

Review

The Biology of Australian Weeds

40. *Bryophyllum* Salisb. species

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Name

The genus name *Bryophyllum* (from the Greek *bryon* + *phyllon*, literally 'moss leaf') refers to the ability of plants to form epiphyllous buds along leaf margins. These buds drop to the ground and form a mat of plantlets.

Specific epithets and common names

There are six species in the genus *Bryophyllum* occurring in Australia. The species epithet *delagoense* refers to Delagoa Bay, the present day Bay of Maputo in Mozambique, where the type specimen was collected in the 1830s. *Bryophyllum delagoense* is commonly known in Australia as mother of millions, mission bells, Christmas bells, frogs' legs or pregnant plant.

There has been a continued debate concerning the usage of *B. delagoense* versus *B. tubiflorum* Harv. The original description given by Ecklon and Zeyher in 1837 was considered by Harvey in 1862 as being incomplete '*nomen nudum*'. Both authors

used the same type specimen. However, the diagnosis of Ecklon and Zeyher, in which they named the species *Kalanchoe delagoensis*, distinguished this species from all others enumerated and the species can be identified by referring to the fragmentary type specimen (Toelken 1985, Toelken and Leistner 1986). The major herbaria in Australia now use *B. delagoense*.

The epithet *daigremontianum* refers to a dedication to a Mr. and Mrs. Daigremont. *Bryophyllum daigremontianum* is commonly known as Mexican hat plant, chandelier plant, mother of thousands or devil's backbone. The epithet *pinnatum* (Latin *pinnatus* 'a feather') refers to its pinnate leaf structure. It is commonly known as green mother of millions, resurrection plant, live leaf plant, air plant, miracle leaf, sprouting leaf, cathedral bells or leaf of life. The epithet *proliferum* (from the French *prolifique* from the Latin *proles* 'that which brings forth') refers to the plant's prolific reproduction. It is commonly

known as prolific mother of millions. The epithet *beauverdii* refers to a dedication to the Swiss botanist Gustave Beauverd (b. 1867 – d. 1942). It is commonly known as Beauverd's widow's thrill. The epithet *fedtschenkoi* refers to a dedication to the Russian botanist Dr. Boris Alexjewitsch Fedtschenko (b. 1873 – d. 1947), Director of the Imperial Gardens of St. Petersburg. It is commonly known as blue mother of millions, hen and chickens, lavender scallops or South American air plant.

Taxonomy

The family Crassulaceae DC. was divided into six sub-families by Berger (1930), one of which (Kalanchoideae) consists of the three genera *Kalanchoe* Adans., *Bryophyllum* Salisb. and *Kitchingia* Baker. However, some authors (Boiteau and Allorge-Boiteau 1995, Rauh 1995) consider all *Bryophyllum* species within a broadly circumscribed *Kalanchoe* while others consider both as 'good genera' based on a larger set of morphological characters (Lauzac-Marchal 1974, Toelken 1985, Wickens 1987, Forster 1997). Genetic studies (Gehrig *et al.* 1997), examination of relative extent of utilization of CAM (Kluge *et al.* 1991, Kluge *et al.* 1993) and cytological differences in haploid number ($x = 17$ or $x = 18$) all support the retention of both genera. This view is accepted here.

There are numerous *Bryophyllum* species in the hands of hobbyists and represented in botanic gardens throughout Australia. A number of species, such as *K. blossfeldiana* Poelln. and *K. tomentosa* Baker, are important in the nursery trade. There are six species and one hybrid of *Bryophyllum* naturalized, as well as two species of *Kalanchoe sensu stricto* naturalized and one possibly native in Australia. These species are listed in Table 1. The *Bryophyllum* and the *Kalanchoe* can be distinguished by the form of the flower head and point of attachment of the filaments to the corolla tube (Figure 1).

Flowers erect or spreading; filaments fused to corolla tube at or above middle	<i>Kalanchoe</i>
Flowers pendent; filaments fused to corolla tube in lower third	<i>Bryophyllum</i>
1. Plants twining; foliage grey-black	<i>B. beauverdii</i>
Plants erect, not twining; foliage pink or green	2
2. Leaves pinnate	3
Leaves simple	4
3. Leaflets 3–5, early leaves often 1-foliate; stems cylindrical	<i>B. pinnatum</i>
Leaflets 7 or more; stems 4-angled	<i>B. proliferum</i>
4. Leaf lamina sub-cylindrical with shallow groove on upper surface	<i>B. delagoense</i>
Leaf lamina flattened	5
5. Leaf lamina >10 cm long and 2.5 cm wide	<i>B. daigremontianum</i>
Leaf lamina <10 cm long and 2.5 cm wide	6
6. Stems and leaves mottled grey and green; lamina <2 cm wide	<i>B. daigremontianum</i> × <i>B. delagoense</i>
Stems and leaves without mottling, bluish, pink-green; lamina > 2 cm wide	<i>B. fedtschenkoi</i>

Figure 1. Key to the naturalized *Bryophyllum* species in Australia after Evett and Norris (1990) and Forster (1992).

Table 1. The *Bryophyllum* and *Kalanchoe* species that have naturalized in Australia.

Species	Chromosome No.	Series ^c	Australian distribution	Native range
<i>B. beauverdii</i> (Raym.-Hamet) A.Berger (= <i>Kalanchoe beauverdii</i> Raym.-Hamet)	34 ^A	V Scandentes	Qld	Madagascar
<i>B. daigremontianum</i> (Raym.-Hamet & H.Perrier) A.Berger (= <i>K. daigremontiana</i> Raym.-Hamet & H.Perrier)	34 ^E	VI Bulbilliferae	Qld, NT	Madagascar
<i>B. delagoense</i> (Eckl. & J.Zeyh.) Schinz (= <i>B. tubiflorum</i> Harv. = <i>K. tubiflora</i> (Harv.) Raym.-Hamet = <i>K. delagoensis</i> Eckl. & J.Zeyh)	68 ^{A,E}	VI Bulbilliferae	Qld, NSW	Madagascar, South Africa
<i>B. daigremontianum</i> (Raym.-Hamet & H.Perrier) A.Berger × <i>B. delagoense</i> (Eckl. & J.Zeyh.) Schinz. (= <i>B. daigremontianum</i> (Raym.-Hamet & H. Perrier) A.Berger × <i>B. tubiflorum</i> Harv.)	51 ^E		Qld	horticultural hybrid?
<i>B. fedtschenkoi</i> (Raym.-Hamet & H.Perrier) Lauz.-March (= <i>K. fedtschenkoi</i> Raym.-Hamet & H. Perrier)	34 ^A	VII Suffrutescentes	Qld	Madagascar
<i>B. pinnatum</i> (Lam.) Oken (= <i>Cotyledon pinnata</i> Lam. = <i>Kalanchoe pinnata</i> (Lam.) Pers. = <i>B. calycinum</i> auct. Aust.)	36? ^A	IX Prolifera	Qld, NT, NSW	Madagascar, Africa
<i>B. proliferum</i> Bowie (= <i>K. prolifera</i> (Bowie) R.Hamet)	34 ^A	IX Prolifera	Qld, NSW	Madagascar
<i>K. longiflora</i> Schltr. ex J.M.Wood	?		NSW, Qld	South Africa
<i>K. lateritia</i> Engl.	34 ^B		Qld	Kenya, Tanzania, Zaire, Mozambique, Zimbabwe, Rwanda, Malawi
<i>K. crenata</i> (Andrews) Haw.	?		WA	tropical Africa, south Africa, Arabia, tropical America, India, Malaysia

^AFriedmann (1971). ^BRaadts (1985). ^CBoiteau and Allorge-Boiteau (1995). ^DKluge *et al.* (1991), Kluge *et al.* (1993). ^EBaldwin (1949).

Description

The following description of *Bryophyllum* taxa that have naturalized in Australia has been compiled from Stanley and Ross (1986), Evett and Norris (1990) and Rauh (1995).

***B. beauverdii*.** Thin, climbing stems to 6 m long; leaves 5–10 cm long and 5–20 mm wide; plantlets formed near leaf apex; black-violet flowers.

***B. daigremontianum*.** Erect, succulent herb; stems stiff, up to c. 45 cm tall. Leaves simple, petioles subcylindrical, up to c. 2.5 cm long; blades ± flat, apex tapering to a blunt point, margin notched, 10 cm × 2.5 cm or larger. Inflorescences terminal; flowers orange-red, c. 5 cm long.

***B. daigremontianum* × *B. delagoense*.** Erect, succulent herb (Figure 2); stems stiff, 30–60 cm tall, occasionally taller, stems and leaves mottled. Leaves simple, petioles succulent, subcylindrical, 1–2.5 cm long; blades folded, apex attenuate, margin notched, 4–8 cm × 0.8–2 cm, often producing plantlets in marginal notches. Inflorescences terminal. Flowers orange-red, 2–3 cm long.

***B. delagoense*.** Erect, succulent herb to 1 m high, occasionally to 3 m (Figure 3), slender with simple stems suckering at the base, stems cylindrical, mottled pinkish brown or greyish. Leaves linear, ± cylindrical, 2.5–15 cm long, grooved longitudinally above, notched towards apex where plantlets are produced, lamina spotted violet-brown. Flowers in a corymbose cluster. Calyx tubular, 5–10 mm long. Corolla tube to 30 mm long, lobes obovate and about a third as long, salmon-coloured to scarlet. Fruit dry, papery, enclosed in the corolla tube, about 1 cm long and deeply divided into four sections. Seeds minute, oval, brown.

***B. fedtschenkoi*.** Plants glabrous, forming tufts. Stems thin, sometimes red-violet, initially prostrate, creeping and rooting, later ascending to erect, up to 50 cm tall and producing long adventitious roots. Leaves numerous, dense, fleshy, flat, ovate to oblong, 1.5–5 cm long and 1–2.5 cm wide, margins crenate, apex rounded, waxy-bluish and brownish to red-violet at the notches with adventitious buds, shortly petiolate. Inflorescences terminal, lax thyrse, stalk base with 1–2 axillary shoots after flowering. Flowers 17–20 mm long, brownish-pink.

***B. pinnatum*.** Stout, glaucous shrub 0.3–2 m high (Figure 4), stems cylindrical erect, little-branched, suckering at the base. Leaves succulent, elliptic, 5–25 cm long, 2–7 cm wide, crenate, lower ones simple, upper ones often pinnate with up to 5 leaflets, young plants often produced in the marginal notches especially after leaf detachment. Inflorescence paniculate. Calyx papery and much-inflated, 25–40 mm long. Flowers pendulous; corolla up to 7 cm long, yellowish-green tinged with pink or reddish, to twice as long as the calyx. Fruits comprised of four slender papery tubes enclosed in the base of the corolla tube. Seeds minute, slender, brown.

