

Biological control of two *Ageratina* species (Asteraceae: Eupatorieae) in South Africa

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Ageratina adenophora (Spreng.) R.M.King & H.Rob. and *Ageratina riparia* (Regel) R.M.King & H.Rob. (Asteraceae: Eupatorieae), originally from Mexico, are invasive in many countries. These plants produce thousands of wind- and water-dispersed seeds which enable them to spread rapidly and invade stream banks and moist habitats in areas with high rainfall. Two biological control agents, a shoot-galling fly, *Procecidochares utilis* Stone (Diptera: Tephritidae), and a leaf-spot fungus, *Passalora ageratinae* Crous & A.R. Wood (Mycosphaerellales: Mycosphaerellaceae), were introduced against *A. adenophora* in South Africa in 1984 and 1987, respectively. Both established but their impact is considered insufficient. Exploratory trips to Mexico between 2007 and 2009 to search for additional agents on *A. adenophora* produced a gregarious leaf-feeding moth, *Lophoceramica* sp. (Lepidoptera: Noctuidae), a stem-boring moth, probably *Eugnosta medioxima* (Razowski) (Lepidoptera: Tortricidae), a leaf-mining beetle, *Pentispa fairmairei* (Chapuis) (Coleoptera: Chrysomelidae: Cassidinae), and a leaf-rust, *Baeodromus eupatorii* (Arthur) Arthur (Pucciniales: Pucciniosiraceae) all of which have been subjected to preliminary investigations. Following its success in Hawaii, the white smut fungus, *Entyloma ageratinae* R.W. Barreto & H.C. Evans (Entylomatales: Entylomataceae), was introduced in 1989 to South Africa against *A. riparia*. Its impact has not been evaluated since its establishment in 1990 in South Africa. By 2009, however, *A. riparia* was rarely observed in the field and *E. ageratinae* was noted to be present over most of the range of the weed, providing circumstantial evidence that the weed has been brought under biological control by *E. ageratinae* in South Africa.

Key words: *Baeodromus eupatorii*, *Entyloma ageratinae*, *Eugnosta medioxima*, invasive weeds, *Lophoceramica*, natural enemies, *Passalora ageratinae*, *Pentispa fairmairei*, *Procecidochares utilis*.

INTRODUCTION

Ageratina adenophora (Spreng.) R.M.King & H.Rob. and *Ageratina riparia* (Regel) R.M.King & H.Rob. (Asteraceae: Eupatorieae), both originally from Mexico, have become invasive in many countries. The two species have some commonalities but they differ in their biology, history of introduction, spread, and their biological control, and are therefore treated separately in this review.

AGERATINA ADENOPHORA

Ageratina adenophora (synonyms: *Eupatorium adenophorum* Spreng., *E. glandulosum* Kunth, *E. pasdadense* Parish) (King & Robinson 1987) commonly called Crofton weed or Mexican devil weed, is a perennial, multi-stemmed soft shrub, native to Mexico, that grows up to three metres in height (Parsons & Cuthbertson 1992; Henderson 2001; Muniappan *et al.* 2009) (Fig. 1). The plant

inhabits moist conditions, such as the edges of slow-flowing streams and waterlogged soaks on steep slopes in high-rainfall areas. It is an extremely aggressive competitor, especially in shaded conditions (Auld & Martin 1975; Zheng *et al.* 2009) although seeds do not germinate in dense shade (Auld & Martin 1975). The plant increases its competitive advantage through allelopathic action (Dhyani 1978) and by altering the soil microbial communities (Yu *et al.* 2005; Niu *et al.* 2007). Stems set roots when in contact with the soil, facilitating the formation of dense stands of plants (Bess & Haramoto 1958; Muniappan *et al.* 2009).

Ageratina adenophora produces terminal clusters of small white flowers during late winter to spring (Henderson 2001). A typical plant can set about 10 000 seeds which are wind- and water-dispersed (Murray & Phillips 2009) and 70 % of which are viable, but not long-lived (Parsons & Cuthbertson 1992; Muniappan *et al.* 2009).

