

Review

The Biology of Australia weeds 59. *Clidemia hirta* (L.) D. Don.

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Name

Clidemia hirta (L.) D. Don (syn. *Melastoma hirta* L.) is in the family Melastomataceae, tribe Miconieae. The Miconieae comprise approximately 1800 species in 19-23 genera and are exclusively neotropical (Michelangeli *et al.* 2008). The genus *Clidemia*, established by David Don in 1823, currently contains about 180 species (Gleason 1939, Manickam *et al.* 2000, Kriebel and Almeda 2009) with new species still being described, particularly from Costa Rica and Panama (Kriebel and Almeda 2009). The species name *hirta* is derived from the Latin word for 'hairy' or 'scrubby'.

Several varieties of *C. hirta* have been described: *C. hirta* var. *hirta*, *C. hirta* var. *elegans* Griseb., *C. hirta* var. *chrysantha* Cogn. and *C. hirta* var. *tiliaefolia* (Gleason 1939, DeWalt and Hamrick 2004). The *elegans* variety is distinguished by broader leaves and a cordate base while the variety *chrysantha* is not readily distinguishable from other varieties (Gleason 1939). *Clidemia hirta* var. *hirta* was introduced into Hawaii (DeWalt and Hamrick 2004). No clidemia species are native to Australia, but some members of the Melastomataceae, including the genera *Medinilla*, *Melastoma*, *Memecylon*, *Osbeckia*, *Otanthera* and *Pternandra* are native to Queensland and other states (APC 2010). Other melastomes such as *Dissotis rotundifolia* (Sm.) Triana, *Tristemma mauritianum* J.F.Gmel. and several *Arthrostemma*, *Tibouchina* and *Miconia* species are considered exotic.

In this review *Clidemia hirta* will be referred to as "clidemia". Common names for clidemia include Koster's curse and soap bush (Randall 2002).

Description

Clidemia is a bushy, perennial evergreen shrub typically reaching 2-3 m in height (DeWalt 2006) (Figure 1). However, its height can vary depending on environmental conditions. In exposed windy areas, clidemia remains a weak upright or scrambling shrub up to 75 cm tall (Smith 1992), but plants growing in moist shaded environments can be densely branched

and reach 5 m into the sub-canopy (Smith 1992, Francis 2007). *Clidemia* roots are shallow, abundant, fine and lateral (Francis 2007).

Clidemia stems, leaves and fruit are covered in spreading, reddish bristly hairs that lighten with age (Whistler 1983, Waterhouse and Mitchell 1998, DeWalt *et al.* 2004a) (Figures 1 and 2). Branchlets are sparsely hirsute (Manickam *et al.* 2000). Leaves are opposite, elliptical, mostly 8–10 cm long, broadest across the middle and cordate or rounded at the base with petioles to 1–3 cm long (Gleason 1939, Wester and Wood 1977, Manickam *et al.* 2000, Yang 2001). The leaf blades are bristly-hairy and wrinkled between the 5(–9) conspicuous longitudinal veins (Whistler 1983, Waterhouse and Mitchell 1998). Leaf margins are toothed to crenate (Gleason 1939, Henty and Pritchard 1988, Michael 1989).

Clidemia flowers are borne on axillary or terminal cymose panicles clustered in the upper leaf-axils (Binggeli 1997, Waterhouse and Mitchell 1998). The pedicels are 2–3 mm long and bristly (Yang 2001). The inflorescence is short, hairy and composed of 6–20 individual flowers (Whistler 1983). Flowers are white and between 1 and 1.5 cm in diameter (DeWalt *et al.* 2004a) (Figure 2a). The 5–7 petals are 6–9 mm long, oval-obovate, obtuse and glabrous (Wester and Wood 1977, Waterhouse and Mitchell 1998, Yang 2001). The calyx has five filiform appendages (Waterhouse and Mitchell 1998). The 8-12 stamens are white, equal or sub-equal and surround a whorl of fimbriate scales (Waterhouse and



Figure 1. An adult clidemia plant approximately 1 m tall in the Julatten infestation (Australia) (Photo: S. Brooks).



Figure 2 – *Clidemia* (a) flowers, and (b) fruit (Photo: T. Sydes).

Mitchell 1998, Yang 2001). The anthers are linear and stigmas are simple and capitate. The style is filiform, up to 7 mm in length and glabrous (Manickam *et al.* 2000, Yang 2001). The ovary is almost completely superior but appears inferior due to being covered by a bristly 5 mm long hypanthium (Henty and Pritchard 1988, Waterhouse and Mitchell 1998, Manickam *et al.* 2000).

The fruit is a berry, 4–5 mm in diameter, 6–7 mm long, ellipsoidal and covered with long patent bristles (Yang 2001, Francis 2007, Shiels and Drake 2011) (Figure 2b). It is red-purple to black-blue, turning deep purple at maturity and weighs on average 214 to 230 mg (Waterhouse and Mitchell 1998, Yang 2001, Kueffer *et al.* 2009, Shiels and Drake 2011). Seeds are ovate, 0.5 mm in diameter, rugose (wrinkled surface) and light yellow to brown with a maximum length of 0.7 mm (Waterhouse and Mitchell 1998, Manickam *et al.* 2000, Bakutis 2005, Shiels and Drake 2011). Teoh *et al.* (1982) reported approximately 36 000 seeds in 1 g while Francis (2007) reported that air-dried seeds weighed an average of 0.00383 g per seed.

History

Worldwide

The earliest introductions of *clidemia* outside its native range appear to have been to Fiji and Java between 1880 and 1896, as a contaminant of coffee plants (Simmonds 1933). *Clidemia* appears to have been primarily transported around the world as a seed contaminant (Binggeli 2001, Randall 2002, Dawson *et al.* 2008) and not usually for agricultural or horticultural purposes (DeWalt 2003). The species may have been deliberately or accidentally introduced via botanical garden specimens to Peradeniya in Sri Lanka in 1894, Amani in Tanzania by 1930 and Wahiawa (Oahu) in Hawaii by 1941 (Dawson *et al.* 2008). Gleason (1939) described *clidemia* as a naturalized weed in the 'Indo-Malaysia' region.

The invasion of *clidemia* in Fiji and subsequent attempts at biological control were well documented in the 1930s by resident Government Entomologist, Hubert Simmonds (Simmonds 1933, 1937) and by the 'coconut entomologist' R.W. Paine (Paine 1934). The species was apparently accidentally introduced into the Waimanu District of Fiji with coffee plants from Brazil between 1880 and 1886. *Clidemia* was first noticed there as a low hedge along wire fences, where the seeds were likely to have been dropped by birds, and subsequently "...spread with such alarming rapidity as to acquire the title of the 'Curse'..." (Simmonds 1937). Simmonds (1933) reports that by 1919 "thousands of acres were covered with it to the exclusion of almost all other growth.....it thrived almost equally well under the shade of coconut and rubber plantations...". In 1920 *clidemia* was declared a noxious weed in Fiji (Patel 1971). By 1922 *clidemia* was said to have "...taken possession of a tract of land that must approximate 3000 acres in extent" (Paine 1934). Paine (1934) also reported dense monocultures of *clidemia* over vast areas of unforested hills.

Clidemia was first observed growing in forests of the Wahiawa area on Oahu, Hawaii (Wester and Wood 1977, Smith 1992) in 1941, having reportedly been cultivated at the Wahiawa botanical gardens (Smith 1992, citing Whitten 1977). It was reported as well established in at least three locations on the island of Hawaii in 1972 (Smith 1992). *Clidemia* was first reported on Molokai in 1973 at 1000–1150 m above sea level and had established on Maui by 1976 (Smith 1992). *Clidemia* was reported on Kauai in 1982 and five confirmed locations and several unconfirmed infestations led Smith (1992) to forecast a rapid expansion beyond the known infested areas, then totalling about 40 ha. Only two plants have been found on Lanai, with the first sighting reported in 1988 (Smith 1992). The species

exhibits high genetic similarity and low genetic differentiation amongst multiple samples collected on four islands in Hawaii (DeWalt and Hamrick 2004). The lack of island-unique alleles on Hawaii suggests that introductions to the different islands came from the same or similar native source populations, most likely from South America or the Caribbean rather than Central America (DeWalt and Hamrick 2004).

Australia

To date there has only been one infestation of *clidemia* discovered in Australia, at Julatten in far north Queensland (Waterhouse 2003, S. Brooks unpublished data 2010). In August 2001, a local government weed officer reported a suspicious melastome to the Australian Quarantine Inspection Service (AQIS) during a trace-forward activity from a newly discovered *mikania* vine (*Mikania micrantha* Kunth) infestation at Speewah (Waterhouse and Hucks 2002, S. Clayton personal communication). Voucher specimens were collected and sent to Queensland Herbarium for verification and permanent storage in August 2001 (AQ 718311).

Following formal identification, approximately 120 plants growing over about 0.5 ha at a former nursery were controlled (Waterhouse and Hucks 2002, Waterhouse 2003, S. Clayton personal communication, P. Davis personal communication). Due to changes in property ownership, no information about the possible time of *clidemia* introduction has been obtained. The origin of *clidemia* at this site is also unknown, but it may have been introduced as a contaminant of palm seeds or packing material imported from Central America or South East Asia (B. Waterhouse personal communication). Some 'within population' leaf samples have been collected locally but there has been no genetic comparison between the Australian and overseas populations. A

small population of *Miconia calvescens* D.C. was found at the same location at the same time.

