Ecology and Management of Alligator Weed, *Alternanthera philoxeroides*

Imogen Eleanor Bassett

A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Biology, The University of Auckland, 2008

Abstract

Invasive plant species in natural ecosystems have been shown to have a wide range of potential impacts on community composition and ecosystem function. Alligator weed (*Alternanthera philoxeroides*) is invasive in New Zealand and elsewhere. An aggressive competitor and difficult to control, its impacts in productive ecosystems are widely documented. However, little information exists about alligator weed's effects in natural ecosystems.

This thesis therefore investigated potential effects of alligator weed on decomposition and nutrient cycling, as well as on invertebrate and plant communities in a "native" ecosystem, thus integrating effects on ecosystem processes and community composition. These aspects were compared between vegetation dominated by alligator weed or by one of two native sedges, *Isolepis prolifer* and *Schoenoplectus tabernaemontani,* in a northern New Zealand lake. In addition, the potential of shading to control alligator weed was assessed.

Herbivory by the biocontrol agent *Agasicles hygrophila* resulted in substantial alligator weed defoliation, differing in timing and magnitude from biomass dynamics of the native sedges. Alligator weed also decomposed faster than either native sedge. Changes in decomposition dynamics led to a shift towards fungivore dominated beetle communities. This illustrates the potentially complex ecosystem effects of biocontrol agents as well as invasive weeds.

Alligator weed decomposition rates and invertebrate communities were more similar to those of *I. prolifer* than *S. tabernaemontani*. This pattern was attributed to the greater chemical and architectural similarity of alligator weed to *I. prolifer* compared with *S. tabernaemontani*. Invasive plants' impacts may thus be partially influenced by the degree of similarity between the invasive species and the dominant vegetation they invade. Alligator weed was associated with decreased cover of native plants, potentially placing them at greater risk of local extinction.

Greenhouse and field experiments showed that shading significantly reduced alligator weed growth. However, clonal support from unshaded areas, and competitive release from less shade tolerant plants, may potentially impede the success of shade based control.

This research demonstrates that alligator weed can have a range of complex and multi-trophic effects in a natural ecosystem. Further, characteristics of both invasive and competing vegetation can influence the success of cultural control methods such as shading.

Acknowledgements

A huge thanks to Jacqueline Beggs and Quentin Paynter who provided me with exceptional supervision throughout this project, and to Landcare Research and the Co-operative Research Centre for Australian Weed Management for providing funding. Numerous other people and organizations also deserve thanks for the assistance they have given me in various ways; Mic Julien, Shon Schooler, Peter Williams, Chris Winks, Richard Toft, Rich Leschen, Grace Hall, Stephen Thorpe, David Toulon, Northland Regional Council, Department of Conservation Northland Conservancy, Ewen Cameron, Paul Champion, Vince Lane, Greg Hoskins, Karikari Estate Vineyards, Guy Forrester. Apologies to anyone else whose assistance I have forgotten to personally acknowledge. Thank you to my wonderful parents, who as ever have provided endless support in all sorts of ways. And lastly a very special thank you to my partner Richard, for all his love and support throughout this process, and for giving up so many weekends to drive for miles and brave mud, eels, leeches…

Table of contents

List of Tables

List of Figures

1 INTRODUCTION

1.1 Overview

Globalisation of human activity has led to increased movement of plant species outside of their native ranges. Not all introduced plants become invasive, with characteristics of both the plant and the receiving environment influencing invasion success. Species that do become invasive, such as alligator weed (*Alternanthera philoxeroides* (Mart.) Griseb., Chenopodiales: Amaranthaceae), may have a range of economic and environmental impacts. These issues are discussed, along with a review of current information on the distribution, ecology and control of alligator weed.

1.2 Invasive species

Increased human international travel and trade over the last 200-500 years has brought with it an increase in the dispersal of other plant and animal species (Mack 2000). Over 25,000 species of plants have been introduced to New Zealand (Taylor and Smith 1997), both deliberately for agriculture, horticulture, forestry or as garden ornamentals, or accidentally, for instance as contaminants in soil, grain or ships' ballast. Many introduced species go on to establish populations in the wild; naturalised exotic vascular plants now outnumber native species in New Zealand (Taylor and Smith 1997; Williams and West 2000). However, naturalised species vary in the extent to which they pose economic or environmental problems. Invasive species are those which proliferate, spread and persist in a new range to the detriment of the environment or pre-existing native ecosystem (Mack 2000; Invasive Species Specialist Group 2004). In contrast, any plant may be considered a weed where it is in the 'wrong' situation, with two broad categories of weeds; economic weeds, and environmental weeds. The terms ‘invasive species’ and ‘environmental weed’ are among a number of names used in the literature for introduced plant species which impact on indigenous systems. The two terms will be used interchangeably in this review.

1.2.1 Economic weeds

Plants that have direct, negative economic impacts, such as control costs and yield losses, may be considered economic weeds. These costs tend to particularly affect primary production industries and represent a significant loss in their productivity. A single invasive species in Idaho rangelands, Yellow star thistle (*Centaurea solsitialis*), was estimated to have economic impacts totalling US$12.7 million (Julia, Holland et al. 2007). The economic cost of weeds in Australia has been estimated at around AU$4 billion in 2001-2 (Sinden, Jones et al. 2004). While this figure excludes many ecosystem goods and services such as water flow, drainage and biodiversity, which are difficult to quantify in monetary terms, it does include weed control costs in natural areas. However, around 97% of costs came from the agricultural sector (Sinden, Jones et al. 2004). Weeds were estimated to cost the American agricultural sector US$26.4 billion annually (Pimental, Lach et al. 2000), around 0.3% of GDP (Bureau of Economic Analysis 2005). In New Zealand in 1993, $90m was spent on herbicide based weed control (Taylor and Smith 1997). In addition, weeds are estimated to cause the New Zealand agricultural sector productivity losses of approximately $340m/year (Taylor and Smith 1997), resulting in a relative cost similar to that in the United States, of around 0.5% of GDP (Statistics New Zealand 2005).

1.2.2 Environmental weeds

Invasion of natural communities by exotic species is often cited as the greatest threat to biodiversity after habitat destruction (Kolar 2001; Shaw 2003). Examples of the damage done by invasive vertebrates such as possums and mustelids are widely recognised in New Zealand (Atkinson and Cameron 1993). However, invasive plant species also pose a considerable threat to conservation areas. Environmental weeds are those which invade natural ecosystems and can cause substantial modifications to indigenous biodiversity and ecosystem function (Williams and West 2000). Environmental weeds contribute to declining biodiversity, and global biotic homogenisation, through the replacement of native, locally distributed species with widespread, non-native species (Olden 2004). Reductions in biodiversity may be viewed at four levels; genetic, species, community and ecosystem level effects (Groves and Willis 1999).

While complete extinctions of plant species may occur only relatively rarely, loss of localised populations, or hybridisation with introduced species may reduce genetic diversity (Groves and Willis 1999). For instance, (Prentis, White et al. 2007) considered hybridisation with the invasive *Senecio madagascariensis* a potential threat to co-occurring populations of the Australian native *Senecio pinnatifolius*. Reduced genetic diversity can affect native species' ability to withstand environmental variation, and increase their risk of extinction from stochastic events, leading to impacts at the species level. Further, species losses are not randomly distributed amongst higher taxonomic groups, with some groups, such as cacti, containing disproportionate numbers of threatened species (McKinney 1999). Loss of genetic diversity may therefore be accelerated, with the loss of whole genera or families with invasion of environmental weeds. Conversely, other taxa, such as Poaceae, contain disproportionate numbers of invasive species, as traits enabling a species to be a successful invader are often shared by closely related species (Daehler 1998; McKinney 1999).

At the species level, weeds are contributing factors in the decline of 59% of New Zealand's threatened native plant species (Dopson, de Lange et al. 1999).Weeds may negatively affect native vegetation by competing for resources such as light, nutrients and space, and altering the frequency and intensity of disturbance. While these can be considered ecosystem level effects, they lead to effects at the species level, and vice versa.

Regeneration is often a particularly vulnerable life stage. Miller and Duncan (2004) reported improved germination of the rare native outcrop plant *Pachycladon cheesemanii* with the removal of weedy vegetation. While initial germination of native trees was not affected by the presence of an invasive grass, *Melinis minutiflora*, seedling survival was reduced by over 50% in plots dominated by the invasive species, compared with plots dominated by native grasses (Hoffmann and Haridasan 2008). Similarly, a reduction in cover of the exotic weed *Tradescantia fluminensis* led to increased abundance and species richness of native seedlings in New Zealand native forest (Standish, Robertson et al. 2001). Native sapling growth in a suburban New Jersey forest was also significantly impaired by the presence of the invasive *Acer plantanoides* as competing saplings, or, more importantly, as a canopy species (Galbraith-Kent and Handel 2008). Weeds may thus cause local species losses or range contractions by impairing regeneration, as well as growth, of native species.

Invasion of a system by exotic plants, and associated changes in recruitment and growth of indigenous species, as discussed above, may lead to community and ecosystem level effects, including altered plant community composition and associated habitat for higher trophic levels, altered ecosystem processes such as decomposition rates and disturbance regimes, and facilitation of other invasive species.

Domination of a plant community by an invasive species alters, and often simplifies, plant communities. For instance, *Acacia longifolia* dominated Portuguese dune ecosystems where it was present, increasing total cover, and decreasing plant species richness (Marchante 2003). Changes in plant community composition and structure may have flow-on effects on animal communities. For instance, arthropod abundance was lower on the invasive vine *Vincetoxicum rossicum* than on two native plants in Ottawa old fields (Ernst and Cappuccino 2005). Similarly, stands of the exotic weed *Mimosa pigra* supported lower abundances of bird and lizard species compared with native sedgeland habitat (Braithwaite, Lonsdale et al. 1989). Simplified communities may suffer a loss of functional diversity, potentially reducing community stability and resistance to environmental change (Olden 2004).

At the ecosystem level, exotic plant species may alter processes such as disturbance regimes and decomposition, which in turn are likely to have effects at community and other levels. One way in which disturbance regimes may be altered by exotic plant species (often grasses) is through increased fuel loads leading to increased frequency and intensity of fires, potentially altering community composition in favour of species able to rapidly regenerate after fire, as well as changing other physical parameters such as soil nutrient levels (D'Antonio and Vitousek 1992; Mack and D'Antonio 1998;

Stoner, Adams et al. 2004). The reverse may also occur, as with the decreased frequency and intensity of fires following invasion of Australian flood plains by the exotic weed *Mimosa pigra* (Mack and D'Antonio 1998).

Another ecosystem process that can be altered by exotic plant invasions is decomposition. Leaf litter decayed faster, and soils contained higher levels of available nitrogen beneath the exotic herb *Tradescantia fluminensis* than under uninfested plots in New Zealand native forest (Standish, Williams et al. 2004). Bitou bush (*Chrysanthemoides monilifera* ssp. *rotundata*) similarly elevated decomposition rates compared with uninvaded coastal vegetation by altering microclimatic conditions such as temperature and humidity, which influence decomposition rates (Lindsay and French 2004). Such changes in ecosystem processes may also facilitate invasions by other exotic species. The nitrogen fixing invasive shrub, *Myrica faya* may facilitate invasion of other exotic weeds in naturally nutrient poor areas by increasing soil nitrogen levels (Vitousek and Walker 1989). This process, where introduced species interact with other introduced species, facilitating one another’s invasion and/or impact, is known as ‘invasional meltdown’ (Simberloff and Von Holle 1999). Similarly, the spread of exotic plants is often aided by the presence of their exotic pollinators or seed dispersers, and vice versa (Simberloff and Von Holle 1999).

1.2.3 Characteristics of Invasive species

The ability of a plant to invade an ecosystem is influenced by characteristics of both the invading plant, and the receiving ecosystem (Pysek and Prach 1994; Williamson and Fitter 1996). Baker (1965) proposed a list of characteristics of the ‘ideal’ weed, including vegetative reproduction, a short juvenile stage, tall growth form and a high tolerance of environmental variation, although no one species is likely to possess them all.

Vegetative reproduction has been found to be positively correlated with invasiveness (Kolar 2001). For instance, with 40% of invasive plants in Hungarian natural systems reproducing vegetatively, this trait was over-represented among invasive plants compared with non-invasive species (Balogh, Botta-Dukat et al. 2003). Vegetative reproduction conveys a number of advantages, including efficient short distance dispersal and site occupation (Balogh, Botta-Dukat et al. 2003). Champion and Clayton (2003) acknowledge the importance of effective dispersal, listing it as a risk factor in assessing invasiveness of aquatic weeds in New Zealand. The factors influencing an 'ideal' weed may be different in aquatic compared with terrestrial environments (Ashton and Mitchell 1989). Asexual methods of reproduction predominate in most aquatic taxa, as sexual reproduction may be difficult in this medium, whereas vegetative fragments have particularly high dispersal potential in water (Grace 1993). A short juvenile stage is also linked to invasiveness (Kolar 2001). Another advantage of reproducing by vegetative fragmentation, is that the non-reproductive juvenile stage can effectively last as long as it takes to grow only a single new leaf node.

Growth form may also be a factor in invasive potential, with invasive species tending to be taller than non-invasive species of comparable life-form (Williamson and Fitter 1996; Reid 1998; Balogh, Botta-Dukat et al. 2003). This is likely to convey an advantage in light capture and shading of competing vegetation. Species also vary in their ability to cope with low light levels. Invaders of forested systems in particular may have lower light requirements than non-invasive species (Balogh, Botta-Dukat et al. 2003).

The ability to tolerate a wide variety of environmental conditions is another key characteristic of many invasive species (Baker 1965; Champion and Clayton 2003). A large native latitudinal range, implying wide environmental tolerance, was positively correlated with invasiveness amongst New England exotic plants (Herron, Martine et al. 2007). Wide environmental tolerance may be particularly important in the survival and spread phases of invasion, following the primary role of reproductive traits in dispersal and establishment (Ashton and Mitchell 1989).

A history of weediness elsewhere, or weediness in closely related species can both be used for predicting invasiveness (Herron, Martine et al. 2007). As previously noted, weediness is not evenly distributed among taxa. Poaceae and Fabaceae are the two families most prominently over-represented amongst invaders of natural areas, while a number of families, including Poaceae, Cyperaceae and Amaranthaceae are over-represented amongst invaders of cultivated land (Daehler 1998). Aquatic families also tend to contain disproportionate numbers of invasive species (Daehler 1998).

Propagule pressure is another factor strongly influencing the invasiveness of plant species. Williamson and Fitter (1996) make the distinction between human and plant based propagule pressure. Many plants are deliberately introduced by humans, with invasiveness positively correlated to introduction effort. The more times a species has been introduced to an area, the more likely it is to have become invasive (Kolar 2001). Accidental introductions often occur as a result of human activity, with the number of human visitors being the strongest correlate of invasions into reserves (Williamson 1996). Natural, or plant based, propagule pressure can also be important in successful invasion. For example, *Rhamnus cathartica* propagule pressure from local trees had a large positive effect on *R. cathartica* seedling cover (Knight and Reich 2005). Similarly, downstream vegetation patches can have more invading species, possibly due to a combination of increased propagule pressure and resource availability downstream (Levine 2000).

1.2.4 Characteristics of invadible environments

In addition to characteristics of the invading species, characteristics of the receiving environment play an important role in invasion success. Relevant characteristics include suitability (i.e. whether the receiving environment fulfils the basic environmental requirements of the invading species), disturbance regime and resource availability, diversity and composition of existing plant communities, and the presence or absence of natural enemies.

1.2.5 Disturbance and invasibility

Disturbance is recognised as a key process in community composition and succession in natural communities (White and Pickett 1985). A disturbance may be defined as any relatively discrete event in time that disrupts ecosystem, community or population structure, and changes resources, substrate availability or the physical environment (White and Pickett 1985). In practise this often means removal of plant biomass, and/or soil disturbance. Disturbance may increase the availability of resources such as nutrients or light by reducing the amount of the resource used by existing vegetation (e.g. by removal of vegetation), or by input of additional resources into the system (e.g. nutrient input by fertilization) (Fox and Fox 1986; Davis, Grime et al. 2000). Increases in available, unused resources generally increase community invasibility (Davis, Grime et al. 2000). However, it is worth noting that some invasive plants increase nutrient levels in soils, thus facilitating their own invasion (Ehrenfeld 2003). Environments which experience periodic disturbances (i.e. fluctuating resource levels) may be more at risk of invasion than those with stable resource levels, as resident vegetation is less able to consistently utilise all available resources (Davis, Grime et al. 2000). Riparian areas may be particularly vulnerable to invasion, due to periodic flooding disturbance (Pysek and Prach 1994).

In addition to natural forms of disturbance such as flooding, human activities often greatly increase disturbance levels. For instance, forest cover has been substantially reduced following colonisation of New Zealand, greatly increasing the amount of light available to many plant communities, while soil disturbance associated with many human activities regularly creates bare sites with little competition from existing vegetation. Human induced disturbance may also create environmental conditions which native species are less well suited to, decreasing their competitive ability relative to some introduced species (Keane and Crawley 2002). Weed invasion tends to be disproportionately concentrated in certain ecosystem types. Weeds are considered a risk factor for 31% of threatened plant species in wetland habitats in New Zealand, compared with only 4% of threatened plants in alpine habitats, where weed invasion is typically lower (Reid 1998). This is likely to in part reflect greater levels of human activity in, and disturbance of, wetland compared with alpine habitats, although differences in other environmental factors such climate and nutrient status may also contribute to this observed effect.

1.2.6 Species richness and invasibility

Just as disturbed environments with increased levels of unused resources may be expected to be more easily invaded, it has been predicted that more diverse, species rich communities should be less easily invaded than species poor communities (Elton 1958). This is because a greater diversity of species may be expected to more fully use all available resources, due to resource use complementarities, thus leaving fewer resources available for the invading species (van Ruijven 2003). This hypothesis has been supported by a number of manipulative experiments, which have shown reduced numbers and performance of invading species with increased resident species diversity (Naeem 2000; Milbau, Nijs et al. 2003; van Ruijven 2003).

However, the apparent effect of species richness on invasibility in some manipulative experiments may have resulted from a ‘sampling effect’; the more species included in a treatment, the higher the chances of a particularly competitive species being included, which can successfully compete with the invading species (Wardle 2001). For instance, the increasing frequency of inclusion of *Leucanthemum vulgare* in more diverse treatments was found to be driving the apparent reduction in *Erigeron canadensis* invasion with increasing species richness (van Ruijven 2003). Thus the effect is arguably not one of species richness per se, but rather driven by a particular species (Wardle 2001). Nevertheless, as previously noted, simplified communities may be less stable and resilient to environmental changes, and thus, even if invasion resistance is driven primarily by one highly competitive species under present conditions, species richness may be important in providing invasion resistance in the longer-term, under changing environmental conditions (Loreau, Naeem et al. 2001).

Alligator weed biomass was lower in species rich treatments than in a monoculture of the strongest competitor (Xu 2004). This author therefore considered that functional group richness did have a role in decreasing invasibility. Functional group richness, rather than overall species richness was found to be inversely correlated to alligator weed invasion success (Xu 2004). This is consistent with the theory of resource use complementarity, as species from different functional groups could be expected to exploit resources more differently than species from the same functional group.

Despite some support from manipulative experiments, Elton’s species richness theory has often not been supported by observational studies, many of which have demonstrated higher levels of invasion in species rich, rather than species poor communities (Levine 2000; Byers and Noonburg 2003). However, this may be because both exotic and native species are responding to the same underlying variation of the physical environment and resources. At the landscape scale, *Rhamnus cathartica* cover was positively related to native species richness, suggesting both native and exotic species were responding to the same underlying environmental variation (Knight and Reich 2005). In contrast, at the 1 m^2 patch scale, *R. cathartica* cover was negatively related to species richness, indicating that viewed on the small scale, where environmental variation is limited, resident species diversity may indeed reduce invasion by *R. cathartica.* Davis, Grime et al (2000) note that both species poor and species rich communities are likely to be susceptible to invasion where fluctuating resource levels are out of equilibrium with existing vegetation.

1.2.7 Enemy release and invasion ability

Another mechanism that has been suggested as a contributing factor in the invasiveness of some introduced species is the enemy release hypothesis. This hypothesis suggests that, on introduction to an exotic region, some species are less regulated by herbivores or other natural enemies than in their native range, leading to increased abundance in their introduced range (Keane and Crawley 2002). This could occur when species are introduced to a new region but their natural enemies are not. The successful control of some weeds by classical biological control programmes has been used to support the enemy release hypothesis (Mack 2000). Some experimental studies have also provided support for the hypothesis, showing higher levels of herbivore damage to plants, and more substantial benefits from enemy control in plants' native compared with introduced ranges, and greater plant vigour in the introduced range (Dewalt, Denslow et al. 2004; Vila, Maron et al. 2005; Ebeling, Hensen et al. 2008). However, although supported in some cases, enemy release is unlikely to contribute to all invasions, being influenced by factors such as habitat type, enemy community in the introduced range, and degree of host plant defences against herbivory (Keane and Crawley 2002; Colautti, Ricciardi et al. 2004; Dewalt, Denslow et al. 2004).

1.3 Alligator weed

1.3.1 Species description and distribution

Alligator weed (Figure 1) is native to the Parana River area of South America (Julien 1995). As an exotic species, alligator weed is established in Australia, New Zealand, south-eastern parts of the United States of America, parts of Asia, including China, India, Thailand and Indonesia, and has more recently been recorded in southern Europe (Julien, Skarratt et al. 1995; Wagh, Ghate et al. 1995; Stewart 1996; Garbari and Pedulla 2001). Climatic conditions are predicted to allow further spread of alligator weed in regions such as Australia, New Zealand, and Europe, with parts of

Africa also potentially susceptible to invasion if the weed were to be introduced there (Julien, Skarratt et al. 1995; Stewart 1996). Alligator weed is thought to be more strongly invasive in temperate regions than in tropical or cold regions, with the optimal temperature for alligator weed growth between about 15-20ºC (Julien, Skarratt et al. 1995), although other authors found maximum shoot emergence and growth occurred at 30°C (Shen, Shen et al. 2005).

Figure 1. Potted alligator weed grown under greenhouse conditions.

Alligator weed is an herbaceous, stoloniferous perennial. A comprehensive description of morphology is provided by Julien (1995). It is not known to produce viable seed in its introduced range (Julien 1995), although viable seed has been reported from plants in the native range (Vogt 1973; Okada, Alonso et al. 1985). Reproduction in the introduced range is therefore entirely vegetative, from both root fragments and stem nodes (Julien, Skarratt et al. 1995). Consistent with its asexual reproduction, genetic diversity of alligator weed was extremely low both within and between populations in China, and also between terrestrial and aquatic habitats also in

China (Xu, Zhang et al. 2003; Ye, Li et al. 2003; Wang, Li et al. 2005; Li and Ye 2006).

A. philoxeroides was originally divided into two varieties; var. *obtusifolia*, and var. *acutifolia* (Pederson 1967). As alligator weed is highly phenotypically plastic, with single plants capable of producing both acute and obtuse leaves depending on environmental conditions, it has been argued that these varietal distinctions are unnecessary (Pederson 1967). However, subsequent work has provided some evidence of different biotypes within the species. A broad-stemmed and a narrow-stemmed biotype maintained morphological differences when grown under varying environmental conditions, with the narrow-stemmed biotype exhibiting greater susceptibility to quinclorac herbicide, possibly due to its greater leaf surface area per unit biomass (Kay and Haller 1982; Kay 1992). Furthermore, both tetraploid and hexaploide cytotypes have been reported in the native range, with the hexaploid cytotype being largely pollen sterile, and much more vigorously weedy than the tetraploid cytotype (Okada, Alonso et al. 1985).

Phenotypic variation of potted alligator weed in conditions ranging from drought to flooding, and also alligator weed growing wild in a variety of habitats in China, was ascribed to plasticity rather than genetic variation (Geng, Pan et al. 2007). Alligator weed showed greater plasticity than the non-invasive congeneric *Alternanthera sessilis* (L.) Roem. & Schult. in both greenhouse and field situations, indicating that alligator weed's plasticity aids its invasiveness by allowing it to tolerate substantial environmental variation (Geng, Pan et al. 2006; Pan, Geng et al. 2006).

1.3.2 Habitat tolerance

In the absence of biocontrol agents, alligator weed growth tends be more prolific in aquatic situations, due to factors such as eutrophication, low interspecific competition, the moderating effect of the aquatic environment on temperature, and the absence of water stress (Julien, Bourne et al. 1992). Alligator weed displays a higher tolerance of low nutrient water than a range of other aquatic weeds (Rogers and Davis 1971; Scarsbrook and Davis 1971). On land, soil moisture influenced biomass, with low lying areas more prone to invasion than drier, elevated sites (Julien, Bourne et al. 1992), and shoot emergence decreasing with decreasing rhizome water content of air-dried rhizomes (Shen, Shen et al. 2005).

Alligator weed fragments growing under low light conditions (160 µmol m^{-2} s^{-1}) in a nutrient solution developed thinner leaves, with greater surface area and a reduced maximum net rate of CO^2 uptake compared with plants grown under high light conditions (790 µmol m^{-2} s^{-1}) (Longstreth, Bolanos et al. 1985). Fragment dry weight exhibited a negative linear relationship to light intensity, with the lowest light treatment imposed averaging 160 µmol m^{-2} s^{-1} (Longstreth and Mason 1984). This model predicted that growth would be zero at approximately 5 mol m^{-2} day^{-1}, or an average of 99 µmol m^{-2} s^{-1} over a 14 hour photoperiod. However, Quimby and Kay (1977) found that in nutrient solution, emersed nodes produced similar root and shoot growth whether grown in light or dark, while Shen, Shen et al (2005) found no difference in shoot emergence, plant height or biomass between fragments planted in light or dark.

Total leaf area and dry weight decreased as salinity increased from 0 to 400 mol m^{-3} NaCl. Increased leaf thickness and a corresponding reduction in leaf area per unit dry weight may have reduced water loss due to osmosis (Longstreth, Bolanos et al. 1984). Alligator weed cells grown in nutrient media with 100 mM NaCl showed slower development of photosynthetic capacity than control cells, leading to fresh weight reductions of 20% after 14 days compared with control cells with no salt added (Mudalige and Longstreth 2006).

Alligator weed suspension cells had greater salinity tolerance than tobacco cells (Balagtas-Burow, Moroney et al. 1993). Similarly, alligator weed appears to be more tolerant of salinity than water hyacinth, with alligator weed gaining a competitive advantage over water hyacinth with increasing salinity (Gangstad 1975). Alligator weed has been noted growing in upper estuarine situations both in New Zealand and Australia (Julien 1995; Stewart 1996), and infestations along Auckland's West Coast may have resulted from floating mats being washed down the coast from the Kaipara region, indicating an ability to tolerate seawater for short periods. Hockley (1974) suggested that alligator weed is able to tolerate salinity up to 10% salt by volume, while Burkhalter, Curtis et al (1972) suggested tolerance of up to 10% of sea strength in still water, and 30% in flowing water. However, in neither case are the primary sources of this information clear.

1.3.3 History and distribution in New Zealand

Alligator weed was first recorded in New Zealand in 1906 (as *Teleanthera* sp*;* see Julien (1995) for previous taxonomy), near the Northern Wairoa River, Dargaville, and is thought to have arrived in the country in ship's ballast (Cheeseman 1906). Viable seed has not been recorded in New Zealand, with the plant spreading by vegetative propagation.

Alligator weed is established in both aquatic and terrestrial situations in New Zealand. Once established within a waterway, alligator weed spreads by stem or root fragments washing downstream. Dispersal between waterways has often been assisted by human movement of boating, fishing and drain clearing equipment (Sainty, McCorkelle et al. 1998). Dispersal into terrestrial habitats may occur as a result of fragments being deposited during floods, or being transported by stock movement. Disposal of weed material following clearance of waterways, and transporting infested soil or turf between sites may also lead to terrestrial invasions (Environment Waikato Biosecurity Group 2005). Several hundred terrestrial infestations throughout Australia occurred as a result of Sri Lankan communities cultivating the plant as a traditional vegetable, having mis-identified it as *A. sessilis* (Gunasekera and Bonila 2001). In New Zealand, alligator weed is widely established in Northland and Auckland, especially around the Kaipara Harbour, and is invading the Waikato and Bay of Plenty regions (Environment Waikato Biosecurity Group 2005).

1.3.4 Legal status

In New Zealand, alligator weed is listed as an Unwanted Organism under the Biosecurity Act 1993 (Anon 2005), and is included on the National Pest Plant Accord List (Anon 2002a). This bans the sale, propagation and distribution of alligator weed throughout New Zealand, with Regional Councils responsible for surveillance within their jurisdiction to enforce this (Anon 2002a). Alligator weed is classified as an Eradication Plant Pest by the Waikato Regional Council, with the council undertaking eradication work with a goal of zero density by 2017 (Environment Waikato 2002). In Australia, alligator weed is classified as a Weed of National Significance (WONS), obliging landholders to control the weed on their property (Anon 2003).

1.3.5 Alligator weed impacts

Alligator weed is considered an economic and potentially also an environmental weed. It has many well documented negative impacts on human activities, including agricultural and horticultural industries, recreational water use, and flood control. Alligator weed also has potential ecological impacts, although these are less well understood.

Growth of alligator weed in drainage channels impedes water flow, increases sedimentation, and exacerbates flooding. Flood damage to structures such as fences may also be increased by the weight of dense mats of weed washing up against them (Philip, Winks et al. 1988; Julien 1995).

Alligator weed steadily increased in occurrence and biomass in pasture during a nine year study in Australia (Julien, Bourne et al. 1992). This was accompanied by a decrease in other plant species, with the authors concluding that alligator weed was competitively displacing pasture species. Grazing by stock reduced apical dominance; stem density increased by 40% (Julien, Bourne et al. 1992). While grazing reduced top biomass by 27%, there was no overall reduction in biomass, implying an increase in allocation to roots.

In addition to displacing valuable pasture species, alligator weed has been linked to photosensitivity in stock, particularly young calves (Anon 1989; Bourke and Rayward 2003). Photosensitivity does not always occur, particularly where adult stock are concerned, with older literature describing alligator weed as an excellent supplementary feed for cattle in America (Alford 1952; Maddox, Andres et al. 1971). The cause of the photosensitivity reaction is unclear, however it has been suggested that a second factor associated with the weed, such as a fungus, rather than the weed itself may explain the inconsistency of this reaction (Bourke and Rayward 2003).

Horticultural crops such as kumara (*Ipomoea batatas*) and rice (*Oryza sativa*) may be invaded by alligator weed (Graham 1976; Vogt, Quimby et al. 1992). Yield losses estimated for various crop species range up to 45% for rice (Shen, Shen et al. 2005). In New South Wales, the transport or sale of soil from land containing alligator weed is prohibited, with alligator weed infestations resulting in the closure of the turf industry in parts of New South Wales (Julien 1995; Anon 2003).

Recreational water use may be affected by the presence of alligator weed, with dense mats impeding boat access, and decreasing the aesthetic appeal of the water for activities such as swimming. Mosquito populations may benefit from habitat provided by alligator weed (Clark 1969; Mitchell 1978). While less of an issue in New Zealand than in countries with mosquito-borne diseases, the presence of southern salt marsh mosquitoes in the Kaipara region illustrates the potential of this to become more of a concern if mosquito borne diseases do establish in New Zealand in the future. Such a scenario demonstrates the potential for alligator weed to facilitate an ‘invasional meltdown’.

While the economic and human use impacts of alligator weed are numerous and well documented, there has been little research into its ecological impacts. Alligator weed is widely recognised as an aggressive competitor, based largely on research comparing it to agricultural or other invasive plant species (Mitchell 1978; Parsons and Cuthbertson 1992; Julien 1995). By extension it is therefore considered likely to disrupt the ecology of banks and shallows by decreasing plant diversity, and altering abiotic conditions such as river flows and light penetration of the water (Julien 1995;

Timmins and Mackenzie 1995). Alligator weed mats in China sampled for co-occurring native vegetation were found to contain 13 native plant species, mostly floating or submersed species (Liu and Yu 2005). Large amounts of decaying plant matter resulting from herbicide application may also deplete oxygen levels in waterways (Hockley 1974; Coffey 1981). Timmins and Mackenzie (1995) suggest loss of spawning sites for native fish, such as inanga, would be a possible consequence of alligator weed invasion in New Zealand. However, there is little research, either in New Zealand or overseas, describing the ecological impacts of alligator weed with regard to native communities.

1.4 Control methods for alligator weed

A range of mechanical, chemical and biological control options are used to manage alligator weed infestations. However, eradication is rarely feasible, except for very small infestations, and control to date is patchy, with all options having their limitations.

1.4.1 Manual control

Mechanical or manual control methods are sometimes used to control alligator weed in aquatic situations and drainage channels. While this may provide relief in the short-term, it has the potential to further the weed's spread in the longer-term, as fragments resulting from mechanical harvesting are likely to establish downstream (Julien 1995). Inappropriate disposal of harvested material also has the potential to spread the weed to new sites. Similarly, cultivation may fragment and spread alligator weed in terrestrial situations. Sainty, McCorkelle et al (1998) suggest that mechanical or manual control techniques be used only for small infestations, where *all* above- and below-ground material can be removed. Alligator weed plants subjected to simulated mowing under greenhouse conditions compensated by re-growing with a higher root to shoot ratio, a higher stem to leaf ratio, and a more prostrate growth form, characteristics which reduce the energetic cost of subsequent mowing or grazing events (Wilson, Yeates et al. 2007). Consequently, mowing or grazing tend to have little impact on alligator weed biomass (Julien, Bourne et al. 1992).

1.4.2 Chemical control

Considerable research has addressed the chemical control of alligator weed (e.g. (Gangstad 1978; Bowmer, McCorkelle et al. 1991; Bowmer and Eberbach 1993). Alligator weed poorly translocates herbicides to underground storage tissue, or to quiescent submerged nodes (Eberbach, Bowmer et al. 1990; Bowmer, Eberbach et al. 1993). Herbicides therefore commonly scorch emergent foliage, but fail to kill the plant, which subsequently resprouts. Rhizome glyphosate concentrations reached inhibiting levels in small, short day length plants, but did not reach critical levels in larger plants grown under long day lengths (Bowmer and Eberbach 1993). Where non-selective herbicides such as glyphosate or dichlobenil remove competing vegetation, alligator weed may even increase in dominance (pers. obs). Control may be more effective where competing vegetation is present and able to suppress regrowth following use of selective herbicides such as metsulfuron (Bowmer, McCorkelle et al. 1989). Eradication is not generally achieved by herbicide use, with repeated applications of herbicide required to maintain control. Herbicide control of aquatic alligator weed is further limited, as many herbicides are not registered for use over water.

1.4.3 Biological control

Simulated herbivory (repeated leaf removal) was found to be more effective at reducing alligator weed above- and below-ground biomass, and at depleting tissue nutrient levels, than either one-off removal of the same total amount of shoot biomass, simulating mowing, or a one-off herbicide application (Schooler, Yeates et al. 2006). However, even under intense repeated defoliation plants continued to accumulate biomass, albeit at reduced rates compared with control plants. Schooler, Yeates et al (2006) therefore predicted that defoliation alone may not be able to control alligator weed, with other control methods, potentially including root feeding biocontrol agents, needed in order to achieve successful control. However, actual herbivory was found to be somewhat more damaging to alligator weed than simulated herbivory restricted to leaf removal, due to stem damage and targeted feeding on new leaves (Schooler, Baron et al. 2006). The previous study may therefore have underestimated the efficacy of some leaf-feeding biocontrol agents.

Three biological control agents have been introduced into New Zealand for control of alligator weed. Of these, the alligator weed flea beetle, *Agasicles hygrophila* (Chrysomelidae) has been the most effective agent. Introduced to sites in the Auckland and Northland regions between 1981 and 1984 (Roberts, Winks et al. 1984a), *A. hygrophila* is now present at alligator weed infestations throughout Northland and Auckland, but has not been recorded at the Bay of Plenty infestations (C. Winks, W. Mead pers.com).

Adult beetles defoliate the plant, and larvae pupate within the stems. *A. hygrophila* has achieved substantial control of emergent alligator weed in still bodies of water such as lakes and dams, and may provide some control in drains. It does not effectively control alligator weed in fast flowing water or areas with frequent flooding, as the beetle is washed away (Coulson 1977; Roberts, Winks et al. 1984a). *A. hygrophila* is also unable to establish on terrestrial infestations, possibly due to the beetle's high humidity requirements (Maddox, Andres et al. 1971; Vogt, Quimby et al. 1992), although it has also been suggested that narrow, lignified stems may restrict pupation of *A. hygrophila* in terrestrial situations (Kay and Haller 1982). The Liverpool City Council in Australia was able to cease herbicide control of alligator weed two years after introduction of the flea beetle to the area (Page and Lacey 2006). This represents an annual saving of around AU$26,000 per annum, as well as reducing the application of chemicals into the environment, illustrating the potential benefits of biological control where it is successful (Page and Lacey 2006).

Globally, *A. hygrophila* is predicted to have a more restricted, temperate distribution than alligator weed, being less adapted to both hot and cold extremes (Julien, Skarratt et al. 1995). Stewart (1996) predicted many North Island locations that may potentially support alligator weed are unlikely to support over-wintering populations of *A. hygrophila*, with all South Island sites unsuitable for the beetle to establish under current climatic conditions. Many other North Island sites may support populations at levels too low to exert substantial control of alligator weed.

The stem-boring moth *Arcolla malloi* (Phycitidae) (formerly *Vogtia malloi*) was initially released to Northland and North Auckland sites in 1984 (Roberts, Winks et al. 1984b), with further releases between 1987 and 1988 (Philip, Winks et al. 1988). *A. malloi* causes distinctive wilting of the stem. As a moth with juvenile stages feeding within hollow alligator weed stems, this species may be less vulnerable to flooding than *A. hygrophila*, which spends most of its lifecycle on the outside of the plant (Roberts, Winks et al. 1984b). While there is little information on the distribution and effectiveness of *A. malloi* in New Zealand (Stewart 1996), it appears to be less common and to have less impact than *A. hygrophila* (pers. obs).

Another beetle, *Disonycha argentinensis* (Chrysomelidae), was released at 17 sites between 1982 and 1984, but failed to establish (Roberts, Winks et al. 1984a). Australian releases in 1980 also failed to establish populations of *D. argentinensis* (Julien 1995). The reasons for this failure are not known. Research is ongoing to establish the cause of previous failures. This might then enable successful future releases, which would aid control as *D. argentinensis* is expected to be more tolerant than *A. hygrophila* of terrestrial situations (Vogt 1973). Research into other potential invertebrate biological control agents is also ongoing. For instance, flea beetles in the genus *Systena*, recorded on alligator weed in its native range, have also been described and investigated for their potential to control alligator weed (Cabrera, Sosa et al. 2005).

There has been considerable research into pathogens with potential as biocontrol agents for alligator weed. A fungus, *Nimbya alternantherae* (Ascomycota), isolated from alligator weed in Brazil, the United States and Puerto Rico, provided significant control of inoculated alligator weed plants under both greenhouse and field conditions (Pomella, Barreto et al. 2007). However, host specificity testing indicated susceptibility of several other plant species, including crops such as spinach which belong to closely related families (Pomella, Barreto et al. 2007). A fungus identified as *Fusarium* sp. (Ascomycota) was isolated from alligator weed plants in China. Inoculation of greenhouse and field grown alligator weed with the *Fusarium* pathogen resulted in mortality within two weeks, indicating strong potential for development as a mycoherbicide (Tan, Li et al. 2002). Inoculation with the pathogen *Sclerotinia sclerotiorum* (Ascomycota) resulted in some increase in shoot necrosis, and so the pathogen is also considered a possible candidate for development as a mycoherbicide against alligator weed (Waipara, Bourdot et al. 2006).

1.5 Thesis aims

Alligator weed is a highly invasive plant, with numerous, well documented impacts on human activities, as discussed in the preceding sections. Although it is also recognised as having potential ecological impacts, there has been little research addressing this issue. This thesis therefore aimed to investigate the potential effects of alligator weed on decomposition and nutrient cycling, as well as on invertebrate and plant communities in a "native" ecosystem, thus integrating effects on both ecosystem processes and community composition. In addition, control of alligator weed is often unsuccessful due to factors such as herbicide resistance. This thesis therefore also sought to investigate the potential of shading as a method of cultural control of alligator weed. Chapters were written as standalone publications. There is therefore some repetition, for instance of site descriptions, among chapters.

Specifically, this thesis tested the following broad hypotheses:

1) That shading will reduce alligator weed growth, but that the presence or absence of interspecific competition and clonal support from unshaded areas will influence the efficacy of shading as a control method.

2) That alligator weed differs in decomposition and biomass dynamics from native vegetation.

3) That differences in decomposition dynamics between alligator weed and native vegetation will have flow-on effects on invertebrate communities.

4) That as an exotic plant species, alligator weed will represent a poorer quality habitat for native invertebrates, particularly habitat specialists, than that provided by native vegetation. Further, that differences in invertebrate communities between alligator weed and native vegetation will reflect differences in plant characteristics such as architecture and chemistry.

5) That alligator weed invasion will be associated with negative impacts on native vegetation, such as reduced native species richness and cover.

2 CLONAL SUPPORT AND INTERSPECIFIC COMPETITION AS POTENTIAL INFLUENCES ON GROWTH OF AN INVASIVE PLANT IN SHADED ENVIRONMENTS

2.1 Introduction

2.1.1 Disturbance and light availability

The ability of a plant species to colonise or invade a particular environment is influenced by the characteristics of the receiving environment as well as those of the invading species (Davis, Grime et al., 2000). The degree of disturbance experienced by a plant community is one of the key environmental characteristics governing community invasibility (Fox and Fox, 1986). All communities are exposed to some degree of natural disturbance, and this is recognised as affecting patterns of community colonisation and succession through fluctuating levels of resource availability and competition (White and Pickett, 1985). Disturbance may increase the availability of resources such as nutrients or light by reducing the amount of the existing resource used by vegetation (e.g. by removal of vegetation), or by input of additional resources into the system (e.g. nutrient input by fertilization) (Fox and Fox, 1986; Davis, Grime et al., 2000). Increases in available, unused resources generally increase community invasibility (Davis, Grime et al., 2000).

Human colonisation and development has resulted in substantially increased levels of disturbance in many habitats. By the late 20th century, only around 23% of New Zealand's land area was under forest cover**,** compared with around 85% before human colonisation (Taylor and Smith, 1997). This has resulted in substantially increased light penetration to many herb and shrub communities. For instance, median lighting at water level was only 2.9% of full sunlight in streams running through native forest, compared with 42% for streams running through pasture (Davies-Colley and Quinn 1998). This increase in open habitats thus facilitates the invasion of many exotic plant species that are adapted to high light environments. In recognition of this, the attainment of a closed canopy is often an early goal of ecological restoration projects or riparian management, in order to reduce the dominance of exotic weedy species at a site (Clewell, Rieger et al. 2005).

2.1.2 Plant responses to low light levels

Plants exposed to low irradiance commonly exhibit a range of shade avoidance and/or tolerance mechanisms, such as elongation of shoots, increased leaf area with low leaf mass per unit area, low chloroplast numbers and changes in chlorophyll a:b ratios. These changes enable plants to outgrow their neighbours and maximise light capture (Salter, Franklin et al. 2003). Similarly, root to shoot ratios often decrease, representing a proportional increase in allocation of resources to above-ground parts of the plant, and biomass overall also decreases (Maule, Andrews et al. 1995; Weihe 1997). With this potential to decrease plant biomass, decreasing light levels has been found to be a useful tool in managing invasive weed species such as *Tradescantia fluminensis* (Standish 2002).

However, shade tolerance varies greatly among plant species. Clonal species in particular can have an advantage invading environments with patchily distributed resources, which light levels are, particularly in riparian environments, since parts of the plant receiving abundant resources may be able to transfer resources to parts of the plant in suboptimal conditions (Friedman and Alpert 1991). For instance, shading of

Solidago canadensis ramets connected to unshaded ramets initially led to elevated photosynthesis rates in the unshaded ramets, with the resulting photosynthates being transferred to the shaded ramets (Hartnett and Bazzaz 1983).

2.1.3 Alligator weed

Alligator weed (*Alternanthera philoxeroides*, Amaranthaceae) is an aggressive, clonal invader of aquatic margins and damp ground. Alligator weed shows limited translocation of herbicides (Bowmer and Eberbach, 1993), and to date effective biological control is achieved only in aquatic environments (Sainty, McCorkelle et al., 1998). Cultural control methods, including manipulating shade and competition, may therefore be important in managing species such as alligator weed. Although restricted translocation of herbicide suggests physiological integration may be limited in this species, its capacity to share valuable resources (rather than herbicide) has not been tested.

2.1.4 Alligator weed and low light levels

Alligator weed in the field has been reported as both shade tolerant (Longstreth, Bolanos et al, 1985; Timmins and Mackenzie, 1995), and shade intolerant (Davis, Stanley et al. 1983). Laboratory observations are similarly conflicting. Grown in a nutrient solution, fragment dry weight exhibited a negative linear relationship to light intensity, down to an average of 160 µmol m^{-2} s^{-1} (Longstreth and Mason, 1984). This model predicted that alligator weed growth would cease at approximately 5 mol m^{-2} day^{-1}, equating to an average of 99 µmol m^{-2} s^{-1} over the 14-hour photoperiod used in this experiment. In contrast, emersed nodes, also in a nutrient solution, produced similar root and shoot growth whether grown in light or dark (Quimby and Kay, 1977). Although not in a replicated experiment, Gangstad (1978) reported continued growth after one year in complete darkness, suggesting a much higher degree of shade tolerance than that predicted by Longstreth and Mason (1984). Similarly, potted rhizomes grown with or without light exposure exhibited similar shoot emergence rates, plant height and biomass 20 days after planting (Shen, Shen et al. 2005).

These studies focused on shade tolerance in the absence of interspecific competition, and mostly in nutrient solutions, rather than rooted in a solid substrate under field conditions. This study aims to investigate the effects of varying light levels on alligator weed growth in field-like conditions. Specifically, the ability of alligator weed to establish and compete with other plant species is examined under light levels comparable to those of stream margins in forested environments. The role of clonal support as a mechanism for enhanced growth under patchy shade conditions is also investigated.

2.2 Methods

2.2.1 Experiment 1: Shade and competition under greenhouse conditions

The effect of varying light intensity and competition on the growth of alligator weed was evaluated in a greenhouse experiment. Three shade treatments and three competition treatments were combined in a full factorial design. The shade treatments were achieved by creating cylindrical shade cloth covers for individual pots, on wire mesh frames 500 mm high, and 350 mm diameter. These treatments were: full sun, partial shade (single layer of shade cloth, mean light level 30.6% +/- 2.4% of full sun, measured with LI-250 light meters; LI-COR Biosciences, Lincoln, Nebrasca, USA) and full shade (two layers of shade cloth, mean light level 6.7% +/- 1.6% of full sun). The partial shade treatment was within the range of light intensities at water level in pasture streams in the North Island (Davies-Colley and Quinn 1998). The mean light intensity in the fully shaded treatment was similar to the median level of light recorded for streams in *Pinus radiata* plantations (6% at water level), and is within the range of light levels reported for streams and stream edges in native forest (Maule, Andrews et al., 1995; Davies-Colley and Quinn, 1998).

As alligator weed in pastures and adjoining riparian edges most commonly competes with introduced pasture grasses, a rye grass (*Lolium perenne* L.)/ fine fescue (*Festuca ovina hirtula* L) turf was chosen for the competition treatments. The three competition treatments were no competition (bare ground), patchy, and full competition. Patchy competition was intended to simulate bare patches within pastures resulting from stock treading. Patchy and full competition were achieved by covering two diagonally opposite, or all four quarters of the pot respectively with turf grass.

Alligator weed stems were collected from a single site in northwest Auckland (36° 44.5′ S, 174° 26.7′ E) and rooted in water. For each treatment combination, eight replicate pots (diameter 180 mm, height 150 mm) were filled with King's potting mix. A single, randomly allocated alligator weed node, with 0-5 mm of stem growth and at least one leaf, was planted into the centre of each pot. Roots were 5-25 mm long at planting, measured from the node to the furthest root tip. Pots were placed in a randomised block design within the greenhouse, with temperatures varying between 12 and 30°C over the period of the experiment. Pots stood in 50 mm of water, and were surface watered every 2-3 days as required.

At the end of the four week experiment, primary shoot length was measured, along with total shoot length, which was defined as the length of the primary stem, plus the length of all lateral stems from the point of branching to the base of the furthest node.

Plants were then removed from the soil. Primary root length was measured from the basal node to the furthest root tip, and root dry mass was determined after oven drying for 24 hours at 70˚C. Root parameters were measured only for alligator weed plants grown without competition, as it was impossible to reliably disentangle alligator weed roots and grass roots where the two were grown together. Dry shoot mass was also determined for both alligator weed and grass in all treatments, again by weighing following oven-drying at 70˚C for 24 hours.

2.2.2 Experiment 2: Shade and competition under field conditions

A second experiment examined the response of alligator weed to varying light levels in a pasture situation in north-west Auckland (36˚ 44.5′ S, 174˚ 26.7′ E).

Three treatments were investigated: no shade, part shade and full shade. The no shade treatments were marked out as permanent quadrats 0.5 m x 0.4 m in size. The shade treatments were achieved by constructing wooden frames 0.5 m x 0.4 m in internal area, 1 m tall, and covered by shade cloth. The partial shade treatments were covered by two layers of 30-50% shade cloth, while the full shade treatments were covered with three layers of 50-70% shade cloth. Mean light levels, measured with LI-250 light meters, were 43.7% +/- 9.1% and 7.7% +/- 4.4% of full sun in the partial shade and full shade treatments respectively. A gap of 100 mm was left uncovered at the bottom of the sides to minimise differences in treatments resulting from altered microclimate (Saitoh, Seiwa et al. 2002), and to minimise exclusion of potential herbivores. The area was also fenced to exclude cattle for the duration of the experiment. Treatments were assigned in a stratified random design throughout the study area, with 8 replicates per treatment.

To test whether shade treatments altered other environmental variables, temperature and relative humidity as well as light were measured at 30-minute intervals by three Hobo H8 data loggers in each treatment.

As it is not possible to measure biomass extractively in the same plot both before and after an experiment, biomass was sampled from ten 0.5 x 0.4 m quadrats randomly selected from throughout the site prior to the beginning of the experiment. To provide a measure of initial biomass of both alligator weed and other plant species at the site, all above-ground vegetation was removed from within each quadrat. This was sorted into alligator weed and 'other' (being all other plant species present) and dried for 24 hours at 70˚C, and weighed to determine dry mass. Plots sampled for biomass at the beginning of the experiment were then not used in the experiment.

At the beginning and end of the experiment, all plants were identified within the treatment quadrats. Percentage cover of alligator weed and other species was estimated from random points imposed on digital photographs of each quadrat using Digital Sampling Method, Version 1.00 (Landcare Research, New Zealand) as follows: 100 points on each photograph were randomly generated and each was categorised, according to whether it scored positive for alligator weed vegetation or competing vegetation. Alligator weed percentage cover was then calculated as the sum of randomly generated points that scored positive for alligator weed vegetation. At the end of the experiment, biomass was extractively measured from all quadrats as described above.

Length of the fifth internode from the growing tip was measured for 10 randomly selected alligator weed stems from each quadrat. This internode was chosen as it was consistently reflective of the size of more mature internodes rather than the new internodes near the growing tip, but was close enough to the tip to be consistently present in all stems.

2.2.3 Experiment 3: Shade and clonal support under greenhouse conditions

An additional greenhouse experiment was conducted to clarify conflicting results from the first two experiments. Alligator weed stolons were grown in plant troughs (450 mm long, 180 mm wide and 130 mm deep), such that the end nodes of each stolon grew at each end of the trough, with the two ends being connected below ground. Three shade treatments were imposed: full shade, where the entire trough was shaded; partial shade, where half the trough was shaded; and no shade, where the entire trough was unshaded. Both shade treatments used chicken wire frames covered in shade cloth that were placed over the entire or half of the trough. The two shade treatments did not differ in shade intensity, having an overall mean photosynthetic photon flux density (PPFD) of 11.8% +/- 0.53% of full sunlight, as measured by LI-250 light meters (t-test, p = 0.081).

Plant responses were measured at only one pre-designated end of each trough (being the shaded end in the partially shaded treatment). At the start of the experiment, all plants had 2-4 stems (mean 3), each with two nodes. Troughs were arranged in a random block design within the greenhouse, and watered every 2-3 days as required. The experiment ran for six weeks. At the conclusion of the experiment total stem length and total above ground biomass were measured from the pre-designated half of each trough. Minimum and maximum temperatures were recorded for three replicates in each shade treatment, using minimum/maximum thermometers.

2.2.4 Analyses

One-way ANOVAs were used to assess the effect of a single factor on continuous data where ANOVA assumptions were satisfied. Tukey's HSD *post hoc* tests were used for pair-wise comparisons. Where multiple internodes were measured per plot in the field experiment, data were averaged for each replicate before analysis to avoid pseudoreplication (Hurlbert 1984). Where unequal variances (as indicated by Levene's tests) could not be overcome by transformation for single factor data, data were analysed using the Brown-Forsyth test which does not assume homogeneity of variance, and is relatively robust to departures from normality (Clinch and Keselman 1982). Games-Howell *post hoc* tests were used as these also do not assume homogeneity of variance. These analyses were performed in SPSS v. 15.

PERMANOVA was used to assess the effects of two factors on continuous data where unequal variances (as indicated by Levene's tests) could not be overcome by transformation, making the data unsuitable for 2-way ANOVAs. Unlike conventional ANOVAs, PERMANOVA does not assume homogeneity of variance (Anderson 2005).

Cover data were square root transformed to down-weight strongly dominant species. Bray-Curtis similarity coefficients among plots were then calculated on the transformed data. These were used to perform an ANOSIM to determine the relative similarity among treatments compared with within treatments. ANOSIM produces a global R statistic and p-value, indicative of overall differences. R statistics close to one indicate a high degree of separation of treatments, while an R value close to zero indicates there is as much variation within groups as among groups (Clarke and Warwick 2001). Pair-wise R statistics and p-values are then provided to determine where differences lie. The R statistic is at least, if not more, important than the p-value in determining whether any differences which may be detected are of a meaningful magnitude (Clarke and Warwick 2001). These results were presented graphically on a non-metric multi-dimensional scaling (nMDS) plot. Data points which fall closely together on this graph are more similar in composition than those which fall further apart. These analyses were conducted in PRIMER v. 5 (Clark and Gorley, 2001).

2.3 Results

2.3.1 Experiment 1: Shade and competition under greenhouse conditions

Primary stem length decreased with increasing shade, from a mean (± one standard error) of 262 ± 20 mm in the no shade treatment, to 26 ± 6 mm in full shade (2-way PERMANOVA; $F_{2,63} = 67.7$; $P < 0.001$, all pair-wise comparisons significant at $P < 0.001$). Increasing competition also reduced primary stem length, although less substantially than shading, from a mean of 169 ± 26 mm with no competition, to 116 ± 22 mm with full competition (2-way PERMANOVA; $F_{2,63} = 4.1$; $P = 0.022$); however, none of the pair-wise comparisons were significant. There was no evidence of an interaction between shade and competition affecting primary stem length.

Total stem length showed a similar pattern to primary stem length. However, total stem length appeared to be a more sensitive response variable than primary stem length, and there was a significant interaction between shade and competition (2-way PERMANOVA; $F_{4,63} = 3.3$; $P = 0.019$, Figure 2). In the absence of competition, light levels explained 88% of the variation in alligator weed total shoot length, with all *post hoc* pair-wise comparisons between shade levels significant at $P < 0.001$ (Figure 3). If this relationship extended outside the range of shade levels studied, light levels would have to be reduced to 0.24% of full sun to restrict alligator weed stem length to zero in the absence of competition.

With part or full competition, both part and full shade treatments differed from the no-shade treatment ($P < 0.01$ and < 0.001 respectively with part competition and $P = 0.014$ and < 0.001 respectively with full competition).

Without shade, full competition reduced total stem length (mean = 281 ± 54 mm) compared with plants without competition (mean = 568 ± 48 mm; $P < 0.01$). In contrast, under full shade, competition had no effect on total stem length.

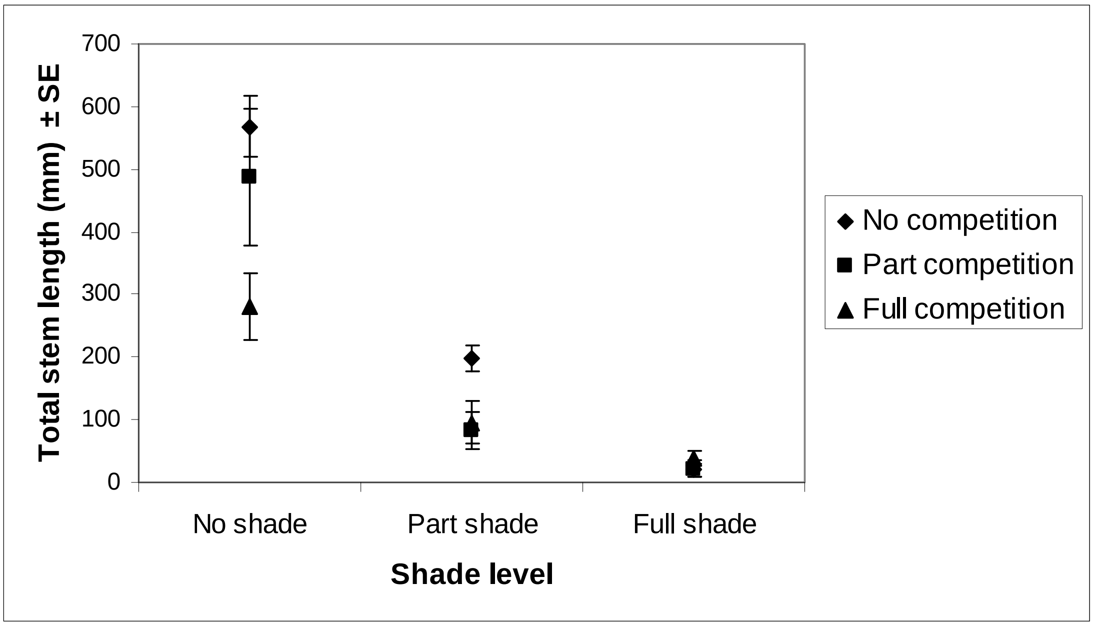

Figure 2. Effect of shade level and interspecific competition on total stem length of alligator weed plants grown under greenhouse conditions.