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Fig. 1. *Ageratina adenophora* shoot and inflorescence (A), and *Ageratina riparia* leaf (B). (Drawn by G. Condy, South African National Biodiversity Institute, Pretoria. First published in Kluge (1991).)

Ageratina adenophora is reported to produce seed by means of apomixis (Noyes 2007). It is therefore likely that there is limited genetic variation within populations, especially in its introduced range, which in turn may make it easier to control. Apart from suppressing biodiversity (Niu *et al.* 2007), it reduces the carrying capacity of pastures, is poisonous to horses (O'Sullivan 1979, 1985; Parsons & Cuthbertson 1992; Muniappan *et al.* 2009) and has the potential to reduce water flow in streams.

It is reported to be invasive in areas of China, Nepal, Pakistan, Thailand, India, Philippines, Malaysia, Singapore, Burma, Vietnam, Indonesia, Brunei, the United States of America (including Hawaii), Tahiti, Australia, New Zealand, Papua

New Guinea, Nigeria, Zimbabwe and South Africa (Osborn 1924; Auld 1970, 1972; Kluge 1991; Sun *et al.* 2004; Muniappan *et al.* 2009). Muniappan *et al.* (2009) recently reviewed the international status of, and biological control efforts against, *A. adenophora*.

The first record of *A. adenophora* in South Africa (from the Limpopo Province) dates back to 1958 (Pretoria National Herbarium) (Henderson 2006). It was most likely introduced and spread in the 1940s as an ornamental (Kluge 1991). By the early 1990s, the plant was naturalized in the Western Cape Province and in the Magaliesberg region of the North West Province, but was considered as invasive only in the mist belt region of KwaZulu-Natal (Bennett & Van Staden 1986; Kluge 1991).

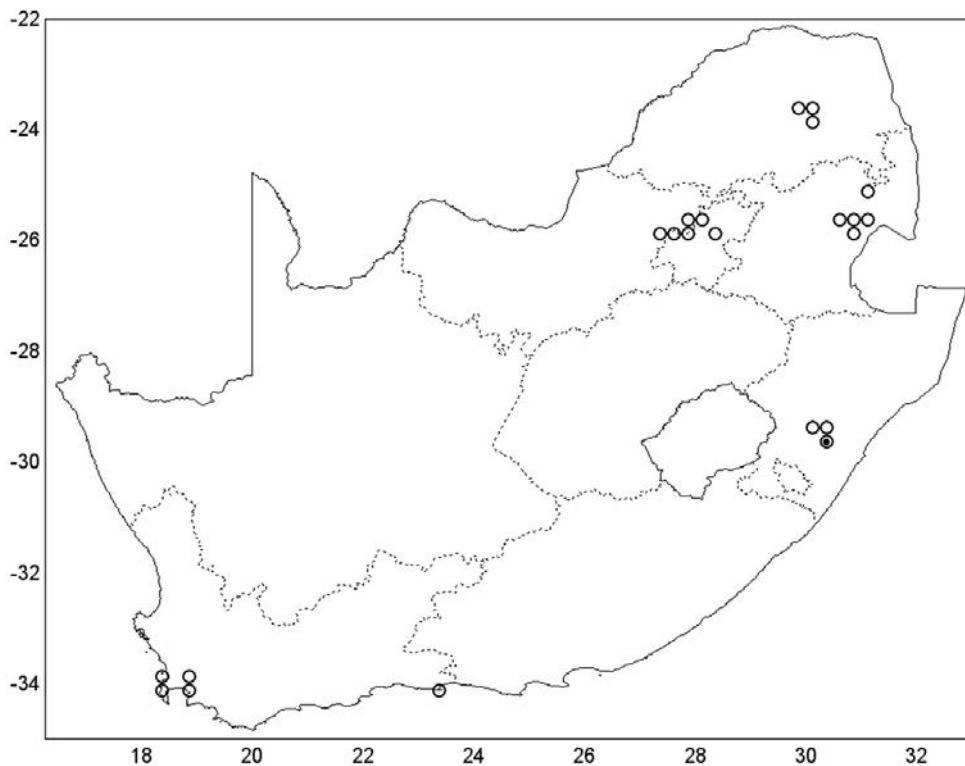


Fig. 2. Distribution of *Ageratina adenophora* (O) and *Ageratina riparia* (• in circle) in South Africa. (Drawn by L. Henderson; data source: SAPIA data base, ARC-Plant Protection Research Institute, Pretoria.)