Distribution

Native

Clidemia is native to the humid, tropical lowlands of Central and South America and the Caribbean Islands, (Figure 3). It is found across a broad neo-tropical native range from southern Mexico, through Costa Rica to northern Argentina, with an altitudinal distribution from sea level to approximately 1500 m (Wester and Wood 1977, Waterhouse and Mitchell 1998, Randall 2002, DeWalt *et al.* 2004a).

Introduced - worldwide

Clidemia is now widely spread in locations that have climatic conditions similar to its native range (DeWalt 2003) (Figure 4). It is a serious weed on many tropical and sub-tropical oceanic islands (Brunei, Singapore, Ascension, Comoros, Mauritius, Madagascar, Réunion, Seychelles, Sri Lanka, Mayotte, Fiji, Palau, American Samoa, Samoa, Solomon Islands, Bougainville (Papua New Guinea), Tonga, Vanuatu, Hawaii and Wallis and Futuna), and countries including Indonesia, India, Malaysia, Thailand and Tanzania (Wester and Wood 1977, Hancock and Henderson 1988, Henty and Pritchard 1988, Sheil 1994, Binggeli 1997, Swarbrick 1997, Waterhouse and Mitchell 1998, Meyer 2000, Kueffer and Vos 2003, Napompeth 2004, PIER 2004, Varnham 2006, Linnebjerg *et al.* 2009).

In tropical Asia, the species has been described as a 'super-invader' as it is the only exotic plant species to invade closed-canopy native forests in Singapore (Teo *et al.* 2003), at Pasoh in Malaysia (Peters 2001) and in Sri Lanka (Ashton *et al.* 2001). In Papua New Guinea, *clidemia* is considered a 'sleeping weed' (Orapa 2006). *Clidemia* was recorded in Pingtung County in southern Taiwan in 1998, growing in a disturbed woodland or secondary forest amongst bamboo (*Bambusa stenostachya* Hack.) and shade-intolerant species at altitudes between 100 and 150 m (Yang 2001). This is the only known infestation in Taiwan and its source is unknown (Yang 2001).

By 1960, Plucknett and Stone (1961) reported that collections had been made on Oahu but the species was uncommon. However, observations reported by Wester and Wood (1977) suggest rampant spread over hundreds of hectares on Oahu in the 1960s. By 1972 it had formed monospecific sub-canopy stands in native forests (Tunison 1991, Smith 1992, Conant 2009). Wester and Wood (1977) considered that *clidemia* had spread to over 31 350 ha on Oahu, in areas receiving more than 1270 mm annual precipitation. The estimated area of infestation on Oahu was



Figure 3. Distribution of *clidemia* in its native neotropical range. Black triangles represent collection records, primarily from the Missouri Botanical Gardens, TROPICOS database.

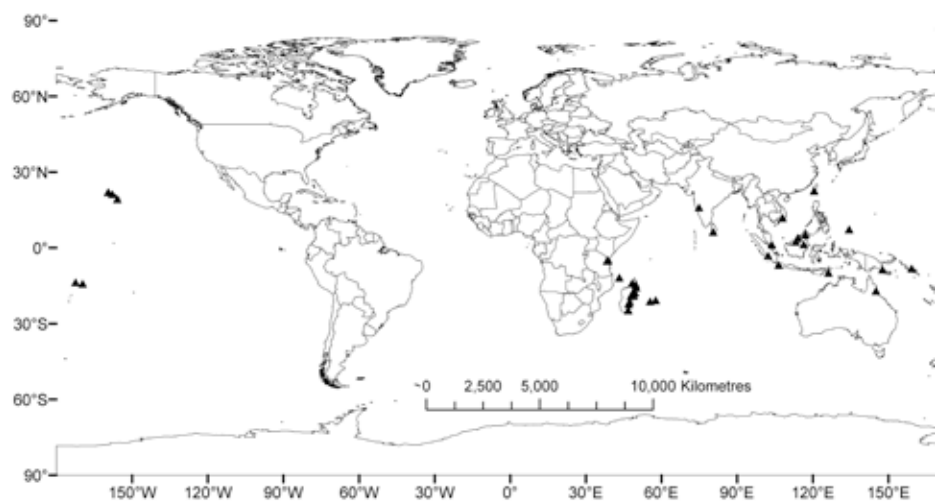


Figure 4. Locations (triangles) where *clidemia* has been recorded as invasive.

revised upward to an estimated 100 000 ha by Smith (1992), as it had been recorded between 11 m and 1340 m above sea level and reached the extent of its possible range. In 1974 the estimated infestation size on Molokai was about 5 ha (Wester and Wood 1977) but it had spread to 6300 ha by 1992 (Smith 1992). Clidemia spread to approximately 200 ha on eastern Maui by 1992 (Smith 1992) and an estimated 21 800 ha by 2004, including into the Haleakala National Park (Medeiros 2004). These reports highlight the rapid expansion (measured in decades) of the distribution of clidemia on Hawaiian Islands. In spreading across the Hawaiian Islands clidemia had become the most common woody invasive plant in wet forests (DeWalt and Hamrick 2004).

Introduced - Australia

The Australian infestation is 16.4 km inland from the wet tropical coast in far north Queensland near the rural township of Jullatten. It is on private properties (16°36'S, 145°20'E), 4 km west of the Riflemead Forest Reserve, at approximately 435 m elevation and is surrounded by extensive tracts of rugged forested land in the Wet Tropics World Heritage Area. Creeks within the infestation broadly flow away from the coast and south west to Rifle Creek near Mount Molloy, which flows west to the Mitchell River then to the Gulf of Carpentaria. At discovery, mature and seedling plants were also found at low density away from the creek line, suggesting that seed was being spread by birds (Waterhouse 2003); further searches suggested flood-borne dispersal of seed may also have occurred (Waterhouse and Hucks 2002). The species occurs in a range of microsite conditions, including open paddocks, riparian forested vegetation and forest edges, and occasionally in well shaded forest interiors. Several hundred hectares around the infestation are searched annually (Brooks *et al.* 2009). Plants are found coarsely scattered over approximately 120 ha, while the cumulative net area (Global Positioning System waypoints plus a 5 m buffer) occupied by clidemia is less than 6 ha (S. Brooks unpublished data 2010).

Habitat

Clidemia occurs in a range of habitats over its broad geographic range. Peters (2001) observed clidemia growing in primary forest beneath closed canopies, along steep embankments with exposed soils and near trails in heavy shade in La Mucuy National Park (c. 2200 m elevation) in Venezuela; he did not observe any plants in tree fall gaps. In Caparo Forest Reserve in Venezuela (c. 150 m elevation), clidemia was observed primarily along trails, in undisturbed forest understorey but seldom in full sunlight. However, in Costa Rica clidemia is found only in highly disturbed sites and in pastures, along roadsides and sometimes

in tree plantations, not in old-growth forest (Peters 2001, Wester and Wood 1977). Within its native range Francis (2007) also considered clidemia to be a colonizer of disturbed habitats such as roadsides, pastures, fence lines, plantations, burnt areas, land slip areas, river banks and tree-fall mounds.

Clidemia occurs in dense, monospecific stands in wet environments in Hawaii, and as low density populations in undisturbed habitats (Smith 1992). It ranges from areas of heavy cover (gullies and other protected areas) where only a few large individuals exist, to open situations where solid stands of short stunted plants occur (Smith 1992).

Teo *et al.* (2003) reported that clidemia was the only weed identified during surveys of tall secondary forest and primary rain forest in Singapore and was mostly found in steep areas with shallow soils, gaps and lit forest margins, although plants also persisted under a closed canopy. In Malaysia, clidemia has invaded forest within the relatively undisturbed Pasoh Forest Reserve; however, it is found there almost exclusively in well lit gaps (Peters 2001). Clidemia was also a common weed in secondary forests forming in rice paddies abandoned 18 years ago and present in riparian forests abandoned 30 years ago, on a tropical flood plain of peninsular Malaysia (Hashim *et al.* 2010). In the closed forests of the East Usambara Mountains of Tanzania, clidemia was scattered but formed dense patches in areas with some direct sunlight (Sheil 1994), although in the same region Dawson *et al.* (2011) recorded it as an invader of disturbed and intact forest plots with a median canopy cover of 92.6% ($n = 157$).

On Silhouette Island in the Seychelles, Gerlach (2004) identified a rapid decline in clidemia density between 1990 and 2000 in mid-altitude forest plots as the canopy thickened and gaps closed. However, over the same timeframe, clidemia spread and increased in abundance from focal points of introduction in the mid-altitude forests towards low-altitude forest (Gerlach 2004). Though frequent in most forest types and on rugged wet mountain peaks, less clidemia was observed in drier coastal areas of Silhouette Island (Gerlach 1993). Since the first detection of clidemia on Mahe (Seychelles) in 1993, isolated plants and large patches have been found in closed canopy forests, disturbed forest floors, open canopy forests, dense grasslands and along roads and paths (Kueffer and Zemp 2004). Linnebjerg *et al.* (2009) recorded clidemia in mature lower mountain moist forests on Mauritius.

In surveying Fijian wetland vegetation, Ash and Ash (1984) occasionally recorded clidemia in transitional freshwater and dryland forest habitats and frequently in wetland patches within open dryland veg-

etation. Clidemia has also been recorded amongst sedges (Cyperaceae) on the occasionally flooded margin of a Fijian upland peat swamp (Southern *et al.* 1986), as well as in upland rainforest plots (Tuiwawa *et al.* 2008).

In documenting the first record of clidemia in India (1961), Nayar (1966) notes 'luxuriant' clidemia growth along rice-fields and water courses in Trivandrum district of Kerala.

In north Queensland, clidemia is found in forested creek banks and creek beds, but also in open pasture and forest regrowth (see above).

