Austral Ecology (2000) **25**, 563–569

Inhibition of *Ageratina riparia* (Asteraceae) by native Australian flora and fauna

BRIAN J. ZANCOLA,* CLYDE WILD AND JEAN-MARC HERO
School of Environmental and Applied Sciences, Griffith University, PMB 50, Queensland 9726, Australia (B.Zuncola@mailbox.gu.edu.au)

Abstract We investigated the influence of native flora and fauna on the establishment and persistence of the exotic weed *Ageratina riparia* (Asteraceae) in disturbed and regenerating rainforests on the Springbrook plateau of south-eastern Queensland. The height and ground cover of *A. riparia* was positively associated with light availability beneath the rainforest canopy and negatively associated with forest leaf litter biomass. Regenerating rainforest with the associated increases in litter and decrease in light availability could therefore inhibit the establishment and density of *A. riparia*. The red-necked pademelon, *Thylogale thetis*, browsed extensively on *A. riparia*, but the pattern of browsing was not associated with light availability, forest leaf litter biomass or density of *A. riparia*. Browsing and incidental damage by *T. thetis* breaks up the broad stands of *A. riparia*. The physical damage caused by *T. thetis*, and the inhibition to establishment and density of *A. riparia* by native plant species, combine to reduce the environmental threat associated with *A. riparia*.

Key words: *Ageratina riparia*, biocontrol, creeping crofton weed, *Eupatorium riparium*, hamakua pamakani, herbivory, interaction, mistflower, pademelon, *Thylogale thetis*.

INTRODUCTION

Much of the research on exotic weeds concentrates on the search for effective biocontrols and assessment of detrimental effects on native plant species or agricultural systems (Julien 1992), such as the consumption of exotic weeds by livestock (e.g. Everist 1974). Some work, principally concerned with the spread of weeds, has also been undertaken on birds (Humphries *et al.* 1991). However, little is known about how native animals, particularly herbivores, interact with exotic weeds (Johnson 1977, Wahungu *et al.* 1999). Native herbivores may adapt their behaviour and/or diet to exploit these new resources and hence act as a biological control. Direct predation and incidental damage by herbivores can indirectly modify resource allocations within plants, altering nutritional value and growth pattern (Danell *et al.* 1994). This study examines the interactions between native flora and fauna and the exotic weed *Ageratina riparia* Asteraceae (King & Robinson 1970) that became dominant after the conversion of subtropical rainforest to grazing pasture in south-east Queensland, Australia. Research that examines how exotic species modify new environments, and the new ecological interactions they generate, will become increasingly important as more exotic plant species become naturalized.

Ageratina riparia

Ageratina riparia is commonly known as mistflower, creeping crofton weed or hamakua pamakani. Native to Mexico, *A. riparia* has been widely distributed around the world as an ornamental (Barreto & Evans 1988) and is a serious weed problem in mesic locations in Australia, Hawaii, India and New Zealand. In Australia, the distribution of *A. riparia* is from southern subcoastal Queensland to the central coast of New South Wales, where it is frequently found in areas with high rainfall. Its southward dispersal is most probably limited due to sensitivity to frost, and its northward dispersal by high temperatures (Wild 1985). *Ageratina riparia* is a persistent weed along roadsides, trails, waterways and areas of continual disturbance, such as bare slopes and areas with partial shading or canopy gaps, and can dominate the ground cover in such locations (Stanley & Ross 1986; Tripathi & Yadav 1987). A single plant of *A. riparia* can produce 7000 to 10 000 seeds per season and the seeds can be dispersed by wind and water (Stanley & Ross 1986; Barreto & Evans 1988; Morin *et al.* 1997) or by becoming attached to animals. Native plant species less than 1 m in height may be smothered by *A. riparia* and the seedlings of taller plant species are deprived of light (Humphries *et al.* 1991). The key feature of *A. riparia* that makes it a threat to native plant species is its sprawling pattern of growth. Juvenile plants grow a single primary stem, developing branches as the plant matures. Branches of adjacent *A. riparia* plants

---

*Corresponding author.

intertwine producing a blanket effect, giving effectively 100% ground cover. The longer branches on *A. riparia* tend to droop over adjacent plants. Nodes on the drooping branch develop adventitious roots and new stems from that point (Tripathi & Yadav 1987; Queensland Department of Lands 1990). *Ageratina riparia* has also been shown to have some allelopathic capacity (Rai & Tripathi 1984), which could inhibit the regeneration of at least some native plants.