Ageratina adenophora has been recorded as invasive from many additional localities over the last two decades, including sites in Gauteng, Mpumalanga and Limpopo provinces (Fig. 2) and is becoming denser and spreading (Henderson 1995, 2001; Heystek 2008, 2009).

Biological control of *A. adenophora*

Biological control research on *A. adenophora* in South Africa has been a mix of reliance on two already-established agents, with some assessment of their performance, and investigations into new potential agents obtained during surveys in Mexico.

Already-established agents

The first surveys in Mexico for natural enemies of *A. adenophora* were conducted in 1923 and 1924, and resulted in the release of the shoot-galling tephritid fly *Procecidochares utilis* Stone (Diptera: Tephritidae) into Hawaii, as recommended by Osborn (1924). The fly was reported to be host-specific (Haseler 1965) and has been intentionally

released in seven countries for the control of *A. adenophora*. It failed to establish in only one of these countries, Thailand, and has further spread to Nepal from India (Julien & Griffiths 1998) and then on to China (Wan & Wang 1991; Muniappan *et al.* 2009). Kluge (1991) reviewed the biological control initiatives in South Africa, focusing on the release and establishment of *P. utilis* in 1984.

Van Staden & Bennett (1991) found galling of stems by *P. utilis* creates a sink for photosynthates which explains the reduced reproductive vigour of galled plants (Bennett & van Staden 1986). Effective control of the weed was achieved in Hawaii, except in high-rainfall areas (Julien & Griffiths 1998). The fly is also credited with a decline in the abundance of the weed in New Zealand (Hill 1989). Lack of sufficient levels of control by *P. utilis* in various other countries is often ascribed to high levels of parasitism, amongst other factors (Zhang *et al.* 2008; Muniappan *et al.* 2009). Bennett (1986) found 76% of flies parasitized by three parasitoid species in KwaZulu-Natal Province, South Africa. However, parasitism levels were

lower (about 30%) in the early summer of 2010 in the Magaliesberg, North West Province (F. Heystek, unpubl.) and more work is required to ascertain the extent of the impact of natural enemies on the abundance of *P. utilis* in areas where it is introduced.

The other agent introduced and established in South Africa in 1987 is a fungal pathogen, which was identified as a *Phaeoramularia* sp. at the time. It has since been described as *Passalora ageratinae* Crous & A.R. Wood (Mycosphaerellales: Mycosphaerellaceae) (Crous *et al.* 2009). It was first observed in Australia and was assumed to have been accidentally introduced there along with shipments of the gall-fly, *P. utilis*, from Hawaii, which had originated in Mexico (Dodd 1961). *Passalora ageratinae* is so far only known from Australia and South Africa (Crous *et al.* 2009). An isolate of *P. ageratinae*, was obtained from Australia and released in South Africa following limited host-specificity testing on seven plant species in the Eupatorieae (Morris 1989). It established and proliferated on the outskirts of Pietermaritzburg, KwaZulu-Natal, (Morris 1991). An introduction was also made in the southwestern Cape in the Jonkershoek valley near Stellenbosch and it was widely released much later in the Magaliesberg region of the North West Province. Currently *P. ageratinae* remains common in the Pietermaritzburg area of KwaZulu-Natal Province, and has also been observed in all areas where the weed has been found (Fig. 2). It was never released in Limpopo or Mpumalanga provinces, and therefore must have dispersed about 300 km on its own from its closest known source in the Magaliesberg. In the Western Cape it has established near Stellenbosch, despite an earlier report to the contrary (Morris 1991), and has since spread to Cape Town.