Climatic requirements

Clidemia will grow under climatic conditions associated with both the dry and wet tropics (Binggeli 1997) and is found in mesic (1270 mm rainfall y^{-1}) to very wet (7600 mm y^{-1}) areas (Wester and Wood 1977). While clidemia prefers moist environments, it has been reported growing in areas where annual rainfall is <1000 mm (Smith 1992, Francis 2007). The infestation in Australia occurs in an area where the estimated annual mean precipitation is 1616 mm ($n = 68$) (BOM 2011), with a distinct wet (median monthly rainfall >120 mm from December to March) and dry season (median monthly rainfall <20 mm from July to September).

A CLIMEX (Sutherst and Maywald 1985, Sutherst *et al.* 2007) model (parameters in Appendix 1) of the potential distribution of clidemia in Australia includes humid coastal sites in the Northern Territory and much of north-eastern Queensland. The most climatically suitable sites, however, are along the south-east coast of Queensland between Maryborough and Brisbane (Figure 5).

Substratum

The various habitats occupied by clidemia indicate a tolerance for disturbed, mountain, forest and waterlogged soils. If the site has adequate moisture, clidemia will tolerate a wide range of soil properties (Francis 2007), including soils of volcanic origin such as ultisols, red-yellow latosols or inceptisols (Singhakumara *et al.* 2000, DeWalt *et al.* 2004b). The clidemia site in north Queensland has loamy soil, specifically soil type Um4.43 map unit LN1, a deep yellowish red or yellow friable loam with an A2 and B horizon (Isobell *et al.* 1968).

Plant associations

Clidemia grows well under both native and introduced plant species (Tunison 1991). On Oahu, clidemia has been observed under introduced trees such as *Lophostemon confertus* (R.Br.) Peter G. Wilson & J.T. Waterh., *Eucalyptus robusta* Sm., *Psidium cattleianum* Sabine and *Melaleuca quinquenervia* (Cav.) T. Blake and under native species such as *Metrosideros collina* (J.R. and G. Forst) and

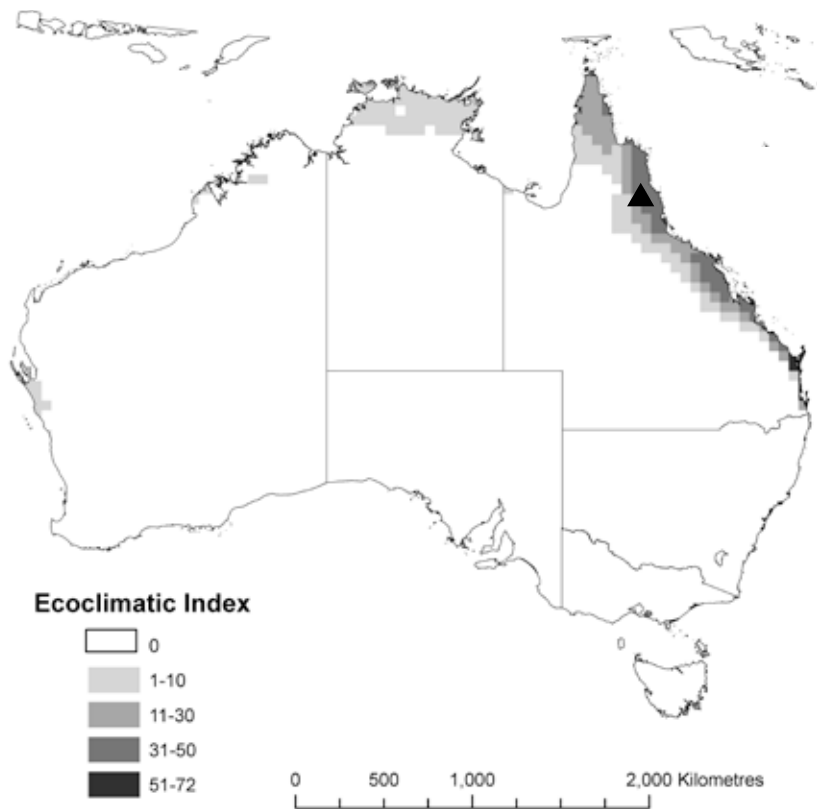


Figure 5. Potential distribution of clidemia in Australia based on climatic conditions (CLIMEX). Larger Ecoclimatic Index (EI) values reflect increasing climatic suitability. A triangle represents the location of the only known infestation in Australia. CLIMEX parameters are shown in Appendix 1.

Acacia koa A. Gray (Wester and Wood 1977). All tropical island forests of any composition appear suitable for clidemia invasion, particularly if subjected to some form of disturbance (Binggeli 1997).

The single known Australian infestation occurs on cleared, disturbed and forested land (Brooks *et al.* 2009) where the predominant forest type is regional ecosystem 7.11.1a, typically a mesophyll vine forest of lowlands and foothills on metamorphic soils of moderate fertility in wet rainfall zones (Queensland Herbarium 2009).

Growth and development

Clidemia is more abundant in much of its introduced range than in its native range and occurs in a greater range of environmental conditions (Wester and Wood 1977, DeWalt *et al.* 2004a). DeWalt *et al.* (2004a) assessed growth, biomass allocation and photosynthetic parameters of clidemia in plants from its native range (Costa Rica) and invaded area (Hawaii). They found no evidence that the genotypes differed in ways that might account for observed differences in abundance and occurrence in habitats between the introduced and native ranges (DeWalt *et al.* 2004a). However, DeWalt *et al.* (2004b) suggest the expanded distribution and vigour of clidemia in its introduced range may be partly attributed to an ecological response to the release from natural enemies.

Morphology

Clidemia can reach 5 m in height in moist shaded habitats, whereas in exposed areas the species rarely grows to more than 1 m (Tunison 1991). When it occurs on very steep slopes it can adopt a 'pendant' habit up to 15 m in length (Smith 1992). Takahashi and Rustandi (2006) found that clidemia increased its crown area in response to canopy openings and its height growth rate in gaps was higher than seven other sub-montane native species studied in Indonesia (Takahashi and Mikami 2008). These authors also found that leaf longevity for clidemia (<6 months) was relatively short compared to the other native species and suggested that avoidance of self-shading by having shorter-lived leaves and increasing crown area was advantageous to the invading species.

Physiology

Clidemia has been shown to be relatively tolerant of low-light conditions. In an experimental study conducted in Hawaii with both native and invasive species (including two other invasive melastomes, *M. calvescens* and *Tibouchina herbacea* (DC.) Cogn., clidemia was the only species to maintain a positive relative growth rate (RGR) under low light conditions (Baruch *et al.* 2000). In a treatment where the species was also subjected to water stress, its RGR in high light conditions was $0.0284 (\pm 0.001 \text{ SE}) \text{ g}^{-1} \text{ d}^{-1}$, compared to $0.0105 (\pm 0.001) \text{ g}^{-1}$

d^{-1} in low light conditions. In a watered treatment the RGR was $0.0315 (\pm 0.001) \text{ g}^{-1} \text{ d}^{-1}$ and $0.0076 (\pm 0.001) \text{ g}^{-1} \text{ d}^{-1}$ in high and low light respectively. In low light, clidemia also reduced specific leaf mass while increasing specific leaf area, a response common to melastomes (Denslow *et al.* 1990) and a strategy that may permit light to reach deeper chloroplasts in the leaf mesophyll. This appears to be an important adaptive trait in shaded habitat and has been explained as a response to increase carbon capture and recover internal carbon balances (Baruch *et al.* 2000). In response to water stress, clidemia showed a decrease in total biomass and leaf-area ratio and an increased root-shoot ratio (Baruch *et al.* 2000).

A study by Peters (2001) at the Pasoh Forest Reserve (Malaysia) reported clidemia exhibited significantly higher relative growth rates in gaps and gap edges than under closed canopies.

Dawson *et al.* (2011) reported a specific leaf area of $310.5 \text{ cm}^2 \text{ g}^{-1}$ dry weight for clidemia and calculated the concentrations of six leaf nutrients. The decomposition rate of clidemia litter from Hawaii was the highest ($k\text{-value year}^{-1} = 8.19$) of 11 species measured by Allison and Vitousek (2004a), including five native Hawaiian species and five invasive species (which included two other melastomes, *M. calvescens* and *T. herbacea*). In addition, the authors found that clidemia litter had a much greater tendency to release nutrients during decomposition, when compared to leaf litter of native species. More than 50% of the initial N and P of clidemia litter was lost by 86 days; litter of native species had lost less than 10% by this time. These results suggest clidemia litter could contribute to positive feedbacks between invasions and nutrient cycling in Hawaiian ecosystems (Allison and Vitousek 2004b).

Phenology

In Australia, when grown under favourable shade-house conditions from young transplanted seedlings, clidemia flowered after a minimum of 266 days (average 382 ± 46 days) and fruited after a minimum of 365 days (average 456 ± 41 days) (Graham and Setter 2007). In the field, the minimum time to flowering was slightly higher at 275 days (Graham and Setter 2007). At fruiting the average plant height in shade-house conditions was 45 cm (± 8) and average basal diameter was 8.3 mm (± 2.2) (Graham *et al.* 2008). When data on size at first flowering from Graham and Setter (2007) are combined with data from reproductive plants encountered in the field, there is a range of basal diameters (6 to 19.1 mm) and heights (38 to 240 cm) at which plants may mature, but most plants with basal diameters greater than 12 mm are mature ($n = 119$; S. Brooks unpublished data).