The gall-forming fly *Procecidochares alani* (Diptera: Tephritidae) was introduced into several countries as a biocontrol agent for *A. riparia* but with limited success (Julien 1992). In Australia *P. alani* was released in 1987 and is now parasitized by native parasitoid wasps (Queensland Department of Lands 1990). The combination of *P. alani*, the caterpillar *Oidaematophorus beneficus* and the leaf spot fungi *Entyloma ageratinae* or *Entyloma compositarum* has produced successful control in Hawaii (Morin *et al.* 1997). Results from the introduction of the fungi into New Zealand in November 1988 (Vervoort 1998) will be considered before any potential release in Queensland, Australia (R. MacFadyen, personal communication).

Predation by *Thylogale thetis*

Ageratina riparia is subject to resource stresses created by neighbouring plants and intracompetitive stresses (Grime 1977; Yadav & Tripathi 1985; Wahungu *et al.* 1999). Interference due to predation and incidental damage from native fauna can also influence the growth of *A. riparia*. Initial observations demonstrated that *A. riparia* is regularly eaten by the red-necked pademelon, *Thylogale thetis* Macropodidae (Lesson 1827), although we found no published reference of any native Australian mammal feeding on *A. riparia*.

Thylogale thetis have distinct variations in diurnal and nocturnal feeding behaviour (Johnson 1977). During daylight hours, *T. thetis* enters the cover of the forest to browse, and from nightfall to dawn they move out into pastures to graze. The nocturnal grazing behaviour of *T. thetis* is well studied (Johnson 1977), as is their digestive system (Dellow 1982; Dellow & Hume 1982a,b; Dellow *et al.* 1983, 1988). Information about diurnal browsing behaviour is more generalized and anecdotal (Johnson 1977; Dawson 1989; Jarman & Phillips 1989). *Thylogale thetis* selectively eats different plant species and which part of these plants it consumes (Johnson 1977; Wahungu *et al.* 1999). For example, when browsing on the leaves of *Solanum mauritianum* (wild tobacco), *T. thetis* ate the leaf petiole and mid vein while avoiding the leaf blade (Johnson 1977; Wahungu *et al.* 1999). When *S. mauritianum* was sprayed with a glyphosate-based herbicide, browsing rates increased and the leaf blade was consumed, with apparent detrimental side-effects on the coordination and judgement of the animals. Similar effects are evident with *A. riparia* after herbicide treatment (C. H. Wild & J. Ward, unpublished data), suggesting that the control of weeds with herbicide can potentially be detrimental to native animals.

METHODS

Study area

The study was conducted between August and October 1998 in the regenerating rainforests of Springbook plateau (latitude 28°13′10″S, longitude 153°15′50″E) in the hinterland of the Gold Coast, Queensland. The elevation of the site varies from 760 to 800 m with a mean average temperature of 14°C and an annual rainfall of about 2500 mm which is spread throughout the year with a summer/autumn maximum.

Most of the area was originally upland tall subtropical rainforest, cleared for dairy farming and converted to kikuyu grass (*Pennisetum clandestinum*) pastures. Much of the area has regenerated back to native forest over the past 30 years. The canopy cover at the site ranged from closed (>90% cover) to fully open, with a mixture of subtropical and warm temperate rainforest tree species. Shrubs and understorey species included lantana (*Lantana camara*), crofton weed (*Ageratina adenophora*), wild native raspberry (*Rubus laciniatus*), wild tobacco (*Solanum mauritianum*) and many species of ferns including common ground fern (*Culcita dubia* (R.Br.) Maxon; Dicksoniaceae) and trim shield fern (*Lastreopsis decomposita* (R.Br.) Tindale; Aspidiaceae).

