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# Successful biological control of mist flower (*Ageratina riparia*) in New Zealand: Agent establishment, impact and benefits to the native flora

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**Abstract**

The white smut fungus (*Entyloma ageratinae*) and the gall fly (*Procecidochares alani*) were released in New Zealand in 1998 and 2001 respectively to suppress mist flower (*Ageratina riparia*). The fungus established and spread rapidly, crossing 80 km of sea to Great Barrier Island within 2 years. The mean number of *P. alani* galls increased exponentially to 1.96/stem at release sites, but dispersal was slow. The impact of the biocontrol agents was monitored once annually from 1998/99 to 2003/04, at up to 51 sites in the North Island. The mean percentage of live leaves infected with fungus rapidly reached nearly 60%. Maximum plant height declined significantly. In heavy infestations, mean percentage cover of mist flower declined from 81 to 1.5%. Galls were only recorded towards the end of the impact study, and at low mean numbers. As mist flower declined, the species richness and mean percentage cover of native plants increased. In contrast, the species richness and mean percentage cover of exotic plants (excluding mist flower) did not change significantly. Many plant species colonizing the plots were important native mid- or late-successional shrubs or trees. With few exceptions, the exotic plant species common in the plots were not weeds that appeared to threaten native forest habitats. There was only a weak "replacement weed effect" from the potentially serious invader African club moss (*Selaginella kraussiana*). These data, together with reports of reduced threats to rare endemic plants from mist flower, suggest this rapid, well-monitored weed biocontrol program was very successful.


*Keywords:* Mist flower; *Ageratina riparia*; *Entyloma ageratinae*; *Procecidochares alani*; Biological control of weeds; Replacement weeds; Native regeneration

## 1. Introduction

Releases of biological control agents against weeds in New Zealand have always been monitored carefully to assess whether agents established, and in some cases quantitative data on the damage that agents inflicted on the target weed have been gathered (Cameron et al., 1989; Fowler et al., 2000a; Memmott et al., 1997). However, good monitoring data on reductions in weed populations, and on what plant species replaced the weed, are almost entirely lacking (Fowler et al., 2000a). This pattern of mixed, often rather poor, monitoring in weed biocontrol is not restricted to New Zealand: worldwide there are few quantitative studies showing that populations of the target weed declined after biological control, and even fewer that went on to show a benefit in terms of replacement by more desirable plant species (Denslow and D'Antonio, 2005; Syrett et al., 2000). Furthermore, the best studied and reported examples appear to involve weeds that were primarily affecting economically productive rangeland such as St John's wort *Hypericum perforatum* L. in the USA (Huffaker and Kennett, 1959). More recently, exotic weeds that affect indigenous biodiversity have become increasingly targeted by biological and other control methods. For such weeds, the

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lack of published data showing beneficial or otherwise outcomes seems even more pronounced. For example, in New Zealand, despite increased resources being focused on exotic weeds affecting indigenous biodiversity, we could only find a few examples where benefits to the indigenous flora were quantified after weed control of any sort: recovery of indigenous plants after control of old man's beard, *Clematis vitalba* L. (Ogle et al., 2000); mixed-short term results after chemical control of Japanese honeysuckle *Lonicera japonica*, climbing dock *Rumex sagittatus* Thunb., and bone-seed *Chrysanthemoides monilifera* (L.) Norl. (Williams et al., 1998); and, unpublished benefits to indigenous plants in a sand dune ecosystem after chemical control of marram grass *Ammophila arenaria* (L.) Link (M. Hilton pers. comm.). This paucity of data on tangible benefits to indigenous plant communities after any form of weed control appears to be a worldwide phenomenon, e.g., Luken (1996) states "unfortunately there are few studies where long-term effects of management practice, specifically plant removal, have been documented in terms of community response".

The recent introduction into New Zealand of two biocontrol agents against the weed mist flower, *Ageratina riparia* (Regel) R. King and H. Robinson (Asteraceae), provided an opportunity to monitor the impacts of these agents. Biocontrol agents were introduced to Hawai'i in the 1970s where they quickly controlled mist flower in rangelands (Trujillo, 1985). It was hoped that similar rapid success would be achieved in New Zealand. In Hawai'i, four biocontrol agents were released (Julien and Griffiths, 1998), and three established; a white smut fungus, *Entyloma ageratinae* Barreto and Evans (Ustilaginomycetes); a gall fly, *Procecidochares alani* Steyskal (Tephritidae); and a plume moth *Oidaematophorus beneficus* Yano and Heppner (Pterophoridae). These agents reportedly greatly reduced mist flower populations, thus rehabilitating the rangelands (Trujillo, 1985), and although quantitative monitoring data are lacking, this project is regarded as highly successful (Evans, 2002; Julien and Griffiths, 1998; Morin et al., 1997; Rosskopf et al., 1999).

Morin et al. (1997) compared climate data from sites in Hawai'i where mist flower was effectively biologically controlled, with data from areas in New Zealand where the weed was causing problems, and concluded that the biocontrol agents should be active in the latter. It was recommended that the fungus and the gall fly should be introduced to New Zealand, and that if needed, the plume moth could be brought in later (Morin et al., 1997). After favorable results in host range tests, *E. ageratinae* was released in New Zealand in November 1998 and *P. alani* in February 2001 (Fröhlich et al., 1999, 2000; Winks and Fowler, 1999).

Mist flower was a popular ornamental plant and consequently was spread well beyond its native range in Central America. It naturalized in many tropical and warm temperate countries, and became a serious invasive weed in many regions including Hawai'i, South Africa, and northern Australia. It is a perennial herb or subshrub, growing to ~1 m tall. It prefers a warm, moist habitat, can grow in sun or shade, produces numerous small white flowers in the spring, and spreads by wind- and water-borne seeds. In New Zealand, mist flower occurs as a weed of forest margins, open places, poorly managed pasture, wetlands and stream banks, mostly in the northern half of the North Island (Anonymous, 1999). Stock mostly avoid grazing the plant, but it can be toxic to horses (O'Sullivan et al., 1985). It is also common beside walking tracks and along river systems in native forests, where it can form large, dense mats of semi-woody stems which smother native plants and prevent their regeneration (Anonymous, 1999). In two specific examples, mist flower was reported to be a threat to the survival of two endemic plants, *Hebe bishopiana* (Petrie) Hatch and *Hebe acutiflora* Cockayne (de Lange, 1996). *H. bishopiana* is endemic to the Waitakere Ranges and is classified as nationally vulnerable, with the main threats being invasion of its habitat by mist flower, and to a lesser extent the related weed *A. adenophora* (Sprengel) R. King et H. Robinson and two exotic pampas grasses, *Cortaderia* spp. (de Lange et al., 1999). The second threatened endemic plant species, *H. acutiflora*, has been classified as nationally endangered or vulnerable over the last 15 years. Mist flower had almost eliminated *H. acutiflora* from Kerikeri Falls, where it was first collected, and had started invading the habitat of *H. acutiflora* in nearby Puketi Forest (Fig. 1), its only other known site (P. de Lange, Department of Conservation, New Zealand, personal communication).

Given these impacts on indigenous flora, it was considered particularly important to monitor the success or otherwise of the mist flower biological control program in New Zealand. In addition, the importance of having good assessment data from new weed biocontrol programs cannot be overemphasized, particularly given the much more rigorous assessment of environmental risks/benefits in modern applications to release biocontrol agents in New Zealand (Fowler et al., 2000b). The aims of this monitoring program were to (1) assess agent establishment and dispersal; (2) measure the levels of attack by the agents and changes to mist flower infestations; and (3) monitor changes in native and exotic vegetation if mist flower was suppressed. This paper presents the final analyses of this monitoring program following on from the preliminary reports in Fröhlich et al. (2000) and Barton née Fröhlich et al. (2004).

## 2. Materials and methods

### 2.1. Agent establishment and dispersal

*Entyloma ageratinae* was released at nine sites (Fig. 1) in the northern half of North Island in November–December 1998 (Fröhlich et al., 2000). Release sites were each visited 2–4 times over the first 14 months to assess whether or not the fungus had established. In addition, selected regional

council and Department of Conservation staff were asked to report whether the mist flower fungus was present on mist flower in their region and/or submit a sample to Landcare Research for microscopic detection of spores (conidia). Reports that the fungus was present were accepted without the need for a sample only if the observer was known to be familiar with the characteristic white conidia. Once the presence of the fungus was confirmed, the distance between the point of collection and the nearest release site was determined.

*Procecidochares alani* was released at 34 sites (Fig. 1) across the North Island from February 2001 to June 2004. In total, 11,630 flies were released, with the sizes of individual releases varying from 30 to 600 flies. In three cases, two separate releases were made at the same sites 1–4 weeks apart. In Table 1 these repeat releases have been summed per site. All releases used just the adult stage. Thirty gall fly release sites have been revisited to assess the presence/absence of galls. Dispersal of the gall fly was not quantitatively monitored, but casual observations were made between release sites, and when mist flower sites were being visited for other reasons.

