Review Article

Hawaii's successful biological control strategy for mist flower *(Ageratina riparia)* - can it be transferred to New Zealand?

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ABSTRACT

The biological control programme against mist flower in Hawaii is considered one of the most successful undertaken anywhere in the world. Published literature and unpublished reports on the Hawaiian programme, and other biological control programmes against mist flower in Australia and South Africa are reviewed and summarized. Climate data from sites in Hawaii where mist flower infestations have been significantly reduced by biological agents were used to extrapolate optimum conditions for maximum activity of agents. Overall, the most important control agent for mist flower in Hawaii appears to be the fungus *Entyloma ageratinae*, followed by the gall fly *Procecidochares alani* and then the plume moth *Oidaematophorus beneficus*. The feasibility of introducing these successful agents from Hawaii to New Zealand was examined. The annual rainfall in New Zealand is sufficient to support high activity of the agents, especially the fungus. Temperatures should be adequate for half the year, and ideal in summer. A biological control programme could be established for mist flower in New Zealand by introducing the fungus, followed by the gall fly.

INTRODUCTION

The biological control programme against *Ageratina riparia* (Asteraceae) (synonym *Eupatorium riparium*; Asteraceae) in Hawaii is considered one of the most successful undertaken anywhere in the world (Julien, 1992). Despite this, there is little published or easily accessible information about how control was achieved, or what the benefits have been. However, observational data were carefully recorded for many years in the State of Hawaii Department of Agriculture files, and some generalizations can be drawn from these data.

Ageratina riparia is a freely branching perennial herb or subshrub belonging to the family Asteraceae (Webb *et al.*, 1988). It is called Hamakua pamakani in Hawaii and mist flower in most other countries where it occurs. An aggressive, fast-growing plant, mist flower produces abundant flowers and seeds, which are dispersed by wind and water. Mature plants in Australia are reported to produce between 10,000 and 100,000 seeds annually (Parsons & Cuthbertson, 1992). Mist flower has no feed value, is slightly toxic to grazing animals, and is allelopathic (Connor, 1977; Rai & Tripathi, 1984; Parsons & Cuthbertson, 1992). It is a native of Central America but has become a serious weed in many countries including Bermuda, Jamaica, parts of Africa, the United States, Hawaii, Australia, Papua New Guinea, Indonesia, Southeast Asia, Portugal, India, Sri Lanka, some Pacific Islands and New Zealand (Holm *et al.*, 1979; Parsons & Cuthbertson, 1992).

This plant was accidentally introduced to Hawaii in 1925 (Haselwood & Motter, 1966; Davis *et al.*, 1992). By 1972, 52,000 ha of rangeland were infested on the island of Hawaii, and ranchers were increasingly alarmed by the aggressive nature of the weed and the prolific production of windblown seed (Davis *et al.*, 1992). A biological control programme for mist flower began in Hawaii in 1955 (Davis, 1970) and is reviewed in detail in this paper. Two insects (a plume moth, *Oidaematophorus beneficus* Yano & Heppner (Pterophoridae), and a gall fly, *Procecidochares alani* Steyskal (Tephritidae)) and a fungus (*Entyloma ageratinae* Baretto & Evans; Ustilaginales: Tilletiaceae) were introduced in the mid 1970s, and within 10 years substantial biological control of mist flower had

been achieved in the Hawaiian Islands, returning weed-infested rangeland to productive use. Previously dense stands of mist flower were reduced to isolated patches of moribund, stunted plants, growing on dry rocky outcrops where there was little competing vegetation. This level of control has been maintained ever since (Matayoshi, 1981; Trujillo, 1985; Davis *et al.*, 1992). The fungus was subsequently introduced to South Africa, and the gall fly to Queensland and Norfolk Island (Morris, 1991; Julien, 1992; R. McFadyen, pers. comm.). The success of these introductions has not been closely monitored.

Mist flower is abundant in the north of the North Island in New Zealand. It is highly invasive, forming thickets that hinder regeneration in native habitats. The feasibility of introducing the successful biological control strategy from Hawaii to New Zealand is examined in this paper. The most likely barrier to such a transfer is the possible unfavourable environmental conditions in New Zealand. The Hawaiian Islands lie between latitudes 19°N and 22°N, and coastal regions have a tropical climate. However, the islands are mountainous and the temperate climate that exists at higher elevations (where mist flower occurs) resembles that of northern New Zealand. This paper summarizes existing information on the status of the weed in New Zealand and its control agents in Hawaii, and sets out to answer three questions: which control agents are responsible for successful control of mist flower in Hawaii, would the New Zealand climate limit their performance, and which should be considered for introduction to New Zealand.

STATUS OF MIST FLOWER IN NEW ZEALAND

Mist flower was first recognized as a garden escapee in northern parts of the North Island of New Zealand in 1933, when it was observed to be well-established near Russell, Bay of Islands (Allan, 1933) (Figure 1). At the time, Allan (1933) stated that this naturalized exotic plant "does not spread very rapidly, is easy to control, and it is not likely to give any serious trouble". In 1954, Hoy (1960) surveyed the northern regions and found small infestations of mist flower growing in shaded areas near Russell, in the Mangamuka Gorge, and near Te Rerenga on the Coromandel Peninsula. Mist flower was not considered a problem at the time but scientists were speculating that it could become important in the future (Hoy, 1960). In 1988, mist flower infestations were common north of Auckland and local in south Auckland, Lower Hutt and Wellington City (Webb *et al.*, 1988).

Recent information provided by the regional councils and the Department of Conservation in New Zealand, shows that mist flower is extremely widespread in the Auckland and Northland Regions, except in the far north (north of Kaitaia), occurs to a lesser extent in the Waikato Region (on the Coromandel Peninsula), and has just recently been sighted in the Bay of Plenty Region.