Study sites

A 6 ha study area (Fig. 1) was established in a valley that had considerable variation in the relative abundance of *A. riparia* on both north- and south-facing slopes. Twelve sites (approximately 950 m^2) were established. The sites were stratified across the north-facing slope, along the creek and across the south-facing slope (Fig. 1). Each site contained three classes based on the growth of *A. riparia*: (i) high growth (plants $\geq$0.2 m in height and $\geq$70% ground cover), low growth (plants $\leq$0.2 m in height with $\leq$70% ground cover), and (iii) areas where *A. riparia* was absent. Two locations were randomly selected within each of these densities of *A. riparia* at each site (2 points × 3 density classes × 12 sites = 72 points).

Variables measured

Habitat

Total canopy gap fraction (insolation) data was collected via hemispheric photography adapted from

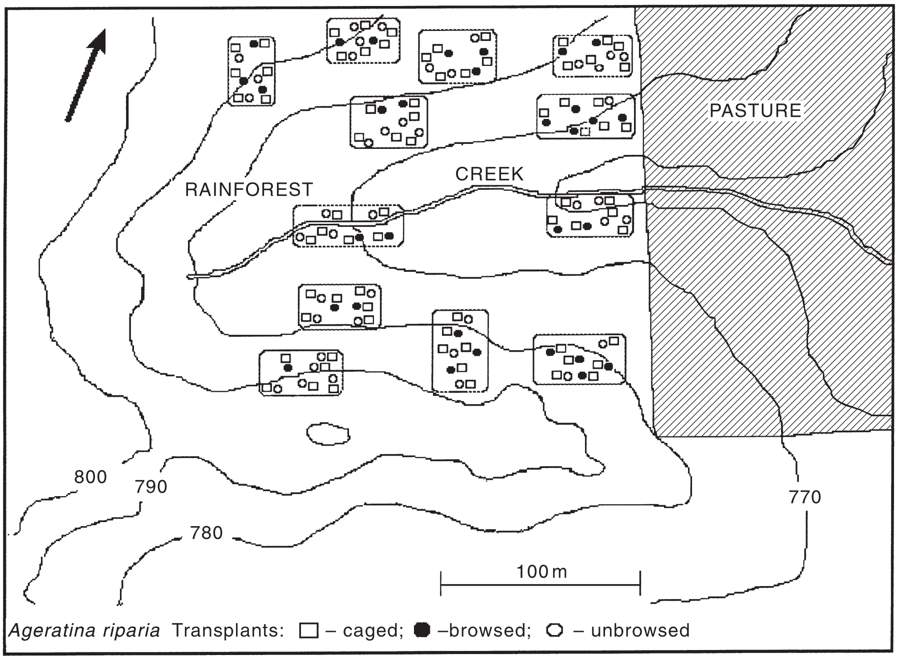

Fig. 1. Generalized topography and map of study area (contour lines indicate elevation in metres). Each of the twelve study sites indicated by the large rectangles contains six data points. Every caged *Ageratina riparia* transplant is paired (1 m distance) with an uncaged *A. riparia* transplant and count as one data point. Two data points are located in each of the nil, low and high density stands of *A. riparia* within each study site.

Frazer *et al.* (1997) in the first week of August 1998. A 153° semi-fisheye lens was attached to a Sony digital still camera (MVC-FD73, Japan). Each photo was centred on magnetic north (11° east of true north) and the ecliptic (62° at this latitude) to include the summer and winter limits of travel of the sun across the sky. The digital photographs were converted to black and white images and masked to include only the area of sky traversed by the sun during the year. The numbers of black and white pixels were counted by custom software written in-house, the ratio of white to total pixels gave an index of insolation. This measure is an index of the amount of direct sunlight received by each point during the year.

The forest litter biomass was collected from 0.2 m × 0.2 m quadrats centered on each field point, over the same period of time that the hemispherical photographs were taken. It was then oven dried at 60°C for three days and weighed.