An attempt was made to measure the impact of *P. ageratinae* on *A. adenophora* along the Easterkloof stream between S25°50'11.9" E27°31'23.2" and S25°49'39.0" and along the Kloofwaters stream between S25°50'02.5" E 27°26'21.5" and S25°50'008", E27°26'22.1" in the Magaliesberg (Buccellato 2004). Plant biomass and area covered by the weed were reportedly not affected by the incidence of the fungus which infected between 22–95 % of the plants and 10–50 % of leaves per infected plant. This finding, together with observations of continual spread of the weed and its potential to invade a much larger area, showed there was a need for

additional agents to reduce the extent of the problem.

Surveys for additional biological control agents

Surveys by staff of the Agricultural Research Council-Plant Protection Research Institute (ARC-PPRI) in Mexico were conducted during August/September 2007, October 2008, and February/March 2009 to find insect herbivores and pathogens with the potential to be used as biological control agents of *A. adenophora*. In 2007, the surveys were undertaken when *A. adenophora* was not in flower, making it difficult to locate plants and to distinguish them from congeners. At the same time, search effort was diffused because six other plant species were surveyed and only 15 *A. adenophora* sites were found. The focus during the 2008 survey was on pathogens associated with *A. adenophora* and natural enemies of two *Tithonia* species. The 2009 survey was specifically aimed at *A. adenophora* and timed to coincide with its flowering period in Mexico. In all, 35 sites were located, of which 31 were surveyed for potential candidates.

The insects found during the recent surveys were probably mostly the same, still unnamed, species observed and described during the survey by Osborn (1924) who had predicted that *P. utilis*, a cecidomyiid midge that develops in flowers, and a flower- and seed-feeding tortricid moth held most potential as candidates to control *A. adenophora* in Hawaii. No cecidomyiids were encountered during the 2007 or 2009 surveys, but three tortricid species, feeding on leaves were collected and *P. utilis* was encountered frequently. Adults of an apionid beetle species were collected in large numbers from flowers in 2009 but did not breed in the laboratory.

Since 2007, at least 11 coleopteran species, five lepidopteran species, two hemipteran species, two dipteran species and two pathogen species have been reared in the Pretoria ARC-PPRI quarantine facility from samples of *A. adenophora* that were collected in Mexico. Those that may have potential for biological control of *A. adenophora* include an unidentified stem-boring species of Mordellidae and some species of Curculionidae (Coleoptera), but too few individuals were obtained to initiate cultures. Besides these species, a pathogen and three insect species were obtained in suitable quantities to start laboratory cultures for further investigation.

Where possible, host-specificity testing was initiated on these species by observing the way they associated with six indigenous plant species from three genera within the tribe Eupatorieae (Retief 2002) and a further ten commercially important ornamental and food crop species in the Asteraceae (Germishuizen *et al.* 2006; Klopper *et al.* 2006).

Baeodromus eupatorii (Arthur) Arthur
(Puccinales: Puccinosiraceae)

The leptosporic, microcyclic rust fungus, *B. eupatorii*, is known from Mexico, Guatemala and Honduras on several species of *Ageratina*, including *A. adenophora* (Buriticá & Hennen 1980). No information on its biology was found. The fungus was seen at four localities in the mountainous interior of Michoacán Province, Mexico, during October 2008 and in February 2009. The majority of leaf infections observed during October 2008 were immature, having pycnia but no telia, whereas four months later the latter were well developed.

Using a method of Morin *et al.* (1993), telia germinated under quarantine conditions. Small orange lesions developed within two weeks in which pycnia were produced. Telia subsequently developed abaxially when these pycnia were cross-fertilized. This culture could not be maintained and was lost before host-specificity tests were initiated.