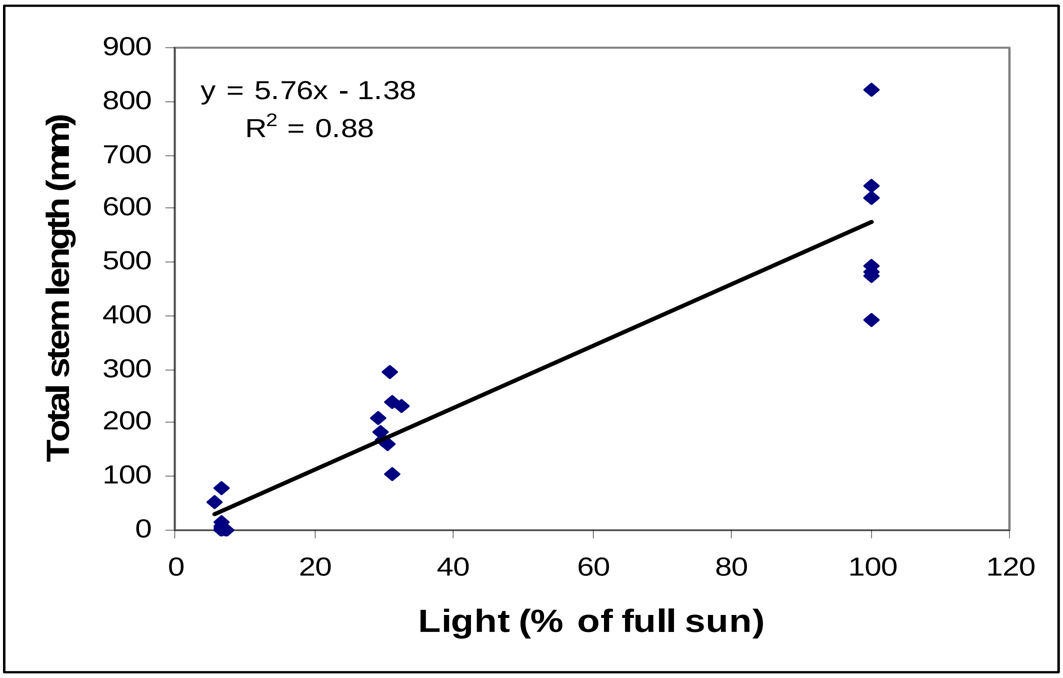

Figure 3. Relationship between light intensity and total stem length of alligator weed plants grown under greenhouse conditions in the absence of competition (Experiment 1).

Increasing shade significantly reduced shoot dry mass from a mean of 0.86 ± 0.10 g for unshaded plants to 0.15 ± 0.02 g in part shade and 0.03 ± 0.01 g in full shade. *Post hoc* tests indicated all pair-wise comparisons were different at the 0.001 level (2-way PERMANOVA, $F_{2,63} = 66.9$; $P < 0.001$). There was no evidence of an interaction between shade and competition on shoot dry weight, which did not differ among competition levels.

Primary root length in plants without competition also decreased with increasing shade level, from a mean of 274 ± 11 mm in the unshaded treatment, to 40 ± 14 mm in the full shade treatment (ANOVA, $F_{2,23} = 49.4$; $P < 0.001$). Tukey's *post hoc* tests indicated that root length in no-shade and part-shade treatments differed significantly at $P < 0.05$, while root length in full shade differed from that in both other treatments at $P < 0.001$. Root dry weight also decreased with increasing shade, dropping from a mean of 0.16 ± 0.02 g without shade to 0.001 ± 0.0005 g in full shade (Brown-Forsyth test $statistic_{2,7.3} = 45.8$, $P < 0.001$). Root dry weight differed among all shade treatments ($P \leq 0.001$ in all Games-Howell pair-wise comparisons). Root dry weight appears more sensitive to shading than primary root length, being proportionally more restricted by both intermediate and full shade. Dry weight root:shoot ratio decreased with increasing shade although this was not significant (ANOVA, $F_{2,23} = 1.9$, $P = 0.175$)

Log transformed grass dry mass also declined with increasing shade (ANOVA, $F_{2,44} = 143.8$; $P < 0.001$). All pair-wise comparisons were significantly different at $P < 0.001$ (Tukey's *post hoc* tests). Median grass dry mass dropped from 12.39 g without shade, to 0.36 g (or 2.9% of unshaded mass) under full shade. This is slightly less of a reduction than that of median alligator weed dry shoot mass, which at full shade was restricted to only 1.64% of unshaded mass. However, visual observation suggested grass was more heavily restricted than alligator weed by shading, with substantial discolouration and rotting of the grass, whereas no senescence of alligator weed shoots was observed. Comparing shoot mass over this length of time may have overestimated grass tolerance of shading, due to inclusion of dying material (although clearly dead material was removed prior to weighing). If the experiment had been continued for longer, grass shade tolerance might have compared less favourably with that of alligator weed.

2.3.2 Experiment 2: Shade and competition under field conditions

There was no difference in cover composition among the three treatments at the beginning of the experiment (Global R: -0.019; P = 0.60). However, at the end of the experiment, cover composition was differentiated on the basis of shade treatment (Global R: 0.41; P = 0.001; Figure 4). Full shade plots were distinguished from both no shade and part shade plots (pair-wise R = 0.71 and 0.49 respectively, p = 0.001 in both cases). In contrast, unshaded and partly shaded plots were not differentiated on the basis of cover composition (pair-wise R = 0.01, p = 0.38).

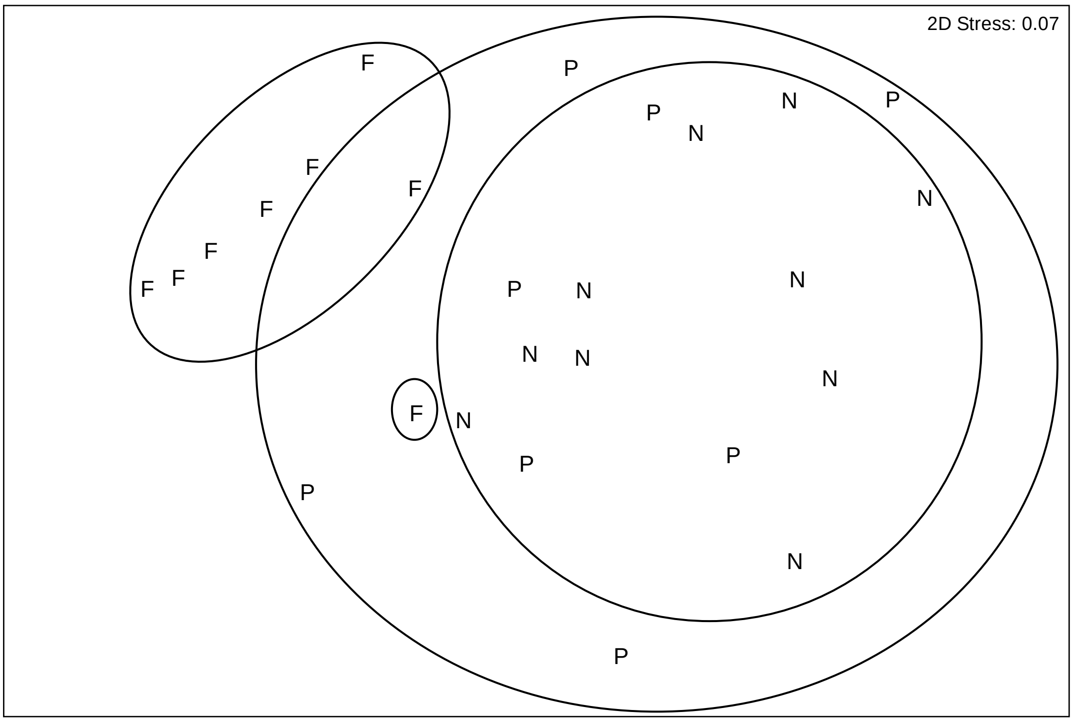

Figure 4. Separation of cover composition by shade treatment at the end of the experiment. Stress provides a measure of goodness of fit, with low stress values indicating reliable ordinations (Clarke and Warwick 2001). Data points falling close together are similar in cover composition. N = no shade, P = part shade, F = full shade.

The separation of full shade plots from unshaded and partly shaded plots reflects the higher shade tolerance of alligator weed compared with most of the other plant species present. Percentage cover of alligator weed was higher in full shade plots (mean 90 ± 3%) compared with unshaded or partly shaded plots (means 50 ± 6% and 59 ± 7% respectively, not significantly different from each other) (Brown-Forsyth test $\text{statistic}_{2,\ 12.9} = 9.08$, $P = 0.003$; Games-Howell *post hoc* tests $P < 0.001$ and < 0.05 for full shade compared with no shade and part shade respectively). Conversely, grass cover was substantially reduced in the full shade treatment compared with the unshaded and partly shaded treatments (ANOVA, $F_{2,23} = 7.1$; $P < 0.01$; Tukey's $P < 0.01$ and 0.05 respectively), with the slightly outlying F plot in the final cover nMDS (Figure 4) reflecting a higher proportion of grass in this plot compared with other full shade plots.

Alligator weed dry mass increased significantly from pre-experiment levels (mean 88 g/m^2) in all three treatments during the course of the experiment (Brown-Forsyth test $\text{statistic}_{3,19.7} = 8.2$, $P = 0.001$; Games-Howell *post hoc* tests, $P < 0.05$ in all pair-wise comparisons with initial biomass, Figure 5**).** However, there were no differences in dry mass among shade treatments at the end of the experiment (Games-Howell *post hoc* tests, $0.17 < P < 0.97$). As with percentage cover, other pasture species' dry mass followed a contrasting pattern to alligator weed dry mass (Brown-Forsyth test $\text{statistic}_{3,23.7} = 25.3$, $P < 0.001$). Dry mass of other pasture species increased during the course of the experiment in the unshaded treatment only (Games-Howell *post hoc* test, $P = 0.015$), remaining unchanged in the partly shaded treatment (Games-Howell *post hoc* test, $P = 0.95$), and decreasing substantially in the fully shaded treatment (Games-Howell *post hoc*, $P < 0.001$). As a result of the contrasting responses of alligator weed and other plant species, the proportion by mass of alligator weed in the full shade treatments (81 ± 3%) was higher than in the initial pasture (20 ± 3 %), or either the unshaded (28 ± 4%) or part shaded (32 ± 5%) treatments (ANOVA, $F_{3,31} =$

55.5; $P < 0.001$; Tukey's *post hoc* tests, $P < 0.001$ for full shade treatment compared with all other treatments).

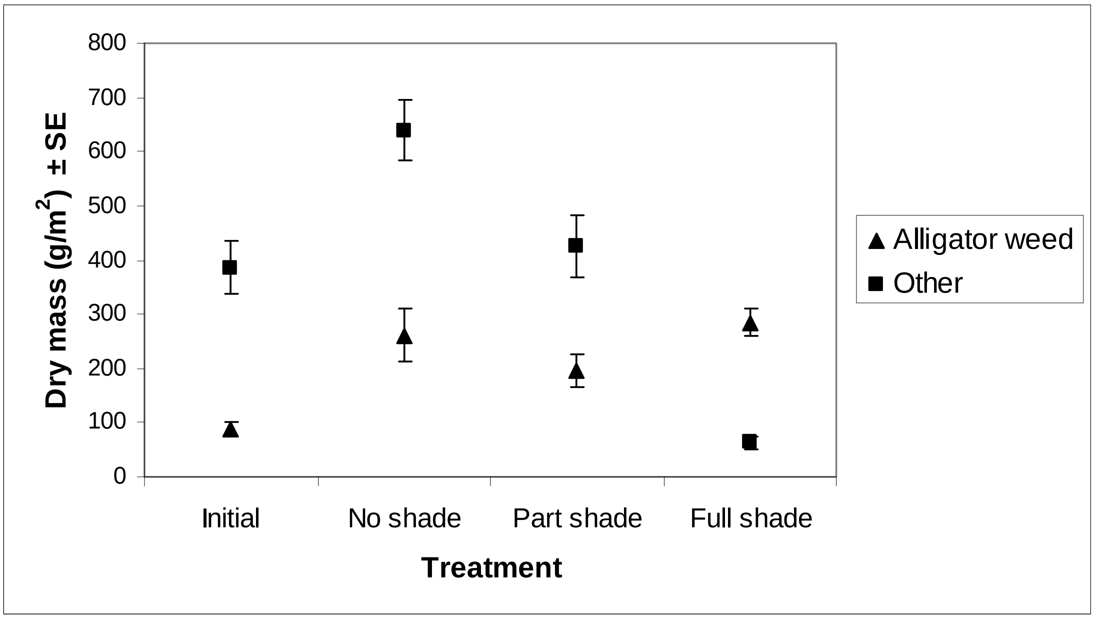

Figure 5. Above-ground biomass of alligator weed and all other vegetation at the beginning of the field experiment (Initial) and at the end of the experiment following three different shade treatments.

Length of the fifth internode below the growing tip increased with increasing shade, from a mean of 87 ± 2 mm in the unshaded treatment, to 119 ± 3 mm in full shade (ANOVA, $F_{2,23} = 15.9$; $P < 0.001$), with all treatments differing at the 0.05 level.

Mean temperature overall was higher in both shaded treatments compared with the unshaded treatment (ANOVA, $F_{2,6} = 21.7$, $P < 0.01$; Tukey's *post hoc* tests, $P < 0.01$), but did not differ between the part and full shade treatments (Tukey's *post hoc* test $P = 0.99$). Neither maximum or minimum temperatures differed among shade treatments (ANOVA, $F_{2,6} = 3.4$, $P = 0.10$ and ANOVA, $F_{2,6} = 2.7$, $P = 0.15$). Humidity was lower in the unshaded treatment (mean = 38.4 ± 0.81%) compared with either the partly or fully shaded treatments (mean = 79.4 ± 0.72 and 90.2 ± 4.9% respectively, Brown-Forsyth test statistic$_{2,2.2} = 88.4$, $P = 0.008$, Games-Howell *post hoc* tests, P <

0.05 in both cases). Humidity did not differ between the two shaded treatments (Games-Howell *post hoc* test, $P = 0.27$).

2.3.3 Experiment 3: Shade and clonal support under greenhouse conditions

Above-ground biomass differed among all shade treatments (Brown-Forsyth test $\text{statistic}_{2,7.8} = 16.2$, $P < 0.001$; Figure 6). Biomass differed most between unshaded and fully shaded plants (Games-Howell *post hoc* test $P < 0.01$), and was intermediate in shaded plants receiving clonal support from unshaded parts of the plant (Games-Howell *post hoc* tests $P < 0.05$ and 0.001 compared with unshaded and fully shaded plants respectively).

Total stem length of unshaded plants (mean = 0.77 ± 0.12 m) was greater than that of fully shaded plants (mean = 0.39 ± 0.05 m) (Kruskal Brown-Forsyth test $\text{statistic}_{2,11.2} = 6.3$, $P = 0.015$; Games-Howell *post hoc* tests $P < 0.046$). Total stem length of shaded plants receiving clonal support from unshaded plants (mean = 0.45 ± 0.05 m) did not differ from that of unshaded or fully shaded plants (Games-Howell *post hoc* tests, $P = 0.09$ and 0.66 respectively). Primary stem length did not differ between shade treatments (Brown-Forsyth test $\text{statistic}_{2,\,16.1} = 3.4$, $P = 0.72$).

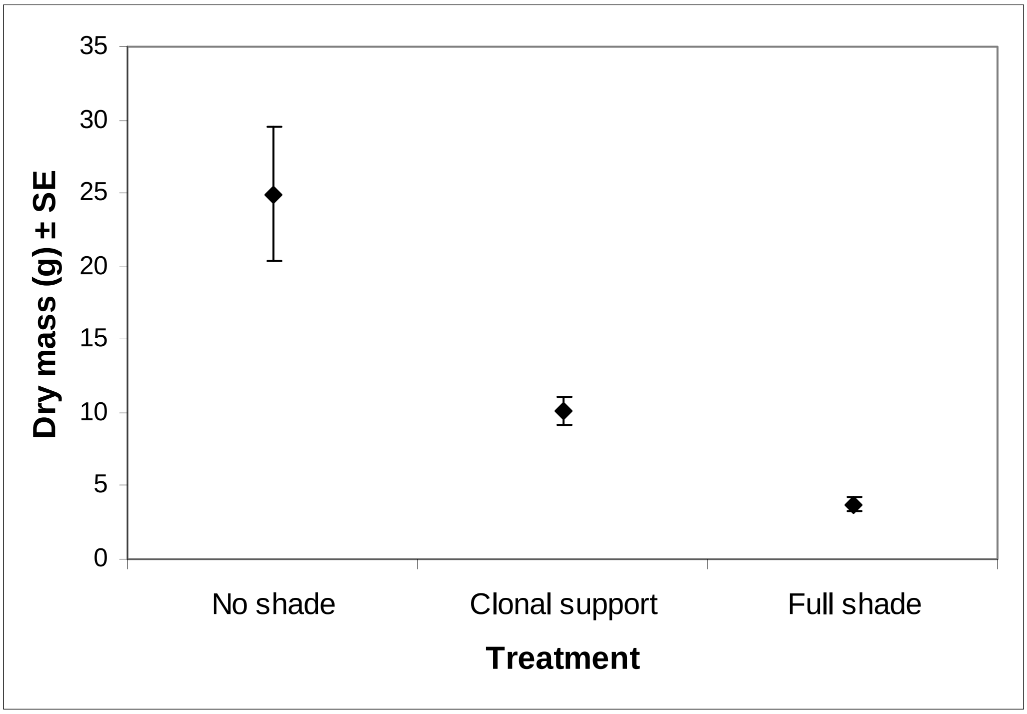

Figure 6. Effect of no shade, full shade and full shade off-set by clonal support from outside the shaded area on above-ground biomass of alligator weed plants grown under greenhouse conditions.

Neither minimum nor maximum temperature differed among shade treatments (ANOVAs, $F_{2,8} = 1.26$, $p = 0.35$ and $F_{2,8} = 1.95$, $P = 0.22$ respectively). Temperatures ranged from 8 – 31˚C.

2.4 Discussion

2.4.1 Alligator weed responses to shade under greenhouse conditions

Alligator weed showed significant reductions in growth when exposed to low light levels under greenhouse conditions. In the absence of competition, light levels explained 88% of the variation in alligator weed total stem length, while shoot dry mass in full shade pots was reduced to around 3% of the biomass of plants exposed to full sun. This is comparable to the response of *Tradescantia fluminensis* biomass, which showed an 86% drop at 2-5% of full sunlight, compared with its biomass response in full sunlight (Standish, 2002), although this was recorded over a 17-month period. Similar reductions in biomass were also observed in the invasive annual grass *Microstegium vimineum* when light levels were reduced to 16% of full light (Cole and Weltzin, 2005).

In the full shade treatment, with an average PPFD of 27 µmol m^{-2} s^{-1}, alligator weed growth continued, albeit slowly, well below 99 µmol m^{-2} s^{-1} PPFD, at which Longstreth and Mason (1984) predicted that dry weight per plant would be zero. If the relationship between total stem length and light observed in the greenhouse continued outside the range of conditions tested here, stem length would be reduced to zero at 0.24% of full sunlight. This is low even compared with the levels of shade (1 -30% of full sunlight) recorded under intact forest canopies in New Zealand (Maule, Andrews et al. 1995; Ebbett and Ogden 1998). This may indicate that, under otherwise favourable conditions, alligator weed is tolerant of lower light levels than previously reported, consistent with Timmins and Mackenzie's (1995) assessment of the plant as shade tolerant. However, it is likely that alligator weed growth would be slowed to a rate that would substantially reduce its invasibility at light levels above this compensation point.

2.4.2 Alligator weed responses to shade under field conditions

The reductions in alligator weed growth observed under shade in greenhouse conditions were not repeated in the field. In fact, full shading in the field resulted in a substantial increase in the relative dominance of alligator weed. A number of factors may have contributed to these conflicting results, including clonal support, release from competition, and changes in other environmental variables.

First, alligator weed subjected to shading in the field was linked by stolons and roots to parts of the plant outside of the shaded experimental area. The subsequent greenhouse experiment found evidence that clonal support of shaded alligator weed by unshaded parts of the plant does occur, with biomass of clonally supported plants intermediate between that of entirely shaded or unshaded plants. This indicates clonal support is likely to have been a contributing factor in the lack of differences between shaded and unshaded plants in the field, with shaded plants receiving photosynthates from outside the shaded area. An additional field experiment was initiated to test for the occurrence of clonal support under field conditions, by severing connections with unshaded parts of the plant. However, this experiment had to be abandoned due to damage by stock. Further research confirming the occurrence of clonal support under field conditions, and determining the distance over which it can occur would be useful in guiding any future attempts at control by shading.

In addition to clonal support, release from competition may have contributed to continued alligator weed growth in shaded field conditions. The first greenhouse experiment indicated that competition from pasture grasses can significantly restrict alligator weed growth in full sun. The effects of competition on alligator weed growth were no longer evident under high shade in the greenhouse. However, this is likely to reflect the rapid senescence of the competing grasses under full shade, effectively rendering the competition treatment negligible in the full shade conditions.

Similarly, all other pasture species in the field experiment, with the exception of *Ranunculus* sp., were more sensitive to shading than alligator weed was, with very few competing plants remaining in the high shade treatment. In contrast, non-alligator weed species comprised 50% of cover in the full sun treatment. As competition from pasture grasses was shown to restrict alligator weed growth, this loss of competition under shaded conditions is likely to have somewhat offset the negative effects of shading. A similar effect has been observed in herbicide trials, where alligator weed regrowth following herbicide application was luxuriant in the absence of competition, whereas in the presence of competing sedges and rushes, regrowth was suppressed (Bowmer, McCorkelle et al., 1989).

2.4.3 Potential confounding factors

These two factors, clonal support and competitive release, are thus considered likely to have played an important role in causing the non-significant effect of shading on alligator weed biomass in the field. Other factors, such as differences in other environmental variables may also have contributed to some extent. Shaded treatments tended to have warmer temperatures than unshaded plots. While alligator weed grows less vigorously in hot tropical climates than in warm temperate locations, optimal temperatures for growth are considered to be between 15 and 20 ˚C (Julien, Skarratt et al., 1995). Overall mean temperatures in both shade treatments were within this range, whereas the overall mean temperature in unshaded plots was only 12˚C. However, there was no difference in temperature between part and full shade treatments. If temperature was playing a key role in offsetting the effect of shade then we would expect to have seen decreased growth in the full shade compared with part shade treatment, as occurred in the greenhouse, given the lack of temperature differences between these two treatments. Similarly, there was no evidence of a difference in humidity between the two shaded treatments, so it is unlikely to have compensated significantly for the decrease in available light. Soil moisture was not measured in this experiment, but Benayas, Lopez-Pintor, et al. (2002) noted increases in soil moisture following artificial shading.

More favourable levels of other environmental factors such as humidity and soil moisture may therefore have counteracted some of the negative effects of shading in the field experiment, thus also contributing to the high alligator weed biomass recorded from full shade plots. However, they appear unlikely to be the primary explanation of the unexpected response of alligator weed to high shade.

2.4.4 Implications

The ability of alligator weed to support parts of the plant in suboptimal light indicates that alligator weed may have a competitive advantage invading into patchily shaded environments. Resource sharing has previously been recorded in other clonal species from a variety of life forms and taxonomic groups. Growth reductions in dwarf bamboo (*Sasa palmata*) grown under low light conditions were partially offset when connected to clone parts in full sun (Saitoh, Seiwa et al., 2002). This mechanism is thought to contribute to this species' ability to exploit canopy gaps and thus persist in a shaded understorey environment.

Under field conditions, plants will experience variations in the levels of a range of resources, rather than simply one at a time, and these resources may not vary independently (Stuefer and Hutchings 1994). In other plant species, resource sharing has also been demonstrated for nutrients such as nitrogen (Friedman and Alpert 1991), and it is possible that alligator weed is able to share more than just photosynthates. However, as previously noted, alligator weed has been shown to translocate herbicides poorly (Bowmer and Eberbach, 1993). This may indicate alligator weed is not able to utilise clonal support as effectively as some other clonal species. This could be tested by comparing clonal support of alligator weed and other clonal species grown with patchy distributions of other resources. However, it may also be that alligator weed transports herbicides and photosynthates by different pathways (e.g. xylem vs phloem). Given that clonal support does appear to have the potential to aid alligator weed growth in low light environments, if shading is considered as a control option it may be important that as much of the infestation as possible is simultaneously subjected to shade.

Artificial shading was the most effective of three methods trialed for control of *Tradescantia fluminensis* (Standish, 2002). While shading does also have the potential to reduce alligator weed growth, it may be unable to provide significant control on its own, depending on the presence or absence of shade tolerant competing species. In riparian situations, alligator weed often grows in competition with high light demanding species such as grasses. Where shade is imposed in such situations, increases in growth due to loss of competition, and facilitated by clonal support from outside the shaded area, may outweigh any reduction in growth achieved by shading. In monocultures, shade tolerances of *Carex hystericina* and the invasive *Phalaris arundinacea* appeared to be similar (Perry and Galatowitsch 2004). However, when grown in competition, *P. arundinacea* became relatively more competitive in lower light conditions. These authors therefore concluded that while reducing light levels by the establishment of a cover crop might slow *P. arundinacea* invasion, it would be unlikely to benefit the native sedge community. This highlights the importance of competition from species that are not only shade tolerant in monoculture, but are also strong competitors under these conditions.

Translocation of herbicide was greatest in larger alligator weed plants grown under long day lengths, but glyphosate concentrations in the rhizomes of these plants fell well below levels required for successful control, as the glyphosate was effectively diluted by the size of the plant (Bowmer and Eberbach, 1993). In contrast, the small biomass of plants grown under reduced day lengths led to higher concentrations of glyphosate in the rhizomes. Therefore, if shading and/or competition can reduce plant size, this may be useful in enhancing the efficacy of herbicide control.

The strong growth of alligator weed in full shade in the field suggests that, under the right conditions, alligator weed is able to grow in light levels in the range of those of both native and exotic forests within New Zealand. However, intact forest sites are seldom likely to be characterised by clonal support from unshaded areas, or lack of competition by shade tolerant species. This may, however, be influenced by a range of factors including the degree of forest fragmentation, disturbance regimes, and plant community composition. In addition to unrelated factors such as lower rates of human-mediated dispersal into forested areas than into more urbanized environments, continuous shade and the presence of shade tolerant competing species may combine to provide waterways in forested catchments with some measure of protection from alligator weed invasion.

This research illustrates how an invasive plant's attributes, such as the potential for clonal support, along with those of associated competing species, such as shade tolerance, may affect the utility of shading as a control measure.

3 ALLIGATOR WEED AND ITS BIOCONTROL AGENT JOINTLY AFFECT DECOMPOSITION DYNAMICS IN A NORTHLAND LAKE.

3.1 Introduction

3.1.1 Influence of plant traits on nutrient cycling

Invasive weeds have the potential to alter ecosystem processes such as decomposition and nutrient cycling. Nutrient cycling may be altered by weeds when their growing seasons and patterns of resource use differ from those of native vegetation. For instance, invasive plant species often share traits such as rapid growth rates, high tissue nutrient concentrations and high specific leaf area (Allison and Vitousek 2004). For example, with high photosynthetic rates, tissue nitrogen levels, and biomass, along with extended growth in the mid-dry season compared with native grasses, Gamba grass (*Andropogon gayanus*) decreased the seasonal availability of nitrate in invaded Australian savannas compared with the availability of nitrate in nearby uninvaded areas (Rossiter, Setterfield et al. 2004).

As well as altering nutrient cycling due to different patterns of growth and nutrient uptake or fixation, invasive weeds may alter nutrient cycling by changing decomposition dynamics. Those characteristics listed above often represent a trade-off of low structural or chemical defences in favour of rapid growth (Cornelissen, Perez-Harguindeguy et al. 1999). The effects of limiting defences such as leaf “toughness” may extend past senescence, facilitating rapid decomposition. Thus, leaf litter decomposition rates vary among plant species with differing chemical constituents (Boulton and Boon 1991). Substances such as lignin and cellulose are highly resistant to degradation (Rowland and Roberts 1994). Conversely, high levels of nitrogen and phosphorous have been associated with faster initial decomposition rates, as these are often limiting nutrients for microbial growth (Berg and McClaugherty 2003).

3.1.2 Weeds and nutrient cycling

The combination of traits such as rapid growth rates and high nutrient concentrations, outlined above, represents a strategy of high productivity and rapid nutrient cycling common among invasive plants. For instance, two invasive species, *Buddeleja asiatica* and *Myrica faya* had high photosynthetic rates and leaf nitrogen concentrations, and decomposed rapidly compared with two native plant species in Hawaii (Matson 1990). In contrast, many non-invasive plants, particularly evergreen species, employ a more resource-conservative strategy, producing more resistant, longer lived leaves which take longer to break down following senescence (Cornelissen, Perez-Harguindeguy et al. 1999). While many invasive plants may therefore elevate nutrient cycling rates compared with indigenous flora, some other invasive species have the reverse effect. For instance, by accumulating large amounts of above-ground biomass, and decomposing more slowly than native species, *Aegilops triuncialis* was found to slow down rates of nutrient cycling in a serpentine grassland (Drenovsky and Batten 2007). A similar pattern was recorded following *Holcus lanatus* invasion of Californian prairie (Bastow, Preisser et al 2008). This effect was attributed to reduced feeding on the invasive litter by an invertebrate decomposer compared with native litter, along with high productivity and biomass accumulation by the invasive plant.

In addition, weed invasion may alter environmental factors, such as moisture, temperature and habitat availability. Such environmental factors may in turn influence the activity of decomposing organisms so the net effect of weed invasion is a change in decomposition rates in general, not just of the invasive litter. For instance, Lindsay and French (2004) attributed elevated decomposition rates beneath introduced bitou bush (*Chrysanthemoides monilifera* ssp. *rotundata*) to altered microclimatic conditions, with the litter environment being moister and darker beneath the invasive vegetation. Similarly, leaf litter decayed faster, and soils contained higher levels of available nitrogen beneath the exotic herb *Tradescantia fluminensis* than under uninfested vegetation in New Zealand native forest, attributed to altered microclimatic conditions (Standish, Williams et al. 2004).

3.1.3 Weed biocontrol and nutrient cycling

While some attention has been given to the effects of invasive plants themselves on nutrient cycling, there has been little investigation of the role of biological control agents in altering nutrient regimes or other ecosystem processes (Denslow and D'Antonio 2005). Instead, research into non-target impacts of weed biocontrol have generally centred around feeding of biocontrol agents on non-target host species, or interactions (direct or indirect) with other invertebrate species (Paynter, Fowler et al. 2004; Louda, Rand et al. 2005). However, where biological control agents alter patterns of weed growth and senescence, they have the potential to affect ecosystem processes such as nutrient cycling. This may be particularly the case given that the aim of most biological control is to reduce weed numbers, rather than completely eradicate them, meaning that the weed and the control agent are likely to continue to co-exist and cycle together within a system indefinitely.

3.1.4 Alligator weed

Aquatic alligator weed (*Alternanthera philoxeroides*) is characterised by very rapid growth beginning in spring, forming a dense mat of vegetation over the water's surface. As a fleshy herb, the architecture of alligator weed differs markedly from that of native sedge and rush species commonly occurring in the same elevation zone in Northern New Zealand lakes. Further, the chemical composition of alligator weed was also expected to differ markedly from that of native sedge species, based on the much greater apparent "toughness" of sedge vegetation, an attribute which is linked to high levels of decomposition-retarding substances such as lignin and cellulose (Graca and Zimmer 2005).

In New Zealand, aquatic alligator weed is fed on by an introduced biological control agent, the alligator weed flea beetle (*Agasicles hygrophila*, Coleoptera: Chrysomelidae). Herbivory by the flea beetle causes rapid senescence of large amounts of aquatic alligator weed in a short period of time during summer in the warmer parts of its range (Stewart, Chapman et al. 2000). This was expected to be uncharacteristic of patterns of litter input exhibited by native vegetation in such ecosystems.

This study investigated whether rates of alligator weed decomposition differed from those of two native sedges, *Schoenoplectus tabernaemontani* and *Isolepis prolifer,* in a Northern New Zealand lake. The influence of vegetation cover type on decomposition rates was also investigated, along with the role of macroinvertebrate decomposers. In addition, biomass of alligator weed and both sedges was measured monthly to quantify litter inputs into the system.

3.2 Methods

3.2.1 Study site

Decomposition rates and biomass fluctuations were investigated in marginal vegetation at Lake Rotokawau, on the Karikari Peninsula, Northland, New Zealand (34˚52' S, 173˚19' E; Figure 7). Lake Rotokawau is 21.3 ha in area, shallow, with an iron-pan base (Champion, Wells et al. 2005). Vegetation at Lake Rotokawau is characterized by small-scale patchiness, with individual patches dominated by a single plant species, be it alligator weed or a native species (Chapter 6).

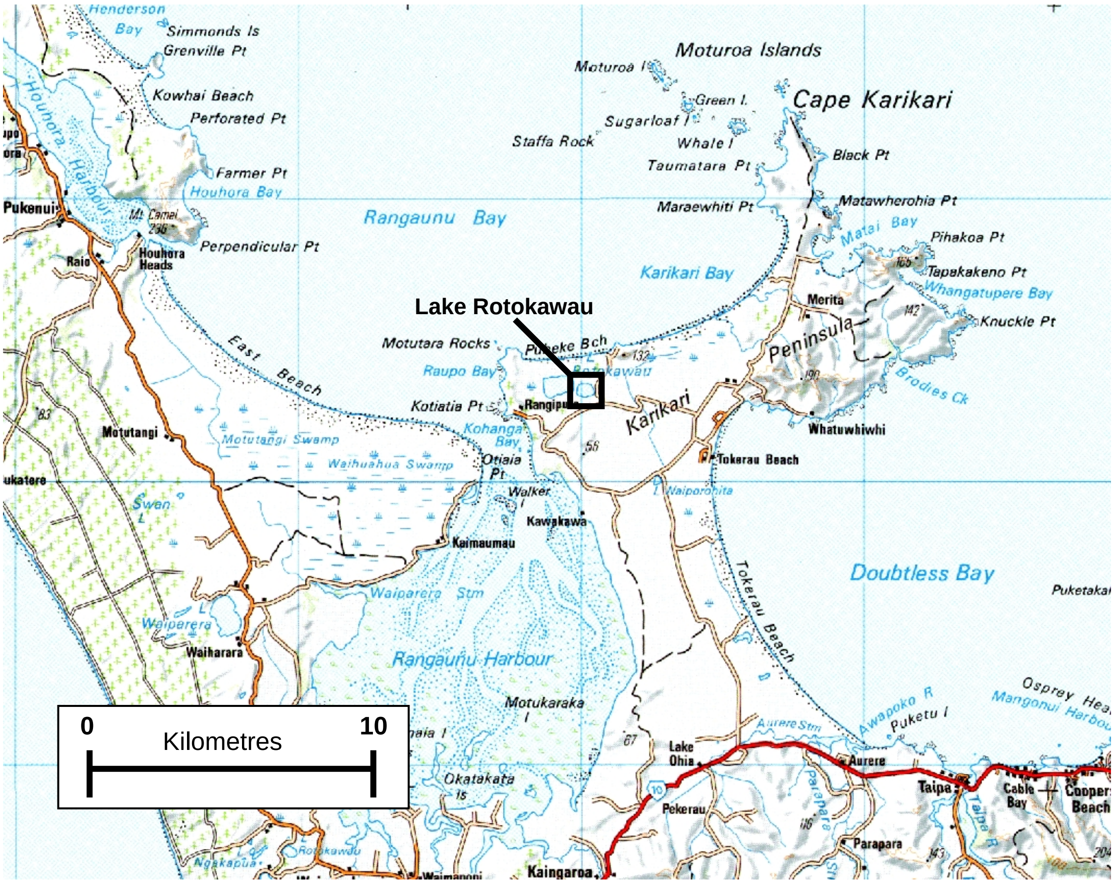

Figure 7. Location of study site; Lake Rotokawau, Karikari Peninsula, Northland, in New Zealand's upper North Island (map reference NZMS262).

3.2.2 Biomass

Seasonal variation in above-ground biomass of alligator weed at Lake Rotokawau was compared with that of two native sedge species, *Schoenoplectus tabernaemontani* and *Isolepis prolifer*. Both species are common at the site, and in similar ecosystems within the region. Above-ground biomass was harvested monthly in five replicate patches dominated by each species. Patches of the three species were interspersed, with each alligator weed patch close to a patch of at least one of the sedge species. Vegetation harvesting was achieved by removing all above-ground (including submerged) vegetation from a 0.25 x 0.25 m quadrat in each replicate patch. Due to the extractive sampling technique, each 0.0625 m^2 quadrat was sampled only once, to avoid affecting subsequent months' measurements, with a new, randomly selected quadrat sampled in each patch each month. Plant material was oven-dried at 70˚C for 24 hours, then weighed to obtain dry mass.

3.2.3 Litter bag study

Decomposition of alligator weed litter was compared with that of litter from the two native sedge species *S. tabernaemontani* and *I. prolifer*. Alligator weed litter was compared with litter from more than one native species to gain a better understanding of the difference between the invading and native litters, as there is likely to be some difference between litter of any two species. The litters of the two native species were kept separate, as combining litters from different species has been shown to alter decomposition rates (Swan and Palmer 2004), and the patchy nature of the vegetation at the site means that the litters of the two species are less likely to be decomposing together.

To investigate whether vegetation cover influenced decomposition rates of litter decomposing below it, litter of all three species was placed in bags under alligator weed vegetation. Alligator weed litter was also placed under each of the two native sedge species, and litter from each sedge species was placed under conspecific vegetation. Litter from the sedges was not placed under the other sedge species as this was not relevant to the question of interest.

Two different litter bag mesh sizes were used to examine the role of macroinvertebrates in decomposition at the site. Small mesh bags were made of 1 mm mesh polyester, thus excluding macroinvertebrates. The large mesh bags were made of 4 mm mesh nylon, allowing access to macroinvertebrates.

The litter to be used in the decomposition experiment was not oven-dried because drying at high temperatures may affect subsequent microbial activity (Boulton and Boon 1991). Therefore, fresh material of each species was collected and air-dried in a laboratory for three weeks, to reach a constant weight. Subsamples were then oven-dried at 70˚C for 24 hours to get oven-dried mass, and the difference used to convert air-dried weights of litter bags to oven-dried weights. Litterbags were individually weighed and numbered, then filled with 2.5 g ± 0.06 g of air-dried litter, sealed and re-weighed. Litter bags were individually sealed in ziplock bags, and transported to the field site.

Fifteen replicate bags of each treatment were placed in the field in December, to coincide with the beginning of alligator weed litter input occurring as a result of herbivory by the biological control flea beetle *Agasicles hygrophila*. Five replicate bags of each treatment were removed after each of three, five and ten weeks. Bags were sealed in individual ziplock bags and returned to a laboratory, where they were gently washed to remove mud, then oven-dried at 70˚C for 24 hours and weighed to determine final dry weight. It is recognised that mass loss from litter bags does not represent complete decomposition so much as disintegration (Boulton and Boon 1991), however, litter bags are a useful and widely used method of estimating differences in decomposition rates.

3.2.4 Litter chemistry

Litter samples were analysed to determine nitrogen, phosphorous, potassium, fibre, cellulose and lignin contents of fresh leaves, and of leaves after each of three, five and ten weeks decomposition. Analyses were performed by the Landcare Research Environmental Chemistry Laboratory. The nitrogen, phosphorous and potassium contents were obtained using a modified semi-micro Kjeldahl method (Blakemore, Searle et al. 1987), while fibre, cellulose and lignin were obtained using the acid detergent fibre-sulphuric acid procedure (Rowland and Roberts 1994). All chemical results are expressed as percentages of litter oven-dried at 105˚C.

3.2.5 Invertebrates

Large mesh litter bags were inspected under a Leica Zoom 2000 microscope (up to 45x magnification), and all invertebrates, including those dislodged during washing, were removed and stored in ethanol.

3.2.6 Environmental measurements

Minimum and maximum surface water temperatures were to be measured during the decomposition experiment, but due to rapidly dropping lake levels during this period, the majority of thermometers became exposed above the water surface. Minimum and maximum water temperatures are therefore not presented here. However, spot water temperature readings were conducted between 9 -10 am at both the start and finish of the decomposition experiment, in conjunction with dissolved oxygen measurements. Dissolved oxygen levels and spot temperature readings were measured in each vegetation type, using a Mettler Toledo MO128 dissolved oxygen meter. This was carried out in December, prior to alligator weed senescence, with one reading at each of the five replicate patches of each vegetation type. Dissolved oxygen and water temperature were measured again in March, when substantial amounts of alligator weed were decomposing in the water. One reading was taken at each of ten replicate patches of each vegetation type, as analyses from December indicated that five replicates might not be sufficient to detect potential differences.

Minimum and maximum air temperatures were measured monthly from January 2005 at 0.1 – 0.2 m above water level, in four of the five replicate plots of each vegetation type. Temperature data could only be analysed for three of the months over which it was recorded due to sample sizes being reduced by thermometers being stolen, damaged, or inundated by water.

Water samples were taken from within ten replicate patches of each vegetation type in November 2006 when alligator weed biomass was at its peak, and then again in March 2007 following alligator weed senescence. Total nitrogen and phosphorous in the water were determined by persulphate digestion (Hosomi and Sudo 1986) by the Landcare Research Environmental Chemistry Laboratory. Water depth was measured bimonthly in each of the five replicate patches of each vegetation type used for the decomposition and biomass experiments.

3.2.7 Analyses

Due to the unbalanced design, differences in decomposition rates were analysed using two-way ANOVAs to test for differences between litter type and date within each cover type, or cover type and date within each litter type. For analyses within a cover type, data under alligator weed and *S. tabernaemontani* were not normally distributed, and this could not be overcome by transformation. However, with sixty data points in each of these data sets, some deviation from normality can be ignored based on the Central Limit Theorem (Fowler, Cohen et al. 2001). Similarly, unequal variances in litter data from alligator weed sites could not be overcome by transformation. The alpha level was therefore lowered to 0.001 for both the Levene's test and effects testing (Underwood 1981). This allowed the data to pass the Levene's test, with a lower p-value required to attribute differences between treatments to differences in means rather than spread.

For analysis of the effect of cover within litter type, alligator weed litter data also showed heteroscedasticity. Unequal variances could not be overcome by transformation, and the Levene's test p-value was too small to allow a lower alpha level to be used. However, we can trust in the non-significance of the interaction term, as heteroscedasticity is likely to lead to overly generous indications of significance rather than conservative results (Underwood 1981). Furthermore, the graphed results do not indicate an interacting trend. Games-Howell *post hoc* analyses were performed for the factors that were significant, as this test does not assume equal variances.

Two-way ANOVAs were used to test for differences in invertebrate abundance between cover types after different decomposition times within each litter type separately, and for differences in invertebrate abundance among litter types with different cover and decomposition times. Data were log (n+1) transformed due to the absence of invertebrates from some litter bags.

Due to the small quantities of litter remaining following decomposition, only a single sample was tested for chemical composition from each litter species at each removal date. Differences in chemical composition therefore could not be confirmed by statistical tests, and are indicative only. Environmental data were analysed using one-way or two-way ANOVAs as appropriate. All analyses were performed in R v 2.0.1 (Ihaka and Gentleman 1996).

3.3 Results

3.3.1 Biomass

Alligator weed above-ground biomass peaked in December 2006 (Figure 8, Figure 9). Following the peak, alligator weed biomass dropped to its lowest point in March and stayed low throughout autumn and winter, increasing again in spring, exhibiting a similar pattern to the previous year (Figure 8, Figure 10). The rapid peak and trough biomass cycle exhibited by alligator weed equated to a 1.5 kg/m^2 drop in biomass over the three months from December 2006 to March 2007.

In contrast, *I. prolifer* biomass peaked in late summer/autumn when alligator weed biomass was at its lowest, and varied by 0.85 kg/m^2 over the course of an entire year (Figure 8). *S. tabernaemontani* annual biomass fluctuations showed a more similar seasonal pattern to those of alligator weed than did *I. prolifer*, peaking in late spring/early summer. However, as with *I. prolifer*, the magnitude of *S. tabernaemontani* biomass fluctuations was much smaller than for alligator weed. *S.*

tabernaemontani biomass dropped by only 0.38 kg/m^2 over the December 2006 – March 2007 period.

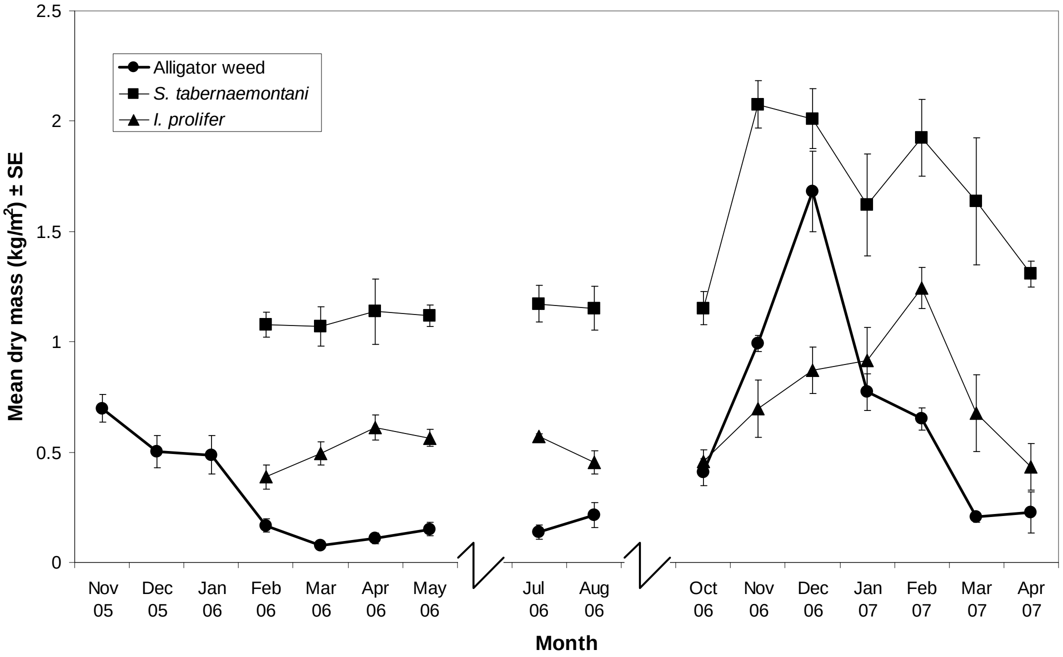

Figure 8. Seasonal variation in mean above-ground biomass. Bars indicate standard error.

Figure 9. Alligator weed near its peak biomass, November 2005.

Figure 10. Decomposing alligator weed, February 2006.

3.3.2 Litter mass loss over time

There were no significant effects of bag mesh size on litter mass loss in any comparisons. Data for both mesh sizes were therefore combined in all further analyses.

Alligator weed litter decomposed much more rapidly than litter from either native sedge species. Under alligator weed cover, more than 60% of alligator weed litter was lost from litter bags within the first three weeks of the experiment, with *S. tabernaemontani* not losing this much litter over the entire duration of the experiment (Figure 11). There was no interaction between removal date and litter type for litter decomposing beneath alligator weed (2-way ANOVA; $F_{4,75} = 0.36$, $p = 0.84$). Mean litter loss differed with both removal date and litter species independently, even using the lower alpha level of 0.001 (date $F_{2,75} = 13.0$, litter $F_{2,75} = 42.7$; $p < 0.001$ in both cases). Litter loss was greatest for alligator weed litter and least for *S. tabernaemontani*, with *I. prolifer* litter loss intermediate between the two (Tukey's $p < 0.001$ in all pair-wise comparisons).

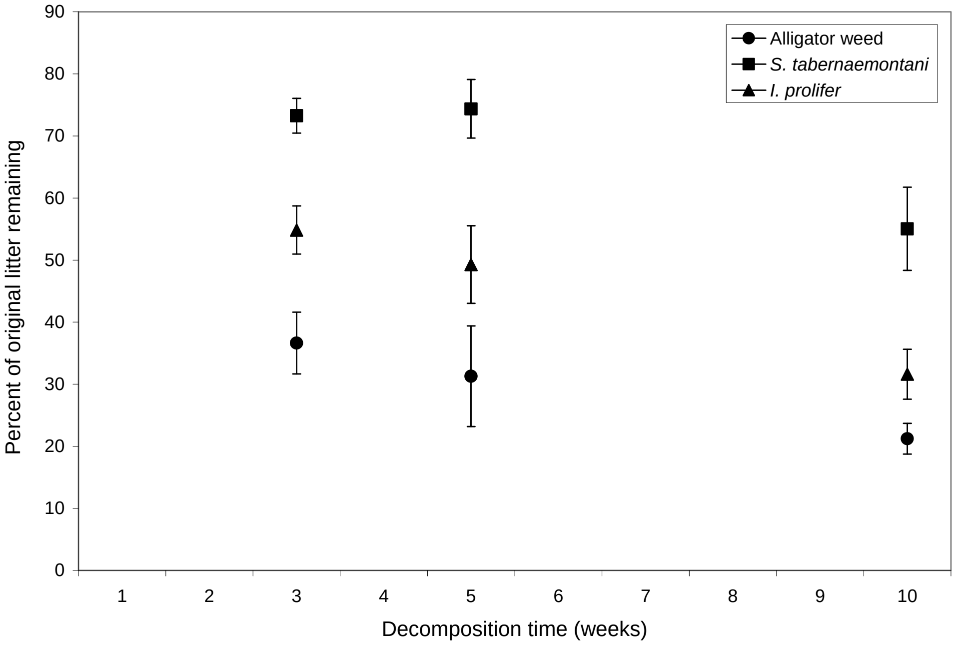

Figure 11. Differences in mean decomposition among litter types, under alligator weed vegetation cover, combining both bag sizes. Bars indicate standard error. All three litter species differ significantly within each date.

Litter decomposing beneath *S. tabernaemontani* showed an interaction between removal date and litter type ($F_{2,47} = 8.56$, $p < 0.001$). At each removal date, alligator weed litter loss was greater than was litter loss from *S. tabernaemontani* bags ($p < 0.001$ in all Tukey's pair-wise comparisons; Figure 12). *S. tabernaemontani* litter loss differed among all removal dates, indicating sustained litter breakdown over the course of the experiment ($p < 0.01$ in all Tukey's pair-wise comparisons). In contrast, alligator weed litter loss did not differ between any of the removal dates. Over 70% of alligator weed litter was lost in the first three weeks of decomposition under *S. tabernaemontani* cover. This suggests that the bulk of rapid decomposition of alligator weed occurred within the first three weeks, with decomposition then slowing to non-significant levels for the remainder of the experiment.

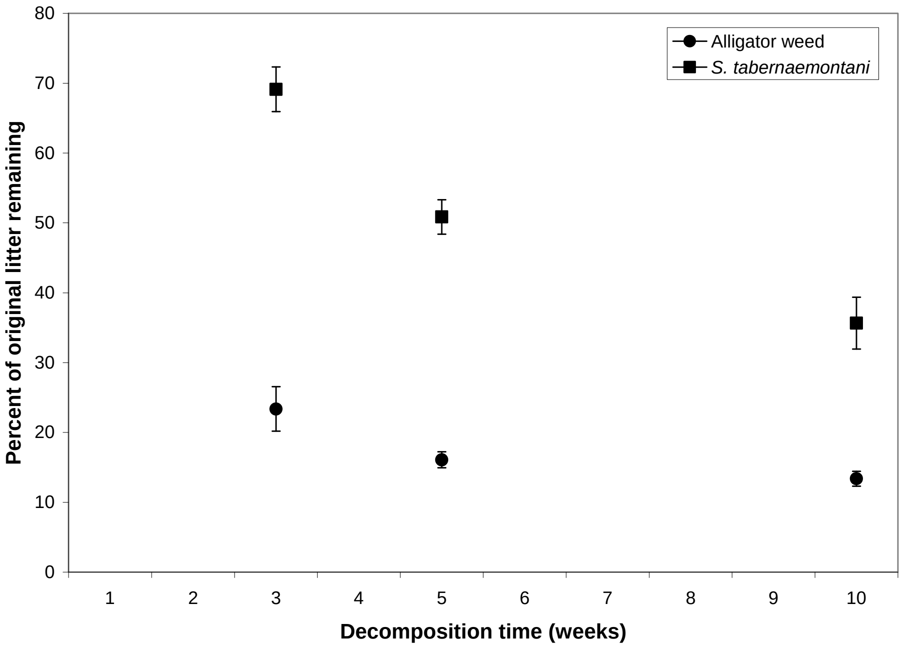

Figure 12. Differences in mean decomposition among litter types, under *S. tabernaemontani* vegetation cover, combining both bag sizes. Bars indicate standard error.

Litter decomposing beneath *I. prolifer* also showed an interaction between removal date and litter type ($F_{2,45} = 5.16$, $p < 0.01$; Figure 13). Alligator weed litter loss after three weeks decomposition was less than that at either five or ten weeks' decomposition (Tukey's $p < 0.05$ and < 0.001 respectively). However, there was no difference in alligator weed litter loss between weeks five and ten, indicating that decomposition had slowed by this stage of the experiment. There were no differences in *I. prolifer* litter among removal dates. Five *I. prolifer* bags were not recovered at week ten, reducing the number of replicates for this treatment to five (both bag sizes included). In addition, *I. prolifer* reproduces vegetatively from the ends of culms, and neighbouring plants had grown vigorously into some of the litter bags removed at ten weeks. This made determination of the original litter difficult. The combination of these two factors may account for the apparent increase in mean percent of litter remaining in this treatment, which is clearly spurious. This data point is excluded from all further analyses.

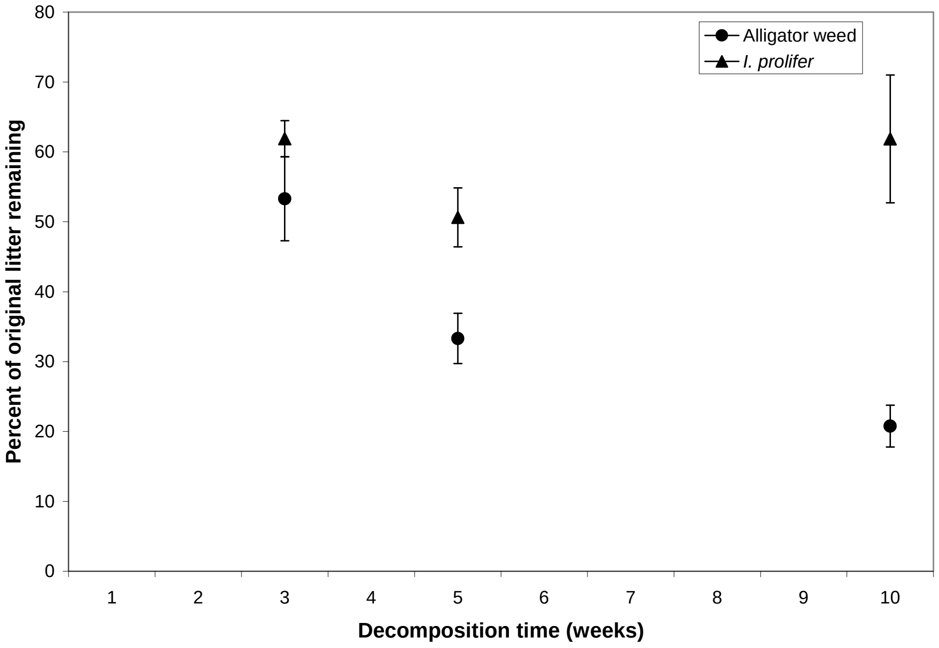

Figure 13. Differences in mean decomposition among litter types, under *I. prolifer* vegetation cover, combining both bag sizes. Bars indicate standard error.

3.3.3 Effect of vegetation cover

Vegetation cover type ($F_{2,73} = 15.28$, $p < 0.001$) and removal date ($F_{2,73} = 14.74$, $p < 0.001$) affected alligator weed litter loss independently (interaction $F_{4,73} = 2.03$, $p = 0.1$; Figure 14). Games-Howell *post hoc* tests indicated that litter loss was greater under *S. tabernaemontani* vegetation than under either alligator weed (Games-Howell *post hoc*, $p < 0.01$) or *I. prolifer* (Games-Howell *post hoc*, $p < 0.001$), with no difference between alligator weed and *I. prolifer*.