Ageratina riparia

Ageratina riparia density was measured using an index of plant volume calculated by multiplying the modal height and percentage ground cover of *A. riparia* at each point. Digital photographs of *A. riparia* ground cover were taken in the first week of August 1998 at each point from a standard height of 0.5 m above the *A. riparia* canopy. The image was loaded into the shareware digital image processing software, PAINT SHOP PRO. The image was edited to convert any *A. riparia* into white pixels and the remainder of the image to black pixels. The ratio of white to total pixels indicated the *A. riparia* percentage ground cover.

Thylogale thetis

The population of *T. thetis* resident in the study area was estimated to be 10–14 individuals, based on visual identification of adult males, females and juveniles. Aggregations of 3–6 individuals were frequently observed in the forest. All observations of *T. thetis* feeding behaviour were opportunistic events during the fortnightly monitoring of the study area. The building of hides or other such observation platforms was not feasible due to visibility being limited to 5–10 m in the forest.

Ageratina riparia *transplant experiment*

A transplant experiment adapted from Reader (1992) was used to examine browsing by *T. thetis*. Cuttings of *A. riparia* (approximately 90 mm in height) were grown in a greenhouse for 3 weeks until sufficient roots had developed. Seventy-two of these cuttings were then transplanted on 8 August 1998 into the same field points used for the previous data collection 6 points per site × 12 sites. Cuttings were individually protected by a small wire mesh exclosure made of 50 mm woven mesh, secured in place by wooden stakes. The size (diameter 0.3 m, height 0.9 m) and design of the exclosure would permit exclusion of *T. thetis*, the only large herbivore in the area, while admitting small herbivores, particularly invertebrates. An additional 72 cuttings were transplanted at a 1 m distance from each exclosure transplant. Every transplant received 1 L of water when planted. Frequent rain ensured that there was no need for additional watering. Each fortnight, the growth of the transplants was measured and any damage recorded. Browsing was defined as a single event of the plant stem being cropped (it was a dichotomous variable) indicating whether a transplant had been browsed or not in the twelve-week period between August to October 1998.

Data analysis

The relationship between native flora (insolation and forest leaf litter biomass) and *A. riparia* density (volume index) was analysed by multiple linear regression. The data for forest leaf litter biomass was log transformed. The influence of these three variables (insolation, forest leaf litter biomass and *A. riparia* volume index) on *T. thetis* browsing was analysed using multiple logistic regression. The proportion of available transplants eaten in each fortnight was calculated and differences compared by ANOVA.

RESULTS

Influence of native plants

The *A. riparia* volume index was related positively to insolation, and related negatively to forest leaf litter biomass (Table 1). Insolation and forest leaf litter biomass were not significantly correlated with each other ($r = -0.174$, $P = 0.072$).

Browsing by *Thylogale thetis*

Browsing was not associated with insolation ($P = 0.16$), forest leaf litter biomass ($P = 0.51$) or *A. riparia* volume index ($P = 0.87$). The explanatory capacity of these variables is very small, for example, multiple $R^2 = 0.05$ (Table 2).

Browse rate of transplants located in the three density classes of *A. riparia* were similar (Fig. 2). There was no significant difference ($F_{2,15} = 0.69$, $P = 0.52$) in the proportion of transplants eaten between high, low and nil areas of *A. riparia*. There are no evident spatial trends in the location of browsing, as browsing occurred in all 12 sites (Fig. 1). The browsing rate was high, with nearly 50% of the uncaged transplants being browsed in 12 weeks. None of the transplants protected by exclosures were browsed, all grew and appeared healthy, although some did receive incidental damage such as bent or broken stems perhaps as a result of rapidly moving animals colliding with the exclosures.

Table 1. Multiple linear regression model of *Ageratina riparia* volume index on insolation and forest leaf litter biomass

Variable	Beta	SE	*P*
Insolation	0.355	0.096	0.00001
Log (leaf litter biomass)	–0.451	0.096	0.00042

$R^2 = 0.385$ (adjusted $R^2 = 0.367$).