Lophoceramica sp.
(Lepidoptera: Noctuidae)

The gregarious leaf-feeding larvae of this species were found at eight of the 15 sites surveyed in 2007 in the Michoacán and Jalisco provinces, Mexico, and once in the Michoacán Province during the winter-spring 2009 survey. Adults were identified as *Lophoceramica* sp. by M.G. Pogue, National Museum of Natural History, U.S.A. The moths are pale beige-brown in colour with a wingspan of about 30 mm. In the laboratory, females laid batches of up to 60 eggs and covered them with white fluffy scales on the underside of leaves. Larvae fed gregariously during the first few instars, often grouping in large numbers in a single folded leaf, drawn into a roll, using silken threads. Larger larvae dispersed and then developed singly, by partially cutting a leaf-stalk and forming a hanging leaf roll in which they remained during the day. Larvae in captivity passed through five, but

sometimes up to eight, instars. Pupation occurred on the soil surface in leaf litter that the larva incorporated into a silken cocoon. The developmental duration from egg to adult, for males and females, was about two months. Owing to the gregarious feeding of larvae, entire potted plants (50–70 cm) were stripped of their leaves within days by offspring from two females.

Host-specificity tests conducted so far on *Lophoceramica* sp. have included larval survival trials on 11 plant species on which development and pupation occurred on five species, all Asteraceae. Second-instar larvae developed to pupation in about 40 days on *A. adenophora*, *Senecio madagascariensis* Poir. and *Senecio tamoides* DC., and in almost 50 days on *A. riparia* and *Adenostemma viscosum* J.R.Frost & G.Frost (*Adenostemma* = *Ad.*). Oviposition occurred on four of nine plant species included in adult multiple-choice oviposition trials. Compared with *A. adenophora*, *Adenostemma caffrum* DC., had about 26 % as many eggs, followed by *C. odorata* with 14 % as many eggs and the other species had fewer than 2 % as many eggs. The culture was lost before testing was completed but this agent is now regarded as nonspecific and of low priority for further consideration.

Pentispa fairmairei (Chapuis)
(Coleoptera: Chrysomelidae: Cassidinae)

Adults of this leaf-mining beetle were collected at only one of the 15 sites surveyed, in Jalisco Province, Mexico, during the 2007 summer survey. A single adult was found during the 2009 winter-spring survey, from a different locality in the same province. *Pentispa fairmairei* adults (identified by C.L. Staines, Center for Systematic Entomology, U.S.A., June 2009) are approximately 6 mm long, black, with mostly orange elytra that have a black terminal transverse band. In the laboratory, females laid eggs singly, mostly on the perimeter of the underside of leaves, and often covered the egg with frass. The larva hatched after a week and mined between the epidermal layers of the leaf, causing a clearly visible blotch mine which in some cases eventually covered the whole lamina. Typically, one mine occurred per leaf, but on occasion a few mines developed on the same leaf. Pupation took place within the leaf and adults emerged approximately 30 days after the eggs were laid.

Lewis *et al.* (2002) and Morris *et al.* (2004) reared *P. fairmairei* from several Asteraceae. Staines *et al.*

(1998) listed various species from nine genera as food plants, and Palmer & Pullen (1995) collected adults off *Lantana camara* L. (Verbenaceae). Host-specificity testing was initiated prior to final identification of the beetles. In multiple-choice tests with ten Asteraceae species, oviposition occurred on *A. adenophora*, *Ad. caffrum* and *Helianthus tuberosus* L. (Jerusalem artichoke) (Asteraceae). Larval development, up to the adult stage, occurred equally successfully on *H. tuberosus* as on *A. adenophora*. Owing to a lack of specificity, *P. fairmairei* is not being considered as a biological control agent.

(?)*Eugnosta medioxima* (Razowski)
(Lepidoptera: Tortricidae).

Adults of this moth were tentatively identified in August 2010 by J. Razowski (Institute of Systematics and Evolution of Animals, Poland). He had originally described the species in 1986 as belonging to the genus *Carolella* Busck, from a female collected from Mexico in 1955, without any host records (J. Razowski 1986, and pers. comm.).