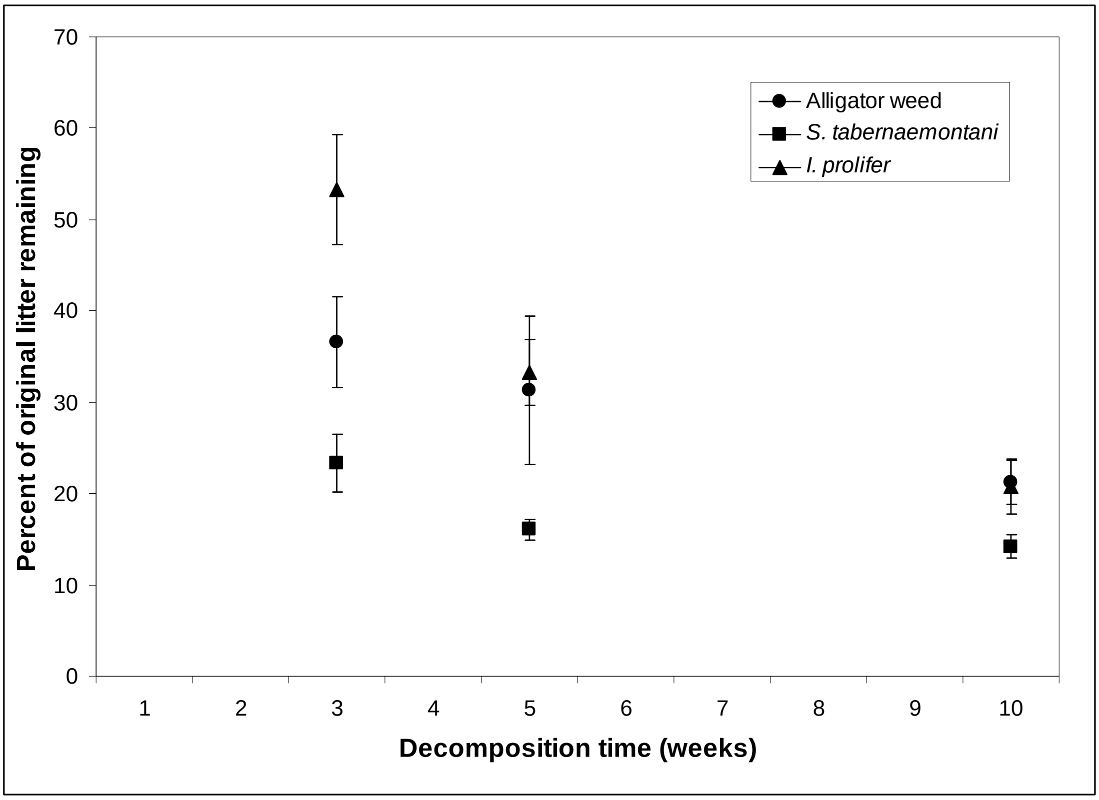

Figure 14. Alligator weed litter decomposition under different vegetation cover types. Bars indicate standard error.

S. tabernaemontani litter loss was also affected by both vegetation cover type and removal date independently, using an alpha level of 0.001 to allow differences to be attributed to means rather than spread, (cover $F_{1, 50} = 19.91$ and date $F_{2, 50} = 18.17$; $p < 0.001$ in both cases). More *S. tabernaemontani* litter remained under alligator weed cover than under *S. tabernaemontani* cover at all removal dates.

Excluding the spurious data from *I. prolifer* at week 10, decomposition time alone affected the amount of *I. prolifer* litter remaining (two-way ANOVA, $F_{2,43} = 14.95$, $p < 0.001$), with no effect of vegetation cover type or an interaction between the two factors ($F_{1,43} = 1.13$, $p = 0.29$ and $F_{1,43} = 0.48$, $p = 0.49$ for cover type and interaction respectively).

3.3.4 Litter chemistry

Fresh alligator weed litter had proportionally less fibre and cellulose than both *S. tabernaemontani* and *I. prolifer*, although the significance of these differences cannot be tested with these data (Figure 15 and Figure 16). Lignin levels were similar between fresh alligator weed and *S. tabernaemontani*, both being somewhat higher than those in fresh *I. prolifer* litter (Figure 17). The proportion of both lignin and fibre increased in all litter species as decomposition time increased, while cellulose contents showed little variation with time.

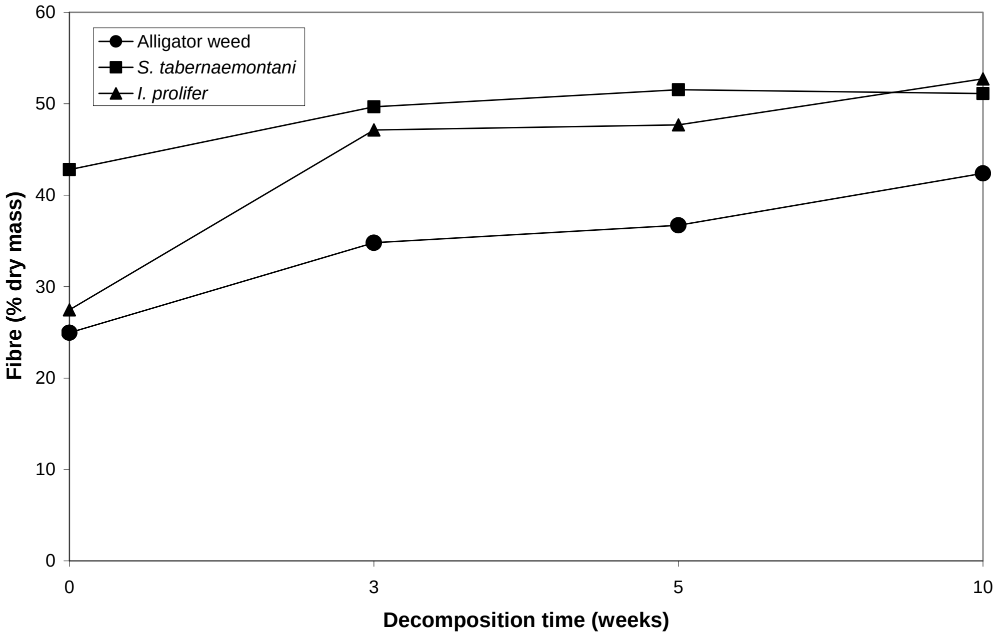

Figure 15. Fibre content of fresh (decomposition time zero) and partially decomposed litter of alligator weed and native sedges.

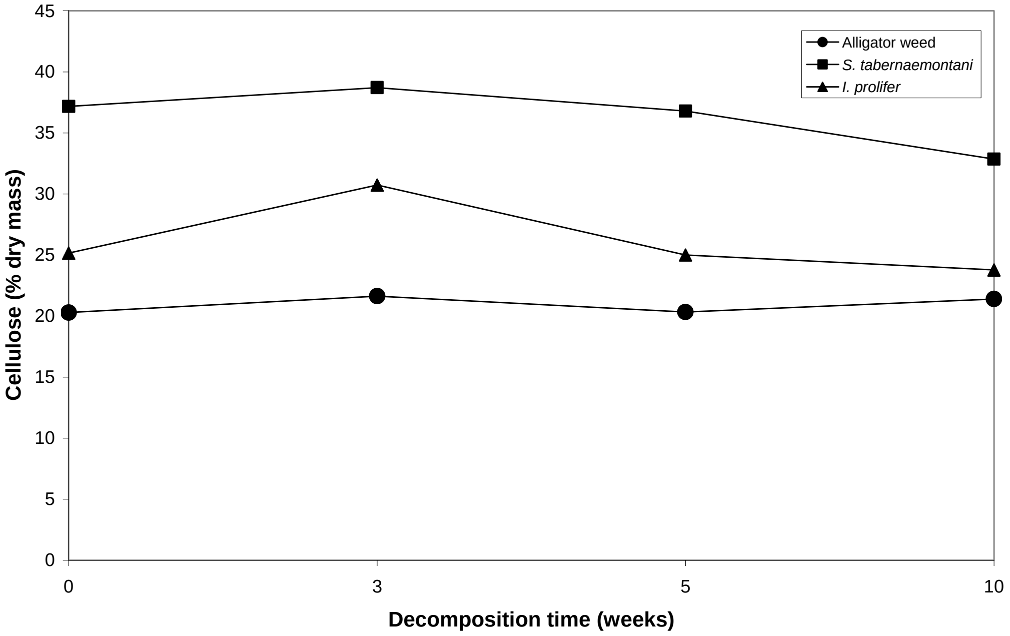

Figure 16. Cellulose content of fresh (decomposition time zero) and partially decomposed litter of alligator weed and native sedges.

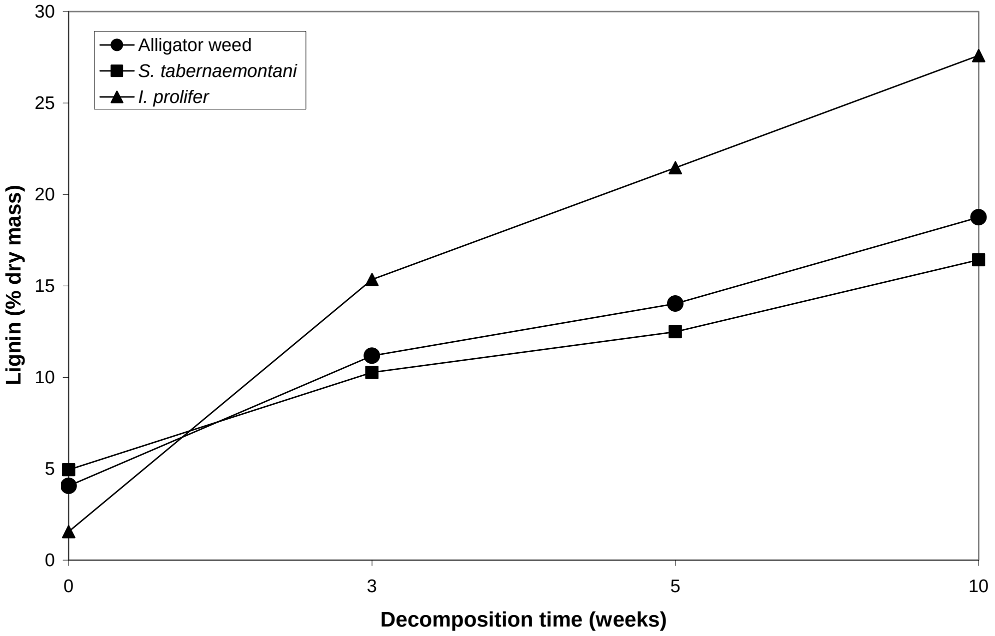

Figure 17. Lignin content of fresh (decomposition time zero) and partially decomposed litter of alligator weed and native sedges.

Fresh alligator weed litter had proportionately higher nitrogen, phosphorous and potassium levels than *S. tabernaemontani* litter, but was more similar to *I. prolifer*, particularly in nitrogen and phosphorous (Table 1). In all three species, the proportion of nitrogen within the litter samples initially decreased with decomposition, and then increased and stabilised after further decomposition.

Table 1. Chemical composition of fresh litters. All values expressed as percent of total dry mass.

Litter species	Fibre	Cellulose	Lignin	Nitrogen	Phosphorous	Potassium
Alligator weed	25.0	20.3	4.1	2.1	0.29	5.2
S. tabernaemontani	42.8	37.2	4.9	1.0	0.12	1.8
I. prolifer	27.5	25.1	1.6	2.7	0.28	3.4

In November 2005, alligator weed covered an estimated 1681.6 m^2 at Lake Rotokawau (Chapter 6). Between November 2005 and February 2006, 0.53 kg/m^2 dry mass of alligator weed entered the system, either consumed by the flea beetle or as abscised stems and leaves. If the nitrogen content of that litter is taken to be the same as that of fresh litter collected for litter bags (2.1% by dry weight), then 0.01 kg/m^2 of nitrogen would have been released into the environment once this litter decomposed, equating to 16.8 kg of nitrogen throughout the whole lake. In 2006 alligator weed biomass peaked in December. Between December 2006 and February 2007 1.45 kg/m^2 dry mass of alligator weed was released into the system. Assuming a similar level of alligator weed coverage, this equates to an estimated 0.03 kg/m^2 or 51.2 kg throughout the lake. Similarly substantial inputs from alligator weed could be expected for the other nutrients (Table 2).

Table 2. Estimated nutrient inputs from alligator weed foliage during peak herbivory periods. Calculations are based on foliage nutrient concentrations presented in Table 1.

	November 2005 - February 2006		December 2006 – February 2007	
Nutrient input	Kg/m^2	Kg/whole lake	Kg/m^2	Kg/whole lake
Nitrogen	0.01	16.8	0.03	51.2
Phosphorous	0.002	2.6	0.004	7.1
Potassium	0.03	46.4	0.08	126.8

3.3.5 Invertebrate abundance

A total of 934 invertebrates were collected from litter bags, belonging to 14 orders or higher taxa (Appendix 1). Log plus one transformed total invertebrate numbers differed with decomposition time for litter decomposing beneath *I. prolifer* cover (2-way ANOVA, $F_{2,20} = 27.86$, $p < 0.001$, Figure 18). Tukey's *post hoc* tests indicated that there were more invertebrates per litter bag after three weeks' decomposition (median = 17 invertebrates per bag), than after five or ten weeks' decomposition (median = 7 and median = 1 invertebrates per bag respectively). Invertebrate numbers from litter decomposing beneath either alligator weed or *S. tabernaemontani* did not differ with either decomposition time or litter type (2-way ANOVAs, $p > 0.18$ in all cases).

Length of decomposition time also significantly affected the number of invertebrates on *I. prolifer* litter regardless of vegetation cover (2-way ANOVA, $F_{2,21} = 5.30$, $p = 0.014$ for the effect of date, Figure 19). There were more invertebrates on *I. prolifer* litter after three weeks' decomposition, than after 10 weeks' decomposition (Tukey's post hoc test, $p = 0.011$).

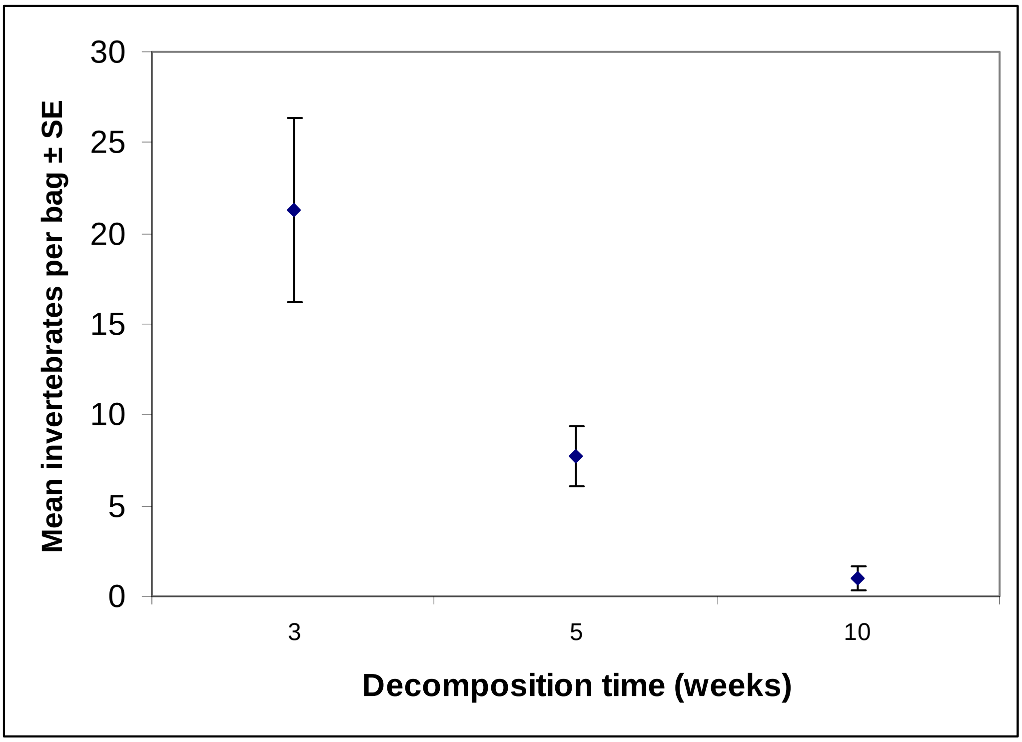

Figure 18. Effect of decomposition time on mean number of invertebrates per litter bag decomposing beneath *I. prolifer* cover, both litter type combined. Error bars indicate one standard error.

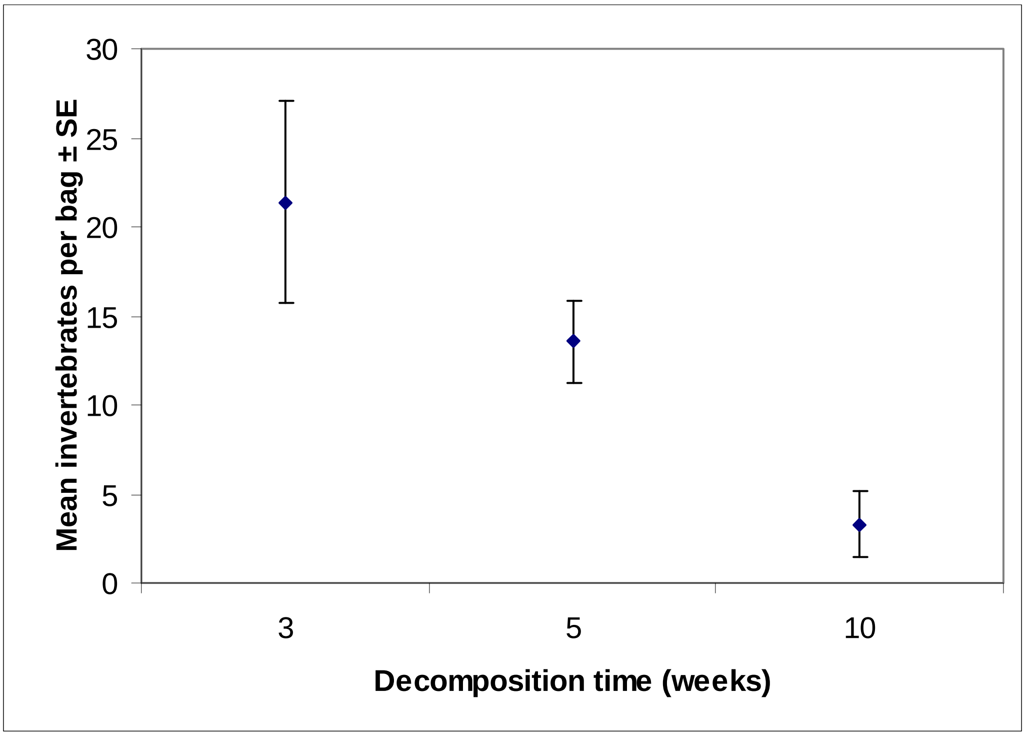

Figure 19. Effect of decomposition time on mean invertebrate numbers per litter bag for *I. prolifer* litter under both cover types combined. Error bars indicate one standard error.

Decomposition time and vegetation cover interacted to affect log plus one transformed invertebrate numbers on alligator weed litter (2-way ANOVA, $F_{4,32}$ = 3.74, p = 0.013 for interaction term, Figure 20). After three weeks decomposition there were more invertebrates on alligator weed litter under *I. prolifer* cover (median = 10.9 invertebrates per litter bag, mean = 14.5) than there were on alligator weed litter under *S. tabernaemontani* cover (median = 0 invertebrates per litter bag, mean = 0.3; Tukey's post hoc test, p < 0.01). Neither decomposition time nor vegetation cover significantly affected invertebrate numbers recorded on *S. tabernaemontani* litter.

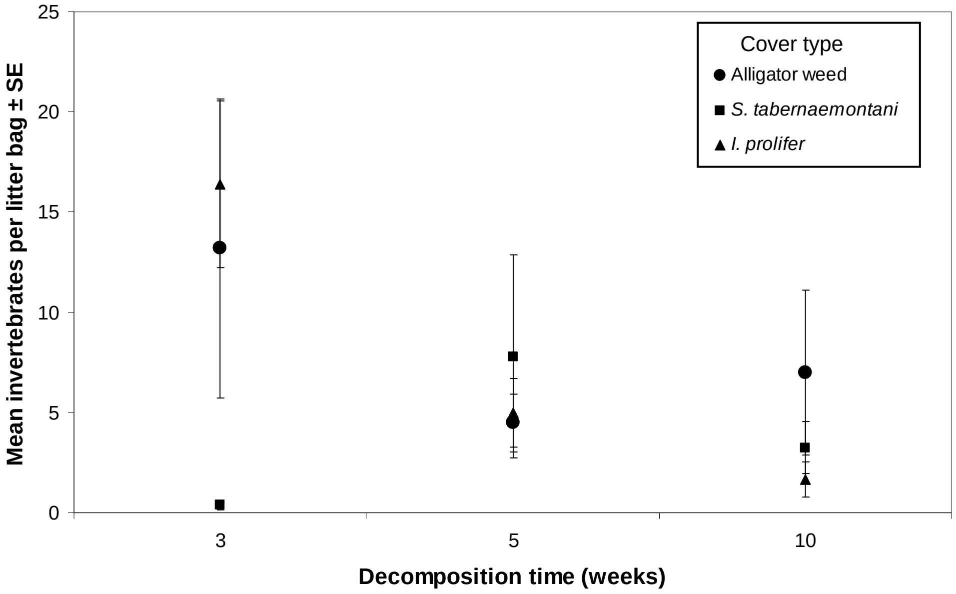

Figure 20. Effect of decomposition time on mean invertebrate numbers on alligator weed litter under different vegetation cover types. Error bars indicate one standard error.

3.3.6 Environmental analyses

In February, water temperature was lower in *I. prolifer* patches (mean = 22.3 ± 0.15˚C) than in either alligator weed (mean = 24.4 ± 0.31˚C) or *S. tabernaemontani* patches (mean = 23.9 ± 0.29˚C) (ANOVA, $F_{2,26}$ = 15.46, p < 0.001; both pair-wise comparisons with *I. prolifer* p < 0.001). There were no significant differences in water temperature in December, although the same trend was observed as in February (ANOVA, $F_{2,11} = 2.58$, $p = 0.12$).

Minimum air temperatures were higher in *S. tabernaemontani* plots than in *I. prolifer* plots in September (ANOVA, $F_{2,9} = 6.55$, $p = 0.018$; Tukey's pair-wise $p = 0.014$; Figure 21), and compared with both alligator weed and *I. prolifer* in January (ANOVA, $F_{2,6} = 15.43$, $p < 0.01$; Tukey's pair-wise $p < 0.01$ in both cases). There was no evidence of a difference in minimum air temperature in July (ANOVA, $F_{2,6} = 3.00$, $p = 0.13$). No differences in maximum air temperature were detected (one-way ANOVAs, $p > 0.61$ in all months).

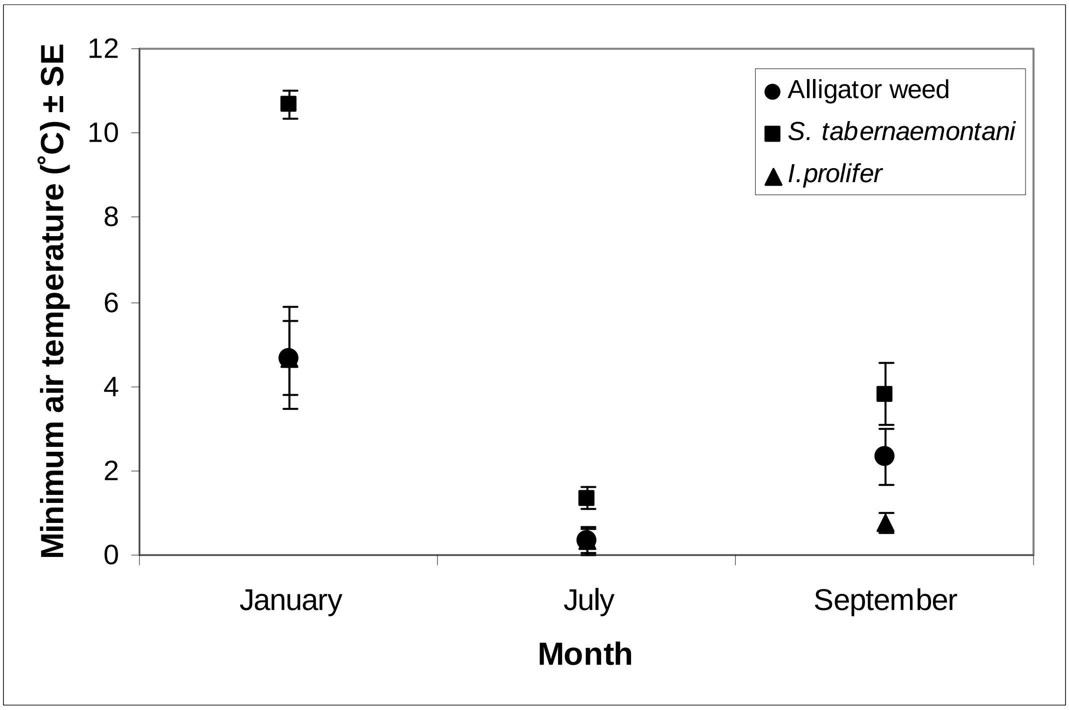

Figure 21. Minimum air temperatures within 1 m^2 plots dominated by alligator weed or native sedges.

Dissolved oxygen varied with vegetation type ($F_{2,37} = 23.00$, $p < 0.001$), being lower in water sampled beneath *I. prolifer* cover (mean = 19% ± 9.0), than under either *S. tabernaemontani* (mean = 99.9% ± 7.2; Tukey's *post hoc* test $p < 0.001$), or alligator weed (mean = 67.4% ± 8.7; Tukey's *post hoc* test $p < 0.001$), but not differing significantly between alligator weed and *S. tabernamontani* (Tukey's *post hoc* test $p = 0.12$).

In contrast, there was no effect of sampling date on dissolved oxygen levels (two-way ANOVA, $F_{1,37} = 1.43$, $p = 0.24$), with dissolved oxygen following alligator weed senescence similar to that prior to senescence (mean for all vegetation types combined = 66% and 54% respectively). There was no evidence of an interaction between sampling date and vegetation type affecting dissolved oxygen ($F_{2,37} = 1.39$, $p = 0.26$).

Both nitrogen and phosphorous concentrations in water samples differed among vegetation types (two-way ANOVAs $F_{2,53} = 4.43$, $p = 0.02$ and $F_{2,53} = 4.16$, $p = 0.02$ respectively; Figure 22 and Figure 23). Water samples from *S. tabernaemontani* sites contained less nitrogen than those from either alligator weed or *I. prolifer* sites (Tukey's *post hoc* tests, $p = 0.022$ and $p = 0.045$ respectively). Similarly, water samples from *S. tabernaemontani* sites contained less phosphorous than those from alligator weed sites (Tukey's *post hoc* test, $p = 0.019$).

There was no effect of sampling date on either nitrogen or phosphorous ($F_{1,53} = 0.24$, $p = 0.62$ and $F_{1,53} = 0.03$, $p = 0.87$ respectively; Figure 23). No interaction between sampling date and vegetation type was detected for either nitrogen or phosphorous content in water samples (two-way ANOVAs; $F_{2,53} = 0.09$, $p = 0.91$ and $F_{2,53} = 0.19$, $p = 0.82$ for nitrogen and phosphorous respectively).

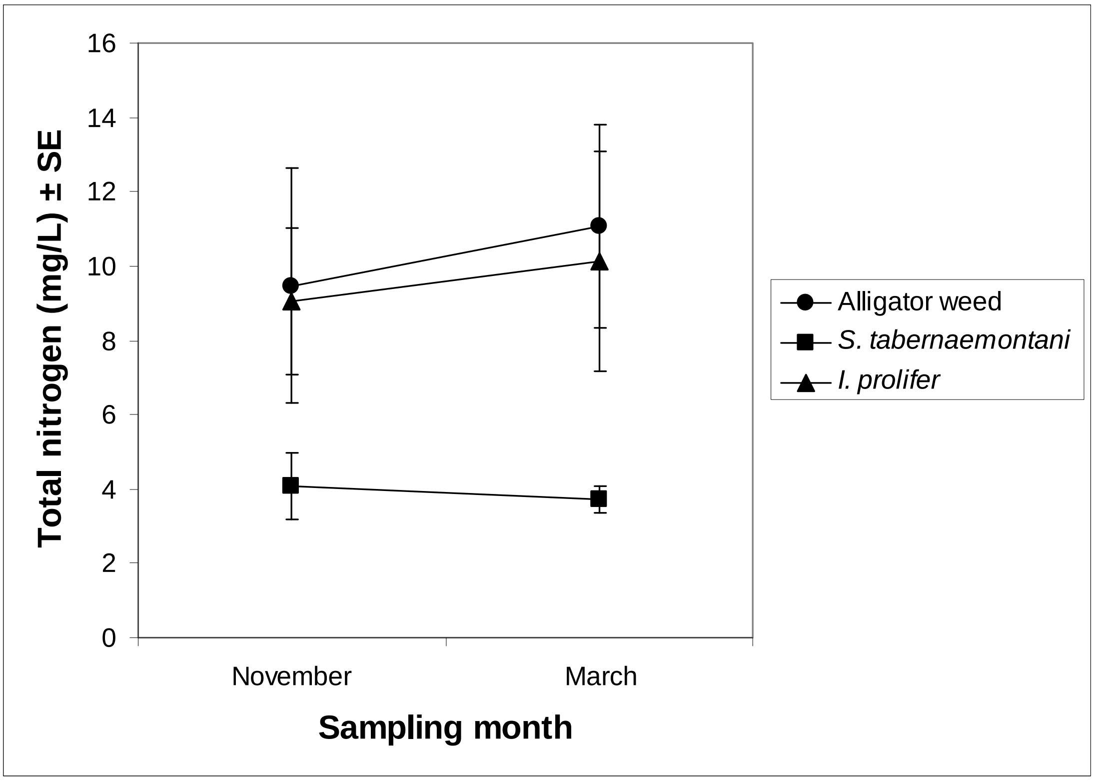

Figure 22.Total nitrogen in water samples from patches dominated by different vegetation types before and after alligator weed senescence.

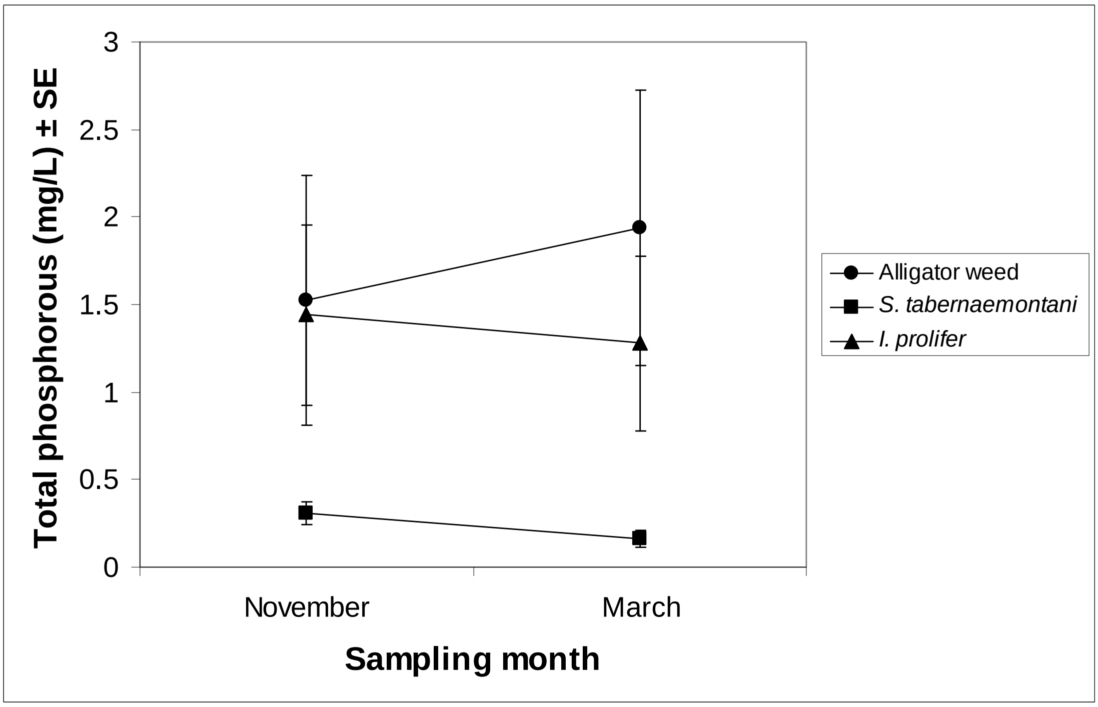

Figure 23.Total phosphorous in water samples from patches dominated by different vegetation types before and after alligator weed senescence.

3.4 Discussion

This study demonstrates that alligator weed has the potential to alter nutrient cycling within invaded lake systems, but evidence of this being translated into actual effects within the study ecosystem is equivocal, since this system is already compromised by the effects of other exotic species and eutrophication.

3.4.1 Effect of litter type

Alligator weed litter decomposed significantly faster than that of two common sedge species. The rate of alligator weed decomposition was comparable to reported rates of decomposition for other mesophyllous aquatic species such as water hyacinth (*Eichhornia crassipes* (Mart.) Solms-Laub.), with the most rapid decomposition occurring in the first 2-3 weeks, and subsequent decomposition slowing, often to non-significant levels (Battle and Mihuc 2000; Xie, Qin et al. 2004).

Differences in decomposition rates among litter types may in part relate to differences in chemical composition. Fresh alligator weed litter had higher nitrogen and phosphorous concentrations than *S. tabernaemontani*, along with lower fibre, cellulose and lignin levels, all of which have been linked to higher decomposition rates in other plant species (Goncalves Jr, Santos et al. 2004). Goncalves Jr, Santos et al. (2004) found *Nymphaea ampla* decomposed approximately 26 times faster than *Typha domingensis*, which they attributed to higher nitrogen and phosphorous levels in *N. ampla*, along with a lower percentage of cell wall fraction. Fresh *I. prolifer* litter was intermediate between alligator weed and *S. tabernaemontani* in the proportions of many chemical constituents in its litter. This is consistent with its intermediate decomposition rate compared to the other species studied here.

Similarly, leaf litter from two invasive species, *Buddeleja asiatica* and *Myrica faya,* decomposed faster than that of two Hawaiian native plants (Matson 1990). Alligator weed shares with these and many other invasive plant species traits such as high growth rates and tissue nutrient levels and low structural defences (Allison and Vitousek 2004), thus resulting in more rapid decomposition than many native species.

As litter decomposed, changes in the proportions of different chemical constituents were consistent with those observed in other studies. The trend across all litter species towards increasing proportions of lignin and fibre with increasing decomposition time has been observed in other species, as these substances are generally slow to break down. Nitrogen levels tend to drop initially, then rise and plateau (Baerlocher 2005). This pattern was displayed by all three litter types tested here.

3.4.2 Implications of alligator weed biomass dynamics

Alligator weed growth and decomposition is consistent with the trend observed elsewhere of invasive species with rapid growth rates, high leaf nutrient levels and rapid decomposition combined in a high productivity, rapid nutrient cycling strategy (Cornelissen, Perez-Harguindeguy et al. 1999; Allison and Vitousek 2004). For instance, in Hawaii, six invasive plant species were found to decompose faster than five native species (Allison and Vitousek 2004).

In addition to decomposing faster than the native sedge species, alligator weed decomposition was characterized by a large input of litter over a very short space of time. This contrasts with both the sedge species, which showed smaller and more gradual seasonal changes in biomass. A large input of litter and frass from the biocontrol agent, along with rapid litter breakdown, is likely to result in a sharp peak in nutrients being released into the lake, in a manner uncharacteristic of the native vegetation. Altering nutrient cycling in this way may have a range of consequences, potentially including facilitating further invasion by alligator weed, other weed species, and/or algal blooms, illustrating the process of ‘invasional meltdown’, where invasive species facilitate the establishment of additional invasive species (Simberloff and Von Holle 1999; O'Dowd, Green et al. 2003).

Despite this potential, no evidence was detected of water quality changes coinciding with alligator weed senescence. Peaks in nutrient input, if they did occur, may have been masked by increased productivity elsewhere within the system. For instance, substantial algal blooms occurred at Lake Rotokawau around the time of peak alligator weed senescence (Figure 24), but were not observed to the same extent at two nearby uninvaded lakes. The algal bloom at Lake Rotokawau could have been exacerbated by alligator weed decomposition, as has been documented elsewhere as a result of herbivore induced litter input. Application of insecticide to *Hydrilla verticillata* and native aquatic plants reduced algal blooms in artificial ponds by reducing nutrient input from herbivory-induced leaf decomposition (Nachtrieb, Grodowitz et al. 2007).

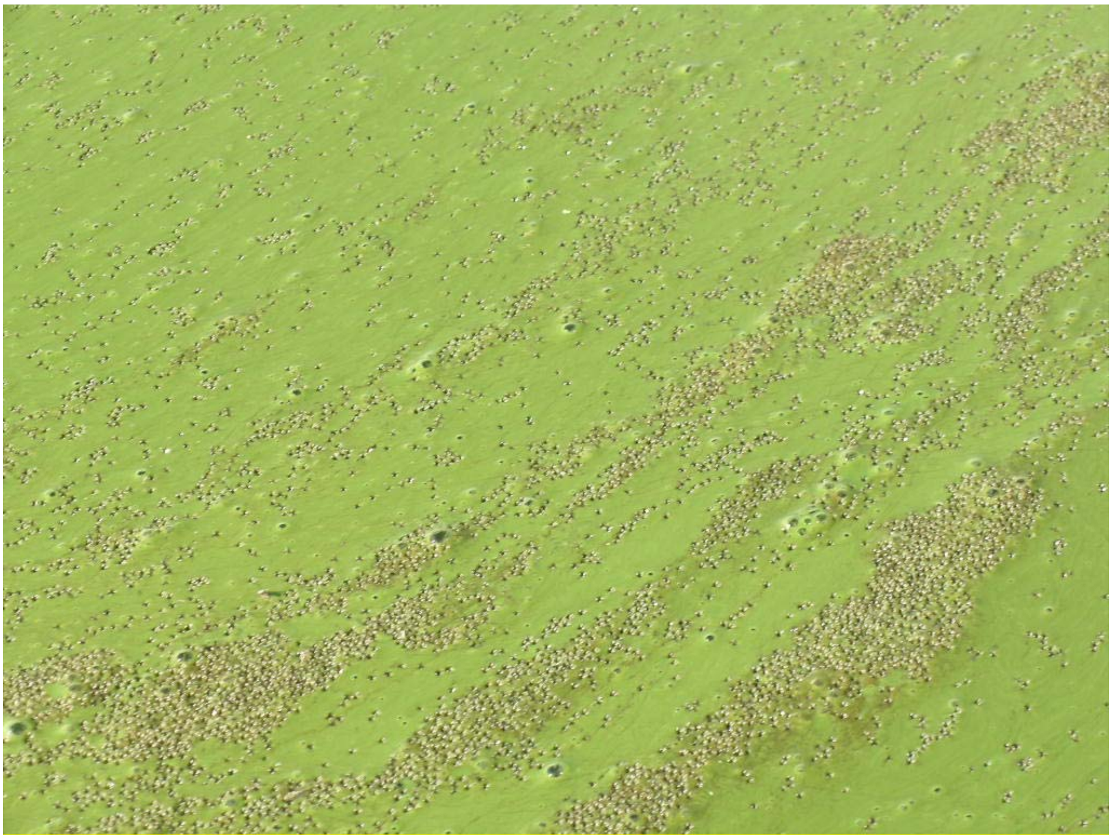

Figure 24. Water surface, Lake Rotokawau February 2006, showing thick algal growth.

The Lake Rotokawau study site is surrounded by farmland (both cattle and sheep), and hosts large numbers of swans and other birds. Alligator weed is therefore not the only major source of nutrients into the water, and indeed the lake has been classified as hypertrophic (Northland Regional Council 2005). Alligator weed decomposition thus may not be having a significant effect on ecosystem processes at this particular site, since it is already a highly modified and degraded site. However, although it may be more aggressive in highly eutrophic environments, alligator weed does tolerate low nutrient environments better than other weeds such as water hyacinth (*Eichhornia crassipes*) and eurasian milfoil (*Myriophyllum spicatum*) (Rogers and Davis 1971). Where alligator weed does invade less nutrient rich waterways it may significantly alter nutrient cycling, particularly if it is accompanied by the biocontrol agent *A. hygrophila*.

3.4.3 Role of the Alligator weed flea beetle

In terrestrial situations within New Zealand, where *A. hygrophila* herbivory does not occur, alligator weed typically shows strong continued growth throughout summer and dies back somewhat over winter. Similarly, uncontrolled aquatic alligator weed in China reaches peak biomass in summer, followed by a winter die-back (Liu, Wu et al. 2004). This is in sharp contrast to the substantial summer senescence observed in this study as a result of *A. hygrophila* herbivory. The change in biomass dynamics caused by the flea beetle is important not only in the volume of litter decomposing, but also in the timing of litter input, with decomposition rates generally faster in summer due to warmer conditions.

Evaluation of non-target effects of biological control agents has tended to focus on host specificity and effects on non-target hosts, with little known about their potential to affect ecosystem processes (Denslow and D'Antonio 2005). However, Paynter (2006) observed a 20% increase in *Mimosa pigra* leaf fall following the introduction of biological control agents. This suggests that changes in litter fall dynamics and nutrient cycling resulting from weed biological control may not be confined to alligator weed and its agent *A. hygrophila*.

Herbivory has also been found to increase nitrogen levels in litter, and decrease lignin: N ratios, thus producing litter higher in nutrients and consequently faster to break down (Berg and Laskowski 2006a). Flea beetle herbivory could thereby further elevate litter decomposition rates as well as affecting the volume and timing of litter input, although this is likely to be of lesser significance.

3.4.4 Alternative pathways for nutrients

Nutrients released by alligator weed dieback may have followed a number of alternative pathways rather than simply direct decomposition as examined in this study. Similarly, various factors may have affected the accuracy of the estimated biomass inputs.

As *A. hygrophila* herbivory often only partially severs damaged stems, some reabsorption of nutrients from leaves back into the rest of the plant may occur before leaf abscission (Berg and Laskowski 2006b). In contrast, in this experiment, fresh vegetation was cut from the plant to ensure the decomposition had not been initiated prior to the experiment. Therefore, natural litter could be expected to release fewer nutrients into the environment than those recorded here from fresh vegetation. Conversely, insect herbivory can increase rates of ‘greenfall’, where green leaf fragments enter the system as litter. These tend to be higher in nitrogen and phosphorous than senescent leaves, thus accelerating decomposition rates (Fonte and Schowalter 2005). Furthermore, as the substantial drop in alligator weed biomass results from flea beetle herbivory, a potentially large proportion of nutrients would cycle through beetles. Invertebrate frass can be quite recalcitrant (Prescott 2005), thus potentially extending the period of time over which nutrients would be released into the environment

This system is not stable, and some continued alligator weed growth occurred despite herbivory, making current calculations conservative in terms of the total biomass of plant material entering the system during the sampling period. The chemical composition of alligator weed itself may also vary to some extent between different environments, potentially influencing decomposition rates.

Because *A. hygrophila* is strongly limited to aquatic environments, herbivory along the terrestrial edge of the 25 m^2 quadrats sampled for the estimate of total alligator weed cover (Chapter 6) is likely to have been less than that recorded by biomass fluctuations, as these measures were taken in the optimal central area of alligator weed's distribution. This may have led to over estimation of the total volume of weed decomposing, and hence nutrient inputs.

The factors governing the amount of nutrients being released into the environment as a result of alligator weed herbivory and decomposition are therefore complex and this study provides only a broad characterisation of the patterns of decomposition at this site.

3.4.5 Cover type

Across all treatments there was a pattern of most rapid decomposition beneath *S. tabernaemontani*, followed by alligator weed, with slowest decomposition beneath *I. prolifer*, although there were no detectable differences between litter mass loss beneath alligator weed and *I. prolifer*. The differences in decomposition rates between vegetation cover types may be related to moisture and/or temperature levels. While absolute water depth was similar between vegetation types, *I. prolifer* and alligator weed grow forming dense mats that, while anchored in the ground by roots, float near the water's surface. In the case of *I. prolifer*, this mat is particularly dense and difficult to penetrate. Litter bags set at the base of these plants therefore dried out more often than those in *S. tabernaemontani* dominated areas. This is consistent with the trend in published studies towards faster decomposition rates in humid or aquatic environments compared with dry terrestrial situations (Battle and Mihuc 2000; Lindsay and French 2004). While temperature data was limited, it suggests that *S.*

taernaemontani patches may have been somewhat warmer than alligator weed or *I. prolifer*. Decomposition rates tend to be elevated in warmer environments, due to enhanced activity of microbial and invertebrate decomposers (Berg and McClaugherty 2003). Thus both temperature and moisture may have contributed to the more rapid litter loss observed under *S. tabernaemontani* cover than either of the other two species.

In reality, loose litter entering the lake in areas dominated by alligator weed may be more easily washed deeper into the water than was the case with litter bags. In contrast, *S. tabernaemontani* culms often decompose considerably while still upright and largely emergent above water (pers. obs), thus potentially decomposing more slowly than observed in this study due to drier conditions, and also reabsorbing a higher proportion of nutrients. The difference in decomposition rates particularly beneath alligator weed and *S. tabernaemontani* may therefore be to some extent an artefact of the experimental design. However, *I. prolifer* forms such an impenetrable mat that litter is more likely to be retained amongst the vegetation rather than washing into the water. The slower decomposition observed under this vegetation type therefore may be experience under natural conditions as well. This thick mat structure, with considerable volumes of associated trapped organic matter, is also likely to have contributed to the very low dissolved oxygen levels recorded in *I. prolifer* dominated plots.

As there were substantial differences in decomposition rates beneath the two native species, with alligator weed cover intermediate between the two, this study indicates that, as a vegetation cover, the environment provided by alligator weed is within the range of those provided by native vegetation types in this system, with regards to its effect on litter decomposition rates. This contrasts with other invasive plant species which have been found to substantially alter decomposition rates beneath them compared with native vegetation cover. For instance, litter decomposed almost twice as fast beneath mats of the invasive herb *Tradescantia fluminensis* as it did in non-*T. fluminensis* infested plots (Standish, Williams et al. 2004). Altered microclimate was thought to have strongly influenced this increase in decomposition rates. Similarly, elevated decomposition rates beneath *Chrysanthemoides monilifera* compared with native vegetation were attributed to changes in microclimate, including moisture levels (Lindsay and French 2004). This effect of moisture levels is consistent with the differences between vegetation cover types observed at Lake Rotokawau, except that at Lake Rotokawau moisture and temperature beneath the invasive alligator weed fell within the range of microclimates provided by native vegetation.

3.4.6 Invertebrates

The lack of observed differences in decomposition between large- and small-mesh litter bags may indicate that the 1 mm mesh size is not small enough to exclude important microinvertebrate decomposers, or juvenile stages of larger species. Alternatively, microbial decomposition may play the more dominant role in decomposition at the site. This would be consistent with findings that microbes were the primary decomposers in stagnant backwater areas, with invertebrates more important in faster flowing riverine sites (Battle and Mihuc 2000). That microbes may be the primary decomposers in this system, particularly in alligator weed dominated patches, is also supported by the dominance of fungivorous beetles present in litter bags at week three (Chapter 4), and the increase in predatory Coleoptera and Araneae towards the end of the experiment. These trends suggest that many of the invertebrates collected were feeding first on microbial decomposers, and then on lower trophic levels of invertebrates, rather than directly on the litter itself.

The sedge species had higher cellulose levels, which freshwater invertebrates typically have difficulty digesting (Gessner 2005), making litter such as *S. tabernaemontani* less attractive as a food source. As *S. tabernaemontani* litter had higher levels of less palatable compounds, it may have required some time decomposing before becoming palatable. This may have been responsible for the trend towards increasing invertebrate numbers on *S. tabernaemontani* litter over the course of the experiment, in contrast to decreasing numbers on both alligator weed and *I. prolifer*. A similar pattern was observed when comparing invertebrate colonisation of *Typha domingensis* and *Nymphaea ampla* litterbags in a Brazilian coastal lagoon. Invertebrate colonisation peaked much earlier on the faster decomposing *N. ampla* than on the slow decomposing *T. domingensis* (Goncalves Jr, Santos et al. 2004).

3.4.7 Conclusions

Alligator weed decomposition and biomass dynamics differ markedly from those of native sedge species within this ecosystem, with greater seasonal variations in biomass, and input of large amounts of rapidly decomposing litter over a short time frame. Despite this, current data did not provide any evidence of these differences being translated into flow-on ecosystem impacts, such as detectable changes in water chemistry. However, the magnitude of differences detected indicates that the already degraded state of the study ecosystem may have masked potentially substantial effects of alligator weed on nutrient dynamics, particularly in conjunction with its biocontrol agent. Nevertheless, this study highlights the potential of not only invasive species, but also their biocontrol agents, to alter ecosystem processes in invaded systems.

4 INDIRECT EFFECTS OF AN INVASIVE PLANT AND ITS BIOCONTROL AGENT ON BEETLE COMMUNITIES THROUGH ALTERED DECOMPOSITION DYNAMICS AND FUNGAL RESOURCES

4.1 Introduction

4.1.1 Epiphytic taxa and their effects on invertebrate host plant choice

Invertebrate habitat preferences are known to be influenced not only directly by plants themselves, but also by the relative abundance of epiphytic organisms, such as fungi and algae, hosted by the plants. Epiphytic algae are an important food source for many aquatic invertebrates, and can therefore have a strong role in structuring aquatic invertebrate communities (Lalonde and Downing 1992; Douglas and O'Connor 2003). For example, the plants *Polygonum amphibium* and *Myriophyllum spicatum* were found to host invertebrate faunas dominated by periphyton grazers, attributed to their extensive surface area supporting rich algal biomass, in contrast to *Typha latifolia*, on which plant miners were more abundant (Learner, Wiles et al. 1989). Conversely, the exotic para grass (*Urochloa mutica*) hosted similar epiphytic invertebrate communities to native grasses, attributed to their structural similarity and therefore similar flora of epiphytic alga (Douglas and O'Connor 2003).

In addition to algae, epiphytic fungi may also influence invertebrate communities. About half of all recognized beetle families are primarily fungivorous or feed on plant material which has been altered by fungal activity (Lawrence 1989). The abundance of some fungivorous beetles on nine tree species in a Queensland rainforest was significantly related to bark roughness, indicating that tree species with a more heterogeneous bark environment hosted more numerous and/or diverse fungal communities, with fungi then influencing the beetle communities (Menzel, Kitching et al. 2004). Similarly, the abundance of microbe-feeding nematodes varied between plant species, and was related to differences in the fungal communities that they hosted (Wardle, Yeates et al. 2003).

Fungi may play a particularly strong role in structuring invertebrate communities on decaying, rather than living, plant material (Jonsell, Weslien et al. 1998). Invertebrates inhabiting decaying material may have feeding preferences for certain species of fungi, or the litter colonised by them (Lodge, Hawksworth et al. 1996). For instance, caddisfly larvae preferentially fed on aspen leaves colonized by certain hyphomycete fungi compared with other species of fungi (Arsuffi and Suberkropp 1984). The nutrient status of the environment can also influence the invertebrate community via microbial activity. Gulis, Ferreira et al (2006) found fungal biomass associated with decomposing oak leaf-litter increased faster and peaked higher in eutrophic than oligotrophic streams. High nutrient levels increased microbial activity and resultant leaf conditioning was considered to have contributed to higher invertebrate abundance in eutrophic streams.

4.1.2 Weed invasion, decomposition and associated invertebrates

The decomposition dynamics of weedy plant species in comparison to native vegetation have been investigated in a number of systems. Weed species such as *Tradescantia fluminensis* and *Chrysanthemoides monilifera* ssp. *rotundata* decompose at different rates to native vegetation, and alter microclimatic conditions, thereby influencing rates of litter decomposition in ecosystems the invade (Lindsay and French 2004; Standish, Williams et al. 2004). Similarly, the effects of weed invasion on invertebrate communities has received some attention, including for some of the same weed species for which decomposition dynamics have been studied, with invertebrate community composition, if not abundance, typically varying between native and invasive vegetation types (Toft, Harris et al. 2001; Harris, Toft et al. 2004; Ernst and Cappuccino 2005; Lindsay and French 2006; Wilkie, Cassis et al. 2007).

However, the two areas of investigation have rarely been linked, and it is often unclear how or whether changes in decomposition dynamics with weed invasion may be affecting invertebrate communities. Pitfall trapped invertebrates in lowland native forest remnants in New Zealand's North Island showed marked differences between *T. fluminensis* invaded plots and uninvaded plots (Standish 2004). In particular, several groups of fungivorous beetles showed a preference for uninvaded plots. Similarly, fungal feeding Aphelenchidae nematodes at the same site were also less abundant in *T. fluminensis* plots than in uninvaded plots (Yeates and Williams 2001). These results suggest that the altered decomposition environment beneath *T. fluminensis* (Standish, Williams et al. 2004) was affecting the fungal community present in these plots, with flow-on effects on fungal feeding invertebrates. In contrast, differences between the same plots were not apparent for Malaise-trapped invertebrates, which might be expected to be less influenced by decomposition and microhabitats immediately above the soil surface (Toft, Harris et al. 2001).

4.1.3 Alligator weed, decomposition and associated invertebrates

Alligator weed (*Alternanthera philoxeroides*) is an emergent aquatic and terrestrial weed. Alligator weed may influence lake margin invertebrate decomposer communities due to the weed's documented effects on decomposition (Chapter 3). Aquatic alligator weed is characterised by very rapid growth beginning in spring, forming a dense mat of vegetation over the water's surface. In New Zealand, aquatic alligator weed is fed on by an introduced biological control agent, the alligator weed flea beetle (*Agasicles hygrophila*). Herbivory by the flea beetle causes rapid dieback of large amounts of aquatic alligator weed in a short period of time during summer in the warmer parts of its range (Stewart, Chapman et al. 2000). The resulting litter input into the system is uncharacteristic, both in timing and magnitude, compared with litter inputs from the co-occurring native sedges *Schoenoplectus tabernaemontani* and *Isolepis prolifer* (Chapter 3). In addition to this, alligator weed litter has been found to decompose much more quickly than either native sedge species (Chapter 3). No differences in decomposition rates were detected between litter bags which allowed access to, or excluded, macroinvertebrates (Chapter 3). This suggested that microbial decomposers played a dominant role in decomposition, as has been found to be the case in other studies, particularly in other slow moving or warm climate water bodies (Collier and Winterbourn 1987; Battle and Mihuc 2000). Nevertheless, invertebrates may still be an important part of this ecosystem that is potentially disrupted by the invasion of alligator weed.

The beetle communities hosted by alligator weed were compared with those on the two native sedge species *S. tabernaemontani* and *I. prolifer* to determine whether the abundant resource represented by this pulse of decomposition influenced invertebrate communities. Specifically, this study aimed to test the hypothesis that beetle community composition on alligator weed would be more heavily dominated by taxa related to decomposition than on either native sedge species.

Two native plant species were chosen for comparison with alligator weed as both the decomposition dynamics and invertebrate communities of any two plant species might be expected to vary to some extent, and using two native species thus provided a better measure of the variation which could be expected within the native system. *Schoenoplectus tabernaemontani* and *Isolepis prolifer* are both abundant at the study site, Lake Rotokawau. However, the two sedges differ considerably in tissue chemistry, which influences both decomposition rates and invertebrate feeding preferences. *I. prolifer* is lower in fibre and cellulose and higher in nitrogen, phosphorous and potassium than *S. tabernaemontani*, thus being more similar to the chemical composition of alligator weed tissue (Chapter 3). Therefore, it was expected that alligator weed would support a decomposer community more similar to *I. prolifer* than to *S. tabernaemontani*.

4.2 Methods

4.2.1 Study site

The Northland region of New Zealand contains a large number of small, shallow lakes formed between stabilised sand dunes (Anon 2002b). This study was conducted at one such lake, Lake Rotokawau on the Karikari Peninsula (34˚52' S, 173˚19' E). Lake Rotokawau is 21.3 ha in area, with an iron-pan base (Champion, Wells et al. 2005). Water depth in the marginal vegetation zone sampled at Lake Rotokawau ranged between a mean of 0.24 ± 0.05 m in March and 0.69 ± 0.03 m in July. The land on the Karikari Peninsula surrounding this lake, as with much of Northland, is predominantly a highly modified agricultural landscape. Lake-margin vegetation at Lake Rotokawau is characterized by small-scale patchiness, with individual patches dominated by a single plant species, be it the invasive alligator weed or a native species.

4.2.2 Coleoptera

Coleoptera was selected as the focal taxon as it is a well described, functionally diverse order, as well as being species rich, representing approximately 50% of described insect species in New Zealand (Watt 1982). Coleoptera communities have been shown to respond to differences in vegetation cover (Gardner-Gee 2004; Harris, Toft et al. 2004), and the existence of these previous studies provides greater potential for comparison with previous research than exists for some other insect groups (Hutcheson and Kimberley 1999). In addition, Coleoptera represented a substantial proportion of the invertebrates collected from both the sampling techniques outlined below.

4.2.3 Coleoptera sampling methods

Beetles were sampled using emergence traps to gain an overview of the communities present in each vegetation type. In addition to this, beetles were sampled from litter bags to more explicitly examine the beetle communities associated with decomposition within the different vegetation types.

4.2.4 Emergence traps

Emergence traps are designed to catch the emerging adults of invertebrates that have spent juvenile life stages in the ground and/or water. They have the advantage of capturing highly mobile or nocturnal species, which might not have been collected successfully from the litter bags.