Mist flower occurs in a wide range of habitats (e.g. forest margins and clearings, waste places, damp banks, stream sides, fresh water wetlands, river systems, roadsides and unimproved pasture) providing there is enough moisture and light. However, severe infestations are more commonly found in river systems and damp areas. Mist flower can tolerate some shading but does not appear to grow in deep shade. It is also seldom found in open sites exposed to high light intensity. In dry habitats, plants tend to be stunted and wilt rapidly during drought. In the Auckland Region, for example, healthiest infestations occur in areas with a mean annual rainfall of 1600 to 2000 mm (L. Vervoort, pers. comm.). Mist flower is also reported to prefer low soil fertility. In Northland, mist flower infestations have been seen to retreat when poor, heavily infested pastures were fertilized. This suggests that the weed is a poor competitor (J. Craw, pers. comm.).

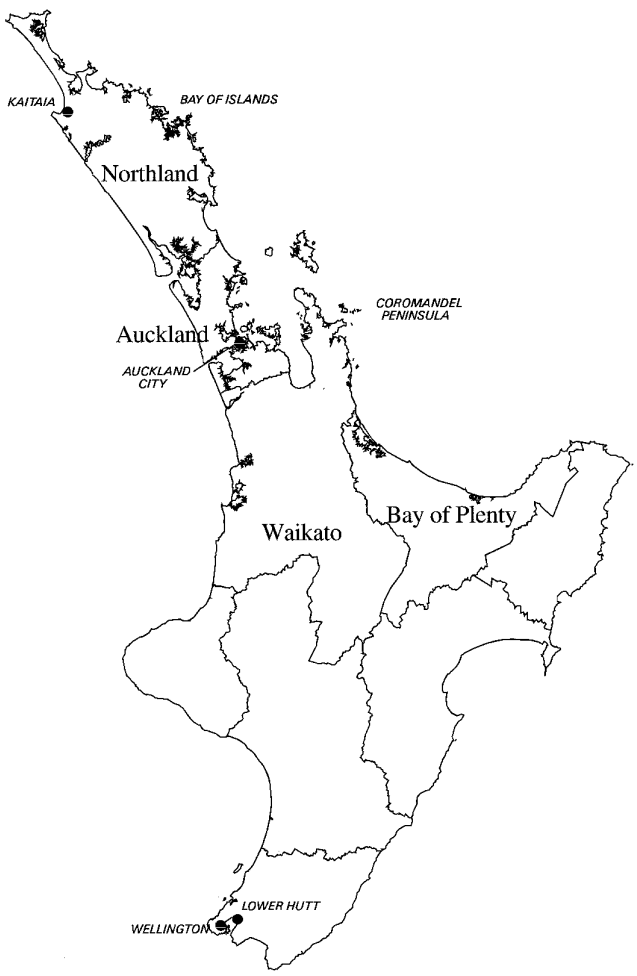

Figure 1. Map of the North Island of New Zealand. Key locations mentioned in the text are indicated.

Mist flower is a major threat to conservation areas because it can prevent forest regeneration and destroy natural communities by producing persistent mats of semi-woody stems. It particularly threatens plant communities on riverbanks in forests. It can also severely affect ecosystems by causing rapid build up of sediment on alluvial flats or destabilizing steep land gullies and stream banks (L. Forrester, pers. comm.).

REVIEW OF BIOLOGICAL CONTROL

The State of Hawaii Department of Agriculture and the Department of Plant Pathology of the University of Hawaii at Manoa were primarily responsible for gathering information on natural enemies of mist flower. Little of this information has been formally published, but is contained in detailed and extensive unpublished reports and correspondence of the State of Hawaii Department of Agriculture. We have reviewed all unpublished material, and much of it is published here for the first time. We have also interviewed all available staff who were involved in the project, and their views are incorporated. Published accounts are also reviewed here. Unpublished information about subsequent programmes in Australia and South Africa is incorporated.

Insects of mist flower

From 1955 to 1965, numerous insects were collected from *Ageratina* species, mainly in Mexico (Table 1). A few insects were studied in quarantine in Hawaii but only one, the tephritid fly *Xanthaciura connexionis* Benjamin, was released and it did not establish (Davis, 1961, 1966, 1970). In the early 1970s, the expanding area of rangeland infested by mist flower made chemical control impractical and stimulated ranchers to fund further searches for natural enemies in Mexico and tropical America (Davis *et al.*, 1992).

Table 1. Insect species recorded on mist flower (*Ageratina riparia*) and investigated as possible biological control agents by the State of Hawaii Department of Agriculture.[1]

ORDER / Family / *Species*	Plant parts collected from	Country of origin	Status in Hawaii Quarantined	Released	Established
COLEOPTERA (beetles)					
Apionidae					
Apion pauper Sharp	terminals & stems	Mexico	1965		
Curculionidae (weevils)					
Baris aerea (Boheman)	terminals & stems	Mexico	1965		
Baris ?corrusca (Boheman)	terminals & stems	Mexico	1965		
Rhodobaenus sanguineus (Gyllenhal)	stems	Mexico	1973		
Tychius sp.	terminals	Mexico	1965		
DIPTERA (flies, midges)					
Agromyzidae (leaf miners)					
Calycomyza allecta Melander	leaves	Mexico	1965		
Cecidomyiidae (midges)					
Clinodiplosis sp.	leaves	Mexico	1973		
Lasioptera sp.	flowering branches	Mexico	1965		
Tephritidae(flies)					
Paroxyna sp.	flower heads	Mexico	1965		
Procecidochares alani Steyskal (gall fly)	stems	Mexico	1973	1974	1974
Xanthaciura connexionis Benjamin[2]	flower heads	Mexico		1955, 1960	
HETEROPTERA (plant-sucking bugs)					
Lygaeidae					
Nysius sp.	leaves	Mexico			
Miridae					
Paraproba sp.	leaves	Mexico			
Phytocoris sp.	leaves	Mexico			
Proba sp.	leaves	Mexico			
Proba fraudulenta Stal	leaves	Mexico			
HOMOPTERA (aphids and leafhoppers)					
Aphididae					
Aphis gossypii Glover	foliage	India			
Aphis spiraecola Patch	foliage	Mexico & India			
Brachycaudus helichrysi (Kaltenbach)	foliage	Mexico			
Hyperomyzus sp.	foliage	Mexico			
Lipaphis erysimi (Kaltenbach)	foliage	Mexico			
Macrosiphum sp.	foliage	Mexico			
Myzus ornatus Laing	foliage	Mexico			
Cicadellidae					
Empoasca sp.	leaves	Mexico			
LEPIDOPTERA (moths & butterflies)					
Geometridae (loopers)					
Eupithecia sp.[2]	flower heads	Mexico	1965		
Gracillariidae (leaf miners)					
Gracillaria sp.	leaves	Mexico	1965		
Phyllonorycter sp.	leaves	Mexico	1965		
Pterophoridae (plume moths)					
Oidaematophorus sp.	leaves	Mexico	1959, 1965		
Oidaematophorus beneficus Yano & Heppner	leaves	Mexico	1972	1973	1973
Tortricidae (leaf rollers)					
Phtheochroa sp.	leaves	Mexico	1965		
Templemania millistriata Walsingham	foliage	Mexico	1965		
Templemania sarothrura (Felder & Rogenhofer)	foliage	Mexico	1965		
THYSANOPTERA (thrips)					
Thripidae					
Frankliniella inutilis Priesner	flower heads	Mexico			
Frankliniella minuta (Moulton)	flower heads	Mexico			
Frankliniella occidentalis (Pergande)	flower heads	Mexico			