### 2.2. Levels of attack by the agents, and changes to mist flower infestations

This study was carried out on two scales: intensively in the Waitakere Ranges 10 km west of Auckland and extensively at a range of release sites for the mist flower fungus. The gall fly had been released too recently to expect



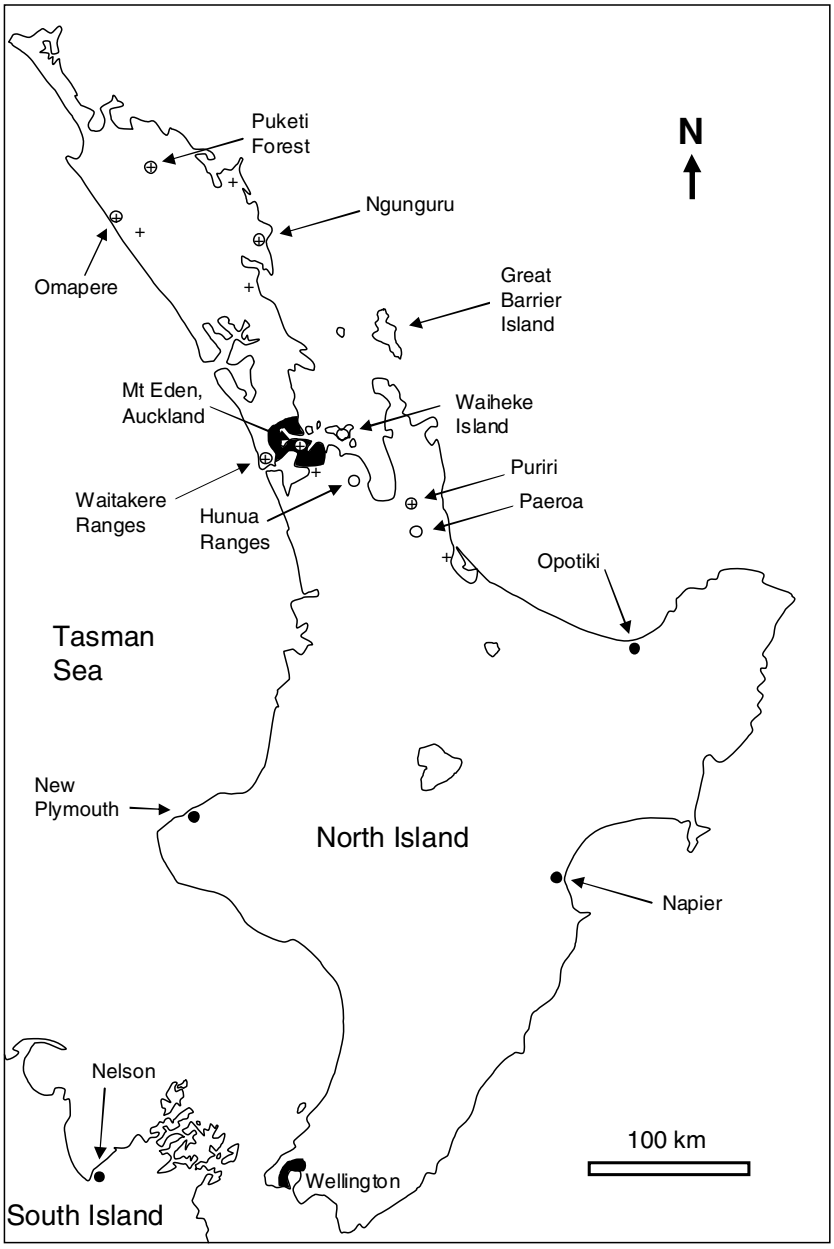


Fig. 1. Map of Northern New Zealand showing initial mist flower fungus release sites (○), gall fly release sites (+, several sites with multiple releases nearby) and other sites examined in the study (●).

Table 1
Release size and establishment success at the sites where mist flower gall fly was released

| Number of adult flies per release | Number of sites checked/unchecked | Percentage of checked sites where gall fly established (%) |
|---|---|---|
| 30 | 4 (+1 unchecked site) | 100 |
| 90–120 | 7 (+1 unchecked site) | 86 |
| 270 | 5 (+1 unchecked site) | 100 |
| 400–500 | 6 (+1 unchecked site) | 67 |
| 600–700 | 6 | 100 |
| 1000–1100 | 2 | 100 |

Similar size releases were aggregated into categories for clarity.

changes in mist flower infestations as a result of its impact so an extensive study at release sites was not carried out. Instead, numbers of galls were counted annually at three sites where releases were made in February 2001.

The intensive study was started in October–November 1998, just before the first release of *E. ageratinae*. Ten plots were established along each of 11 walking tracks in the Waitakere Ranges (Fig. 2). Tracks were selected randomly except that very long tracks were avoided to minimize access times, tracks close to ones already selected were avoided, and the Karamatura Track was deliberately included because it was the only area in the Waitakere Ranges where releases of agents were planned. Along each track, the first plot was centered at a point 500 m from the start of the track, and subsequent plots were centered at incremental 500 m intervals. Each plot comprised a 50-m length of track and the land within 5 m on either side of the track, making an area of 500 $m^2$. Cleared walking tracks (typically 1–2 m wide) were used for ease of access, and because mist flower grows abundantly near disturbed areas such as track edges and riparian zones. All plots were revisited in October–November of 1999, 2001 and 2003. On each visit, if mist flower was found, then five mist flower plants were randomly selected from within the plot. On each of these plants, the following were counted: (1) total number of living leaves; (2) total number of attached dead leaves;

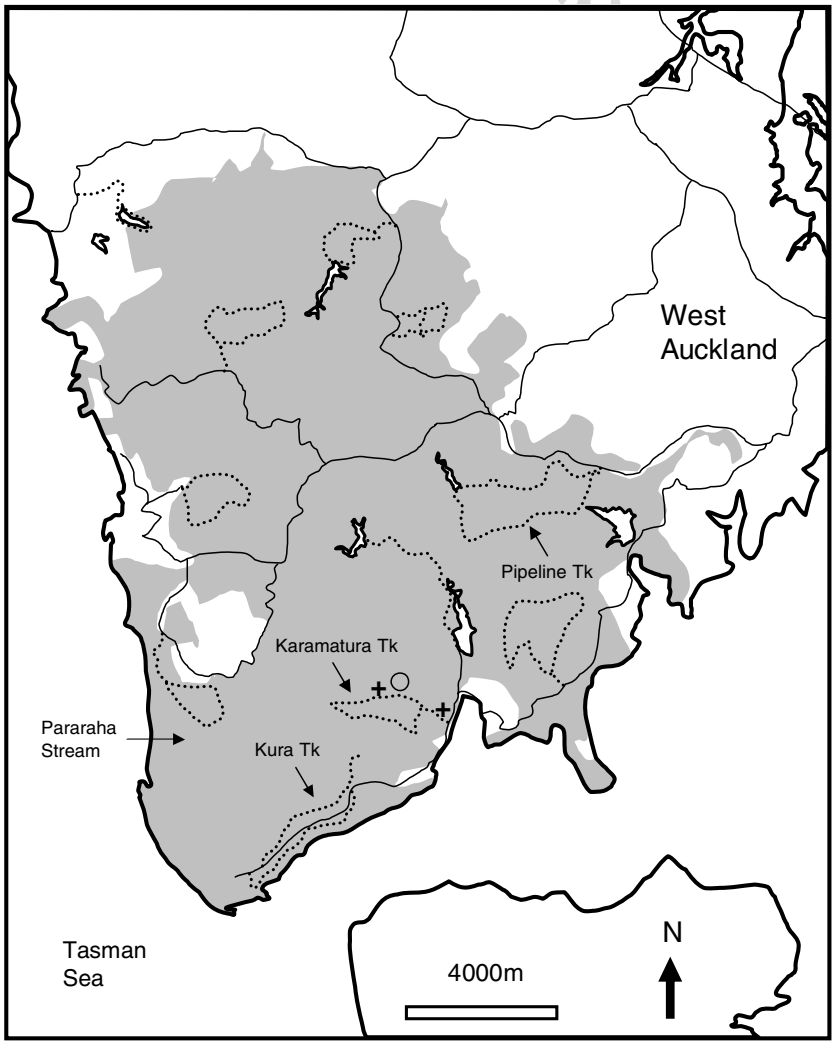


Fig. 2. Detailed map of the Waitakere Ranges. Regional Park land is shaded in grey. Thick black lines are coastal or lake shorelines. Thin black lines show selected roads. Dotted lines indicate the walking tracks used in the intensive study. The Pipeline and Kura Tracks were used for the vegetation change study. The Karamatura Track runs along the stream where the mist flower fungus was released in November 1998 (site marked ○), and where several gall fly releases were made in Feburary 2001 (sites marked +). One gall was seen alongside the Pararaha Stream in Feburary 2002. Further details in text.

(3) number of live leaves with externally visible infections of *E. ageratinae*; (4) total number of *P. alani* galls; and (5) number of stems per plant. In addition, the height of the tallest mist flower plant within each plot was measured and the area of each plot covered by mist flower foliage was estimated visually. If mist flower was not recorded in the plots, then a note was made if it was present along other parts of the track.

The extensive study comprised nine permanent plots, each $15 \times 5$ m (75 $m^2$) with the point of release of *E. ageratinae* at its center. Sampling (as above, except that maximum plant height data were not collected in the first year) was carried out once a year per plot, between October and February in the southern hemisphere summers of 1998/99, 1999/00, 2000/01 and 2001/02.

At the three release sites in the Karamatura Valley where the gall fly had been released in February 2001, the numbers of galls were counted by destructively sampling mist flower stems in two $0.5 \times 0.5$ m wire quadrats placed within 5 m of each release site. The quadrat was randomly placed, given the constraint that only sites with dense mist flower stems were used. Sampling was carried out in April 2001, May 2002 and May 2003.

