Prerelease Assessment of Impact on Biomass Production of an Invasive Weed, Lygodium microphyllum (Lygodiaceae: Pteridophyta), by a Potential Biological Control Agent, Floracarus perrepae (Acariformes: Eriophyidae)

JOHN A. GOOLSBY,^{1,2} RYAN ZONNEVELD,³ AND ANNE BOURNE⁴

ABSTRACT A prerelease assessment of impact by a potential biological control agent, *Floracarus perrepae* Knihinicki and Boczek, on the invasive weed, *Lygodium microphyllum* (Cav.) R. Br., was conducted in a 2-yr field study in their native range—Australia. Thirty-two pairs of test plants were planted in a field plot with two levels of shade, with one plant in each pair treated biweekly with the miticide abamectin. The mite caused a significant reduction in biomass of above ground stems and leaves and below ground roots and rhizomes. The mean leaf longevity was significantly longer for the treated versus the mite infested untreated plants. Populations of native predator mites were low throughout the study; however, the mite pathogen *Hirsutella thompsonii* Fisher was common in the second year of the study, but neither reduced the impact of *F. perrepae*. Based on its potential to cause significant damage to *L. microphyllum* under field conditions in the native range and extremely narrow field host range, *F. perrepae* is an excellent candidate for biological control of this invasive fern in Florida.

KEY WORDS predictive studies, biological control weeds, Florida Everglades restoration

PREDICTING THE IMPACT OF natural enemies is an important but underdeveloped part of the science of biological control (Shea and Possingham 2000, Wratten and Gurr 2000). Assessment of potential impact caused by candidate agents is one of the tools that can be used in the prioritization and selection process in a biological control program. Prioritizing the agents that show the greatest potential to control the target organism could potentially minimize the numbers of species released in a program (Hoddle and Svrett 2002, Balciunas 2004). Limiting the number of species released may reduce risk to nontarget species and improve success (McEvoy and Coombs 1999, Strong and Pemberton 2001). These ideas are part of "The Code of Best Practices for Classical Biological Control of Weeds," which proposes that only agents with the potential to control the target should be selected (Balciunas 2000).

Few biological control programs have attempted to quantitatively assess the impact on plant biomass of a candidate biological control agent before release. Waloff and Richards (1977), in an 11-yr insecticidal exclusion study in Britain, showed that broom, Cytisus scoparius L. Link (=Sarothamnus scoparius), when protected from insect attack, outgrew plants exposed to the native insect fauna. Balciunas and Burrows (1993), also using chemical exclusion, showed a reduction in biomass of the sapling paperbark trees, Melaleuca quinquenervia (Cav.) S. T. Blake, by naturally occurring herbivores. Cage studies have also been used to show the impact of agents. Kleinjan et al. (2003), in greenhouse cage studies, measured the direct impact on the tuber biomass of bridal creeper, Asparagus asparagoides L., related to above-ground feeding by the cicadellid Zygina sp. This study was used in the prioritization process of the bridal creeper biological control program, which led to selection of this agent for release. Zugina sp. has become established, and initial reports of impact are positive (Batchelor and Woodburn 2002). Briese (1996) assessed the potential impact of the weevil, Lixus cardui Olivier, on the growth of the Onopordum spp. thistles using field cage studies. *Lixus cardui* was found to reduce plant height and biomass by up to 50%, and the plants produced 80% fewer viable seeds. Postrelease studies of L. cardui in Australia confirm the earlier predictions of impact (Swirepik and Smyth 2002). Field studies in the native range of the thistle, Carduus nutans L., were conducted to assess the impact of root-feeding insects (Sheppard et al. 1995). The studies showed that two weevils, Hadroplontus trimaculatus F. and Trichosirocalus horridus Panzer, mainly al-

Environ. Entomol. 33(4): 997-1002 (2004)

¹ USDA-ARS, Australian Biological Control Laboratory, CSIRO Long Pocket Laboratories, 120 Meiers Rd., Indooroopilly, Queensland 4068, Australia.