[1] Compiled from Davis (1961, 1966, 1970), Nakao *et al.* (1975) and Nakao & Funasaki (1976).
[2] Recovered from flower heads of *Ageratina adenophora,* a close relative of mist flower.

Table 2. Plant species tested for host-specificity of the gall fly *Procecidochares alani* before introduction for biological control of mist flower (*Ageratina riparia*) in Hawaii and Australia.[1]

Family	Sub-family	Tribe	Species	Country
Asteraceae	Asteroideae	Eupatorieae	*Ageratina adenophora*	Hawaii, Australia
			Mikania scandens	Australia
		Anthemideae	*Chrysanthemum* sp.	Hawaii, Australia
		Astereae	*Aster* sp.	Hawaii
		Heliantheae	*Bidens pilosa*	Hawaii
			Carthamus tinctorius	Australia
			Dahlia sp.	Hawaii, Australia
			Eclipta prostrata	Australia
			Helianthus annuus	Hawaii, Australia
			Wedelia trilobata	Hawaii
		Inuleae	*Helichrysum ramosissimum*	Australia
		Tageteae	*Tagetes* sp.	Hawaii
	Cichorioideae	Cardueae	*Arctium lappa*	Hawaii
		Lactuceae	*Lactuca sativa*	Hawaii, Australia
Anacardiaceae			*Mangifera indica*	Australia
Annonaceae			*Annona reticulata*	Australia
Apiaceae			*Apium graveolens*	Australia
			Daucus carota	Australia
Brassicaceae			*Brassica oleracea*	Australia
			Brassica campestris	Australia
Bromeliaceae			*Ananas comosus*	Australia
Caricaceae			*Carica papaya*	Australia
Chenopodiaceae			*Beta vulgaris*	Australia
Convolvulaceae			*Ipomoea batatas*	Australia
Cucurbitaceae			*Cucurbita maxima*	Australia
Fabaceae			*Arachis hypogaea*	Australia
			Centrosema pubescens	Australia
			Glycine max	Australia
			Macroptilium atropurpureum	Australia
			Phaseolus vulgaris	Australia
Lauraceae			*Persea americana*	Australia
Liliaceae			*Allium cepa*	Australia
Linaceae			*Linum usitatissimum*	Australia
Malvaceae			*Gossypium* sp.	Australia
Mimosaceae			*Acacia concurrens*	Australia
Musaceae			*Musa paradisiaca*	Australia
Myrtaceae			*Eucalyptus curtisii*	Australia
Passifloraceae			*Passiflora edulis*	Australia
Pinaceae			*Pinus elliottii*	Australia
Poaceae			*Cenchrus ciliaris*	Australia
			Saccharum officinarum	Australia
			Sorghum bicolor	Australia
			Triticum sp.	Australia
			Zea mays	Australia
Proteaceae			*Macadamia integrifolia*	Australia
Rosaceae			*Fragaria vesca*	Australia
			Malus sylvestris	Australia
			Prunus persica	Australia
			Rosa sp.	Australia
Rutaceae			*Citrus sinensis*	Australia
Solanaceae			*Lycopersicon esculentum*	Australia
			Nicotiana tabacum	Australia
			Solanum tuberosum	Australia
Theaceae			*Camellia sinensis*	Australia
Vitaceae			*Vitis vinifera*	Australia
Zingiberaceae			*Zingiber officinale*	Australia

[1] Compiled from Nakao & Hin Au (1974) and Wild (1985, 1986).

Two insects with potential as control agents, the gall fly *P. alani* and the plume moth *O. beneficus*, were transferred to Hawaii for closer examination, and were eventually released (Nakao *et al.*, 1975; Nakao & Funasaki, 1976).

Procecidochares alani is a fly that forms galls in the growing points of mist flower. Flies insert whitish, elongated eggs into the pair of leaves at the tip of the stem. Nakao & Hin Au (1974) conducted developmental studies at 22.4-24.2°C. Eggs hatched after three to five days, and larvae moved to the base of the leaves and penetrated the tender stem tissue. As the larvae matured, galls formed, and development was completed in approximately 21 days. Immediately before pupation, each larva gnawed an exit corridor through the gall, leaving only the surface layer covering a 'window' in the gall. Adults emerged in 14-21 days, breaking through the 'window'. Adults could mate and lay eggs immediately, and survived for about two weeks.

This gall fly was collected as an unnamed *Procecidochares* sp. from stem galls of *Ageratina pazcuarense* near Mexico City in 1973 (W. Rose, pers. comm. in Trujillo, 1985), and shipped to Hawaii for further evaluation. It was later described by Steyskal (1974) as *P. alani*. It can only be distinguished from *Procecidochares utilis* Stone, the gall-forming fly used for biological control of *Ageratina adenophora* (called Mexican devil weed in New Zealand, Maui pamakani in Hawaii, and crofton weed in Australia and South Africa), a species closely related to mist flower, by microscopic differences in the venation of the wing tip, and the external and internal genitalia (Steyskal, 1974).