### 2.3. Changes in native and exotic vegetation as mist flower was suppressed

This study used the Pipeline Track (Fig. 2) because mist flower was only patchily distributed along it. In December–January 1999/00, 10 plots with a reasonably dense cover of the weed, a few meters from the cleared track, were selected. Each plot was then paired with a similar plot (1–10 m away) with very little if any mist flower. At the start of the study, and in subsequent years, any mist flower plants found growing in these control plots were carefully removed. Each control plot was selected to be as similar as possible to its paired "mist flower present" plot, and as best we could ascertain contained suitable habitat for colonization by the weed. All plots had an area of 4 $m^2$, but their dimensions were either $2 \times 2$ m, or $4 \times 1$ m, depending on the availability of suitable habitat. A further 10 plots with mist flower present were established along the Kura Track (Fig. 2). The Kura Track had an extensive cover of mist flower in 1999/2000, with the weed appearing to have colonized almost all suitable habitat, so it was not possible to find matched plot sites without mist flower. The Pipeline Track and Kura Track were approximately 6.5 and 5 km, respectively, from the Karamatura Valley release site, where *E. ageratinae* was released in November 1998 (Fig. 2).

In December–February each summer from 1999/00 to 2003/04, all plants up to 2 m tall in each plot were identified to species or recognizable taxonomic unit (RTU), and classified as native or exotic according to the Allan Herbarium New Zealand Plant Names Database (Landcare Research, 2000). Percentage cover of each species was assessed visually from 2000/01 onwards. As plants differed in height and their foliage overlapped, the sum of individual percentage cover scores for all of the species in a given plot could be greater than 100%. All plots were also sampled in the same way as the intensive and extensive studies detailed above, except that to avoid disturbance to the plots the five randomly selected mist flower plants were selected from just outside the plot boundaries. Field data were collected by a different person each year, except that the same person worked in 2000/01 and 2001/02.

### 2.4. Data analysis

The analysis was carried out using the Linear Mixed Effects procedure (Pinheiro and Bates, 2000) in the statistical package S-Plus (Insightful Corporation, 2002). Numbers of species in the plots were transformed using the $\ln(x+1)$ transformation to stabilize the error variance. Serial correlations (due to repeated observations on the same plots) were modeled using first-order autocorrelations. Initially models with random intercepts and common slopes were fitted and subsequently a random intercept and slope model was fitted. The best models were chosen by Akaike's Information Criterion (Burnham and Anderson, 2002). Random slope models did not improve the overall fit of the models and random intercept models were retained. For the analyses of percentage infected/dead leaves, maximum mist flower height and percentage cover of mist flower, data from the intensive and extensive studies, and from the mist flower-present plots (in the vegetation change study) along the Pipeline and Kura Tracks, were analyzed together. Percentage data were not transformed because most of the data fell in the 20–70% range and fitted models did not predict percentages under 0% or over 100%. The analysis of gall fly abundance (as galls/stem) combined data from the Karamatura Valley release sites with data from the intensive study sites (plots with no mist flower were excluded) and the mist flower-present plots along the Kura Track. No galls were found in plots along the Pipeline Track or at the extensive study sites. Hawai'ian data for mean galls per stem was calculated from the mean number of galls per plant and the mean number of stems per plant measured by Hapai (1977).

## 3. Results

### 3.1. Agent establishment and dispersal

*Entyloma ageratinae* developed damaging infestations at all nine of the sites where it was released in November–December 1998. After establishing at all these sites, the fungus dispersed rapidly. For example, within 2 years it had crossed the Hauraki Gulf to reach Great Barrier Island (Fig. 1), about 80 km from the nearest release site, apparently without deliberate human intervention. By June 2004 (5.5 years after its release) all North Island mist flower sites from which reliable reports had been received, or that had been visited (during formal surveys or casually), had plants that were infected by the fungus. Even small, apparently

isolated populations of the weed found in Opotiki, New Plymouth, Napier and Wellington were infected, again without known human intervention (Fig. 1; Barton, 2004). The most distant site, at Wellington, is 440 km from the nearest release. The only place in the South Island where mist flower is known to occur is in Nelson, on the north coast (Fig. 1). By June 2004, the fungus had not yet been found in Nelson.

*Procecidochares alani* was recorded after passing through at least one generation at 26 of the 30 sites that were revisited: an establishment rate of 87%. Four sites were not revisited due to time constraints. Successful overwintering occurred at atleast 16 sites. Gall flies were not recovered at only four sites. The number of flies per release did not appear to influence establishment success (Table 1). Dispersal was not formally assessed but was noted sporadically. For example, in October 2001, one gall was recorded on the five sampled plants in one study plot, 250 m from the site where a release had been made the previous February. Longer distance dispersal has also occurred: in February 2002 one gall was found on mist flower alongside the Pararaha Stream in the Waitakere Ranges (Fig. 2). This represents dispersal of about 5 km (the distance to the nearest release site, where the fly was released 1-year earlier), across a forested ridge at 300–400 m altitude with little or no suitable habitat for mist flower.

### 3.2. Levels of attack by the agents, and changes to mist flower infestations

The percentage of live leaves that were infected with the fungus could reach high levels very soon after the arrival of the agent in a plot. For example, the highest percentage infection rates for leaves were 60.4% in 1999/00, 78.1% in 2000/01, 84.0% in 2001/02, 58.0% in 2002/03 and 94.5% in 2003/04. Overall, there appeared to be a leveling off of the mean percentage of live leaves attacked, and an asymptotic model provided a good fit to the data (Fig. 3; $y = 57.78 - 60.09e^{-0.66x}$, $R^2 = 0.59$, $F_{(3,232)} = 380$, $P < 0.001$). The model estimated the asymptote in percentage infected leaves as $57.78 \pm 3.41$ (SEM). The data from all three studies have been combined in this analysis, because there was quite high variability between studies and years. In particular, there was an unexplained decrease in the percentage leaves infected in the vegetation change plots in the final 2 years of the study (▼ Fig. 3).

The percentage of leaves attached to each plant that were dead was variable across years and plots, showing no obvious trend with time. For example, the mean percentage of dead leaves in the vegetation change plots reached a maximum of 30.7% in the Pipeline Track plots in 2000/01, but was lower in all plots in subsequent years, dropping to a mean of only 7.6% in the Kura Track plots in 2002/03.

Galls caused by *P. alani* on mist flower were first recorded quantitatively at the Karamatura Valley release sites in March 2001, two months after adult flies had been released. The number of galls per mist flower stem

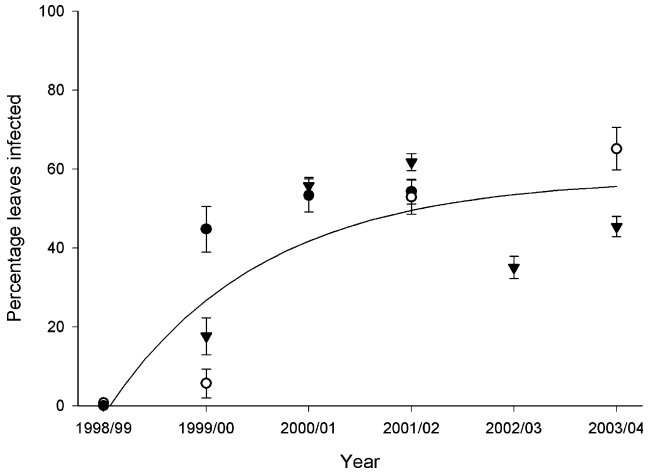


Fig. 3. Mean percentage of live leaves infected with mist flower fungus in the intensive study (○), extensive study (●) and mist flower vegetation change study (▼). An asymptotic model provided a good fit to the data ($R^2 = 0.59$, $P < 0.001$). Error bars = SEM. See text for further details.

increased exponentially over the next two years, quickly surpassing the mean 0.46 galls/stem reported in a 3-year study from three sites in Hawai'i, where the gall fly was considered to have contributed to the successful suppression of mist flower (Fig. 4, Hawai'ian data extracted from Hapai (1977)). On the last sampling occasion at the Karamatura Valley sites in May 2003, the mean galls per stem had reached 1.96, or 44.7 per 0.25-$m^2$ quadrat. No galls were recorded from the extensive study sites at any sampling date, which was not surprising as there were no gall fly release sites within 1 km of any of these nine sites, and sampling of these sites ceased in 2001/02. Galls were first recorded in the intensive study and vegetation change plots in October–November 2001 and December–January 2001/

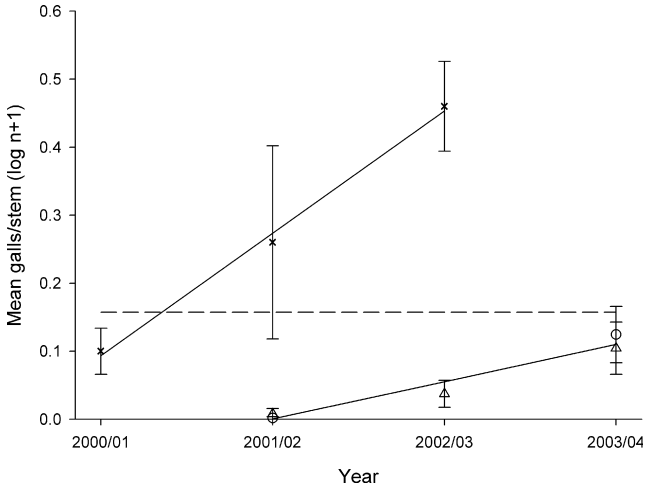


Fig. 4. Mean numbers of galls of *P. alani* recorded at release sites in the Karamatura Valley (×), in intensive study plots (○) and in the vegetation change plots (△). The horizontal dashed line is the mean galls/stem measured in Hawai'i (see text for more details). The illustrative trend lines are from linear regressions through the means. One line was used for the means for the intensive and vegetation change studies as they were not significantly different. Error bars = SEM.