Field observations

All existing areas of *A. riparia* contained some evidence of browsing. Areas of frequent browsing were apparent by the cropped appearance of the *A. riparia* plants and the debris of leaf laminae and stem tips. Browsing in high volume areas resulted in the defoliation of plants on the edges of the stands, leaving only the woody stems. In several cases, entire stands of *A. riparia* were defoliated. Browsing in low volume areas tended to produce a ‘lawn’ of *A. riparia*, as the plants were repeatedly cropped close to the ground. In all areas, regrowth of browsed plants was evident in the development of new branches. We observed that with *A. riparia*, the manner of browsing by *T. thetis* was consistent: an initial bite severed the stem at the third or fourth internode below the apical meristem and the stem was

Table 2. Multiple logistic regression of insolation, leaf litter biomass and *Ageratina riparia* volume index as predictors of *Thylogale thetis* browsing on *A. riparia* transplants in the open. The dependent variable is defined as transplants ‘browsed’ or ‘not browsed’ after 84 days

Variable	Beta	*P*
Entire model		0.35
Insolation	8.343	0.16
Leaf litter biomass	–0.776	0.51
Volume index	–0.0001	0.87
Constant	–1.907	0.090

Cox and Snell $R^2 = 0.045$; Nagelkerke $R^2 = 0.059$.

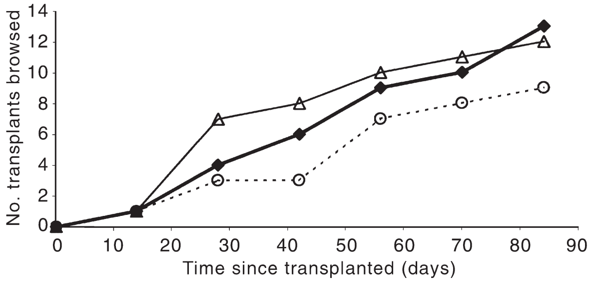

Fig. 2. Cumulative number of browsed transplants from all sites combined, separated into the three classes of *Ageratina riparia* densities. Transplants in high density area (◆, plants ≥0.2 m in height with ≥70% groundcover). Transplants in low density area (△, plants <0.2 m in height with <70% groundcover). Transplants in nil density area (○, absence of *Ageratina riparia*).

then inverted and eaten. The leaves were discarded (often with the petioles removed), as was the apical meristem.

Stands of *A. riparia* were criss-crossed with trails created by *T. thetis*. Continuously utilized trails were clear of vegetation; disused trails through *A. riparia* stands generally closed over within a few months.

On heavily overcast days, *T. thetis* was consistently observed to move out of the forest to the edges of roadsides, pastures and into the larger canopy gaps to feed. However, these areas of more open forest canopy cover are generally avoided by *T. thetis* during their diurnal browsing.

DISCUSSION

A significant positive relationship between insolation and *A. riparia* volume index indicates that higher levels of light availability were associated with greater volumes of *A. riparia*. This result is consistent with the distribution of the plant, which is found in dense stands in canopy gaps and on forest fringes. The *A. riparia* volume index was significantly negatively associated with forest leaf litter biomass, with high levels of forest leaf litter biomass associated with the absence of *A. riparia*. It is possible that the accumulated litter may inhibit seed germination or seedling growth of the weed (Tripathi & Yadav 1987). Seed germination inhibition could also be due to allelopathic compounds (chemical intervention) being released by the decaying litter or by limiting the resources required by seeds (physical intervention), such as contact with soil or moisture (Xiong & Nilsson 1997). Alternatively, it is possible that seed germination does occur and the seedlings die due to lack of light or exposure to allelochemicals after being buried by the decaying litter. This study did not explore these processes.

Insolation and forest leaf litter biomass were not correlated. The independence of the two variables is most probably due to the diversity of the forest canopy species and, because some species drop more litter than others, the density of the canopy does not ensure high forest leaf litter biomass. The combination or interaction of low light and high forest leaf litter biomass inhibits the establishment and/or the density of *A. riparia*, and this limits the abundance of *A. riparia* within regenerating rainforest in this region.