Gall-forming flies are generally regarded as monospecific. Because of this, only 10 plants that were closely related to mist flower were included in safety tests conducted in Hawaii (Nakao & Hin Au, 1974) (Table 2). Test plants and mist flower plants were placed in screened cages measuring $40 \times 40 \times 60$ cm, and exposed to 25 adult flies for three to four days. Test plants were examined for egg shells after 10 days, and after 20 days, growing tips were dissected to search for larvae. Two series of tests were conducted for each plant species. Eggs were laid on *A. adenophora* and the eggs hatched. However there were no signs of gall formation and no larvae were found when stems were dissected. There was no egg laying or development on any other species. On the basis of these results, the fly was first released at Hualalai Ranch, on the island of Hawaii in April 1974 (Nakao & Funasaki, 1976). From June until March 1975, 94 releases averaging 2500 flies were made at 22 sites (Matayoshi, 1975). Galls were found in July 1974, and the fly established easily. Three years after release, Otsuka (1977) found that 74-82% of stems at three sites on Oahu Island had galls. Matayoshi (1977) reported that most galls were formed from June to December, as stems completed elongation, and that almost every shoot bore galls on the tip and side branches. Attack was rare from January to April because new shoots were rare (Matayoshi, 1977). The fly was found from sea level to 1600 m above sea level (a.s.l.), but galls were most numerous from 500 to 1000 m a.s.l. Galls retarded stem elongation, reducing competitive ability and causing mist flower to be out-competed by associated vegetation (Matayoshi, 1978, 1979). However, it was difficult to distinguish the relative roles played by the gall fly and the fungus (Matayoshi, 1979). Galls can be heavily parasitized. Hapai (1977) recorded five parasitoid species at one site, where she often reared more parasitoids than flies from samples.

The impact of galls on the growth and abundance of mist flower has been measured in both laboratory and field trials (Hapai, 1977). In the laboratory, the presence of a gall on the growing tip of the plant reduced final stem length to 45% of that of uninfested stems. The presence of a gall on the growing tips caused an increase in branching, but many of the branches bore galls as well. The weight of foliage produced overall was not significantly different between stems with and without galls. At two of three field sites, Hapai (1977) recorded in November 1976 that 81% and 84% of stems had galls. However, the number of stems produced per plant did not decline. During Hapai's study, the plume moth invaded the sites in May 1976, and the fungus was established by November 1976. On the next sampling occasion, few stems had galls, and the number of stems per plant had fallen dramatically, probably as a result of competition from the fungus. The study was conducted from November 1975 to February 1977. Over that time, the abundance of mist flower at the three sites fell from 50 to four, 18 to seven, and 55 to 17 stems / m^2. Over the same period Hapai (1977) recorded progressive replacement of mist flower with other vegetation. As the fungus did not invade until late in this study, it is likely that the gall fly was achieving some level of control in its own right.

Following the spectacular success of the biological control programme for mist flower in Hawaii, *P. alani* was introduced to Queensland, Australia in 1986 (Parsons & Cuthbertson, 1992; R. McFadyen, pers. comm.). Before introduction was approved, host range tests were conducted (Wild, 1985, 1986). Unlike the host range tests conducted in Hawaii, which concentrated on plants related to mist flower, Queensland tests concentrated on economically important plants, and species native to Australia (Table 2). No galls formed on any of the plants tested. The fly established and spread quite widely, but is now heavily parasitized by the same parasitoids that attack the gall fly of *A. adenophora* (R. McFadyen, pers. comm.).

Oidaematophorus beneficus is a plume moth, the larvae of which feed on the leaves of mist flower. Their tufted, narrow, brown-and-white striped wings are distinctive as they are not folded, but protrude at right angles to the body. Eggs are creamy-white, elliptical, 0.45 mm long and 0.3 mm across (Yano & Heppner, 1983). Nakao *et al.* (1973) conducted developmental studies at 22.8-24.7°C. They found that larvae hatch in five to seven days, and feed *in situ* on the underside of the leaf before moving to the new leaves at the terminals of shoots. There they begin to consume all parts of the new leaves. Larval development takes 30-35 days. Maturing larvae move to older leaves once young growth is destroyed. There is a short pre-pupal period during which the mature larva (10 mm in length) attaches itself with silk to dried plant material, usually at the base of the plant, where it pupates. Moths emerge after 10 days, and commence laying eggs three days after emergence. Longevity varies from 14 to 28 days, and the sex ratio is 1:1.

Yano & Heppner (1983) claim that this insect was unsuccessfully released in Hawaii in 1959 and 1965, but this cannot be confirmed from other sources (Davis, 1966, 1970). It was found on mist flower at Contreras, Mexico (40 km southwest of Mexico City) in 1972, and shipped to Hawaii for further study. In two sets of tests, the ability of larvae to survive on 36 plant species of 20 families was measured (Nakao *et al.*, 1973). The plants selected for testing were mostly of economic or social importance, with less emphasis on related plants within the same family (Table 3). The larvae in the first test were less than half-grown while those in the second were nearing maturity. Ten larvae were placed on a bouquet of test-plant foliage in a gallon jar. Trace to light feeding was observed on a number of plants, but despite the relative maturity of the larvae, all died within a short period of time. None was able to complete development on any plant tested. Tests on selected economic plants were repeated with the same results (Nakao *et al.*, 1973, 1975). On the basis of this evidence of host specificity, the first releases of plume moth were made in October 1973 at Mount Kaala, Oahu Island and at Kona, Island of Hawaii (Nakao *et al.*, 1975; Nakao & Funasaki, 1976). One species not tested was *A. adenophora* presumably because it is a weed in Hawaii. Recently, plume moth larvae were collected from heavily damaged leaves of this species growing in the shade (Conant, in press).