02, respectively. There was a highly significant increase in gall numbers over time both in the Karamatura Valley sites (Fig. 4; $F_{(1,16)} = 15.29$, $P = 0.001$) and in the intensive and vegetation change studies (Fig. 4; $F_{(1,74)} = 15.31$, $P < 0.001$). The rate of increase in gall numbers was not significantly different in the intensive and vegetation change studies, but it was significantly faster at the Karamatura sites (Fig. 4; $F_{(2,88)} = 4.58$, $P = 0.013$), probably because of unknown differences between the sites, years or a combination of both.

The mean height of the tallest mist flower plant in each plot, although rather variable over time, showed a marginally statistically significant overall decline from 1998/99 to 2003/04 (Fig. 5; $F_{(1,174)} = 3.96$, $P = 0.048$). However, when the three different studies were compared, it was clear that the data for the intensive study showed no significant trend (slope $= -0.19$, $t_{172} = 0.08$, 172, $P = 0.94$), the data for the extensive study approached statistical significance (slope $= -15.46$, $t_{172} = 1.81$, $P = 0.07$), and it was only in the vegetation change plots that there was a highly significant decrease in the mean height of the tallest mist flower plant (slope $= -12.08$, $t_{172} = 5.37$, $P < 0.001$). There is no obvious explanation for these differences. Given the variability in the overall data, the separate lines for each study have not been used in Fig. 5, and instead an overall regression line through the means of all three studies was used for illustrative purposes.

In 1998/99, mist flower was found in 20 of the 110 plots distributed along 7 of the 11 walking tracks in the intensive study in the Waitakere Ranges. The weed was recorded outside the plots in the remaining four tracks. Mist flower was recorded from the same 20 plots in 1999/2000 as in 1998/99 (the first year of sampling), but also in an additional two plots where it had apparently been absent in 1998/99. From 2000/01 onwards there were eight instances where mist flower apparently disappeared from plots, but also three examples where the weed was re-recorded in plots, and one example of the plant being recorded for the first time in a new plot. Mist flower was still present at the end of the study at all the release site plots, and in all the plots along the Pipeline Track. However, there was a dramatic, and highly significant, overall reduction in the mean percentage cover of mist flower (Fig. 6; $F_{(1,151)} = 54.29$, $P < 0.0001$). There was only one consecutive year (1998/99 to 1999/2000) in one set of plots (intensive study) where mean percentage cover of mist flower increased. This first year in the intensive study was the only date in all three study types where sampling was undertaken before the release of the mist flower fungus. This increase in percentage cover of mist flower was consistent with the view that the weed was still expanding in density prior to the biological control program starting (Anonymous, 1999), and hence the data from this first year were excluded from the analysis. After this first year, the fungus proceeded to colonize the plots in the intensive study: by 1999/2000, the fungus was found in four of the 22 plots with mist flower present. By the following year, 2000/01, the fungus was recorded in all plots in the intensive study that had mist flower present.

When the three different studies were examined, it was clear that although the percentage cover of mist flower in the intensive study decreased from 1999/2000 to 2003/04, the trend failed to reach statistical significance in the analysis using the mixed effects models (Fig. 6; Slope $= -1.31$, $t_{198} = 1.22$, $P = 0.22$). This was caused by the high proportion of plots at the start of the study where the percentage cover of mist flower was very low: In 1999/2000 mist flower cover was <2% in 13 of the 23 plots where mist flower was present at any time during the study, and cover exceeded 10% in only four plots. However, by the end of the study, percentage cover of mist flower had dropped in 22 of the 23 plots, with the highest cover in a plot only reaching 5.4%, and with 18 of the 23 plots with <1% cover. Overall the mean cover data for the 23 plots were 4.41% in 1998/99,

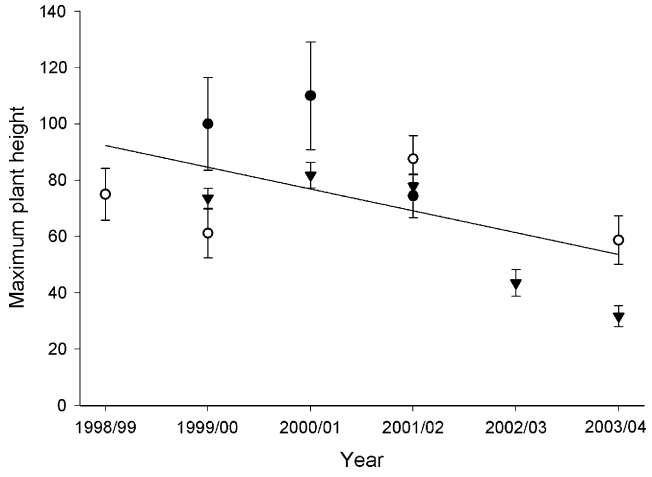


Fig. 5. The maximum height (cm) of mist flower plants recorded in the intensive study (○), extensive study (●) and vegetation change study (▼). The decline over time was significant ($P < 0.05$). Error bars = SEM.

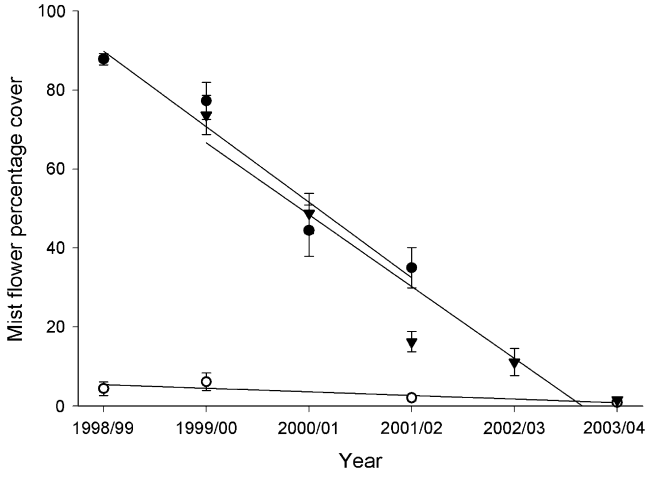


Fig. 6. The percentage cover of mist flower in the intensive study (○), extensive study (●) and vegetation change study (▼). A mixed effects model showed a significant decrease in the percentage cover of mist flower with time ($P < 0.0001$). Error bars = SEM.

6.12% in 1999/2000, 2.08% in 2001/2002 and 0.86% in 2003/04. Thus, there was a drop in mean percentage cover of mist flower of 85.9% over the period when the fungus was impacting on the weed (1999/2000 to 2003/04). A simple non-parametric sign test between the data from 1999/2000 and 2003/04 showed that percentage cover declined significantly between these years (declines in 22 of the 23 plots, $P < 0.001$, two-tailed sign test). In contrast, the trends for reducing percentage cover of mist flower in the extensive and vegetation change studies in Fig. 6 were statistically highly significant in the mixed effect model (extensive study; slope $= -19.11$, $t_{198} = 8.75$, $P < 0.001$: vegetation change study; slope $= -18.27$, $t_{198} = 17.45$, $P < 0.001$) and not significantly different from each other ($t_{198} = 0.85$, $P = 0.73$).

The mean percentage cover of mist flower in the intensive study in 1998/99 or 1999/2000 was clearly much lower than at the start of the extensive or vegetation change studies (Fig. 6). When the intercepts of the three lines were compared, the intensive study was highly significantly lower than either of the other two studies ($P < 0.001$ in both comparisons). This difference occurred simply because the release sites in the extensive study and the quadrats (containing mist flower) along the Pipeline and Kura Tracks (in the vegetation change plots) were all selected to have high percentage cover of the weed, whereas the sites along the tracks in the intensive study were randomly selected. In the intensive study, plots where mist flower was not recorded at all from 1998/99 to 2003/04 were excluded from this analysis, as the large number of zeros would have further obscured the trend in plots with mist flower infestations.