In assessing the growth of clidemia

from seeds planted in mid-July 2001 in a fertilized and watered common garden, Dewalt *et al.* (2004a) found that plants of Costa Rican and Hawaiian parentage grown in high light environments all had flowers and immature fruit when harvested in the second week of August 2002. Plants from both areas grown under low light conditions had not flowered by the time that this trial concluded. The dry mass of the total reproductive parts on the Hawaiian-sourced plants was double that of the Costa Rican plants at the time of harvesting, which could be due to an earlier onset of flowering, though that information was not recorded. A greater, earlier reproductive effort could contribute to the greater abundance of clidemia in the introduced habitats (DeWalt *et al.* 2004a).

Melo *et al.* (1999) observed 10 native clidemia plants in a field situation (Recife, Brazil) twice weekly between January 1993 and January 1995; they reported that flower production peaked in April and May, but fruit was produced for most of the year.

In Hawaii (altitude 820 m in the Kipahulu Valley, Maui), Medeiros (2004) selected 25 mature plants for a phenological study. The heights of these plants ranged from 55 to 126 cm (average 84 cm) and basal diameters ranged from 9 to 37 mm (average 15 mm). In every month between May 1996 and April 1997 the production of buds, flowers, immature fruit or ripe fruit was recorded for these plants. Overall, ripe fruit production peaked between November and January. Eleven of the larger plants produced ripe fruits every month, while some smaller plants did not produce flowers between December and March or ripe fruits from May through July. On Oahu, Bakutis (2005) recorded the presence of mature and immature fruits on 15 clidemia plants monthly between June 2003 and June 2004; fruits were observed all year round. Mature fruit were present on all plants in all months except during September, October and November 2003 and June 2004, when 70% or more of plants

exhibited mature fruit. Peters (2001) noted that clidemia's year-round reproduction may contribute to its invasiveness at the Pasoh Forest Reserve, where most native plants show some periodicity to their reproduction by fruiting one to two times per year.

Reproduction

Floral biology and pollination

Physical separation between the anthers and stigma is thought to largely prevent self fertilization in many Melastomataceae, including clidemia (Renner 1989). Clidemia also has low pollen viability (Melo *et al.* 1999). This species reproduces both by cross-fertilization (allogamy) (Ferreira *et al.* 1994) and by agamospermy, a form of apomixis where seeds are produced without fertilization and are genetically identical to the parent plant (Renner 1989, Melo *et al.* 1999, DeWalt *et al.* 2004a, Mendes-Rodrigues *et al.* 2008). The proportion of seeds produced through apomixis versus sexual reproduction is not known in either the native or invasive ranges (DeWalt 2003). Mendes-Rodrigues *et al.* (2008) identified polyembryony in clidemia, reporting means between different populations of 1.04 and 1.26 embryos per seed from fresh and buried seed samples. In germinating seed collected from glass-house-cultivated plants collected from the Australian infestation, two seedlings have occasionally been observed arising from single seeds in petri dishes (S. Setter personal communication). The combination of apomixis and polyembryony led Mendes-Rodrigues *et al.* (2008) to suggest that a single seed could initiate a clidemia infestation. The invasive capacity of clidemia in Hawaii is not limited by low genetic diversity (Dewalt and Hamrick 2004). With similarly low genetic diversity values also identified in native Costa Rican clidemia populations, DeWalt and Hamrick (2004) warn that the level of genetic variation in clidemia is unrelated to invasiveness.

In its native range, clidemia is reported

to be pollinated by bees from two families, Apidae (*Bombus*, *Trigona*, *Euglossa*, *Melipona fulva* Lepageletier and *M. lateralis* Erichson) and Halictidae (*Augochloropsis hebescens* Smith, *A. callichroa* Cockerell) (Renner 1989, Ferreira *et al.* 1994, Melo *et al.* 1999). The low frequency oscillation of bees' wings is thought to be the most likely mechanism that allows pollen to escape the anthers (Renner 1989). In Brazil, anthesis begins at about 1800 h and ends at about 0900 h the following morning (Ferreira *et al.* 1994).

DeWalt *et al.* (2004a) stated that clidemia does not exhibit clonal growth. However, there have been reports of leaves and stem fragments developing roots on moist shaded soil (e.g. Smith 1992, citing A.C. Medeiros personal communication), indicating a capacity for vegetative propagation.

Seed production

Clidemia is a prolific seeder with more than 300 seeds per fruit found in studies across three countries (Table 1).

Medeiros (2004) estimated an average production of 4586 fruits per plant y^{-1} under field conditions (range 2191–8011). This equates to an average of over 3.8 million seeds per plant y^{-1} , and over 10.3 million seeds $y^{-1} m^{-2}$ of mature clidemia infestation. Bakutis (2005) reported that clidemia seed comprised 90.5% of the total seed rain and more than 2600 seeds m^{-2} , sampled over 11 months across native, transitional and alien dominated vegetation types on Oahu. Clidemia accounted for more than 80% of the 'dispersed' seed rain in the vegetation types assessed by Bakutis (2005). In Australia, shade house-raised plants were also found to produce an average of 284 fruits per plant ($n = 18$) over the first six months of reproductive maturity, rising to an average of 967 fruits per plant ($n = 10$) over the first 12 months of maturity (Patane and Setter 2009).

Seed germination

Ground disturbance appears to provide an excellent environment for germination and establishment of clidemia: within two years disturbed areas can become smothered with clidemia (Wester and Wood 1977). In Hawaii, areas dug up by feral pigs show large numbers of seedlings within two months of disturbance; these areas become dense thickets of clidemia within six months (Smith 1992). In Sri Lanka, Singhakumara *et al.* (2000) found germination was highest in partially shaded areas (valley and ridge), although some clidemia germinated in seedling trays exposed to full sun. Fresh clidemia seed ($n = 150$) averaged 88% germination over four months when cultivated in petri dishes in incubators set at alternating 12 h regimes of 30°C with lights on and 20°C of darkness (K. Patane personal communication, S. Brooks unpublished data).

Table 1. Studies reporting the number of clidemia seeds per fruit.

Location	Mean seeds per berry (sample size)	Range	Source
Maui	832 (50)	618 to 932	Medeiros (2004)
Oahu	408 (15)	Not stated	Bakutis (2005)
Hawaii	412 (10)	300 to 900	DeWalt (2006)
Oahu	360 (57)	Not stated	Shiels and Drake (2011)
Mauritius	Not stated	700 to 1200	Linnebjerg <i>et al.</i> (2009)
Queensland*	801 (50)	300 to 1200	K. Patane, personal communication (2009)

*Berries were collected from plants grown under shade-house conditions.

Seed bank longevity

Mendes-Rodrigues *et al.* (2008) assessed viability of clidemia seed collected from two locations, Araguari and Uberlandia in the state of Minas Gerais, Brazil. Seed from Uberlandia was also collected two years earlier and buried in local soil (Uberlandia University Garden) or stored under dry laboratory conditions. Germination of all four samples (two fresh and two stored) was high and not significantly different (range 87.7–94.2%), with 93.1% of seed germinating after being recovered from permeable packets that had been buried for two years. The authors concluded that storage conditions did not alter seed germination. Germination of the buried seed commenced and concluded in a shorter time frame than the other samples. Also in the Uberlandia area, Pereira-Diniz and Ranal (2006) studied the germinable soil seed bank of a gallery forest. They found small numbers of germinable clidemia seed at soil depths from surface to 30–35 cm and in several microhabitats. Although this vegetation type is regularly flooded, the authors consider that at the greater depths sampled, several species (including clidemia) form a persistent seed bank. In the Bragantina area of Brazil, Vieira and Proctor (2007) found clidemia seed made considerable contributions to the total soil seed bank and seed rain in a primary forest and in 5, 10 and 20 year old secondary forests, although the species was not recorded in censuses of nearby plants. These studies indicate that clidemia develops a persistent soil seed bank across different forest ages in its native Brazil. Similarly, Peters (2001) reported that clidemia seed was identified in soil samples 20 years prior to plants being recorded in the Pasoh Forest Reserve (Malaysia).

Bakutis (2005) found clidemia seedlings comprised 99% of all germinants ($n = 51\ 940$) from soil samples collected from three vegetation types at a seed rain study site on Oahu. As the mean density of clidemia in the soil seed bank (32 110 – 43 148 seeds m^{-2}) was much greater than the seed rain (2 600 seeds m^{-2}), Bakutis (2005) considered that clidemia formed a relatively persistent seed bank. Medeiros (2004) also reported evidence of a wide-spread and persistent seed bank on Maui, when clidemia seedlings emerged in plots with limited local mature plants and/or no experimental seed input. Further anecdotal reports indicate that clidemia also develops a seed bank persisting for at least 3 years (Medeiros 2004) and seedling emergence may occur up to 10 years after the removal of mature plants (Smith 1992).

The single known Australian infestation was discovered and first controlled in 2001, with seedling recruits from an active soil seed bank still being recorded in 2011, despite limited fresh seed produced in the immediate vicinity of the core infestation

since 2004 and probably since 2001 (Brooks *et al.* 2009). Field observations indicate that clidemia can quickly develop a wide-spread and persistent seed bank in a variety of vegetation types, even with a low local abundance of mature plants.

Dispersal

Birds, mammals and floodwaters can cause rapid spread from established sites, adding to the difficulty in locating outlying plants (Waterhouse 2002, Waterhouse and Hucks 2002, P. Lawler personal communication). Local movement of clidemia seed may also be aided by feral pigs (*Sus scrofa* L.) and mongooses *Herpestes javanicus* (E. Geoffroy Saint-Hilaire) (Syn. *H. auropunctatus*) where present (Smith 1992). Feral pigs may carry seeds on their pelage and hooves or they may disperse clidemia seed by disturbing the soil looking for roots, fruit or worms to eat, or by eating clidemia fruit and moving to new areas (Smith 1992, Peters 2001, W. Dorney personal communication). Soil disturbance by feral pigs appears to aid the creation of dense thickets of clidemia in Hawaii (Smith 1992).