In summer 2007, small (<5 mm) larvae were collected in soft shoots at a site in Michoacán Province, Mexico. After collection, larval survival was low (approximately 30 %) as the young, cut shoots decayed readily. During the 2009 winter–spring survey, many larvae were found at one locality, in Jalisco Province. These were larger and occurred in thicker shoots and had better survival rates (just over 50 %) which aided in the initiation of a colony in quarantine. Adults are approximately 6 mm in length with a wingspan of about 12 mm. Females are pale beige-brown, with two darkened triangles forming a chevron pattern on the forewings, with a nearly-black fringe around the wings. Forewings of males do not have the distinctive triangular pattern and become progressively darker towards the wing tip, which is almost black.

Eggs were laid on shoot tips and leaf midribs. Hatched larvae burrowed from the midrib into the petiole, initially spirally just below the surface and then in the centre downwards into stems, working frass out through openings, chewed at irregular intervals. Occasionally a few larvae were found in a single stem. Tunnelling may extend into the crown of the plant. Tunnelled stems characteristically wilted after a few days of larval activity and gradually dried out, usually dying within three to four months. Pupation takes place within the stem

and adults emerge through window-like patches that have been left by the larvae. Most often, pupal casts are characteristically left partly protruding from the stem, but occasionally are pulled out and fall to the ground as the adult emerges.

Larvae are extremely damaging, with ten being more than enough to destroy a large (approximately 70 cm high) multi-stemmed potted plant. Development from egg to adult takes about 3–4 months, with female development taking approximately two weeks longer than that of the males. In partially-completed multiple-choice tests, oviposition and full development occurred only on *A. adenophora* and not on any of the five other test plant species which included *A. riparia*, *Ad. caffrum*, *Senecio angulatus* L.f., *Senecio deltooides* Less. and *S. tamoides*. Additional material is to be collected in Mexico to allow completion of host-specificity work on this promising candidate.

AGERATINA RIPARIA

Ageratina riparia (creeping Crofton weed or mist-flower) (synonyms: *Eupatorium riparium* Regel) (King & Robinson 1987), originally from Mexico, is a weak-stemmed, perennial, creeping herb that grows up to 1 m in height. Unlike those of *A. adenophora*, the leaves are narrowly ovate and three-nerved from the base (Fig. 1 – leaf inset), but, like *A. adenophora*, this species produces terminal flat-topped showy clusters of small white flowers in late winter to spring. These give rise to wind- and water-dispersed seeds (Parsons & Cuthbertson 1992; Henderson 2001).

Ageratina riparia is recorded as naturalized in parts of the U.S.A. (including Hawaii), Australia, New Zealand, the Canary Islands, Madagascar, Mauritius, Reunion, Spain, southeast Asia, including India, Indonesia, Peru and Africa (including South Africa) (Parsons & Cuthbertson 1992). It is shade tolerant and frost sensitive and grows in damp areas, on stream banks, in forest clearings and edges, and pastures in high-rainfall areas (Parsons & Cuthbertson 1992). In Australia, *A. riparia* is mostly invasive in areas with an annual rainfall of ≥ 1700 mm per year (Parsons & Cuthbertson 1992) and in Hawaii it has invaded areas with between 750 and 8000 mm of rain per year (Trujillo 2005; Morin *et al.* 1997).

Morris (1991) reviewed the introduction and early spread of *A. riparia* in South Africa. The oldest known specimen was collected in 1955, from Chase Valley, Pietermaritzburg, KwaZulu-Natal

Province (Hilliard 1977). The weed had spread to Town Bush, also in the Pietermaritzburg area, by 1974, and then into the nearby Hilton and Sweetwaters, before the early 1980s (all these localities are encompassed by the solid dot in Fig. 2).

Two roadside surveys in the greater Pietermaritzburg area during 2009 showed that, although widespread within its known limited range (Fig. 2), *A. riparia* was nowhere a significant invader. Only small numbers of plants were recorded at most localities, and the largest infestation found was approximately 60 m². No plants were found in the original area of invasion, namely Chase Valley, which has been transformed by extensive urbanization and plantations of *Eucalyptus* species (Myrtaceae) and *Acacia mearnsii* De Wild. (Mimosaceae).