By September 1974, 20,000 larvae and adults had been distributed to many sites from sea level to over 1600 m a.s.l. (Matayoshi, 1975). The plume moth established rapidly, and

Table 3. Plant species tested for host-specificity of the plume moth *Oidaematophorus beneficus* before introduction for biological control of mist flower (*Ageratina riparia*) in Hawaii.[1]

Family	Sub-family	Tribe	Species
Asteraceae	Asteroideae	Eupatorieae	*Ageratina adenophora*
		Anthemideae	*Chrysanthemum* sp.
		Astereae	*Aster* sp.
			Bellis perennis
		Heliantheae	*Argyroxiphium sandwicense*
			Bidens sp.
			Dahlia sp.
			Dubautia sp.
			Helianthus annuus
			Wedelia trilobata
			Zinnia elegans
		Inuleae	*Helichrysum bracteatum*
		Senecioneae	*Ligularia tussilaginea*
		Tageteae	*Tagetes* sp.
	Cichorioideae	Arctoteae	*Arctotis stoechadifolia*
		Cardueae	*Arctium lappa*
		Lactuceae	*Lactuca sativa*
Anacardiaceae			*Mangifera indica*
Araceae			*Colocasia esculenta*
Bromeliaceae			*Ananas comosus*
Caricaceae			*Carica papaya*
Convolvulaceae			*Ipomoea batatas*
Cucurbitaceae			*Cucumis sativus*
Euphorbiaceae			*Euphorbia pulcherrima*
Fabaceae			*Phaseolus vulgaris*
Lauraceae			*Persea americana*
Malvaceae			*Hibiscus* sp.
Musaceae			*Musa* sp.
Myrtaceae			*Psidium guajava*
Orchidaceae			*Dendrobium* sp.
Poaceae			*Saccharum officinarum*
Proteaceae			*Macadamia integrifolia*
Rosaceae			*Rosa* sp.
Rubiaceae			*Coffea arabica*
Rutaceae			*Citrus* sp.
Sapindaceae			*Litchi chinensis*
Solanaceae			*Lycopersicon esculentum*

[1] Compiled from Nakao *et al.* (1973, 1975).

was most active in August, coinciding with the period of maximum growth (Matayoshi, 1977). It was readily found from 500 to 1300 m a.s.l. (Matayoshi, 1976, 1978), completely defoliated mist flower at Volcano, Island of Hawaii (E. Yoshioka, pers. comm.), and caused 'impressive' damage on non-ranchland sites, especially in the shade (Matayoshi, 1978, 1979). The fungus established shortly after the moth and masked the potential effect of the moth on plants at most sites (Matayoshi, 1977). The plume moth did not perform well in the warmer climates that exist at low altitude in Hawaii, possibly because of egg parasitism there (Matayoshi, 1985).

Pathogens of mist flower

A few herbarium specimens of diseased mist flower from tropical America, collected prior to the initiation of the biological control programme in Hawaii, exist at the International Mycological Institute, UK (Baretto & Evans, 1988). The causal agent of the disease symptoms on these specimens has been classified under various genera of Deuteromycotina (= Mitosporic fungi, see Hawksworth *et al.*, 1995): *Cercospora* sp., *Cercoseptoria* sp., *Gloeocercospora* sp., *Pseudocercosporella* sp., *Ramularia* sp. and *Cercosporella* sp.

Two plant disease surveys of mist flower were conducted in July-August 1973 and November 1974 in Vera Cruz State, Mexico by a plant pathologist from the University of Hawaii (Trujillo, 1985). A rust fungus was found on mist flower in El Mirador during the second survey but was not introduced to Hawaii "because of insufficient biological information" (Trujillo, 1985). At the end of 1974, another exploration was made in the Blue Mountains, Jamaica, where a fungus had been reported to attack mist flower (Leather, 1967). Following preliminary studies in Jamaica, the fungus was imported into Hawaii on living plant material for further studies and to conduct host range tests in quarantine. The fungus was originally identified as a new species of *Cercosporella* Sacc. (a genus of Mitosporic fungi), *Cercosporella ageratinae* (Trujillo, 1975), but in later years Trujillo (1985) stated that "the non-septate character of the conidia places the pathogen in a genus other than *Cercosporella*". In 1988, results from two taxonomic investigations were published and described the mist flower pathogen as *Entyloma compositarum* Farlow (Trujillo *et al.*, 1988) and as the new species *E. ageratinae* (Baretto & Evans, 1988) in the order Ustilaginales of the division Basidiomycota (Hawksworth *et al.*, 1995), far removed from its original disposition. The latter study was conducted at the request of the Department of Lands, Queensland, Australia, which was considering importing the fungus and required additional taxonomic details to comply with regulations (Baretto & Evans, 1988;

Table 4. Plant species tested for host-specificity of the fungus *Entyloma ageratinae* before introduction for biological control of mist flower (*Ageratina riparia*) in Hawaii and South Africa.[1]