### 3.3. Changes in native and exotic vegetation as mist flower was suppressed

A total of 122 species or RTUs of native plants and 26 of exotic plants (excluding mist flower) were recorded in the vegetation change study plots along the Pipeline and Kura tracks from 1999/2000 until 2003/04. All species or RTUs recorded in 10% or more of the plots over the study, or with a maximum percentage cover of 10% or more in any plot, are listed in Table 2. The most frequent plant species was the endemic palm *Rhopalostylis sapida* H. Wendl. and Drude, which was recorded in nearly 90% of plots over the study period (with a maximum percentage cover of 70%). The highest percentage cover in any plot reached by a native plant species (80%) was by *Elatostema rugosum* A.Cunn, which typically forms dense, almost monospecific, stands in moderately shaded, damp areas in native forest such as the Waitakere Ranges. A wide range of native, mid-successional woody shrubs and small trees were commonly recorded, including *Geniostoma rupestre* J.R. Forst and G. Forst (73.1% of plots), *Coprosma arborea* Kirk (42.5% of plots), *Coprosma grandifolia* Hook.f. (40.0% of plots) and *Myrsine australis* (A.Rich.) Allan (38.8% of plots). The important native mid-successional small tree, *Kunzea ericoides* (A.Rich.) Joy Thomps., reached a maximum percentage cover of 70% and occurred in 21.3% of plots. The most frequent canopy tree species were *Dacrycarpus dacrydioides* (A.Rich.) de Laub., *Knightia excelsa* R.Br. and *Hoheria populnea* A.Cunn which were each recorded in 30–40% of plots. Other significant native tree species recorded from the plots but not listed in Table 2 because they were below the 10% frequency or cover thresholds, included *Fuchsia excorticata* (J.R. Forst and G. Forst) L.f. (Kōtukutuku, Onagraceae), *Cordyline banksii* Hook.f. (cabbage tree, Agavaceae), *Metrosideros fulgens* Sol. ex Gaertn. (rātā, Myrtaceae), *Prumnopitys ferruginea* (D.Don) de Laub. (miro, Podocarpaceae), *Dacrydium cupressinum* Lamb. (rimu, Podocarpaceae), *Podocarpus totara* G.Benn. ex D.Don (tōtara, Podocarpaceae), *Agathis australis* (D.Don) Lindl. (kauri, Araucariaceae), and *Phyllocladus trichomanoides* D.Don (tānekaha, Phyllocladaceae).

The most frequent exotic plant species, recorded in 58.8% of plots, was the African club moss, *Selaginella kraussiana* (Kunze) A. Braun, which also reached a maximum percentage cover of 90%. This was only just below the maximum percentage cover of 95% recorded for mist flower. Hence *S. kraussiana* was subjected to separate analyses described at the end of this section. All the other exotic plant species listed in Table 2 are low-growing herbaceous plants or grasses, with the exception of *Ulex europaeus* L. and *Rubus fruticosus* L., neither of which are considered to be major weeds that could interfere with natural succession in recovering secondary-growth forest that is predominant in the Waitakere Ranges. Other weed species that were relatively infrequent (<10% of plots), but that occurred at relatively high levels of maximum percentage cover, were *Vinca major* L. (greater periwinkle, maximum cover 35%) and *Erigeron karvinskianus* DC. (Mexican daisy, maximum cover 15%). The only other exotic plant species or RTUs recorded that are weeds or potential weeds in regenerating forest were *Cortaderia jubata* (Lemoine) Stapf (pampas grass, Poaceae), *Paraserianthes lophantha* (Willd.) I.C.Nielsen (brush wattle, Mimosaceae), *Hakea* sp. (needle bush, Proteaceae) and *Salix fragilis* L. (crack willow, Salicaeae), all of which were uncommon (maximum percentage cover <0.5%).

Given that mist flower percentage cover ranged from zero (in the control plots) to a maximum of 95% in the paired mist-flower-present plots, it was not surprising that there was a highly significant negative relationship between native species richness and percentage cover of mist flower at the start of the study (Fig. 7; slope $= -0.09$, $t_{18} = 4.22$, $P < 0.001$). However, this relationship became non-significant by 2000/01 onwards as mist flower percentage cover declined.

The mean species richness data from the mist-flower-present and paired control plots over the 5-year study are presented in Fig. 8. Initially (as expected from Fig. 7) there is lower native species richness in the plots with mist flower present compared with the control plots. Overall, the reduced species richness of native species on the mist-flower-present plots was statistically significant (Fig. 8a;

Table 2
Plant species or recognizable taxonomic units (RTU) recorded in the study in 10% or more of the study plots or at maximum percentage cover of 10% or more in any plot

| Scientific name/ RTU | Māori or English name | Family | Plant type | Percentage of plots with species or RTU | Max percentage cover in a plot |
|---|---|---|---|---|---|
| *Rhopalostylis sapida* H. Wendl. and Drude | Nikau | Arecaceae | Palm | 89.4 | 70 |
| *Oplismenus hirtellus* (L.) P.Beauv. | | Poaceae | Grass | 75.0 | 10.5 |
| *Geniostoma rupestre* J.R. Forst and G. Forst | Hangehange | Loganiaceae | Shrub | 73.1 | 20 |
| *Carex* spp. | | Cyperaceae | Sedge | 61.3 | 40 |
| *Selaginella kraussiana* (Kunze) A.Braun[a] | African club moss | Selaginellaceae | Club moss | 58.8 | 90 |
| *Blechnum novae-zelandiae* T.C. Chambers and P.A. Farrant | Kiokio | Blechnaceae | Fern | 45.0 | 65 |
| *Hedycarya arborea* J.R. Forst and G. Forst | Porokaiwhiri, pigeonwood | Monimiaceae | Tree | 43.1 | 8 |
| *Centella uniflora* (Col.) | | Umbelliferae | herb | 42.5 | 20 |
| *Coprosma arborea* Kirk | Māmāngi | Rubiaceae | Shrub | 42.5 | 9 |
| *Coprosma grandifolia* Hook.f. | Kanono | Rubiaceae | Shrub | 40.0 | 18 |
| *Myrsine australis* (A. Rich.) Allan | Māpou | Myrsinaceae | Shrub | 38.8 | 7 |
| *Dacrycarpus dacrydioides* (A. Rich.) de Laub. | Kahikatea | Podocarpaceae | Tree | 38.1 | 5 |
| *Knightia excelsa* R. Br. | Rewarewa | Proteaceae | Tree | 36.3 | 4 |
| *Hoheria populnea* A. Cunn | Hohere, lacebark | Malvaceae | Tree | 34.4 | 25 |
| *Lotus pedunculatus* Cav.[a] | Birdsfoot trefoil | Fabaceae | Herb | 28.8 | 20 |
| *Prunella vulgaris* L.[a] | Self-heal | Lamiaceae | Herb | 27.5 | 5 |
| *Doodia media* R.Br. | Pukupuku | Blechnaceae | Fern | 25.0 | 60 |
| *Gahnia* sp. | Cutty grass | Cyperaceae | Sedge | 24.4 | 40 |
| *Melicytus ramiflorus* J.R. Forst and G. Forst | Māhoe, whiteywood | Violaceae | Tree | 24.4 | 30 |
| *Carpodetus serratus* J.R. et G. Forst | putaputawētā, Marbleleaf | Grossulariaceae | Tree | 22.5 | 8 |
| *Pseudopanax crassifolius* (Sol. ex A.Cunn) Koch | Horoeka, lancewood | Araliaceae | Tree | 22.5 | 5 |
| *Coprosma rhamnoides* A. Cunn | | Rubiaceae | Shrub | 21.9 | 12 |
| *Kunzea ericoides* (A. Rich.) Joy Thomps | Kanuka | Myrtaceae | Tree | 21.3 | 70 |
| *Macropiper excelsum* (G. Forst) Miq. | Kawakawa | Piperaceae | Shrub | 17.5 | 10 |
| *Ulex europeaus* L.[a] | Gorse | Fabaceae | Shrub | 16.9 | 4 |
| *Pratia angulata* (G. Forst) Hook.f. | Pānakenake | Campanulaceae | Herb | 15.6 | 2.5 |
| *Anthoxanthum odoratum* L.[a] | Sweet vernal | Poaceae | Grass | 15.0 | 10 |
| *Cyathea dealbata* (G.Forst) Sw. | Ponga | Cyatheaceae | Tree fern | 14.4 | 30 |
| *Ptychomnion aciculare* (Brid.) Mitt. | | Ptychomniaceae | Moss | 14.4 | 55 |
| *Coprosma spathulata* A. Cunn | | Rubiaceae | Shrub | 13.8 | 5 |
| *Sophora chathamica* Cockayne | Kowhai | Fabaceae | Tree | 13.8 | 10 |
| *Breutelia pendula* (Sm.) Mitt. | | Bartramiaceae | Moss | 13.1 | 40 |
| *Coprosma robusta* Raoul | Karamū | Rubiaceae | Shrub | 13.1 | 12 |
| Liverwort (unidentified) | | | Liverwort | 13.1 | 20 |
| *Rubus fruticosus* L.[a] | Blackberry | Rosaceae | Climber | 11.3 | 7 |
| *Hypnodendron* spp. | Umbrella moss | Hypnodendraceae | Moss | 25.0 | 25 |
| *Paesia scaberula* (A. Rich.) Kuhn | Mātātā | Dennstaedtiaceae | Fern | 10.6 | 6 |
| *Pteris* sp. | Brake fern | Pteridaceae | Fern | 10.6 | 10 |
| *Uncinia* sp. | Hook grass | Cyperaceae | Sedge | 17.5 | 10 |
| *Hebe* spp. | | Scrophulariaceae | Shrub | 10.0 | 5 |
| *Leucopogon fasciculatus* (G. Forst) A. Rich. | Mingimingi | Epacridaceae | Shrub | 10.0 | 4 |
| *Oxalis* sp.[a] | Wood sorrel | Oxalidaceae | Herb | 10.0 | 1 |
| *Elatostema rugosum* A. Cunn | Parataniwha | Urticaceae | Herb | 3.1 | 80 |
| *Rhabdothamnus solandri* A. Cunn | | Gesneriaceae | Shrub | 6.3 | 35 |
| *Vinca major* L.[a] | Greater periwinkle | Apocynaceae | Herb | 3.8 | 35 |
| *Hypopterygium rotulatum* (Hedw.) Brid. | | Hypopterygiaceae | Moss | 3.1 | 25 |
| *Cyathea medullaris* (G. Forst) Sw. | Mamaku | Cyatheaceae | Tree fern | 1.9 | 20 |
| *Asplenium bulbiferum* Forst f. Prodr. | Mouku | Aspleniaceae | Fern | 5.6 | 15 |
| *Erigeron karvinskianus* DC.[a] | Mexican daisy | Asteraceae | Herb | 3.1 | 15 |
| *Microlaena avenacea* (Raoul) Hook.f. | Bush rice grass | Poaceae | Grass | 1.9 | 15 |
| *Melicytus novae-zelandiae* (A.Cunn) P.S. Green | Māhoe, whiteywood | Violaceae | Tree | 3.1 | 12 |
| *Cyperus* sp.[a] | | Cyperaceae | Sedge | 3.8 | 10 |

[a] Species non-native to New Zealand.