One emergence trap was erected in each of four replicate patches of each of the three vegetation types. Traps were constructed using a chicken wire frame encompassing 0.5 x 0.5 m of ground, rising 1 m vertically and covered with a 1 mm^2 nylon mesh. At the top, plastic framing formed a pyramidal shape. PVC piping from the apex led to a removable 400 ml collecting jar partially filled with glycol (50% solution) as a preservative. Using preservative allowed for longer time intervals between collection dates, and prevented captured individuals from climbing back out of the trap or eating one another (Southwood and Henderson 2000). Collecting jars were replaced monthly, with sampling running from early January 2006 – early April 2006, and then again from early October 2006 – early April 2007. Sampling was suspended during winter. Traps were moved to a new, adjacent, position within each patch between the two sampling seasons to prevent the second season's catch being diminished due to inaccessibility of the trap area for breeding throughout the first trapping period.

4.2.5 Litter bags

Invertebrates were also sampled from the litter bags used for the decomposition experiment, the methodology of which is outlined in Chapter 3. Litter bags were returned to the laboratory after 3, 5 or 10 weeks decomposition. There they were inspected under a Leica Zoom 2000 microscope (up to 45x magnification), and all invertebrates detected were removed and stored in ethanol.

4.2.6 Invertebrate sorting

Invertebrates collected from both emergence traps and litter bags were sorted to order level, and then members of the order Coleoptera were sorted to morphospecies. Coleoptera were then identified to species level by S. Thorpe (independent taxonomist) and R. Leschen (Landcare Research). Where possible, published literature was used to assign beetles to one of the following trophic groups; phytophage, predator, fungivore, scavenger, or detritivore. Knowledge of the ecology of many New Zealand invertebrates is currently lacking, so the ecology can be inferred only from taxonomic relationships (Hutcheson 1999). Trophic assignation was based on information on higher taxonomic levels where no information was available for individual species. Where adult and juvenile functional groups were known to differ, beetles were assigned to the category corresponding to their adult state, as all beetles were caught as adults on the given vegetation type.

4.2.7 Analyses

Differences in beetle community composition between vegetation types were investigated using PRIMER v.5. Data was square root transformed to down-weight the importance of very abundant species, thus allowing rarer species to exert some influence on the calculation of similarity (Clarke and Warwick 2001). A similarity matrix was then created from data using the Bray-Curtis coefficient (Clarke and Gorley 2001). ANOSIM was used to test for differences in beetle community composition among plant species. ANOSIM produces a global R statistic and p-value, indicative of overall differences. R statistics closer to one indicate a high degree of separation of treatments, while an R statistic close to zero indicates there is similar variation within groups as between groups. Pair-wise R statistics and p-values are then provided to determine where differences lie. The R statistic is at least, if not more important than the p-value in determining whether any differences which may be detected are of a meaningful magnitude (Clarke and Warwick 2001). Data was plotted in a non-metric Multi-Dimensional Scaling (MDS) plot to allow a visual assessment of separation among host plant species. Data points which fall closely together on these graphs are more similar in composition than those which fall further apart.

Differences in the functional group composition of beetle individuals and species from emergence traps were tested for using Chi squared tests, or, where minimum count assumptions were violated, Fisher's Exact tests. Bonferroni corrected pair-wise Fisher's Exact tests were then used to determine where differences lay. These analyses were conducted for all months combined as preliminary analyses indicated similar trends across different months.

Similarly, Chi squared or Fisher's Exact tests were used to test for differences in functional group composition of beetle individuals and species from litter bags. Differences were tested for between vegetation cover types, for all litter types and lengths of decomposition combined, between litter types for all cover types and lengths of decomposition combined, and between lengths of decomposition for all litter and cover types combined. Litter, cover types and decomposition time were analysed separately due to the unbalanced design. Again, Bonferroni corrected pair-wise Fisher's Exact tests were then used to determine where differences lay. Chi squared and Fisher's exact tests were performed in R v 2.0.1.

4.3 Results

4.3.1 Emergence traps

A total of 987 individual beetles were collected from emergence traps, belonging to 47 species or higher taxa (Appendix 2). Twenty-eight species or higher taxa were present on alligator weed, totalling 437 individuals. A total of 136 individuals, belonging to 23 species or higher taxa were collected from *S. tabernaemontani.* A further 414 individuals, from 26 species or higher taxa were collected from *I. prolifer* emergence traps. Beetle community composition pooled over the entire sampling period showed considerable differentiation among vegetation types (ANOSIM, Global R = 0.500, p = 0.001). All pair-wise comparisons between vegetation types were significant at $p < 0.05$. However, the beetle communities associated with alligator weed and *I. prolifer* were both distinct from that associated with *S. tabernaemontani* (pair-wise R-values = 0.604 and 0.646 respectively), but showed little separation from each other (pair-wise R-value = 0.406; Figure 25).

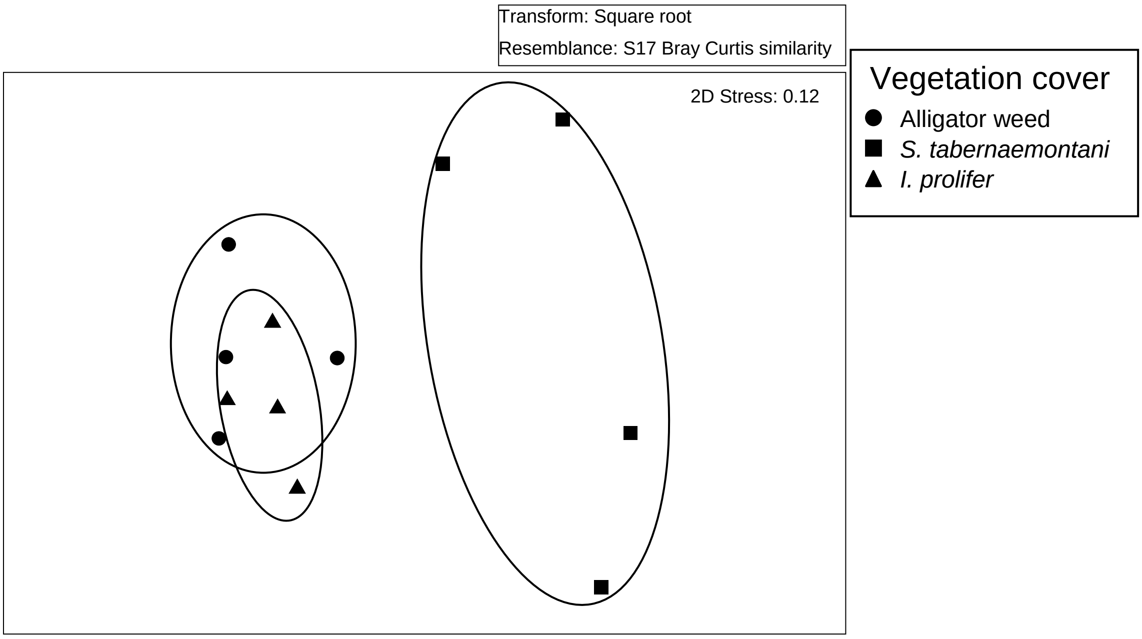

Figure 25. Separation of Coleoptera communities with vegetation type, for all months combined. Points falling closer together are more similar in composition than those falling further apart. Stress provides a measure of goodness of fit, with low stress values indicating reliable ordinations (Clarke and Warwick 2001).

SIMPER analyses indicated that the high abundance of beetles from the family Scirtidae in both alligator weed and *I. prolifer* traps distinguished the beetle communities in both these vegetation types from *S. tabernaemontani*, contributing 12% and 17% to the total differentiation for alligator weed and *I. prolifer* respectively. In contrast, the traps in *S. tabernaemontani* were distinguished by relatively high numbers of the gorse seed weevil *Exapion ulicis*, which was rare in both the other vegetation types.

Functional group composition of beetle individuals collected from emergence traps differed with vegetation type (Chi-squared test, $X^2 = 92.55$, df = 8, $p < 0.001$), with all pair-wise comparisons between vegetation types significant (Bonferroni corrected Fisher's Exact tests, $p < 0.001$ in all pair-wise comparisons). Detritivores, represented by the family Scirtidae, dominated the beetle fauna of both alligator weed and *I. prolifer*, but were less dominant in *S. tabernaemontani* traps (Figure 26). Fungivores comprised approximately a third of all individuals on both alligator weed and *S. tabernaemontani*, but a smaller proportion on *I. prolifer*. Seven families were represented by fungivorous individuals, with the most abundant species (*Sericoderus* sp., an exotic species, and *Holopsis* sp., a native species) belonging to the family Corylophidae. Phytophagous individuals, predominantly from the families Brentidae and Curculionidae, were the most abundant functional group in *S. tabernaemontani* traps, but were less dominant in samples from alligator weed and *I. prolifer*. Scavengers and predators contributed only a small proportion of individuals on all vegetation types.

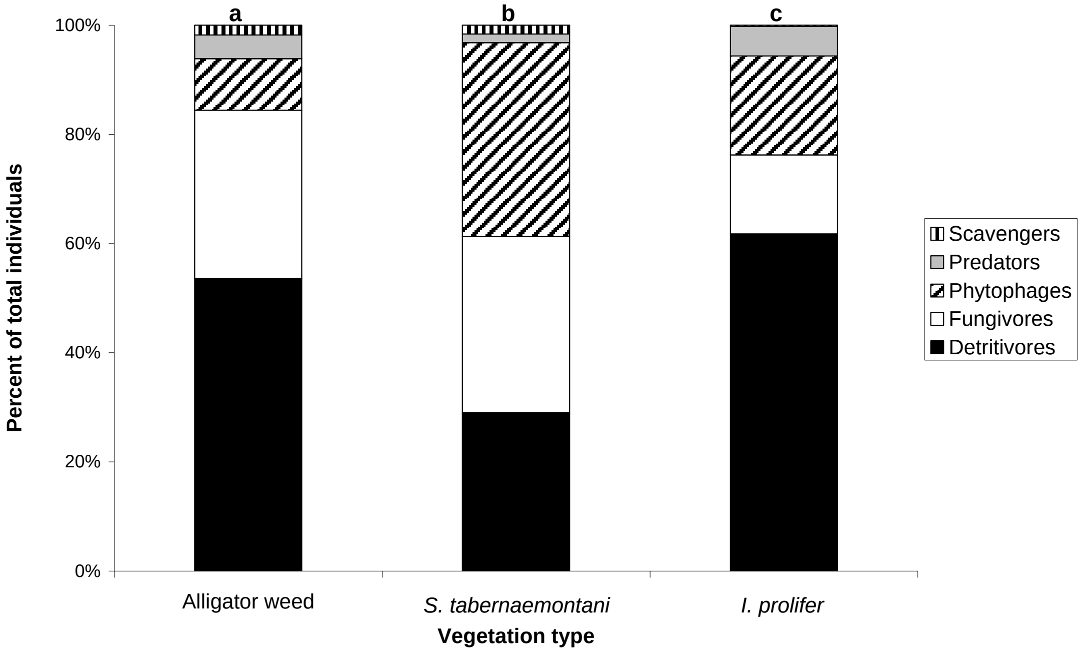

Figure 26. Functional group composition of Coleoptera individuals collected from emergence traps, all months combined. Vegetation types with different letters differ in functional group composition at $p < 0.001$.

In contrast to functional composition at the individual level, functional composition of beetles at species or higher taxonomic level did not differ among vegetation types, with phytophagous and fungivorous guilds the most species rich across all vegetation types (Fisher's Exact test, $p = 0.92$; Figure 27). Despite being dominant in terms of abundance, decomposers were represented by only a single taxonomic unit. Species diversity of decomposers is, however, probably under-represented here, as Scirtidae are treated here as a single unit due to difficulty in achieving finer taxonomic resolution (Dugdale and Hutcheson 1997), but the family is represented in these samples by more than one species (S. Thorpe pers. comm.). Fungivorous beetles on alligator weed comprised a lower proportion of species richness than of total abundance, reflecting the relatively high abundance of *Sericoderus* sp. In contrast, fungivores on *I. prolifer* were represented by more species than on alligator weed, but at much lower abundance. Similarly, phytophagous beetles made up a much higher proportion of species richness than of total abundance on both alligator weed and *I. prolifer*. Predatory beetles were also represented by relatively high species richness across all vegetation types, but with only low abundance.

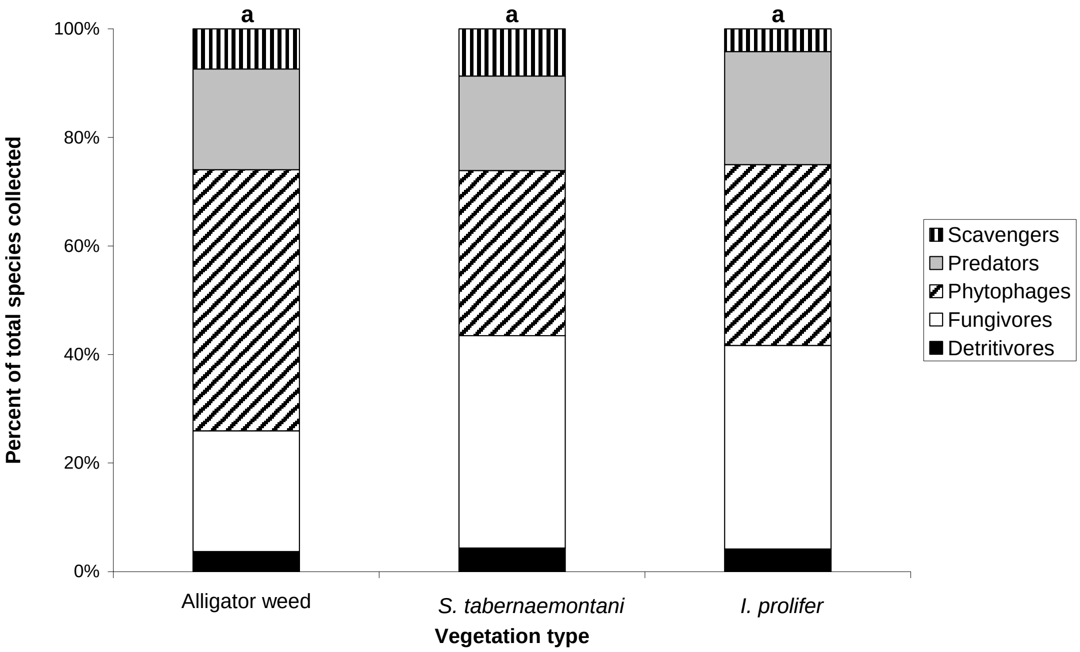

Figure 27. Functional group composition of Coleoptera species (or higher taxonomic unit) collected from emergence traps, all months combined. No differences between vegetation types were detected at the 0.05 level.

4.3.2 Litter bags

In total, 122 individual beetles, belonging to 13 species or higher taxa, were collected from litterbags (Appendix 3). Nine species or higher taxa of beetles, totalling 90 individuals, were collected from litter bags from beneath alligator weed. Eighteen individuals from five species or higher taxa were collected from bags beneath *S. tabernaemontani*. Seventeen individuals from six species or higher taxa were collected beneath *I. prolifer*.

The proportions of different functional groups among Coleoptera individuals collected from litterbags varied between vegetation cover types (Fisher's Exact test, p

< 0.001; Figure 28). Pair-wise tests indicated that litter bags decomposing under alligator weed cover were strongly dominated by fungivorous beetles (82% of individuals), leading alligator weed cover to differ from both *S. tabernaemontani* (6% of individuals fungivorous; Bonferonni corrected pair-wise Fisher's Exact test, p < 0.001) and *I. prolifer* cover (43% of individuals fungivorous; Bonferonni corrected pair-wise Fisher's Exact test, p < 0.01). In contrast, scavengers comprised a higher proportion of individuals collected from beneath the two sedge species, which did not differ from each other in functional composition of beetles (Bonferonni corrected pair-wise Fisher's exact test, p = 0.096). The functional group distributions of beetle *species* under different cover types did not, however, vary (Fisher's Exact test, p = 0.81; Figure 29). Again, this result may have been influenced by a lack of taxonomic resolution for some groups.

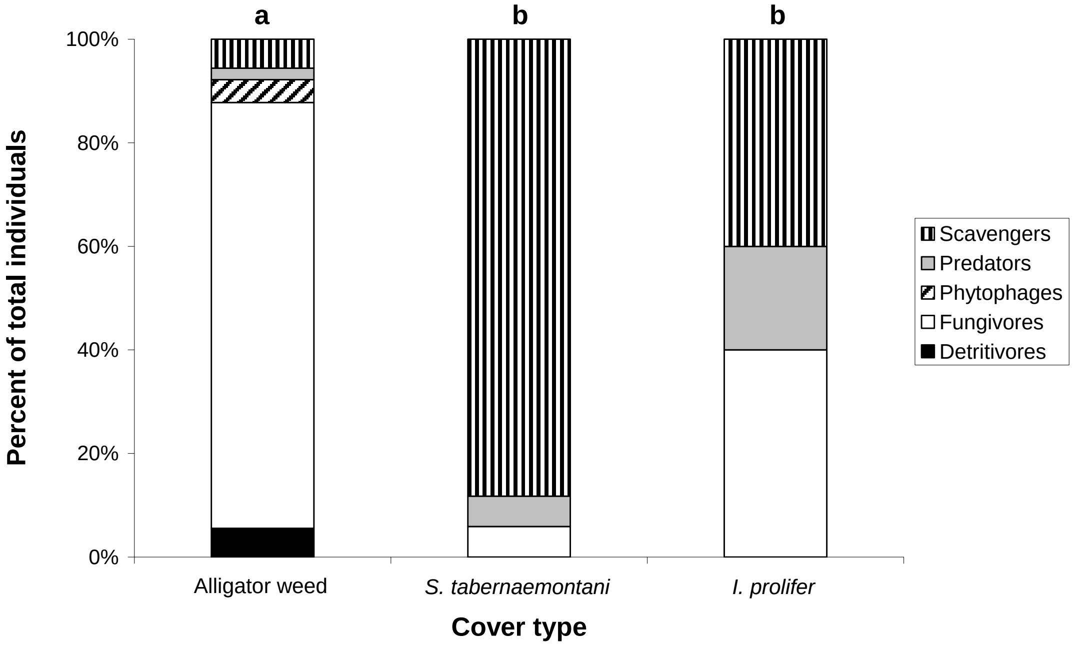

Figure 28. Functional group proportions of beetle individuals collected from litter bags with varying cover type, all litter types combined. Cover types with different letters differ in functional group composition at p < 0.01.

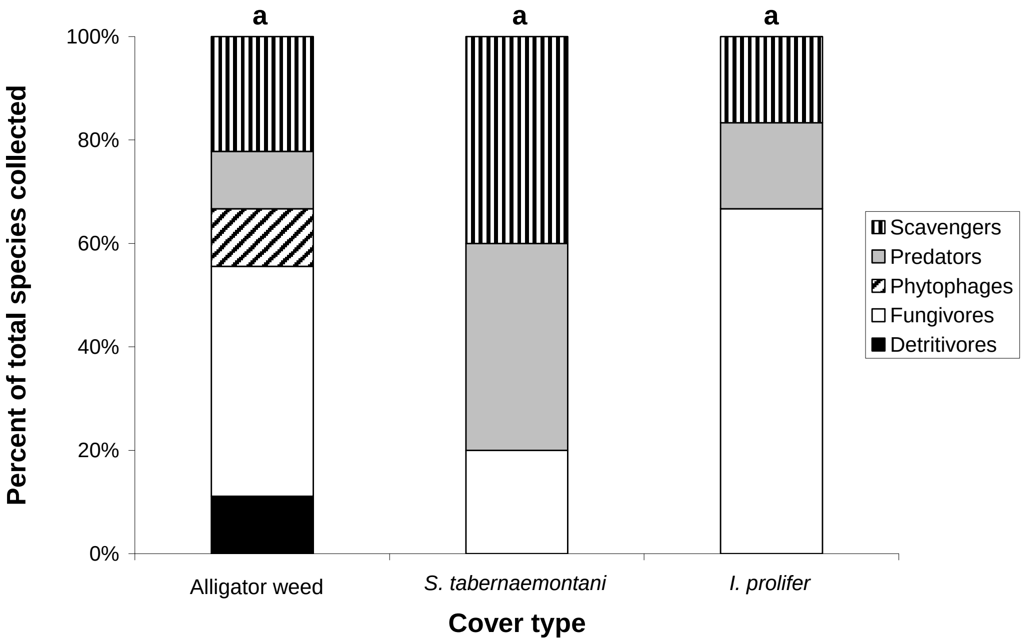

Figure 29. Functional group proportions of beetle species collected from litter bags with varying cover type, all litter types combined. No differences between cover types were detected at $p < 0.05$.

The proportions of different functional groups among Coleoptera individuals also varied with litter type (Fisher's Exact test, $p < 0.001$; Figure 30). The clearest difference was between alligator weed and *I. prolifer* litters (Bonferonni corrected pair-wise Fisher's exact test, $p < 0.001$). Beetles from *S. tabernaemontani* litter also differed from those on *I. prolifer* (Bonferonni corrected pair-wise Fisher's exact test, $p < 0.05$) but did not differ from those on alligator weed (Bonferonni corrected pair-wise Fisher's exact test, $p = 0.62$). Fungivorous beetles comprised over half the individuals from all litter types. These largely came from beneath alligator weed cover, with litter bags under both the sedge species more frequently completely lacking beetles than samples under alligator weed. Scavengers were common on alligator weed and *S. tabernaemontani* litter, but were absent on *I. prolifer* litter. As with cover type, the functional group distributions of beetle *species* on different litter types did not vary (Fisher's Exact test, $p = 0.79$; Figure 31).

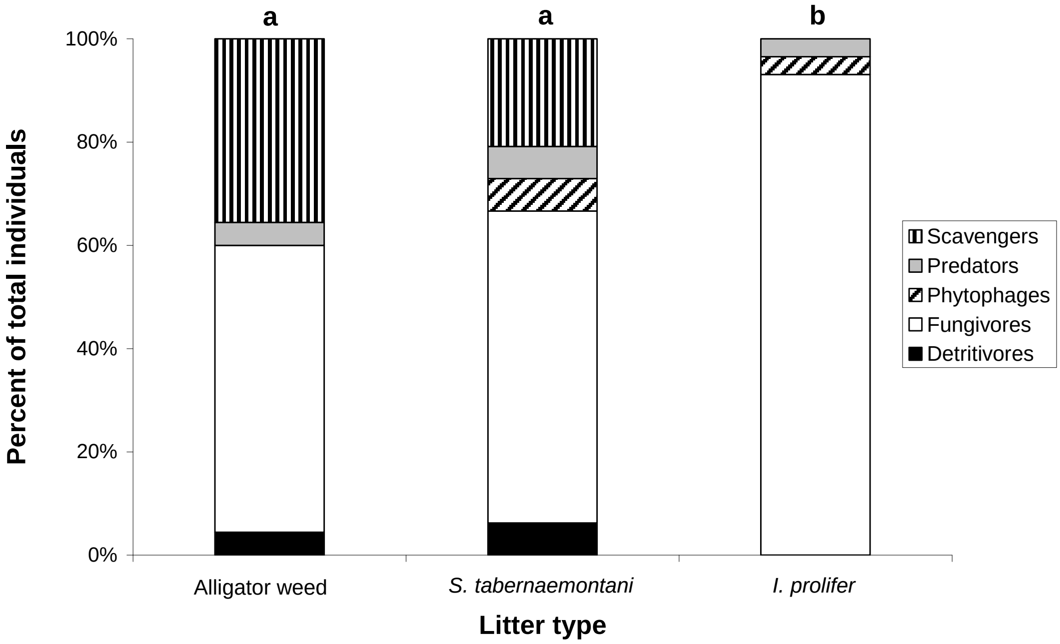

Figure 30. Functional group proportions of beetle individuals collected from litter bags with varying litter type, all cover types combined. Litter types with different letters differ in functional group composition at $p < 0.05$.

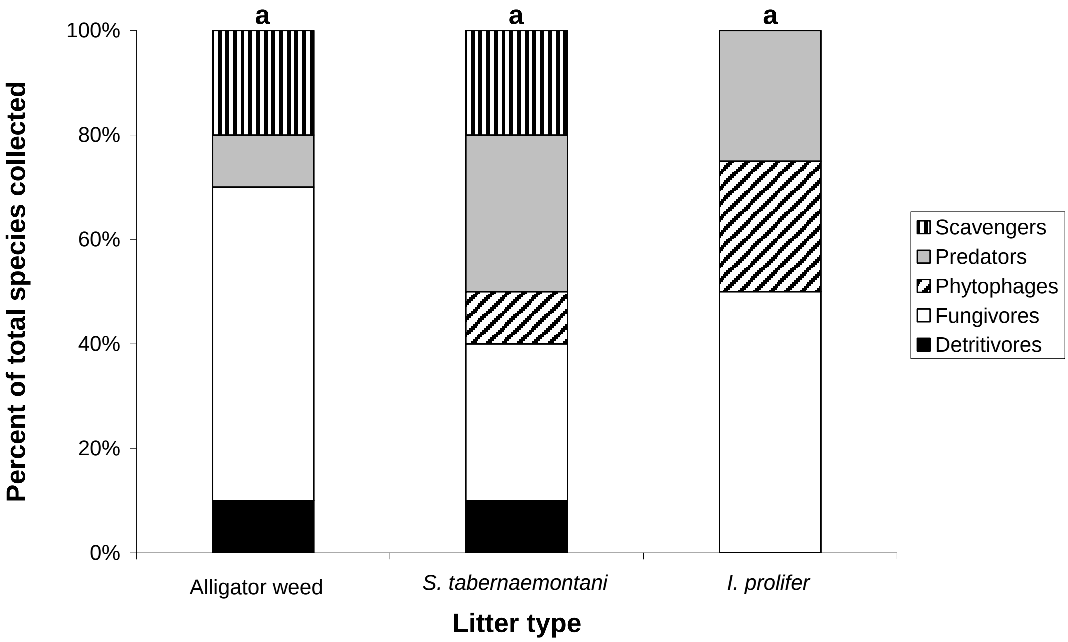

Figure 31. Functional group proportions of beetle species collected from litter bags with varying litter type, all cover types combined. No differences between litter types were detected at $p < 0.05$.

Functional group composition of individuals also differed between dates (Fisher's Exact test, $p < 0.001$; Figure 32). Pair-wise comparisons indicated that functional group composition differed between litter bags which had decomposed for three weeks and those which had decomposed for five or ten weeks (Bonferonni corrected pair-wise Fisher's exact tests, $p < 0.001$ and 0.01 respectively), but there was no evidence of a difference in functional group composition between five and ten weeks decomposition (Bonferonni corrected pair-wise Fisher's exact test, $p = 0.10$). Phytophagous beetles were only present at three weeks' decomposition. Fungivorous beetles strongly dominated the fauna at three weeks, then decreased in numbers with increasing decomposition time. Scavengers were most numerous after five weeks' decomposition, and predators were entirely absent at three weeks but became more common with increasing decomposition time, although always remaining in low numbers.

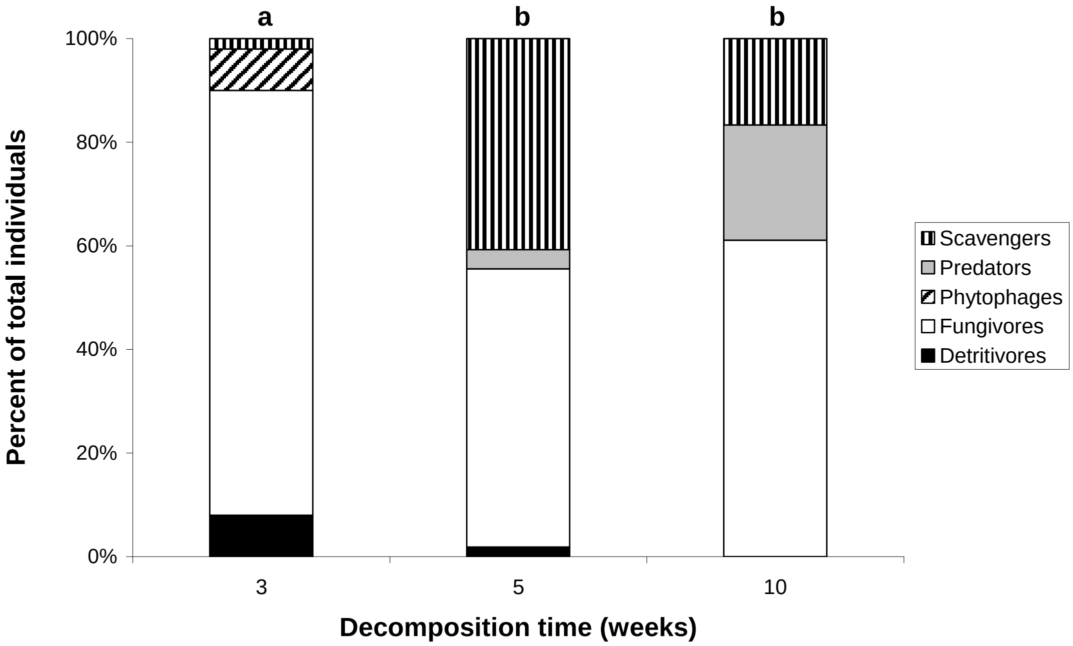

Figure 32. Functional group proportions of beetle individuals collected from litter bags after varying decomposition time, all cover and litter types combined. Dates with different letters differ in functional group composition at $p < 0.01$.

The functional group distributions of beetle *species* in litter bags removed after different decomposition times did not, however, vary (Fisher's Exact test, p = 0.18; Figure 33).

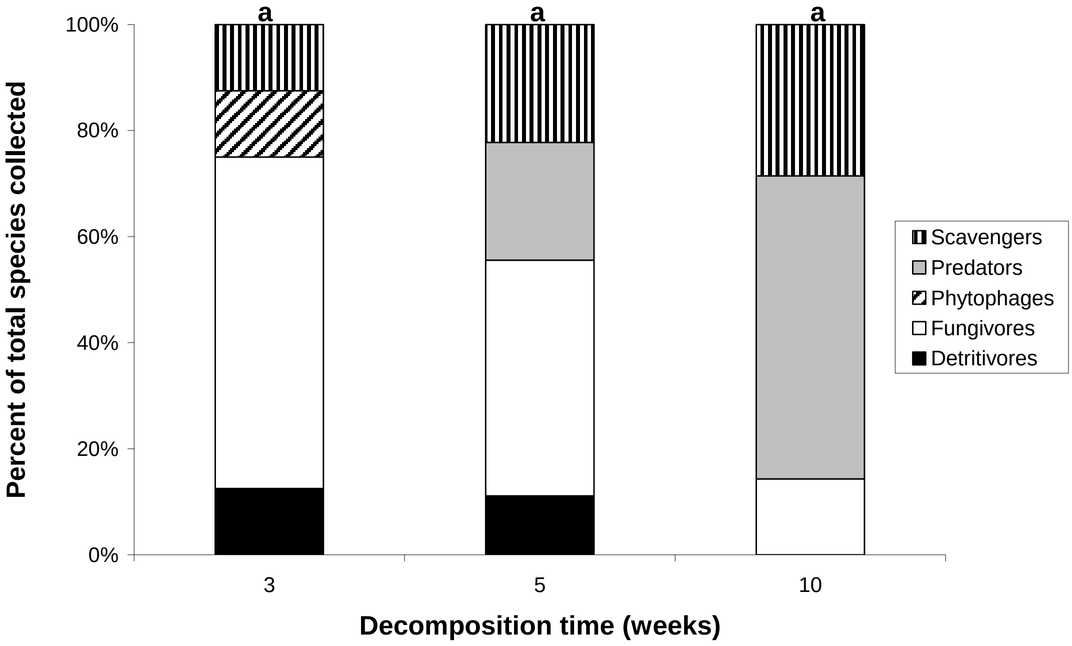

Figure 33. Functional group proportions of beetle species collected from litter bags after varying decomposition time, all cover and litter types combined. No differences between dates were detected at p < 0.05.

4.4 Discussion

4.4.1 Dominance of fungivorous and detritivorous beetles on alligator weed

Alligator weed hosted a beetle fauna more strongly dominated by decomposition-associated taxa than was the case for either native sedge species. Fungivores and detritivores together made up 84% of the beetles collected from alligator weed emergence traps, versus 61% and 76% from *S. tabernaemontani* and *I. prolifer* traps respectively. While emergence trap data is presented here for all months pooled, the dominance of fungivores in alligator weed emergence traps was particularly pronounced in mid to late summer, coinciding with the pulse of decomposition caused by *A. hygrophila* herbivory. Similarly, the dominance of fungivorous beetles (but not detritivores) was even more pronounced in litterbags removed from beneath alligator weed vegetation than was the case for emergence traps. Fungivorous beetles dominated all litter types decomposing beneath alligator weed, but were not prominent on alligator weed (or native) litter decomposing under the native sedge species. Thus it appears that the mats of decomposing alligator weed created an environment which supported a more abundant and/or diverse fungal flora than was present in areas dominated by either sedge species, with flow-on effects evident in the beetle communities supported by alligator weed. Both native and exotic fungivores (Appendices 2 and 3) responded positively to the fungal resource putatively provided on alligator weed.

Both fungivores and detritivores can dominate beetle communities in other ecosystems with increased levels of disturbance and decomposing plant material, both being, for instance, more abundant in forest patches with edge disturbance effects than in less fragmented forest (Davies, Melbourne et al. 2001). Exotic *Pinus radiata* plantations in New Zealand's central North Island, characterised by high growth rates and frequent human imposed disturbance, were also found to be dominated by detritivorous beetle species (Hutcheson and Jones 1999). These authors concluded that recycling of the fungi/wood decay complex rather than live plant material played the main role in structuring beetle communities in this habitat

Despite making up the overwhelming majority of individuals caught in alligator weed emergence traps, fungivores and detritivores comprised less than one third of the species collected from these traps. This reflects the very high abundance of a few species, particularly the exotic *Sericoderus* sp. (Corylophidae) which appears to have been especially well adapted to take advantage of the fungal resource apparently provided by alligator weed. Species of this genus elsewhere commonly occur in grass cuttings and mouldy hay (Lawrence and Britton 1991), which represent similar environments, albeit entirely terrestrial, to the mats of decomposing alligator weed. In addition, species richness of detritivores is likely to have been under represented here as all members of the family Scirtidae have been treated as a single taxa due to difficulties in achieving a finer degree of taxonomic resolution (Dugdale and Hutcheson 1997), but are in fact likely to be represented by more than one species and be native in provenance (S. Thorpe pers. comm.).

Beetle community composition from *S. tabernaemontani* emergence traps was strongly separated from beetle communities from both alligator weed and *I. prolifer* traps, which clustered closely together in the MDS plot. Although to a lesser extent than for alligator weed emergence traps, fungivores and detritivores did also comprise a substantial component within *I. prolifer* traps. This sedge forms dense, floating mats which trap large amounts of decomposing organic matter, again providing a considerable resource for decomposition associated taxa. In contrast, *S. tabernaemontani* stands have a taller, more open structure, which tended to have little associated organic matter.

In further contrast to the other two vegetation types, *S. tabernaemontani* emergence traps collected relatively high abundances of phytophagous beetles. However, this may represent spill-over from adjacent vegetation more than an actual preference for *S. tabernaemontani*. The gorse seed weevil, *Exapion ulicis*, which was highly abundant in two *S. tabernaemontani* traps in December 2006 and January 2007 feeds only on gorse (*Ulex europaeus* L.) in New Zealand, but has been observed in high numbers on other vegetation presumably due to wind movement (Kuschel 2003). Similarly, various species of Curculionidae collected from *S. tabernaemontani* traps are known to feed on other plant species, including *Storeus albosignatus* on *Acacia longifolia* (May 1987) and *Sitona lepidus* on clover (*Trifolium* spp.) (Barratt, Barker et al. 1996). Both of these plant genera were found in surrounding vegetation. Thus, the strong separation of *S. tabernaemontani* emeregence traps from alligator weed and *I. prolifer* in the MDS plot and functional group analyses may have somewhat over-represented the biologically relevant differences between these species. Harris, Toft et al (2004) recorded similar effects of the surrounding vegetation matrix when comparing invertebrates between introduced gorse and native kanuka. Several of the species found in greater abundance in one or other vegetation type were known to be associated with other plant species found in or adjacent to that vegetation type but not the other.

The fungivorous component of the beetle fauna in litter bags decreased with increasing decomposition time, consistent with an abundant fungal resource involved in the early conditioning of leaves, diminishing as decomposition became more complete. In contrast, predators increased with decomposition time, presumably as a result of an accumulating prey resource. Predatory beetles contributed a higher proportion of species than individuals across all vegetation types, in both litter bags and emergence traps. This is consistent with other studies which have also found beetles from higher trophic levels to be present at low densities (Hutcheson and Jones 1999).

As this study was conducted at only a single invaded study site, the results cannot be generalised to other alligator weed invasions. However, it seems likely that decomposition-associated invertebrate taxa would be affected in any system in which the presence of alligator weed and its biocontrol agent resulted in a large pulse of decomposition uncharacteristic of the decomposition dynamics of the native vegetation.

4.4.2 Integrating the effects of weed invasion on diverse ecological metrics

Numerous studies have identified effects of weed invasion on decomposition or invertebrate communities, and often both have been shown for the same weed species. Detritivore abundance tended to be higher in invasive gorse (*Ulex europaeus*) than native kanuka (*Kunzea ericoides*) stands (Harris, Toft et al. 2004). Although decomposition rates were not measured in this study, the increased detritivore abundance was attributed to abundant dead wood and litter within gorse patches and it is probable that decomposition dynamics differ between gorse and kanuka. In the case of *Tradescantia fluminensis*, differences in fungal-feeding invertebrate taxa including beetles and nematodes (Yeates and Williams 2001; Standish 2004) can be assumed to be linked to the altered decomposition environment created by mats of the invasive weed (Standish, Williams et al. 2004). Beetle communities beneath the invasive giant knotweed were more heavily dominated by detritivores than were communities beneath native vegetation (Topp, Kappes et al. 2008). This was attributed to the abundant litter generated by the invasive plant.

The current study similarly identifies a mechanism by which the altered decomposition dynamics of alligator weed can be seen to be affecting the invertebrate communities hosted by it. The strong response of fungivorous or detritivorous species to invasion by alligator weed and other invasive plant species, suggests that these functional groups may be particularly likely to be affected by weed invasions that alter the decomposition environment of an ecosystem. In contrast, despite the strong role of bacteria in decomposition in many ecosystems, bacterial feeding nematodes were not found to differ between native and weedy vegetation in the manner exhibited by fungivorous nematodes (Yeates and Williams 2001). Altered decomposition dynamics observed for other weedy species may therefore also have flow-on effects on invertebrate communities, especially fungus-associated taxa.

4.4.3 Indirect effects of biological control on invertebrate communities

Alligator weed decomposes faster than either of the native sedges studied here (Chapter 3). However, the pulse of decomposition making this resource available within the system depends, both in terms of timing and magnitude, on the presence of the biological control agent *A. hygrophila* in addition to the weed itself. The biocontrol agent is therefore indirectly affecting not only an ecosystem process (decomposition; Chapter 3) but also the composition and abundance of other invertebrates.

While pre-release testing for biological control agents is now comprehensive with respect to predicting potential feeding on non-target plants (Pemberton 2000), indirect effects of biocontrol agents on other ecosystem components are less well documented and less easily predicted. Biocontrol agents may be preyed on or parasitized by native species. For example, deer mice in a Montana grass-land preferentially fed on spotted knapweed seedheads containing larvae of a gall fly biocontrol agent, thus shifting mouse habitat use for parts of the year from native vegetation to weed-invaded areas (Pearson, McKelvey et al. 2000). This habitat shift may then have had flow-on effects to other ecosystem components. Similarly, native parasitoids, maintained at high population levels by the presence of an introduced biocontrol agent host, could potentially negatively impact native invertebrate hosts (Willis and Memmott 2005). Biocontrol agents are also known to indirectly affect other invertebrate species by competing with them for food, as with the non-host-specific weevil *Rhinocyllus conicus*, introduced to North America to control exotic thistles. Where the weevil developed on native thistle hosts, its presence was related to decreased abundance of a native fly which pupates within thistle flower heads (Louda, Rand et al. 2005).

The effect of *A. hygrophila* on beetle communities represents yet another mechanism for indirect effects of a biological control agent on other invertebrates: by altering decomposition dynamics it apparently increased habitat availability for fungi which themselves provided an enhanced resource for fungivorous invertebrates. This finding highlights the diverse and intricate nature of potential ‘ripple’ effects of biological control introductions, and supports Fowler, Syrett et al’s (2000) observation that an accurate catalogue of ecosystem effects resulting from biocontrol introductions would be impossible to predict *a priori* given the unpredictability and complexity of interactions between a newly introduced organism and its receiving environment(s). However, effects on decomposition and associated decomposer communities may be among those which could be commonly expected to occur as a result of introducing herbivores for biocontrol, as such introductions may often result in altered cycling of biomass and litter as demonstrated in this study and elsewhere (Paynter 2006).

Further, the effects of *A. hygrophila* documented here suggest that while ecosystem effects of biocontrol introductions are likely to be complex and difficult to predict, they may also be of sufficient magnitude and reach within an ecosystem to warrant consideration in the agent selection process. Louda and Stiling (2004) note that ineffective releases do not help the pest problem, yet potentially carry multiple ecological risks. Current biological control agent selection protocols emphasise testing host specificity over potential effectiveness (Schooler, Clech-Goods et al. 2006). In finding the parasitoid *Sphecophaga vesparum vesparum* to be ineffective at controlling *Vespula* wasps in New Zealand, Beggs, Rees et al (2008) suggested that pre-release assessment of agents' likely impacts on the target host would result in more effective agents being introduced. This would improve the balance of ecological benefits compared with risks arising from biological control introductions.

4.4.4 Conclusions

The results of this study support the initial hypothesis that the beetle fauna on alligator weed would be more dominated by decomposition-related taxa than would be the case on either native sedge species. The hypothesis that the beetle fauna on alligator weed would be more similar to that on *I. prolifer* than *S. tabernaemontani* was also supported. The pulse of decomposing alligator weed occurring in summer apparently hosted a strong fungal community which in turn supported high numbers of some fungivorous beetles. In concert with other studies, it suggests that fungivorous taxa may be particularly sensitive to changes in decomposition dynamics resulting from weed invasion. The study highlights the linkages between various ecosystem components, and the way in which weed impacts on one aspect of an ecosystem can be expected to have follow-on effects for other components. This study also highlights the potentially complex 'ripple' effects of biological control agents, as well as their target weeds, on other components of their receiving ecosystems.

5 RESPONSE OF LAKESIDE INVERTEBRATE COMMUNITIES TO CHANGES IN PLANT ARCHITECTURE ASSOCIATED WITH INVASION BY AN EXOTIC WEED

5.1 Introduction

5.1.1 Role of plant architecture in determining invertebrate habitat choice

Plant identity can have a major influence on the structure of invertebrate communities. Invertebrate abundance and composition can be influenced by differences in plant architecture and chemistry (often reflecting taxonomic differences), which may alter the amount of suitable habitat, food, attachment sites or degree of shelter from predators and the environment offered by a given plant species.

Some phytophagous invertebrates are restricted to feeding on a single plant species, or a few closely related or chemically similar species, with plant taxonomic diversity an important determinant of invertebrate diversity (Siemann, Tilman et al. 1998). Within herbivorous species, certain guilds, such as leaf-miners and gall-formers, tend to show higher rates of host specificity (Memmott, Fowler et al. 2000).

Plants with more complex architecture may provide a greater diversity of resources, and thereby support higher invertebrate numbers than more architecturally simple plant species (Lawton 1983). For instance, in aquatic systems, plants with highly dissected leaf architecture may host high invertebrate numbers because they host abundant epiphytic algae and provide refuges from predation (Kelly and Hawes 2005; Hornung and Foote 2006).

5.1.2 Effect of differences in architecture and/or chemistry between native and exotic vegetation

Where exotic plant species differ in chemistry and/or architecture from native plants, they may host different invertebrate communities from the pre-existing vegetation. However, relatively little is known about the effects of weed invasion on invertebrate communities (Ernst and Cappuccino 2005). The enemy release hypothesis predicts that introduced plants may become invasive because they host fewer herbivores than they do in their native range, as fewer of the herbivores with which the plant has co-evolved will be present in the introduced range, and many herbivores native to the plant's introduced range, particularly specialist herbivore species, will be unable to utilise the exotic plant (Keane and Crawley 2002). This hypothesis has been supported by surveys which have found higher overall herbivore numbers and particularly higher numbers of specialist species on plants in their native compared with introduced ranges (Memmott, Fowler et al. 2000; Cripps, Schwarzlander et al. 2006). Guild composition of herbivores may also differ on exotic compared with native vegetation. For instance, herbivores on *Lepidium draba* in its introduced range were predominantly generalist sap-suckers, with root feeders and gall formers completely absent (Cripps, Schwarzlander et al. 2006).

The enemy release hypothesis also predicts that introduced plant species should host lower numbers of invertebrates in comparison to the surrounding native vegetation, as many of the herbivores present in the introduced range will be adapted to feed on native vegetation but not the introduced plant (Keane and Crawley 2002). This prediction was supported by the lower abundance of phytophages detected in stem samples from the invasive vine *Vincetoxicum rossicum* than from nearby native plant species (Ernst and Cappuccino 2005). Similarly, herbivore abundance (excluding an introduced biocontrol agent) was lower on introduced gorse (*Ulex europeaus*) than on native kanuka (*Kunzea ericoides*) in New Zealand's South Island (Harris, Toft et al. 2004). However, in a review paper, Colautti, Ricciardi et al (2004) found that this pattern is by no means exhibited in the majority of studies. While the results of some studies did support the prediction, many studies in fact found higher numbers of enemies (including pathogens as well as invertebrates) on invasive rather than native species. This suggests that introduced plants can represent naïve hosts for enemies from outside of the plant's native range.

While the enemy release hypothesis predicts differences in herbivore abundance with weed invasion, invertebrates belonging to other trophic groups, including predators, may also be affected. As they are not feeding directly on the introduced plant, architecture and other factors may be more influential than taxonomy in determining predator abundance. Web-building spiders in particular are known to be tightly correlated with architectural features of vegetation which meet their specific web attachment requirements (Rypstra, Carter et al. 1999). Web-builders were 80% less abundant in invasive *Phragmites australis* stands than native *Spartina alterniflora*, whereas hunting spiders showed only a 25% decrease in abundance (Gratton and Denno 2005). As well as being directly affected by plant architecture, predatory invertebrates may be affected by differences between plant species in the abundance and/or composition of lower trophic groups of invertebrates. In a meta-analysis, Langellotto and Denno (2004) found that seven out of nine predatory guilds showed increased abundance with increased habitat complexity. In contrast, Hornung and Foote (2006) found predator abundance in Canadian wetlands was higher in simple rather than complex vegetation, which they suggested may be due to the increased hunting success of visually oriented predators in less complex vegetation.

5.1.3 Exotic plants as habitat for native invertebrates

Another corollary of the enemy release hypothesis is that introduced plant species represent a low quality habitat for native invertebrates relative to native vegetation, and thus invasion of an area by an introduced plant species could be expected to lead to a reduction in the proportion and/or abundance of native invertebrates. Consistent with this, several studies have shown that abundance and diversity of native New Zealand invertebrates is low in pasture (dominated by exotic plant species) compared with native forest or scrub, with pasture sites instead dominated by exotic invertebrates (Crisp, Dickinson et al. 1998; Harris and Burns 2000; McLean and Jones 2006).

However, native invertebrate numbers are not always lower on exotic than native vegetation. While herbivore abundance was lower than on the native vegetation, overall invertebrate abundance was at least as high on gorse as on native kanuka stands (Harris, Toft et al. 2004). A high degree of architectural and/or taxonomic similarity between an introduced plant and the native vegetation it is invading may contribute to similar invertebrate communities in the two vegetation types. Gorse and kanuka were found to be quite structurally different, which is likely to have contributed to the differences in invertebrate community composition detected despite similar levels of total abundance. In contrast, para grass (*Urochloa mutica*) hosted comparatively similar epiphytic invertebrates to those on native grasses in northern Australia, which was attributed to the high degree of structural similarity between the native and invasive plant species (Douglas and O'Connor 2003). Similarly, the prevalence of native Brassicaceae in North America was thought to allow some native herbivore species to utilise the weed *Lepidium draba* by being pre-adapted to closely related plant species (Cripps, Schwarzlander et al. 2006).

5.1.4 Alligator weed

Alligator weed (*Alternanthera philoxeroides*) is an herbaceous perennial weed invasive in New Zealand and elsewhere. Extensive surveys have been undertaken for potential biocontrol agents within its native range in South America. These have recorded over 40 species of insects on alligator weed (Maddox, Andres et al. 1971). Of those, several have been introduced as biocontrol agents in parts of its exotic range. In New Zealand, the most successful of these has been the alligator weed flea beetle (*Agasicles hygrophila*: Chrysomelidae). Beyond the presence of introduced biocontrol agents, little is known about the invertebrate fauna hosted by alligator weed outside of its native range.

This study aimed to examine the invertebrate communities hosted by alligator weed in lake-margin vegetation in northern New Zealand, and to compare them with invertebrates found on two native sedge species, *Schoenoplectus tabernaemontani* and *Isolepis prolifer*, in the same environment (Figure 34). These two sedge species were chosen as they were both relatively abundant at the study site, and differ considerably in architecture and chemistry. *S. tabernaemontani* is a tall sedge, growing to approximately 2 m in height (Johnson 1998), whereas *I. prolifer* is much shorter, reaching heights of 60 cm or less (Johnson 1998), similar to those attained by alligator weed. Moreover, *S. tabernaemontani* stands are comprised of simple, thick vertical culms that are widely spaced, whereas *I. prolifer* mats are a much denser network of inter-arching culms, many of which end in vegetatively proliferating juveniles, thus giving much more structural complexity, again more similar to that of the many branches and leaves of alligator weed. Further, *I. prolifer* tissue is lower in fibre and cellulose and higher in nitrogen, phosphorous and potassium than *S. tabernaemontani*, more in line with the chemical composition of alligator weed tissue (Chapter 3).

Figure 34. The two native sedges in which invertebrate communities were investigated for comparison with those on alligator weed; *Schoenoplectus tabernaemontani* (left) and *Isolepis prolifer* (right).

Specifically, this study aimed to test five hypotheses relating to the invertebrate communities hosted by alligator weed compared with the two native sedge species. These were: (1) that invertebrate abundance would be higher on the more architecturally complex alligator weed and *I. prolifer* than on *S. tabernaemontani*. (2) That as an exotic plant species, alligator weed would host a lower proportion of native invertebrates than hosted on the native sedge species. (3) That differences in plant architecture and/or a higher abundance of lower trophic levels of invertebrates would result in a higher abundance of predators on alligator weed compared with *S. tabernaemontani*. (4) That specialist herbivores (excluding introduced biocontrol agents) would be under-represented on alligator weed compared with the native sedges, and that this would be reflected in changes in herbivore guild composition. (5) That generalist herbivores would be shared across all plant species.

5.2 Methods

5.2.1 Study site

The Northland region of New Zealand contains a large number of small, shallow lakes formed on iron pans or between stabilised sand dunes (Anon 2002b; Hunt 2007). Their margins are generally characterised by a patchy mosaic of sedges, rushes and raupo (Hunt 2007). The Karikari Peninsula hosts several of these lakes, and three of them were chosen for this study. These were Lake Rotokawau (34˚52' S, 173˚19' E), Vineyard Lake (34˚ 51′ 46′′ S, 173˚ 23′ 03′′ E), and Lake Waiporohita (34˚ 53′ 56′′ S, 173˚ 20′ 52′′ E). Lake Rotokawau was chosen as the primary study site as it is heavily invaded by alligator weed. In contrast, Vineyard Lake and Lake Waiporohita are free or almost free of alligator weed respectively, and were chosen to provide some comparison for invertebrate communities on the same native plant species in similar systems but in the absence of alligator weed. It was not possible to obtain multiple invaded and uninvaded lakes for comparison as alligator weed is often actively controlled, and other invaded lakes were sufficiently geographically isolated as to vary substantially in a number of physical and biological characteristics. Lake Rotokawau is 21.3 ha in area, while the smaller Lake Waiporohita is 5.6 ha. Both lakes have an iron-pan base (Champion, Wells et al. 2005). The Vineyard Lake is approximately 0.3 ha in area and appears to be of anthropogenic origin. Water depth fluctuated seasonally at each lake (Table 3).

Table 3. Range of water depths at different lakes as measured in the centre of five replicate 0.25 m x 0.25 m quadrats used to sample vegetation for epiphytic invertebrates.

Lake	Water depth (m)	
	March 2006	July 2006
Lake Rotokawau	0.24 ± 0.05	0.69 ± 0.03
Lake Waiporohita	0.06 ± 0.01	1.17 ± 0.07
Vineyard Lake	0.34 ± 0.05	0.51 ± 0.09

The land on the Karikari Peninsula surrounding these lakes, as with much of Northland, is predominantly a highly modified agricultural landscape. Lake-margin vegetation at all three sites is characterized by small-scale patchiness, with individual patches strongly dominated by a single plant species, be it the invasive alligator weed or a native species. Five replicate patches each of alligator weed, *S. tabernaemontani* and *I. prolifer* were selected from within Lake Rotokawau. Five replicate patches of *S. tabernaemontani* were also selected at Lake Waiporohita, and likewise five patches of *I. prolifer* were selected at the Vineyard Lake, these being in each case the only one of the three study plants present at these two lakes respectively.

5.2.2 Excised vegetation

Invertebrates were sampled by cutting all vegetation at ground-level from a 25 cm x 25 cm quadrat (0.0625 m^2 in area) in each replicate patch. Lake levels fluctuated during the course of sampling, but in almost all months at least part of the vegetation removed from each plot was submerged below the water-line, and this was collected in addition to that part of the plant which was emergent above the water. All excised vegetation was sealed in ziplock bags and transported in chilly-bins back to a University of Auckland laboratory, where it was refrigerated to minimise decomposition of plant and animal matter, and to reduce invertebrate activity and resulting predation. All vegetation was visually inspected under a Leica Zoom 2000 microscope (up to 45x magnification) as soon as possible after collection. All invertebrates detected were removed, and placed into 70% ethanol.

This procedure was repeated monthly from February – April 2006 and then again from October 2006 – April 2007. Each month, vegetation was removed from the same five replicate patches of each vegetation type, but from a different, randomly selected 0.0625 m^2 quadrat within each patch to prevent previous months' extractions from affecting samples. Sampling was suspended during winter partly because invertebrate activity is often reduced in cooler months (Hutcheson and Jones 1999), and also due to increased difficulty accessing study sites in the lake environment over winter due to elevated water levels and strong winds and waves.

5.2.3 Emergence traps

In this chapter, invertebrate communities were also analysed from the same emergence traps used to sample invertebrate responses to altered decomposition dynamics (Chapter 4). The methodology used for emergence trapping is thus outlined in Chapter 4. Emergence traps are designed to catch the emerging adults of invertebrates that have spent juvenile life stages in the ground and/or water. This trapping method was expected to better capture highly mobile taxa that may be disturbed by the collector in the bagged vegetation method, as well as those species that might be nocturnally active. It also allowed continuous sampling throughout each month, rather than a one-off collection date each month as in the bagged vegetation method. Emergence trapping was used only at Lake Rotokawau.

5.2.4 Invertebrate sorting

To provide an over-view of invertebrate communities on different vegetation types, invertebrates from both sampling methods were sorted to order level following the key given by Harvey (1989). Members of the Classes Gastropoda, Oligochaeta and Hirudinidea were sorted only to Class level due to difficulties in accurately identifying specimens to order level. Where possible, juveniles were identified to order level. Where this was not possible they were classified as “unidentified juvenile”.

5.2.5 Hemiptera

The order Hemiptera is comprised of predominantly herbivorous species, and is thus likely to be strongly influenced by plant community composition. Hemiptera collected from excised vegetation were therefore sorted to morphospecies and then identified to species level by S. Thorpe (independent taxonomist), D. Toulon (Hort Research) and R. Henderson (Landcare Research). Where possible, species were categorised as native or exotic based on information in the Checklist of New Zealand Hemiptera (Larivière 2005), and classified by feeding habit based on the available literature. Differences in Hemipteran biomass between vegetation types were examined by oven-drying five randomly selected individuals from each species at 70˚C for 24 hours and then weighing them to determine dry mass. An average dry mass for the species was then determined from these five measurements. Where less than five individuals were caught from a given species, all individuals caught were dried and weighed.

5.2.6 Araneae

The order Araneae was used to examine the effects of vegetation type on predatory invertebrates. Preliminary analyses suggested that, in particular, members of the genus *Tetragnatha* played a strong role in differentiating vegetation types. This order was therefore sorted into two categories, being *Tetragnatha* spp. (identified by G. Hall, Landcare Research) and “other” spiders.

5.2.7 Coleoptera

Coleoptera from emergence traps were used as an additional focus group as they represented a substantial component of emergence trap catches from all vegetation types. In addition, Coleoptera are a well described, functionally diverse order, as well as being species rich, representing approximately 50% of described insect species in New Zealand (Watt 1982). Coloepteran communities have been shown to respond to differences in vegetation cover (Gardner-Gee 2004; Harris, Toft et al. 2004)**,** and the existence of previous studies in this area provides greater potential for comparison with previous research than exists for some other insect groups (Hutcheson and Kimberley 1999). Coleoptera were sorted to morphospecies. They were then identified to species level by S. Thorpe (independent taxonomist) and R. Leschen (Landcare Research). Where possible, published literature was used to categorise beetles as native or exotic.