***B. proliferum*.** Erect, succulent shrub ± woody base 1–3.5 m high, stems 4-angled. Leaves pinnate, to 45 cm long; leaflets 7–11, oblong-lanceolate with subdentate-crenate margins, 3.5 × 7.5–15 cm long, base oblique, apex nearly obtuse; petiole ± cylindrical, channelled above. Inflorescences terminal. Flowers in paniculate cymes. Calyx nearly campanulate, to 25 mm long, lobes shorter than the tube. Corolla tubular to urn-shaped, to 25 mm long, yellow or greenish-yellow with a red tip or pink tinge.

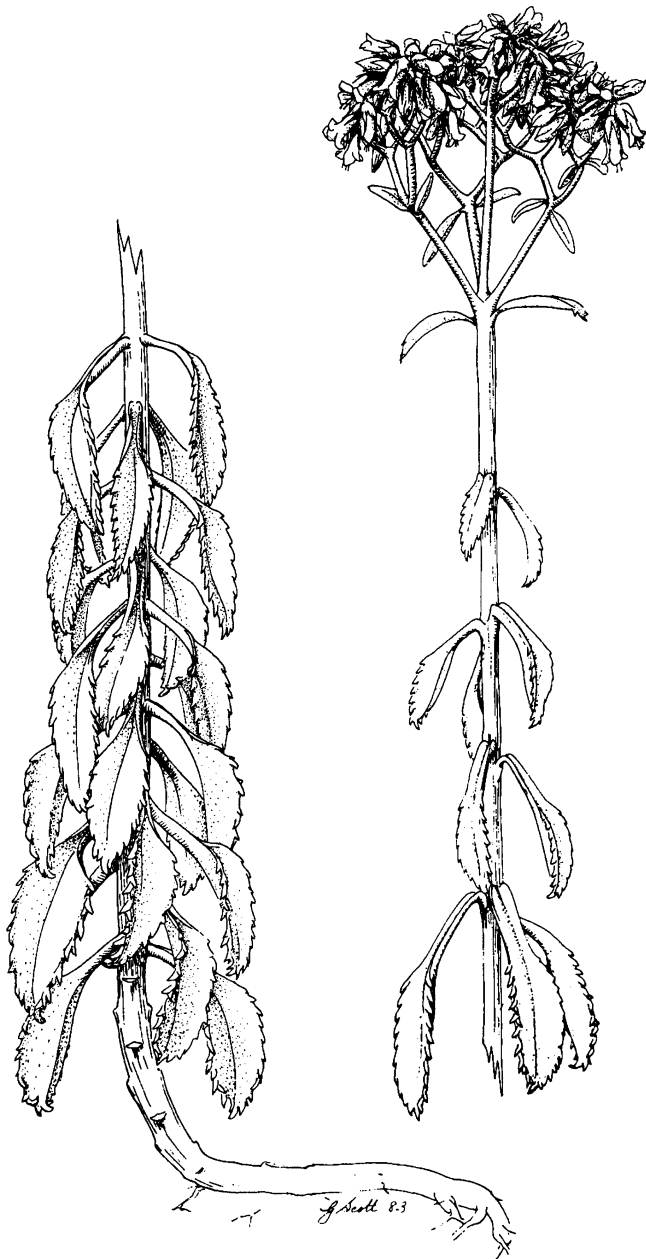


Figure 2. *Bryophyllum daigremontianum* × *Bryophyllum delagoense* (Artists Dr. G. Scott and R. Lenahan).

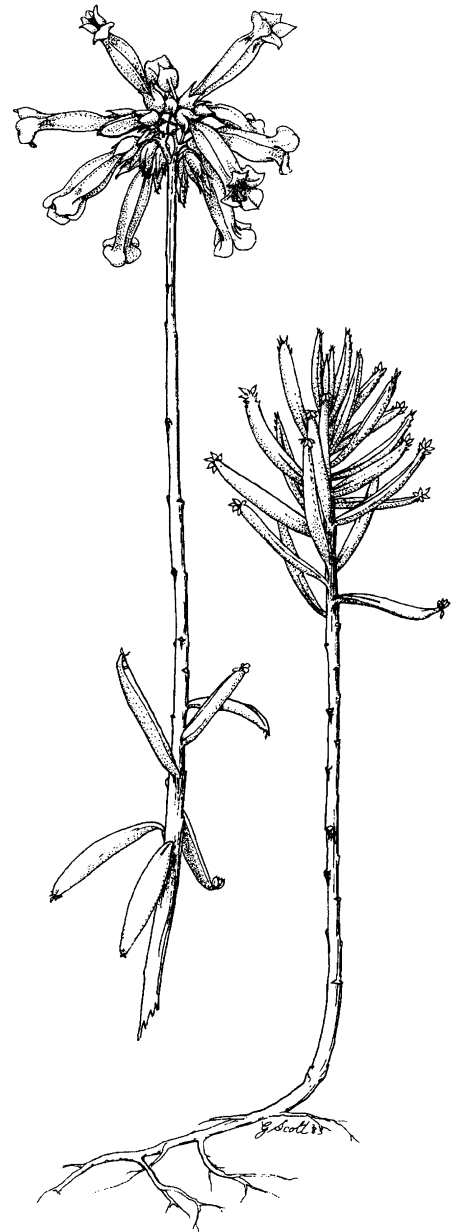


Figure 3. *Bryophyllum delagoense* (Artist Dr. G. Scott).

Cytology

Examination of the naturalized *Bryophyllum* species in their native range (Table 1) has shown a haploid chromosome number of $x=17$ for the genus except for *B. pinnatum*, which has a haploid number $x=18$. All are diploid except for *B. delagoense*, which is a tetraploid ($2n=68$) both in its native range (Friedmann 1971) and in cultivation in the USA (Baldwin 1949) (Table 1). No cytological study has been reported on Australian material.

History

Various species of *Bryophyllum* and *Kalanchoe* have been popular pot and garden plants in Australia because of their colourful winter flowers and drought tolerance (Forster 1985). Some species have escaped from cultivation through dumping of garden rubbish and have become naturalized

(Stanley and Ross 1986, Forster 1997, Forster 1998). The dates of first introductions to Australia are unknown. Both *B. pinnatum* and *B. proliferum* are mentioned by Bailey (1885) in his census of the Brisbane Botanic Garden and Bowen Park (the garden of the Queensland Acclimatisation Society). In 1885, von Mueller reported that *B. pinnatum* was collected in North Queensland in the vicinity of the Endeavour River. He implied that this was a field collection.

Councillor Peter Jeffrey of the Chinchilla Shire Council relates a typical history of the introduction and spread of *B. delagoense*. The first reported outbreak of *B. delagoense* in Chinchilla Shire was in 1940 at Baking Board, a small railway settlement 8 km west of Chinchilla. Railway fettlers grew the plant in their garden, as plants not requiring a lot of water were in

demand. Tennis tournaments were held at Baking Board and participants and spectators from the district took the plants home with them. From homestead gardens the plant was placed in dumps, which were usually in gullies, and hence it washed down into local seasonal watercourses. The council started control programs in the early 1980s and declared the plant a noxious weed under local bylaws in 1988.

The Murgon Shire Council in south-eastern Queensland first raised concerns about the weed potential of *B. delagoense* in 1956. The oldest specimens in the Queensland Herbarium of *B. delagoense* and its hybrid, *B. daigremontianum* × *B. delagoense* were collected in 1957 and 1965 respectively (Queensland Herbarium database 1999, R. Henderson personal communication).

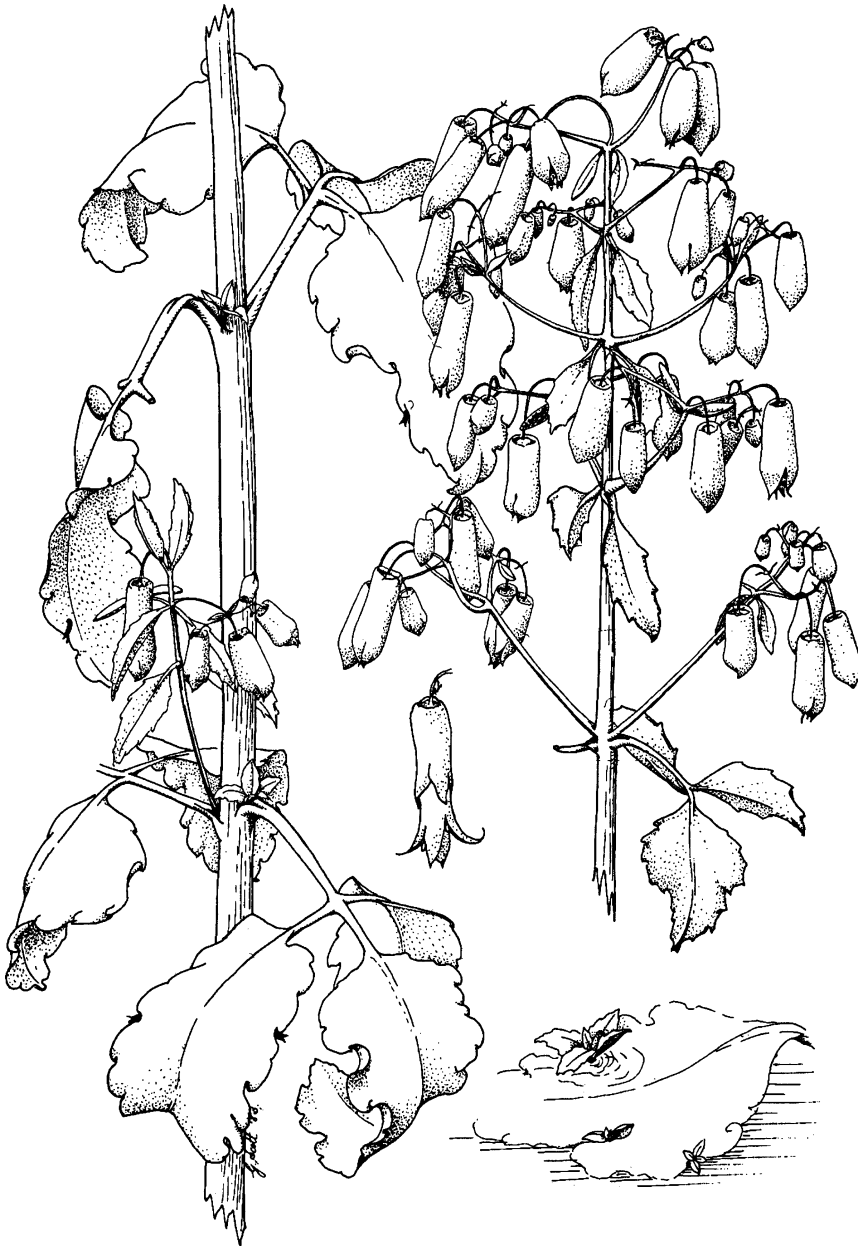


Figure 4. *Bryophyllum pinnatum* (Artist Dr. G. Scott).