$F_{(1,18)} = 6.50$, $P = 0.02$), but more important is the significant mist flower × year interaction (Fig. 8a; $F_{(1,78)} = 6.19$, $P = 0.02$). This shows that the species richness of native plants in the plots where mist flower is in decline (mist flower present) becomes increasingly similar over the study period to the native species richness in the control plots (mist flower absent). Most of this effect is due to the increase in native species richness (from a mean of 10.4 in

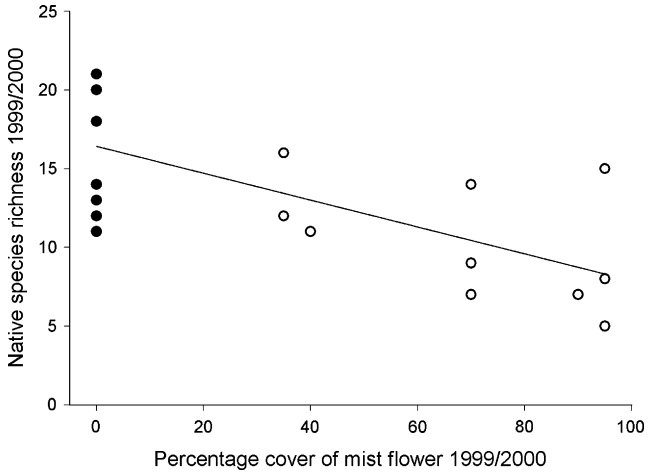


Fig. 7. The relationship of native species richness to the percentage cover of mist flower in 1999/2000. Plots with a higher percentage cover of mist flower at the start of the vegetation change study in 1999/2000 had fewer species of native plants ($P < 0.001$). Control plots had no mist flower (●) whereas plots with mist flower present (○) had 35–95% cover of the weed.

1999/2000 to 13.5 in 2003/04) in plots that initially had abundant mist flower. However, there was also a small reduction in the native species richness (from a mean of 16.6 in 1999/2000 to 15.3 in 2003/04) in the control plots over time (Fig. 8a).

The species richness of exotic plants in the plots was much lower (mean per plot type in each year ranging from 2.1 to 3.3) than that of native species (range from 10.4 to 16.5). These figures and the subsequent analysis exclude mist flower itself. There was no significant difference between the exotic plant species richness in plots with mist flower present or absent from 1999 to 2003 (Fig. 8b; $F_{(1,18)=}0.18$, $P = 0.68$). There was a small, but highly statistically significant, reduction in the species richness of exotic plants in both plot types over the same time period (Fig. 8b; $F_{(1,78)} = 12.60$, $P < 0.001$). The mist flower × year interaction was not significant for exotic plant species richness (Fig. 8b; $F_{(1,78)} = 0.001$, $P = 0.97$). With the very low species richness of exotic plants in the study, these significant reductions only represent changes in average species richness of exotic plants from 3.2 to 2.1 in control plots, and 3.3–2.4 in plots where mist flower was present but declining.

The mean percentage cover of native species in the mist flower present and paired control plots from 2000/01 to 2003/04 is presented in Fig. 9a. Initially there was lower native species percentage cover in the plots with mist flower compared with the plots without mist flower. Overall, the reduced percentage cover of native species on the mist-flower-present plots compared to the control plots approached statistical significance (Fig. 9a; $F_{(1,18)} = 3.63$, $P = 0.07$), but more important is the significant mist flower × year interaction ($F_{(1,58)} = 5.55$, $P = 0.02$). This shows that the percent cover of native plants in the plots where mist flower is in decline (mist flower present) becomes increasingly similar to the percentage cover of native species in the control plots. Although the percentage cover of native

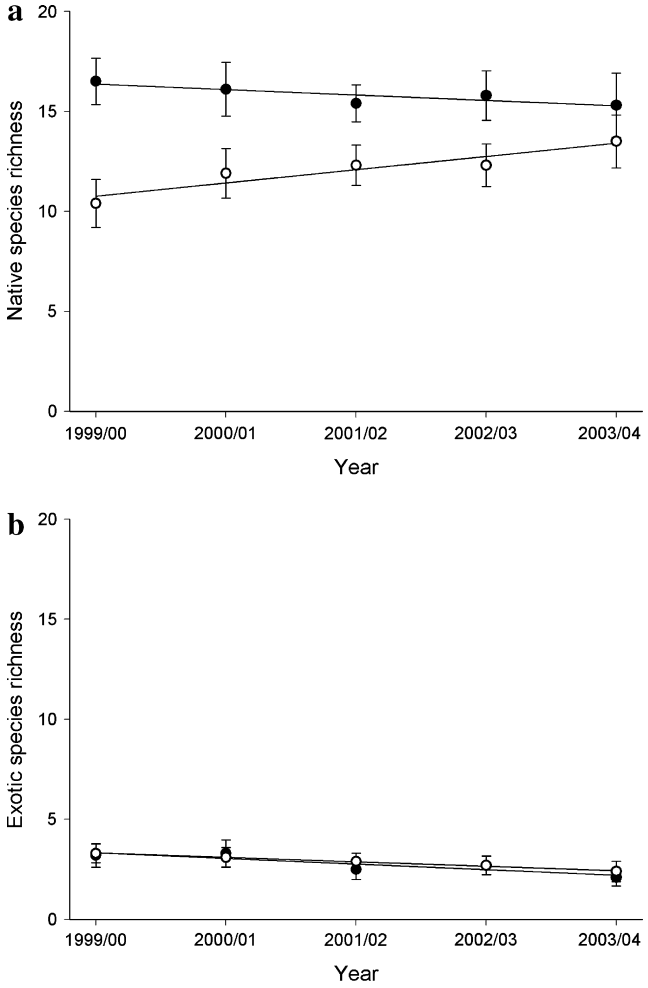


Fig. 8. Mean species richness of native (a) and exotic (b) plant species in control plots without mist flower (●) and in paired plots where mist flower was initially present (○). As mist flower declined in percent cover from 1999/2000 to 2003/04 (see Fig. 6), the species richness of native plants in the two plot types became gradually more similar (Fig. 8a, interaction term $P < 0.05$). This change in percentage cover of mist flower did not have any effect on the species richness of exotic plants (Fig. 8b). Illustrative trend lines are from regressions through means. Error bars = SEM.

species increases in both plot types from 2000/01 to 2003/04, the important effect is that it increases at a significantly faster rate in the plots where mist flower was initially present but is in decline, compared with the control plots where mist flower was absent. There were also highly significant differences in percentage cover throughout the observation period (Fig. 9a; $F_{(1,58)} = 18.82$, $P < 0.001$). The mean percentage cover of exotic plant species in the mist-flower-present and control plots showed no significant trends (Fig. 9b; $P > 0.1$) for mist flower, year, and mist flower × year interaction.

The mean percentage cover of native plant species ranged from 33.4 to 68.1% which, in any plot type and year, was almost always higher than the percentage cover of exotic plant species, which varied from 18.8 to 55.6%. The contrast between these mean percentage cover data and the mean species richness is interesting: mean species richness

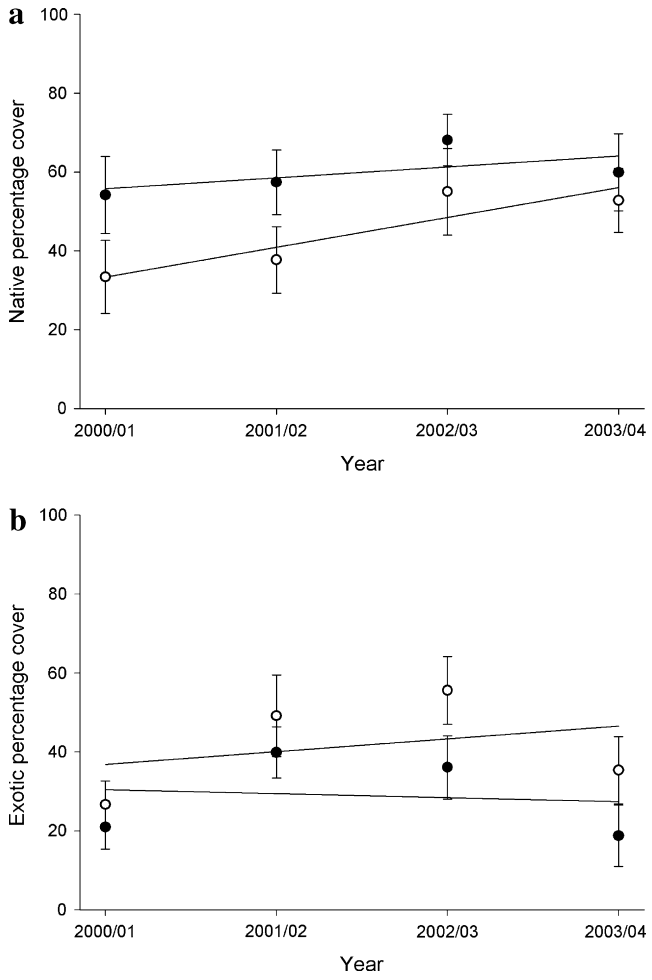


Fig. 9. Percentage cover of native species (a) and exotic species (b) in plots with mist flower initially present (○) compared with paired control plots without mist flower (●). Illustrative trend lines are from regressions through means. Error bars = SEM.

of native plants was usually around four times higher than the mean species richness of exotic plants (Fig. 8a and b), whereas the equivalent data for mean percentage cover were much more similar (Fig. 9a and b). Put another way, it seems that the relatively few exotic plant species recorded in the plots are achieving a comparatively high percentage cover in comparison to the more-species-rich native plants.