Levels of insolation within the forest also showed no correlation with the feeding pattern of the pademelon, which mainly feeds at night. Field observations, however, pointed to more subtle browsing behaviour during the day. When *T. thetis* individuals were observed browsing in daylight, they generally avoided areas of more open forest canopy. This behaviour changed on heavily overcast days, when feeding occurred in large canopy gaps and other open areas. This was possibly masked in the analysis, which measured browsing activity over several days and nights. These subtle differences in behaviour, however, do not appear to have had an impact on the overall levels of browsing of *A. riparia*.

Forest leaf litter biomass did not influence the browsing of *T. thetis*. Recently fallen leaves and fruits comprise a part of the native browse diet of *T. thetis* (Johnson 1977; Dawson 1989, Jarman & Phillips 1989) and higher concentrations of these could be expected in areas with high forest leaf litter biomass. An increase in the time spent in an area due to the availability of native browse would have been reflected in a higher incidence of browsed transplants in the area. It appears therefore that *T. thetis* are actively selecting *A. riparia* independently of the availability of other dietary resources. The *A. riparia* volume index was also non-significant in relation to *T. thetis* browsing, suggesting that there was no preference towards any specific density of *A. riparia* (Fig. 2).

The combination of these three factors generally provided three distinct browsing macrohabitats for *T. thetis*. The 'high growth' areas provided abundant *A. riparia*, dense lateral cover and minimal forest canopy cover. 'Low growth' areas gave a mix of native browse and *A. riparia*, minimal lateral cover with moderate to heavy forest canopy cover. Areas with 'nil growth' of *A. riparia* provided only native browse (apart from the transplants), no lateral cover with moderate to heavy canopy cover. *Thylogale thetis* showed no preference for any of these macrohabitats or to other habitats associated with topography. Evidently, therefore, *A. riparia* is suitable for browsing for this species at any density or location.

Field observations indicate that the damage to *A. riparia* stands via browsing can range from minimal to extensive. Frequent browsing by *T. thetis* results in the denuding of the *A. riparia* plants, reducing the ground cover, and the redirection of resources toward regrowth. Damage to stands of *A. riparia* caused by *T. thetis* is increased with the incidental damage due to the formation and use of their trails, which is a common trait of *T. thetis* (Troughton 1951, Johnson 1977). The repeated loss of above-ground biomass combined with the negative influences of insolation and forest leaf litter biomass must put *A. riparia* on a reduced competitive standing.

This exploratory study points to a number of questions that need to be examined before the extent of the interaction of *T. thetis* and *A. riparia* can be fully understood. For example, it is unknown what proportion *A. riparia* contributes to the daily browse diet of *T. thetis*. Whether utilization of the *A. riparia* as an alternate food source is consistent throughout the year or varies seasonally is also unknown. If *A. riparia* does provide an abundance of browse throughout the year, this may influence the size of *T. thetis* populations, as reproductive success is influenced by food availability (Johnson 1977).

Chromenes, toxic secondary metabolite compounds, have been identified in the aerial parts of *A. riparia* (Banerjee *et al.* 1985; Abou-Mandour *et al.* 1996). These compounds are believed to have antimicrobial and antifeedant properties (Ratnayake Bandara *et al.* 1992; Abou-Mandour *et al.* 1996). The effects of these toxins on *T. thetis* are unknown. Unlike the grazing animals used in published toxicity tests, such as sheep (Everist 1974) and horses (Gibson & O'Sullivan 1984), *T. thetis* is a grazer/browser (Johnson 1977; Hume 1978) and must have evolved mechanisms to avoid or metabolize some plant toxins (Freudenberger *et al.* 1989; Foley *et al.* 1995). The selective manner in which *T. thetis* only eats parts of *A. riparia* may be an indication of toxin detection and avoidance, alternately there may be some chronic disorders induced by the regular consumption of *A. riparia* tissue.