Family	Sub-family	Tribe	Species	Country
Asteraceae	Asteroideae	Eupatorieae	*Adenostemma perrottetii*	South Africa
			Ageratina adenophora	Hawaii, South Africa
			Ageratum houstonianum	South Africa
			Chromolaena odorata	South Africa
			Eupatorium macrocephalum	South Africa
			Stomatanthes africanus	South Africa
		Anthemideae	*Achillea* sp. (var. Cloth of gold)	South Africa
			Achillea millefolium	South Africa
			Achillea ptarmica	South Africa
			Chrysanthemum sp.	Hawaii, South Africa
		Astereae	*Aster novi-belgii*	South Africa
			Bellis perennis	South Africa
		Calenduleae	*Calendula* sp.	Hawaii
			Calendula officinalis	South Africa
		Heliantheae	*Bidens pilosa*	South Africa
			Cosmos sulphureus	South Africa
			Gaillardia pulchella	South Africa
			Helianthus annuus	South Africa
			Wedelia trilobata	Hawaii
		Senecioneae	*Ligularia tussilaginea*	Hawaii
		Tageteae	*Tagetes* sp.	Hawaii
	Cichorioideae	Lactuceae	*Lactuca sativa*	Hawaii
			Lactuca serriola	South Africa
Agavaceae			*Cordyline fruticosa*	Hawaii
Anacardiaceae			*Mangifera indica*	Hawaii
Apocynaceae			*Plumeria obtusa*	Hawaii
Araceae			*Anthurium andraeanum*	Hawaii
Arecaceae			*Cocos nucifera*	Hawaii
Brassicaceae			*Brassica oleracea*	Hawaii
Bromeliaceae			*Ananas comosus*	Hawaii
Caricaceae			*Carica papaya*	Hawaii
Chenopodiaceae			*Beta vulgaris*	Hawaii
Convolvulaceae			*Ipomoea batatas*	Hawaii
			Ipomoea sp.	Hawaii
Cucurbitaceae			*Cucumis sativus*	Hawaii
Euphorbiaceae			*Euphorbia pulcherrima*	Hawaii
Fabaceae			*Phaseolus vulgaris*	Hawaii
Lauraceae			*Persea americana*	Hawaii
Malvaceae			*Hibiscus* sp.	Hawaii
Musaceae			*Musa* sp.	Hawaii
Myrtaceae			*Meterosideros collina*	Hawaii
			Psidium guajava	Hawaii
Orchidaceae			*Dendrobium* sp.	Hawaii
Passifloraceae			*Passiflora edulis*	Hawaii
Poaceae			*Bambusa* sp.	Hawaii
			Saccharum officinarum	Hawaii
			various grasses (3 spp.)	Hawaii
Polemoniaceae			*Phlox* sp.	Hawaii
Proteaceae			*Macadamia integrifolia*	Hawaii
Rosaceae			*Rosa* sp.	Hawaii
Rubiaceae			*Coffea arabica*	Hawaii
			Gardenia jasminoides	Hawaii
Sapindaceae			*Litchi chinensis*	Hawaii
Scrophulariaceae			*Antirrhinum* sp.	Hawaii
Solanaceae			*Lycopersicon esculentum*	Hawaii
			Solanum melongena	Hawaii
Verbenaceae			*Lantana camara*	Hawaii
			Stachytarpheta jamaicensis	Hawaii

[1] Compiled from Trujillo (1975, 1985) and Morris (1989, 1991).

R. McFadyen, pers. comm.). The fungus is referred to as *E. ageratinae* in this paper.

Entyloma ageratinae produces angular, reddish-brown lesions with yellow margins on the upper surface of leaves. The fungus sporulates heavily only on small, circular to angular, lesions on the lower leaf surface. The spores give the lesion a 'woolly white' appearance (Trujillo, 1985). Lesions coalesce and become dark brown as the disease progresses, and entire leaves eventually die.

The fungus is reported to grow and form spores on artificial culture medium but only very slowly (Trujillo, 1975; Baretto & Evans, 1988). Artificially produced spores have a similar structure and form to those produced on plants, but are not as pathogenic (Trujillo, 1975). Spores germinate and penetrate the leaf of mist flower within 24 h if temperatures and humidity conditions are optimum (Trujillo *et al.*, 1988). The fungus penetrates the surface on both sides of the leaves, grows into the spaces between cells, and produces fruiting bodies that emerge through the stomata on the lower surface. Spore formation occurs seven to 10 days after inoculation of leaves and gradually stops as the lesion ages.

In laboratory studies, infection of detached mist flower leaves by the fungus was optimum at 18°C and 100% relative humidity (Trujillo, 1985). In a subsequent study, Trujillo *et al.* (1988) found no difference in the number of lesions produced by the fungus at 16°C and 20°C. No lesions developed with temperatures above 22°C or below 10°C (Trujillo, 1985). Spore formation on lesions was also influenced by temperature and was abundant when diseased leaves were at 18°C but reduced by half at 16°C and 20°C. Trujillo (1985) estimated that approximately 70 spores were produced in each lesion.

Prior to the release of the fungus in Hawaii, a series of tests were conducted in terrariums in the laboratory to determine its host range (Trujillo, 1975, 1985). A wide range of plants from 29 families was tested and none developed any symptoms after inoculation with the fungus (Table 4). The closely related *A. adenophora* did not develop any disease symptoms in those tests.

The fungus was first released in November 1975 at various elevations on Mount Tantalus, Oahu Island and Palani Ranch, Island of Hawaii by 'painting' leaves with a spore suspension (Trujillo, 1985). Within 12 days of inoculation, lesions appeared on inoculated leaves at the Tantalus sites (elevations 450, 500 and 550 m a.s.l.). Spores produced on these lesions landed on other leaves and caused additional lesions at 20 days after release. On Palani Ranch, numerous lesions developed within 15 days after artificial inoculation of leaves at elevations of 900 and 1100 m a.s.l. Six weeks after release of the fungus at Tantalus, disease symptoms were observed as far as 4 km from the initial inoculation sites. This spectacular spread was not expected and was probably due to a major tropical storm that affected the area a few weeks after the release (Trujillo, 1985). Spores of the fungus are spread by wind currents and readily germinate upon landing on a humid surface.

The high rainfall and favourable temperature for the fungus at the initial release sites and the presence of a large infestation of mist flower are likely to have favoured the development of severe disease epidemics. Trujillo (1985) estimated that the mist flower infestations at Tantalus dropped from 70-80% cover to less than 1% in nine months. In other areas where temperatures and rainfall were sub-optimum, control of mist flower took longer (from three to eight years). The fungus has been observed over the years to perform best at sites that received at least 1500 mm of rain annually and where temperatures range from 10°C to 20°C (E. Trujillo, pers. comm.).

In 1989, the fungus was introduced into South Africa to control a small but rapidly spreading infestation of mist flower in a district of Natal (Morris, 1991). Safety tests conducted before the release of the fungus focused on plants within the Eupatorieae sub-tribe (including some native South African species) and a number of recorded hosts of the pathogen *E. compositarum*, which is closely related to the mist flower pathogen (Morris, 1989, 1991) (Table 4). No symptoms developed on any of the test plants except for *A. adenophora*. However, lesions on this host plant were smaller (less than 1 mm in diameter) than those developing on mist flower

Table 5. Selected sites on the islands of Hawaii and Oahu where a reduction in mist flower (*Ageratina riparia*) infestations has been linked to a specific biological control agent.[1]