Biological control of *A. riparia*

Biological control agents have been introduced against *A. riparia* in Hawaii, Australia, South Africa (Julien & Griffiths 1998) and New Zealand (Barton *et al.* 2007). Hawaii introduced four agents: the white smut fungus, *Entyloma ageratinae* R.W. Barreto & H.C. Evans (Entylomatales: Entylomataceae), a pterophorid moth, *Oidaematophorus beneficus* Yano & Hepner (Lepidoptera: Pterophoridae), a shoot-galling fly, *Procecidochares alani* Steyskal (Diptera: Tephritidae), and another tephritid fly, *Xanthaciura connexionis* Benjamin (Diptera: Tephritidae) (Julien & Griffiths 1998). *Procecidochares alani* was introduced into Australia in 1986 and *E. ageratinae* was introduced into South Africa in 1989 (Morris 1991; Parsons & Cuthbertson 1992). Both these agents were introduced into New Zealand, *E. ageratinae* in 1998, and *P. alani* in 2001 (Barton *et al.* 2007).

Morris (1991) reviewed the early stages of the biological control programme in South Africa and the taxonomy of the agent, *E. ageratinae*, which was originally collected in Jamaica from where it was introduced into Hawaii before being supplied to South Africa. It was released at a single site in Hilton in November 1989, and was well established at that site by April 1990 (Morris 1991). Although the impact of the fungus on the weed has never been formally assessed, Olckers (2004) recorded that it had only had a negligible impact on the weed.

By contrast, *E. ageratinae* is considered to have been a highly successful biological control agent of *A. riparia* in both Hawaii (Trujillo 2005) and New

Zealand (Barton *et al.* 2007), reducing large dense infestations dramatically within just a few years of introduction. The fungus causes early leaf-drop, significantly curbing both growth and reproduction of the plants. Infection occurs within a temperature range of 10–20 °C (Trujillo 1985). In the high-rainfall areas of Hawaii (1500–8000 mm per year) with suitable temperatures, plant densities were reduced by 80 % within nine months of release (Trujillo 1985, 2005; Morin *et al.* 1997). Similarly, in New Zealand, sudden declines in plant densities occurred both in areas where the weed was well established and where it was rapidly spreading.

Recent observations in South Africa indicate that initial assessments were incorrect and that *E. ageratinae* has had a substantial impact on the abundance of *A. riparia*. The fungus was present at 18 of 19 localities where the plant was observed and plant densities in South Africa are equivalent to those now apparent in both Hawaii and New Zealand (A.R. Wood, unpubl.).

CONCLUSIONS

The rate of invasion and abundance of *A. adenophora* in certain areas may have been retarded by the early introduction of *P. utilis* and *P. ageratinae*, as these agents occasionally reach high densities (Buccellato 2004; F. Heystek, unpubl.). Certainly the impact of these two agents on the target weed is valued elsewhere (Dodd 1961; Auld 1969). In Australia, despite low levels of damage to mature plants (Auld 1969), the biological control agents are credited with having halted the very rapid spread of the weed compared to that prior to their introduction (Dodd 1961). However, the continual spread and densification of *A. adenophora* in South Africa are indicative of a need for greater levels of biological control. Surveys in the plant's native range revealed a potential suite of natural enemies, of which the damaging stem-boring moth, (?)*E. medioxima*, and the rust fungus, *B. eupatorii*, appear to be host-specific and warrant further investigation.

It is unlikely that *A. riparia* would ever have become a major weed in South Africa as a large proportion of the country receives less than 750 mm annual rainfall which is highly seasonal. However, there are large areas with suitable climate and habitat for the plant. The introduction of the smut fungus, *E. ageratinae* seems to have

reduced the plant's abundance in the confined area over which it was common and could be preventing its further spread. This highlights the prudent strategy of introducing successful agents in the early stages of invasion by alien plants (Olickers 2004).

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