² E-mail: john.goolsby@csiro.au.

³ CSIRO Entomology, Australian Biological Control Laboratory, 120 Meiers Rd., Indooroopilly, Queensland 4068, Australia.

⁴ CSIRO Entomology, 120 Meiers Rd., Indooroopilly, Queensland 4068, Australia.

tered plant architecture, whereas the syrphid fly, *Cheilosa corydon* Harris, reduced seed production by 45%. Although *C. corydon* was prioritized in the biological control program, rearing difficulties in quarantine prevented further study of this potential agent.

In our study, the impact of a single species of a native herbivorous mite on its native host plant was measured in a field plot study before its release as a biological control agent. Although the study was conducted in the native range within close proximity to native stands, the plot itself was not a natural stand. We chose to create the study site to standardize plant size, provide optimal growing conditions, and avoid ethical concerns related to destructive sampling and chemical use in natural areas. The study was conducted for 2 yr to evaluate long-term impacts of the mite on the fern. These studies were intended to (1)confirm field observations that plant damage was caused by the mite, (2) measure the mite's impact on plant biomass production, and (3) make predictions about the mite's efficacy as a biological control agent.

The target weed in this study is Lygodium micro*phyllum* (Cav.) R. Br. (Lygodiaceae, Pteridophyta), the Old World climbing fern. It is native to the Old World wet tropics and subtropics of Africa, Asia, Australia, and Oceania (Pemberton 1998). It is an aggressive invasive weed in moist habitats of southern Florida (Pemberton and Ferriter 1998) and is classified as a Category I invasive species by the Florida Exotic Plant Pest Council (Langland and Craddock Burks 1998). Exploration for natural enemies of this weed was conducted between 1997 and 2002 in Australia, China, India, Indonesia, Malaysia, New Caledonia, Singapore, Taiwan, Thailand, and Vietnam. Two species of mites and 20 insect species were collected (Goolsby et al. 2003). The eriophyid mite, *Floracarus* perrepae Knihinicki and Boczek, was given the highest priority for further evaluation as a biological control agent. This was because of the fact that it was the most widely distributed of the herbivores and appeared, from field observations, to have a significant debilitating impact on the plant over time. Feeding by the adults and immatures causes formation of leaf roll galls, which leads to necrosis and defoliation of L. microphyllum pinnules, and seems to limit plant growth. Although the use of eriophyid mites in biological control of weeds shows great promise, several authors, including Briese and Cullen (2001), have stated that there are not yet any dramatic successes that can be attributed to the singular impact of an eriophyid. Bearing this in mind, we sought to measure the impact of F. perrepae on L. microphyllum in an experimental field setting in the native range.

Materials and Methods

The field study was conducted over two seasons from March 2001 to March 2003. A plot of land at Commonwealth Scientific and Industrial Research Organization Long Pocket Laboratories in Indooroopilly, Queensland (27°30.70' S and 152°59.81' E), measuring 30 m by 5 m, was used for the layout of 64 *L. micro*- phyllum test plants. Orientation of site length was approximately east to west and received full sun. The site was leveled before planting, and 30-liter pots were arranged in a grid with plant pot centers 1 m apart along the column and the columns 1.5 m apart. This used the available space and arranged the plant pots in a grid that was 3 columns by 22 rows. The plot was split into four blocks on the basis of different shading from adjacent buildings; each block had 16 pots. The plot was shaded with black shade cloth on a metalframed structure. Blocks 1-3 were covered with two layers of 25% shade cloth (heavy shade), overlaid to represent field light levels in Melaleuca quinquenervia swamp forests (J.A.G., unpublished data). Block 4 had only one layer of shade cloth (light shade). A trellis was constructed over each pot to allow for growth of the climbing fern. The trellis was constructed with 1.8-m-high tomato stakes and galvanized chicken wire. Each trellis was oriented north by south to allow for maximum sunlight capture. Each pot was drip irrigated and controlled by an electronic timer. The amount of water was adjusted by season to account for plant growth. A 100-mm-thick layer of pine bark mulch was used to top dress the entire site to keep weeds to a minimum.