Agent	Site	Elevation (m a.s.l.)	Mean annual rainfall (mm)
Entyloma ageratinae fungus	Parker Ranch[2]	793	2000-3000
	Hualalai Ranch[2]	1037-1373	1000-1500
	HueHue Ranch[2]	793-915	1000-1500
	Palani Ranch[3]	1037	750-1000
	Honomalino Ranch (Captain Cook)	732-1220	1000-1500
	Volcano	1220	2000-3000
	Glenwood	793	4000-5000
	Tantalus (Oahu)	396-518	3000-4000
Procecidochares alani gall fly	Parker Ranch[2]	793	2000-3000
	Hualalai Ranch[2]	1037	1000-1500
	HueHue Ranch[2]	793-915	1000-1500
	Palani Ranch[3]	793	1000-1500
	Kahuku Ranch[2]	793-915	1000-1500
	Hilo to Honokoa	61-214	3000-4000
Oidaematophorus beneficus plume moth	Volcano	1220	2000-3000
	Glenwood	793	4000-5000
	Ahualoa[3]	671	2000-3000
	Mount Kaala (Oahu)	1220	1500-2000

[1] Compiled from Matayoshi (1978, 1979) and E. Yoshioka (pers. comm.).
[2] Open sites.
[3] Sites under tree canopy.

and took approximately five days longer to begin producing spores (Morris, 1989). Within 18 months of release, the fungus had spread throughout the region infested with mist flower and plants were severely defoliated (Morris, 1991).

TEMPERATURE AND RAINFALL REQUIRED FOR OPTIMAL AGENT ACTIVITY

To judge the likely performance of each agent in New Zealand, we defined the climatic conditions prevailing at Hawaiian sites where mist flower control could be reliably attributed to a particular agent. Information about levels of control were obtained from reports of informal monitoring and eye-witness accounts. Table 5 describes the sites where staff involved in the programme observed major impact on mist flower infestations within 10 years of agent introduction (Matayoshi, 1978, 1979; E. Yoshioka, pers. comm.). The climates prevailing at these 'best' sites were assumed to be optimum conditions for agent performance.

No maps of mean annual temperature have been published for the Hawaiian Islands because there are few official temperature stations (Nullet & Sanderson, 1993). Assistance was sought from the Department of Geography of the University of Hawaii at Manoa to estimate mean annual temperatures at selected sites (T. Giambelluca, pers. comm.). By plotting mean annual temperatures from official weather stations established on the island of Lanai against elevation, we were able to estimate the mean annual temperature prevailing at the selected sites. These official stations were established at elevations of 950, 1650, 2130, 2600 and 3000 m a.s.l. between 1988 and 1990 on the west-northwest facing flank of the mountain as part of the Halenet I network (T. Giambelluca, pers. comm.). The mean annual temperature data from these stations are based on records taken until February, 1995. The mean annual temperature data for the town of Lahaina (elevation 14 m a.s.l.) on the neighbouring island of Maui were used since the Halenet I network does not have a station at sea level and because temperatures are relatively uniform at sea level in the Hawaiian Archipelago (Nullet & Sanderson, 1993; T. Giambelluca, pers. comm.).

The mean monthly temperatures at these official weather stations do not fluctuate much during the year; the lowest mean monthly temperature is recorded in February or March, and the highest mean monthly temperature in August or September. On average, the mean monthly temperatures at each station varied within 2.1°C above or below the mean annual temperature.

The optimum range of temperature for each agent was determined by estimating the mean annual temperature at the sites with the lowest and highest elevations (Table 5), using graphs constructed with data from official weather stations. In the years following its introduction to Hawaii, the fungus was reported to be most active and damaging at elevations between 396 and 1373 m a.s.l. which correspond to a mean annual temperature of 14.7°C to 21.4°C ± 2.1°C. The gall fly was particularly active at elevations between 61 and 1037 m a.s.l., where temperature ranged from 17.0°C to 23.8°C ± 2.1°C. In contrast, the plume moth performed better at higher elevations between 671 and 1220 m a.s.l. where cooler temperatures prevailed, 15.7°C to 19.5°C ± 2.1°C.

Mean annual rainfall data for each site were obtained from rainfall maps of each island (Giambelluca *et al.*, 1986), to determine the minimum mean annual rainfall required for the optimum activity of each agent (Table 5). Based on the rainfall maps, the fungus performed well at sites that received more than 750 mm of rain annually. Although the presence of available water is not a prerequisite for insects, the gall fly was observed to be most active at sites with more than 1000 mm mean annual rainfall, and the plume moth was most active at a mean annual rainfall of more than 1500 mm.