Regenerating rainforest may displace *A. riparia* due to the accumulation of high forest leaf litter biomass and a decreased level of light at ground level. There is an apparent inverse relationship between density of stands of *A. riparia* and insolation. This suggests that once rainforest plant species can outgrow *A. riparia*, they are capable of displacing it or, at the least, reducing its density. Browsing by *T. thetis* could be the key to successful rainforest regeneration if it enables natural plant successional processes to operate (Wahungu *et al.* 1999). The combination of *T. thetis* pathways disturbing the blanket cover of *A. riparia*, and the selective browsing of individuals on *A. riparia* stems, reduces the biomass and ground cover of *A. riparia* and creates the potential for native plant species to establish.

ACKNOWLEDGEMENTS

We thank Mark Watson, Cuong Tran and the other volunteers who helped in the collection of field data.

REFERENCES

Abou-Mandour A. A., Raab U. & Proksch P. (1996) Production and accumulation of chromenes in tissue cultures of *Ageratina riparia* (Asteraceae). *J. Appl. Bot.* **70,** 40–4.

Banerjee S., Jakupovic J., Bohlmann F., King R. M. & Robinson H. (1985) Chromenes from *Ageratina riparia*. *Phytochemistry* **24,** 2681–3.

Barreto R. W. & Evans H. C. (1988) Taxonomy of a fungus introduced into Hawaii for biological control of *Ageratina riparia* (Eupatorieae: Compositae), with observations on related weed pathogens. *Trans. Br. Mycol. Soc.* **91,** 81–97.

Dannell K., Bergstrom R. & Edenius L. (1994) Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. *J. Mammal* **75,** 833–44.

Dawson T. J. (1989) Diets of Macropodiod marsupials: general patterns and environmental influences. In: *Kangaroos, Wallabies and Rat-Kangaroos*. (eds G. Grigg, P. Jarman & I. Hume) pp. 129–42. Surrey Beatty and Sons Chipping Norton, Australia.

Dellow D. W. (1982) Studies on the nutrition of Macropodine marsupials III. The flow of digesta through the stomach and intestine of Macropodines and sheep. *Aust. J. Zool.* **30,** 751–65.

Dellow D. W. & Hume I. D. (1982a) Studies on the nutrition of Macropodine marsupials. I. Intake and digestion of lucerne hay and fresh grass, *Phalaris aquatica*. *Aust. J. Zool.* **30,** 391–8.

Dellow D. W. & Hume I. D. (1982b) Studies on the nutrition of Macropodine marsupials. II. Urea and water metabolism in *Thylogale thetis* and *Macropus eugenii*, two wallabies from divergent habitats. *Aust. J. Zool.* **30,** 399–406.

Dellow D. W., Nolan J. V. & Hume I. D. (1983) Studies on the nutrition of Macropodine marsupials. V. Microbial fermentation in the forestomach of *Thylogale thetis* and *Macropus eugenii*. *Aust. J. Zool.* **31,** 433–44.

Dellow D. W., Hume I. D., Clarke R. T. J. & Bauchop T. (1988) Microbial activity in the forestomach of free-living Macropodid marsupials: comparisons with laboratory studies. *Aust. J. Zool.* **364,** 383–95.

Everist S. L. (1974) *Poisonous plants of Australia*. Angus and Robertson, Sydney.

Foley W. J., Mclean S. & Cork S. J. (1995) Consequences of biotransformation of plant secondary metabolites on acid-base metabolism in mammals – a final common pathway. *J. Chem. Ecol.* **21,** 721–43.

Frazer G. W., Trofymow J. A. & Lertzman K. P. (1997) A method for estimating canopy openness, effective leaf area index, and photosynthetically active photon flux density using hemispherical photography and computerized analysis techniques. Canadian Forestry Service, British Columbia.

Freudenberger D. O., Wallis I. R. & Hume I. D. (1989) Digestive adaptations of kangaroos, wallabies and rat-kangaroos. In: *Kangaroos, Wallabies and Rat-Kangaroos*. (eds G. Grigg, P. Jarman & I. Hume) pp. 179–87. Surrey Beatty & Sons Chipping Norton, Australia.