Lygodium microphyllum plants with rhizomes 3–5 cm in length infested with *F. perrepae* were harvested from a native stand along Running Dog Creek, near Logan, Queensland (27°07.30' S and 152°58.50' E). Voucher specimens *L. microphyllum* and *F. perrepae* are lodged at the Queensland Herbarium, Brisbane, and Agricultural Scientific Collections Unit, Orange, New South Wales, respectively. The plants were placed in pots and allowed to grow for a period of 2 mo. From this collection, a subset of plants was identified for uniformity. Sixty-four *L. microphyllum* with uniform infestations of *F. perrepae* were ranked by size, and plants of approximately the same size were selected as pairs. Eight pairs of plants were allocated to each of four plots.

The *L. microphyllum* plants were transplanted into the 30-liter pots using a commercially available organic potting mix, with a ratio of 85 parts (1–10 mm composted pine bark) organic material to 15 parts medium grade washed river sand. Osmocote Plus Exact (Scotts Co., Marysville, OH) (15N-4P-7.5K + micronutrients) 5- to 6-mo slow release fertilizer was added at the time of planting. Five months after the start of the experiment, leaf samples were analyzed for nutrient levels and were compared with samples from field sites. Additional fertilizer was added to test plants on two occasions to maintain similar nutrient levels to natural stands. On 21 September 2001, each pot received a soluble fertilizer (Aquasol; 23N-4P-8K + micronutrients, Hortico Pty. Ltd., Homebush, Australia) and 5- to 6-mo slow release Osmocote Plus Exact, at label rates. In the second year of the study (16 August 2002), 10 g of isobutylidene diurea (IBDU; -31% N) was added to each pot. Weeds were removed regularly from the pot surface to reduce competition for nutrients and water.

of mites in leaf	curls by sample date	e ^a on untreated and	plants treated	with miticide

Untreated			Treated					
Date	Percentage leaves curled	Mean no. of adults and nymphs in curls	Mean no. of predator mites per curl	Percentage of curls with mite pathogen	Percentage leaves curled	Mean no. of adults and nymphs in curls	Mean no. of predator mites per curl	Percentage of curls with mite pathogen
6/01	84	71.0	0.03	0	10	1.5	0	0
10/01	69	51.4	0	0	1	0.5	0	0
12/01	92	69.1	0.04	0	30	12.8	0.01	0
3/02	38	27.2	0.09	10	7	2.0	0	0
6/02	65	15.5	0.26	50	15	2.0	0.01	12
10/02	63	16.0	0.03	52	3	0.7	0	7
12/02	62	20.6	0.05	16	11	0.3	0	6
3/03	93	33.5	0.07	31	20	0.4	0.03	0

^a The table shows pooled means for the 3 mo before destructive sampling.

One plant from each pair was randomly selected to receive the treatment, a biweekly application of a miticide for the duration of the experiment. Treated plants were sprayed with the miticide abamectin, Vertimec (Syngenta, Basel, Switzerland), at a rate of 4 ml/liter. A plastic curtain was used to prevent overspray onto nearby plants. All plants also received a weekly application of *Bacillus thuringiensis* Dipel, to control Lepidoptera larvae, especially *Spodoptera* spp.

Table 1. Percentages of leaves curled and numbers of

A pair of plants from each of blocks 1–3 was harvested every 3 mo, with two pairs of plants harvested from block 4 at 6-mo intervals over the two seasons of growth. Above-ground leaves and stems were separated from below ground roots in separate drying bags. Dry weights were recorded after 2 wk in a drying oven at a temperature of 50°C. Below-ground biomass was further processed using sieves and hand sorting to remove extraneous material clinging to root fibers. After completion of this process, the remaining biomass was dried again, and weights were recorded after a period of \sim 2 wk.