Distribution

All *Bryophyllum* spp. are native to Madagascar. *Bryophyllum delagoense* is naturalized in southern Africa (Toelken 1985), US Virgin Islands (Ting 1989), East Africa (Wickens 1987), Hawaii (Holm *et al.* 1991), Florida and Texas (Biota Of North America Program 1999) and Australia. In Australia, it is naturalized in Queensland (Stanley and Ross 1986) and New South Wales (Evetts and Norris 1990), from the coast to well inland (Figure 5). A survey of Queensland in 1980 estimated an infested area of 10 000 ha (Armstrong 1981). *B. daigremontianum* is naturalized in the US Virgin Islands (Ting 1989), Florida and Hawaii (Biota Of North America Program 1999) and in Queensland (Forster 1998, Figure 5). The hybrid is naturalized and common in both Queensland and New South Wales (Figure 5). It is also naturalized in the Cayman Islands (G.R. Proctor

unpublished) and Guadeloupe (J.M. Moullec unpublished).

Bryophyllum beauverdii is reported from Hawaii (Biota Of North America Program 1999) and the Moreton region of Queensland (Forster 1992, Figure 6). *Bryophyllum pinnatum* is naturalized widely in the tropics. Its extensive distribution relative to the other species is due, in part, to its medicinal usage by early navigators (Boiteau and Allorge-Boiteau 1995). It is present in the US Virgin Islands (Ting 1989), Florida and Hawaii (Holm *et al.* 1991, Biota Of North America Program 1999), New Guinea and Melanesia (Forster 1998), Taiwan (Yamagishi *et al.* 1988), tropical east Africa (Wickens 1987), Indonesia, Seychelles and Cook Islands (Bär *et al.* 1997), Puerto Rico, Dominican Republic, Fiji, Jamaica and Mauritius (Holm *et al.* 1991). It is found in coastal Queensland and northern and central

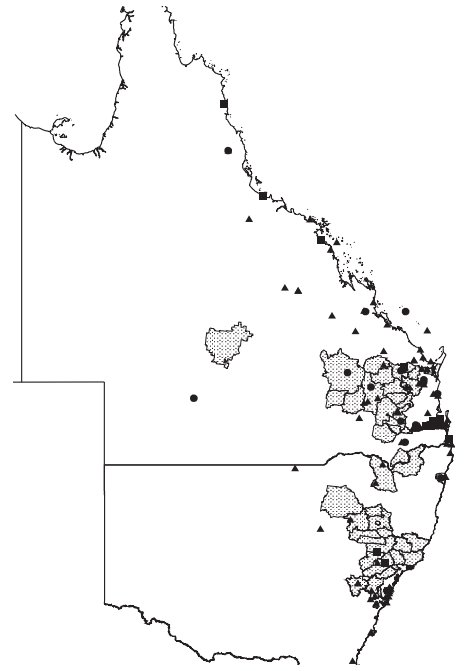


Figure 5. Distribution of *Bryophyllum delagoense* (▲), *B. daigremontianum* × *B. delagoense* (●) and *B. daigremontianum* (■) in Queensland (Queensland Herbarium database 1999) and New South Wales. Shaded areas indicate local government areas within which *B. delagoense* and the hybrid are declared noxious weeds.

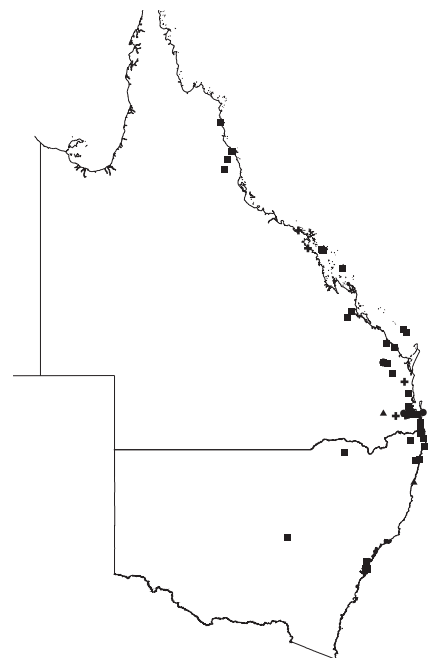


Figure 6. Distribution of the other naturalized *Bryophyllum* species in Queensland (Queensland Herbarium database 1999) and New South Wales. *B. beauverdii* (●), *B. fedtschenkoi* (+), *B. pinnatum* (■) and *B. proliferum* (▲).



Figure 7. Typical habitat of *Bryophyllum delagoense*, Mungle Creek Flora and Fauna Protection Area, northern New South Wales.

coastal New South Wales (Figure 6) (Evelt and Norris 1990), and also occasionally inland in areas of higher humidity (Armstrong and Swarbrick 1983). *Bryophyllum proliferum* is naturalized in tropical east Africa (Wickens 1987), north coastal New South Wales (Evelt and Norris 1990) and the Darling Downs, Burnett, Callide and Moreton regions of Queensland (Forster 1998, Figure 6). *Bryophyllum fedtschenkoi* has been reported as naturalized in tropical east Africa (Wickens 1987), Florida and Hawaii (Biota Of North America Program 1999), and Queensland (Forster 1998, Figure 6).

Habitat

In Madagascar, *B. delagoense* is never found growing as a weed in disturbed areas, but always occurs as a natural element in very specific habitats. This species is mostly found on open granite outcrops, where the plants grow on the rock face in direct sunlight (L.L. Dreyer and D. Du Puy unpublished). In Queensland and northern New South Wales, *B. delagoense* distinctly prefers the leaf litter within the drip/shade zone of trees, with few plants growing in open bare areas (Figure 7). When plants do grow in open areas they



Figure 8. Typical microhabitat for *B. delagoense* establishment under fallen log, Chinchilla Queensland.

require a sheltered/moist microclimate with organic matter for establishment, such as under a fallen branch or log (Figure 8). Many infestations are associated with tree-lined roadsides where mechanical work has disturbed the soil surface and spread plantlets from existing infestations.

Climatic requirements

In Madagascar, *B. delagoense* is more commonly found in the drier southern region (L.L. Dreyer and D. Du Puy unpublished). This region is characterized by either a temperate sub-humid climate (annual rainfall from 950 to 1600 mm, a well defined dry season and a mean annual temperature of 17–28°C, with sharp annual and daily fluctuations) or a semi-arid climate (annual rainfall between 500 mm and 900 mm, a 7 month dry season and a mean annual temperature from 25–26°C) (Paulian 1984). A CLIMEX® model (Sutherst and Maywald 1999) based on the known distribution of *B. delagoense* in Madagascar and elsewhere (Boiteau and Allorge-Boiteau 1995, A. Witt personal communication) indicates an extensive potential range in Australia (Figure 9). The parameters for this model are presented in Appendix A. *B. delagoense* appears to be frost intolerant in Australia. In frost prone areas, the main infestations are limited to protected areas under tree canopies. *B. beauverdii* and *B. fedtschenkoi* have a similar climate range in Madagascar to that of *B. delagoense* (Boiteau and Allorge-Boiteau 1995). It might be assumed that the potential distribution of these two species in Australia would be similar to the predicted potential range of *B. delagoense* (Figure 9).

Bryophyllum daigremontianum, in its native range, has been reported only from around Toliara (Toliara), south-western Madagascar. This is a subarid region,

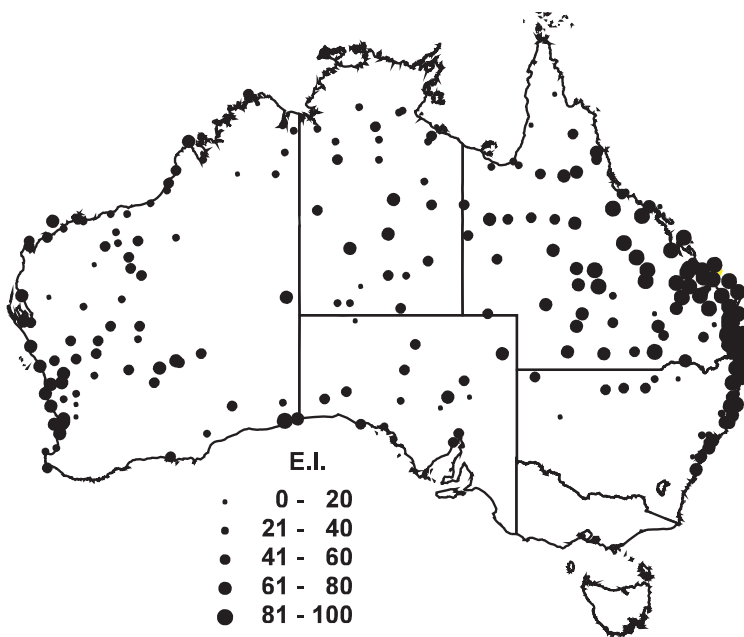


Figure 9. Predicted suitability of sites in Australia for *B. delagoense* using Ecological Index (E.I.) from CLIMEX (Sutherst and Maywald 1999) based on the Madagascan distribution of this species and tested against known world distribution. Size of circle indicates level of suitability predicted by this model.

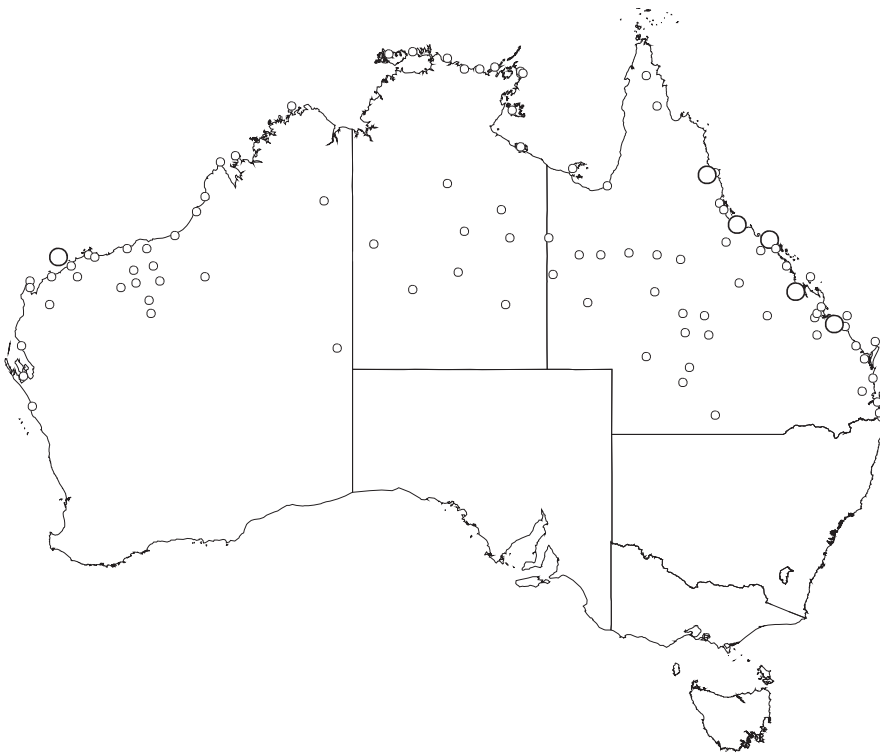


Figure 10. Climate match of sites in Australia with Tulear (Toliara), south-west Madagascar using CLIMEX (Sutherst and Maywald 1999). Match index is based on similarity of humidity, temperature and rainfall totals and patterns. Smaller symbol indicates a match index of 40–60, larger symbol index of 61–80. Suitability of these Australian sites for the growth and maintenance of *B. daigremontianum* populations may be inferred from this level of closeness of climate match.