In a captive feeding trial, Shiels and Drake (2011) showed that when black rats (*Rattus rattus* L.) ate clidemia fruit, the seed was intact and viable after passing through the rats' gut. Shiels and Drake (2011) suggest the minute seeds may be too small to be chewed, as there was no significant difference in the viability of eaten and uneaten seed. By combining observations of black rats voluntarily eating the fruit, passing viable seed and clidemia fruit removal from field enclosures, Shiels and Drake (2011) concluded that black rats and possibly other small vertebrates spread clidemia. Medeiros (2004) also found clidemia seed in rat droppings and found seed that had passed through rats was highly germinable, although he suspected that overall clidemia fruit consumption was low.

In Singapore, long-tailed macaques (*Macaca fascicularis* Raffles) have been observed feeding on clidemia fruit in the Bukit Timah Nature Reserve (Lucas and Corlett 1998). In Indonesia, clidemia seeds have been retrieved from detritus excavated from the burrows of the land crab *Geocarcoidea lalandii* H. Milne-Edwards (Whittaker 1995).

Clidemia is abundant along roadsides in Hawaii. Human vectors via foot traffic and vehicular movement probably assisted in the rapid spread of the species (Wester and Wood 1977, Smith 1992). People who work in or use the forests, including hikers and pig hunters, are also thought to contribute to the long-distance dispersal of clidemia in Hawaii, as plants have been discovered along walking trails (Smith 1992).

The Australian infestation occurs at a former nursery which was established as

a wholesale business, although most stock was sold at local markets (P. Davis personal communication). At the time of discovery clidemia was seen as a nuisance plant and not thought to have been deliberately cultivated for sale (P. Davis personal communication). Since discovery of the Australian infestation, ongoing activities such as implementing property plans and field hygiene procedures have been established to limit the potential spread from this infestation (Brooks *et al.* 2009).

Dispersal by birds

Across clidemia's invasive range, its berries are avidly eaten by both native and alien frugivorous birds (Nayar 1966, Gerlach 1993, Mandon-Dalger *et al.* 2004, Medeiros 2004, Linnebjerg *et al.* 2009, HDOA 2010). Bakutis (2005) classified 39% of clidemia seed collected in traps as 'dispersed' by birds, while the remaining 61% of seed trapped was considered to have fallen from plants less than 3 m from the traps.

When capturing birds near a clidemia infestation on Maui, Medeiros (2004) found an average of 314 clidemia seeds in faecal samples from seven of nine exotic Japanese white-eye (*Zosterops japonicus* Temminck) and an average of 101 clidemia seeds from six captured red-billed leiothrix (*Leiothrix lutea* Scopoli). Samples from one of the nine captured native finches (Amakihi) (*Hemignathus virens* Cabanis) also contained some clidemia seeds (Medeiros 2004). Under experimental cage conditions, birds were offered and ate clidemia fruit. The mean passage time for clidemia seeds through eight Japanese white-eyes was 112 min (maximum 210 min) and 50 min (maximum 90 min) through three red-billed leiothrix (Medeiros 2004). Germination from seeds collected from faecal samples of captive Japanese white-eyes (64.7%) and red-billed leiothrix (71.5%) was similar to that recorded for uneaten seeds (67.3%).

In red-whiskered bulbul (*Pycnonotus jocosus* L.) captive feeding trials on Mauritius, clidemia germination success and speed was greater after gut-passage when compared to physically cleaned seeds, although more than 60% of seeds germinated in both treatments (Linnebjerg *et al.* 2009). Seeds were passed in an average of 12.7 min ($n = 31$), with a maximum retention time of 68 min (Linnebjerg *et al.* 2009). Mandon-Dalger *et al.* (2004) also found clidemia seed in 95% of red-whiskered bulbul droppings and up to 2000 clidemia seeds per dropping on Reunion Island. In another captive feeding trial, 89% of clidemia seeds germinated after passing through the gut of exotic red-whiskered bulbuls (Mandon-Dalger *et al.* 2004). Mandon-Dalger *et al.* (2004) and Linnebjerg *et al.* (2009) both reported that removal of fruit pulp is essential for clidemia germi-

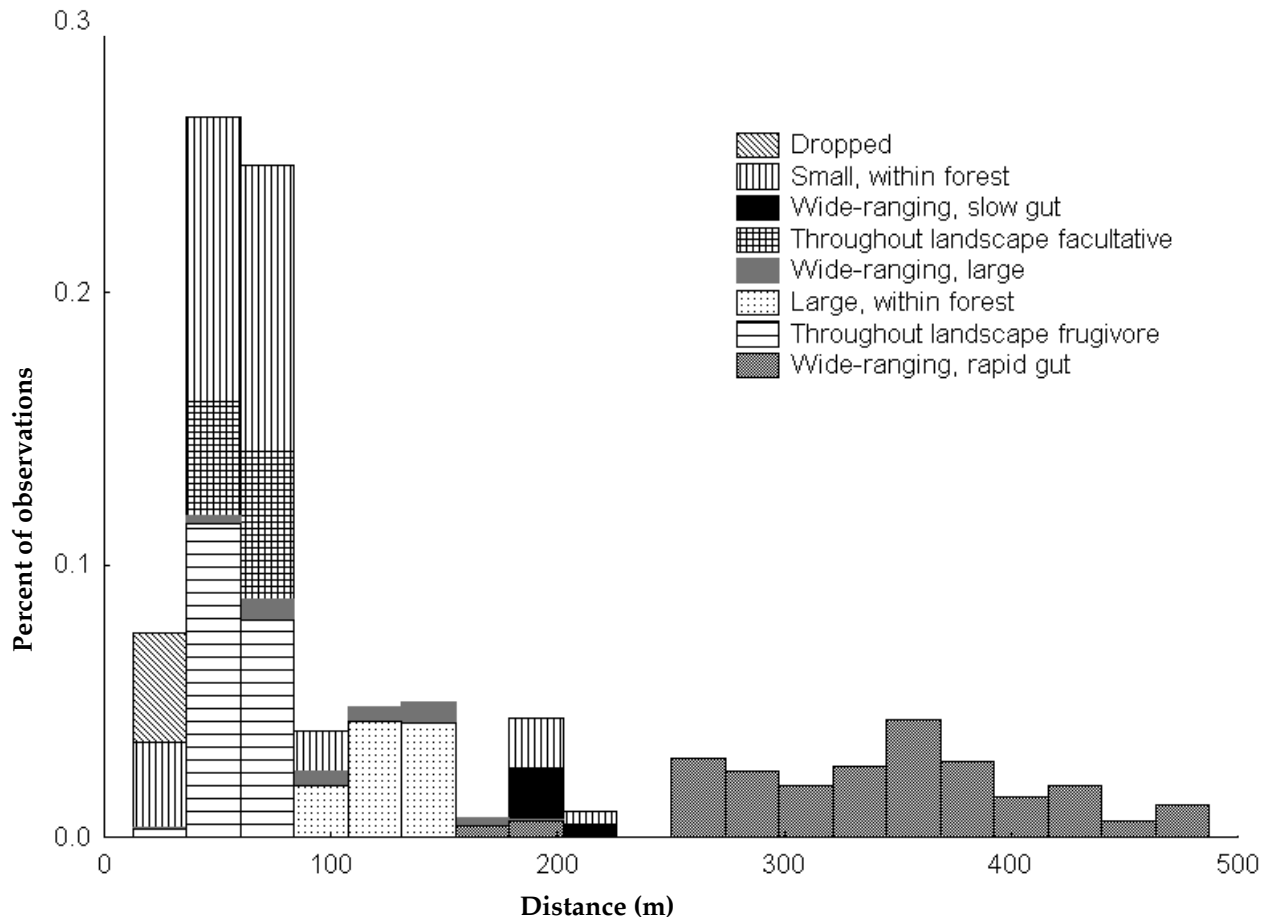


Figure 6. Dispersal curve for clidemia in Australia showing the estimated percent of observations of fruit removal by different frugivores.

Values are based on observations made on similar fruited native species.

Representative bird species in each group include: **Small, within forest:** bowerbirds, spotted catbird. **Wide-ranging, slow gut:** topknot pigeon, cuckoo-shrikes. **Throughout landscape, facultative:** bridled, Macleay's and yellow-spotted honeyeaters. **Wide-ranging, large:** pied imperial pigeon, common koel, pied currawong. **Large, within forest:** fruit doves, orioles. **Throughout landscape frugivore:** mistletoe bird, Lewins honeyeater, silvereve. **Wide ranging, rapid gut:** figbird, metallic starling.

nation. Kueffer *et al.* (2009) suggest that birds in the Seychelles may be more attracted to clidemia berries, as these have 1.6 times the sugar and protein than the average of indigenous plant berries. The native Seychelles bulbul, *Hypsipetes crassirostris* Newton may be the main dispersal agent of clidemia on Silhouette Island (Gerlach 1993).

Frugivorous animals are thought to be one of the main vectors for the spread of clidemia within the Australian infestation (Brooks *et al.* 2009). Frugivorous birds found in the general vicinity of the local infestation include the emerald dove (*Chalcophaps indica* L.), the superb fruit-dove (*Ptilinopus superbus* Temminck), the pied (Torresian) imperial-pigeon (*Ducula bicolor* Scopoli), the metallic starling (*Aplonis metallica* Temminck), figbirds (*Sphocotheres vieilloti* Vigors & Horsfield) and the wompoo fruit-dove (*Ptilinopus magnificus* Temminck) (P. Lawler personal communication, B. Waterhouse personal communication, D. Westcott personal communication).