To determine mite population levels on the plants, one newly expanded mature sterile pinnule (leaflet) was randomly selected from each plant, and the numbers of curled (with mites) and uncurled subpinnae (leaves) were recorded. Pinnules were marked with a dot of paint to prevent recounting in subsequent months. To determine the density of mites within curls, a single leaf curl was harvested in an unbiased manner from each plant, and the numbers and life stages of *F. perrepae* were counted. We also identified and counted the predator mites within each curl and assessed the presence or absence of the mite pathogen, Hirsutella thompsonii Fisher. Observations and counts of mites and pathogens within the curl of the infested subpinnule were undertaken using a dissecting microscope at $\approx 100 \times$. Representative adult F. perrepae and predator species were removed and placed in 70% ethanol for identification. To measure longevity of the pinnules on plants in both treatments, one newly formed pinnule from each plant was tagged each month, and its development was followed until senescence and abscission.

A split plot analysis of variance (ANOVA) was done on the dry weights. Shade and time were assessed between pairs and treatment differences, and their interaction with shade and time was assessed within pairs. Blocks were excluded from the analysis because it was determined that they no effect on the plants in high shade. Total dry weight, dry weight of leaves, and the dry weight of roots were analyzed. All the weights were log-transformed for the analysis to make the variance independent of the mean. Estimates of treatment differences of dry weights between pairs are shown on the log scale. Back transformation of these differences gives an unbiased estimate of the proportional change in dry weight between treated and untreated plants. Means are reported as \pm SE throughout, unless otherwise noted.

Results

The miticide was effective in controlling *F. perrepae* on the treated plants (Table 1), although a minor amount of plant damage from the mite was experienced. It is likely that *F. perrepae* dispersed by air from the untreated to the treated plants. Once settled on the leaves of the treated plants, mites were able to occasionally survive and induce curls, but successful development was uncommon. Two species of predator mites, *Tarsonemus* sp. and a tydaeid sp., were found in the curls, but their numbers remained low throughout the study. The predator mites in the test plot were the same species that are common at field sites in southeast Queensland (J.A.G., unpublished data). The mite pathogen, *H. thompsonii*, was present in the field plot in the second year of the study.

Floracarus perrepae caused a significant reduction in biomass of *L. microphyllum* throughout the 2-yr study. Figure 1 shows the mean total weights of the treated and untreated plants for each sample date. The three dry weight analyses were very similar. In all analyses, shade and its interaction with other factors were not significant. Time was a significant effect ($F_{1,23} = 128.87$, P < 0.0001 in total dry weight), as expected, because of growth of the plants during the study. There was a small but significant interaction between time and treatment ($F_{1,23} = 2.98$, P < 0.02). The treatment effect was strongest ($F_{1,23} = 131.01$, P < 0.0001) for total dry weight. Ignoring the interaction between

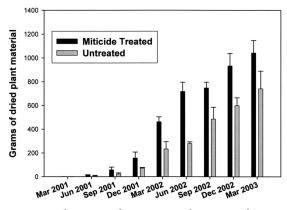


Fig. 1. The impact of *F. perrepae* on biomass production of *L. microphyllum* in a 2-yr chemical exclusion study conducted in the native range of the mite and fern. Treated plants received monthly applications of Agrimec miticide. Bars represent the mean total dry weights of roots, stems, and leaves \pm SE.

time and treatment, estimated treatment differences of dry weights on the log scale were as follows: total, -0.26 ± 0.03 ; leaves, -0.29 ± 0.04 ; roots, -0.19 ± 0.04 . Back transformation of the logs show that overall the mite caused a 49% (95% CI, 42–56) reduction in aboveground stems and leaves with a 35% (95% CI, 23–45) reduction of roots and rhizomes. The relative biomass of the fern above and below ground is seen in the mean weight of the 64 plants at harvest. Average aboveground dry weight was greater, at 297 \pm 31.9 g, compared with below ground, at 123 \pm 13.0 g.