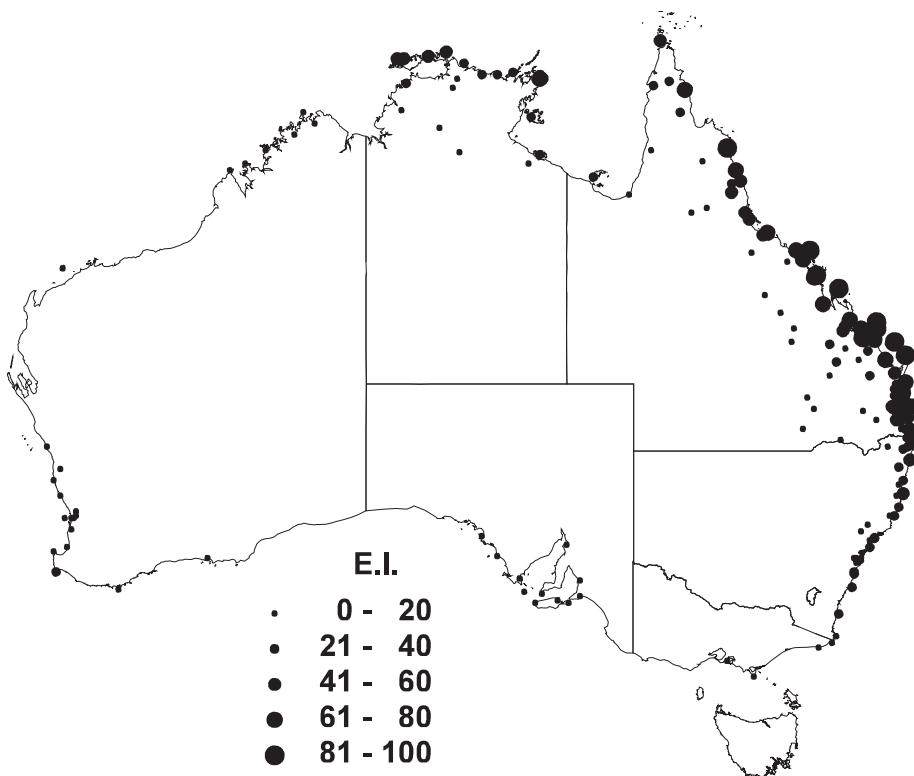


Figure 11. Predicted suitability of sites in Australia for *B. pinnatum* using Ecological Index (E.I.) from CLIMEX (Sutherst and Maywald 1999) based on the Madagascan distribution of this species and tested against known world distribution. Size of circle indicates level of suitability predicted by this model.

which has an average annual rainfall of 350 mm, falling irregularly as occasional rains. This region has a mean annual temperature of about 26°C with maximum temperatures to around 40°C (Paulian 1984). A distribution map for *B. daigremontianum* based on a match of the rainfall and temperature patterns of Tulear (Toliara) using CLIMEX® indicates a potential for utilization of the drier areas of inland Australia (Figure 10).

The hybrid, *B. daigremontianum* × *B. delagoense* could be expected to have a climatic requirement within the range of requirements of its parent species.

The more moisture reliant *B. pinnatum* and *B. proliferum* occur in the temperate humid and subhumid climates of the central highlands of Madagascar, with annual rainfalls of 1000–2000 mm (Paulian 1984). These species, particularly *B. pinnatum*, are relatively drought intolerant and may become almost totally defoliated during periods of extended drought (Forster 1985). A potential distribution for *B. pinnatum* was modelled with CLIMEX® (Figure 11, Appendix A). It is assumed that the potential range for *B. proliferum* is similar to that of *B. pinnatum*.

Substratum

In Madagascar, *B. delagoense* is strongly associated with granite outcrops, with sand as a secondary substrate. There is only one instance of it being collected on limestone (D. DuPuy and J. Moat unpublished). In Queensland, *B. delagoense* is associated with dry skeletal soils or rock faces, shallow stony soils in open forest country or loose sand near the seashore. However, it may be found on a broad range of soils, from sand to heavy clay, where surface organic matter occurs (Batianoff and Franks 1998, Queensland Herbarium database 1999).

The *B. daigremontianum* specimens in the Queensland Herbarium collection (Queensland Herbarium database 1999) are frequently collected from sand dunes. *Bryophyllum fedtschenkoi* is found on sand, loamy sand and lithosols (Queensland Herbarium database 1999). *Bryophyllum pinnatum* is associated with loamy sand, alluvial soils, clay loams and skeletal soils (Queensland Herbarium database 1999) and where soil moisture persists with surface organic matter.

Plant associations

In Madagascar, *B. delagoense* and *B. daigremontianum* are commonly associated with *Xerophyta* spp., *Zornia glochidiata* Reichb. ex DC. and *Senecio* spp. (L.L. Dreyer and D. Du Puy unpublished) in xerophilous bush or 'spiny desert' of the south and south-west (Guillaumet 1984). The other *Bryophyllum* species are associated with savannah and steppe forests of the central highlands and western slopes

(Guillaumet 1984). In Queensland, most of the *Bryophyllum* spp. are associated with open eucalypt forests, brigalow (*Acacia harpophylla* Benth.) woodlands or *Casuarina* communities. *B. beauverdii* has been collected from gallery or fringing rainforest (Queensland Herbarium database 1999).

A typical open forest association of *B. delagoense*, at Nudley State Forest near Chinchilla is white cypress pine (*Calitris collumellaris* F.Muell.), rusty gum (*Angophora costata* Hochr. ex Britten), wilga (*Geijera parviflora* Lindl.), belah (*Casuarina cristata* Miq.), gum top box (*Eucalyptus moluccana* Wall. ex Roxb.) and brigalow (*Acacia harpophylla*), with an understorey of sandalwoods (*Eremophila* spp.) and other native shrubs and grasses.

A typical association for *B. pinnatum* is at Nundah Creek near Brisbane in a coastal heath verging on mangrove swamps. Dominant species include *Eucalyptus terebinthifolius* Sm., *E. racemosa* Cav. and *Casuarina equisetifolia* L., with *Melaleuca quinquenervia* (Cav.) S.T.Blake and *M. nodosa* (Gaertn.) Sm. Broad-leaf pepper (*Schinus terebinthifolius* Raddi), *Asparagus* spp., *Lantana camara* L. and *Passiflora* sp. also invade this area (Sparkes *et al.* in press).

Growth and development

Morphology

Cattle trodden or uprooted *Bryophyllum* spp. exhibit a gravitropic response and reorientate to the vertical. This effect has been studied in detail in *B. pinnatum* stems (Meichenheimer and Nackid 1994). It was analysed in terms of instantaneous curvature along the stem, relative growth rates, and epidermal cell dimensions. Analysis of epidermal cell dimensions revealed that, in general, there was a redistribution of cell elongation potential to the lower side of the gravistimulated stem but no evidence for overall enhancement of cell expansion in response to gravity (Meichenheimer and Nackid 1994).

The epidermal structure, distribution of stomata, and the ontogenetic types of stomata in vegetative and reproductive organs of *B. delagoense* and *B. daigremontianum* were described by Jeong and Kim (1987). The cell walls were thick and arched or sinuous in the leaves, bracts, sepals, epiphyllous buds, petals and ovaries. The cell walls in the stems, petioles, pedicles and peduncles were thick and straight. The subsidiary cell walls were thin and mostly arched. The number of stomata was greater on the epidermis of the leaves (20.2–22.7 mm⁻²) than on the epiphyllous buds (13.5–17.6 mm⁻²). The density and size of stomata on the upper or lower surfaces of the leaves or epiphyllous buds of *B. delagoense* did not vary greatly. However, the stomatal density on the surfaces of *B. daigremontianum* leaves was very different (19.8 mm⁻² upper compared to lower 29.9 mm⁻²).

The naturalized *Bryophyllum* spp. (except for *B. delagoense* and the hybrid) have a decussate phyllotaxis (leaves opposite with successive pairs at right angles). Shoots of *B. delagoense* can show up to six different phyllotactic patterns, starting with decussate and progressing to tricusate (leaves in whorls of three leaves set at an 120° angle with each successive triplet of leaves set at 60° to the preceding triplet) (Gomez-Campo 1974). *B. daigremontianum* constantly exhibits a fully decussate pattern (Gomez-Campo 1974). The hybrid has a phyllotaxis largely identical to *B. delagoense*. However, it has a longer juvenile stage, i.e. decussate pattern (Gomez-Campo 1974).

Hellendoorn and Lindenmayer (1974) assumed that these changes in phyllotaxis of *B. delagoense* were due to changing rates of production of an inhibitor on the apical surface, or alternatively to changing apical size. Observations on the structure of the apex supported the latter assumption. Mirror asymmetry in the position of the first two leaves was also observed and found to be necessary for computer models to simulate the progression of phyllotaxis patterns during growth of *B. delagoense*.

Perennation

Many *Bryophyllum* spp. are semelparous biennials or triennials. Semelparity is a distinct life history where a single sexual reproductive event is followed by plant death. *B. delagoense*, *B. daigremontianum* and the hybrid can be bi- or triennials depending on the season of establishment and environmental and intra-specific effects. In the case of *B. pinnatum* and *B. proliferum* the entire plant may not die but re-shoot from near the ground level. These species may be considered as short-lived perennials. *B. fedtschenkoi* and *B. beauverdii* should be considered as perennials.

Physiology

All *Bryophyllum* spp. utilize crassulacean acid metabolism (CAM) that is a unique ecophysiological adaptation to arid or otherwise water stressed environments. CAM was first described from *B. pinnatum*. Since then, *B. delagoense*, *B. daigremontianum* and *B. fedtschenkoi* have been studied so extensively as model systems in the elucidation of this metabolic pathway, that they have formed the basis for many generalizations on the mechanisms and ecological significance of CAM (Kluge and Brulfert 1996). CAM plants capture carbon dioxide from the atmosphere during the night and photosynthesize this CO₂ to carbohydrates during the following light period (Winter and Smith 1996).