A likely bird-dispersal histogram for

clidemia in Australia is shown in Figure 6. This histogram is based on extensive research on fruit removal rates for similar-fruited native species, gut passage times and bird movement data in the Wet Tropics of Queensland (Westcott *et al.* 2005, Westcott and Dennis 2006). The dispersal distance is likely to extend to at least 500 m, driven primarily at the 'long-distance' end by figbirds and metallic starlings.

Population dynamics

Six weeks after a fire on Oahu, Wester and Wood (1977) established four plots (40 m² each) and recorded the cover, number and composition of the flora present in the plots 1.5, 13.5, 25.5 and 80 months after the fire. Although only present in two plots at the time of the first assessment, clidemia quickly re-established to dominate three of the plots 13.5 months after the fire and more than 300 stems per plot were recorded 80 months after the fire.

DeWalt (2006) monitored population growth rates of clidemia over a four year period at two locations in Hawaii. One site was an older infestation of clidemia growing under a dense canopy, while the

other was a recent invasion in an open forest. Both populations grew quickly, with population growth rates (λ) greater than 1.0 over the time period. Seedling survival was in the range of 81–97%, with significantly higher values in the older site; post-seedling stage survival was close to 100% in all years at both locations (DeWalt 2006). DeWalt (2006) noted that these survivorship rates are high compared with most other tropical plants, and even other invasive plants, and suggests that this is because there are fewer natural enemies at the seedling stage in Hawaii. Graham and Setter (2007) also recorded high seedling survival rates for transplanted clidemia in a shade-house experiment (97.5%) and tagged plants at a field site (75%). McMahon and Metcalf (2008) used DeWalt's (2006) transition matrices for clidemia in matrix population models to estimate the transient population dynamics of the species. They found that clidemia showed population generation times between 9 and 59 years, with an open-canopy site having shorter generation times than a closed-canopy site.

Importance

Michael (1989) listed clidemia in the top 23 weeds posing the greatest potential quarantine threat to northern Australia. This ranking process took into consideration the weed's importance and degree of risk of introduction (Michael 1989). Since inception of the Northern Australia Quarantine Strategy (NAQS) in 1989, clidemia has been searched for during NAQS surveys throughout northern Australia and adjoining landmasses (Waterhouse 2002), and included in subsequent editions of the NAQS weeds 'target' list (*viz.* Waterhouse & Mitchell 1998, Brown *et al.* 2008). A modified version of the Australian and New Zealand weed risk assessment system has been used to predict potential risk of weed species to Hawaiian and other Pacific Island ecosystems (Daehler *et al.* 2004). Clidemia was given a 'reject' score in this assessment, indicating the species poses a high risk of becoming a serious invader in these ecosystems (PIER 2004).

Clidemia can be found in pastures, plantations and orchards, wasteland, roadsides, dryland crops, wetlands, national parks and along stream banks (Swarbrick 1997, Waterhouse 2003). Conant (2009) concludes clidemia has great potential to cause large-scale negative impacts on agricultural and environmental land uses. Similarly, according to DEEDI (2010), clidemia has the potential to cause millions of dollars worth of damage to primary production in Queensland and irreversible damage to sensitive habitats and native plant communities, especially in the Wet Tropics region. Clidemia's growth along trails and roadsides increases maintenance costs, whilst also reducing the aesthetic, educational and recreational value of forest lands (Wester and Wood 1977, Binggeli 1997, 2001).

Detrimental

Environmental impacts. Meyer (2000) considers clidemia a dominant invader of several Pacific Islands, including Hawaii, Samoa, Wallis and Futuna and Fiji. Meyer (2000) also believes that clidemia is capable of invading less disturbed habitats of high ecological and conservation importance, such as native montane forests. This threat is already being realized on islands in the western Indian Ocean. Kueffer and Vos (2003) list clidemia as one of the most problematic invasive plants on the Comoros archipelago and Reunion Island and identify it as a species that is invading undisturbed mountain forests which have the most intact forest canopies in the region. Clidemia is considered a major threat to high biodiversity, relatively pristine mountain mist forest and upland areas of the Seychelles (Kueffer and Zemp 2004).

Medeiros (2004) estimated that clidemia occupies 21 848 ha on East Maui, including

6 037 ha of native rain forest (24% of total rainforest) and 46% of Haleakala National Park's native rainforest, and could fully invade vulnerable East Maui native rainforest (below 1500 m elevation) in less than 160 years.

Dense clidemia infestations can influence successional processes (Sheil 1994) and Smith (1992) suggested rare sub-canopy species could be displaced by clidemia. In Hawaii, most plants below the clidemia canopy disappear, even those normally able to survive shady conditions (*i.e.* mosses, liverworts and soil-binding, mat-forming plants such as *Leucobryum gracile* Sull. and *Rhizogonium spiniforme* Hedw. Bruch.) (Smith 1992). Follett *et al.* (2003) recorded dieback of the native fern (*Dicranopteris linearis* Burm. f. Underwood) in Hawaiian rainforests where clidemia was the most common invasive species. Wester and Wood (1977) also recorded clidemia excluding *D. linearis*, primarily where the fern had previously been removed or in disturbed areas such as trails. Singhakumara *et al.* (2000) suggest that clidemia occupies the growing space of the closely related *Melastoma malabathricum* L. in mixed dipterocarp forest in Sri Lanka. Clidemia could also be causing some ecological modification at the Pasoh Forest Reserve in Malaysia through suppressing native plants that are dependent on gap regeneration (Peters 2001).

In addition to invading native forests and cleared land, clidemia has the ability to undermine rehabilitation efforts such as those documented by Ashton *et al.* (2001), Shono *et al.* (2006), Ostertag *et al.* (2008) and Tomimura (2008). In south western Sri Lanka, clidemia was found in 95% of quadrats sampled beneath a pine plantation (Tomimura 2008). This dominance jeopardized a planting that was intended to serve as a cover crop for native species regeneration adjacent to a World Heritage Listed Area. With densities of up to 98 individuals m⁻², clidemia abundance was negatively correlated with both understory species richness and mid- and over-story species richness (Tomimura 2008).

Agricultural impacts. Clidemia has become a serious weed in plantation crops including coconut, rubber, cocoa, tea, cassava and oil palm, in at least 16 countries causing large increases in weed control costs (Waterhouse and Norris 1987, Chee and Faiz 1990, Waterhouse 1997, Binggeli 1997, 2001). Clidemia is a weed in Indonesian tea plantations where the accidental harvesting of clidemia leaves can reduce tea yields (Santosa *et al.* 2009). The weed also occurs in the understorey of forestry plantations of *Pinus caribaea* Morelet in Sri Lanka, *Acacia mangium* Willd. in Indonesia and *Eucalyptus* species in Hawaii (Saharjo and Watanabe 1999, Ostertag *et al.* 2008,

Tomimura 2008). In Australia, Michael (1989) expected tea, other plantation crops and disturbed forest areas to be especially vulnerable to clidemia impacts.

Clidemia has been recorded in banana plantations in Martinique, St Vincent, the Lesser Antillies and Hawaii (Quénéhervé *et al.* 2006, Isaac *et al.* 2009, USDA 2010). In Martinique, clidemia serves as a transitional host for the burrowing nematode *Radopholus similis* (Cobb), which reduces yield and the production period (Quénéhervé *et al.* 2006).

Clidemia can also invade pastures rapidly and displace more palatable species in grazing systems (Khusahry *et al.* 2004, Conant 2009). Chee and Faiz (1990) reported that sheep would not eat clidemia growing in 3- to 10-year old Malaysian rubber plantations, increasing the cost of, and reliance on chemical control.

Unpublished documents prepared in support of the Australian eradication program targeting this species suggest that clidemia has the potential to become a major pest of horticultural plantations of tea, bananas, pawpaws and other crops, as well as becoming a problem for the cattle and dairy industries in Queensland (B. Wilson personal communication).

Clidemia is a common browsing plant for grazing animals in some locations, with relatively high nutritional value (Murdiati *et al.* 1990). However it contains substantial concentrations of hydrolyzable tannin, which is readily processed in the stomach to sugar moieties and small phenolic compounds that are absorbed and may cause toxicity (Murdiati *et al.* 1990). Goats (*Capra aegagrus hircus* Erxleben, 1777) fed with clidemia leaves were less active and spent more time lying down than control animals. Murdiati *et al.* (1990, 1991) documented the likely chemical effects and pathological changes in the liver, kidney and gastrointestinal tract consistent with hydrolyzable tannin toxicity, as well as the possible mitigation of these effects in clidemia-fed ruminants.

Beneficial

Across its native range clidemia can provide food for wildlife and aid revegetation projects (Conant 2009). As a widespread species, no direct threats to the conservation of native clidemia have been identified. Native clidemia fruit is consumed by people in the Oriete area of southern Ecuador (Van Den Eyden *et al.* 2003) and harvested from the forest for food around Iquitos in Peru (Vaquez and Gentry 1989). Clidemia berries are fleshy and sweet with a weak blueberry flavour and are 73% water; they also contain 210 mg of fibre, 73 mg of protein and 380 mg of sugar g⁻¹ of pulp (Francis 2007, Kueffer *et al.* 2009, HDOA 2010). Clidemia is an edible herb commonly consumed for its medicinal properties in Sabah, Malaysia (Ali *et al.*

2006). Fresh clidemia leaves are used by the Betsimisaraka people in north-eastern Madagascar to stop bleeding and dried crushed leaves were taken to ease lung pains (Quansah 1988). Ganzhorn (1998) indicates that the foraging behaviour of the lemur *Microcebus murinus* Miller was altered by the local removal of clidemia on Madagascar. Year round fruit production of clidemia also provided a food source for the endemic black-and-white ruffed lemurs (*Varecia v. variegata* Kerr.) of Madagascar after a cyclone depleted their native food resources (Ratsimbazafy 2002). Despite issues with toxicity, clidemia is noted as a common ruminant browse plant in Indonesia (Murdiati *et al.* 1990).