Leaf longevity was significantly different between miticide-treated and untreated plants. Leaves on untreated plants lived on average 162.4 \pm 7.4 (n = 37) and 220.8 \pm 13.2 (n = 37) d on treated plants. Leaves with mite-induced curls developed the characteristic necrotic lesions seen in natural stands of *L. microphyllum* infested with *F. perrepae*. Dr. Roger Shivas (Plant Pathologist, Queensland Department of Primary Industries) analyzed the diseased leaves. The pathogens isolated were typical saprophytic fungi. Further analysis for viruses and viroids was negative.

After 6 mo of the study, nutrient levels in leaf tissue fell below background levels assayed from native stands of *L. microphyllum* (Table 2). Fertilizer applications brought them up to slightly higher levels compared with natural stands in Queensland, but similar to levels in Florida where the plant is a vigorously growing invasive weed.

Discussion

Floracarus perrepae had a significant impact on L. *microphyllum* in our study. The damage and impact on the plant was consistent over the 2-yr period. Although there was a significant interaction between the treatment effect and time, this was only observed in the last guarter of the experiment. In the last guarter, the difference in the size of the treated and untreated plants began to narrow. This may be because of the untreated plants becoming slightly root bound and lacking additional trellis to climb upward. The impact of F. perrepae was not different between the two shade levels. Although the plants appeared smaller in the low-shade block, the proportional differences between treated and untreated were the same as in the high shade blocks. We set up the low-shade block to replicate the higher light levels that F. perrepae might encounter in Florida. In Florida, L. microphyllum is often found growing in nearly full sun and across the canopies of tree islands. It does not seem that these conditions will negatively affect the mite. The impact of F. perrepae was greater on the above-ground biomass (leaves and stems) than roots. The mite did not visibly alter plant architecture. However, we may have been able to measure a difference in height of the climbing vines if we would have used taller trellises.

During our exploration in Australia and Asia for potential biological control agents, F. perrepae seemed to cause considerable debilitation and defoliation of L. microphyllum (Goolsby et al. 2003). We could not be certain if this effect was caused by the action of the mite. The effects of *F. perrepae* in the biomass plot confirm the plant damage we observed in the field across its native range. The differences observed in longevity of the leaves between treated and untreated plants illustrate this impact. Leaves infested with active colonies of the mite undergo rapid necrosis and senescence, but may not abscise immediately. In retrospect, we should have measured the date at which infested leaves became necrotic instead of the date of abscission. This measure may have been a better indicator of leaf damage and impact of the mite. However, it seems logical that this persistent damage to the leaves by the mite reduces the photosynthetic ability of the plant, which in turn limits the growth of the plant. The damage caused by F. perrepae is not readily apparent, but when measured over the long-term, its significance is clearly evident.

Population levels of *F. perrepae* in the biomass plot were higher than found in natural stands (J.A.G., unpublished data). This may be caused by the low levels

Table 2.	Nutrient	levels in	L. micropl	hyllum	leaf tissue
----------	----------	-----------	------------	--------	-------------

Sample location	Percent N \pm SD	Percent P \pm SD	Percent K \pm SD
Biomass plot untreated before fertilization	2.03 ± 0.13	0.17 ± 0.01	1.46 ± 0.23
Biomass plot treated before fertilization	1.70 ± 0.03	0.14 ± 0.01	1.27 ± 0.05
Biomass plot untreated after fertilization	2.68 ± 0.11	0.30 ± 0.13	2.03 ± 0.18
Biomass plot treated after fertilization	2.85 ± 0.04	0.32 ± 0.02	1.49 ± 0.18
Natural stand (Queensland, Australia)	1.91 ± 0.20	0.19 ± 0.02	2.41 ± 0.11
Weedy stand (Florida, USA)	2.64	0.29	2.19

of predation experienced in the biomass plot (Table 1). Although we identified the same species of predators that occur in nearby natural stands of *L. microphyllum*, other factors in the biomass plot environment did not allow them to reach high population levels. This is fortuitous because this low level of predation may be similar to what *F. perrepae* will encounter in Florida in the absence of its indigenous predator species.