CAM has been observed in *B. delagoense* only in the older (succulent) phyllodia and not in the younger (non-succulent) ones at the apex of the plant (Kluge and Ting

1978). CAM plants can be divided into two distinct metabolic groups based on the C₄-acid decarboxylases found in the plant and the use of soluble sugars versus polysaccharides as the carbon reserve (Black *et al.* 1996). *Bryophyllum delagoense* and *B. daigremontianum* utilize starch and other glucans, such as dextrin, as the carbohydrate pool (Sutton 1975).

In some species, CAM is regulated by water status; at high external water potential malate accumulation can be completely suppressed, while it progressively increases as water potential decreases, e.g. in *B. daigremontianum* (Luttge *et al.* 1975). On the other hand, full hydration of *B. delagoense* leaves does not prevent malate accumulation (Kluge *et al.* 1980).

Very low night temperatures inhibit net dark CO₂ fixation. In *B. daigremontianum* and *B. delagoense*, net CO₂ uptake is zero at about 5°C nocturnal. The optimal temperature range for CO₂ uptake for most CAM plants is 15° to 22°C (Kluge and Ting 1978). The former temperature has been shown to be optimal for full stomatal opening (Jewer *et al.* 1985).

Many *Bryophyllum* species show a high phenotypic variability in CAM expression with water relations, light intensity, photoperiod and the diel temperature regime being major modulating factors (Kluge and Brulfert 1996). Carbon isotope ratios (δ¹³C values) of the biomass of a plant is a convenient method to obtain information about the frequency and variability of photosynthetic carbon assimilation pathways (Kluge *et al.* 1993). The δ¹³C values for *B. daigremontianum* (-13.14 to -21.21%) and *B. pinnatum* (-12.96 to -23.22%) show acquisition of external carbon by both the PEP and C₃ pathways when external conditions such as light and water are altered. This occurs both in the laboratory and field situations (Luetttge *et al.* 1991) and this should facilitate the occupation of ecological niches where such changes frequently occur (Kluge *et al.* 1993). There is no data, however, for *B. beauverdii* or the hybrid, *B. daigremontianum* × *B. delagoense*. The other naturalized *Bryophyllum* spp. in Australia are all obligative CAM plants.

The success of *Bryophyllum* spp. in Australia appears to be due in part to their ability to withstand drought. *B. daigremontianum* shows a marked reduction in daily water loss within 6 days of drought, using CAM to restrict transpiration and net CO₂ uptake to the dark period. Translocation of water from old to young leaves is an additional mechanism, which reduces the negative effects of drought on the water relations of young leaves. Solutes are also transported from old to young leaves of the plant via the phloem. Xylem tension was higher in young than in old leaves; thus, water translocation could have occurred via xylem elements. Since transport of organic matter in the

phloem is also linked to water flow, phloem transport additionally may contribute effectively to the balance of the water budget in young leaves (Schafer and Luttge 1987).

Bryophyllum delagoense leaves that are affected by drought at an immature stage develop an enhanced resistance to water loss (Ayerbe and Gomez Campo 1977). This drought hardening is manifest in a permanent alteration in leaf geometry, especially the surface to volume ratio, while wax secretions also appear to be higher. New growth following the hardened stage shows similar symptoms for a certain distance along the stem (Ayerbe and Gomez Campo 1977). Water deficiency has a greater influence on productivity than does deficiency of nitrogen. In laboratory experiments *B. delagoense* was much more sensitive to drought than *B. daigremontianum*, which corresponds to their distributions in Madagascar, where *B. daigremontianum* is found in the drier south-west and *B. delagoense* in the areas of higher rainfall (Widmann *et al.* 1990).

Australian soils are low in nutrients due weathering and leaching. In mineral nutrition experiments, *B. daigremontianum* growth was not affected by phosphorus deficiency but was markedly affected by nitrogen or potassium deficiency (Nozzolillo 1970). Under low nitrogen conditions the biomass of both *B. daigremontianum* and *B. delagoense* were reduced by more than 75% when compared to high nitrogen conditions. Nitrogen deficiency did not have such a strong effect when plants were short of water. Under combined drought and nitrogen deficiency the biomass of *B. daigremontianum* was reduced by 40% and *B. delagoense* by 25%. Further studies by Widmann *et al.* (1993) showed that *B. daigremontianum* and *B. delagoense* neither took up nor used nitrate when water was limited.

Phenology

Bryophyllum delagoense is classified as a long-short-day plant, requiring exposure to a period of long day length followed by short days to induce flowering. It was shown by Teske (1980) that *B. delagoense* requires several successive changes in the length of the photoperiod to induce flowering. A single change at 6 or 12 months from long day to continuous short day did not induce flowering, even after 39 months; but a second long short day change resulted in flowering by 18 to 20 months. Holding the plant at short day and treating with gibberellic acid resulted in flowering after 7 months (Teske 1980). Flowering took place only during short day (SD) conditions and no influence of temperature was observed.

On the other hand, *B. daigremontianum*, which is also classified as a long-short-day plant, flowers under several photo-

periodic conditions, including continuous exposure to long day and after transition from a short-day to a long-day exposure. The flowering of *B. daigremontianum* is conditioned by sufficient long day (LD) exposure followed by one of two factors: the shortening of the day or the lowering of the temperature (Teske 1980). Zeevaart and Lang (1962) suggested that transfer of *B. daigremontianum* from LD to SD would induce flowering provided that the night temperature does not exceed 15°C. It was further demonstrated by Van de Pol (1972) that plants initiate flowering only 'when the sum of the temperature times hours per 24 hours is 472 or less'.

Forster (1985) recorded the flowering of *Bryophyllum* species at Didcot (25° 28' 58" S, 151° 52' 2" E) in south-eastern Queensland over a period of 7 years (Table 2). Most of the naturalized species flower from May till September, except *B. beauverdii*, which commences flowering in July and *B. proliferum*, for which flowering extends into October. In Brisbane (153° 1' 36" S, 27° 28' 19" E) some *B. delagoense* populations are still in flower in October (M. Hannan-Jones unpublished).

Mycorrhiza

None known.

Reproduction

Pollination

In Madagascar, sunbirds *Nectarinia* sp. (Nectariniidae) have been observed visiting the flowers of *B. delagoense* (A. Witt personal communication). However, in Australia, honeybees *Apis mellifera* have been observed entering the corolla tube of *B. delagoense* flowers and emerging covered with pollen (M.A. Hannan-Jones and M. Rogers unpublished). To access the nectary the bee has to push itself completely up the corolla tube, brushing past the stamens. Bees can only enter fully opened flowers and were seen to abandon their efforts to enter some flowers when the fit was too tight. Nothing is known about floral visitors or pollination requirements of any of the other naturalized *Bryophyllum* species in Australia.

Seed production and dispersal

Seed production is prolific in all species except the hybrid, with a single plant of *B. delagoense* capable of producing up to 20 000 seeds from its inflorescence (M.A. Hannan-Jones unpublished). Plantlets and seeds may be spread short distances by rain-wash, with further movement along watercourses, especially during periods of flooding (F.D. Panetta unpublished). The minute seeds adhering to fur or feathers of passing animals and birds may also aid the spread. This is indicated by local uphill spread above flood lines from main infestations.

Physiology of seeds and seed germination

Cumulative germination of freshly collected *B. delagoense* seeds was 29% after 10 days and 57% after 38 days; an attempt to germinate these same seeds after 5 months storage demonstrated only 4% germination after 21 days (T.R. Armstrong unpublished). The seeds of the hybrid can be viable, but with very low germinability (M.A. Hannan-Jones unpublished).

Vegetative reproduction

Bryophyllum delagoense reproduces vegetatively from epiphyllous buds on the pegs at the apex of the leaves and sometimes forms vegetative buds on the senescing inflorescences after seed set. *B. daigremontianum* and *B. daigremontianum* × *B. delagoense* form epiphyllous buds in the indentations along the leaf edges. *B. daigremontianum* × *B. delagoense* forms vegetative buds on the inflorescences more readily than does *B. delagoense*.

Bryophyllum delagoense, *B. daigremontianum* and *B. daigremontianum* × *B. delagoense* produce epiphyllous buds very readily, whereas in other species buds are formed only under stress (Toelken and Leistner 1986). Leaves of all species can produce epiphyllous buds after they are dislodged from the parent plant.

The formation of epiphyllous buds in *B. daigremontianum*, *B. delagoense* and their hybrid occurs only under long-day conditions (Purohit and Nanda 1971). The photoperiod in which a parent leaf develops

Table 2. Flowering calendar of *Bryophyllum* spp. cultivated at 'Nora Creina', Didcot, south-eastern Queensland (Forster 1985).

Species	Month ^A				
	June	July	August	September	October
<i>B. beauverdii</i>		+	+	+	
<i>B. daigremontianum</i>	+	+	+	+	
<i>B. daigremontianum</i> × <i>B. delagoense</i>	+				
<i>B. delagoense</i>	+	+			
<i>B. fedtschenkoi</i>	+	+	+	+	
<i>B. pinnatum</i>	+	+	+	+	
<i>B. proliferum</i>	+	+	+	+	+

^A Flowering did not occur outside these months.

determines whether initiation of epiphyllous buds occurs. Long days allow epiphyllous bud initiation and growth, although once mature, the leaf appears to be largely unresponsive to photoperiod in that the transfer from short to long days does not elicit bud initiation (Henson and Wareing 1977). The long day requirement for formation of epiphyllous buds in *B. daigremontianum* vanishes as soon as the leaves are cut from the plant; epiphyllous buds then form on the excised leaves in both long and short days.

According to Naylor (1932), the primordia for the epiphyllous buds already exist in the leaf notches. These remain dormant until favourable conditions for plantlet formation occur (Yarbrough 1932). Initiation of physical and chemical changes in leaves in response to favourable environmental conditions causes bud release from dormancy. An increased cytokinin/auxin ratio appears to be responsible for bringing about the effect. This is supported by the studies on endogenous levels of these hormones (Henson and Wareing 1977), as well as cytokinin-caused promotion and auxin-caused inhibition of budding, when applied exogenously to *B. pinnatum* (Mohan Ram 1963, Houck and Rieseberg 1983), *B. daigremontianum* (Saniewski and Puchalski 1988) or to *B. delagoense* (Purohit and Nanda 1971, Bisaria 1981). Consequently, increased indoleacetic acid (IAA) oxidase activity may be one of the significant metabolic changes associated with bud release (Houck and Rieseberg 1983). El Shafey (1991) found that the most significant difference in growth regulators between *B. daigremontianum* and *Kalanchoe tomentosa* (which forms epiphyllous buds only on detachment of the leaves from the parent plant) was increased IAA-oxidase activity in the former.

The hormonal requirements for the extension growth of the initiated epiphyllous bud are different from those that trigger their release from dormancy. The extension of excised buds of *B. delagoense* was stimulated by gibberellic acid (GA_3) but inhibited by IAA and kinetin (Purohit *et al.* 1969, Nanda and Jain 1972). Conversely, GA_3 inhibits the production of roots on the buds, whereas IAA promotes production of roots (Nanda and Jain 1972).