5.2.8 Analyses, Hypothesis 1: Differences in invertebrate abundance

For excised vegetation, differences in total invertebrate abundance and Hemiptera abundance at Lake Rotokawau were assessed using two-way ANOVAs, testing for effects of vegetation type and sampling month. Differences in abundance on each of the two sedge species were compared in separate two-way ANOVAs between Lake

Rotokawau and the other lake at which the sedge was present, testing for the effects of lake location and sampling month. This provided a measure of whether invertebrate abundance on these plant species at Lake Rotokawau (invaded by alligator weed) might be similar to abundance on the same species at other, uninvaded lakes in the region. Where necessary, data were log plus one transformed to overcome heteroscedasticity.

Six out of the twelve emergence traps were stolen in October 2006, and a further three lost their collecting jars due to high winds. Sample size was therefore reduced in this month to one trap in each vegetation type. Similarly, the following month's sample size was reduced to two traps in each of alligator weed and *S. tabernaemontani*, and one in *I. prolifer* due to the time required to replace stolen traps. Further damage occurred to traps in both February and March 2007 due to strong winds, reducing *n* from 12 to 8 and 7 in February and March respectively.

Exploratory analyses indicated no consistent seasonal trends in total invertebrate or beetle abundance across all traps in any of the vegetation types. The mean number of individuals caught per month, averaged over the whole sampling period, was therefore obtained for each replicate trap by dividing the total number caught in that trap by the number of months for which data was obtained for that trap. One-way ANOVAs were then performed, examining the effect of vegetation type on the mean number of invertebrates or beetles per trap per month.

Tetragnatha sp. and total spider abundance from bagged vegetation were both log (n+1) transformed due to heteroscedasticity. Transformed *Tetragnatha* sp. data still failed Levene's test for homogeneity of variance. Differences were therefore assessed by lowering the alpha level to 0.005, at which Levene's test was no longer significant

(Underwood 1981). This allowed results to be confidently attributed to differences in means rather than variance. Two-way ANOVAs were used to examine differences in *Tetragnatha* sp. and total spider abundance between months and vegetation types. Differences in the proportion of spiders belonging to *Tetragnatha* sp. between vegetation types were assessed by pair-wise Chi-squared tests between vegetation types. Bonferroni of Holm corrections were used to adjust for multiple comparisons, and Yates' continuity correction to prevent p-values being underestimated in 2 x 2 tables (Glantz 2005). Similarly, Chi-squared tests followed by Bonferroni corrected pair-wise Fisher's exact tests were used to examine differences among vegetation types in the proportions of Tetragnathids and other spiders in emergence traps. For both sampling methods, proportions of Tetragnathids were examined for data from all months pooled, as preliminary analyses indicated similar trends occurred across all months.

5.2.9 Analyses, Hypothesis 2: Proportions of native invertebrates

Chi squared tests, or, where minimum count assumptions were violated, Fisher's Exact tests, were used to test for differences in the proportions of native and exotic individuals and species between vegetation types for both Hemiptera from excised vegetation and Coleoptera from emergence traps. These were done for all months pooled, as similar trends were exhibited across all months. Bonferroni corrected Fisher's Exact tests were then used to determine where pair-wise differences lay.

5.2.10 Analyses, Hypotheses 3, 4 and 5: Functional group composition

Hemiptera community composition was investigated using PRIMER v.5. Data was square root transformed to down-weight the importance of the very abundant species, thus allowing rarer species to exert some influence on the calculation of similarity

(Clarke and Warwick 2001). A similarity matrix was then created from data using the Bray-Curtis coefficient (Clarke and Gorley 2001). ANOSIM was used to test for differences in Hemiptera community composition between plant species. ANOSIM produces a global R statistic and p-value, indicative of overall differences. R ranges from -1 to 1. R statistics closer to one indicate a high degree of separation of treatments, while an R statistic close to zero indicates there is similar variation within groups as between groups. Pair-wise R statistics and p-values are then provided to determine where differences lie. The R statistic is at least, if not more important than the p-value in determining whether any differences which may be detected are of a meaningful magnitude (Clarke and Warwick 2001). Data was also plotted in a non-metric Multi-Dimensional Scaling (MDS) plot to allow a visual assessment of separation between treatments. Data points which fall closely together on these graphs are more similar in composition than those which fall further apart.

Differences in mean abundance of predatory Hemiptera at Lake Rotokawau were tested using a one-way ANOVA, testing for an effect of vegetation type. As with proportions of native invertebrates, differences in trophic guild composition of Hemiptera were also tested for using Fisher's Exact tests, followed by Bonferroni corrected pair-wise Fisher's Exact tests. Unless otherwise stated, all analyses were conducted using R v 2.0.1.

5.3 Results

5.3.1 Hypothesis 1: Differences in invertebrate abundance

A total of 7316 invertebrates were collected from excised vegetation. These belonged to 20 orders and higher taxa plus unidentified juveniles (Appendix 4).Total invertebrate abundance per vegetation sample from Lake Rotokawau was affected by an interaction between sampling month and vegetation type (Two-way ANOVA, $F_{18,115} = 1.86$, $p < 0.05$). However, Tukey's pair-wise testing within each level of the two factors found no evidence of any pair-wise differences ($p > 0.32$ in all pair-wise cases, Figure 35).

Comparing abundance on the same sedge species at different lakes, no differences in total invertebrate abundance were detected between *S. tabernaemontani* at Lakes Rotokawau and Waiporohita (Two-way ANOVA; effect of lake, $F_{1,78} = 2.41$, $p = 0.13$). Invertebrate abundance (log(n +1) transformed) on *I. prolifer* was affected by an interaction between sampling month and lake (Two-way ANOVA, $F_{9,78} = 2.08$, $p < 0.05$, but Tukey's pair-wise testing within each level of the two factors found no evidence of any pair-wise differences ($p > 0.16$ in all pair-wise cases).

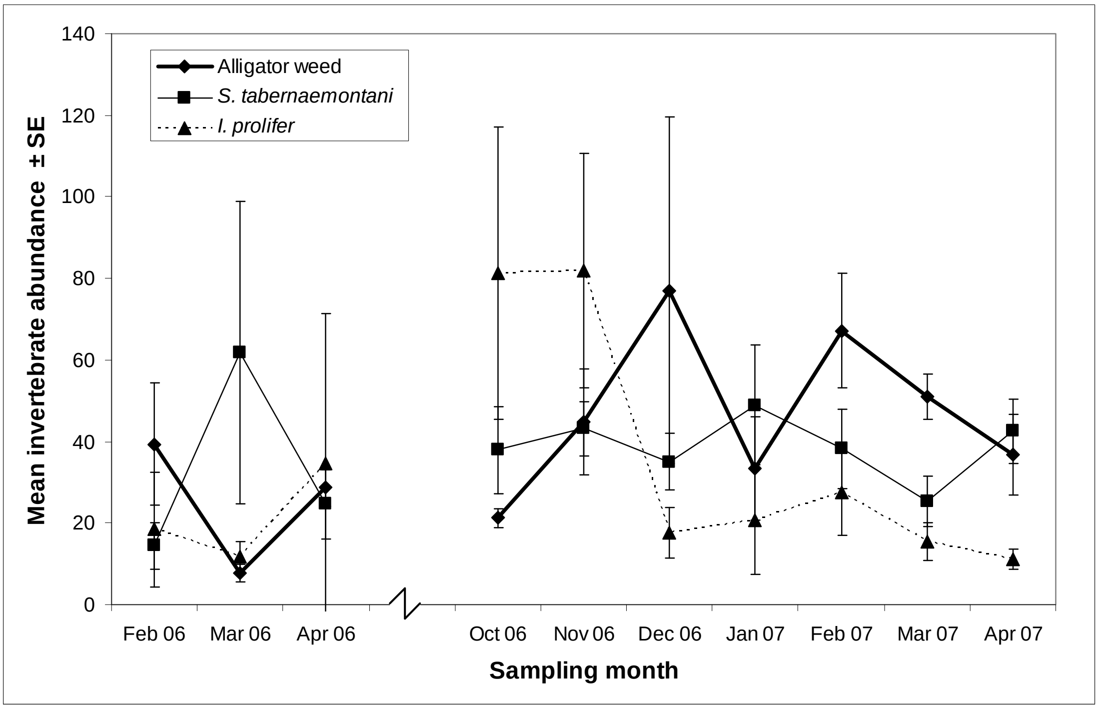

Figure 35. Mean invertebrate abundance per 0.0625 m^2 of excised vegetation for each vegetation type at Lake Rotokawau. See text for sample size.

A total of 4713 invertebrates were collected from emergence traps between January 2006 and March 2007, belonging to 19 orders and higher taxa plus unidentified juveniles (Appendix 4). Mean invertebrate numbers per trap per month differed between vegetation types ($F_{2,9} = 4.82$, $p < 0.05$; Figure 36). Mean invertebrate numbers per trap per month from alligator weed traps were higher than those from *S. tabernaemontani* (Tukey's post hoc test, $p < 0.05$).

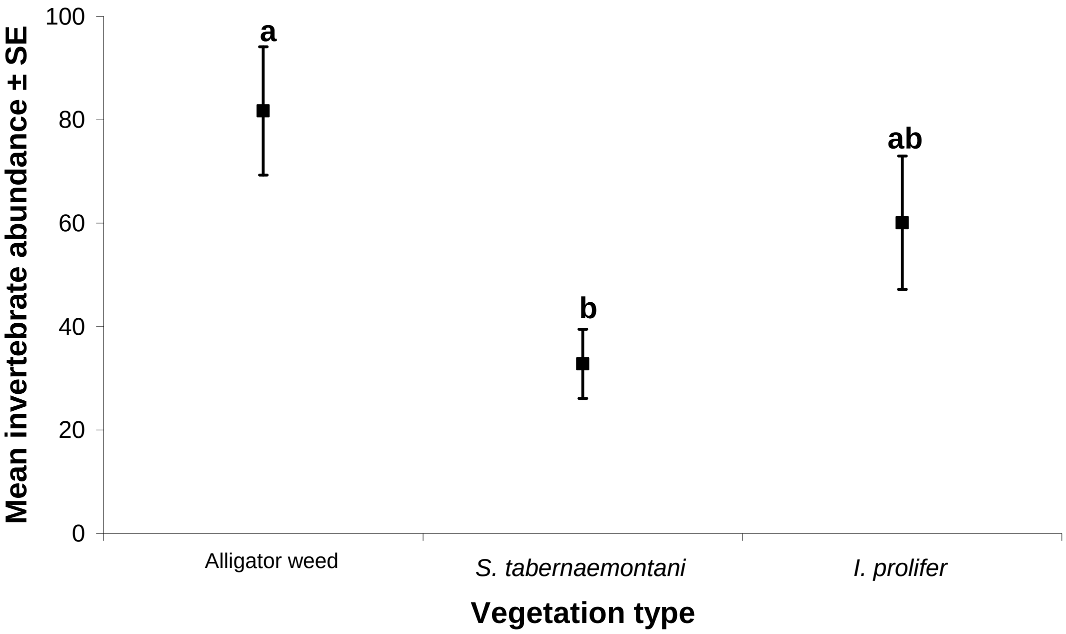

Figure 36. Mean invertebrate abundance per emergence trap per month for different vegetation types at Lake Rotokawau. Vegetation types with different letters differ at $p < 0.05$. See methods for sample size.

Hemiptera abundance (log(n + 1) transformed) at Lake Rotokawau showed a significant interaction between vegetation type and month (two-way ANOVA, $F_{18,116} = 2.08$, $p < 0.05$; Figure 37). Hemiptera abundance was lower on alligator weed than *S. tabernaemontani* in April and December 2006 and January and February 2007 (Tukey's pair-wise comparisons, $p < 0.05$ in each case). Abundance was also lower on *I. prolifer* than on *S. tabernaemontani* in January 2007 (Tukey's $p < 0.05$).

Comparing Hemiptera abundance (log(n + 1) transformed) on the same sedge at different lakes, abundance on *S. tabernaemontani* was affected by an interaction between vegetation type and month (two-way ANOVA, $F_{9,77} = 2.30$, $p < 0.05$). However, abundance did not differ between lakes in any individual month (Tukey's p > 0.5 in all months). In contrast, Hemiptera abundance on *I. prolifer* was higher at Lake Rotokawau than at the Vineyard Lake (two-way ANOVA, $F_{1,76} = 5.91$, $p < 0.05$). No differences were detected between vegetation types in the mean number of beetles per trap per month ($F_{2,9} = 1.86$, $p = 0.21$; Figure 38).

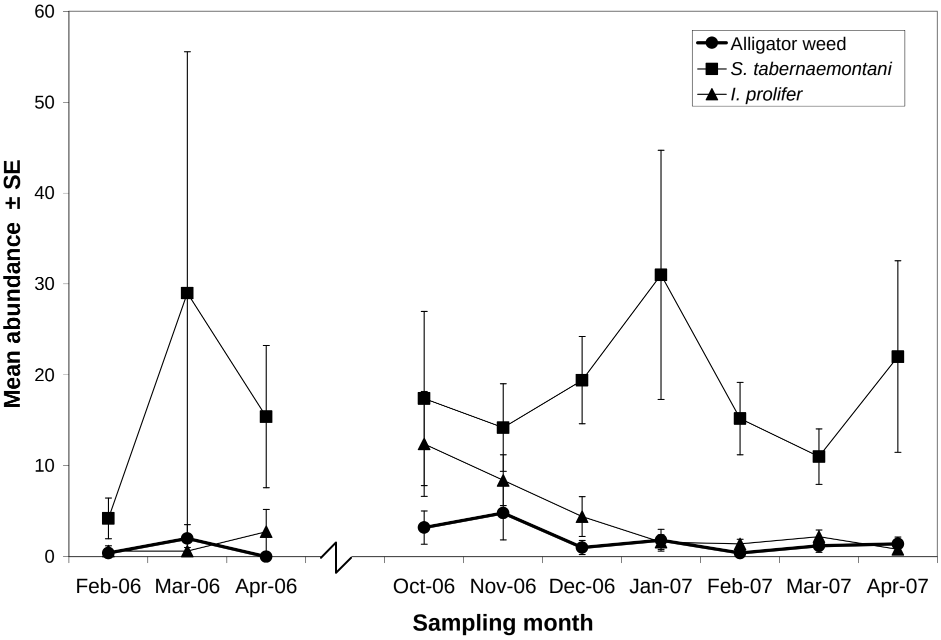

Figure 37. Mean Hemiptera abundance per 0.0625 m^2 of excised vegetation. See text for sample size.

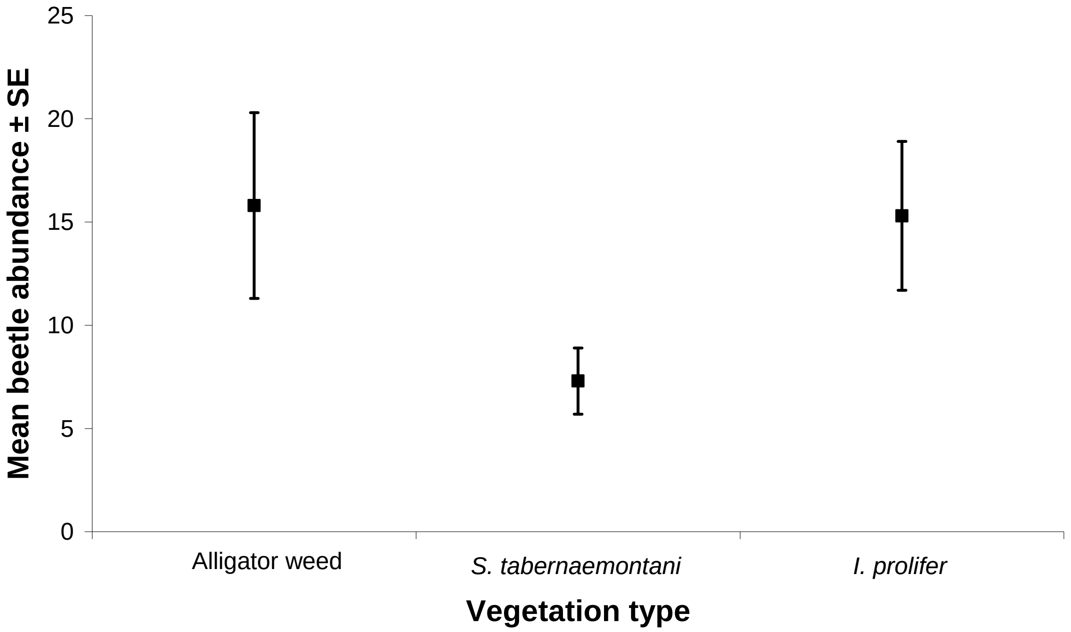

Figure 38. Mean Coleoptera abundance per emergence trap per month. No differences were detected between vegetation types at $p < 0.05$. See methods for sample sizes.

Total spider abundance (log(n + 1) transformed) was affected by an interaction between sampling month and vegetation type (Two-way ANOVA, $F_{36,197} = 1.90$, $p < 0.01$). In five of the ten months over which sampling occurred, the median number of total spider numbers collected from excised vegetation was higher in *S. tabernaemontani* samples from Lake Rotokawau than in at least one other vegetation type (Table 4). In each of these cases the median number of spiders was zero in the other vegetation type(s). There were no differences in total spider numbers between months within any vegetation type (Tukey's *post hoc* tests, $p > 0.08$ in all pair-wise cases).

Table 4. Months and vegetation types in which total spider abundance from excised vegetation differed significantly in pair-wise tests. LR = Lake Rotokawau, LW = Lake Waiporohita, VL = Vineyard Lake.

Month	Median total spider numbers		Pair-wise p-value
	S.tabernaemontani Lake Rotokawau	Other plots	
March 2006	4	*I. prolifer* (LR) = 0	< 0.01
December 2006	5	*S.tabernaemontani* (LW) = 0	< 0.05
February 2007	7	Alligator weed = 0	< 0.05
March 2007	4	*S.tabernaemontani* (LW) = 0 *I. prolifer* (VL) = 0	< 0.05 < 0.05
April 2007	9.5	Alligator weed = 0 *S.tabernaemontani* (LW) = 0 *I. prolifer* (VL) = 0	< 0.01 < 0.001 < 0.001

Differences in total spider numbers were strongly influenced by differing abundances of spiders from the genus *Tetragnatha* in the different vegetation types. As with total spider numbers, *Tetragnatha* sp. abundance was influenced by an interaction between vegetation type and sampling month (Two-way ANOVA, $F_{36,197} = 2.71$, $p < 0.001$). Again, the significant interaction term simply reflected variation between months in the number of other treatments with which *S. tabernaemontani* plots differed, with no differences observed between any of the other plots (Table 5). In seven of the ten months over which sampling occurred, *Tetragnatha* sp. abundance was higher in *S. tabernaemontani* samples from Lake Rotokawau than in at least one other vegetation type. There were no differences in *Tetragnatha* sp. between months in any vegetation type (alpha = 0.005; $p > 0.01$ in all pair-wise cases).

Table 5. Months and vegetation types in which *Tetragnatha* sp. abundance from excised vegetation differed significantly in pair-wise tests. LR = Lake Rotokawau, LW = Lake Waiporohita, VL = Vineyard Lake.

Month	Median *Tetragnatha* sp. abundance		Pair-wise p-value
	S. tabernaemontani Lake Rotokawau	Other plots	
March 2006	4	Alligator weed = 0 *I. prolifer* (LR) = 0 *I. prolifer* (VL) = 0	< 0.001 < 0.001 < 0.001
April 2006	3	Alligator weed = 0 *I. prolifer* (LR) = 0 *I. prolifer* (VL) = 0	< 0.001 < 0.001 < 0.001
December 2006	4	*S.tabernaemontani* (LW) = 0 *I. prolifer* (LR) = 0 *I. prolifer* (VL) = 0	< 0.001 < 0.001 < 0.001
January 2006	4.5	*I. prolifer* (VL) = 0	< 0.001
February 2007	6	Alligator weed = 0 *S.tabernaemontani* (LW) = 0 *I. prolifer* (LR) = 0 *I. prolifer* (VL) = 0	< 0.001 < 0.001 < 0.001 < 0.001
March 2007	4	*S.tabernaemontani* (LW) = 0 *I. prolifer* (LR) = 0 *I. prolifer* (VL) = 0	< 0.001 < 0.001 < 0.001
April 2007	6.5	Alligator weed = 0 *S.tabernaemontani* (LW) = 0 *I. prolifer* (LR) = 0 *I. prolifer* (VL) = 0	< 0.001 < 0.001 < 0.001 < 0.001

In addition to variations in abundance, the *proportion* of the total spiders caught which belonged to the genus *Tetragnatha* also varied between vegetation type for data pooled across all months for both sampling techniques (Chi-squared tests; excised vegetation $X^2 = 147.34$, df = 4, $p < 0.001$, Figure 39; emergence traps Chi-squared test; $X^2 = 94.25$, df = 2, $p < 0.001$; Figure 40). Pair-wise testing indicated that from excised vegetation Tetragnathids made up a greater proportion of the spiders caught on alligator weed than on *I. prolifer* from either Lake Rotokawau or the Vineyard Lake (pair-wise chi-squared tests, Bonferroni adjusted $p < 0.001$ and $p < 0.01$ respectively). However there was no difference in the proportion of Tetragnathids in spiders collected from alligator weed and *I. prolifer* using emergence traps (pair-wise Chi-squared test, Bonferroni corrected $p = 6.2$).

In contrast, the proportion of Tetragnathids in the spider fauna from *S. tabernaemontani* vegetation at either Lake Rotokawau or Lake Waiporohita was higher than for alligator weed, or *I. prolifer* at either Lake Rotokawau or the Vineyard Lake (pair-wise chi-squared tests, Bonferroni adjusted $p < 0.001$ in all cases). Similarly the proportion of Tetragnathids in the spider fauna from *S. tabernaemontani* emergence traps was higher than for either alligator weed or *I. prolifer* traps (pair-wise Chi-squared tests, Bonferroni corrected $p < 0.001$ in both cases).

For excised vegetation, the proportion of Tetragnathids in the spider fauna did not differ between the same plant species from different lakes (Bonferroni corrected p-values: *S. tabernaemontani* Lake Rotokawau/Lake Waiporohita $p = 6.3$; *I. prolifer* Lake Rotokawau/Vineyard Lake $p = 8.6$).

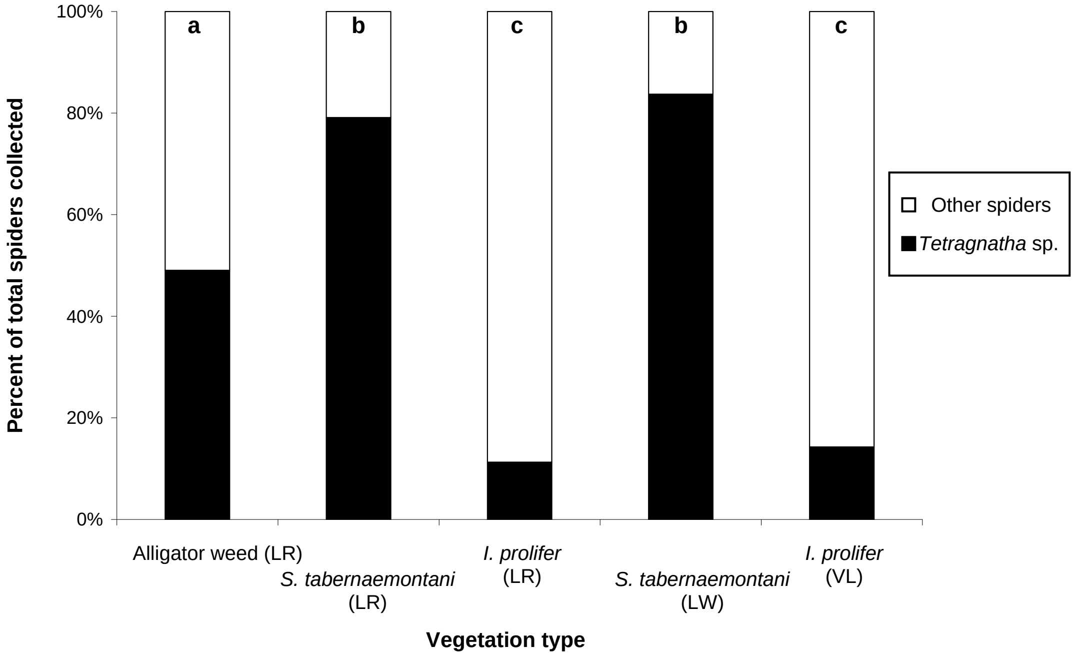

Figure 39. Proportion of spiders belonging to the genus *Tetragnatha* in total spider catch from excised vegetation of different types, data pooled across all months sampled. Vegetation types with different letters differ in the proportion of Tetragnathid spiders at the 0.01 level.

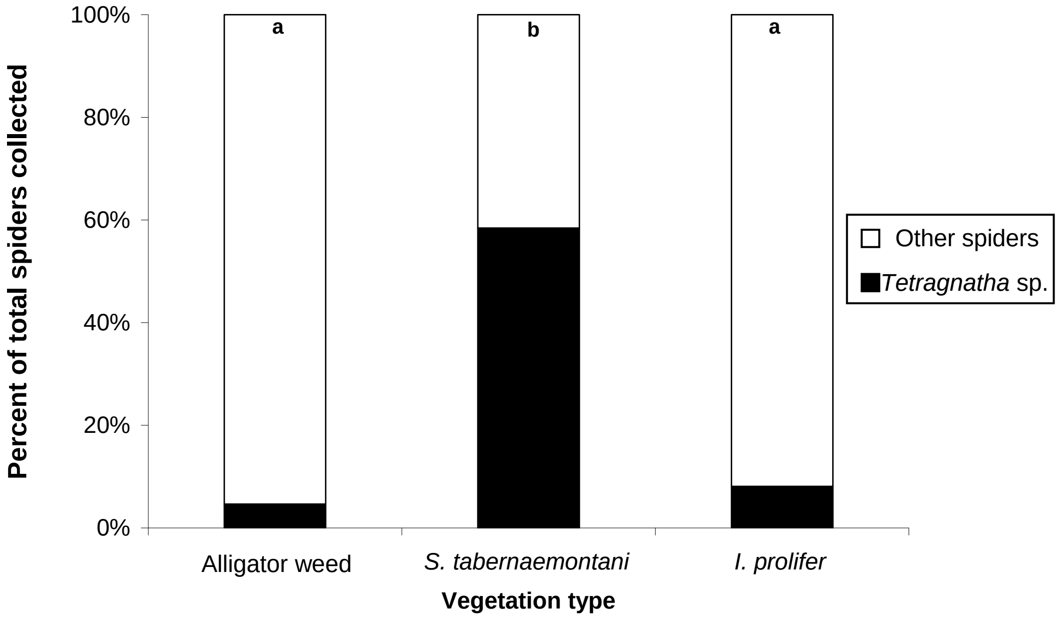

Figure 40. Proportion of spiders belonging to the genus *Tetragnatha* in total spider catch from emergence traps, data pooled across all months sampled. Vegetation types with different letters differ in the proportion of Tetragnathid spiders at the 0.001 level.

5.3.2 Hypothesis 2: Proportions of native invertebrates

The proportion of native Hemiptera individuals differed with vegetation type (Chi-squared test, $X^2 = 406.67$, df = 4, $p < 0.001$; Figure 41; Appendix 5). *I. prolifer* at Lake Rotokawau was strongly dominated by native Hemiptera, having a higher proportion of native individuals than all other vegetation types (Bonferroni correct pair-wise Fisher's Exact tests, $p < 0.001$ in all cases). While *I. prolifer* at the Vineyard Lake had a lower proportion of native individuals than did the same sedge at Lake Rotokawau, it was still dominated by native individuals, thus differing from alligator weed and *S. tabernaemontani* at both lakes (Bonferroni correct pair-wise Fisher's Exact tests, $p < 0.01$ in all cases). Alligator weed and *S. tabernaemontani* from both lakes were dominated by exotic Hemiptera, and did not differ from each other in this respect (Bonferroni correct pair-wise Fisher's Exact tests, $p > 0.29$ in all cases).

Although differences were detected in the proportions of native and exotic Hemiptera individuals, no differences were detected in the proportions of native and exotic Hemiptera *species* hosted by different vegetation types, for all sampling dates combined (Fisher's exact test, $p = 0.901$; Figure 42). With the exception of the *I. prolifer* treatments, the proportion of native species tended to be higher than the proportion of native individuals, due to high abundances of some species. Notably, the differences between the individual and species levels reflect high abundances of the native species *Cymus novaezelandiae* and *Microvelia* sp. in *I. prolifer* plots, and high abundances of the exotic aphid *Rhopalosiphum padi* in alligator weed and *S. tabernaemontani* plots and the mealy bug *Pseudococcus longispinus* in *S. tabernaemontani* plots.

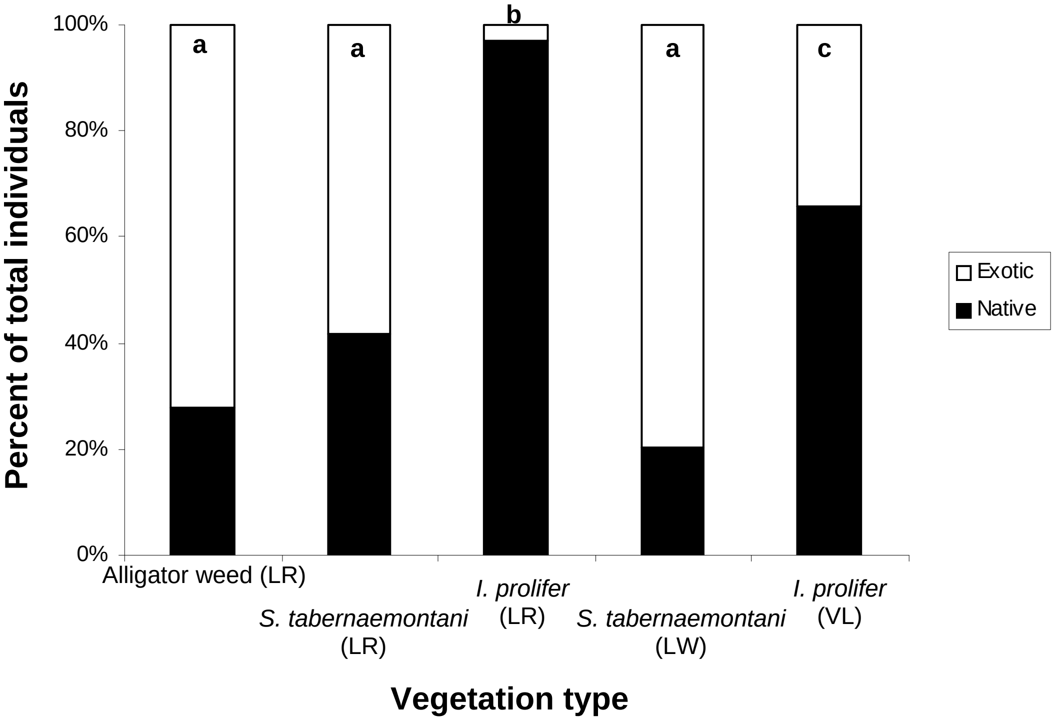

Figure 41. Proportions of native and exotic Hemiptera individuals collected from excised vegetation, all months combined. Vegetation types with different letters differ at $p < 0.01$. LR = Lake Rotokawau, LW = Lake Waiporohita, VL = Vineyard Lake.

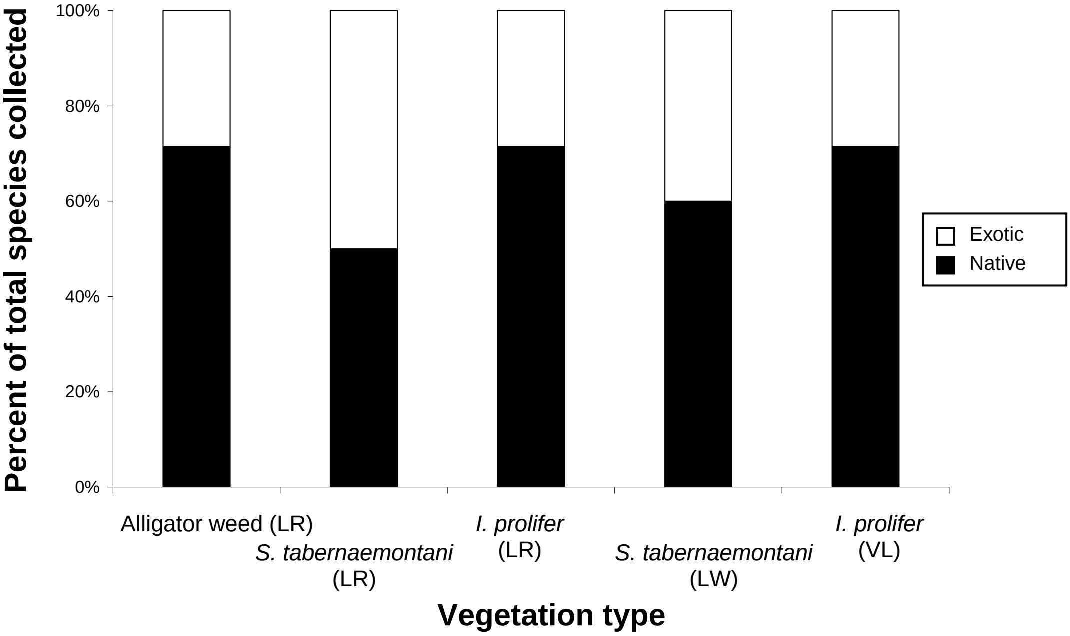

Figure 42. Proportions of native and exotic Hemiptera species collected from excised vegetation, all months combined. No differences were detected at $p = 0.05$. LR = Lake Rotokawau, LW = Lake Waiporohita, VL = Vineyard Lake.

Biomass of Hemiptera samples was even more dominantly native than at the species level, being at least 70% of total biomass in all vegetation types, including those *S. tabernaemontani* treatments strongly numerically dominated by exotic individuals (Figure 43). Even without lowering the alpha level for effects testing to 0.01 to accommodate some departure from normality, there was no evidence of any differences between vegetation types in the proportion of Hemiptera biomass made up by native species, for all months combined (ANOVA, $F_{2,20} = 2.08$, $p = 0.12$).

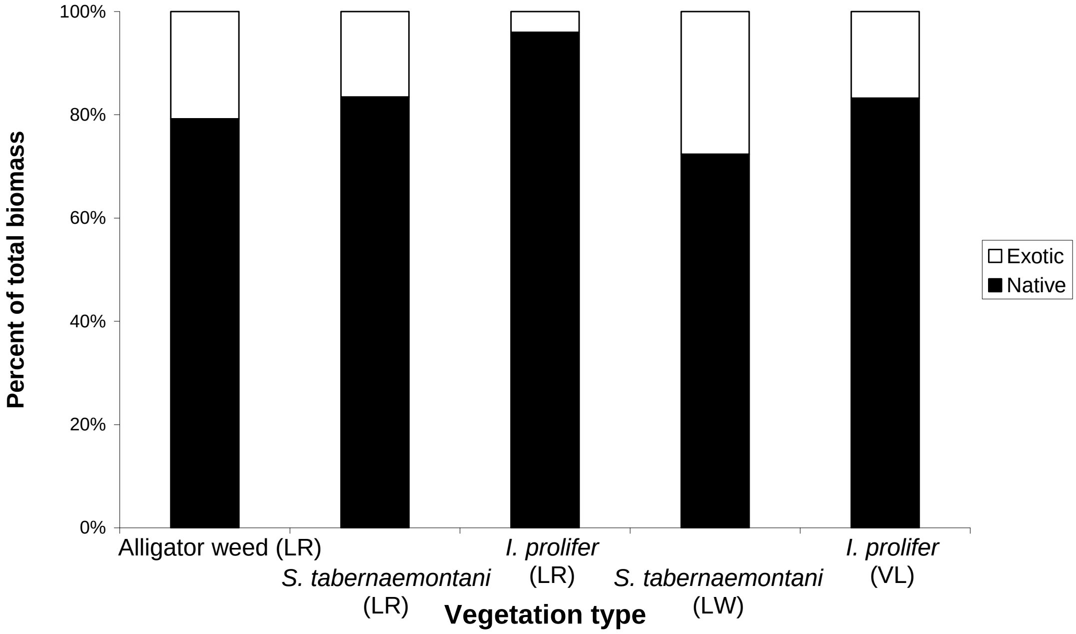

Figure 43. Proportions of native and exotic total Hemiptera biomass from different vegetation types, all months combined. No differences in mean proportion of native biomass were detected among vegetation types. LR = Lake Rotokawau, LW = Lake Waiporohita, VL = Vineyard Lake.

The proportion of native beetle individuals caught in emergence traps (all months combined) varied with vegetation type (Chi-squared test, $X^2 = 92.02$, df = 2, $p < 0.001$; Figure 44; Appendix 2), with all vegetation types differing in pair-wise comparisons (Bonferroni corrected Fisher's Exact tests, $P < 0.001$ in all cases). *I. prolifer* traps were strongly dominated by native individuals, particularly members of the family Scirtidae. While native beetles still outnumbered exotics in alligator weed traps, they were less dominant than in *I. prolifer* traps. In contrast, over half the beetles collected from *S. tabernaemontani* traps were exotic.

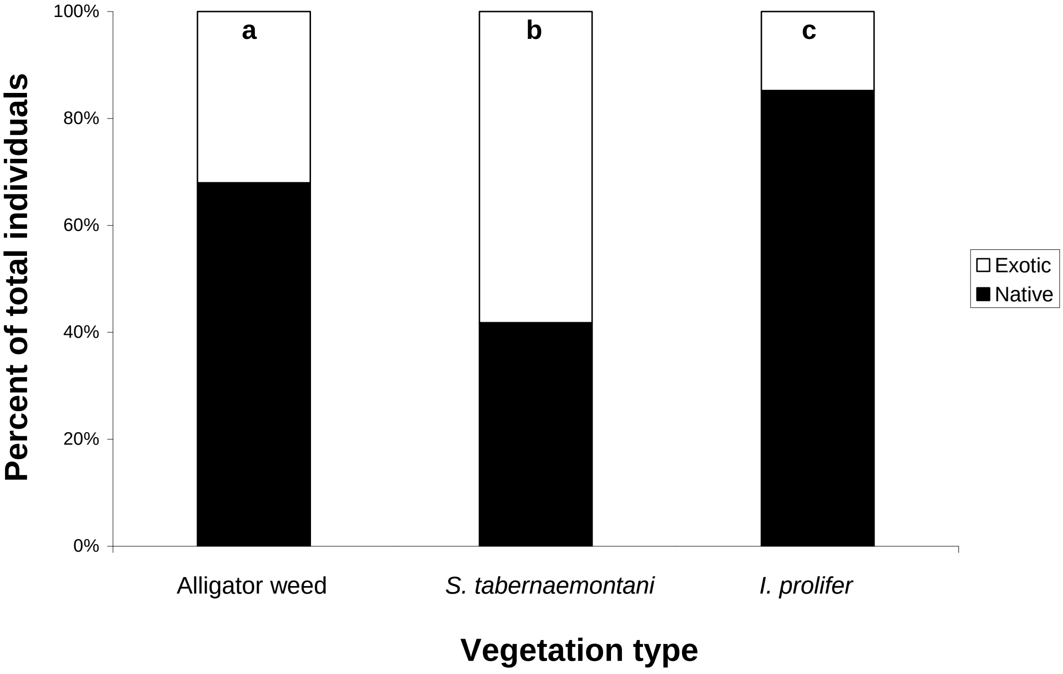

Figure 44. Proportions of native and exotic Coleoptera individuals collected from emergence traps in different vegetation types, all months combined. Vegetation types with different letters differ at the 0.001 level.

Although the proportions of native and exotic Coleoptera individuals differed between vegetation types, as with Hemiptera there was no evidence of any differences in the proportions of native and exotic Coleoptera *species* hosted by the different plant species, for all sampling dates combined (Fisher's Exact test, $p = 0.60$; Figure 45). However, unlike the Hemipteran assemblages, which were dominated by natives at the species level, but with exotic species more numerically abundant than natives, Coleoptera tended to be dominated by exotic species in all vegetation types both in terms of abundance and species richness. Similarly, there was no evidence of any differences between vegetation types in the proportion of beetle biomass (log transformed) comprised of native species for all months combined (ANOVA, $F_{2,9} = 1.97$, $p = 0.19$). However, the trend towards a higher proportion of native individuals in *I. prolifer* traps was reflected in a similar though non-significant trend for biomass, with the mean proportion of native biomass higher (56%) in *I. prolifer* traps than in alligator weed or *S. tabernaemontani* traps (13 and 11% native respectively). The total proportion of native biomass was also higher in *I. prolifer,* reflecting the high abundance of native Scirtidae in *I. prolifer* traps (Figure 46). The dominance of exotic Coleoptera in alligator weed and *S. tabernaemontani* traps was more pronounced when the response variable was biomass than at the individual or species level. However, this trend is not significant, even in regards to biomass.

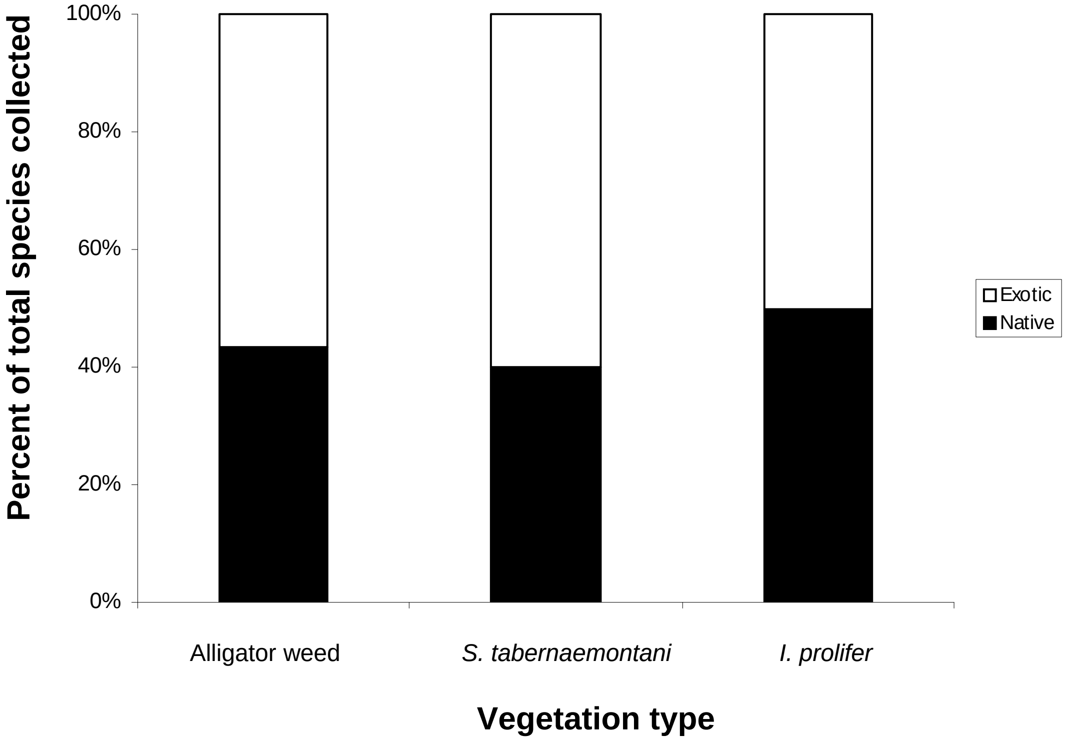

Figure 45. Proportions of native and exotic Coleoptera species collected from emergence traps in different vegetation types, all months combined. No differences among vegetation types were detected at the 0.05 level.

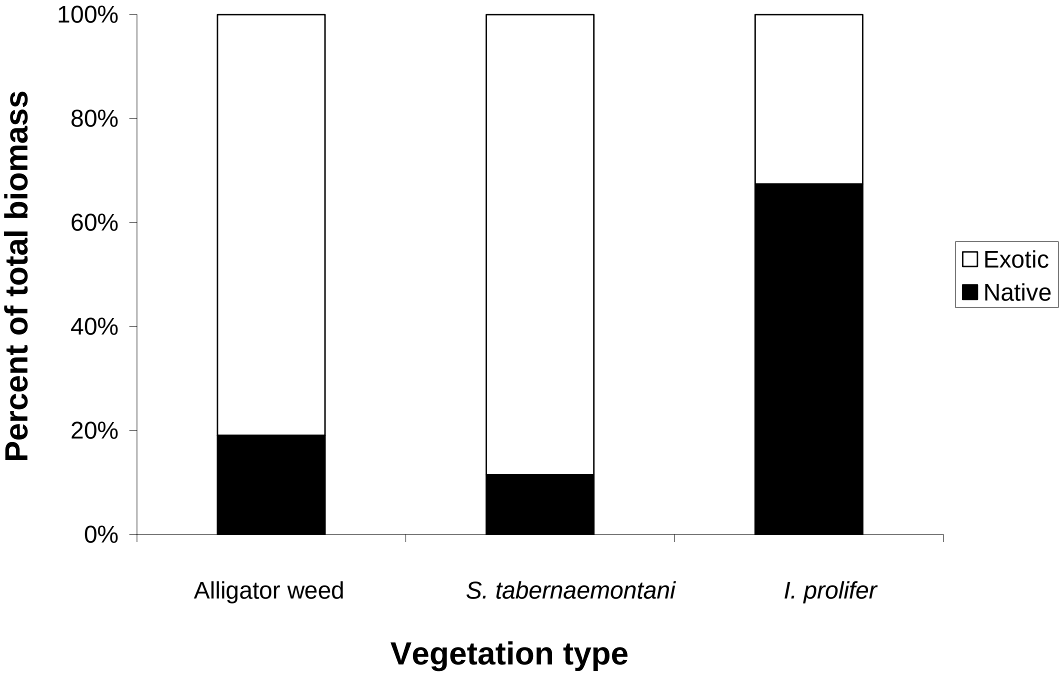

Figure 46. Proportions of total Coleoptera biomass from emergence traps comprised of native and exotic species, all months combined. No differences in mean proportion of native biomass per trap were detected among vegetation types.

5.3.3 Hypotheses 3, 4 and 5: Functional group composition

Hemipteran community composition showed differentiation between vegetation types (ANOSIM, Global R = 0.695, p = 0.001). All pair-wise comparisons between vegetation types were significant, except between *S. tabernaemontani* at the different lakes. However, the low R-value comparing invertebrates from alligator weed with those from *I. prolifer* at the Vineyard Lake indicates that the difference between these two communities, though significant, is not of a meaningful magnitude (Table 6, Figure 47). *S. tabernaemontani* samples from both lakes were characterised by high numbers of aphids and mealy bugs. *I. prolifer* at Lake Rotokawau was dominated by *Cymus novaezelandiae* as well as *Microvelia* sp. which were also common on *I. prolifer* at the Vineyard Lake. Alligator weed hosted a relatively impoverished

Hemiptera fauna compared with either sedge species. Pentatomids were more abundant on alligator weed than on either sedge. In addition to members of this family, alligator weed was characterised by aphids, though at much lower numbers than on *S. tabernaemontani*, and *Microvelia* sp., though again at much lower numbers than on *I. prolifer*.

Table 6. Pair-wise differentiation of Hemiptera communites between vegetation types. R values give a comparative measure of the degree of separation of pair-wise comparisons, ranging from -1 to 1. R values close to one indicate complete separation of vegetation types, while values close to zero imply little or no separation (Clarke and Warwick 2001). R values > 0.5 are highlighted in bold. LR = Lake Rotokawau, LW = Lake Waiporohita, VL = Vineyard Lake.

Vegetation types compared	Pair-wise R statistic	p-value
Alligator weed (LR) – *S. tabernaemontani* (LR)	**0.79**	< 0.01
Alligator weed (LR) – *I. prolifer* (LR)	**0.89**	< 0.01
Alligator weed (LR) – *S. tabernaemontani* (LW)	**0.84**	< 0.01
Alligator weed (LR) – *I. prolifer* (VL)	0.34	< 0.05
S. tabernaemontani (LR) – *I. prolifer* (LR)	**1**	< 0.01
S. tabernaemontani (LR) – *S. tabernaemontani* (LW)	0.12	0.19
S. tabernaemontani (LR) – *I. prolifer* (VL)	**0.7**	< 0.01
I. prolifer (LR)– *S. tabernaemontani* (LW)	**1**	< 0.01
I. prolifer (LR) – *I. prolifer* (VL)	**0.61**	< 0.01
S. tabernaemontani (LW) – *I. prolifer* (VL)	**0.79**	< 0.01

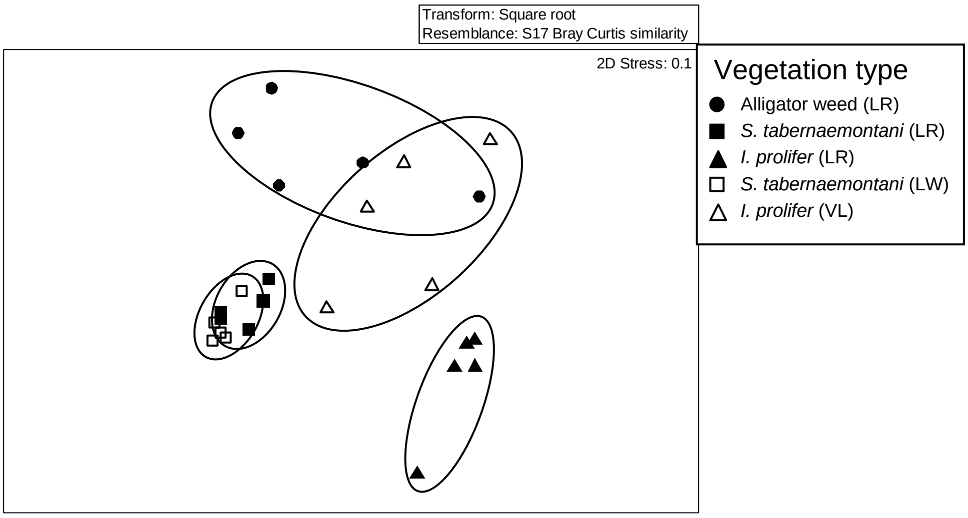

Figure 47. Grouping of Hemiptera communities by vegetation type, all months combined. Points falling closer together are more similar in composition than those falling further apart. Stress provides a measure of goodness of fit, with low stress values indicating reliable ordinations (Clarke and Warwick 2001). All vegetation types differ significantly at $p < 0.05$ except the two *S. tabernaemontani* treatments. LR = Lake Rotokawau, LW = Lake Waiporohita, VL = Vineyard Lake.

No differences were observed between vegetation types at Lake Rotokawau in the mean abundance of predatory Hemiptera per 0.0625 m^2 of vegetation (ANOVA, $F_{2,12} = 2.18$, $p = 0.16$). However, the proportions of phytophagous and predatory Hemiptera did vary with vegetation type (Fisher's Exact test, $p < 0.001$; Figure 48). *S. tabernaemontani* at each lake hosted a higher proportion of phytophagous individuals than did alligator weed at Lake Rotokawau or *I. prolifer* at either lake (Bonferroni corrected pair-wise Fisher's Exact tests, $p < 0.001$ in all pair-wise comparisons), reflecting the very high abundance of aphids on *S. tabernaemontani* and also a non-significant trend towards lower predator abundance on *S. tabernaemontani* than other vegetation types. In contrast, alligator weed did not differ from *I. prolifer* at either lake in the proportions of predatory and phytophagous Hemiptera.

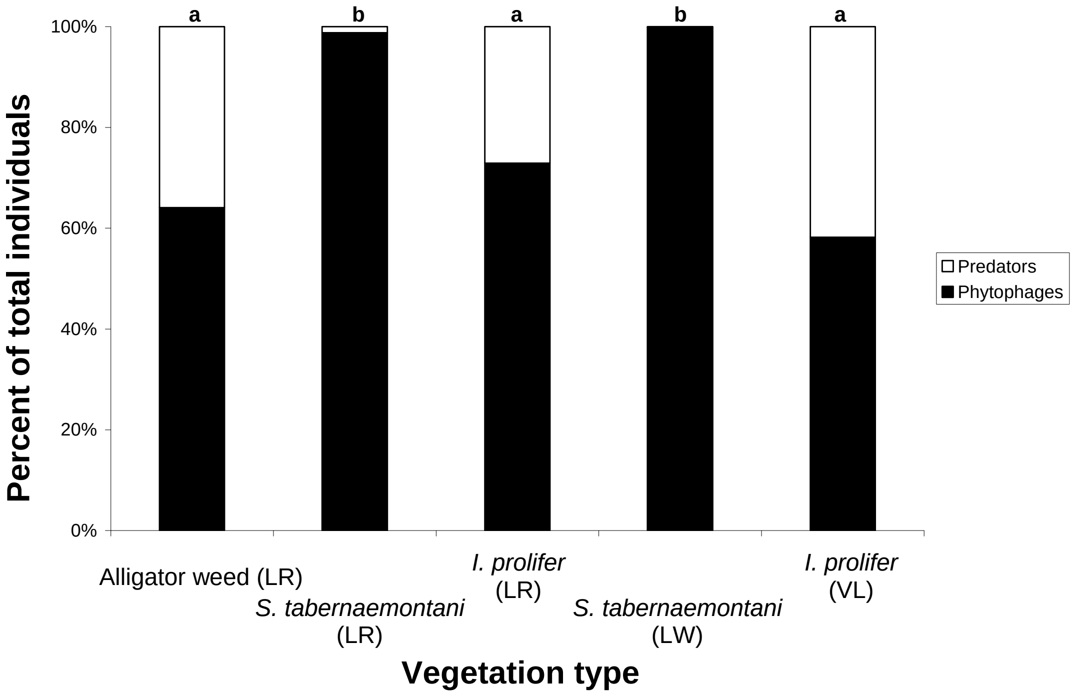

Figure 48. Proportions of predatory and phytophagous Hemiptera individuals collected from excised vegetation, all months combined. Vegetation types with different letters differ at $p < 0.001$. LR = Lake Rotokawau, LW = Lake Waiporohita, VL = Vineyard Lake.

However, at the species level there were no differences between vegetation types in the proportions of phytophagous and predatory Hemiptera collected (Fisher's exact test, $p = 0.38$; Figure 49). This indicates that differences at the individual level reflect the very high abundance of aphids and, to a lesser extent, also mealy bugs in *S. tabernaemontani* samples.

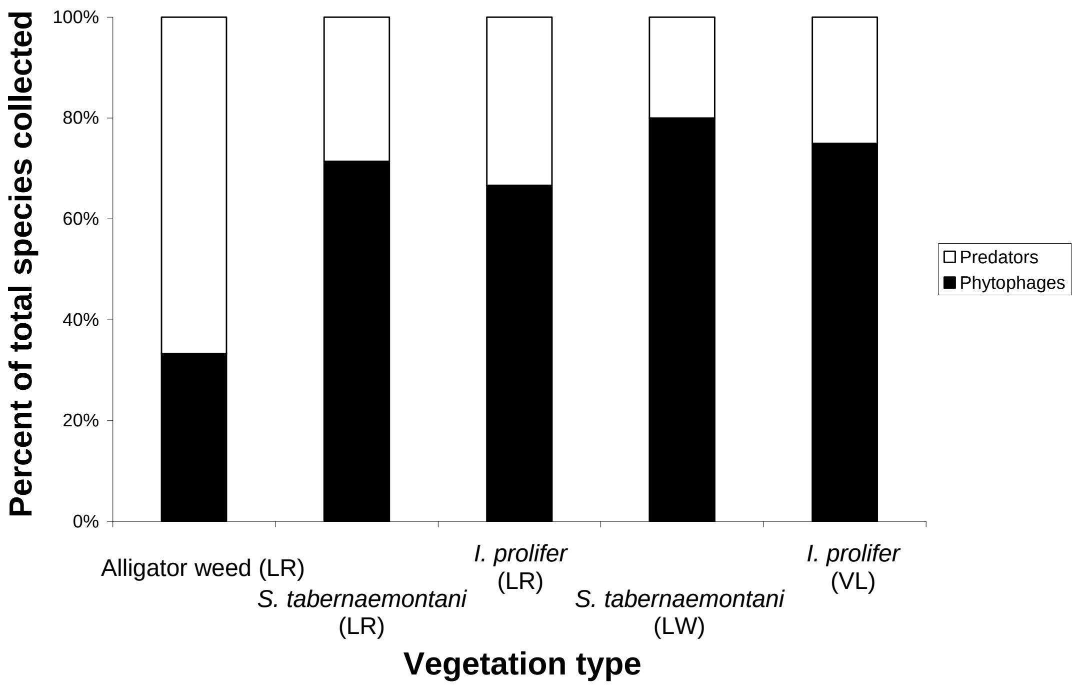

Figure 49. Proportions of predatory and phytophagous Hemiptera species collected from excised vegetation, all months combined. No significant differences were detected between vegetation types. LR = Lake Rotokawau, LW = Lake Waiporohita, VL = Vineyard Lake.

Within the phytophagous Hemiptera, there were also differences in the proportions of feeding guilds between vegetation types (Fisher's Exact test, $p < 0.001$). *I. prolifer* at Lake Rotokawau hosted a higher proportion of seed feeders than any other vegetation type (Bonferroni corrected pair-wise Fisher's Exact tests, $p < 0.001$ in all pair-wise comparisons; Figure 50). This reflected the complete absence of aphids from this vegetation type, and a high abundance of *Cymus novaezelandiae*. No other significant differences were detected. This dominance of seed-feeders underlies the much greater separation of Hemiptera communities on *I. prolifer* at Lake Rotokawau than at the Vineyard Lake when compared with Hemiptera on alligator weed at Lake Rotokawau (Figure 47).