The mite pathogen, *H. thompsonii*, was common in the second year of the study. Although it caused considerable mortality to *F. perrepae* populations, the level of plant damage was relatively unchanged (Table 1). *Hirsutella thompsonii* occurs in Florida, where it is a natural control for citrus rust mite, *Phyllocoptruta oleivora* (Ashmead) (Muma 1955, McCoy and Couch 1982). Therefore, we should expect this pathogen to infect *F. perrepae* if it is released in Florida. Based on our experience in Australia with a locally occurring strain of *H. thompsonii*, it does not seem that this pathogen will greatly minimize the impact of *F. perrepae* on *L. microphyllum* in Florida.

In summary, the assessment of F. perrepae shows that it can have significant impact on the target weed L. microphyllum, and therefore, it was prioritized in our selection process. In this biological control program, we will attempt to first release agent(s) with the greatest potential to control the target organism, which may ultimately limit the numbers of species released in the program. The potential benefits of this strategy include an efficient use of resources and a reduction of risk to nontarget species.

Acknowledgments

The authors thank G. Fichera, D. Mira, and K. Waterworth (Commonwealth Scientific and Industrial Research Organization Entomology) for plant culture; A. Oles, L. Vallely, P. Feeney, and P. Mischler (Berea College) for help in sorting and weighing the biomass samples and Syngenta for supplying the abamectin. We also thank R. Pemberton and T. Center (USDA-ARS, Ft. Lauderdale, FL) and M. Julien (Commonwealth Scientific and Industrial Research Organization Entomology, Indooroopilly, Queensland) for project support. M. Lonsdale (Commonwealth Scientific and Industrial Research Organization Entomology, Canberra, Australia) gave valuable advice on experimental design. We also thank T. Widmer (USDA-ARS, Montpellier, France), J. Balciunas (USDA-ARS, Albany, NY, USA), R. Van Klinken (Commonwealth Scientific and Industrial Research Organization Entomology, Darwin, Australia), and J. Makinson (Commonwealth Scientific and Industrial Research Organization Entomology, Indooroopilly) for reviewing and making helpful comments on the manuscript.

References Cited

- Balciunas, J. K. 2000. Code of best practices for classical biological control of weeds, p. 435. *In* N. R. Spencer (ed.), Proceedings, X International Symposium Biological Control of Weeds, July 4–14, 1999, Bozeman, MT. Montana State University, Bozeman, MT.
- Balciunas, J. K. 2004. Are mono-specific agents necessarily safe? The need for pre-release assessment of probable

impact of candidate biocontrol agents, with some examples. *In* Proceedings of the XI International Symposium on Biological Control of Weeds, (J. M. Cullen, D. T. Briese, D. J. Kriticos, W. M. Lonsdale, L. Morin, and J. K. Scott, eds.). CSIRO Entomology, Canberra, Australia, pp. 252–257.