Recently, Batygina *et al.* (1996) found that epiphyllous bud development in *B. daigremontianum* and *B. pinnatum* proceeds via embryoidogenesis (i.e. somatic embryos). In both species, all vegetative propagule organs arise from dormant meristem derivatives, but there are morphogenetic differences at the latest developmental stages (in relation to adventitious root initiation). In both species, vegetative propagule development proceeds through globular, heart-shaped

and torpedo-shaped stages. Comparative morphological and embryological analysis of vegetative propagules and sexual embryos in these two species revealed a strong similarity in their developmental patterns, notwithstanding their morphological variability.

Hybrids

The only recognized hybrid in Australia is *B. daigremontianum* × *B. delagoense*, which was produced by the hobbyist A.D. Houghton of San Fernando, California (Houghton 1935). The maternal (seed bearing) plant was *B. daigremontianum* and the paternal (pollen bearing) plant was *B. delagoense*. The cross was made by careful emasculation, bagging and hand pollination. Material derived from this cross was examined cytologically many years later and shown to be a triploid ($2n = 51$) (Baldwin 1949). The cultivar name 'Houghton's hybrid' has been used (Forster 1985) and the hybrid is still available for sale in the USA under the name *Kalanchoe houghtonii*. Its common names include devil's backbone (Batianoff and Franks 1998), coconut plant, good luck plant, hybrid mother of millions, cross-bred mother of millions and hybrid life plant. The hybrid is second to *B. delagoense* in the extent of its infestations in Australia and is also naturalized in the Cayman Islands (G.R. Proctor unpublished) and the Lesser Antilles (J.M. Moullec unpublished).

Boiteau and Allorge-Boiteau (1995) in their monograph on Madagascan *Kalanchoe sensu lato* did not report any natural

hybrid between these two species although they report the spontaneous hybrids, *B. daigremontianum* × *B. rosei* R.Hamet & H.Perrier, *B. beauverdii* × *B. delagoense* and *B. daigremontianum* × *B. crenatum* (Baker) R.Hamet. The National Herbarium, Pretoria, RSA (PRE) and the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar (TAN), do not have any specimens of *B. daigremontianum* × *B. delagoense* (L.L. Dreyer and D. Du Puy unpublished).

Population dynamics

The majority of seedlings and plantlets surrounding a patch of mature flowering plants appear to be held in a juvenile state (M. Rogers and M.A. Hannan-Jones unpublished). This effect may be caused by allelochemicals (see below) or by competition for resources. After the mature plants in the stand have flowered and started dying back, a number of the more advanced juveniles break through the inhibitory effect and rapidly grow and flower after the next LD/SD cycle. Mature plants and more advanced juveniles contribute epiphyllous plantlets to the juvenile pool as a continuous rain during LD conditions, continuing right up to flowering. Establishment of these plantlets is dependent on climatic and substrate conditions in the weeks after detachment from the parent plant. As the parent plant dies back post flowering it also releases a rain of seed that can germinate under suitable, albeit unknown, conditions. Otherwise, mortality seems to be confined to seedlings and less advanced juveniles. The



Figure 12. Dense *B. delagoense* stand under *Acacia harpophylla* at Mungle Creek, NSW.

relative contributions of the seedlings and the plantlets to the establishment, regeneration and overall population dynamics of *B. delagoense* is unknown.

Importance

Detrimental

Invasiveness. Batianoff and Franks (1997) include *Bryophyllum* spp. in their list of the twelve most invasive ornamental plants of coastal Queensland fore dunes. Their general observations and the study of six transects on the Sunshine Coast in 1982 and 1997, indicate that *Bryophyllum* spp. may become widespread and troublesome in the near future if precautions are not taken (Batianoff and Franks 1998). A case study of the flora changes on Lady Elliot Island, a coral cay on the Great Barrier Reef, showed 'changes to the current vegetation structure by the widespread occurrence of *Lantana camara* L., *Bryophyllum tubiflorum* [= *delagoense*] and *Euphorbia cyathophora* Murray' (Batianoff 1998). However, Batianoff postulated that the removal of *Lantana* and *Bryophyllum* might not only aid the spread of native species such as *Abutilon asiaticum* (L.) Sweet ex G. Don and *Ficus opposita* Miq., but also provide new habitat for other weeds.

Reports from property managers on the Darling Downs and in central Queensland indicate the *B. delagoense* is still spreading down the river drainage systems with each successive flood event. With each large flood the infestations are also being moved further out onto the flood plains. At Mungle Creek, New South Wales, dense infestations of *B. delagoense* that originated from a garden planting, about two kilometres upstream, now interfere with the regeneration of southern remnant stands of *Acacia harpophylla* in a flora reserve (Figure 12). Near Dingo in central Queensland, *B. delagoense* is of concern for its competition with native herbs and forbs which are the diet of the endangered macropod, bridled nail-tailed wallaby *Onychogalea fraenata* Gould which has a restricted range within a heavily infested reserve.

Toxicity. *Bryophyllum delagoense*, *B. daigremontianum* × *B. delagoense*, *B. pinnatum* and *B. proliferum* caused 41 recorded poisoning incidents affecting 379 cattle in Queensland between 1960 and 1984 (McKenzie and Armstrong 1986). The vast majority of cattle mortalities have occurred in the south-eastern corner of Queensland, in an area bounded by Goondiwindi in the south-west and Rockhampton in the north. These were caused by *B. delagoense* or *B. daigremontianum* × *B. delagoense*. From 1990 to 1999 there were 25 reported incidents of *B. delagoense* poisoning of cattle in New South Wales for the loss of 25 animals (F.J.A. Neilson *et al.* unpublished). Two cattle deaths from ingestion of *B.*

pinnatum have been reported in New South Wales (Reppas 1995).

Most poisonings occur when *Bryophyllum* spp. are flowering between May and October, which is usually a dry time of year. Cattle have generally been poisoned when they have been placed under unusual or stressful conditions (McKenzie and Armstrong 1986). Shifting cattle to new paddocks, droving past infested rubbish dumps and breaking into abandoned gardens commonly have led to poisoning events. Less frequently, being crowded into infested parts of paddocks by floods, or cold weather, or running out of available feed in droughts has caused cattle to eat lethal amounts of this plant (McKenzie 1987).

The single most extensive loss of stock has been reported from New South Wales (W. Hetherington personal communication). A mob of about 775 weaner cattle, bred on the New England Tableland, was placed in a travelling stock reserve near Moree after 8 weeks travelling. The stock reserve and adjoining paddock had flowering *B. delagoense*. The cattle removed all the flower heads in the stock reserve and within reach across the fence line. Over the next 20 days 122 deaths occurred. Interestingly, local cattle in that adjoining paddock were not affected by the *B. delagoense*.

Field cases and experimental results indicate that ingestion of the flowering stage is most responsible for poisonings in Australia. The median lethal doses of *B. delagoense* flowers, roots and leaf plus stem were 0.7, 2.3 and 5.0 g dry matter per kg live weight respectively (McKenzie and Dunster 1986). The main life-threatening lesion is myocardial. The effects on the alimentary tract are less important. Both experimental and field *B. delagoense* poisonings produced anorexia, depression, ruminal atony, diarrhoea, heart rate and rhythm abnormalities, dyspnoea and death. Increased plasma concentrations of urea, creatinine and glucose and decreased chloride have been measured. Both natural and experimental cases had myocardial degeneration and necrosis with haemorrhages of the heart and alimentary tract. Cattle with severe dyspnoea had atelectasis and emphysema of the lungs. Some cattle had mild nephrosis.

Three bufadienolides (cardioglycosides), Bryotoxins A, B and C have been isolated from *B. delagoense* and identified by their chemical and spectrometric properties (Capon *et al.* 1985, Capon *et al.* 1986). Bryotoxin B had previously been identified from *B. daigremontianum* and named daigremontianine (Wagner *et al.* 1985). Smaller amounts of more polar toxins were isolated but the identity and structures of these compounds have not yet been fully elucidated. The symptoms of intoxication of laboratory animals

poisoned with these purified bryotoxins (McKenzie *et al.* 1989) resemble those of animals poisoned with the crude extracts of *B. delagoense* and so it is presumed that these bufadienolides are the toxic principles (Oelrichs *et al.* 1992).

McKenzie and Dunster (1987) demonstrated that most cattle recover if treated within 24 hours after eating potentially lethal doses of *B. delagoense*. The treatment consists of the administration of a slurry of activated carbon (activated charcoal) or bentonite in electrolyte replacement solution given by stomach tube and anti-arrhythmic drugs given parenterally. This cured nine of 11 calves dosed 7–24 hours previously with a lethal amount (20 g kg⁻¹) of *B. delagoense* flower heads. Two of another four calves treated 26–36 hours after dosing with flowers survived. Activated carbon was effective at a single dose of 5 g kg⁻¹. Calves were rehydrated with oral electrolyte replacement solution at 150 mL kg⁻¹ in divided doses over 24 hours. Tachycardia was treated with intravenous lignocaine (200 mg doses) or propranolol (5 mg doses) and atrioventricular block with atropine (0.5 mg kg⁻¹). This treatment can be more expensive than most poisoned animals are worth.

Bryophyllum species are toxic to species other than cattle. *Bryophyllum* plants produce almost identical clinical and pathological effects in sheep in laboratory experiments, with a median lethal dose for wethers of 20 g wet weight per kg live weight. Leaves of *B. delagoense*, *B. daigremontianum* and *B. fedtschenkoi* were toxic to 2-week-old chickens at 8–12 mg per g of body weight. There was a case of severe diarrhoea in a child who ate flowers of *B. delagoense* (Williams and Smith 1984).

Allelopathy. Mature plants of *B. daigremontianum* display an allelopathic influence on the growth and development of their own plantlets (Groner 1974) and other species of plants (Groner 1975). Groner (1975) observed the inhibition of plantlets growing within the root zone of their mother plants in natural habitats in Madagascar as well as in pots. Stem elongation of such plantlets was a third to one tenth of that of sister plantlets growing in isolation.

Extracts of *B. daigremontianum* inhibited the germination and survival rates of seedlings of *Digitaria sanguinalis* (L.) Scop., *Panicum miliaceum* L., *Setaria italica* (L.) P. Beauv., *Trifolium incarnatum* L., *Lactuca sativa* L., *Allium cepa* L. and *Chrysanthemum hortorum* Bailey (Groner 1975) but not *Zea mays* L., *Triticum aestivum* L. and *Avena sativa* L. The effects varied from species to species but included delays in germination, reduction in total germination, leaf chlorosis, stunting and reduction in flowering and seeding.

Nair *et al.* (1988) showed that the leaves and roots of *B. daigremontianum* contain ferulate esters of higher fatty alcohols and the potting mix from potted plants contained free ferulic acid released from the roots or from the leaf litter. They postulated that the free ferulic acid binds in the topsoil and acts on the young *B. daigremontianum* and other plantlets, but is ineffective on the parent plant.