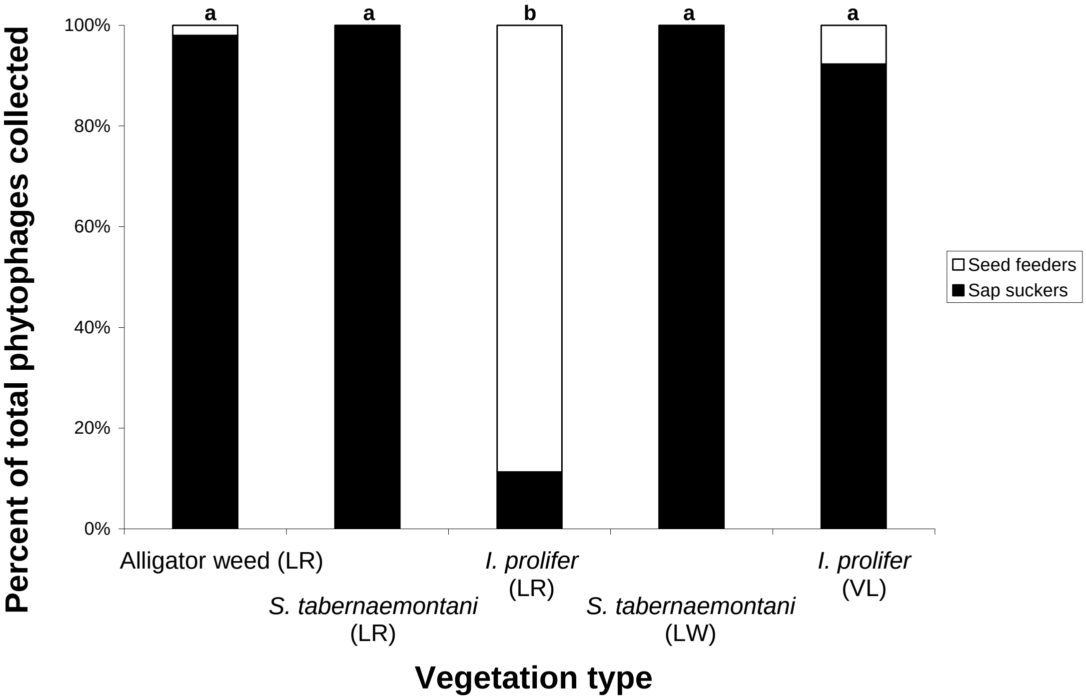

Figure 50. Proportions of sap sucking and seed feeding individuals among phytophagous Hemiptera collected from excised vegetation, all months combined. Vegetation types with different letters differ at $p < 0.001$. LR = Lake Rotokawau, LW = Lake Waiporohita, VL = Vineyard Lake.

Again, at the species level these differences in guild composition were no longer evident, with no differences detected between vegetation types, although this probably reflects the low numbers of species collected (Fisher's Exact test, $p = 0.27$; Figure 51).

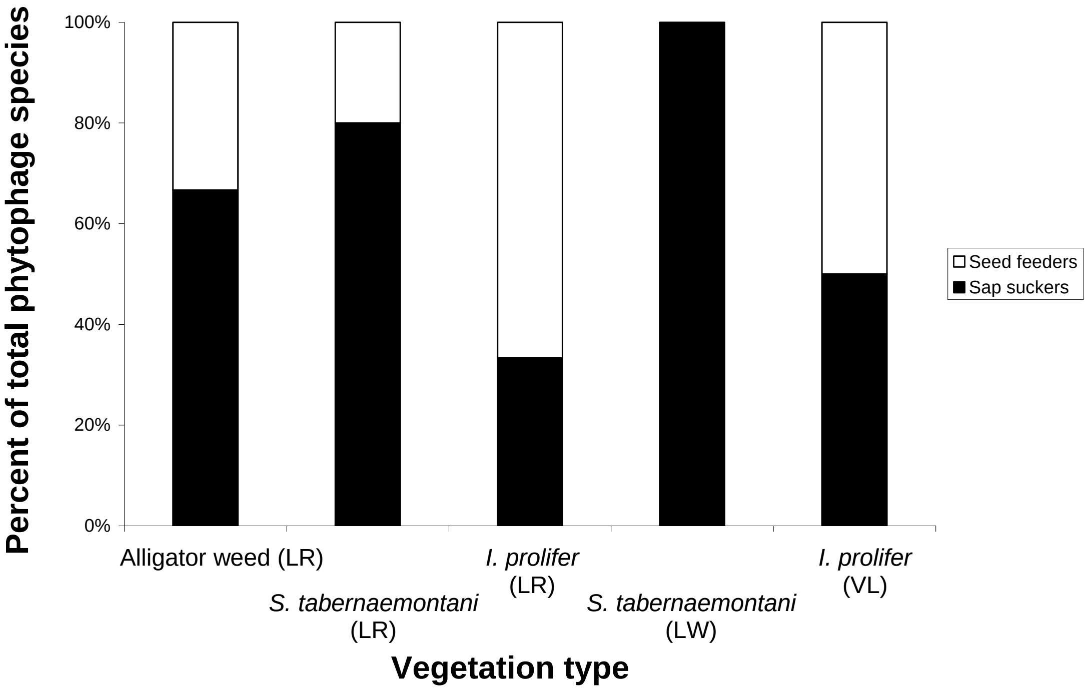

Figure 51. Proportions of sap sucking and seed feeding species among phytophagous Hemiptera collected from excised vegetation, all months combined. No differences were detected between vegetation types. LR = Lake Rotokawau, LW = Lake Waiporohita, VL = Vineyard Lake.

5.4 Discussion

5.4.1 Invertebrate abundance

Invertebrate abundance was predicted to be higher on the more architecturally complex alligator weed and *I. prolifer* than on the simple vegetation structure provided by *S. tabernaemontani*. While this prediction received some support from total invertebrate abundance from emergence traps, it was not supported in other cases. Total invertebrate abundance from excised vegetation and beetle abundance from emergence traps did not vary between vegetation types, although beetle abundance did show a non-significant trend towards lower abundance on *S. tabernaemontani* than the other two vegetation types. Further, both Hemiptera and spider abundance was lower on alligator weed than on *S. tabernaemontani*. However, in both these orders there were no differences in abundance between alligator weed and *I. prolifer,* supporting the hypothesis that abundance would be more similar between these two species than in comparison to *S. tabernaemontani.*

These results indicate that invertebrate responses to vegetation type are taxa specific, depending on their different ecological requirements. In examining responses of large and small snails to artificial substrate types of uniform surface area but differing shape, (Kershner and Lodge 1990) found more usable surface area was available to the large snails in some treatments due to the ability of its foot to span distances which the smaller snail could not, thus leading to differing habitat preferences between the two species.

The results from the current study are consistent with other studies which have also found contrasting responses to weed invasion across different invertebrate taxa. For instance, while some orders, including Ephemeroptera, Hemiptera and Odonata were detected at lower abundances in invasive *Hymenachne amplexicaulis* sites than in native vegetation in Queensland, Coleoptera (including native species) showed the reverse trend, being more abundant in the invaded sites (Houston and Duivenvoorden 2002). Similarly, *Chrysanthemoides monilifera* ssp. *rotundata* invasion of native shrublands resulted in increases in abundance of some invertebrate taxa including earthworms and millipedes, along with reductions in other taxa such as spiders and ants, although the authors attributed these differences to differing responses to altered microclimate as well as habitat structure (Lindsay and French 2006). Thus, while plants’ architecture and other attributes will influence invertebrate assemblages, they do so in interaction with characteristics of the invertebrates as well, rather than in isolation.

5.4.2 Native invertebrates

While metrics such as overall abundance and species richness may remain similar between native and exotic vegetation, species *composition* often changes (Sax 2002). This was indeed evident for Hemiptera communities in this study, which showed clear separation between vegetation types in ANOSIM analyses. As an exotic plant species, alligator weed was predicted to host a lower proportion of native invertebrates than hosted by either of the native sedge species studied. However, the proportions of native and exotic individuals hosted by alligator weed varied between invertebrate taxa, with over half the beetles collected from alligator weed being native, compared with less than a third of Hemiptera individuals. In both cases, alligator weed did host a lower proportion of native individuals than *I. prolifer*, which was strongly dominated by native Hemiptera and Coleoptera. This therefore supported the prediction of a less native fauna on alligator weed than on at least one of the native sedges. However, this prediction was not borne out in relation to the other native sedge, *S. tabernaemontani*, which hosted predominantly exotic Hemiptera and Coleoptera. In fact, *S. tabernaemontani* hosted an even more exotic-dominated Coleoptera fauna than did alligator weed.

While numerous studies have shown that invertebrate species composition varies between exotic and native plants (Samways, Caldwell et al. 1996; Toft, Harris et al. 2001; Douglas and O'Connor 2003; Kelly and Hawes 2005; Jayawardana, Westbrooke et al. 2006; Lindsay and French 2006), few studies have explicitly compared biostatus (native/exotic) of invertebrates between specific exotic and native plant species. Invasive gorse (*Ulex europaeus*) supported a fauna strongly dominated by New Zealand natives when examined across several invertebrate orders, comparable to the levels of native species detected in native Kanuka (*Kunzea* *ericoides*) stands (Harris, Toft et al. 2004). This study indicates that exotic plants do not necessarily represent a poor quality habitat for native invertebrates, as might be expected. However, the reduction in native invertebrate dominance on alligator weed compared with *I. prolifer* suggests that alligator weed does not represent as suitable a habitat for some native species compared with some native plants within these lake systems. Further, the species *composition* of native invertebrates on both gorse and alligator weed differed from that on nearby native vegetation, suggesting that a subset of native invertebrates may be better than others at utilising exotic plants as habitat.

The similarly high level of adventive individuals on *S. tabernaemontani* as on alligator weed, and the dominance of adventive beetles at the species level across all three vegetation types, is likely to reflect the highly modified pastoral landscape within which the study site was set. Several studies have shown that abundance and diversity of native New Zealand invertebrates is low in pasture compared with native forest or scrub (Crisp, Dickinson et al. 1998; Harris and Burns 2000; McLean and Jones 2006). It would be interesting to see whether alligator weed would attract an unusually exotic fauna relative to native plants in a less modified system where a greater native species pool was available. Kuschel (1990) found many native beetles were absent on native plants in Auckland gardens, despite being abundant on the same plant species in bush areas within the same suburban region, suggesting that the matrix of surrounding vegetation and/or landuse history has a strong influence on whether beetles will occupy even suitable plant hosts such as *S. tabernaemontani*.

Although alligator weed and *S. tabernaemontani* hosted a lower proportion of native Hemiptera and Coleoptera individuals than *I. prolifer* did, there were no differences among vegetation types in the proportion of native biomass or species in either invertebrate order. Species which occur in locally high densities were largely responsible for the differences in the proportions of native Hemiptera individuals. Native *Microvelia* sp. commonly live and feed in aggregations (Jackson and Wallis 1998), and so tended to be collected in relatively high numbers on *I. prolifer*. Similarly, exotic aphids and mealy bugs tended to be found in high numbers on *S. tabernaemontani*. Although aphids and mealy bugs occurred in high densities, they are very small in size, and thus contributed relatively little to total Hemiptera biomass, thus accounting for the lack of differences in the proportion of native biomass among vegetation types.

The different proportions of native Hemiptera at individual and species levels reflect relatively low densities of native species on both alligator weed and *S. tabernaemontani*. Native species which are maintaining a presence in this modified landscape but are occurring only at low densities may be at risk from stochastic events, potentially representing a slow decline in native biodiversity from the system, although long-term monitoring would be required to verify this.

5.4.3 Predator abundance

Hornung and Foote (2006) found that different functional groups responded differently to plant architecture, with herbivores and predators showing contrasting responses to increasing habitat complexity. This study hypothesised that, as with overall invertebrate abundance, predator abundance would be lower on the structurally simple *S. tabernaemontani* than on alligator weed or *I. prolifer*. However, this prediction was not supported by the *Tetragnatha* spider data.

Tetragnathid spiders showed a preference for *S. tabernaemontani* habitat over either alligator weed or *I. prolifer*. Web-building spiders are known to be tightly correlated with architectural features of vegetation which meet their specific web attachment requirements (Rypstra, Carter et al. 1999). Web-builders were 80% less abundant in invasive *Phragmites australis* stands than native *Spartina alterniflora*, whereas hunting spiders showed only a 25% decrease in abundance (Gratton and Denno 2005). Members of the *Tetragnatha* genus in Hawaii and North America have also been shown to be highly habitat specific (Aiken and Coyle 2000; Vandergast and Gillespie 2004). The tall, simple culms of *S. tabernaemontani* appeared to provide ideal camouflage for Tetragnathids. In addition, they allowed the creation of larger webs spanning across open, elevated spaces, which allow the interception of alate species and would not be possible in either of the shorter, denser plant species. The slightly higher proportion of Tetragnathids on alligator weed compared with *I. prolifer* may reflect spill-over from *S. tabernaemontani*, rather than an actual habitat preference, as alligator weed plots were more frequently located contiguous to *S. tabernaemontani* stands than were *I. prolifer* plots.

However, there was some support for predicted patterns of predator abundance from other predatory taxa. “Other spiders”, predominantly members of the family Pisauridae, appeared to prefer the more architecturally complex plant species over *S. tabernaemontani*. Spiders belonging to this family construct their characteristic, dense “nurserywebs” on scrub, grass or sedge vegetation to protect their young (Forster and Forster 1999), rather than slinging large, prey catching webs across open spaces as do Tetragnathids.

It therefore appears that, as with invertebrates more generally, predator ecology interacts with plant architecture in determining predator abundance, with different taxa responding differently to different habitats. Tolonen, Hamalainen et al.(2003)

also documented differing responses of various predatory invertebrate taxa to variation in vegetation complexity, with Tanypodinae (Chironimidae) abundant in sparsely vegetated sites, whereas Odonata, Corixidae and Dytiscidae were more abundant in dense vegetation. Further, intra-guild predation (wolf-spiders predating predatory mirids) was higher in structurally simple vegetation compared with structurally complex vegetation, which provided refuges for the mirids (Finke and Denno 2002). Structurally complex shrubs were also found to support more species and guilds of spiders than simple vegetation (Hatley and MacMahon 1980). Structurally simple vegetation such as *S. tabernaemontani* may therefore advantage large, dominant invertebrate predators such as Tetragnathid spiders, at the expense of other predatory taxa, thus contributing to observed differences in responses to vegetation complexity across different predatory taxa.

5.4.4 Specialists versus generalists

Alligator weed was predicted to host fewer specialist herbivores than the native sedges, with generalist species shared across the vegetation types. Alligator weed did host the lowest number of herbivorous Hemiptera species of any vegetation type, and hosted no unique species, with all those found on alligator weed also occurring on at least one sedge species. However, even those herbivores collected from a single sedge species, such as *Nysius huttoni* which was collected only from *S. tabernaemontani* at Lake Waiporohita, are generalist herbivores which have previously been collected from a range of other host plants (Lariviere and Larochelle 2004).

This lack of specialist Hemipteran herbivores could be explained by two alternative hypotheses; either these lakes have historically been generalist dominated systems, or, any specialist species previously present have been lost due to factors such as habitat modification. In either case, it is possible that habitat specialists are present in taxa other than Hemiptera. There is a lack of records of host specific herbivores of any invertebrate taxa associated with either of the two sedge species studied here, or Northland dune lake vegetation in general. However, very little information is available on the feeding preferences and ecology of many invertebrates in New Zealand (Hutcheson 1999), and the absence of evidence for specific herbivores from this system by no means represents evidence of their absence. The benthic invertebrate fauna of South Island lakes has, however, been found to be dominated by generalist taxa (Wissinger, McIntosh et al. 2006), while the same trend has been reported for New Zealand stream invertebrates (Thompson and Townsend 2000).

Conversely, studies in other ecosystems have shown a trend towards increased dominance of habitat generalists with increasing habitat loss or modification. For instance, in the Northern hemisphere, the practice of clear-cutting in forestry has been associated with a move towards generalist-dominated Carabid beetle communities (Niemela, Koivula et al. 2007; Nitterus, Astrom et al. 2007). Similarly, butterfly community composition in California changed from predominantly specialist to predominantly generalist species as the proportion of landscape in oak woodland decreased and residential development increased (Niell, Brussard et al. 2007). Insect pollinator communities also became more generalist-dominated as forest cover in the Ontario landscape was replaced by agricultural ecosystems (Taki and Kevan 2007). This trend in other studies towards generalist dominance in modified ecosystems suggests that the generalist dominated fauna at Lake Rotokawau may reflect the highly modified agricultural landscape in which it is set.

In keeping with the generalist nature of the Hemiptera fauna at the site, there was very little guild diversity within the herbivorous Hemiptera collected. In all vegetation types sap sucking species dominated at the species level, and this was true at the individual level as well for all vegetation types except *I. prolifer* at Lake Rotokawau, which hosted a high abundance of the seed-feeding *Cymus novaezelandiae*. The high abundance of this species reflects a response to the abundant seed resource available on *I. prolifer*, which alligator weed does not provide, as it generally does not set seed in New Zealand. Other studies which have found a greater diversity of phytophagous guilds in part reflect a wider range of taxa than examined here (Memmott, Fowler et al. 2000; Ernst and Cappuccino 2005), but the lack of specialist species across vegetation type or feeding guild suggests that the depauperate guild diversity recorded here is also a reflection of a highly modified generalist-dominated system.

This study was conducted in only a single invaded ecosystem, and thus results cannot be generalised to other sites invaded by alligator weed. However, I would hypothesize that invertebrate communities would be increasingly affected by alligator weed invasion the more dominant the weed became in any system. Further, the more the weed differed taxonomically, structurally and/or chemically from existing vegetation, the more likely it would host altered invertebrate communities.

5.4.5 Conclusions

Alligator weed hosted an invertebrate fauna distinct in composition from that on either of two native sedges. However, across a range of taxa and metrics, invertebrate communities on alligator weed were more similar to those on *I. prolifer* than *S. tabernaemontani*. This supports the premise underlying the initial hypotheses of this study; that the greater degree of architectural and/or chemical similarity of alligator weed to *I. prolifer* would lead to more similar invertebrate communities between alligator weed and this sedge compared with *S. tabernaemontani*. Thus the extent to which an invasive plant species will affect invertebrate communities may depend at least in part on the extent to which it differs architecturally and/or chemically (or taxonomically) from the native vegetation which it is invading. Several of the hypotheses being tested, including those relating to abundance and biostatus, gained only equivocal support, with responses differing among invertebrate taxa. These results suggest that we can expect invertebrate responses to invasive plants to be variable among invertebrate taxa with different ecological requirements. The equivocal support for hypotheses relating to biostatus and functional specialisation also suggests that the characteristics of the ecosystem and surrounding landscape matrix in which the study was set may have served to overshadow potential differences between this invasive weed and the native vegetation.

6 EFFECTS OF ALLIGATOR WEED INVASION ON PLANT COMMUNITY COMPOSITION IN LAKE-MARGIN VEGETATION

6.1 Introduction

6.1.1 Weed invasion as one of many threats to wetland ecosystems

Wetland ecosystems have been heavily impacted by human activities, with around 90% of New Zealand's former wetlands lost to drainage and development (Taylor and Smith 1997). Those that remain are often highly degraded, due to a number of factors, including eutrophication, weed and pest invasion, stock access and vegetation clearance. Many wetlands, particularly in the North Island, are now set within a predominantly pastoral landscape. Clearance of surrounding native vegetation has often led to changes in water quality, including increased light penetration and more variable temperatures (Quinn, Boothroyd et al. 2004). In addition, many waterways are highly eutrophic due to use of agricultural fertilisers in the surrounding catchments. The combination of elevated light and nutrient levels makes many wetlands highly vulnerable to invasion by exotic weeds and algal blooms (Taylor and Smith 1997).

6.1.2 Weed impacts on plant communities

Weed invasion, in wetlands and other ecosystems, has the potential to negatively impact plant communities. Weeds are contributing factors in the decline of 59% of New Zealand's threatened native plant species (Dopson, de Lange et al. 1999). Domination of a plant community by an invasive species alters, and often simplifies, the community. For example, *Myriophyllum spicatum* invasion lead to the loss of 13 of 20 native species over an 11 year period, due to its dense canopy formation and subsequent overshadowing of native species (Boylen, Eichler et al. 1999). Similarly, native seedling abundance and species richness was lower in sites with high cover of the exotic weed *Tradescantia fluminensis* (Standish, Robertson et al. 2001). This highlights the particular vulnerability of the regeneration life-stage to the effects of invasive species, through reduced seed banks, germination success, and survival. Similarly, seed banks in New Zealand lakes had lower numbers and species richness of seeds at sites dominated by submerged exotic weed species compared with sites dominated by indigenous vegetation (de Winton and Clayton 1996). This was attributed to displacement of seed-setting adult plants, and low dispersal ability of many submerged plant species.

Certain plant species may be disproportionately affected by weed invasion compared with others. For instance, local plant species losses following *Clematis vitalba* invasion tend to be those which were already nationally threatened or uncommon, or of restricted distribution (Ogle, La Cock et al. 2000). Likewise, invasive grasses were linked to decreased recruitment of the endangered herb, *Oenothera deltoides* ssp. *howellii*, apparently due to inhibition of germination due to reduced soil disturbance. Weed invasions may therefore affect biodiversity at larger, regional scales as well as locally.

6.1.3 Invasibility and plant species richness

Species diversity was suggested by Elton (1958) as a protective factor against invasion by exotic species, supported by the often devastating impact of exotic species on depauperate island ecosystems. More diverse ecosystems were expected to have greater resource use complimentarity, leaving fewer unused resources available for invading species (van Ruijven 2003). This theory has been supported by some experimental work manipulating species richness e.g. (Naeem 2000; van Ruijven 2003), although in some cases this effect may relate to sampling effects such as the increasing frequency of occurrence of a single, highly competitive species in more diverse plots (Wardle 2001). Increased functional group diversity (corresponding to greater resource use complimentarity) has also been shown to decrease invasibility even where species richness alone did not (Xu 2004).

In contrast, some studies, particularly those correlating invader abundance with species richness in the field have found exotic and native plant species richness to be positively correlated (Hager and Vinebrooke 2004; Houlahan and Findlay 2004). In many cases, this is likely to be because both native and exotic species respond similarly to the same environmental factors (e.g. nutrient levels) (Levine 1999). The scale at which studies are conducted may also influence the conclusions drawn. Negative relationships between invasive species cover and native species richness at small scales may become positive at large, landscape scales, indicating that they are indeed responding positively to the same underlying environmental variables (Byers and Noonburg 2003).

In addition, just as native species may be responding to the same variables as an invasive species, so other non-native species are also likely to respond similarly. Removal of a given invasive species may therefore result not in replacement by native species, but rather, replacement by other invasive exotics. This was observed following purple loose-strife removal, where it was replaced by the exotics *Agrostis stolonifera* and *Phalaris arundinacea* (Morrison 2002).

6.1.4 Alligator weed and plant communities

Alligator weed (*Alternanthera philoxeroides* (Mart.) Griseb.) is an aggressive invader of both terrestrial and aquatic environments. In pasture ecosystems, alligator weed has been shown to steadily increase in biomass and displace other species (Julien and Bourne 1988). Alligator weed literature reviews typically note that this species decreases plant diversity and disrupts the ecology of invaded sites (Julien 1995; Timmins and Mackenzie 1995). However, these conclusions are based on research in pastoral ecosystems and casual observations in native systems. Little quantitative data has been collected on the ecology of alligator weed in natural ecosystems. The research which has been conducted in this area has largely come from China. Although a range of native species were recorded growing within floating alligator weed mats in China (Liu and Yu 2005), another study found that diversity decreased with increasing dominance of alligator weed (Cheng and Qiang 2006). Within New Zealand, while invasive plants are widely acknowledged to have negative impacts on native vegetation, there is a paucity of quantitative research documenting this which is not just confined to alligator weed (Ogle, La Cock et al. 2000).

The present study aimed to investigate the role of alligator weed in a “native” ecosystem in New Zealand. Ideally, plant communities would have been measured in a number of lakes with and without alligator weed invasion. However, there were insufficient invaded native ecosystems which were similar enough in ecosystem type to be usefully used as replicates, and at which active alligator weed control was not planned during the period of this study. Therefore this study is restricted to a description of a single invaded ecosystem, Lake Rotokawau on the Karikari Peninsula in Northland.

In Northern New Zealand, including Lake Rotokawau, aquatic alligator weed is partially controlled by an introduced biological control agent, the alligator weed flea beetle (*Agasicles hygrophila*: Chrysomelidae). In the presence of the flea beetle, alligator weed biomass tends to follow a distinct annual cycle. Weed biomass builds up in spring prior to the emergence of a large beetle population. Weed biomass then peaks in early summer before substantial dieback occurs midsummer as a result of biocontrol. Continued herbivory and then cooler temperatures combine to keep alligator weed biomass at low levels until the following spring (Stewart 1996).

Specifically, this study sought to address the following three hypotheses: 1) That areas dominated by alligator weed would support reduced cover and richness of native plant species. 2) That native plant species would be positively correlated with exotic species over large spatial scales, reflecting similar responses to underlying environmental variation, but that natives and exotics would be negatively correlated over smaller areas. 3) That exotic plants rather than native plants would be advantaged by temporary reductions in alligator weed cover.

6.2 Methods

6.2.1 Study site

This study describes the plant communities of Lake Rotokawau on the Karikari Peninsula in Northland (34° 52′ 14′′ S, 173° 19′ 19′′ E), particularly in relation to the presence of alligator weed within the system. Lake Rotokawau is 21.3 ha in area, with an iron-pan base (Champion, Wells et al. 2005).

6.2.2 Plant community composition

Plant communities at Lake Rotokawau were surveyed at two spatial scales, as the scale of study will often influence the trends detected in vegetation composition (Byers and Noonburg 2003). To assess plant community composition on a broad scale, 5 m x 5 m plots were examined at 50 m intervals around the entire circumference of the lake. This resulted in a total of 28 replicate 25 m^2 plots. Plots were centred on the elevation level occupied by alligator weed. Water depth was measured at the centre of each 25 m^2 plot bimonthly, from January 2005 to November 2006. Water was shallowest in March (mean 0.24 ± 0.05 m), rising over winter to a mean of 0.69 ± 0.03 m.

All emergent vascular plants within each quadrat were identified, and assigned a percentage cover score from 1-5, following a modified Braun-Blanquet scale (Table 7). Cover was assigned to categories as this makes data collection easier, while providing statistical results similar to unclassed data, and does not aim to achieve an unrealistic level of accuracy (Wikum and Shanholtzer 1978; McCune and Grace 2002). All cover assessments were conducted by a single observer, and calibrated regularly against printed cover diagrams, thus reducing the chances of observer bias. Cover measurements in 25 m^2 plots were repeated at three monthly intervals from November 2005 to September 2006, providing seasonal data on plant communities.

Plant community composition at Lake Rotokawau was also studied within 1 m^2 plots. This scale was chosen as vegetation at the site is characterised by small-scale patchiness, with single species strongly dominating small patches of vegetation. This scale of study therefore allowed comparison of plant communities between patches of vegetation dominated by alligator weed, and those patches dominated by native species. Two native sedge species were chosen for comparison with alligator weed. These were *Schoenoplectus tabernaemontani* and *Isolepis prolifer*. Having two native species provided a clearer indication of how patches dominated by alligator weed differed from a range of native vegetation types at the site. Five replicate plots in each of the three vegetation types were monitored bimonthly from November 2005 to September 2006. Again, all emergent vascular plants within each quadrat were identified, and assigned a percentage cover score from 1-5, following the modified Braun-Blanquet scale.

Table 7. Modified Braun-Blanquet cover scale used for both 1 m^2 and 25 m^2 vegetation plots.

Cover Score	Percentage Cover
1	0 - 4%
2	5 – 24%
3	25 – 49%
4	50 – 74%
5	75 – 100%

6.2.3 Environmental measurements

Depth was also measured at each corner of the 25 m^2 plots during each quarterly vegetation cover measurement. Total nitrogen and phosphorous were measured in water from patches dominated by alligator weed, *S. tabernaemontani* or *I. prolifer* in November 2006 and March 2007. At each date, 400 ml water samples were taken from 10 replicate patches of each vegetation type, including from each of the 1 m^2 vegetation plots. Water samples were frozen and transported to the Landcare Research environmental chemistry laboratory, where they were analysed by persulphate digestion to measure total nitrogen and phosphorous (Hosomi and Sudo 1986).

Minimum and maximum air temperatures were measured in four replicate 1 m^2 plots for each vegetation type, using maximum and minimum thermometers. Temperature was recorded, and thermometers reset, monthly from January 2005. Temperature data could only be analysed for three of the months over which it was recorded due to sample sizes being reduced in other months by thermometers being stolen, damaged, or displaced.

6.2.4 Analyses

For each bimonthly survey, differences in native and exotic plant species richness between 1 m^2 plots were analysed by one-way ANOVA, testing for an effect of dominant vegetation type. Where data failed Levene's test for homogeneity of variance, differences were assessed by lowering the alpha level to one at which Levene's test was no longer significant (Underwood 1981). Where all treatments had zero variance, analysis of variance could not be performed.

Because of the highly synchronised nature of alligator weed cover, and the low numbers of native species present within alligator weed dominated plots, it was not possible to correlate native species cover or richness with alligator weed in 1 m^2 plots in any single month. Instead, native and exotic richness from successive months were plotted against alligator weed and *I. prolifer* cover to give a visual representation of annual trends in species richness in relation to biomass dynamics of the dominant vegetation type.

For each season separately, t-tests were used to compare native, exotic and total species richness between 25 m^2 plots from Lake Rotokawau with or without alligator weed present. Comparisons were not made between dates, as samples were not independent, and this comparison was not of primary interest.

For 25 m^2 plots with alligator weed present, alligator weed cover score was regressed against native, exotic, and total species richness for each season separately. Sites without alligator weed present were excluded from this analysis. This investigated the effect of increased alligator weed dominance at sites where it was present, acknowledging that uninvaded sites may differ from invaded sites in other ways which may also influence the diversity of other species present at these sites. In May, July and November, only a single data point represented alligator weed cover scores in the highest cover bracket for that month. This outlying data point was removed from analyses as in each case it exerted disproportionate influence on the trend line, as indicated by Cook's distance. As well as species richness, alligator weed cover scores were also regressed against total native or exotic cover score (being the total of all cover scores in each of these categories for each plot), and the proportion of species or cover (excluding alligator weed) which were native. This tested whether native species were disproportionately affected by increasing alligator weed dominance. All these analyses followed the data manipulations outlined above with respect to species richness correlations.

Simpson's Index ($1 - \lambda$) was calculated using cover data as the measure of abundance. Simpson's index was chosen as it emphasises common species, or the relative evenness of samples and is relatively robust to small sample size (McCune and Grace 2002). This was then also regressed against alligator weed cover score. Again, sites with alligator weed absent were excluded from analyses, as was the highest cover category in months when this was represented by a single data point which, when included, exerted disproportionate influence on the trend line, as indicated by Cook's distance.

Native and exotic plant species richness were regressed against each other for each month separately to determine whether there was a relationship between the two. This was done for both plot sizes. Native species richness and total cover score were also regressed against exotic cover score (excluding alligator weed) to examine whether exotic cover affected the two parameters differently. This was done for both 1 m^2 and 25 m^2 plots.

Differences between 1 m^2 vegetation types for environmental variables temperature and water quality were analysed using one-way ANOVAs for each month separately as they were repeated measures which were not independent from measures in other months. Differences between months were not measured as the data were not independent, and seasonal variations in temperature were not in themselves of interest in this study. Total nitrogen data was log-transformed due to heteroscadisticity indicated by Levene’s test.

Alligator weed cover, all other exotic cover and native cover were each regressed against the mean depth of the two bottom corners, the mean depth of the two top corners, and the difference between the two (i.e. a rough proxy for the degree of slope within the plot). All univariate analyses were performed using R v. 2.0.1 (Ihaka and Gentleman 1996), while Simpson’s diversity index was calculated in Primer v.5 (Clarke and Gorley 2001).

6.3 Results

6.3.1 Alligator weed cover in 25 m^2 plots

In summer, alligator weed was present in 27 of the 28 25 m^2 plots at Lake Rotokawau, while in all other seasons it was present in 24 of the plots, though not always the same

24 plots. Alligator weed cover scores from spring, when alligator weed cover was highest, were back-transformed to their minimum cover percentage, using 1% as the minimum for the less than 5% category. These minimum values were used to provide a conservative estimate of total alligator weed coverage in the elevation zone sampled. Using this approach, alligator weed covered an average of 22.6 ± 4.0% of the 25 m^2 plots. If this is representative of alligator weed cover over this entire elevation zone, then in spring alligator weed is estimated to have covered 1681.6 m^2.

Plots with “high” alligator weed cover in winter (cover score = 2) were more likely to have higher alligator weed cover in spring (mean cover score in spring = 3) than sites with “low” (cover score = 1) alligator weed cover in winter (mean cover score in spring = 2) ($t = 2.11$, $p < 0.05$, $n=20$, after removal of one extreme outlier). In other words, sites which retained relatively high alligator weed cover in winter tended to be those which had the heaviest and most consistent cover throughout the year.

6.3.2 Species richness and cover in 25 m^2 plots within season

A total of 23 native vascular plant species, and 22 exotic plant species were recorded from 25 m^2 plots at Lake Rotokawau, over the entire study period (Appendix 6). Native and exotic species richness separately were each greater in 25 m^2 plots with alligator weed present than in plots where alligator weed was not detected, as was total species richness (Table 8, Table 9, Table 10). This was the case in all seasons except summer, during which only one plot was free of alligator weed.

Table 8. Native species richness in 25 m^2 plots with and without alligator weed at Lake Rotokawau. †Only one replicate available, therefore comparison of means not performed.

Season	Mean native species richness		t-statistic	Degrees of freedom	p-value
	Non- alligator weed sites	Alligator weed sites			
Spring	2.5 ± 0.29	3.8 ± 0.40	-2.55	26	0.021
Summer	1.0†	3.7 ± 0.38	NA	NA	NA
Autumn	1.5 ± 0.29	3.6 ± 0.37	-2.24	26	0.034
Winter	1.5 ± 0.29	3.5 ± 0.34	-2.43	26	0.022

Table 9. Exotic species richness in 25 m^2 plots with and without alligator weed at Lake Rotokawau. †Only one replicate available, therefore comparison of means not performed.

Season	Mean exotic species richness		t-statistic	Degrees of freedom	p-value
	Non- alligator weed sites	Alligator weed sites			
Spring	1.0 ± 0	3.8 ± 0.35	-7.84	26	< 0.001
Summer	1.0†	4.9 ± 0.36	NA	NA	NA
Autumn	2.0 ± 1.1	5.0 ± 0.42	-2.68	26	0.013
Winter	2.3 ± 0.95	5.0 ± 0.38	-2.67	26	0.013

Table 10. Total species richness in 25 m^2 plots with and without alligator weed at Lake Rotokawau. †Only one replicate available, therefore comparison of means not performed.

Season	Mean total species richness		t-statistic	Degrees of freedom	p-value
	Non- alligator weed sites	Alligator weed sites			
Spring	3.5 ± 0.29	7.5 ± 0.64	-5.76	26	< 0.001
Summer	2†	8.6 ± 0.63	NA	NA	NA
Autumn	3.5 ± 0.96	8.6 ± 0.65	-3.08	26	< 0.01
Winter	3.8 ± 0.85	8.5 ± 0.56	-3.34	26	< 0.01

Using only plots where alligator weed *was* present, the total native cover score decreased with increasing alligator weed cover score in spring (Figure 52). In contrast, there was no evidence of a relationship between alligator weed cover score and "other exotics" cover score in any month. Nor were any relationships detected between alligator weed cover score and native, exotic or combined species richness in any month, or the proportion of native species or cover (of total non-alligator weed species).

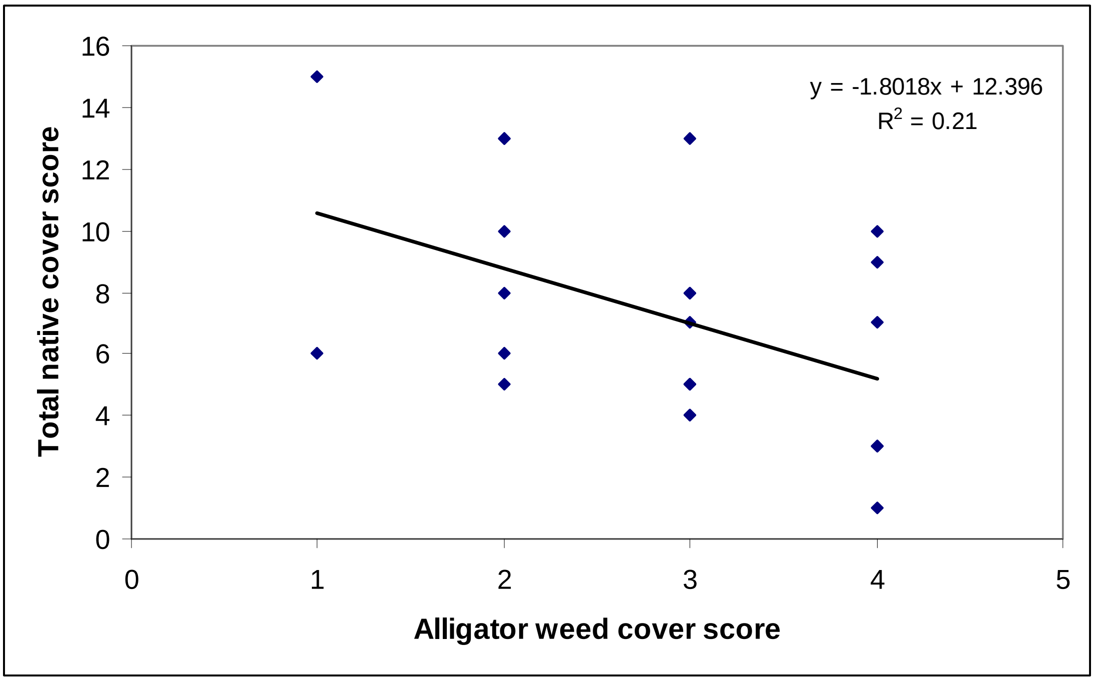

Figure 52. Relationship between total native cover score per plot and alligator weed cover scores in 25 m^2 plots from Lake Rotokawau, spring 2006, p = 0.028. Only plots with alligator weed present were included in the analysis, n = 24.

6.3.3 Species richness and cover in 25 m^2 plots between seasons

Mean exotic species richness was higher in winter (mean = 4.6 ± 0.39 exotic species per 25 m^2 plot), when alligator weed cover was low, than in spring (mean = 3.4 ± 0.36 exotic species per plot; paired sample t-test, $t_{27} = 3.45$, $p < 0.01$; Figure 53). In contrast, there was no evidence of a difference in native species richness between winter and spring (mean = 3.3 ± 0.32 and 3.6 ± 0.35 native species per plot respectively; paired sample t-test, $t_{27} = -1.30$, p = 0.20). Total other exotic cover per plot was also higher in winter than in spring (mean exotic cover score = 6.1 ± 0.65 and 4.3 ± 0.51 respectively; paired sample t-test, $t_{27} = 4.45$, $p < 0.001$; Figure 54). Total native cover per plot did differ between winter and spring, but showed the reverse trend to that of exotic cover, increasing from a mean score of 5.9 ± 0.48 in winter to 6.8 ± 0.60 in spring (paired sample t-test, $t_{27} = -2.20$, $p < 0.05$).

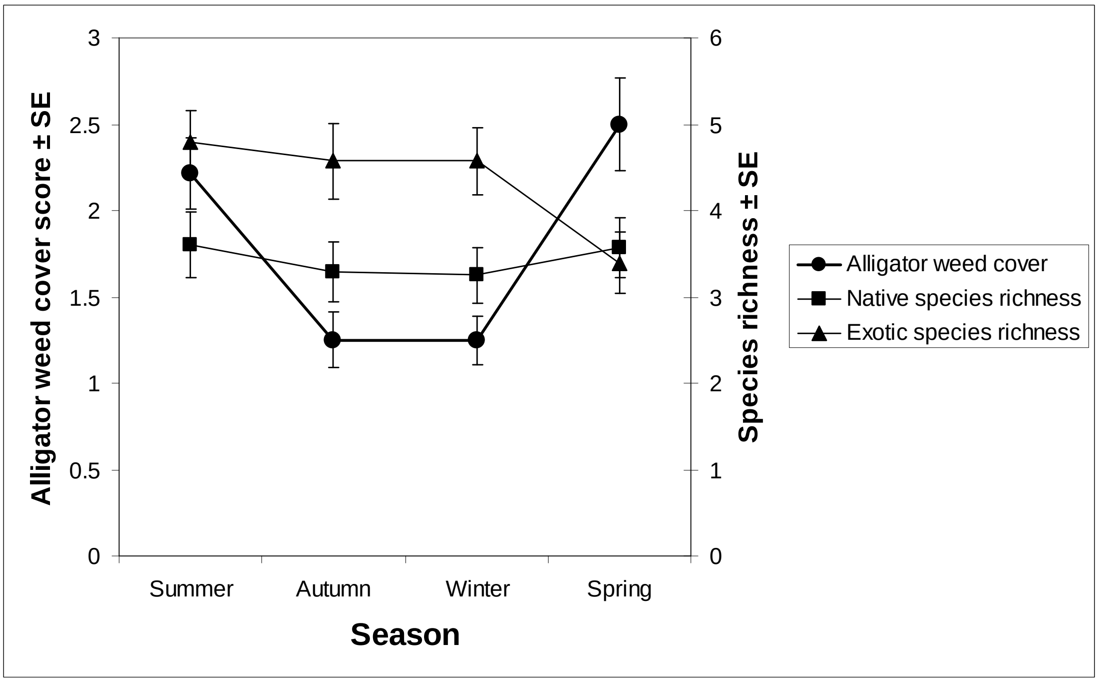

Figure 53. Mean alligator weed cover score along with mean native and exotic species richness for 25 m^2 plots from Lake Rotokawau, measured quarterly over one year.

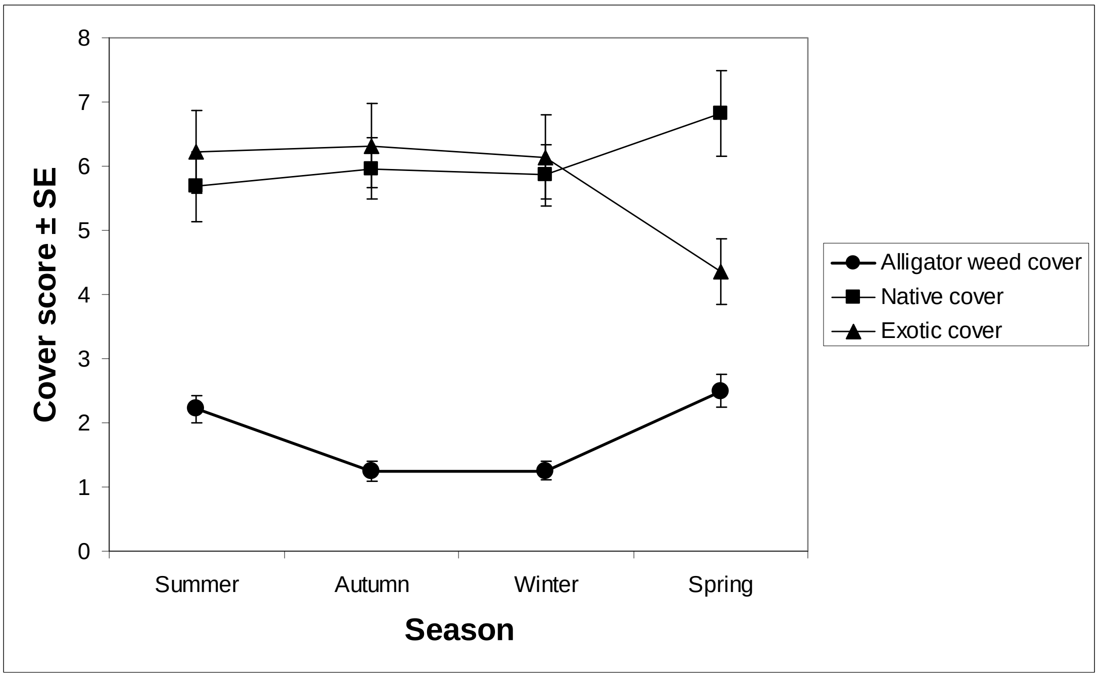

Figure 54. Mean alligator weed, total native, and other exotics cover scores for 25 m^2 plots from Lake Rotokawau, measured quarterly over one year.

6.3.4 Native species richness in 1 m^2 plots

No *S. tabernaemontani* or *I. prolifer* 1 m^2 plots were found to contain additional native plant species other than the one dominant species for which they were selected. However, native species were often lacking entirely from alligator weed dominated plots. Native species richness was therefore lower in 1 m^2 plots dominated by alligator weed than those dominated by either *S. tabernaemontani* or *I. prolifer* in January and May (ANOVAs using $\alpha = 0.01$, $F_{2,12} = 16$, $p < 0.01$ in both cases; Tukey's $p = 0.01$ in all pair-wise comparisons with alligator weed). The same trend, though not significant, was also evident in November, March, July and September.

6.3.5 Exotic species richness in 1 m^2 plots

In both September and November, exotic plant species richness was highest in *I. prolifer* dominated plots (ANOVAs, $F_{2,12} = 5.1$ and 4.9; $p = 0.025$ and 0.028 respectively; Figure 55). In both months, exotic species richness was higher in *I.*

prolifer than in *S. tabernaemontani* plots (Tukey's *post hoc* test; p = 0.023 (September) and p = 0.024 (November)), with alligator weed plots intermediate between, and not different from, the two native treatments. However, for the remainder of the year (January – July), exotic species richness was highest in alligator weed dominated plots, although this trend was significant only in May (ANOVA, $F_{2,12}$ = 4.2, p = 0.042; Figure 55). The difference in May was only statistically significant between alligator weed and *I. prolifer* dominated plots (Tukey's *post-hoc* p = 0.043).

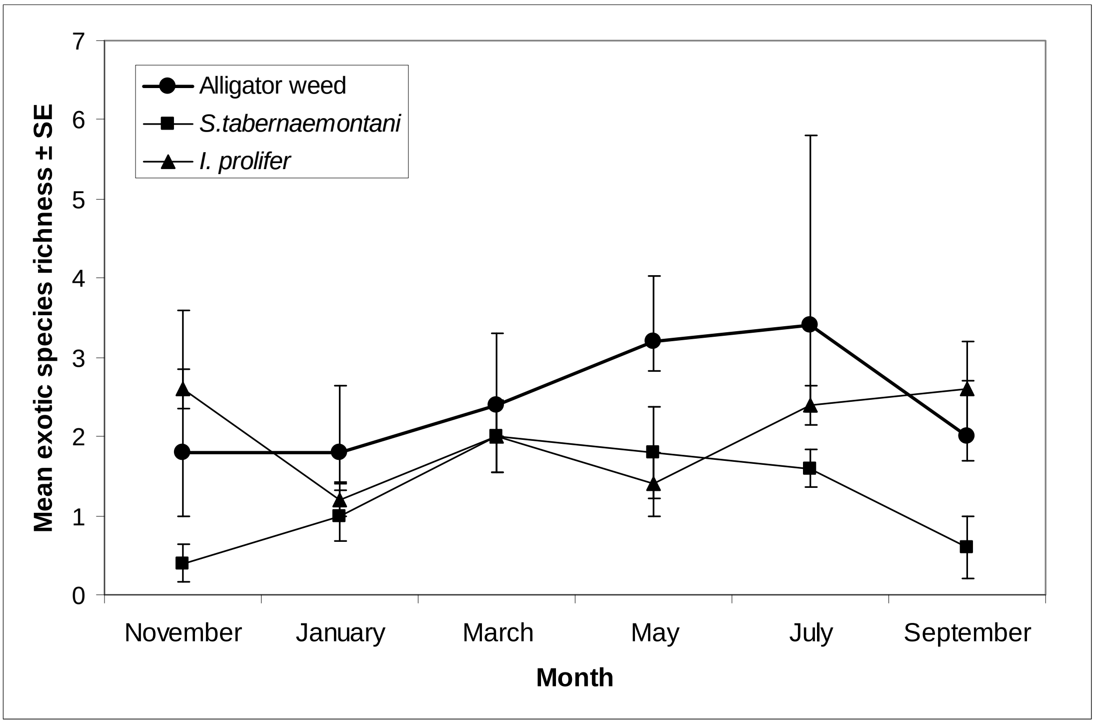

Figure 55. Mean exotic species richness (including alligator weed) in 1 m^2 plots dominated by alligator weed or native sedges, Lake Rotokawau. Error bars indicate one standard error.

In alligator weed plots, exotic species richness showed an inverse trend to that of alligator weed cover, while native species richness showed little annual variation (Figure 56). Four native species were observed in alligator weed plots during the course of sampling. Two of these were *I. prolifer* and *Typha orientalis*. Both appeared occasionally as small plants which had apparently been dislodged and moved during storms, relodging within alligator weed plots. In addition, the small herbs *Glossostigma elatinoides* and *Myriophyllum propinquum* were observed repeatedly within a minority of alligator weed plots. Those exotics commonly recorded from alligator weed plots included *Polygonum persicaria*, *Ludwigia peploides*, *Azolla pinnata*, *Spirodella punctata*, *Paspalum distichum* and *Lotus* sp.

Similarly, in *I. prolifer* plots, exotic species richness also appeared to be inversely related to *I. prolifer* cover, with no additional native species present within plots on any sampling date (Figure 57). Exotic species richness peaked in different months in alligator weed compared with *I. prolifer* dominated plots. In each case this coincided with lowest cover scores for the dominant species. *Polygonum persicaria* was the most dominant exotic within *I. prolifer* plots, with *Spirodella punctata* also abundant in late winter and spring.

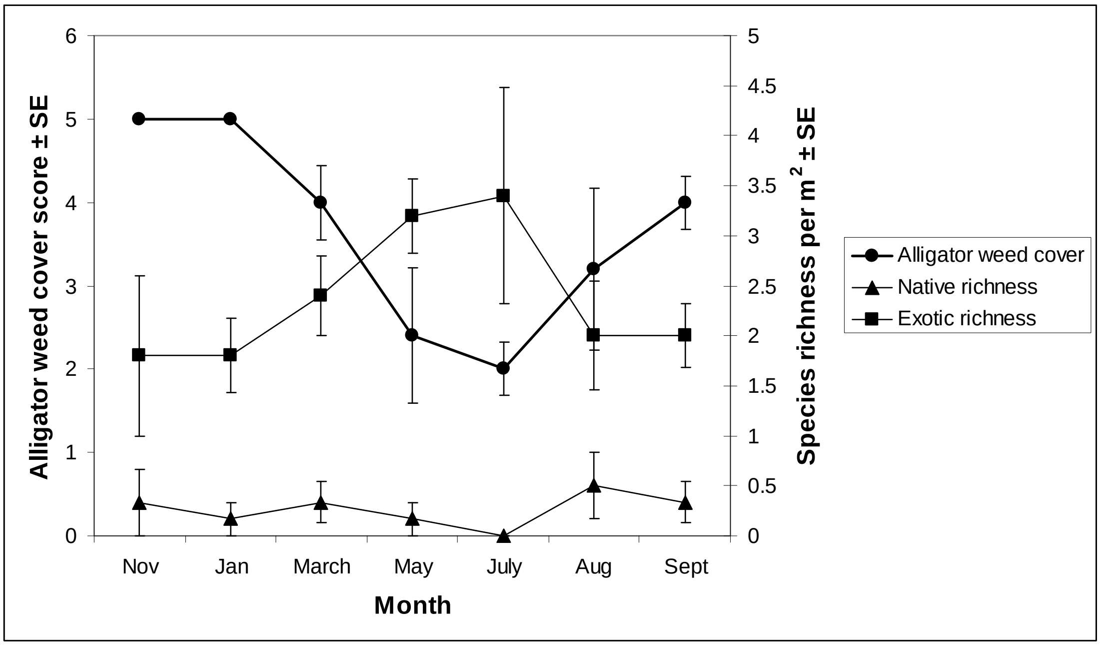

Figure 56. Mean alligator weed cover score, exotic and native species richness from 1 m^2 alligator weed plots, Lake Rotokawau. Exotic species richness includes alligator weed. Error bars indicate one standard error.

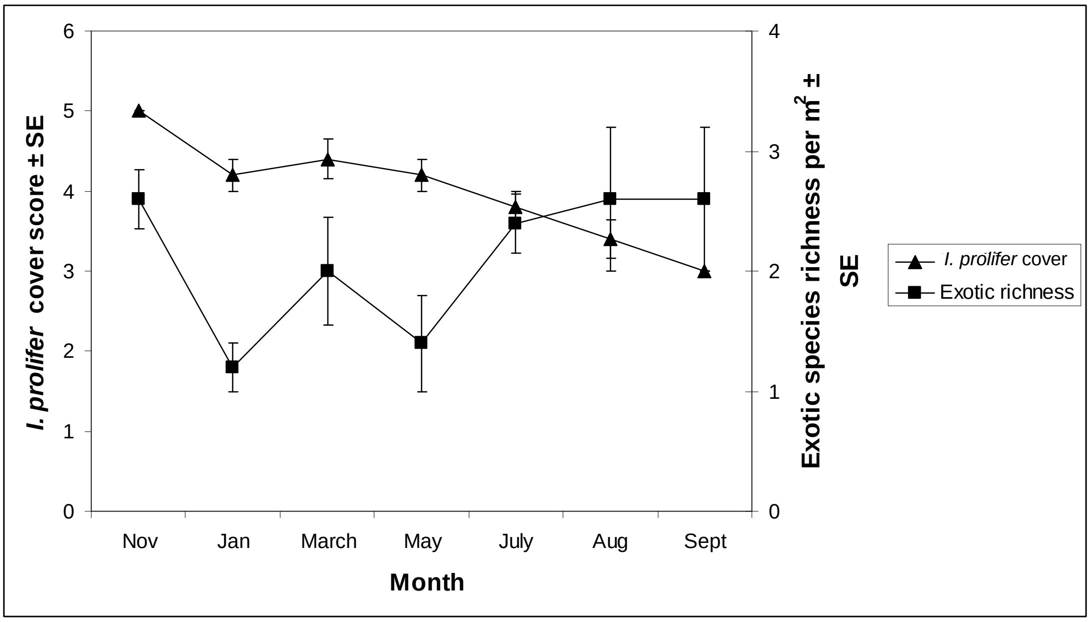

Figure 57. Mean *I. prolifer* cover score and exotic species richness from 1 m^2 *I. prolifer* plots. Lake Rotokawau. No additional native species were found in *I. prolifer* plots. Error bars indicate one standard error.

6.3.6 Diversity

There was weak evidence of a quadratic relationship between alligator weed cover score and Simpson's evenness scores for 25 m^2 plots in spring (Figure 58). In no other season were any relationships between alligator weed cover and diversity detected.

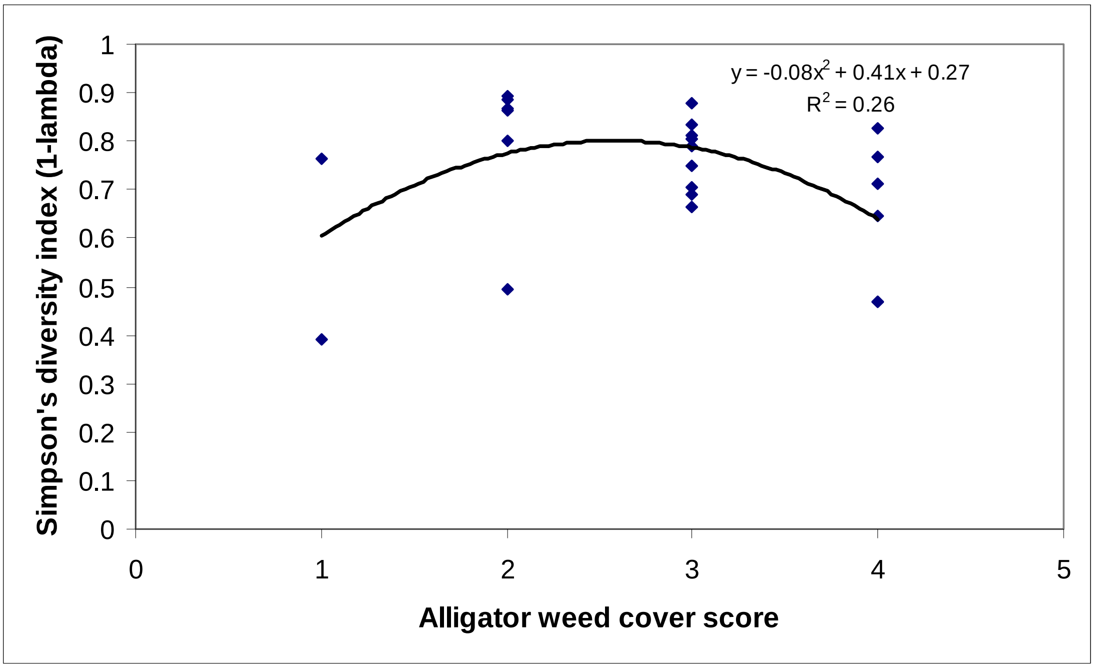

Figure 58. Relationship between Simpson's diversity index and alligator weed cover score in 25 m^2 plots, Lake Rotokawau, November 2006 (p = 0.052). Sites where alligator weed was completely absent have been excluded, as has the single site with an alligator weed cover score of five. Therefore n = 23.