Gibson J. A. & O'Sullivan B. M. (1984) Lung lesions in horses fed mistflower (*Eupatorium riparium*). *Aust. Vet. J.* **61,** 271.

Grime J. P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **111,** 1169–94.

Hume I. D. (1978) Evolution of the Macropodidae digestive system. *Aust. Mammal* **2,** 37–42.

Humphries S. E., Groves R. H. & Mitchell D. S. (1991) Plant invasions of Australian ecosystems – a status review and management directions. National Parks and Wildlife Service, Canberra.

Jarman P. J. & Phillips C. M. (1989) Diets in a community of Macropod species. In: *Kangaroos, Wallabies and Rat-Kangaroos*. (eds G. Grigg, P. Jarman & I. Hume) pp. 143–9. Surrey Beatty & Sons Chipping Norton, Australia.

Johnson K. A. (1977) Ecology and management of the red-necked pademelon, *Thylogale thetis*, on the Dorrigo plateau of northern New South Wales. PhD Thesis. University of New England, Armidale.

Julien M. H. (1992) *Biological control of weeds: a world catalogue of agents and their target weeds. 3rd ed.* CAB International in association with Australian Centre for International Agricultural Research, Wallingford.

King R. M. & Robinson H. (1970) Studies in the Eupatorieae (Compositae). XIX. New combinations in *Ageratina*. *Phytologia* **19,** 208–29.

Morin L., Hill R. L., Matayoshi S. & Whenua M. (1997) Hawaii's successful biological control strategy for mist flower

(*Ageratina riparia*) – can it be transferred to New Zealand? *Biocentral News Inf.* **18,** 3.

Queensland Department of Lands (1990) *Mistflower* Eupatorium riparium *and its control*. *Pestfact*. Queensland Department of Lands, Brisbane.

Rai J. P. N. & Tripathi R. S. (1984) Allelopathic effects of *Eupatorium riparium* on population regulation of two species of *Galinsoga* and soil microbes (*Galinsoga Ciliata, Galinsoga Parviflora*, India). *Plant and Soil* **80,** 105–17.

Ratnayake Bandara B. M., Hewage C. M., Karunaratne V., Wannigana G. P. & Adikaram N. K. B. (1992) An antifungal chromene from *Ageratina riparia*. *Phytochemistry* **31,** 1983–5.

Reader R. J. (1992) Herbivory as a confounding factor in an experiment measuring competition among plants. *Ecology* **73,** 373–6.

Stanley T. D. & Ross E. M. (1986) *Flora of South-Eastern Queensland, Volume 2*. Queensland Department of Primary Industries, Brisbane.

Tripathi R. S. & Yadav A. S. (1987) Population dynamics of *Eupatorium adenophorum* Spreng and *Eupatorium riparium* Regel in relation to burning. *Weed Res.* **27,** 229–36.

Troughton E. G. (1951) The kangaroo family. The pademelons or scrub wallabies – I. *Australian Museum Magazine, 15 September 1951*. pp. 218–22.

Vervoort L. (1998) Mistflower fungus latest weapon in arsenal. *Auckland Regional Council Media Release*. http://www.arc.govt.nz.

Wahungu G. M., Catterall C. P. & Olsen M. F. (1999) Selective herbivory by red-necked pademelon *Thylogale thetis* at rainforest margins: factors affecting predation rates. *Aust. J. Ecol.* **24,** 577–86.

Wild C. H. (1985) Host specificity report on *Procecidochares alani* Steyskal (Diptera: tephritidae), an agent for the biocontrol of mistflower (*Ageratina riparia* (Rigel) King & Robinson: Asteraceae) in Australia. *Internal Report: The Alan Fletcher Research Station*. Queensland Department of Lands, Brisbane.

Xiong S. & Nilsson C. (1997) Dynamics of leaf litter accumulation and its effects on riparian vegetation: a review. *Bot. Rev.* **63,** 240–64.

Yadav A. S. & Tripathi R. S. (1985) Effect of soil moisture and sowing density on population growth of *Eupatorium Adenophorum* and *Eupatorium Riparium*. *Plant and Soil* **88,** 441–7.