Similarly, the leaf extracts of *B. pinnatum* inhibited the root length of mung bean *Vigna radiata* (L.) R. Wilczek cuttings by 38.1%; inhibited the rooting rate, root number, and root length of pea cuttings by 14.2, 23.5 and 26.9% respectively; and inhibited the germination rates of Indian mustard *Brassica juncea* (L.) Czern. and wild cabbage *Brassica oleracea* var. *caulorapa* DC. seeds by 42.0 and 53.6%, respectively (Huang *et al.* 1997).

The intra- and inter-specific acting allelochemicals of *B. daigremontianum*, *B. delagoense* and *B. pinnatum* were isolated and identified as p-hydroxybenzoic-, protocatechuic-, gallic-, p-coumaric and caffeic acid. By measuring stems and primary roots of *Bryophyllum* daughter plants, the intra- and inter-specific inhibitory activities of authentic compounds were demonstrated (Bär *et al.* 1997). Bär *et al.* (1997) also demonstrated the inter-specific allelopathic effect between mature, one-year old 40 cm high *B. daigremontianum* and plantlets of *B. delagoense*. Plantlets up to 12 cm distant from the base of the *B. daigremontianum* plant were severely retarded in growth; from that distance onwards the plantlets showed increasingly more normal growth. The allelopathic effect was more pronounced for *B. delagoense* than for *B. daigremontianum* (Bär *et al.* 1997).

Bryophyllum delagoense is not known to suppress good pasture in open situations in Australia but herbaceous species in shady situations may be at risk. Grasses under shade can also be suppressed (M.A. Hannan-Jones unpublished).

Beneficial

Medicinal. In Madagascar, *B. delagoense* is known as Tsiaba and the locals have two medicinal uses for the leaves: bathing with crushed leaves to alleviate fatigue and chewing the leaves to get rid of froth (white saliva) from the lips (J.J. Marohasy personal communication). In Mexico, *B. delagoense* is popularly used as a postcoital vaginal rinse. When tested *in vitro* with human spermatozoa ($\sim 30 \times 10^6$ spermatozoa mL⁻¹), the crude aqueous extract of *B. delagoense* leaves produced instantaneous agglutination and immobilizing effects (Taboada *et al.* 1992). *B. proliferum* is widely used in Madagascan traditional medicine for the treatment of various skin diseases; the methanolic extract yields several flavonoid glycosides (Razanamahefa *et al.* 1992).

Morton (1990) has reviewed the medicinal uses for *B. pinnatum*. In Africa, India and South America it is used for the treatment of insect bites, wounds, ulcers, abscesses and burns, inflammations, swellings and discolourations (Safford 1905, Kirtikar and Basu 1935, Dalziel 1937, Dastur 1950, Chopra *et al.* 1956, Boakye-Yiadom 1977); rheumatic afflictions, erysipelas and boils (Quisumbing 1951); smallpox, diarrhoea, dysentery, lithiasis and phthisis (Nadkarni 1954); whitlow (Gaind and Gupta 1971) and cholera (Siddiqui *et al.* 1989); mange and as a cold remedy, especially for small children (Walker and Sillans 1961); for bronchitis (Quisumbing 1951); as a diuretic (Oliver-Bever 1986); for conjunctivitis, earache and sore throats (Oliver-Bever 1986); in the induction of labour and the removal of ovarian cysts (Onwuliri and Anekwe 1992). In west tropical Africa, the leaf juice is fed into a newborn infant's mouth, while an infusion is drunk by the child and the mother (Dalziel 1937). In Singapore, the juice is given as a febrifuge (Burkill 1935). Apart from making concoctions, decoctions and infusions of plant parts, some leaves are regularly eaten in soups as a tonic for the stomach and kidneys.

The many ethnobotanical uses of *B. pinnatum* have led to investigations into its chemical composition and properties. The aqueous extract of *B. pinnatum* yielded bryophyllin B, with activity against the *in vitro* growth of tissue culture cells (Yamagishi *et al.* 1989). The methanolic extract of *B. pinnatum* has shown potent cytotoxicity *in vitro* against tumour cell cultures (Yamagishi *et al.* 1988), significant anti-ulcer activity in nine experimental animal models (Pal and Chaudhuri 1991) and a potent central nervous system depressant action (Pal *et al.* 1999). The juice expressed from warmed leaves of *B. pinnatum* has potent antibiotic activity against *Staphylococcus aureus*, *Bacillus subtilis*, *Escheichia coli* and *Pseudomonas aeruginosa* (Boakye-Yiadom 1977). The ethyl acetate extract of *B. pinnatum* showed appreciable antimutagenic activity (Obaseiki-Ebor *et al.* 1993).

Onwuliri and Anekwe (1992) found that *B. pinnatum* (Tables 3 and 4) is a rich source of some elements, important in the maintenance of human health. This high content of essential elements plus the physiological activities mentioned above explain the traditional medicinal roles attributed to the plant.

The extensive studies into the activity of *B. pinnatum* have led to the isolation and identification of various chemical classes, such as hydrocarbons (Gaind and Gupta 1974), phenolic components (Gaind and Gupta 1973), triterpenoids and phenanthrenes (Siddiqui *et al.* 1989) and sterols (Akihisa *et al.* 1991). Gaind and Gupta (1971) also reported the presence of three flavonoid glycosides in pulverized leaves: glycoside A (not defined); quercetin 3-diarabinoside and kaempferol 3-glucoside.

Insecticidal. Tannins serve as feeding deterrents and defence compounds against insect herbivores and pathogens, and accumulate preferentially in peripheral tissue to fulfil these functions. Tannin cells in *B. delagoense* and *B. daigremontianum* are located in the second sub-epidermal layer.

Table 3. Composition of *B. pinnatum*: per cent concentration (dry weight) (means \pm SD; n=3) after Onwuliri and Anekwe (1992).

	Moisture	Ash	Crude lipid	Crude protein	Crude fibre	Carbohydrate
Leaf	90.28 \pm 4.32	21.21 \pm 2.53	12.75 \pm 1.84	11.52 \pm 1.36	10.44 \pm 1.07	44.06 \pm 1.98
Stem	84.51 \pm 1.91	12.68 \pm 1.18	8.53 \pm 0.91	9.56 \pm 0.63	20.23 \pm 2.09	49.00 \pm 3.95
Root	75.10 \pm 2.89	13.92 \pm 1.40	7.12 \pm 0.48	7.45 \pm 0.75	13.32 \pm 1.24	58.15 \pm 1.91

Table 4. Elemental composition of *B. pinnatum*: (in ppm) (means \pm SD; n=3) after Onwuliri and Anekwe (1992).

	Calcium	Iron	Manganese	Magnesium	Potassium	Sodium	Zinc
Leaf	3552 \pm 149	14.55 \pm 1.28	1.03 \pm 0.17	158.0 \pm 10.8	1242 \pm 110.7	4.89 \pm 0.20	7.78 \pm 0.32
Stem	1887 \pm 165.7	11.03 \pm 0.99	0.43 \pm 0.03	137.5 \pm 14.5	1442 \pm 105.8	7.71 \pm 0.42	3.65 \pm 0.15
Root	2982 \pm 116.7	27.40 \pm 0.73	0.95 \pm 0.08	100.5 \pm 8.88	446.5 \pm 76.6	6.28 \pm 0.71	18.56 \pm 1.01

These idioblasts exhibit high levels of chalcone synthase (CHS) activity that indicates that the tannins accumulate in the cells where they are synthesized. In *B. delagoense* these idioblasts form a defensive layer under the surface of the leaf. In addition, idioblasts are more abundant at the abaxial, i.e. the outside orientated surface of the young leaf organs (Karwatzki *et al.* 1993). Paraffin sections of mature leaves of *B. daigremontianum* also show tannin cells scattered throughout the mesophyll rather evenly spaced, as well as the distinct layer of tannin cells below the abaxial epidermis (Balsamo and Uribe 1988).

Leaves of both *B. daigremontianum* and *B. delagoense* were not eaten by starved desert locusts *Schistocera gregaria* Forskal (Singh 1983). Acetone extracts of both of these species yielded an antifeedant, which could inhibit the feeding of *S. gregaria* at 0.5 % concentration.

Legislation

Bryophyllum delagoense (as *B. tubiflorum*) and the hybrid (as *B. daigremontianum* × *tubiflorum*) were declared in 1999 in Queensland under the Rural Lands Protection Act (1985) as Category P4 plants. This requires landowners to prevent the plant from spreading from the places in which they occur in the State or the relevant parts thereof. They are also declared in some Queensland shires under Section 41(2) of the Local Government Act (1936–81) (Figure 5). The costs of compliance, to the community and various levels of government, resulting from this declaration were estimated to be in excess of \$500 000 per year (Anon. 1999).

In New South Wales, *B. delagoense*, *B. pinnatum* and the hybrid are declared noxious weeds under the Noxious Weed Act (1993) in either the W2 (infestations to be suppressed and destroyed) or W3 (infestation size to be reduced; and spread to be prevented) categories in 17 Local Control Authority areas (Figure 5).

Weed management

Herbicides

A screening trial of various herbicides by Armstrong and Prior (1999) showed that at 9 months after treatment (MAT) the following treatments gave greater than 90% control of *B. delagoense* plants: 2,4-D acid (1.05 kg a.i. 1000 L⁻¹ water and 2.1 kg a.i. 1000 L⁻¹ water); 2,4-D amine plus atrazine plus BS1000® non-ionic surfactant (1 kg a.i. + 2 kg a.i. + 1 L 1000 L⁻¹ water); fluroxypyr (0.8 kg a.i. 1000 L⁻¹ and 1.6 kg a.i. 1000 L⁻¹ water); 2,4-D sodium salt plus BS1000® (1.6 kg a.i. + 1 L 1000 L⁻¹ water); 2,4-D amine (1.6 kg a.i. 1000 L⁻¹ water); 2,4-D ester (4 kg a.i. 1000 L⁻¹ high flash kerosene); and triclopyr ester/picloram amine plus BS1000 (1.05 kg a.i./350 g a.i. + 1 L 1000 L⁻¹ water). Complete control of *B. delagoense* plantlets within the same trial plots at 9 MAT was achieved only with fluroxypyr (800 g a.i. 1000 L⁻¹ and 1.6 kg a.i. 1000 L⁻¹ water), 2,4-D acid (2.1 kg a.i. 1000 L⁻¹ water), triclopyr/picloram (1.05 kg a.i./300 g a.i. 1000 L⁻¹ water) and 2,4-D ester (4 kg a.i. 1000 L⁻¹ high flash kerosene).

Armstrong and Prior (1999) also compared the cost and efficacy of various rates of fluroxypyr and metsulfuron methyl with the registered rate of 2,4-D acid (Table 5). Their results showed that fluroxypyr (70 g a.i. 100 L⁻¹ water) and metsulfuron methyl plus BS1000 (3 g a.i. + 100 mL 100 L⁻¹ water) were equally effective as the registered rate of 2,4-D acid at 9 MAT. The relative costs of product only were \$97 ha⁻¹, \$40 ha⁻¹ and \$93 ha⁻¹ respectively.