6.3.7 Native versus exotic species richness

There was a positive linear relationship between native and exotic plant species richness from 25 m^2 plots for each quarter except for July (Figure 59, Figure 60, and Figure 61). Native and exotic species richness from 1 m^2 plots were also positively correlated in November 2005 (Figure 62). In no other month did any 1 m^2 plots contain more than one native species, therefore there were no correlations between native and exotic plant species richness at other dates.

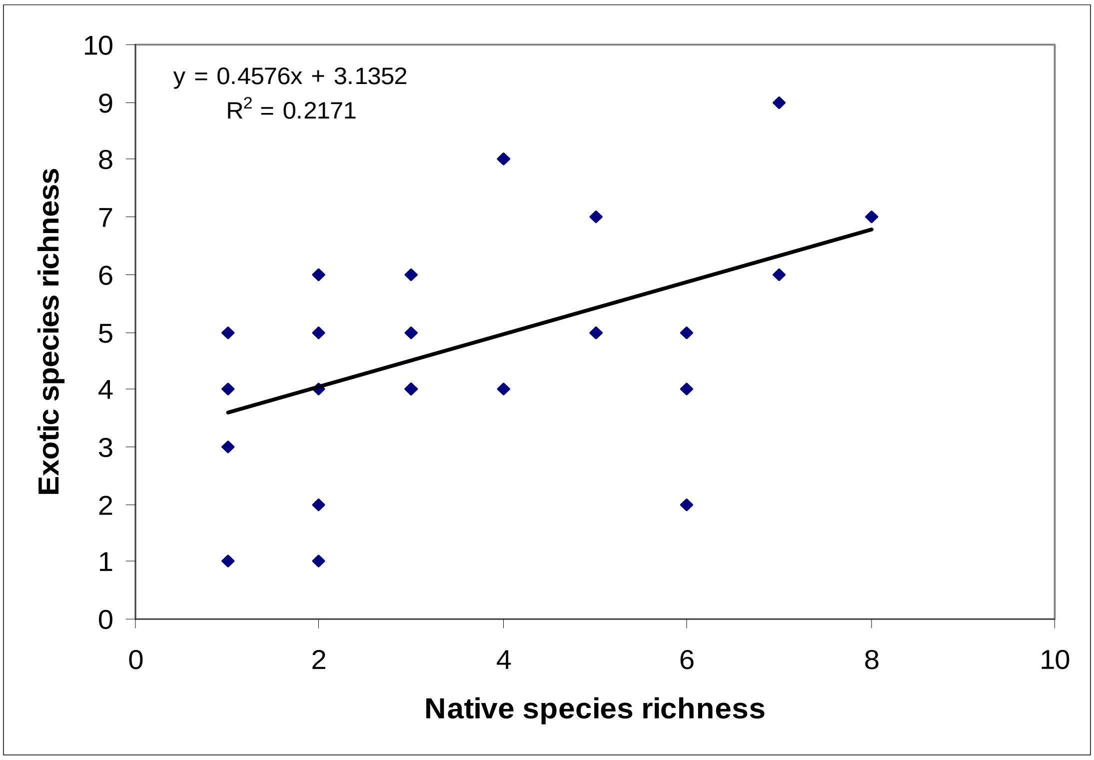

Figure 59. Relationship between native and exotic species richness, 25 m^2 plots, Lake Rotokawau, January 2006 (n = 28; $F_{1,26}$ = 7.21; $p < 0.05$).

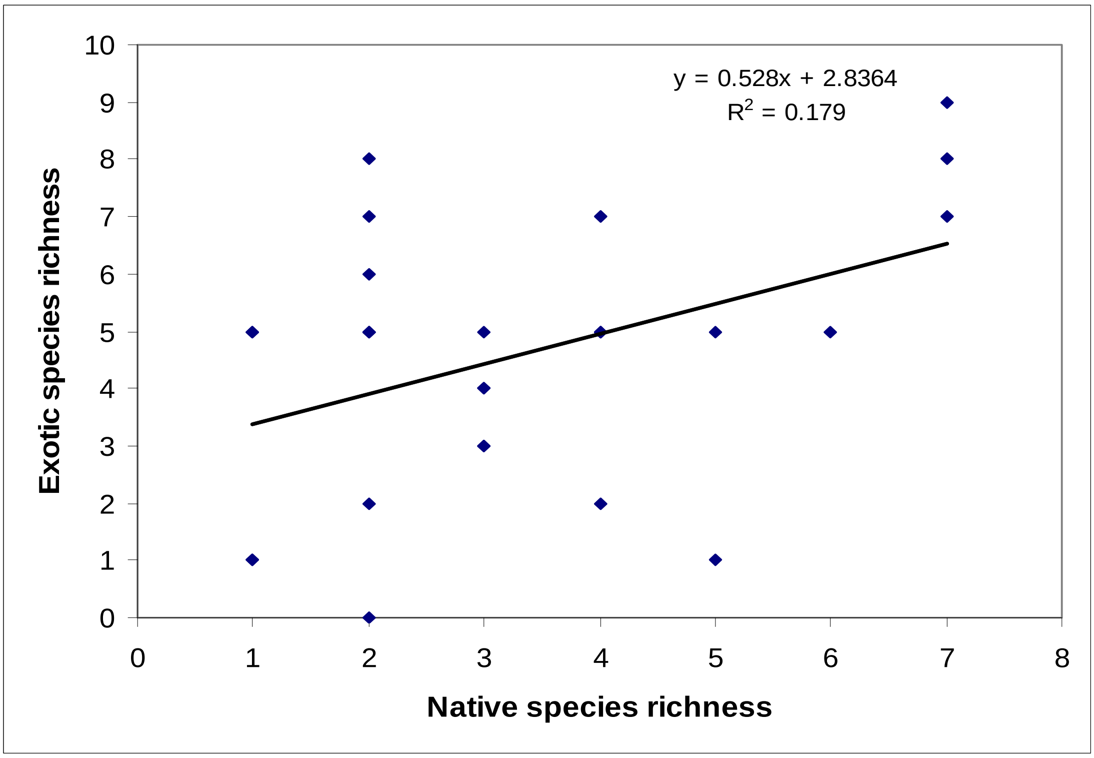

Figure 60. Relationship between native and exotic species richness, 25 m^2 plots, Lake Rotokawau, May 2006 (n = 28; $F_{1,26}$ = 5.67; $p < 0.05$).

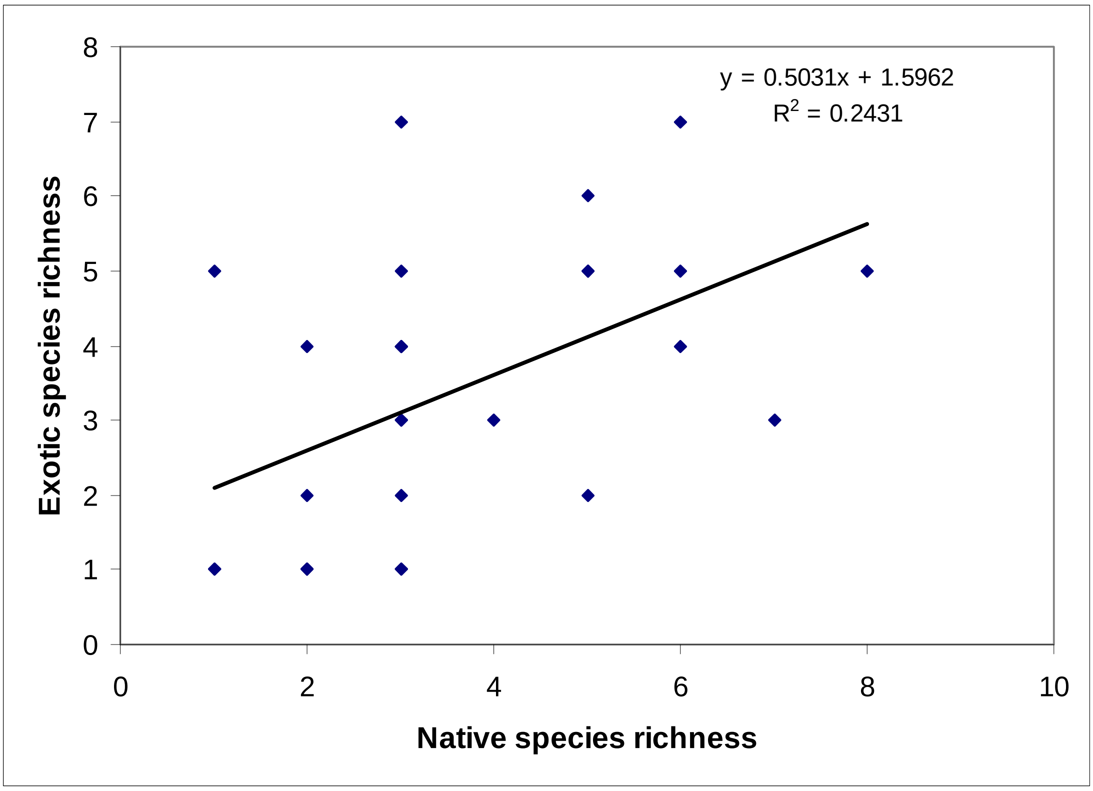

Figure 61. Relationship between native and exotic species richness, 25 m^2 plots, Lake Rotokawau, November 2006 (n = 28, $F_{1,26}$ = 8.35, $p < 0.01$).

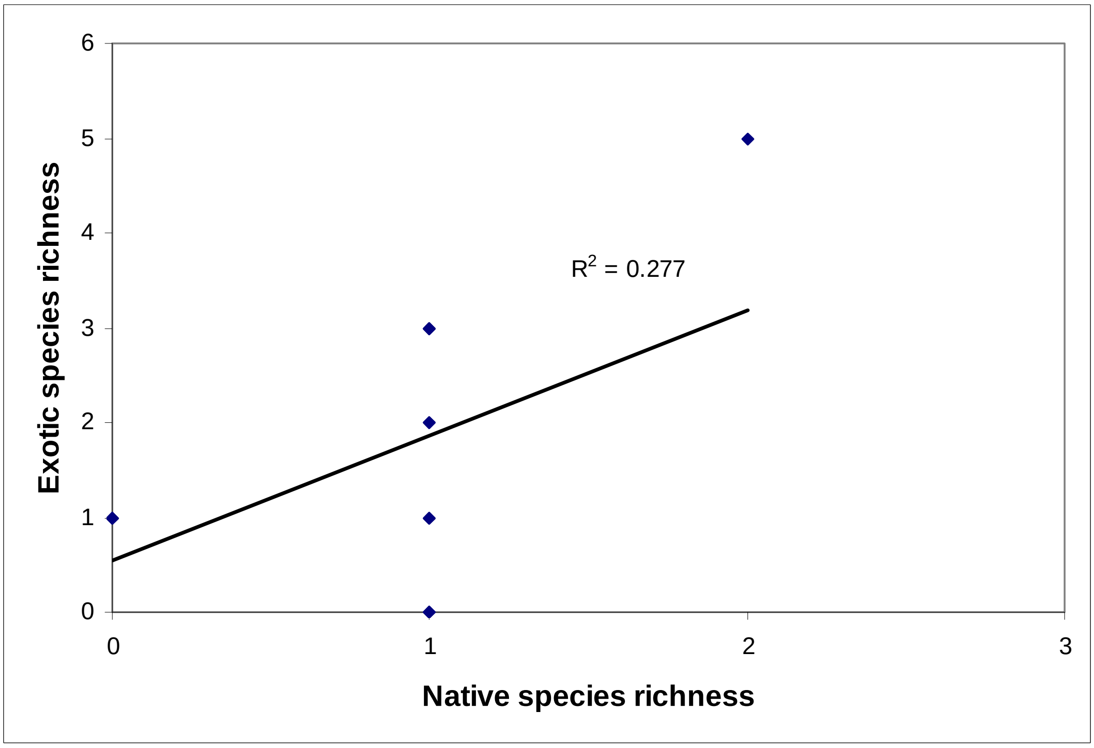

Figure 62. Relationship between native and exotic species richness, 1 m^2 plots, Lake Rotokawau, November 2005 (n = 15, $F_{1,13}$ = 4.98, $p < 0.05$).

6.3.8 Exotic cover excluding alligator weed

Native species richness showed a positive linear relationship to exotic cover (excluding alligator weed) from 1 m^2 plots in November (Figure 63), but not in any other month. Similarly, native species richness displayed a positive linear relationship with exotic cover in 25 m^2 plots in November (Figure 64) and January (Figure 65), but not May or July. Native cover was not significantly related to exotic cover in either plot size in any month.

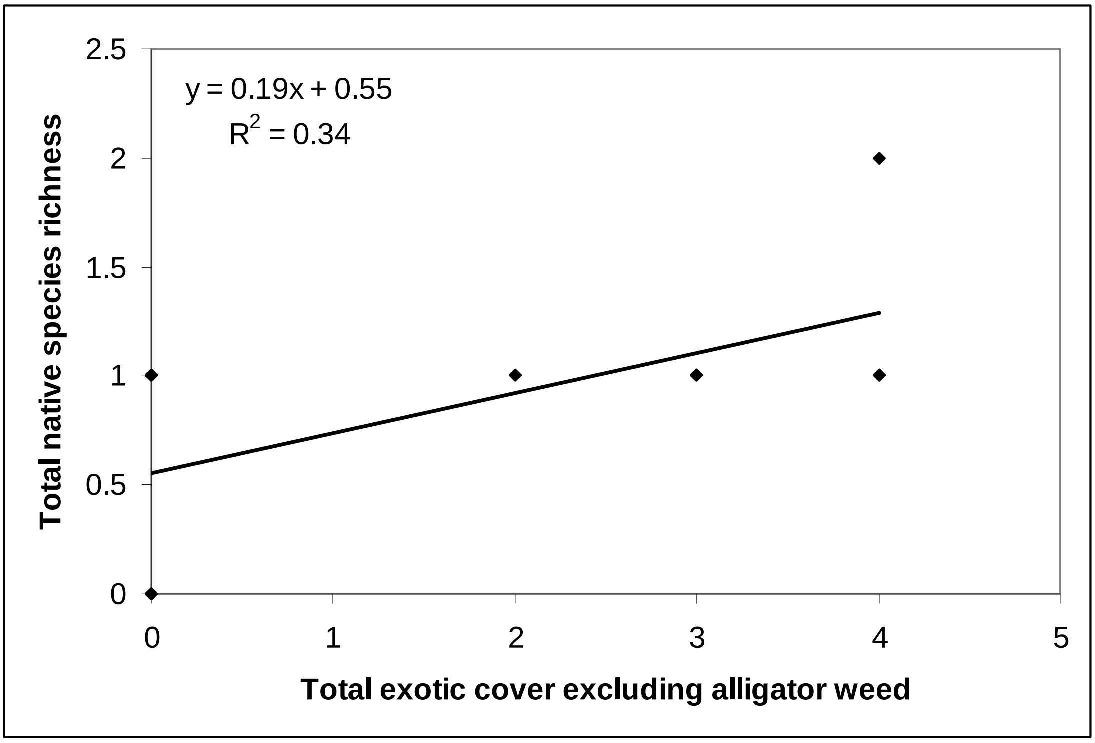

Figure 63. Relationship between native species richness and exotic cover (excluding alligator weed), November 1 m^2 plots, Lake Rotokawau ($n = 15$, $F_{1,13} = 6.57$, $p < 0.05$).

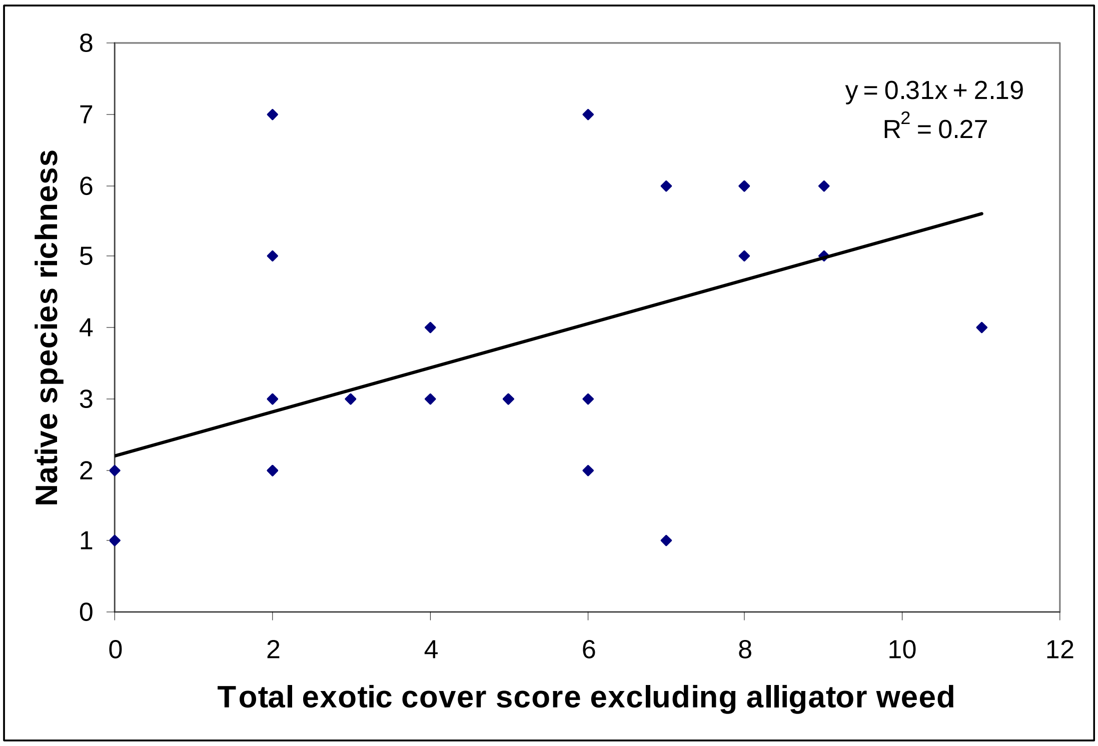

Figure 64. Relationship between native species richness and total exotic cover (excluding alligator weed), 25 m^2 plots, Lake Rotokawau, November 2006 (n = 28, $F_{1,26} = 9.65$, $p < 0.01$).

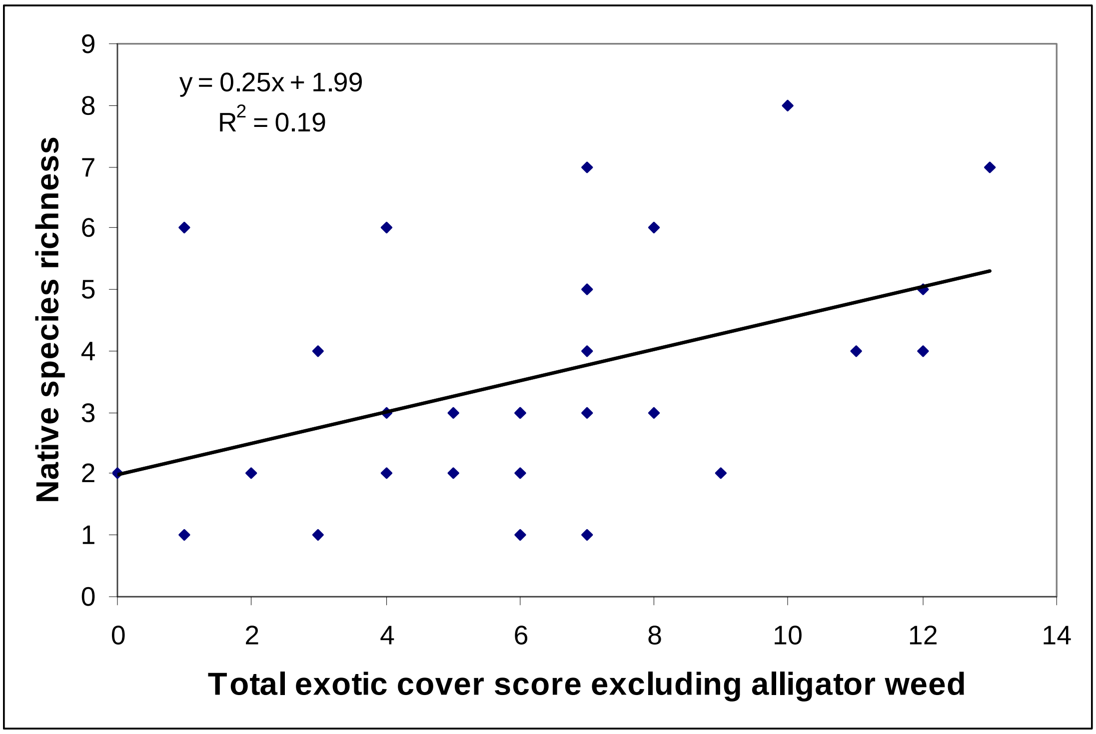

Figure 65. Native Relationship between native species richness and total exotic cover (excluding alligator weed), Lake Rotokawau, 25 m^2 plots, January 2006 (n = 28, $F_{1,26} = 6.03$, $p < 0.05$).

6.3.9 Environmental data 25 m^2 plots

In November, alligator weed cover score showed a significant quadratic relationship with the mean depth of the bottom corners of 25 m^2 plots ($F_{2,25} = 8.88$, $p < 0.01$; Figure 66). Alligator weed cover score peaked when bottom corner depth was 0.065 m. Sites with alligator weed absent, or present at less than 5% cover were all greater than 0.25 m in depth at the bottom of the plot, whereas plots with high alligator weed cover tended to be shallower than 0.25 m at the bottom end of the plot (Fisher's Exact test, $p < 0.001$).

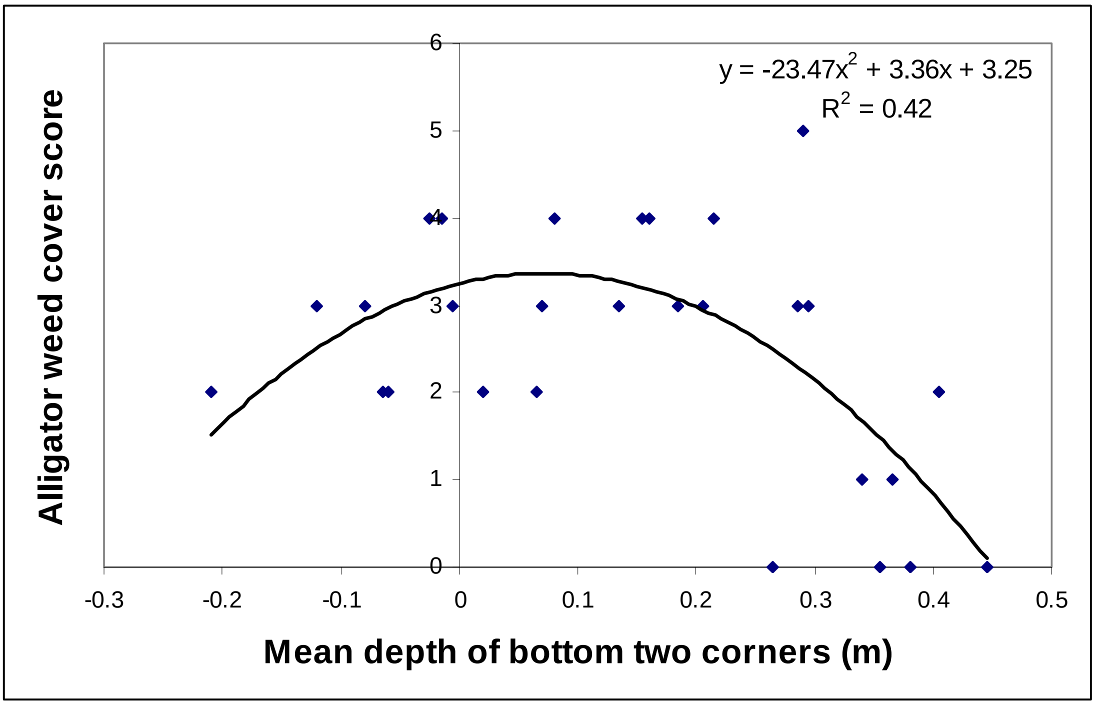

Figure 66. Alligator weed cover score in Lake Rotokawau 25 m^2 plots against water depth at bottom corners of plot, November. Negative numbers indicate height of dry ground above water level, which is shown as zero depth, with positive numbers indicating depth below the water level. N = 28, $F_{2,25} = 8.88$, $p < 0.01$

The difference in elevation between the bottom and top corners of the plots was not itself a significant term, but slightly increased the R^2 value to 0.48 ($F_{4,23} = 5.36$, p <

0.01) when combined with mean bottom depth in a multiple regression given by the following equation:

$$y = 18.78x^2 + 2.04x + 4.46z^2 + 4.41z + 2.68$$

where: y = alligator weed cover score

x = mean bottom corner depth

z = difference between mean top corner depth and mean bottom corner depth

Bottom corner depth and difference between top and bottom corners were not significantly related to alligator weed cover score in any month other than November, although similar but weak quadratic relationships were displayed in all other months. There was no relationship between depth of top corners and alligator weed cover score in November or any other month.

Exotic species richness and total cover score of all exotics excluding alligator weed both showed negative linear relationships to the depth of the bottom plot corners (Figure 67, Figure 68). Native species richness and cover were not significantly related to water depth.

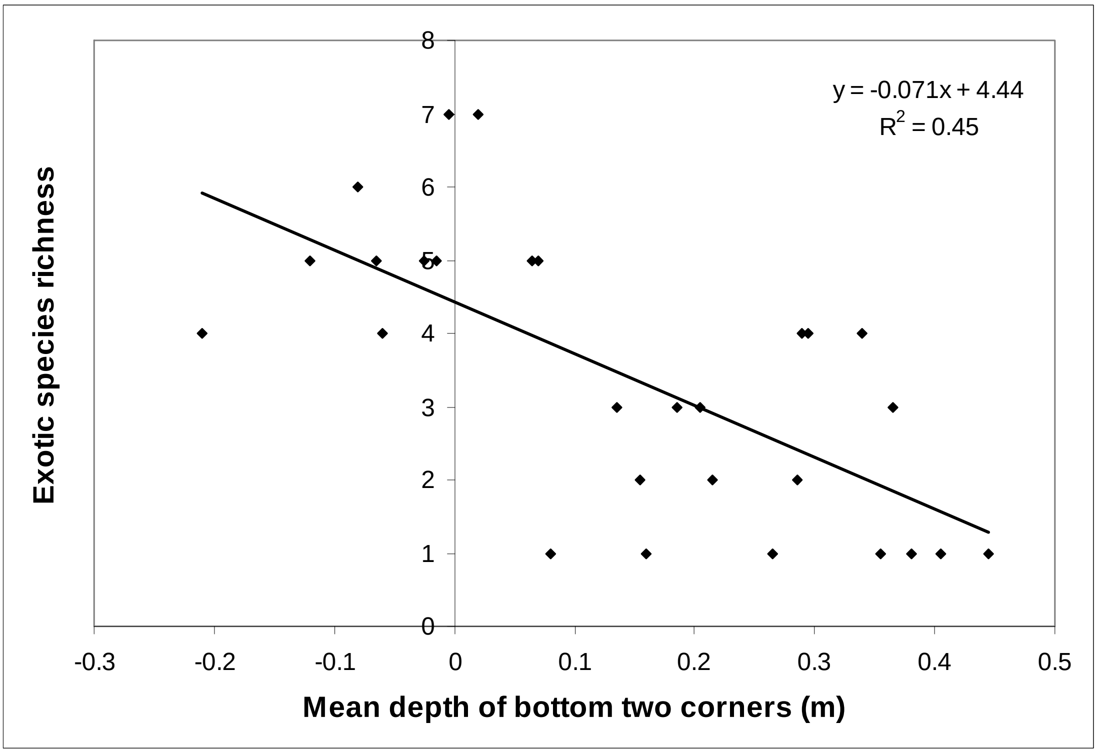

Figure 67. Exotic species richness in 25 m^2 plots with increasing depth of water at bottom corners of plots, Lake Rotokawau, November (n = 28, $F_{1,26} = 21.29$, $p < 0.001$). Negative numbers indicate height of dry ground above water level, which is shown as zero depth, with positive numbers indicating depth below the water level.

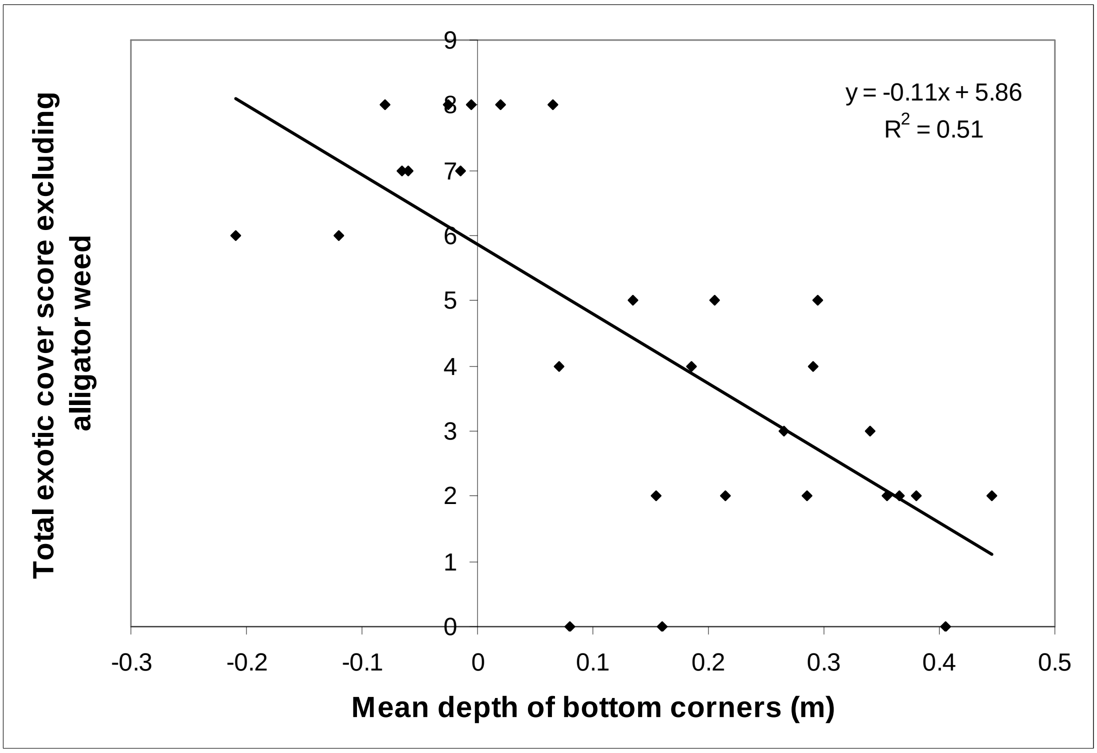

Figure 68. Total cover score of all exotic species other than alligator weed against increasing water depth of bottom corners in 25 m^2 plots, Lake Rotokawau, November (n = 28, $F_{1,26}$ = 27.35, p < 0.001). Negative numbers indicate height of dry ground above water level, which is shown as zero depth, with positive numbers indicating depth below the water level.

6.3.10 Environmental data 1 m^2 plots

There was no evidence of differences between vegetation types in the levels of total nitrogen or phosphorous in water samples from November 2006 (ANOVAs, $F_{2,27}$ = 1.84, p = 0.18 and $F_{2,27}$ = 1.77, p = 0.19 respectively) or March 2007 (ANOVAs, $F_{2,26}$ = 2.63, p = 0.09 and $F_{2,26}$ = 2.51, p = 0.10 for nitrogen and phosphorous respectively).

Minimum air temperatures were higher in *S. tabernaemontani* plots than in *I. prolifer* plots in September (ANOVA, $F_{2,9}$ = 6.55, p = 0.018; Tukey's pair-wise p = 0.014; Figure 69), and compared with both alligator weed and *I. prolifer* in January (ANOVA, $F_{2,6}$ = 15.43, p < 0.01; Tukey's pair-wise p < 0.01 in both cases). There was no evidence of a difference in minimum air temperature in July (ANOVA, $F_{2,6}$ = 3.00, p = 0.13). No differences in maximum air temperature were detected (one-way ANOVAs, p > 0.61 in all months; Figure 70).

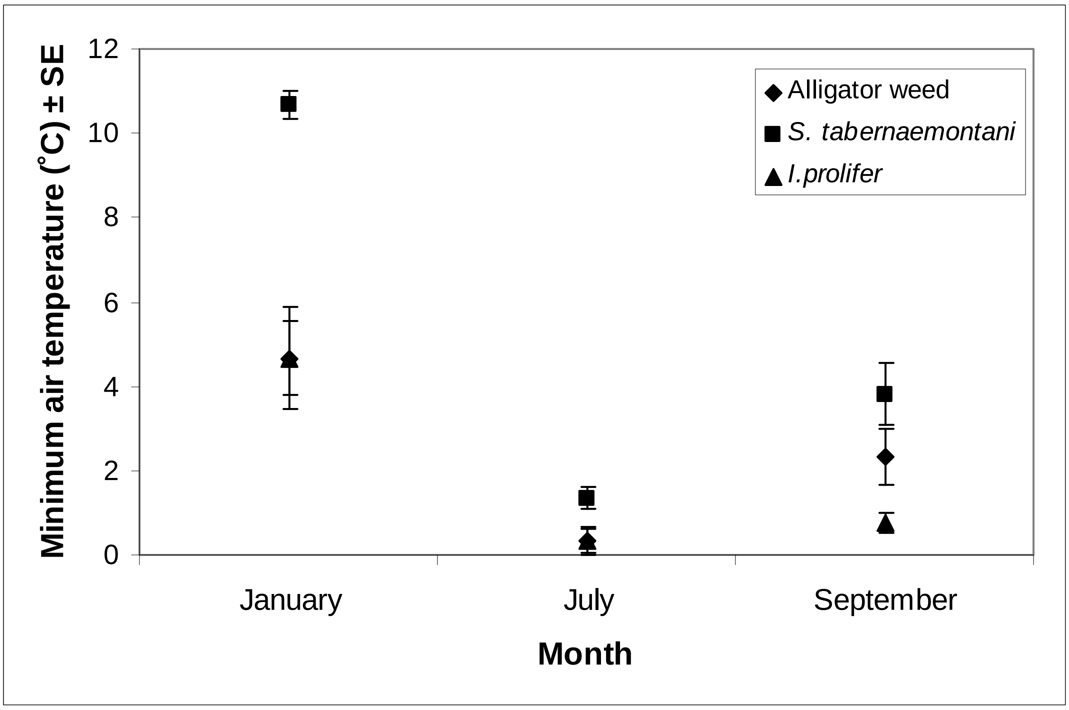

Figure 69. Minimum air temperatures within 1 m^2 plots dominated by alligator weed or native sedges. Error bars indicate one standard error.

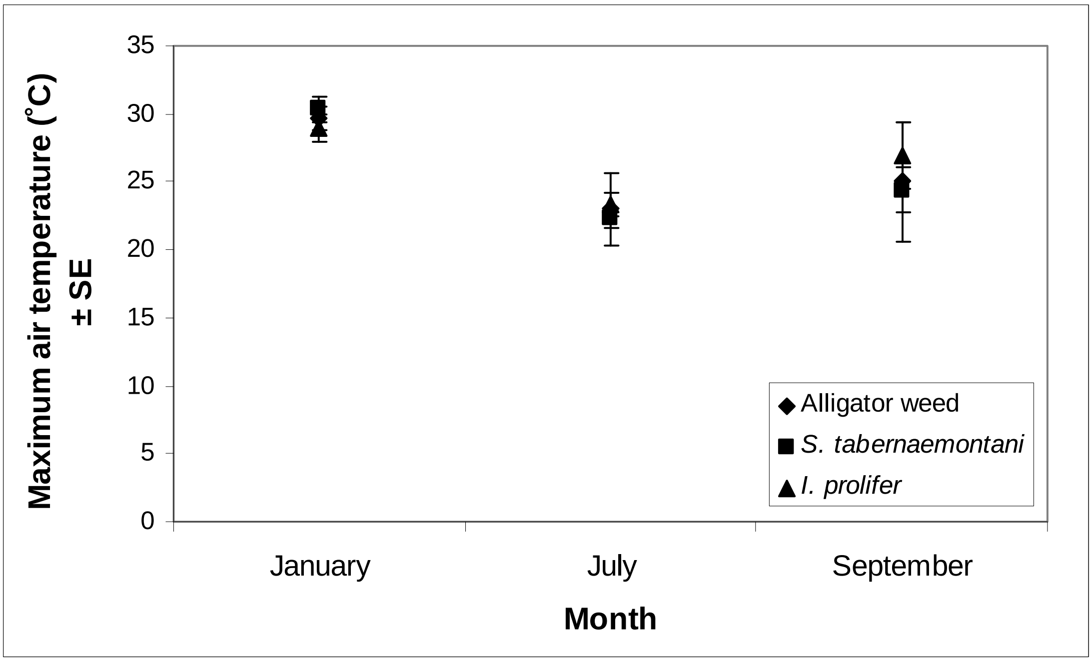

Figure 70. Maximum air temperatures within 1 m^2 plots dominated by alligator weed or native sedges. No differences were significant within any month. Error bars indicate one standard error.

6.4 Discussion

6.4.1 Weed impacts on native diversity

The results indicate some negative correlation of alligator weed cover and native plants, however this was not as consistent across all metrics as predicted by hypothesis one. Total native cover score decreased with increasing alligator weed cover in 25 m^2 plots, while Simpson's diversity index was also reduced under high levels of alligator weed cover. In contrast, native species richness was not significantly related to alligator weed cover in any month. This pattern of a more negative impact of weed species on native cover than on native species richness is similar to that observed by Knight and Reich (2005). This indicates that native species may be able to maintain a presence, as indicated by species *richness*, under heavy infestations of alligator weed or other exotics at this site, probably due to more favourable environmental conditions in heavily invaded areas partially offsetting the negative effects of weed invasion. Nevertheless, this native presence may have limited functional significance, with native *cover* declining with increasing alligator weed invasion. With such reduced cover, some species may be more vulnerable to stochastic events, and species richness may also decline if measured over longer post-invasion time-frames.

The lack of relationship between alligator weed and native cover in 25 m^2 plots in months other than November may in part be due to the small range of alligator weed cover values present in other seasons, reflecting the synchronised annual fluctuations in alligator weed biomass around the lake edge due to alligator weed's uniformly vigorous early season growth followed by intensive herbivory by the flea beetle.

The highly synchronous nature of alligator weed growth also prevented any correlations between alligator weed and native species within 1 m^2 plots. Recording cover data in narrower category bands may have detected differences. However, it is possible that many of the native species sampled reach peak biomass in late spring/early summer, and only at this time of year did a release from alligator weed dominance result in a detectable increase in their growth. These results also suggest that any differences which may have been present are likely to be so slight as to have limited biological importance. Simulated or actual herbivory experiments which maintained alligator weed at a wide range of cover levels for prolonged periods of time might provide a clearer indication of whether lower alligator weed cover levels would in fact have any significant benefits for native cover.

As an observational study, conducted post-invasion, this research correlates alligator weed invasion with current diversity, which may not be the same as diversity at the time of invasion (Levine 1999). Because of the high level of alligator weed dominance in this lake, it is possible that the lack of correlation between alligator weed cover and native species richness may reflect an already impacted native flora, which has been reduced sufficiently throughout the lake for these effects to no longer be evident. Replicated research comparing uninvaded ecosystems and those ranging from lightly/newly invaded to heavily/historically invaded would help to clarify the extent of alligator weed’s impacts on plant communities. However, the logistical problems involved in obtaining suitable sites for this work can be prohibitive, as experienced in this study. Alternatively, greenhouse and/or field based manipulative competition studies could further elucidate the role of alligator weed invasion on the germination and competition dynamics of native flora. It would also be useful to conduct studies over more than one year, to determine the extent to which observed seasonal variations are repeated between years.

As this study was conducted in only a single invaded ecosystem, the results here cannot be generalised to other systems invaded by alligator weed. However, it seems likely that wherever alligator weed attains the level of dominance over large areas that occurred at Lake Rotokawau, native plant species will inevitably be displaced to some extent. It would be interesting to determine how different the responses to alligator weed invasion are for different life forms among the native flora (e.g. herbaceous species versus sedges).

6.4.2 Natives and exotics: Similar responses to environmental gradients?

Native and exotic plants (including alligator weed) often appeared to respond similarly to environmental variation. However, this occurred at both large and small spatial scales, rather than solely at the 25 m^2 scale, as predicted.

Plots with low or absent alligator weed cover consistently displayed lower species diversity than plots with high alligator weed cover in the same month. This may be because the same underlying environmental differences which make these sites less suitable for invasion by alligator weed also make them less able to support highly diverse communities, as has been documented in previous studies (Levine 1999). This is also reflected in the quadratic relationship of Simpson’s diversity to alligator weed cover, with low diversity at relatively inhospitable sites as well as heavily alligator weed dominated sites, and higher diversity in between.

Water depth was one environmental variable that was correlated with alligator weed growth, in a quadratic relationship, indicating that this weed was mostly dominant in the zone between 0.1 m above – 0.3 m below the November 2006 waterline. As a group, other exotic species were also affected by plot depth, but showed a linear rather than quadratic relationship, probably due to the more terrestrial nature of many of the other exotic species present at Lake Rotokawau. Native species richness and cover were not significantly related to water depth, which may reflect differences in habitat requirements between exotic and native species at the site, with fewer herbaceous terrestrial species present amongst the native flora.

In addition, the iron pan rock lake bed makes establishment by plant roots difficult, and in places patches of bare rock are exposed where colonisation is clearly impossible for most plants. At the larger spatial scale these patches would have resulted in lower cover scores for both native and exotic plant species. However, none of the 1 m^2 plots included bare patches, and water depth did not vary significantly. Correlations between native and exotic species at this scale thus suggest that natives and exotics were also responding similarly to additional unmeasured environmental variables. No differences in nitrogen or phosphorous levels were detected among vegetation types at the 1 m^2 scale, thus providing no evidence that alligator weed was occupying sites of differing nutrient status from the native sedge species. This is consistent with other studies which have found similar responses of natives and exotics to nutrient levels to be partially responsible for positive correlations between the two (Houlahan and Findlay 2004). However, elevated nutrient levels have been found to assist other invasive plant species disproportionately compared with natives (Leishman and Thomson 2005), with differences in sediment nutrient levels detected between stands of different species (Templer, Findlay et al. 1998). It is therefore possible that alligator weed may have been found to occupy higher nutrient sites had substrate nutrient samples been taken in addition to water chemistry, or that alligator weed's rapid growth rates serve to mask differences in nutrient levels through rapid nutrient uptake.

6.4.3 Effects of spatial scale

The relationship between native species richness and exotic species richness or cover was found to be positive at both spatial scales, although the evidence at the 1 m^2 scale was relatively weak. This contrasts with other studies, which have found that, while the two may be positively correlated over larger scales (such as the 25 m^2 plots) due to similar responses to environmental variables, when examined on a small scale (such as 1 m^2) native species richness often declines with increasing exotic richness (Byers and Noonburg 2003). This result suggests that even at small spatial scales the effects of environmental gradients are playing a strong role in structuring plant communities at Lake Rotokawau. The small-scale patchiness inherent in this system may also contribute to this lack of difference between the spatial scales compared with other studies conducted in ecosystems which may be more homogenous over larger scales. The low species richness in 1 m^2 sedge plots is consistent with observations of these species growing elsewhere, often in mosaics of small monospecific stands of various sedge and rush species (U.S Army Corps of Engineers 2007).

Alligator weed's cover dominance does, however, suggest some loss of native biodiversity as a result of alligator weed invasion. Alligator weed covered approximately 23% of the lake margin area. The low levels of bare ground throughout the lake suggest that if this area were not occupied by alligator weed, it would most likely be colonised by something else. In combination with the significant negative relationship between alligator weed and native cover (Figure 52), this implies that native biodiversity at Lake Rotokawau may benefit from a reduction in alligator weed cover.

Whether this would in fact happen in the presence of other weed species is doubtful. Exotic species richness and cover increased in winter, when alligator weed cover was reduced, and then decreased again in September as alligator weed cover increased. Peak cover of other exotics in *I. prolifer* plots occurred at a different time from peak cover of other exotics in alligator weed plots, again coinciding with the lowest cover of the dominant plant species. This suggests that the increased cover of other exotics was at least in part a facultative response to increased resource availability, rather than simply a phenological coincidence with low alligator weed levels. In contrast, there was no evidence of native species being able to increase in response to short-term reductions in cover of either alligator weed or *I. prolifer*. Other studies have found that weed removal may simply lead to replacement by other weeds (Morrison 2002). For instance, biological control of *Pistia stratiotes* in Zimbabwe resulted in rapid replacement of this species by other aquatic weeds including *Eichhornia crassipes* (Denslow and D'Antonio 2005). The results of this study indicate that a similar weed replacement effect may well be occurring with alligator weed at Lake Rotokawau, as predicted. Introduced species such as *Polygonum persicaria* and *Paspallum distichum* tended to be the main beneficiaries of reductions in alligator weed cover. This highlights the valuable role of an ecosystem-based management approach rather than solely species by species weed management.

Previous authors have suggested that alligator weed may accelerate terrestrial in-filling of lake margins by growing as a dense mat which traps sediment and acts as a substrate for more terrestrial weedy species (Stewart, Emberson et al. 1996). The high incidence of terrestrial weedy species within 1 m^2 alligator weed plots in this study is consistent with this observation, although long-term monitoring would be required to detect any trend towards lake infilling. Similarly, dense mats of *I. prolifer* served to support several terrestrial exotics, whereas the more open architecture of *S. tabernaemontani* supported fewer additional species overall, and in particular fewer rooted emergent/terrestrial species, with the floating species *Spirodella punctata* more frequently observed in these plots.

6.4.4 Conclusions

Alligator weed dominated the marginal vegetation at Lake Rotokawau. Its extensive coverage, along with a negative relationship with native plant cover indicates that alligator weed is extensively restructuring the plant community at this site, to the detriment of native vegetation. While native species richness was not reduced under heavy alligator weed invasion, probably as a result of the influence of underlying environmental variation, the reduction in native cover with alligator weed invasion is predicted to result in loss of native species in the long-term. An apparent weed replacement effect indicates that ecosystem-based management, rather than simply removal of alligator weed, might be necessary for native species to benefit from weed control measures.

7 THESIS SUMMARY

7.1 Potential of shading as a control method

The first data chapter of this thesis examined the responses of alligator weed to shading and interspecific competition. While alligator weed is considerably more shade tolerant than common pasture grasses, its growth is significantly slowed by shading. To provide satisfactory control, high levels of shade are likely to be needed, although the presence or absence of shade tolerant competitors may strongly influence the degree of shading required for control. Streamside revegetation which combines overhead shading with shade tolerant competitive plantings may substantially reduce alligator weed cover, although this would need to be tested by further experiments. Shading of the entire infestation will be important to the success of any control efforts in order to prevent clonal support from outside the shaded area reducing its effectiveness. Native forest streams may have some degree of protection from aggressive alligator weed invasion due to a combination of overhead shading and shade tolerant native species that may compete strongly with alligator weed. However, maintenance of an intact canopy would be important in preserving this protection.

7.2 A cascade of inter- related effects

The remainder of this thesis examined the ecology of alligator weed within a native ecosystem, Lake Rotokawau. Alligator weed at Lake Rotokawau has a wide range of impacts on ecosystem functions such as decomposition and nutrient cycling (Chapter 3), as well as on community structure across a range of taxa including plants (Chapter

6) and invertebrates (Chapters 4 and 5). Clear linkages can be seen between impacts on different ecosystem components, such as altered decomposition dynamics leading to a fungivore dominated beetle community on alligator weed (Figure 71). Parker, Simberloff et al (1999), recognising the paucity of information synthesising the various impacts of invasive plants, raised the question of how closely related the impacts of invasive species were regarding community characteristics and ecosystem function, and whether the former influenced the latter or vice versa. In the case of alligator weed, the changes in ecosystem function (a pulse of decomposition and altered seasonal patterns of biomass fluctuation) appear to strongly influence the invertebrate community and potentially also the plant community.

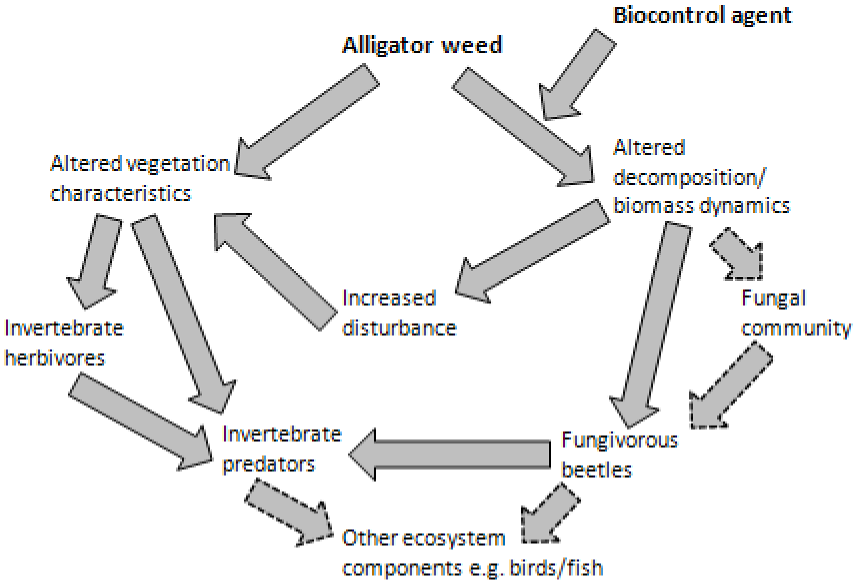

Figure 71. Summary of inter-relationships between effects of alligator weed and its biocontrol agent. Dashed arrows indicate hypothesised effects not directly tested in this thesis.

These results reinforce the way in which, as has been previously demonstrated for other invasive species, both plant and animal, invasive species are unlikely to affect just a single ecosystem component in isolation, instead having complex multi-trophic effects.

The impacts of alligator weed described in this study may therefore also have further flow-on effects on other unstudied ecosystem components such as fish and birds. Vegetation structure influences habitat availability for fish and birds, including refuge, nesting and food resources (Gorman and Karr 1978; Brown and Trosset 1989). In addition, invertebrates represent a key food source for both these vertebrate groups. Many of the bird species observed at Lake Rotokawau are at least partially insectivorous (Moon 2004). Both sedge species were frequently seen being utilised by a range of bird species including pukeko (*Porphyrio porphyrio melanotus*), Australasian bittern (*Botaurus poiciloptilus*), paradise shelducks (*Tadorna variegata*) and black swans (*Cygnus atratus*). *I. prolifer* shoots (with abundant seed heads) were also eaten by birds in large amounts. In contrast, fewer birds were observed utilising the more open and ephemeral alligator weed mats than the native sedges. Where vegetation type and management practices influence the abundance and/or composition of invertebrate prey, as has been demonstrated at Lake Rotokawau, this may be expected to lead to flow-on effects on bird communities (Buchanan, Grant et al. 2006). Other studies of introduced plants demonstrate that bird communities can be restructured by invasions. For instance, introduced plant species in North American prairies were associated with changes in bird communities, with some bird species negatively correlated with introduced vegetation while others responded positively (Wilson and Belcher 1989). These changes were attributed to changes in food supply, including invertebrates and seed sources, as well as altered vegetation structure and diversity, all factors altered by alligator weed invasion at Lake Rotokawau. Similarly, areas dominated by the invasive *Phragmites australis* or

Lythrum salicaria were not utilised by a number of North American marsh birds (Blossey 1999).

7.3 Ability to support native species

Exotic invaders such as alligator weed might be expected to displace native plants, and to provide a lower quality habitat for native fauna than that provided by native vegetation. The native species richness of plants, Coleoptera and Hemiptera was comparable between alligator weed and native dominated vegetation. However, in all these taxa, both plant and invertebrate, abundance or cover of natives was substantially reduced in alligator weed dominated areas, in comparison to at least one of the two native sedges. Thus, native taxa were able to maintain a presence within alligator weed dominated areas, but their numbers were much reduced. Their reduced abundance suggests that many species may be vulnerable to stochastic events. In the long-term, the system may therefore be on a trajectory towards increasing exotic dominance across a range of taxa, as native species in low abundance are periodically lost altogether from the area. Furthermore, as with invertebrate communities on gorse (*Ulex europaeus*) compared with native Kanuka (*Kunzea ericoides*) stands (Harris, Toft et al. 2004), the *composition* of native invertebrates differed from that on native vegetation. This suggests that a subset of native invertebrates may be better than others at utilising exotic plants as habitat. Depending on conservation goals, simply being able to retain generalist native invertebrates on exotic vegetation may not be sufficient.

This study was conducted in a highly modified system; the lake is surrounded by pasture, with high nutrient levels in the water, and lake edge vegetation has been invaded by several other introduced plant species, although to a lesser extent than by alligator weed. The dominance of invertebrate habitat generalists across all vegetation types studied may reflect a loss of specialist invertebrate species as a result of land-use changes, reflecting the role of the wider landscape matrix in addition to local plant cover in determining invertebrate community composition. Thus we might expect that exotic species such as alligator weed may be used as habitat by many native species when found in a matrix of other suitable native vegetation, but that as the dominance of exotic vegetation increases across the landscape, the ability of native species to utilise this habitat will decrease. As Parker, Simberloff et al (1999) note, the total impact of an invader will be strongly influenced by both its range and its abundance within that range.

Studying the impact of alligator weed in an otherwise less modified system than that studied here would provide a more detailed picture of its effects on native species. This may be logistically difficult however, as the imperative for actively controlling alligator weed rather than allowing invasion to continue for study purposes is stronger in more pristine environments. Microcosm experiments could provide some useful information, particularly in regards to competitive interactions with native plant species, while avoiding the problems associated with leaving alligator weed uncontrolled. However, microcosms are less likely to be able to provide realistic information regarding more complex ecosystem interactions such as nutrient cycling and invertebrate communities.

Native plant cover decreased with increasing alligator weed cover, implying that the lower the level at which alligator weed cover can be maintained, the better for native plant species. However, there is no evidence that, once already at reduced levels, native plant species are able to utilise reductions in alligator weed cover, at least in the short-term. Other weedy exotics instead appear to be the main beneficiaries of seasonal reductions in alligator weed cover. This therefore highlights the importance of ecosystem-wide management in efforts to increase native plant cover, rather than single species pest control.

7.4 Similarity to original vegetation

Alligator weed's role within the ecosystem was more similar to *I. prolifer* than *S. tabernaemontani* in a number of measures. Alligator weed and *I. prolifer* decomposed more quickly than did *S. tabernaemontani*. They both also formed mats with abundant associated decomposing organic material, whereas *S. tabernaemontani* was much more open in structure, with less associated organic material and higher dissolved oxygen levels in the surrounding water. These differences led to beetle communities on alligator weed and *I. prolifer* that were more dominated by decomposers than the beetle communities on *S. tabernaemontani*. The composition of other aspects of the invertebrate community was also more similar between alligator weed and *I. prolifer* than *S. tabernaemontani*. For instance, spider communities were heavily dominated by Tetragnathid spiders on *S. tabernaemontani,* but nursery-web spiders dominated on the other two vegetation types. This pattern of effects is attributed to alligator weed's greater degree of chemical and architectural similarity to *I. prolifer* compared with *S. tabernaemontani*.

Relatedness of introduced species to native taxa has long been suggested as potentially influencing exotics' chances of successfully establishing (Mitchell, Agrawal et al. 2006). In line with this, introduced species with native congenerics have been found more likely to become naturalised in New Zealand than those without closely related elements in the native flora, presumably due to similar environmental adaptations (Duncan and Williams 2002). However, for exotic species which do establish, *impacts* appear to often be greater the greater the contrast between the invader and the dominant native vegetation.

Thus, we might expect that exotic plant species' impacts in an invaded ecosystem will in part be mediated by the degree of taxonomic, architectural and/or chemical similarity between the invading and pre-existing vegetation. Such a pattern has been documented for exotic grasses in California, with highly invasive species being, on average, significantly less closely related to native grasses than were non-invasive exotics (Strauss, Webb et al. 2006). The trend of increasing impact with increasing difference between native and invading vegetation may be useful in predicting the degree of impact of potential invaders in novel ecosystems. Across a range of taxa and ecosystem functions we might expect that an invasive species will have more pronounced impacts in ecosystems where it differs greatly from pre-existing vegetation in terms of chemistry and architecture than in systems where it shares many characteristics with the native vegetation. A similar trend is evident for invasive vertebrate species. Introduced mammals, for instance, have had particularly devastating effects on both native plants and animals on oceanic islands such as New Zealand, where mammals are essentially absent from the native fauna (Veblen and Stewart 1982; Atkinson 2006).

It would be interesting to investigate the effects of alligator weed invasion in native systems dominated by different vegetation types, particularly herbaceous species which are more similar to alligator weed than the sedge-dominated vegetation to which it was compared in this study. I would predict that alligator weed might have less impact on invertebrate communities associated with native herbaceous species than detected in this study of native sedges, although factors such as biomass and nutrient cycling regimes of native vegetation are also likely to play a pivotal role in influencing potential differences.

7.5 Role of biological control agent

In addition to invasive weed species themselves, their deliberately introduced biological control agents also represent exotic organisms with potential ecological effects in novel environments. Modern biological control programmes focus on selecting highly specific invertebrates and micro-organisms, including stringent host specificity testing during pre-release assessments in order to avoid or minimise damage to non-target host plants (Sheppard, Shaw et al. 2006). Since rigorous host specificity testing has become standard practice, few released agents have been found attacking non-target species, and those which have generally had minor, transitory or predictable effects (Fowler, Syrett et al. 2000).