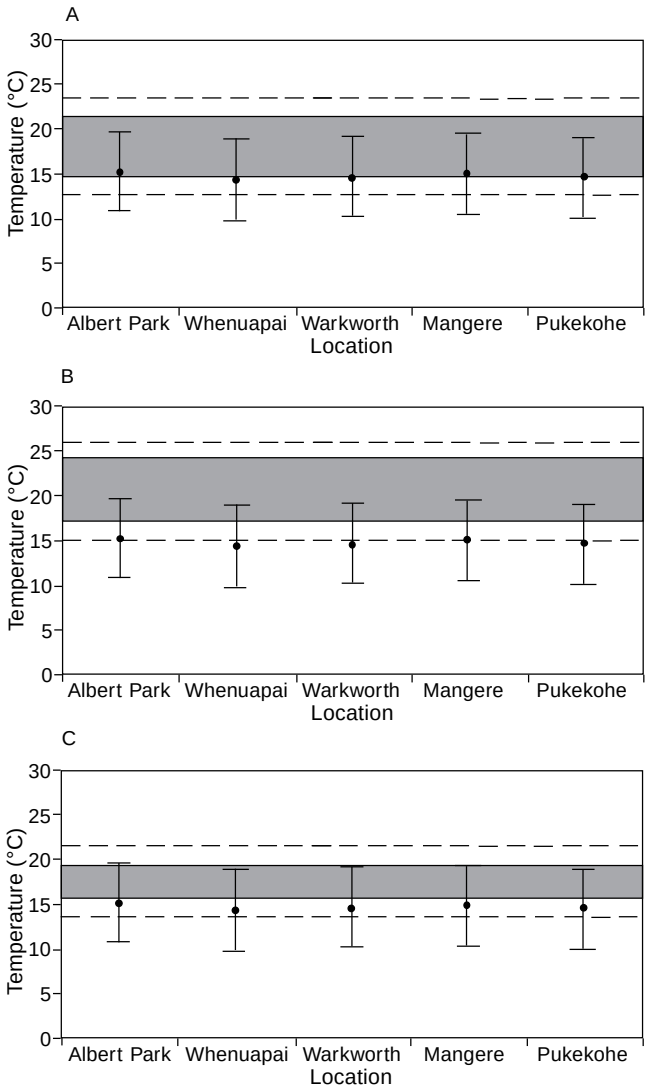

Figure 2. Optimum ranges of temperature (shaded area) and upper and lower limits (dash lines) for best activity of the fungus *Entyloma ageratinae* (A), gall fly *Procecidochares alani* (B), and plume moth *Oidaematophorus beneficus* (C) on mist flower *(Ageratina riparia)* in Hawaii which have been superimposed onto temperature data for five meteorological stations in the Auckland Region in New Zealand. Data points correspond to mean annual temperatures and vertical bars to ranges of mean monthly temperatures for each station.

The optimum range of temperature for each agent, extrapolated from Hawaiian data, was superimposed on data from 20 meteorological stations in Auckland, Northland, Waikato and Bay of Plenty Regions (Anonymous, 1983), to determine whether the climate of northern New Zealand is suitable for the agents (Morin & Hill, 1996). The mean annual temperatures and lowest and highest mean monthly temperatures were similar for the selected meteorological stations located in the four regions of northern New Zealand where mist flower infestations occur. Only data for the Auckland Region are presented here (Figure 2). The upper range of mean monthly temperatures at the selected stations in this region fell within the optimum temperature range for each agent, meaning that temperatures should be adequate for the agents for approximately half of the year, and ideal in the summer.

The mean annual rainfall in most of northern New Zealand ranged from 1000 to 2000 mm (Anonymous, 1985). The annual rainfall in New Zealand is therefore sufficient to support high activity of the biological control agents, especially the fungus. Furthermore, the fungus is likely to benefit from the relatively uniform rainfall pattern in New Zealand. Regular rainfall is likely to assist in the building-up of inoculum and consequently increase the incidence and severity of the disease.

DISCUSSION

The fungus *E. ageratinae* has had a drastic impact in reducing infestations of mist flower in Hawaii (Trujillo, 1985). This spectacular success is likely to be due to its ability to infect plants within a relatively wide range of temperature, produce spores rapidly after infection, spread abundant spores by wind currents, and cause severe necrotic lesions that kill foliage. In addition, resistant biotypes of the weed have not emerged despite the 20 years of constant selection pressure imposed by the fungus on populations in Hawaii (E. Trujillo, pers. comm.). However, like most other pathogenic fungi, *E. ageratinae* requires moisture to infect plants, and thus is limited to wet areas (more than 750 mm annual rainfall).

One of the few quantitative studies undertaken in Hawaii showed that the gall fly alone was capable of stunting mist flower stems, leading to partial suppression of infestations by competing vegetation (Hapai, 1977). This was confirmed in reports from the State of Hawaii Department of Agriculture (Otsuka, 1977; Matayoshi, 1978, 1979). Reduction in plant height resulting from galls on the tips of stems would lessen competition for light with accompanying vegetation. However, the impact of the gall fly may be limited by parasitism. A range of parasitoids destroyed up to 50% of flies in galls in Hawaii (Hapai, 1977), and in Queensland, parasitism is the main factor limiting effectiveness (R. McFadyen, pers. comm.). In New Zealand, it is likely that the single parasitoid thought to limit the effectiveness of the gall fly attacking *A. adenophora* (Hoy, 1960; Hill, 1989) would also attack *P. alani.*

The plume moth was capable of massive defoliation of the weed at some sites in Hawaii when it was first introduced, suggesting that it has value as a control agent (Matayoshi, 1978, 1979).

The relative importance of the control agents in the spectacular control of mist flower in Hawaii is not entirely clear because no formal quantitative studies of the relative impacts of the agents were conducted as the programme proceeded. The fungus adversely affected the performance of the gall fly in Hawaii, probably by destroying sites for egg laying (Hapai, 1977). However, recent observations made in Hawaii suggested that galls are formed on a high proportion of stems before the period of peak activity of the fungus, and that the timing of activity of the agents may be complementary (Morin & Hill, 1996). At most sites visited in 1995, mist flower seedlings were found growing amongst kikuyu grass (*Pennisetum clandestinum*; Poaceae) pasture, most bearing galls on the tips of stems. There were few older plants present, suggesting high rates of seedling mortality, probably caused by the combined effects of the gall fly, the fungus, and competition with the grass.

Once the fungus became established in Hawaii, plume moth declined in importance. The plume moth and the fungus both use leaves as a substrate and we know of no situation where the plume moth out-competes the fungus.

Climate analyses are increasingly used in biological control of weeds to predict the suitability of particular agents to a new area (McFadyen, 1991; McClay, 1996). In our study, the Hawaiian data available were not extensive and precise enough for sophisticated climatic modelling. Nevertheless, the crude climate analysis presented here shows that the general environmental conditions in northern New Zealand should suit the biological requirements of the agents from Hawaii. It is likely, however, that their activity will decrease during the winter months because of sub-optimum temperatures, as has been observed at high elevations in Hawaii. On the other hand, the abundance and regular pattern of rainfall in the north of New Zealand will assist in maintaining low levels of the disease during the winter which should then provide sufficient inoculum to initiate epidemics in the spring as temperatures increase. More detailed data on the effect of temperature on the various stages of development of each agent would be necessary to predict more accurately when and where the agents will be active in New Zealand.

On balance, we believe that the fungus and the gall fly are complementary in their activity, and that both could be introduced into New Zealand. The gall fly may be limited by parasitism, but how much this would affect fly populations is unknown. A decision on introduction of the plume moth should be delayed until we know if there are situations (such as dry sites) where the fungus will not perform well. If introduced to New Zealand, the plume moth would probably also attack *A. adenophora* (Conant, in press), especially in shaded situations.

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