Further examination of the exotic species shows that the majority of the mean percentage cover of exotics is provided by just one species, African club moss *S. kraussiana*. For example, the overall mean percentage cover for exotic species over all plots and years is 35.3%, and the same figure for *S. kraussiana* alone is 31.5%. Consequently, data for *S. kraussiana* were extracted and subjected to further analyses. In the first of these extra analyses we checked to see whether the percentage cover of *S. kraussiana* was negatively correlated with the species richness of native plants, in a similar way to mist flower as shown in Fig 7. From 1999/2000 to 2002/03, there was no relationship between native species richness and percentage cover of *S. kraussiana* in either the mist-flower-present or paired control plots. However, by 2003/04 a significant trend had emerged, with lower native species richness in plots with higher percentage cover of *S. kraussiana* (Fig. 10; slope = −0.10, $t_{18} = 2.43$, $P = 0.03$).

This is a very similar trend to that demonstrated for mist flower in 1999/2000 (Fig. 7) and could indicate that *S. kraussiana* has simply replaced mist flower in terms of its effect on native species richness. However, the crucial difference is that *S. kraussiana* invaded the paired control plots (open symbols in Fig. 10) as well as the plots where mist flower was present but declining (closed symbols in Fig. 10). In fact the plot with the highest percentage cover of *S. kraussiana* (Fig. 10; 70%) in 2003/04 was a control plot. If there was a tendency for *S. kraussiana* percentage cover to increase to replace declining mist flower, i.e. the commonly suggested "replacement" weed problem with successful biological control, then plots with relatively high percentage of mist flower cover at the start of the study should have higher percentage cover of *S. kraussiana* by the end of the study. There is indeed such an effect (Fig. 11; slope = 0.25, $t_{18} = 2.08$, $P = 0.05$) but it is only weakly positive and not quite statistically significant. In earlier years, the same relationship does not even approach statistical significance (*S. kraussiana* percentage cover data from 1999/2000 to 2002/03, plotted against mist flower percentage cover in 1999/2000, all with $P > 0.1$).

## 4. Discussion

Both biocontrol agents released against mist flower in New Zealand established well, and the first to be released, the white smut fungus (*E. ageratinae*), spread particularly rapidly and thoroughly across apparently all of the North Island where its host plant occurs. This confirmed predictions on the geographic extent of spread, based on comparing climate data from montane Hawai'i with northern New

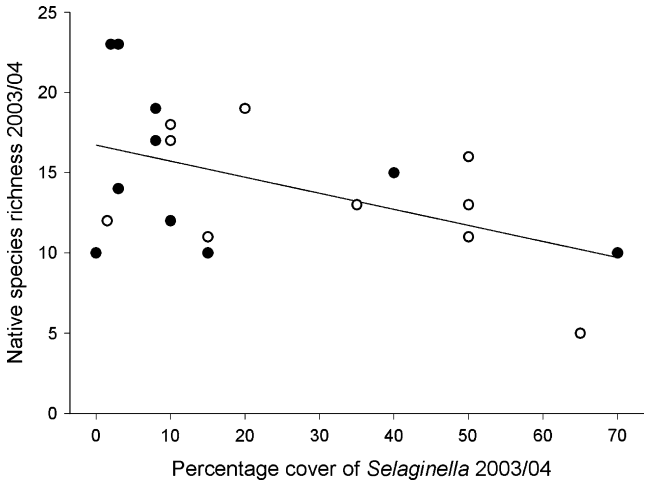


Fig. 10. The relationship between native species richness and percentage cover of *Selaginella kraussiana* that occurred by 2003/04 in the paired mist-flower-present (○) and control (●) plots. Regression line is significant, ($P = 0.03$).

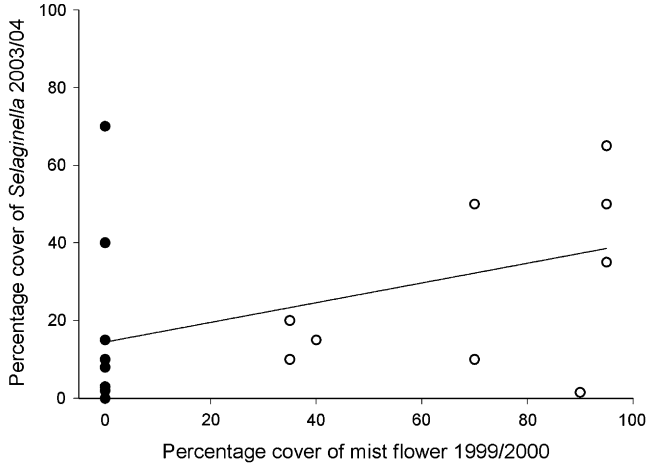


Fig. 11. The weak positive relationship between percentage cover of *Selaginella kraussiana* at the end of the study in 2003, and that of mist flower in plots with mist flower (○) or without mist flower (●), at the start of the study in 1999 (regression line, $P = 0.05$).

Zealand (Morin et al., 1997). We assume the fungus was mostly dispersed via its wind-blown conidia, although on occasions its first occurrences on plants overhanging walking tracks suggested that some dispersal may have occurred via humans and other animals. A gall fly, *Procecidochares utilis* Stone, which is congeneric with the mist flower gall fly, can vector the leaf spot fungus *Cercospora eupatorii* Peck (Dodd, 1961). We have no information on whether the mist flower gall fly can vector the mist flower fungus, but given the rapid spread of the fungus throughout much of North Island before the gall fly was released, any vectoring will only be improving on an already effective dispersal system.

A "snapshot" of the fungal infection levels, measured once each year at a range of sites, showed rapid increases at first, with the mean percentage of live leaves infected leveling off at around 58%. This measure will normally underestimate the effect of the fungus, because many leaves would already be dead as a result of the fungal infection. However, the percentages of attached leaves that were dead were variable across plots and years. This is almost certainly because once dead, mist flower leaves can rapidly fall off the plant if conditions are rainy or windy, with the result that counts of attached dead leaves will often underestimate leaf mortality substantially. The link between the damage caused by the mist flower fungus and the dramatic reduction in the percentage cover of the weed is only correlative in this study. The extremely rapid spread and impact of the fungus made it impossible to randomize and compare sites where the fungus was deliberately released and established with paired control sites. However, glasshouse trials were undertaken to quantify the damage the two agents could inflict on mist flower both independently and together (S.G. Casonato, HortResearch New Zealand, unpublished data) and chemical exclusion studies in the field have also been completed and will be reported in a later paper (S.G. Casonato, personal communication). The glasshouse trials demonstrated that both biocontrol agents are capable of causing significant reduction in the growth of mist flower plants, either together or alone (S.G. Casonato, unpublished data).

The rapidity of mist flower decline can probably be partially attributed to the relatively warm maritime climate in northern New Zealand, allowing the fungus to have many generations per year. The dramatic reduction in the percentage cover of mist flower infestations at all study sites in the 4–5 years after the release of the mist flower fungus, and the high levels of infection of leaves, are consistent with biological control being highly successful. This interpretation also matches results in Hawai'i where the fungus has made a major contribution to the successful biological control of mist flower (Trujillo, 1985). Reports from South Africa, the other country where the mist flower fungus has been released, are more mixed, ranging from reports of severe defoliation (Julien and Griffiths, 1998) to negligible control achieved (Olckers, 2004). This may be a genuine difference resulting from variation in factors such as climate, or might reflect a lack of monitoring in South Africa of emerging weeds such as mist flower, as opposed to already widespread and damaging weeds (Olckers, 2004).

In New Zealand, the gall fly may enhance the impact of the fungus but it did not reach high enough average levels of infestation during this study to be contributing significantly to the reductions in percentage cover of mist flower. However, in isolated cases the levels of galling were high, with up to eight galls being present on one plant. There were also high mean gall numbers close to the earliest release sites in the Karamatura Valley. After 3 years these numbers had exceeded the average numbers of galls per stem reported from Hawai'i, where the gall fly was considered to have contributed to the successful suppression of mist flower. Hence, we suspect that the gall fly may yet contribute to the suppression of mist flower in New Zealand. At present it seems that additional agents, e.g., the plume moth *O. beneficus* which was released in Hawai'i, will not be needed for suppression of mist flower in New Zealand. However, given the slower rate of spread of the gall fly compared with the fungus, it may be worthwhile to make further releases of the gall fly in new areas especially if mist flower infestations are patchy and distant from existing release sites.