- Balciunas, J. K., and D. W. Burrows. 1993. The rapid suppression of the growth of *Melaleuca quinquenervia* saplings in Australia by insects. J. Aquat. Plant Manag. 31: 265–270.
- Batchelor, K. L., and T. L. Woodburn. 2002. Population development and impact of bridal creeper leafhopper Zygina sp. in Western Australia, pp. 381–384. In H. Spafford-Jacob, J. Dodd, and J. H. Moore (eds.), Proceedings of the 13th Australian Weeds Conference, 8–13 Perth, Australia. RG and FJ Richardson, Meredith, Australia.
- Briese, D. T. 1996. Potential impact of the stem-boring weevil *Lixus cardui* on the growth and reproductive capacity of *Onopordum* thistles. Biocontr. Sci. Technol. 6: 251–261.
- Briese, D. T., and J. M. Cullen. 2001. The use and usefulness of mites in weed biological control, pp. 455–465. In R. B. Halliday, D. E. Walter, H. C. Proctor, R. A. Norton, and M. J. Coloff (eds.), Proceedings of the 10th International Congress of Acarology, 5–10 July 1998, Canberra, Australia. CSIRO Publishing, Melbourne, Australia.
- Goolsby, J. A., A. D. Wright, and R. W. Pemberton. 2003. Exploratory surveys in Australia and Asia for natural enemies of old world climbing fern, Lygodium microphyllum: Lygodiaceae. Biol. Contr. 28: 33–46.
- Hoddle, M., and P. Syrett. 2002. Realizing the potential of classical biological control, pp. 395–424. *In* G. Hallman and C. Schwalbe (eds.), Invasive arthropods in agriculture: problems and solutions. Science Publishers, Enfield, NH U.S.A.
- Kleinjan, C. A., P. B. Edwards, and J. H. Hoffmann. 2004. Impact of foliage feeding by *Zygina* sp. on tuber biomass and reproduction of *Asparagus asparagoides* (L): relevance to biological control in Australia. Biol. Contr. 30: 36–41.
- Langland, K. A., and K. Craddock Burks. 1998. Identification and biology of non-native plants in Florida's natural areas. University of Florida, Gainesville, FL.
- McCoy, C. W., and T. L. Couch. 1982. Microbial control of the citrus rust mite with the mycoacaricide, MYCAR. Fla. Entomol. 65: 116–126.
- McEvoy, P. B., and E. M. Coombs. 1999. Why things bite back: unintended consequence of biological control of weeds, pp. 167–195. In P. A. Follett and J. J. Duan (eds.), Non-target effects of biological control. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Muma, M. H. 1955. Factors contributing to the natural control of citrus insects and mites in Florida. J. Econ. Entomol. 48: 432–438.
- Pemberton, R. W. 1998. The potential of biological control to manage Old World climbing fern (*Lygodium microphyllum*), an invasive weed in Florida. Am. Fern J. 88: 176–182.
- Pemberton, R. W., and A. P. Ferriter. 1998. Old World climbing fern (*Lygodium microphyllum*), a dangerous invasive weed in Florida. Am. Fern J. 88: 165–175.
- Shea, K., and H. P. Possingham. 2000. Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management. J. Appl. Ecol. 37: 77–86.
- Sheppard, A. W., J. P. Aeschilimann, J. L. Sagliocco, and J. Vitou. 1995. Below-ground herbivory in *Carduus nutans* (Asteraceae) and the potential for biological control. Biocontr. Sci. Technol. 5: 261–270.

- Strong D. R., and R. W. Pemberton. 2001. Food webs, risks of alien enemies and reform of biological control, pp. 57–74. In E. Wajnberg, J. K. Scott, and P. C. Quimby (eds.), Evaluating indirect ecological effects of biological control. CAB International, Wallingford, UK.
- Swirepik, A. E., and M. J. Smyth. 2002. Biological control of broad-leafed pasture weeds (Paterson's curse, Onopordum, and Nodding thistles). What have we achieved and where to from here?, pp. 373–376. In H. Spafford-Jacob, J. Dodd, and J. H. Moore (eds.), Proceedings of the 13th Australian Weeds Conference, 8–13 September 2002,

Perth, Australia. RG and FJ Richardson, Meredith, Australia.

- Waloff, N., and O. W. Richards. 1977. The effect of insect fauna on growth mortality and natality of broom, Sarothannus scoparius. J. Appl. Ecol. 14: 787–798.
- Wratten, S. D., and G. M Gurr. 2000. Synthesis: the future success of biological control, pp. 405–416. *In* G. Gurr and S. Wratten (eds.), Biological control: measures of success. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Received 22 July 2003; accepted 2 May 2004.