Neat diesel has been trialed on *B. delagoense* at 500 mL m⁻² (P. Whyte unpublished). Observations in the first few weeks after treatment revealed that all plant tips were desiccated and blackened, with many plants defoliated. After 6 weeks, there was much regrowth and at 9 weeks about 50% of the treated plants had obviously survived. Spot spraying with glyphosate (360 g a.i. L⁻¹) at 500 mL m⁻² (15 mL a.i. L⁻¹ + 5 mL L⁻¹ Agral™ 600 surfactant) resulted in 100% mortality of all vegetation after 9 weeks. A cost equivalent

of \$1000 ha⁻¹ makes this mix only suitable for small infestations.

The efficacy of a range of herbicides has been tested on *B. pinnatum* (Sparkes *et al.* in press). 2,4-D dimethylamine salt plus BS1000 (250 g a.i. + 100 mL and 500 g a.i. + 100 mL 100 L⁻¹ water) was the most efficacious. Fluroxypyr (150 g a.i. and 300 g a.i. 100 L⁻¹ water), metsulfuron methyl plus BS1000 (3 g a.i. + 100 mL and 6 g a.i. + 100 mL 100 L⁻¹ water) and triclopyr/picloram (105 g a.i./30 g a.i. 100 L⁻¹) did not prove to be as effective as they were for *B. delagoense*. These authors conjectured the poor results were due possibly to insufficient wetting agent having been used to allow herbicide penetration through the plant's waxy cuticle.

Some data exists on chemical control costs as a result of recent control operations undertaken by the Queensland Department of Natural Resources (QDNR) in Nudley State Forest in Chinchilla Shire, Queensland. The cost of the initial treatment was calculated to be approximately \$170 ha⁻¹ due to the heavily timbered nature of the area. Chinchilla Shire Council have spent an average of \$27 000 (1998 dollars) per year for the last 5 years on the control of *B. delagoense* and the hybrid. This equates to about \$180 ha⁻¹, comprising initial control and subsequent follow up (Anonymous 1999).

Other treatments

Pasture management. To best suppress *Bryophyllum* spp., it is essential to maintain strong pasture competition. Suggested grasses for this purpose include green panic (*Panicum maximum* Jacq. var. *maximum*), Queensland blue grass (*Dichanthium sericeum* (R.Br.) A.Camus), buffel grass (*Cenchrus ciliaris* L.), Katambora Rhodes grass (*Chloris guyana* cv. Katambora), purple pigeon grass (*Setaria incrassata* cv. Inverell) and silk sorghum (*Sorghum halepense* × *S. roxburghii* × *S. arundinaceum*). A reduction in stocking rate can lead to stronger grass production and suppression of *Bryophyllum* spp.

Cultivation. *Bryophyllum delagoense* rarely colonizes areas that have no canopy cover. A radical strategy proposed for eradication of *B. delagoense* from under a brigalow (*A. harpophylla*) canopy on an old mining lease involves strip blade ploughing of the brigalow, followed by sowing of native or improved pasture grasses and burning when fuel load is at a maximum. *Bryophyllum* infestations once cultivated and planted to crops, lawns or pastures are no longer a problem. Such a strategy may be useful if the infested area is to be put back into grazing or crop production, but would not be of use in areas where timber production or environmental values such as biodiversity, soil conservation and down catchment water quality are of

Table 5. Herbicides registered for *Bryophyllum* spp. control in Australia.

Herbicide	Rate for spot or boom application	Comments	State registration
Triclopyr 300 g L ⁻¹ + picloram 100 g L ⁻¹	500 mL in 100 L of water	High volume application; apply with surfactant at flowering	NSW, QLD
Fluroxypyr 200 g L ⁻¹	600 mL in 100 L of water	High volume application; add adjuvant	NSW, QLD
2,4-D amine 500 g L ⁻¹	500 mL in 100 L of water	Thorough, even coverage of leaves and plantlets is necessary. Add a wetting agent	NSW
2,4-D acid 300 g L ⁻¹	7.0 L in 1000 L of water ha ⁻¹	Hand Gun. Thorough, even coverage of leaves and plantlets is necessary	NSW, QLD

concern. This is particularly the case in Queensland brigalow, which is an endangered ecosystem (Wilson 1999).

Cultural control. In a hand weeding experiment, entire *B. delagoense* plants with intact roots came away easily from the leaf litter (P. Whyte unpublished). It was possible to prevent leaves and plantlets from falling to the ground, but even when all obvious plantlets were removed from the leaf litter, over 100 plantlets m² were observed 9 weeks later. It was not determined whether these were from hidden plantlets or from seeds germinating after good rain. All the removed *B. delagoense* were mounded to assess decomposition. After 10 weeks, most horizontal stems were rooting and tips were vertical with new growth. Plants inside the mound showed no signs of decomposition (P. Whyte, unpublished). It is thus advisable to either burn or bag and bury plants pulled up by hand. A hand weeding exercise with *B. pinnatum* (Sparkes *et al.* in press) was costed at \$2095 ha⁻¹. It was noted that the difficulty in removing plants with their root systems intact and the avoidance of leaf fall made this method less efficacious and more expensive than treatment with 2,4-D (approximately \$160 ha⁻¹).

Fire. Infestations and the accompanying debris can be burned after fencing off from grazing or removing stock to obtain sufficient fuel loads, grading firebreaks and obtaining required permits. This encourages grass competition and can prevent domination by *Bryophyllum* spp. for many years, especially if unburnt patches are followed up with herbicide treatment.

Natural enemies

Bryophyllum delagoense is not attacked in the field to any significant amount by insects presently in Australia. In glasshouse situations, scale insects will attack *B. delagoense* and the hybrid, causing the stems to collapse. (M. Hannan-Jones unpublished). An unidentified leaf blotch attacks *B. pinnatum*. *B. proliferum* and *B. pinnatum* are attacked by a mealybug in gardens in Brisbane (M. Hannan-Jones unpublished). *Bryophyllum daigremontianum* is attacked by a powdery mildew in moist situations. Only recently has interest been shown in management of *B. delagoense* and its hybrid with natural enemies. NR&M has nominated *B. delagoense* and the hybrid as targets for biological control and has initiated insect surveys in Madagascar and South Africa.

Insects and mites. The only species recorded attacking *B. delagoense* in Madagascar in any numbers is the weevil *Osphilia tenuipes* Fairmaire. The larvae of this species bore along the main stem of the plant

and pupate *in situ*. Multiple larvae/pupae are generally present per stem (J. Marohasy unpublished). The adults feed on the epiphyllous buds and in the leaf axil. A number of other species have been found attacking *B. delagoense* in Madagascar; these are a lycaenid caterpillar, *Leptomyrina phidias* Fabricius, an unidentified leaf-mining eurytomid wasp, *Eurytoma* sp.; an unidentified eumolpine leaf-feeding beetle; a bagworm *Acanthopsyche* sp.; a leaf hopper *Poecilocarda* sp.; a moth *Agrotis longidentifera ranavalo* Viette; and two scales, *Eriococcus* sp. and an unidentified sp. (Witt and Palmer 2000). A number of these insects have potential as biological control agents.

In its introduced range in South Africa, *B. delagoense* is attacked by insects that have evolved to utilize native African Crassulaceae. These include: the thrips, *Scirtothrips auranthii* Faure; the moth, *Tortrix capensana* Walker; and the lycaenid butterfly, *Leptomyrina hirundo* Wallengren. *Bryophyllum delagoense* is also attacked by two insect species that may themselves have been introduced into South Africa on horticultural taxa of *Sedum*, the weevil, *Alcidodes sedi* (Marshall) and the aphid, *Aphis sedi* Kaltentbach (A. Witt unpublished).

Pathogens. *B. delagoense* is highly susceptible to the pathogen *Agrobacterium tumefaciens* (Smith & Townsend) Conn, and develops tumours in a few days (Napoleao *et al.* 1998). This characteristic forms the basis of a simple, fast, low-cost and reproducible bioassay for screening antagonistic bacteria for the biocontrol of this pathogen.

Bryophyllum pinnatum was observed with a stem blight disease in Pune, India caused by two fungi *Colletotrichum dematium* (Pers. ex Fr.) Grev. and *Colletotrichum* state of *Glomerella cingulata* (Stonem.) Spauld. & Schrenk. The disease symptoms were visible over the entire stem as irregular, discoloured areas that later exhibited growth of punctate or slightly elongated, dark, acervular fruit bodies (Rao *et al.* 1989).

Forty-one species belonging to three genera of the family Crassulaceae were inoculated with basidiospores of *Puccinia benkei* to clarify the host range of this rust fungus (Yamaoka *et al.* 1997). Telia were produced on the leaves of *B. daigremontianum*, *B. delagoense*, and *B. beauverdiei*, which were recognized as new host plants.

Kalanchoe isometric virus (KIV) was identified (Izaguirre-Mayoral *et al.* 1990, Brunt *et al.* 1996 onwards) in crude sap of *B. pinnatum*, *B. daigremontianum* and *B. delagoense* plants showing a mild mosaic on the leaves. The virus could be transmitted mechanically to several test plants but not to healthy *Bryophyllum*. Air tempera-

ture greater than 30°C hindered the infection process. The virus particles occurred in relatively low concentration in the plant sap. Ultrastructural studies of infected leaves of *B. pinnatum* indicated that KIV caused an increase in chloroplast volume, distortion of the grana and reduced the number of thylakoids per granum. KIV infection also impaired the diurnal pattern of CAM synthesis and hydrolysis of starch. In nature, young *Bryophyllum* plantlets acquire KIV through their physical connections with the infected mature leaves.

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Appendix A. CLIMEX® (Sutherst and Maywald 1999) model parameters for *Bryophyllum* spp. based on their Madagascan distribution and tested against known worldwide distribution.

Parameter	<i>Bryophyllum delagoense</i>	<i>Bryophyllum pinnatum</i>
Temperature		
DV0	12.0	15.0
DV1	18.0	22.0
DV2	33.0	33.0
DV3	40.0	36.0
PDD	0.0	0.0
Moisture		
SM0	0.01	0.10
SM1	0.045	0.20
SM2	1.35	1.80
SM3	1.55	2.00
Cold Stress		
TTCS	6.0	13.0
THCS	0.005	0.0005
DTCS	15.0	0.0
DHCS	0.005	0.0
Heat stress		
TTHS	40.0	36.0
THHS	0.05	0.005
DTHS	0.0	0.0
DHHS	0.0	0.0
Dry Stress		
SMDS	0.02	0.2
HDS	0.10	0.0125
Wet Stress		
SMWS	1.4	1.9
HWS	0.05	0.05
Diapause and light and stress interactions not used.		