There was considerable variability in the measured levels of infestation by the fungus and the gall fly between sites and years. This could be genuine site and year differences, or could simply be caused by the fact our sampling at any given site was just on one date, which inevitably varied by a few days or weeks each year. We did expect there to be differences in level of attack by the two agents between sites and between different seasons/years. For example, part of the rationale for releasing the gall fly was we expected it to complement the action of the fungus, which we thought might be most effective in more humid sites/seasons/years. The glasshouse and field trials mentioned above examined the interactions between the two agents, as well as their

direct impacts on the plant (S.G. Casonato, unpublished data).

Although we chose walking tracks in one range of hills for most of our monitoring studies, the reductions in percentage cover of mist flower also occurred at all the release sites, which were geographically spread over a range of habitats in the entire range of the weed in the Auckland and Northland regions of New Zealand. During the study, no other management of mist flower was undertaken in any of the study areas. Furthermore, based on informal contacts with regional councils and the Department of Conservation, it does not appear that there has been any need for other control measures (e.g., herbicide applications) against mist flower in New Zealand since the end of this study in 2003/04.

At the time this program was instigated mist flower was thought to be spreading rapidly into suitable habitats in northern North Island. Unfortunately, the 1998/99 data in the intensive study plots in the Waitakere Ranges are the only pre-biocontrol mist flower data we have. The increase in percentage cover of mist flower and in the proportion of plots occupied from 1998/99 to 1999/2000 is consistent with the view that mist flower was still spreading rapidly prior to the release of the mist flower fungus. There were no other occasions in the entire study when average percentage cover of the plant increased between years. However, there were a few other occasions when mist flower appeared for apparently the first time in plots. Some of these apparent appearances and disappearances of the weed from plots could be a result of sampling error; others may be the result of the germination of mist flower seed arriving from outside of plots, or already present in a seed bank. In cases where new seedlings have germinated, these are likely to quickly succumb to the fungus. The overall trend of increasing cases where the weed disappeared from plots in which it was becoming relatively rare is consistent with the increasing action of highly effective biocontrol agents. It appears that successful biological control may cause local extinction of mist flower, but conversely we would also expect the plant to continue to disperse into optimal habitats in areas of northern New Zealand where it has not yet reached. Given the consistent pattern of reduced percentage cover of mist flower in this study we would not expect new infestations to reach levels where substantial damage to the native flora would occur. For example, we would expect mist flower to spread further in the Waitakere Ranges, and become a minor component of the flora in all intermittently disturbed riparian areas.

A key question, which is seldom addressed in weed control programs, is what are the consequences of a decline in the weed for other native or exotic plant species (Denslow and D'Antonio, 2005; Syrett et al., 2000)? We studied this by comparing plots with high levels of mist flower cover with nearby paired control plots with no mist flower (but that contained habitat that appeared ideal for invasion by mist flower). The results were dramatic: there was an increase in species richness and percentage cover of native plant species in plots where mist flower was declining in percentage cover. There was no detectable response in species richness or percentage cover of exotic plant species. It was particularly encouraging that, by the end of the study in 2003/04, the mean native species richness of plots with declining mist flower had recovered to very nearly the mean level in the control plots. Another positive result in the percentage cover data is that in the plots where mist flower was present, but declining in cover, the overall cover by other species increased markedly, so that by the end of the study, the area of ground covered by species other than mist flower was similar in the two plot types (77.2% in plots without mist flower vs. 88.2% in plots with mist flower). This demonstrates that the activities of the biocontrol agents did not lead to the development of bare ground.

The fact that new exotic species appear not to be able to exploit the reduction in mist flower cover was probably because the Waitakere Ranges are mostly dominated by native species, so propagule pressure from new exotic plant species in these plots was probably very low. The small decline in native species richness in the control plots (without mist flower) and the similar decline in exotic species richness in both plot types, probably represents on going early succession, with smaller-stature native species being outcompeted and naturally self-thinning. This view is consistent with nearly 50% of the most common plant species in the plots listed in Table 2 being native trees or shrubs. The main vegetation in the Waitakere Ranges is regenerating secondary native forest, and the presence of mid- to late-successional species is vital to this continued natural restoration. Weeds that can disrupt this native succession, as mist flower appeared to be able to do, are thus of particular concern. In addition, mist flower had invaded the stream margins, where flooding causes intermittent natural disturbance, creating the habitat essential for a range of rare native plant species such as *H. acutiflora* (discussed further below).

Although there were far fewer exotic plant species than native plant species recorded in the study, the average percentage cover achieved by the exotic species was often rather similar to that achieved by the more-species-rich native plants. In fact the exotic flora in the plots, excluding mist flower, was dominated in terms of both percentage cover and plot occupancy by the invasive African clubmoss *S. kraussiana*. The only other exotic plant species listed in Table 2 that are of concern as potential weeds that could interfere with the regeneration of native forest species and/or invade naturally disturbed riparian habitats are the greater periwinkle (*Vinca major*) and the Mexican daisy (*Erigeron karvinskianus*). These species occurred only sporadically in the plots, but did reach maximum percentage cover levels of 35 and 15%, respectively. These data support the view that these are emerging weed species that need to be monitored and subjected to future management as necessary. In addition, several other exotic plants with potential to be weeds in native forests ecosystems were also recorded less frequently in the study, including the

Argentinean pampas grass (*C. jubata*), the Australian brush wattle (*P. lophantha*), the South African *Hakea* sp. and the European crack willow (*S. fragilis*).

*Selaginella kraussiana* was such a dominant feature of the exotic flora in our study that it was subjected to a separate analysis. Disturbingly, this showed that by the end of the study there was a negative relationship between the species richness of native plant species in the plots and percentage cover of *S. kraussiana*. In fact, this relationship was very similar to that of native species richness and percentage cover of mist flower at the start of the study. Although we had shown that native species appeared to be recovering after mist flower declined, was there also a problem with a replacement weed? The risk of control of a single weed species simply resulting in replacement by one or more other weed species is frequently seen as a potential problem with biological control, but there appear to be rather few documented cases of this phenomenon, or indeed of successful biological control resulting in the return of native plant species (Burdon et al., 1981; Campbell and McCaffrey, 1991; Denslow and D'Antonio, 2005; Doeleman, 1989; Huffaker, 1951; Huffaker and Kennett, 1959; Jayanth and Ganga Visalakshy, 1996). In the current study, while there is evidence that *S. kraussiana* is invading the plots, it is invading both the plots that initially had mist flower abundant *and* the control plots where mist flower was absent. There is a weak replacement weed effect, with a positive relationship between mist flower percentage cover at the start of the study with percentage cover by *S. kraussiana* at the end of the study, but it just failed to reach statistical significance (Fig. 11, $P = 0.05$). Although these trends are all correlations, it seems plausible that *S. kraussiana* is achieving higher percent cover in plots because the native species richness is lower. Furthermore, it is possible that the higher percentage cover of *S. kraussiana* then restricts the increase in native species richness in these plots over time. Experimentally manipulating the abundance of this invasive plant species, and measuring the resultant effects on native species richness, would be one way to test the causality in these correlations. At a wider level, Auckland Regional Council has been sufficiently concerned with the invasiveness of *S. kraussiana* that it has funded a feasibility study into its potential biological control (Barton, 2005).

Given that the vegetation change study was restricted to the Waitakere Ranges, to what extent can we generalize regarding the recovery of native or other exotic species after mist flower suppression in other areas of New Zealand? In at least one case, the suburban release site at Mt Eden in Auckland, it was visually obvious that, as mist flower declined, the main plant species that came to dominate the ground cover were exotic grasses and weeds such as Montpellier broom *Teline monspessulanus* (L.) K. Koch (Fabaceae), and tree privet *Ligustrum lucidum* W.T. Aiton (Oleaceae). Suburban Auckland is dominated by exotic plant species, and native plant species were not expected to benefit from mist flower suppression without active efforts at restoration planting. However, even at Mt Eden, there will have been benefits from the reduced use of herbicides for mist flower control in pasture on this important archeological/cultural site. Generally, the most important impacts of mist flower in New Zealand were in sites where it was suppressing native vegetation, of which the Waitakere Ranges were a good example. Indeed *H. bishopiana*, which was one of the specific examples of endemic New Zealand plant species threatened by mist flower mentioned in the introduction, is endemic to the Waitakere Ranges. *H. bishopiana* is still rated as "nationally vulnerable" (de Lange et al., 2004) but if further mist flower reduction continues, and pampas grass populations can also be reduced, then it may be removed from the "vulnerable" list altogether (de Lange, pers. comm.). The prognosis for the conservation of the other threatened species, *H. acutiflora*, has also improved: its ranking has now dropped to "range restricted," in part because mist flower infestations have declined to the point where they no longer threaten the plant (de Lange pers. comm.). Overall, it seems certain that the suppression of mist flower attributed to successful biological control has benefited native plants in many parts of the Northland and Auckland regions of New Zealand, including areas of very high conservation importance such as Puketi Forest (Best and Bellingham, 1991). This biological control program has been the most rapidly successful and intensively monitored in New Zealand to date, and is an excellent example of the benefits to the indigenous flora that can accrue from the suppression of even a single weed species.



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