Legislation

In 1993 clidemia was declared a P1 plant in Queensland under the *Rural Lands Protection Act 1985*, the highest priority category for a pest plant. Under the legislation, it was an offence to sell clidemia and the species was to be controlled where found. Under the *Land Protection (Pest and Stock Route Management) Act 2002*, clidemia was classified as a Class 1 weed in Queensland, meaning "... the pest is not commonly present in Queensland and if introduced, would cause an adverse economic, environmental or social impact" (Australian Weeds Committee 2008a,b). Clidemia is also a Class C weed (not to be introduced) in the Northern Territory and a prohibited plant in Western Australia (AWC 2008a, 2008b).

Management

In Australia, intensive field surveys are conducted on foot and control is primarily via manual removal (Erbacher *et al.* 2008, Brooks *et al.* 2009). Seedlings are uprooted and tied to nearby trees with flagging tape to help identify active recruitment areas on subsequent surveys. Any reproductive material is carefully removed, bagged and incinerated (Brooks *et al.* 2009). Survey frequency is typically every 10 to 12 weeks. However, different portions of the infested area may be visited monthly or fortnightly (Erbacher *et al.* 2008, M. Jeffery personal communication). Detecting all plants is difficult due to steep terrain, dense understories and high native plant diversity.

Currently the scope of the surveys is determined by a dispersal buffer of at least 500 m around mature plants. Extended surveys are also undertaken to delimit the infestation and to search high-risk areas such as creek lines (Erbacher *et al.* 2008).

Physical control

Manual removal requires careful extraction of the entire plant and root. In moist rainforests, clidemia may resprout when uprooted or damaged, or form roots when certain plant parts touch the forest floor (Tunison 1991, Smith 1992, DeWalt *et al.*

2004a). Clidemia is a vigorous resprouter following damage (DeWalt *et al.* 2004a, Graham *et al.* 2008), which means that mowing or slashing is an ineffective treatment method (Conant 2009). Graham *et al.* (2008) grew clidemia to maturity in favourable shade-house conditions and then cut plants to either ground level (0 cm) or 10 cm above the ground, simulating incomplete removal or damage that may occur during control work. Following cutting, plants were capable of setting seed in as few as 194 days and 86 days for plants cut at 0 cm and 10 cm respectively. More than 90% of cut plants survived and regrew to their pre-cut height in the 12 months after treatment (K. Patane, unpublished data).

Chemical control

Teoh *et al.* (1982) found triclopyr, 2,4,5-T, 2,4-D amine and 2,4,5-T butoxy ethyl ester were effective in controlling clidemia. In rubber and oil palm plantations, 0.7 kg of triclopyr ha⁻¹ applied using a knapsack sprayer was fast acting and caused high mortality. Dicamba, buthidazole and fenoprop far less effective (Teoh *et al.* 1982). All these chemicals are selective, although 2,4,5-T based herbicides are no longer available. CTAHR (2010) also reported that a 1–2% foliar application of triclopyr amine and triclopyr ester at 2 lb per acre (2.24 kg ha⁻¹) with 0.5% crop oil were effective treatments. In rubber plantations, 0.4–0.5 kg of fluroxypyr ha⁻¹ is applied as an overall spray (Kuan *et al.* 1993). Lange-luddeke *et al.* (1983) controlled clidemia in a mature rubber plantation in Malaysia with a boom spray application of 1.0 kg of glufosinate-ammonium ha⁻¹. Glufosinate-ammonium acts via the leaf; the speed of action is faster than that of glyphosate but slower than that of paraquat (Langeluddeke *et al.* 1983). Chuah and Ismail (2010) reported herbicide resistant clidemia biotypes in oil palm plantations at Jerantut (Pahang, Malaysia).

In a trial conducted on Kauai, Hawaii, a 50% triclopyr amine application to cut stumps was found to be effective when assessed one month after treatment (CTAHR 2010), while stumps painted with glyphosate have been found to re-sprout eventually (PIER 2004). Thin-line basal application of triclopyr ester was effective on large plants and drizzle application of triclopyr in oil was effective on clidemia that had been previously cut back (CTAHR 2010).

Fire

Fire, where possible in mesic habitats, may not be suitable as a stand-alone method for clidemia control. Clidemia outnumbered most native species and other weed species two to five years after a fire on Oahu (Wester and Wood 1977). In Sri Lanka, Shibayama *et al.* (2006) found clidemia plants contributed greatly to the density of shrubs in areas of pine plantations that

had been burnt either repeatedly, once or not at all in the previous five years. Saharjo and Watanabe (1999) identified clidemia as one of the less flammable species present in *Acacia mangium* plantations of Southern Sumatra. A fire every two to five years increased the density of *Clidemia sericea* D. Don in Belize (Myanishi and Kellman 1988).

Natural enemies

Biological control of clidemia has been a focus of research since the first introduction of an agent in Fiji in 1930 (Simmonds 1933, 1937). DeWalt's (2003) extensive work addressing mechanisms of clidemia invasion in Hawaii suggests release from natural enemies is a primary cause of the species' successful invasion there (see also DeWalt *et al.* 2004b, DeWalt 2006). DeWalt *et al.* (2004b) found that insect herbivores and fungal pathogens are at least partially responsible for excluding clidemia from forest understories in its native range and therefore certain biocontrol agents have the potential to provide effective control for the species, at least in shaded habitats in Hawaii. Stage matrix models indicate that agents that reduce seedling survival would have the largest effect on population size in the short term but reductions in survival across all life-history stages would cause clidemia population decline (DeWalt 2006). To control clidemia in Hawaiian rainforests, DeWalt (2006) recommended searching for herbivores or pathogens that decrease survival across all vegetative stages, rather than those that decrease seed production. A range of potential biological control agents (insects and pathogens) have been observed on clidemia in Costa Rica (DeWalt 2004, Conant 2009). None of the biological control agents introduced to Hawaii thus far have caused a decline in clidemia abundance in forest understories (DeWalt 2006).

In Trinidad, six Lepidoptera species attacked clidemia seeds, causing malformation, hardening and some premature falling (Waterhouse and Norris 1987). However, several lepidopteran agents released in Hawaii have suffered from parasitism and predation from local invertebrates (Conant 2009).

***Liothrips urichi* Karney.** The most successful biological control agent released to date has been the thrips *Liothrips urichi* (Phlaeothripidae). In its native Trinidad, *L. urichi* are species-specific, even where there are 20 other species of melastome present (Waterhouse and Norris 1987, Cook 2001). *Liothrips urichi* has specialized feeding habits, feeding on petioles and leaf bases (Reimer and Beardsley 1989). Large numbers of thrips concentrate on young terminal shoots before moving down the stem to fresh material (Waterhouse and Norris 1987). At high densities, heavy at-

tack causes complete dieback of all young growth and eliminates seed production (Waterhouse and Norris 1987). Eggs are laid on the undersides of leaves, in axils of young leaves or on terminal stems and buds. Natural predators of *L. urichi* in Trinidad include the midge (cecidomyiid) larvae *Thripsobremia liothrips* Barnes, the parasitic wasp *Tetrastichus gentilei* Del Guircio and the bugs *Heniartes flavicans* and *Macrotrachelia laevis* Champion (Waterhouse and Norris 1987).

In Fiji and Hawaii, *L. urichi* has been particularly successful in open areas and pasture; however it has proven ineffective in shaded areas (Nakahara *et al.* 1992). In 1930, biological control using *L. urichi* began in Fiji; the agent spread rapidly and widely by 1932 (Simmonds 1933, 1937). Simmonds (1937) noted that "...the insect began to increase with astounding rapidity, crossing wide areas of sea and jungle.... the general effect was that by 1934 large areas of what had been very dense curse had been replaced by a mixed growth...". By 1937, clidemia had been permanently impaired in sunny locations. Waterhouse and Norris (1987) note that in Fiji the relative success in controlling clidemia has probably been due to the early establishment of *L. urichi*. A summary of the thrips' effects in Fiji reported that it had established widely and generally reduced clidemia's competitive ability and weeding costs by 75%; however, the thrips was less effective in wet areas and under intense grazing or dense shade (Julien and Griffiths 1998).

Liothrips urichi was introduced to Hawaii (Oahu) from Fiji in 1953 and was considered established when eight days later it was observed breeding on clidemia (Nakahara *et al.* 1992). The thrips were considered effective in controlling or suppressing the growth of juvenile clidemia plants by causing terminal leaf abscission (Reimer and Beardsley 1989), thus preventing the spread of clidemia in open pastures and cultivated land (Nakahara *et al.* 1992 citing Reimer 1985). In Hawaii the most suitable habitats for *L. urichi* are sunny or partly sunny sites and they tend not to occur in shaded areas, such as areas with frequent cloud cover or dense forest cover where clidemia is common (Reimer and Beardsley 1989). This habitat preference results from significantly lower oviposition in shaded than sunny areas (Reimer and Beardsley 1989). In Oahu, Hawaii, two predators adversely affect *L. urichi*: an exotic ant, *Pheidole megacephala* Fabricius and an anthocorid bug *Montandoniella moraguiesii* Puton (Reimer 1988).

Liothrips urichi was introduced to American Samoa (the main island of Tutuila) in 1974 and since this time has established and eliminated clidemia in some areas by inhibiting growth and reducing vigour (Tauili'ili and Vargo 1993). Clidemia is still common and widespread throughout Tu-

tuila, but *L. urichi* prevents this weed from achieving ecological dominance (Cook 2001). Infested plants exhibit a characteristic browning of terminal shoots and leaves, which allows the damage to be spotted from several metres (Cook 2001). *Liothrips urichi* also established on Palau (Babeldaob) after being first released in 1960 (Conant 2009). Several unsuccessful introductions of *L. urichi* were made into the Solomon Islands, where it is unclear why establishment failed (Cock *et al.* 2000).

Other insects. The moth *Carposina bullata* Meyrick (Carposinidae) lays its eggs on flower buds. The larvae feed on the buds and then create webs that can damage flowers and prevent seed maturation (Conant 2009). This moth was imported from Tobago and small releases were conducted between 1995 and 2000 on Oahu and Hawaii. Insects were recovered in 2002, but not since, and the status of establishment remains uncertain (Conant 2009). On East Maui, *C. bullata* was released to control *M. calvescens* which co-occurs with clidemia, and where clidemia could serve as the primary host species for the agent (Medeiros *et al.* 1997).

Ategumia matutinalis (Guenee) (Pyralidae), a leaf-rolling pyralid caterpillar from Puerto Rico and Trinidad, was released on Oahu to control clidemia and Hawaii to control a range of melastomes in 1970-72 (Nakahara *et al.* 1992). Light infestations of this agent were observed from 1974 to 1977 on Oahu, where it is considered established (Nakahara *et al.* 1992, Conant 2009). *Ategumia matutinalis* has not been recovered on Hawaii (Conant 2009). Four introduced parasites may be affecting the survival of this agent (Nakahara *et al.* 1992 citing Reimer 1985). This agent was also released in Palau in 1972, but failed to establish (Schreiner 1989).

The moth, *Antiblemma acclinalis* Hubner (Nocturidae) lays its eggs abaxially and the larvae roll up leaves to feed within them until the third instar moves off the plant and pupates on the ground (Conant 2002, 2009). The first release from Tobago occurred in 1995 on Oahu and Kauai (Conant 2009). The insect was rare on Oahu and no attempt at recovery has been made on Kauai (Conant 2002, 2009).

Mompha trithalama Meyrick (Mompidae) lays its eggs on flowers and fruits and the larvae feed primarily on the immature seeds within a berry (Conant 2009). This agent from Tobago was released on Oahu (1995), Hawaii (1999) and Maui, Molokai and Kauai (2002). The colourful late instar larvae are easy to find and the species is considered established on all the islands where it was released (Conant 2009).

A leaf-feeding beetle from Trinidad, *Liuis poseidon* Napp (Buprestidae), was introduced on Oahu and Kauai (Hawaii) in 1988 and more recently to Maui, Hawaii

and Molokai (Conant and Hirayama 2001, Conant 2009). *Liuis poseidon* favours lightly shaded aspects where the adult feeds on leaves and larvae mine the leaves (HDOA 2010). In 1998, larval mines of *L. poseidon* were observed on the leaves of the weed *Tibouchina herbacea* near the original release site (Conant and Hirayama 2001). Original host specificity testing of the agent did not include any species in the genus *Tibouchina* (Conant and Hirayama 2001). *Liuis poseidon* is considered established on Hawaii (Conant 2009).

Plant pathogens

In 1985, diseased clidemia leaves at a site in Panama were found to be hosting *Colletotrichum gleosporioides* f. sp. *clidemiae* Trujillo (f. sp. = race, or formae specialis) (Trujillo *et al.* 1986). This fungus was isolated and clean clidemia plants were inoculated, resulting in severe premature defoliation and tip dieback after the eighth day (Trujillo *et al.* 1986). Host-range tests indicated that clidemia was the only host of the fungus among the eight genera of melastomes present in Hawaii (Trujillo 2005). In 1986 the pathogen was released from quarantine for use as a bio-herbicide. Due to its poor dispersal capacity, the bio-herbicide is sprayed onto the target plant (Tunison 1991, Norman and Trujillo 1995). Conant (2002) notes that *C. gleosporioides* f. sp. *clidemiae* can cause extensive defoliation when weather conditions are favourable, i.e. cool, windy and rainy. Though it does appear to stress clidemia seasonally, the long-term impact of this pathogen has not yet been quantitatively evaluated (Conant 2002). Manufacturing costs and continuous production of this bio-herbicide remain obstacles for long-term viability (Norman and Trujillo 1995).

Eradication

Mack and Lonsdale (2002) cite the delay in responding to the known threat of clidemia in Hawaii as a prime example of an opportunity lost in the eradication of an invasive species. They suggest the first identification of clidemia in Hawaii in the 1940s, when its reputation in Fiji was already well known, should have prompted a vigorous attempt at eradication. Instead, the delayed response was to attempt control clidemia using *L. urichi*, which may have prevented its further spread into cropland but did not prevent the species from entering the forest, a consequence already recognized in Fiji (Mack and Lonsdale 2002).

Eradication of weed species is more likely to be successful if there are legal barriers to prevent further introductions (Brooks *et al.* 2009). In recognition of the invasiveness of clidemia elsewhere and the potential threat to tropical and humid coastal areas of Australia, the species was declared a weed in Queensland and was

on quarantine watch lists well before the identification of the only known Australian infestation in 2001. Survey and control activities commenced at the Julatten infestation shortly after the identity of the weed was confirmed (Brooks *et al.* 2009) and have continued at this site (K. Erbacher personal communication).

The formal identification of clidemia in Australia, coupled with the discovery of new infestations of other high priority weeds *Limnocharis flava* (L.) Buchenau, *Mikania micrantha* and *Miconia calvescens*, led to a proposal for a nationally cost-shared weed eradication program (The 'Four Tropical Weeds Program' (4TWP)), developed in 2001 and funded from late 2003 onwards (Erbacher *et al.* 2008). Between 2001 and 2004, survey, control and extension activities were conducted by staff from the Queensland Department of Natural Resources and the Mareeba Shire Council (Brooks *et al.* 2009). The 4TWP started employing its own staff in 2004 but still receives assistance from the Tablelands Regional Council and other program stakeholders. The 4TWP is currently managed by Biosecurity Queensland (within the Department of Agriculture, Fisheries and Forestry) with funding received via national cost-share arrangements from the Australian, Queensland, Northern Territory, New South Wales and Western Australian governments. Favourable recommendations from external reviews of the 4TWP in 2006 and 2010 led to continued national funding agreement for another three financial years from mid 2011 (M. Jeffery personal communication).

Activities such as public displays, publicity events, fact sheets, professional awareness and field visits have taken place since 2001 to help identify any further infestations and add confidence as to the extent of the incursion (Brooks *et al.* 2009). Further details of the search strategies, areas, populations and assessments against eradication progress criteria are presented by Brooks *et al.* (2009). The ongoing discovery of small new infested areas and mature plants, as well as the need to accurately survey several hundred hectares annually, means that eradicating the infestation will require considerable resources for years to come. Although the 4TWP stretches across more than 50 active infestations, the single clidemia location accounts for more than 18% of annual field crew effort (S. Brooks unpublished data).

Publications cited in this review show that clidemia is a fecund, bird dispersed perennial shrub that can rapidly invade open and shaded vegetation types and develop a persistent seed bank. Clidemia would be very difficult to eradicate if many more naturalised infestations were discovered in Australia (Brooks *et al.* 2009), due to the biology of the species and the amount of resources required to manage

it. Ominously, Conant (2009) warns that clidemia could be the mesic to hydric habitat equivalent of *Lantana camara* L. across environmental and agricultural land uses.

Acknowledgments

The authors appreciate the time and efforts of Jason Weber (previously Department of Natural Resources and Mines) for the initial reference collection and Adam McKeown and David Westcott (CSIRO Atherton) for extracting the dispersal curve. Local personnel (Biosecurity Queensland and Northern Australian Quarantine Strategy) are also appreciated for their time and input into field visits and records. We thank Barbara Madigan, Dane Panetta, Kim Erbacher, Mick Jeffery, Shane Campbell, Melissa Setter, Barbara Waterhouse and Stephen McKenna for commenting on this manuscript.

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Appendix 1. Parameters used in the CLIMEX model for clidemia.

Index	Parameter	Value	Unit
Moisture Index	SM0	Lower soil moisture threshold	0.3
	SM1	Lower optimum soil moisture threshold	0.8
	SM2	Upper optimum soil moisture threshold	1.75
	SM3	Upper soil moisture threshold	2.2
Temperature index	DVO	Lower threshold	16 °C
	DV1	Lower optimum threshold	22 °C
	DV2	Upper optimum threshold	28 °C
	DV3	Upper threshold	33 °C
Cold Stress	TTCS	Temperature threshold	10 °C
	THCS	Stress accumulation rate	-0.01 week ⁻¹
Heat stress	TTHS	Temperature threshold	34 °C
	THHS	Stress accumulation rate	0.005 week ⁻¹
Wet Stress	SMWS	Threshold soil moisture	2.2
	HWS	Stress accumulation rate	0.005 week ⁻¹
Dry Stress	SMDS	Dry stress threshold	0.3
	HDS	Stress accumulation rate	-0.0001 week ⁻¹

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