However, in addition to non-target feeding, more complex, indirect effects of introduced biocontrol agents are gaining increasing recognition. While effects of introduced biocontrol agents on other *species* have received some attention, little is known about the potential of biocontrol to affect ecosystem processes such as nutrient cycling or fire frequency (Denslow and D'Antonio 2005).

Many of alligator weed’s impacts, particularly on nutrient cycling and beetle community composition, were influenced by the presence of its biocontrol agent, the alligator weed flea beetle. As biocontrol agents generally coexist indefinitely with their target weed, rather than eradicating the weed altogether, similar changes in nutrient and biomass cycling may occur in many other undocumented cases. This research also indicates that, as with impacts of weeds on their own, effects of biocontrol agents detected for one aspect of an ecosystem may represent only part of a ripple effect across various ecosystem components.

The combined effects of alligator weed, which decomposes rapidly, and its control agent, do not necessarily represent the kind of 'invasional meltdown' which may occur with the presence of multiple unwanted exotics (Simberloff and Von Holle 1999). Evidence such as the inverse relationship between native plant and alligator weed cover (Chapter 6), and the potentially extensive coverage attained by uncontrolled alligator weed suggests that alligator weed's impacts on its own are likely to be much more devastating to native biodiversity than those of controlled alligator weed in combination with the flea beetle.

However, it does add to a growing body of research that suggests that while ecosystem effects of biocontrol introductions are likely to be complex and difficult to predict, they may also be of sufficient magnitude and reach within an ecosystem to warrant consideration in the agent selection process. Louda and Stiling (2004) note that ineffective releases do not help the pest problem, yet potentially carry multiple ecological risks. Current biological control agent selection protocols emphasise testing host specificity over potential effectiveness (Schooler, Clech-Goods et al. 2006). In finding the parasitoid *Sphecophaga vesparum vesparum* to be ineffective at controlling *Vespula* wasps in New Zealand, Beggs, Rees et al (2008) suggested that pre-release assessment of agents' likely impacts on the target host would result in more effective agents being introduced. This would improve the balance of ecological benefits compared with risks arising from biological control introductions, without the need to predict, *a priori*, potential ecological effects, a daunting task which would cripple most biocontrol programmes (Fowler, Syrett et al. 2000). Such consideration of potential ecological risks from biocontrol may be particularly important for control programmes within natural, rather than production ecosystems, as species and ecosystem functions within agricultural and other productive ecosystems are frequently already highly modified and dominated by exotic species.

7.6 Conservation management at the study lakes

Alligator weed is a key issue for the management of Lake Rotokawau. This weed covers approximately one quarter of the elevation zone in which it is found, and affects diverse aspects of ecosystem function and composition. However, in the absence of additional successful biocontrol agents or herbicide treatments emerging from continuing research programmes both in New Zealand and overseas, greater control of alligator weed than that already achieved at Lake Rotokawau continues to be difficult (Chapter 1).

Over and above the effects of this particular weed species though, the eutrophic nutrient status of Lake Rotokawau (Anon 2006) is likely to dominate its trajectory. High nutrient levels are likely to exacerbate problems with alligator weed and other weeds and algae. The lake experiences substantial algal blooms in summer. Furthermore, this study has documented a weed replacement effect occurring, at least in the short-term; seasonal reductions in alligator weed are off-set by increases in other weed species. As previously noted, ecosystem based management, rather than simply the control of alligator weed alone, would be required for native species to benefit substantially. Surrounded by farmland, management of the wider catchment to reduce the lake’s nutrient levels represents a vital step in improving the lake’s health and the competitiveness of native vegetation. This applies equally to Lake Waiporohita, which has been classified as hypertrophic by the Northland Regional

Council (Anon 2006). However, alligator weed is present in only a small area of Lake Waiporohita. Therefore in addition to wider landscape scale issues, intensive, preemptive control leading to eradication of alligator weed at this site is also important and feasible in a way which it is not currently at Lake Rotokawau.

8 APPENDICES

8.1 Appendix 1: Invertebrate orders collected from litter bags.

Table 11. Invertebrate orders and higher taxa collected from litter bags, Lake Rotokawau. Invertebrates are given by litter type, all cover types and sampling months combined.

Litter type		
Alligator weed	*S. tabernaemontani*	*I. prolifer*
Acarina Araneae Coleoptera Collembola Diptera Gastropoda Hemiptera Hymenoptera Isopoda Lepidoptera Pseudoscorpionida	Araneae Coleoptera Collembola Gastropoda Hemiptera Pseudoscorpionida Tricladida	Acarina Araneae Blattodea Coleoptera Collembola Diptera Gastropoda Hemiptera Hymenoptera Isopoda Orthoptera Pseudoscorpionida Tricladida

8.2 Appendix 2: Coleoptera species collected from emergence traps

Table 12. Coleoptera species and higher taxa collected from alligator weed emergence traps, all sampling months combined. Functional groups are based on adult behaviour unless otherwise stated.

Family	Species	Provenance	Functional group	Reference
Anthicidae	*Anthicus ?kreusleri*	Exotic	Scavenger	(Werner and Chandler 1995)
Brentidae	*Exapion ulicis*	Exotic	Phytophage	(Kuschel 2003)
Carabidae	*Notagonum* sp.	Unknown	Predator	(Larochelle and Lariviere 2001)
Chrysomelidae	*Agasicles hygrophila*	Exotic	Phytophage	(Klimaszewski and Watt 1997)
Coccinellidae	*Coccinella undecimpunctata*	Exotic	Predator	(Klimaszewski and Watt 1997)
Coccinellidae	*Scymnus loewi*	Exotic	Predator	(Klimaszewski and Watt 1997)
Coccinellidae	Unidentified sp.	Unknown	Predator	(Klimaszewski and Watt 1997)
Corylophidae	*Holopsis* sp.	Native	Fungivore	(Klimaszewski and Watt 1997)
Corylophidae	*Sericoderus* sp.	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Curculionidae	*Microcryptorhynchus sp.*	Native	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Microtribus huttoni*	Native	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Naupactus leucoloma*	Exotic	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Phloeophagosoma pedatum*	Native	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Sericotrogus subaenescens*	Native	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Sitona lepidus*	Exotic	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Steriphus ascitus*	Native	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Steriphus diversipes lineatus*	Native	Phytophage	(Klimaszewski and Watt 1997)

Curculionidae	Unidentified sp. (Cossoninae)	Unknown	Phytophage	(Klimaszewski and Watt 1997)
Elateridae	*Conoderus exsul*	Exotic	Phytophage	(Winks, Fowler et al. 2004)
Elateridae	*Conoderus posticus*	Exotic	Phytophage	(Winks, Fowler et al. 2004)
Elateridae	*Ochosternus zealandicus*	Native	Unknown	(Leschen, Lawrence et al. 2003)
Hydrophilidae	*Enochrus maculiceps*	Exotic	Scavenger	(Klimaszewski and Watt 1997)
Latridiidae	*Melanophthalma* sp. 1	Native	Fungivore	(Klimaszewski and Watt 1997)
Latridiidae	*Cortinicaria* sp.	Unknown	Fungivore	(Klimaszewski and Watt 1997)
Mycetophagidae	*Litargus vestitus*	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Scirtidae	Unidentified spp.	Native	Detritivore (as juvenile)	(Dugdale and Hutcheson 1997)
Silvanidae	*Cryptamorpha desjardinsi*	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Staphylinidae	Unidentified sp. (Pselaphinae)	Unknown	Predator	(Klimaszewski and Watt 1997)

Table 13. Coleoptera species and higher taxa collected from *S. tabernaemontani* emergence traps, all months combined. Functional groups are based on adult behaviour unless otherwise stated.

Family	Species	Provenance	Functional group	Reference
Anthicidae	*Anthicus ?kreusleri*	Exotic	Scavenger	(Werner and Chandler 1995)
Anthribidae	*Sharpius brouni*	Native	Fungivore	(Holloway 1984)
Brentidae	*Exapion ulicis*	Exotic	Phytophage	(Kuschel 2003)
Carabidae	*Hypharpax australis*	Exotic	Predator	(Larochelle and Lariviere 2001)
Coccinellidae	*Coccinella undecimpunctata*	Exotic	Predator	(Klimaszewski and Watt 1997)
Coccinellidae	*Scymnus loewi*	Exotic	Predator	(Klimaszewski and Watt 1997)
Coccinellidae	Unidentified sp.	Unknown	Predator	(Klimaszewski and Watt 1997)
Corylophidae	*Sericoderus* sp.	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Curculionidae	*Eucossonus* sp.	Native	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Novitas* sp.	Native	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Sitona lepidus*	Exotic	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Steriphus ascitus*	Native	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Storeus albosignatus*	Exotic	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	Unidentified sp. (Cossoninae)	Unknown	Phytophage	(Klimaszewski and Watt 1997)
Hydrophilidae	*Cercyon* sp.	Exotic	Scavenger	(Klimaszewski and Watt 1997)
Latridiidae	*Corticaria* sp.	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Latridiidae	*Melanophthalma* sp.1	Native	Fungivore	(Klimaszewski and Watt 1997)
Latridiidae	*Melanophthalma* sp.2	Native	Fungivore	(Klimaszewski and Watt 1997)

Latridiidae	*Aridius* sp.	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Latridiidae	*Cortinicaria* sp.	Unknown	Fungivore	(Klimaszewski and Watt 1997)
Scirtidae	Unidentified spp.	Native	Detritivore (as juvenile)	(Dugdale and Hutcheson 1997)
Silvanidae	*Cryptamorpha desjardinsi*	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Staphylinidae	Unidentified species (Aleocharinae: Gyrophaenina)	Native	Fungivore	(Klimaszewski and Watt 1997)

Table 14. Coleoptera species and higher taxa collected from *I. prolifer* emergence traps, all months combined. Functional groups are based on adult behaviour unless otherwise stated.

Family	Species	Provenance	Functional group	Reference
Anthicidae	*Anthicus ?kreusleri*	Exotic	Scavenger	(Werner and Chandler 1995)
Anthribidae	*Micranthribus atomus*	Native	Fungivore	(Holloway 1984)
Anthribidae	*Sharpius brouni*	Native	Fungivore	(Holloway 1984)
Brentidae	*Exapion ulicis*	Exotic	Phytophage	(Kuschel 2003)
Carabidae	*Euthenarus puncticollis*	Native	Phytophage	(Larochelle and Lariviere 2001)
Carabidae	*Hypharpax australis*	Exotic	Predator	(Larochelle and Lariviere 2001)
Carabidae	*Notagonum* sp.	Unknown	Predator	(Larochelle and Lariviere 2001)
Coccinellidae	*Diomus* sp.	Exotic	Predator	(Klimaszewski and Watt 1997)
Coccinellidae	Unidentified sp.	Unknown	Predator	(Klimaszewski and Watt 1997)
Corylophidae	*Clypastraea pulchella*	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Corylophidae	*Holopsis* sp.	Native	Fungivore	(Klimaszewski and Watt 1997)
Corylophidae	*Sericoderus* sp.	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Curculionidae	*Microtribus huttoni*	Native	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Phloeophagosoma pedatum*	Native	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Sericotrogus subaenescens*	Native	Phytophage	(Klimaszewski and Watt 1997)
Curculionidae	*Sitona lepidus*	Exotic	Phytophage	(Klimaszewski and Watt 1997)
Dermestidae	*Hexanodes vulgata*	Native	Phytophage	(Klimaszewski and Watt 1997)
Elateridae	*Agrypnus variabilis*	Exotic	Phytophage	(Lawrence and Britton 1991)

Elateridae	*Conoderus exsul*	Exotic	Phytophage	(Winks, Fowler et al. 2004)
Latridiidae	*Melanophthalma* sp. 1	Native	Fungivore	(Klimaszewski and Watt 1997)
Latridiidae	Unidentified sp.	Unknown	Fungivore	(Klimaszewski and Watt 1997)
Latridiidae	*Cortinicaria* sp.	Unknown	Fungivore	(Klimaszewski and Watt 1997)
Salpingidae	*Salpingus* sp.	Native	Fungivore	(Klimaszewski and Watt 1997)
Scirtidae	Unidentified spp.	Native	Detritivore (as juvenile)	(Dugdale and Hutcheson 1997)
Silvanidae	*Cryptamorpha desjardinsi*	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Staphylinidae	*Pselaphophus atriventris*	Exotic	Predator	(Klimaszewski and Watt 1997)

8.3 Appendix 3: Coleoptera collected from litter bags beneath different vegetation cover types

Table 15. Coleoptera species and higher taxa collected from litter bags beneath alligator weed cover, all litter types and sampling dates combined. Functional groups are based on adult feeding behaviour unless otherwise stated.

Family	Species	Provenance	Functional group	Reference
Chrysomelidae	*Agasicles hygrophila*	Exotic	Phytophage	(Klimaszewski and Watt 1997)
Corylophidae	*Sericoderus* sp.	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Corylophidae	*Holopsis* sp.	Native	Fungivore	(Klimaszewski and Watt 1997)
Dytiscidae	*Liodessus* sp.	Unknown	Predator	(Klimaszewski and Watt 1997)
Hydrophilidae	*Paracymus pygmaeus*	Introduced	Saprophage	(Klimaszewski and Watt 1997; Hansen 2000)
Hydrophilidae	*Enochrus* sp.	Exotic	Saprophage	(Klimaszewski and Watt 1997)
Latridiidae	*Melanophthalma* sp.	Native	Fungivore	(Klimaszewski and Watt 1997)
Ptiliidae	Unidentified sp.	Unknown	Fungivore	(Klimaszewski and Watt 1997)
Scirtidae	Unidentified sp.	Native	Detritivore (as juvenile)	(Dugdale and Hutcheson 1997)

Table 16. Coleoptera species and higher taxa collected from litter bags beneath *S. tabernaemontani*, both litter types and all sampling dates combined. Functional groups are based on adult feeding behaviour unless otherwise stated.

Family	Species	Provenance	Functional group	Reference
Carabidae	*Notagonum submetallicum*	Native	Predator	(Larochelle and Lariviere 2001)
Coccinellidae	Unidentified sp.	Unknown	Predator	(Klimaszewski and Watt 1997)
Corylophidae	*Sericoderus* sp.	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Hydrophilidae	*Paracymus pygmaeus*	Introduced	Saprophage	(Klimaszewski and Watt 1997; Hansen 2000)
Hydrophilidae	*Enochrus* sp.	Exotic	Saprophage	(Klimaszewski and Watt 1997)

Table 17. Coleoptera species and higher taxa collected from litter bags beneath *I. prolifer* vegetation, both litter types and all sampling dates combined. Functional groups are based on adult feeding behaviour unless otherwise stated.

Family	Species	Provenance	Functional group	Reference
Corylophidae	*Sericoderus* sp.	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Corylophidae	*Holopsis* sp.	Native	Fungivore	(Klimaszewski and Watt 1997)
Hydrophilidae	*Enochrus* sp.	Exotic	Saprophage	(Klimaszewski and Watt 1997)
Latridiidae	*Melanophthalma* sp.	Native	Fungivore	(Klimaszewski and Watt 1997)
Silvanidae	*Cryptamorpha desjardinsi*	Exotic	Fungivore	(Klimaszewski and Watt 1997)
Staphylinidae	*Pselaphophus atriventris*	Exotic	Predator	(Klimaszewski and Watt 1997)

8.4 Appendix 4: Invertebrate orders and higher taxa collected from emergence traps and excised vegetation.

Table 18. Invertebrate orders and higher taxa collected from alligator weed, all sampling months combined.

Sampling method	
Emergence traps	Excised vegetation
Acarina	Acarina
Araneae	Araneae
Coleoptera	Coleoptera
Collembola	Collembola
Diptera	Diptera
Gastropoda	Gastropoda
Hemiptera	Hemiptera
Hymenoptera	Hirudinidea
Isopoda	Hymenoptera
Lepidoptera	Isopoda
Mecoptera	Lepidoptera
Megaloptera	Odonata
Orthoptera	Oligochaeta
Pseudoscorpionida	Orthoptera
Tricoptera	Pseudoscorpionida
	Tricladida
	Tricoptera

Table 19. Invertebrate orders and higher taxa collected from *S. tabernaemontani* at Lake Rotokawau, all sampling months combined.

Sampling method	
Emergence traps	Excised vegetation
Acarina	Acarina
Araneae	Araneae
Coleoptera	Coleoptera
Collembola	Collembola
Diptera	Diptera
Gastropoda	Gastropoda
Hemiptera	Hemiptera
Hymenoptera	Hirudinidea
Isopoda	Hymenoptera
Lepidoptera	Lepidoptera
Mecoptera	Mecoptera
Orthoptera	Neuroptera
Pseudoscorpionida	Pseudoscorpionida
Psocoptera	Psocoptera
Tricoptera	Tricladida
	Tricoptera

Table 20. Invertebrate orders and higher taxa collected from *I. prolifer* at Lake Rotokawau, all sampling months combined.

Sampling method	
Emergence traps	Excised vegetation
Acarina	Acarina
Amphipoda	Araneae
Araneae	Coleoptera
Coleoptera	Collembola
Collembola	Diptera
Diptera	Gastropoda
Gastropoda	Hemiptera
Hemiptera	Hirudinidea
Hymenoptera	Hymenoptera
Isopoda	Isopoda
Lepidoptera	Lepidoptera
Mecoptera	Odonata
Megaloptera	Oligochaeta
Neuroptera	Pseudoscorpionida
Orthoptera	Psocoptera
Plecoptera	
Pseudoscorpionida	

Table 21. Invertebrate orders and higher taxa collected from *S. tabernaemontani* at Lake Waiporohita, all sampling months combined.

Emergence traps	Excised vegetation
N/A	Acarina Araneae Coleoptera Collembola Diptera Gastropoda Hemiptera Hymenoptera Lepidoptera Odonata Psocoptera Tricoptera

Table 22. Invertebrate orders and higher taxa collected from *I. prolifer* at the Vineyard Lake, all sampling months combined.

Emergence traps	Excised vegetation
N/A	Acarina Araneae Coleoptera Collembola Diptera Gastropoda Hemiptera Hymenoptera Isopoda Odonata Orthoptera Psocoptera

8.5 Appendix 5: Hemiptera species collected from excised vegetation

Table 23. Hemiptera species and higher taxa collected from excised alligator weed vegetation, Lake Rotokawau, all sampling dates combined.

Family	Species	Provenance	Functional group	Reference
APHIDIDAE	*Rhopalosiphum padi*	Exotic	Phytophage (sap sucker)	(Chinery 1985)
HYDROMETRIDAE	*Hydrometra strigosa*	Native	Predator	(Lariviere and Larochelle 2004)
LYGAEIDAE	*Nysius huttoni*	Native	Phytophage (sap sucker and seed feeder)	(Lariviere and Larochelle 2004)
MIRIDAE	Unidentified sp.	Unknown	Unknown	
PENTATOMIDAE	*Cermatulus nasalis nasalis*	Native	Predator	(Lariviere and Larochelle 2004)
PENTATOMIDAE	*Dictyotus caenosus*	Exotic	Predator	(Lariviere and Larochelle 2004)
PENTATOMIDAE	*Oechalia schellenbergii*	Native	Predator	(Lariviere and Larochelle 2004)
RHYPAROCHROMIDAE	Unidentified sp.	Unknown	Phytophage (seed feeding)	(Lariviere and Larochelle 2004)
SALDIDAE	Unidentified sp.	Unknown	Predator	(Lariviere and Larochelle 2004)
VELIIDAE	*Microvelia* sp.	Native	Predator	(Lariviere and Larochelle 2004)

Table 24. Hemiptera species and higher taxa collected from excised *S. tabernaemontani* vegetation, Lake Rotokawau, all sampling dates combined.

Family	Species	Provenance	Functional group	Reference
APHIDIDAE	*Rhopalosiphum padi*	Exotic	Phytophage (sap sucker)	(Chinery 1985)
DELPHACIDAE	Unidentified sp.	Unknown	Phytophage	(Lariviere and Larochelle 2004)
HYDROMETRIDAE	*Hydrometra strigosa*	Native	Predator	(Lariviere and Larochelle 2004)
MIRIDAE	Unidentified sp.	Unknown	Unknown	
PENTATOMIDAE	*Dictyotus caenosus*	Exotic	Phytophage	(Lariviere and Larochelle 2004)
PSEUDOCOCCIDAE	*Balanococcus* sp.	Native	Phytophage (sap sucker)	(Cox 1987)
PSEUDOCOCCIDAE	*Pseudococcus longispinus*	Exotic	Phytophage (sap sucker)	(Cox 1987)
VELIIDAE	*Microvelia* sp.	Native	Predator	(Lariviere and Larochelle 2004)

Table 25. Hemiptera species and higher taxa collected from excised *I. prolifer* vegetation, Lake Rotokawau, all sampling dates combined.

Family	Species	Provenance	Functional group	Reference
CERATOCOMBIDAE	*Ceratocombus* sp.	Native	Predator	(Lariviere and Larochelle 2004)
CYMIDAE	*Cymus novaezelandiae*	Native	Phytophage (seed feeding)	(Lariviere and Larochelle 2004)
DELPHACIDAE	Unidentified sp.	Unknown	Phytophage	(Lariviere and Larochelle 2004)
HYDROMETRIDAE	*Hydrometra strigosa*	Native	Predator	(Lariviere and Larochelle 2004)
MIRIDAE	Unidentified sp.	Unknown	Unknown	
PSEUDOCOCCIDAE	*Balanococcus* sp.	Native	Phytophage (sap sucker)	(Cox 1987)
PSEUDOCOCCIDAE	*Pseudococcus longispinus*	Exotic	Phytophage (sap sucker)	(Cox 1987)
RHYPAROCHROMIDAE	*Remaudiereana inornata*	Exotic	Phytophage (seed feeding)	(Lariviere and Larochelle 2004)
RHYPAROCHROMIDAE	Unidentified sp.	Unknown	Phytophage (seed feeding)	(Lariviere and Larochelle 2004)
VELIIDAE	*Microvelia* sp.	Native	Predator	(Lariviere and Larochelle 2004)

Table 26. Hemiptera species and higher taxa collected from excised *S. tabernaemontani* vegetation, Lake Waiporohita, all sampling dates combined.

Family	Species	Provenance	Functional group	Reference
APHIDIDAE	*Rhopalosiphum padi*	Exotic	Phytophage (sap sucker)	(Chinery 1985)
HYDROMETRIDAE	*Hydrometra strigosa*	Native	Predator	(Lariviere and Larochelle 2004)
LYGAEIDAE	*Nysius huttoni*	Native	Phytophage (sap sucker and seed feeder)	(Lariviere and Larochelle 2004)
MIRIDAE	Unidentified sp.	Unknown	Unknown	
PSEUDOCOCCIDAE	*Balanococcus* sp.	Native	Phytophage (sap sucker)	(Cox 1987)
PSEUDOCOCCIDAE	*Pseudococcus longispinus*	Exotic	Phytophage (sap sucker)	(Cox 1987)

Table 27. Hemiptera species and higher taxa collected from excised *I. prolifer* vegetation, Vineyard Lake, all sampling dates combined.

Family	Species	Provenance	Functional group	Reference
APHIDIDAE	*Rhopalosiphum padi*	Exotic	Phytophage (sap sucker)	(Chinery 1985)
CYMIDAE	*Cymus novaezelandiae*	Native	Phytophage (seed feeding)	(Lariviere and Larochelle 2004)
HYDROMETRIDAE	*Hydrometra strigosa*	Native	Predator	(Lariviere and Larochelle 2004)
MIRIDAE	Unidentified sp.	Unknown	Unknown	
PSEUDOCOCCIDAE	*Balanococcus* sp.	Native	Phytophage (sap sucker)	(Cox 1987)
PSEUDOCOCCIDAE	*Pseudococcus longispinus*	Exotic	Phytophage (sap sucker)	(Cox 1987)
RHYPAROCHROMIDAE	*Targarema stali*	Native	Phytophage (seed feeding)	(Lariviere and Larochelle 2004)
VELIIDAE	*Microvelia* sp.	Native	Predator	(Lariviere and Larochelle 2004)

8.6 Appendix 6: Vascular plant species at Lake Rotokawau

Table 28. Vascular plant species observed within 25 m^2 plots at Lake Rotokawau, all sampling dates combined.

Native Species	Exotic Species
Adiantum cunninghamii	*Acacia longifolia*
Adiantum hispidulum	*Ageratina adenophora*
Baumea juncea	*Alternanthera philoxeroides*
Baumea teretifolia	*Aster subulatus*
Blechnum minus	*Azolla pinnata*
Coprosma propinqua	*Bidens frondosa*
Eleocharis acuta	*Carex scoparia*
Eleocharis sphacelata	*Cortaderia selloana*
Empodisma minus	*Cotula coronopifolia*
Gleichenia dicarpa	*Cyperus eragrostis*
Glossostigma elatinoides	*Juncus microcephalus.*
Histiopteris incisa	*Lotus pedunculatus*
Isolepis prolifer	*Ludwigia peploides* subsp. *montevidensis*
Leptospermum scoparium	*Paspalum distichum*
Leucopogon fasiculatus	*Paspalum urvillei*
Lobelia anceps	*Polygonum persicaria*
Muelenbeckia complexa	*Ranunculus* sp.
Myriophyllum propinquum	*Solanum mauritianum*
Phormium tenax	*Solanum* sp.
Pteridium esculentum	*Spirodela punctata*
Schoenoplectus tabernaemontani	*Ulex europeaus*
Schoenus brevifolius	Unidentified species (Asteraceae: Tribe Lactuceae)
Typha orientalis	

9 REFERENCES

Aiken, M. and F. A. Coyle (2000). "Habitat distribution, life history and behaviour of *Tetragnatha* spider species in the Great Smoky Mountains National Park." The Journal of Arachnology **28**(97-106).

Alford, L. W. (1952). "Alligator Weed: A good cattle feed." Chemurgic Digest **11**(9): 10-12.

Allison, S. D. and P. M. Vitousek (2004). "Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i." Oecologia **141**: 612-619.

Anderson, M. J. (2005). PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Auckland, Department of Statistics, University of Auckland.

Anon (1989). "'Spring eczema' link with eaten weed." Dairy Exporter **August 1989**: 37.

Anon (2002a). Auckland Regional Pest Management Strategy 2002-2007. Auckland, Auckland Regional Council.

Anon (2002b). Northland Regional Council State of the Environment Report, Northland Regional Council.

Anon (2003). Weed Management Guide: Alligator Weed - *Alternanthera philoxderoides*, Cooperative Research Centre for Australian Weed Management.

Anon. (2005). Retrieved 14 April, 2005, from http://www.biosecurity.govt.nz/pests-diseases/registers-lists/unwanted-organisms/index.htm.

Anon (2006). Annual Monitoring Report 2005-2006, Northland Regional Council.

Arsuffi, T. L. and K. Suberkropp (1984). "Leaf processing capabilities of aquatic hyphomycetes: Interspecific differences and influence on shredder feeding preferences." Oikos **42**(2): 144-154.

Ashton, P. J. and D. S. Mitchell (1989). Aquatic Plants: Patterns and Modes of Invasion, Attributes of Invading Species and Assessment of Control Programmes. Biological Invasions: A Global Perspective. J. M. Drake and H. A. Mooney, John Wiley and Sons Ltd**:** 111-154.

Atkinson, I. A. E. (2006). Introduced mammals in a new environment. Biological Invasions in New Zealand. R. B. Allen and W. G. Lee. Berlin, Springer-Verlag.

Atkinson, I. A. E. and E. K. Cameron (1993). "Human influence on the terrestrial biota and biotic communities of New Zealand." Trends in Ecology & Evolution **8**: 447-451.

Baerlocher, M. O. (2005). Total Protein. Methods to Study Litter Decomposition: A Practical Guide. M. A. S. Graca, F. Barlocher and M. O. Gessner. Dordrecht, Springer**:** 61-68.

Baker, H. G. (1965). Characteristics and Modes of Origin of Weeds. The Genetics of Colonizing Species. H. G. Baker and G. Ledyard Stebbins. New york, Academic Press**:** 147-172.

Balagtas-Burow, G. E., J. V. Moroney, et al. (1993). "Growth and osmotic adjustment of cultured suspension cells from *Alternanthera philoxeroides* (Mart.) Griseb after an abrupt increase in salinity." Journal of Experimental Botany **44**(260): 673-679.

Balogh, L., Z. Botta-Dukat, et al. (2003). What kind of plants are invasive in Hungary? Plant Invasions: Ecological Threats and Management Solutions. L. E. Child, J. H. Brock, G. Brunduet al. Leiden, The Netherlands, Backhuys Publishers**:** 131-146.

Barratt, B. I. P., G. M. Barker, et al. (1996). "*Sitona lepidus* Gyllenhal (Coleoptera: Curculionidae), a potential clover pest new to New Zealand." New Zealand Entomologist **19**(1): 23-30.

Bastow, J. L., E. L. Preisser, et al. (2008). *Holcus lanatus* invasion slows decomposition through its interaction with a macroinvertebrate detritivore, *Porcellio scaber*. Biological Invasions **10**: 191 - 199.

Battle, J. M. and T. B. Mihuc (2000). "Decomposition dynamics of aquatic macrophytes in the lower Atchafalaya, a large floodplain river." Hydrobiologia **418**: 123-136.

Beggs, J. R., J. S. Rees, et al. (2008). "Evaluating the impact of a biological control parasitoid on invasive *Vespula* wasps in a natural forest ecosystem." Biological Control: doi:10.1016/jbiocontrol.2007.10.016.

Benayas, J. M. R., A. Lopez-Pintor, et al. (2002). "Early establishment of planted *Retama sphaerocarpa* seedlings under different levels of light, water and weed competition." Plant Ecology **159**(2): 201-209.

Berg, B. and R. Laskowski (2006a). "Decomposers: Soil Microorganisms and Animals " Advances in Ecological Research **38**: 73-100.

Berg, B. and R. Laskowski (2006b). "Litter Fall." Advances in Ecological Research **38**: 19-71.

Berg, B. and C. McClaugherty (2003). Plant litter : decomposition, humus formation, carbon sequestration. Berlin, Springer.

Blakemore, L. C. S., P.L. Searle, et al. (1987). Methods for Chemical Analysis of Soils. New Zealand Soil Bureau Scientific Report 80**:** 103p.

Blossey, B. (1999). "Before, during and after: the need for long-term monitoring in invasive plant species management." Biological Invasions **1**: 301-311.

Boulton, A. J. and P. I. Boon (1991). "A Review of Methodology Used to Measure Leaf Litter Decomposition in Lotic Environments: Time to Turn Over an Old Leaf." Australian Journal of Marine and Freshwater Research **42**: 1-43.

Bourke, C. A. and D. Rayward (2003). "Photosensitisation in dairy cattle grazing alligator weed (*Alternanthera philoxeroides*) infested pastures." Australian Veterinary Journal **81**: 361-362.

Bowmer, K. H. and P. L. Eberbach (1993). "Uptake and translocation of ^{14}C-glyphosate in *Alternanthera philoxeroides* (Mart.) Griseb. (alligator weed) II. Effect of plant size and photoperiod." Weed Research **33**: 59-67.

Bowmer, K. H., P. L. Eberbach, et al. (1993). "Uptake and translocation of ^{14}C-glyphosate in *Alternanthera philoxeroides* (Mart.) Griseb. (alligator weed) I. Rhizome concentrations required for inhibition." Weed Research **33**: 53-57.

Bowmer, K. H., G. McCorkelle, et al. (1991). Final Report 31 Jan 1991. National Water research Program Alligator weed Control Project 86/85, Australian Water Research Council and Land and Water Resources Research and Development Corporation.

Bowmer, K. H., G. McCorkelle, et al. (1989). Progress in the Chemical Control of Alligatorweed. 5th Noxious Plants Conference, Northern Rivers College of Advanced Education.

Boylen, C. W., L. W. Eichler, et al. (1999). "Loss of native aquatic plant species in a community dominated by Eurasian watermilfoil." Hydrobiologia **415**: 207-211.

Braithwaite, R. W., W. M. Lonsdale, et al. (1989). "Alien Vegetation and Native Biota in Tropical Australia: the Impact of *Mimosa pigra*." Biological Conservation **48**(3): 189-210.

Brown, B. T. and M. W. Trosset (1989). "Nesting-habitat relationships of riparian birds along the Colorado river in Grand Canyon, Arizona." The Southwestern Naturalist **34**(2): 260-270.

Buchanan, G. M., M. C. Grant, et al. (2006). "The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management." Ibis **148**: 615-628.

Bureau of Economic Analysis. (2005, 29 July 2005). "Current Dollar and "Real" Gross Domestic Product." Retrieved 8 August, 2005, from http://www.bea.doc.gov/bea/dn/home/gdp.htm.

Burkhalter, A. P., L. M. Curtis, et al. (1972). Aquatic Weed Identification and Control Manual. Tallahassee, Florida, Bureau of Aquatic Plant Research and Control, Florida Department of Natural Resources**:** 41-42.

Byers, J. E. and E. G. Noonburg (2003). "Scale Dependent Effects of Biotic Resistance to Biological Invasion." Ecology **84**(6): 1428-1433.

Cabrera, N., A. J. Sosa, et al. (2005). "*Systena nitentula* (Coleoptera: Chrysomelidae), a flea beetle injurious to *Alternanthera philoxeroides* (Amaranthaceae): Rediscription, biology, and distribution." Annals of the Entomological Society of America **98**(5): 643-652.

Champion, P. D. and J. S. Clayton (2003). The evaluation and management of aquatic weeds in New Zealand. Plant Invasions: Ecological Threats and Management Solutions. L. E. Child, J. H. Brock, G. Brunduet al. Leiden, The Netherlands, Backhuys Publishers**:** 429-434.

Champion, P. D., R. Wells, et al. (2005). Northland Lakes Assessment 2004/5, NIWA Client Report: HAM2005-113, NRC05215 Northland Regional Council, NIWA**:** 265.

Cheeseman, T. F. (1906). Manual of the New Zealand Flora. Wellington, John Mackay, Government Printer.

Cheng, L. and S. Qiang (2006). "Influence of *Alternanthera philoxeroides* on the species composition and diversity of weed community in spring in Nanjing." Zhiwu Shengtai Xuebao. **30**(4): 585-592.

Chinery, M. (1985). A Field Guide to the Insects of Britain and Northern Europe. London, Collins.

Clark, W. R. (1969). Controlling Alligatorweed in Tulare County. California Weed Conference.

Clarke, K. R. and R. N. Gorley (2001). PRIMER v5: User Manual/Tutorial. Plymouth, PRIMER-E.

Clarke, K. R. and R. M. Warwick (2001). Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth, PRIMER-E.

Clewell, A., J. Rieger, et al. (2005, 19 January 2007). "Society for Ecological Restoration International: Guidelines for Developing and Managing Ecological Restoration Projects." from http://www.ser.org/content/guidelines_ecological_restoration.asp.

Clinch, J. J. and H. J. Keselman (1982). "Parametric alternatives to the analysis of variance." Journal of Educational Statistics **7**(3): 207-214.

Coffey, B. T. (1981). "Water Weeds." Protect **14**: 2-7.

Colautti, R. I., A. Ricciardi, et al. (2004). "Is invasion success explained by the enemy release hypothesis?" Ecology Letters **7**(8): 721-733.

Collier, K. J. and M. J. Winterbourn (1987). "Breakdown of Kamahi Leaves in Four South Westland New Zealand Streams." Mauri Ora **14**(33-42).

Cornelissen, J. H. C., N. Perez-Harguindeguy, et al. (1999). "Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents." New Phytologist **143**: 191-200.

Coulson, J. R. (1977). Biological Control of Alligatorweed, 1959-1972. A review and evaluation.Technical Bulletin No. 1547, United States Department of Agriculture.

Cox, J. M. (1987). Pseudococcidae (Insecta: Hemiptera). Fauna of New Zealand 11. Wellington, DSIR Science Information Publishing Centre.

Cripps, M. G., M. Schwarzlander, et al. (2006). "Biogeographical comparison of the arthropod herbivore communities associated with *Lepidium draba* in its native, expanded and introduced ranges." Journal of Biogeography **33**: 2107-2119.

Crisp, P. N., K. J. M. Dickinson, et al. (1998). "Does native invertebrate diversity reflect native plant diversity? A case study from New Zealand and implications for conservation." Biological Conservation **83**(2): 209-220.

D'Antonio, C. and P. M. Vitousek (1992). "Biological invasions by exotic grasses, the grass/fire cycle, and global change." Annual Review of Ecology and Systematics **23**: 63-87.

Daehler, C. C. (1998). "The taxonomic distribution of invasive angiosperm plants: Ecological insights and comparison to agricultural weeds." Biological Conservation **84**: 167-180.

Davies-Colley, R. J. and J. M. Quinn (1998). "Stream lighting in five regions of North Island, New Zealand: control by channel size and riparian vegetation." New Zealand Journal of Marine and Freshwater Research **32**: 591-605.

Davies, K. F., B. A. Melbourne, et al. (2001). "Effects of within- and between-patch processes on community dynamics in a fragmentation experiment." Ecology **82**(7): 1830-1846.

Davis, G. J., D. W. Stanley, et al. (1983). Biomass dynamics of *Alternanthera philoxeroides* in a swamp forest stream and floodplain. Symposium on Aquatic Macrophytes, University of Nijmegen.

Davis, M. A., J. P. Grime, et al. (2000). "Fluctuating resources in plant communities: a general theory of invasibility." Journal of Ecology **88**: 528-534.

de Winton, M. D. and J. S. Clayton (1996). "The impact of invasive submerged weed species on seed banks in lake sediments." Aquatic Botany **53**: 31-45.

Denslow, J. S. and C. M. D'Antonio (2005). "After biocontrol: Assessing indirect effects of insect releases." Biological Control **35**: 307-318.

Dewalt, S. J., J. S. Denslow, et al. (2004). "Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*." Ecology **85**(2): 471-483.

Dopson, S. R., P. J. de Lange, et al. (1999). The Conservation Requirements of New Zealand's Nationally Threatened Vascular Plants. Threatened Species Occasional Publication No. 13. Wellington, Department of Conservation.

Douglas, M. M. and R. A. O'Connor (2003). "Effects of the exotic macrophyte, para grass (*Urochloa mutica*), on benthic and epiphytic macroinvertebrates of a tropical floodplain." Freshwater Biology **48**(962-971).

Drenovsky, R. E. and K. M. Batten (2007). "Invasion by *Aegilops triuncialis* (barb goatgrass) slows carbon and nutrient cycling in a serpentine grassland." Biological Invasions **9**: 107-116.

Dugdale, J. and J. Hutcheson (1997). Invertebrate values of kanuka (*Kunzea ericoides*) stands, Gisborne Region. Science for Conservation: 55. Wellington, Department of Conservation.

Duncan, R. P. and P. A. Williams (2002). "Darwin's naturalization hypothesis challenged." Nature **417**: 608.

Ebbett, R. L. and J. Ogden (1998). "Comparative seedling growth of five endemic New Zealand podocarp species under different light regimes." New Zealand Journal of Botany **36**: 189-201.

Ebeling, S. K., I. Hensen, et al. (2008). "The invasive shrub *Buddleja davidii* performs better in its introduced range." Diversity & Distributions **14**(2).

Eberbach, P. L., K. H. Bowmer, et al. (1990). Effect of application droplet size and photoperiod on the absorption and translocation of ^{14}C-Glyphosate in terrestrial alligator weed. Nineth Australian Weeds Conference, Adelaide, The Crop Science Society of South Australia.

Ehrenfeld, J. G. (2003). "Effects of exotic plant invasions on soil nutrient cycling processes." Ecosystems **6**(6): 503-523.

Elton, C. S. (1958). The Ecology of Invasions by Animals and Plants. London, Methuen.

Environment Waikato. (2002). "Regional Pest Management Strategy 2002-2007. ." 17 October 2005, from http://www.ew.govt.nz/policyandplans/rpmsintro/rpms2002/operative5.2.2.htm.

Environment Waikato Biosecurity Group (2005). Alligator weed control 2004/2005. Environment Waikato Technical Report 2005/38. Hamilton, Environment Waikato.

Ernst, C. M. and N. Cappuccino (2005). "The effect of an invasive alien vine, *Vincetoxicum rossicum* (Asclepiadaceae), on arthropod populations in Ontario old fields." Biological Invasions **7**: 417-425.

Finke, D. L. and R. F. Denno (2002). "Intraguild predation diminished in complex-structured vegetation: Implications for prey suppression." Ecology **83**(3): 643-652.

Fonte, S. J. and T. D. Schowalter (2005). "The influence of a neotropical herbivore (*Lamponius portoricensis*) on nutrient cycling and soil processes." Oecologia **146**: 423-431.

Forster, R. and L. Forster (1999). Spiders of New Zealand and their world-wide kin. Dunedin, University of Otago Press.

Fowler, J., L. Cohen, et al. (2001). Practical Statistics for Field Biologists. Chichester, England, John Wiley and Sons Ltd

Fowler, S. V., P. Syrett, et al. (2000). "Success and safety in the biological control of environmental weeds in New Zealand." Austral Ecology **25**(5): 553-562.

Fox, M. D. and B. J. Fox (1986). The susceptibility of natural communities to invasion. Ecology of Biological Invasions. R. H. Groves and J. J. Burdon. Cambridge, Press Syndicate of the University of Cambridge.

Friedman, D. and P. Alpert (1991). "Reciprocal transport between ramets increases growth of *Fragaria chiloensis* when light and nitrogen occur in separate patches but only if patches are rich." Oecologia **86**: 76-80.

Galbraith-Kent, S. L. and S. N. Handel (2008). "Invasive *Acer platanoides* inhibits native sapling growth in forest understorey communities." Journal of Ecology **96**(2): 293-302.

Gangstad, E. O. (1975). Integrated Program for Alligator Weed Management. Aquatic Plant Control Program. Technical Report 10. Integrated program for alligator weed management. Vicksburg, Mississippi, U.S Army Engineers Waterways Experiment Station.

Gangstad, E. O. (1978). Weed control methods for river basin management. West Palm Beach, Florida, CRC Press Inc.

Garbari, F. and M. L. Pedulla (2001). "*Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae), a new species for the exotic flora of Italy." Webbia **56**(1): 139-143.

Gardner-Gee, R. (2004). Assessing restoration success: Invertebrate responses to re-vegetation on Motuora Island. Unpublished Honours Thesis. School of Biological Sciences. Auckland, University of Auckland.

Geng, Y., X. Pan, et al. (2006). "Phenotypic plasticity of invasive *Alternanthera philoxeroides* in relation to different water availability, compared to its native congener." Acta Oecologica **30**: 380-385.

Geng, Y., X. Pan, et al. (2007). "Phenotypic plasticity rather than locally adapted ecotypes allows the invasive alligator weed to colonize a wide range of habitats." Biological Invasions **9**: 245-256.

Gessner, M. O. (2005). Proximate Lignin and Cellulose. Methods to Study Litter Decomposition: A Practical Guide. M. A. S. Graca, F. Barlocher and M. O. Gessner. Dordrecht, Springer**:** 115-120.

Glantz, S. A. (2005). Primer of Biostatistics. New York, McGraw-Hill.

Goncalves Jr, J. F., A. M. Santos, et al. (2004). "The influence of the chemical composition of *Typha domingensis* and *Nymphaea ampla* detritus on invertebrate colonization during decomposition in a Brazilian coastal lagoon." Hydrobiologia **527**: 125-137.

Gorman, O. T. and J. R. Karr (1978). "Habitat structure and stream fish communities." Ecology **59**(3): 507-515.

Graca, M. A. S. and M. Zimmer (2005). Leaf Toughness. Methods to Study Litter Decomposition: A Practical Guide. M. A. S. Graca, F. Barlocher and M. O. Gessner. Dordrecht, The Netherlands, Springer.

Grace, J. B. (1993). "The adaptive significance of clonal reproduction in angiosperms: an aquatic perspective." Aquatic Botany **44**: 159-180.

Graham, W. A. E. (1976). Aquatic weeds. Observations on their growth and control in New Zealand. Victoria, Australia, State Rivers and Water Supply Commision.

Gratton, C. and R. F. Denno (2005). "Restoration of arthropod assemblages in a *Spartina* salt marsh following removal of the invasive plant *Phragmites australis*." Restoration Ecology **13**(2): 358-372.

Groves, R. H. and A. J. Willis (1999). "Environmental Weeds and Loss of Native Plant Biodiversity: Some Australian Examples." Australian Journal of Environmental Management **6**(3): 164-171.

Gulis, V., V. Ferreira, et al. (2006). "Stimulation of leaf litter decomposition and associated fungi and invertebrates by moderate eutrophication: implications for stream assessment." Freshwater Biology **51**: 1655-1669.

Gunasekera, L. and J. Bonila (2001). "Alligator weed: Tasty vegetable in Australian backyards?" Journal of Aquatic Plant Management **39**: 17-20.

Hager, H. A. and R. D. Vinebrooke (2004). "Positive relationships between invasive purple loosestrife (*Lythrum salicaria*) and plant species diversity and abundance in Minnesota wetlands." Canadian Journal of Botany **82**(6): 763-773.

Hansen, M. (2000). "On the identity of *Anacaena tepida* Winterbourn (Coleoptera: Hydrophilidae)." New Zealand Entomologist **23**: 85.

Harris, R. J. and B. R. Burns (2000). "Beetle assemblages of kahikatea forest fragments in a pasture-dominated landscape." New Zealand Journal of Ecology **24**(1): 57-67.

Harris, R. J., R. J. Toft, et al. (2004). "Insect assemblages in a native (kanuka - *Kunzea ericoides*) and an invasive (gorse - *Ulex europaeus*) shrubland." New Zealand Journal of Ecology **28**(1): 35-47.

Hartnett, D. C. and F. A. Bazzaz (1983). "Physiological integration among intraclonal ramets in *Solidago canadensis*." Ecology **64**(4): 779-788.

Harvey, M. S. (1989). Worms to wasps: an illustrated guide to Australia's terrestrial invertebrates. Melbourne, Oxford University press.

Hatley, C. L. and J. A. MacMahon (1980). "Spider community organization, seasonal variation and the role of vegetation architecture." Environmental Entomology **9**(5): 632-639.

Herron, P. M., C. T. Martine, et al. (2007). "Invasive plants and their ecological strategies: prediction and explanation of woody plant invasion in New England." Diversity & Distributions **13**(5): 633-644.

Hockley, J. (1974). "... and alligator weed spreads in Australia." Nature **250**: 704.

Hoffmann, W. A. and M. Haridasan (2008). "The invasive grass, *Melinis minutiflora*, inhibits tree regeneration in a Neotropical savanna." Austral Ecology **33**(1): 29-36.

Holloway, B. A. (1984). Anthribidae (Insecta: Coleoptera). Fauna of New Zealand 3. Lincoln, Manaaki Whenua Press.

Hornung, J. P. and A. L. Foote (2006). "Aquatic invertebrate responses to fish presence and vegetation complexity in western boreal wetlands, with implications for waterbird productivity." Wetlands **26**(1): 1-12.

Hosomi, M. and R. Sudo (1986). "Simultaneous determination of Total Nitrogen and Total Phosphorus in Freshwater Samples Using Persulphate Digestion." International Journal of Environmental Studies **27**: 267 - 275.

Houlahan, J. E. and C. S. Findlay (2004). "Effect of invasive plant species on temperate wetland plant diversity." Conservation Biology **18**(4): 1132-1138.

Houston, W. A. and L. J. Duivenvoorden (2002). "Replacement of littoral native vegetation with the ponded pasture grass *Hymenachne amplexicaulis*: effects on plant, macroinvertebrate and fish biodiversity of backwaters in the Fitzroy River, Central Queensland, Australia." Marine and Freshwater Research **53**: 1235-1244.

Hunt, J. (2007). Wetlands of New Zealand: A bitter-sweet story. Auckland, Random House.

Hurlbert, S. H. (1984). "Pseudoreplication and the design of ecological field experiments." Ecological Monographs **54**(2): 187-211.

Hutcheson, J. (1999). Characteristics of Mapara insect communities as depicted by Malaise trapped beetles: changes with time and animal control. Science for Conservation 135. Wellington, Department of Conservation.

Hutcheson, J. and D. Jones (1999). "Spatial variability of insect communities in a homogenous system: Measuring biodiversity using Malaise trapped beetles in a *Pinus radiata* plantation in New Zealand." Forest Ecology and Management **118**: 93-105.

Hutcheson, J. A. and M. O. Kimberley (1999). "A pragmatic approach to characterising insect communities in New Zealand: Malaise trapped beetles." New Zealand Journal of Ecology **23**(1): 69-79.

Ihaka, R. and R. Gentleman (1996). "R: A Language for Data Analysis and Graphics." Journal of Computational and Graphical Statistics **5**(3): 299-314.

Invasive Species Specialist Group. (2004, 25 March 2004). Retrieved 4 August, 2005, from http://www.issg.org/.

Jackson, R. R. and E. I. Wallis (1998). "Predatory and scavenging behaviour of *Microvelia macgregori* (Hemiptera: Veliidae), a water-surface bug from New Zealand." New Zealand Journal of Zoology **25**: 23-28.

Jayawardana, J. M. C. K., M. Westbrooke, et al. (2006). "Macroinvertebrate communities in willow (*Salix* spp.) and reed beds (*Phragmites australis*) in central Victorian streams in Australia." Marine and Freshwater Research **57**: 429-439.

Johnson, P. a. B., P (1998). Wetland plants in New Zealand. Lincoln, Manaaki Whenua Press.

Jonsell, M., J. Weslien, et al. (1998). "Substrate requirements of red-listed saproxylic invertebrates in Sweden." Biodiversity and Conservation **7**: 749-764.

Julia, R., D. Holland, et al. (2007). "Assessing the economic impact of invasive species: The case of yellow starthistle (*Centaurea solsitialis* L.) in the rangelands of Idaho, USA." Journal of Environmental Management **85**(4): 876-882.

Julien, M. H. (1995). *Alternanthera philoxeroides* (Mart.) Griseb. The Biology of Australian Weeds. R. H. Groves, R. C. H. Shepherd and R. G. Richardson. Frankston, R. G. and F. J. Richardson. **1**.

Julien, M. H. and A. S. Bourne (1988). "Alligator Weed is Spreading in Australia." Plant Protection Quarterly **3**(3): 91-96.

Julien, M. H., A. S. Bourne, et al. (1992). "Growth of the weed *Alternanthera philoxeroides* (Martius) Grisebach, (alligator weed) in aquatic and terrestrial habitats in Australia." Plant Protection Quarterly **7**(3): 102-108.

Julien, M. H., B. Skarratt, et al. (1995). "Potential Geographical distribution of alligator weed and its biological control by *Agasicles hygrophila*." Journal of Aquatic Plant Management **33**: 55-60.

Kay, S. H. (1992). "Response of Two Alligator Weed Biotypes to Quinclorac." Journal of Aquatic Plant Management **30**: 35-40.

Kay, S. H. and W. T. Haller (1982). "Evidence for the existence of distinct alligatorweed biotypes." Journal of Aquatic Plant Management **20**: 37-41.

Keane, R. M. and M. J. Crawley (2002). "Exotic plant invasions and the enemy release hypothesis." Trends in Ecology & Evolution **17**: 164-170.

Kelly, D. J. and I. Hawes (2005). "Effects of invasive macrophytes on littoral-zone productivity and foodweb dynamics in a New Zealand high country lake." Journal of the North American Benthological Society **24**(2): 300-320.

Kershner, M. W. and D. M. Lodge (1990). "Effect of substrate architecture on aquatic gastropod-substrate associations." Journal of the North American Benthological Society **9**(4): 319-326.

Klimaszewski, J. and J. C. Watt (1997). Coleoptera: family-group review and keys to identification. Lincoln, Manaaki Whenua Press.

Knight, K. S. and P. B. Reich (2005). "Opposite relationships between invasibility and native species richness at patch versus landscape scales." Oikos **109**(1): 81-88.

Kolar, C. S. (2001). "Progress in invasion biology: predicting invaders." Trends in Ecology & Evolution **16**(4): 199-204.

Kuschel, G. (1990). Beetles in a suburban environment: a New Zealand case study: The identity and status of Coleoptera in the natural and modified habitats of Lynfield, Auckland (1974 - 1989). Auckland, DSIR.

Kuschel, G. (2003). Nemonychidae Belidae Brentidae (Insecta: Coleoptera: Curculionoidea). Fauna of New Zealand 45. Lincoln, Manaaki Whenua Press.

Lalonde, S. and J. D. Downing (1992). "Phytofauna of Eleven Macrophyte Beds of Differing Trophic Status Depth and Composition." Canadian Journal of Fisheries & Aquatic Sciences **49**(5): 992-1000.

Langellotto, G. A. and R. F. Denno (2004). "Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis." Oecologia **139**: 1-10.

Larivière, M.-C. (2005). Checklist of New Zealand Hemiptera (excluding Sternorrhyncha) www.landcareresearch.co.nz/research/biosystematics/invertebrates/hemwsite/nzhemlist/.

Lariviere, M.-C. and A. Larochelle (2004). Heteroptera (Insecta: Hemiptera): catalogue. Fauna of New Zealand 50. Lincoln, Manaaki Whenua Press.

Larochelle, A. and M.-C. Lariviere (2001). Carabidae (Insecta: Coleoptera): catalogue. Fauna of New Zeland 43. Lincoln, Manaaki Whenua Press.

Lawrence, J. F. (1989). Mycophagy in the Coleoptera: Feeding strategies and morphological adaptations. Insect-fungus interactions. N. Wilding, N. M. Collins, P. M. Hammond and J. F. Webber. London, Academic Press.

Lawrence, J. F. and E. B. Britton (1991). Coleoptera. The Insects of Australia. Burwood, Melbourne University Press: 543-683.

Lawton, J. H. (1983). "Plant architecture and the diversity of phytophagous insects." Annual Review of Entomology **28**: 23-39.

Learner, M. A., P. R. Wiles, et al. (1989). "The influence of aquatic macrophyte identity on the composition of the chironomid fauna in a former gravel pit in Berkshire, England." Aquatic Insects **11**(3): 183-191.

Leishman, M. R. and V. P. Thomson (2005). "Experimental evidence for the effects of additional water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury Sandstone soils, Sydney, Australia." Journal of Ecology **93**(1): 38-49.

Leschen, R. A. B., J. F. Lawrence, et al. (2003). "Coleoptera genera of New Zealand." New Zealand Entomologist **26**: 15-28.

Levine, J. M. (1999). "Elton revisited: a review of evidence linking diversity and invasibility." Oikos **87**(1): 15-26.

Levine, J. M. (2000). "Species Diversity and Biological Invasions: Relating Local Process to Community Pattern." Science **288**: 852-854.

Li, J. and W. H. Ye (2006). "Genetic diversity of alligator weed ecotypes is not the reason for their different responses to biological control." Aquatic Botany **85**: 155-158.

Lindsay, E. A. and K. French (2004). "*Chrysanthemoides monilifera* ssp. *rotundata* invasion alters decomposition rates in coastal areas of south-eastern Australia." Forest Ecology & Management **198**(1-3): 387-399.

Lindsay, E. A. and K. French (2006). "The impact of the weed *Chrysanthemoides monilifera* ssp. *rotundata* on coastal leaf litter invertebrates." Biological invasions **8**: 177-192.

Liu, C., G. Wu, et al. (2004). "Seasonal changes in height, biomass and biomass allocation of two exotic aquatic plants in a shallow eutrophic lake." Journal of Freshwater Ecology **19**(1): 41-45.

Liu, C. and D. Yu (2005). "Occurence of native aquatic plants within floating mats of *Alternanthera philoxeroides*." Journal of Freshwater Ecology **20**(2): 407-408.

Lodge, D. J., D. L. Hawksworth, et al. (1996). Microbial diversity and tropical forest functioning. Biodiversity and Ecosystem Processes in Tropical Forests. G. H. Orians, R. Dirzo and J. H. Cushman. Berlin, Springer**:** 69-100.

Longstreth, D. J., J. A. Bolanos, et al. (1984). "Salinity Effects on Photosynthesis and Growth in *Alternanthera philoxeroides*." Plant Physiology (Rockville) **75**(4): 1044-1047.

Longstreth, D. J., J. A. Bolanos, et al. (1985). "Photosynthetic Rate and Mesophyll Surface Area in Expanding Leaves of *Alternanthera philoxeroides* Grown at Two Light Levels." American Journal of Botany **72**(1): 14-19.

Longstreth, D. J. and C. B. Mason (1984). "The Effect of Light on Growth and Dry Matter Allocation Patterns of *Alternanthera philoxeroides*." Botanical Gazette **145**(1): 105-109.

Loreau, M., S. Naeem, et al. (2001). "Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges." Science **294**: 804-808.

Louda, S. M., T. A. Rand, et al. (2005). "Assessment of ecological risks in weed biocontrol: Input from retrospective ecological analyses." Biological Control **35**: 253-264.

Louda, S. M. and P. Stiling (2004). "The double-edged sword of biological control in conservation and restoration." Conservation Biology **18**(1): 50-53.

Mack, M. C. and C. D'Antonio (1998). "Impacts of biological invasions on disturbance regimes." Trends in Ecology and Evolution **13**: 195-198.

Mack, R. N. (2000). "Biotic invasions: Causes, epidemiology, global consequences, and control." Ecological Applications **10**(3): 689-710.

Maddox, D. M., L. A. Andres, et al. (1971). "Insects to control alligator weed, an invader of aquatic ecosystems in the United States." Bioscience **21**: 985-991.

Marchante, H. (2003). Invasion of the Portuguese dune ecosystems by the exotic species *Acacia longifolia* (Andrews) Willd.: effects at the community level. Plant Invasions: Ecological Threats and Management Solutions**:** 75-85.

Matson, p. (1990). "Plant-soil interactions in primary succession at Hawaii Volcanoes National Park." Oecologia **85**: 241-246.

Maule, H. G., M. Andrews, et al. (1995). "Sun/shade acclimation and nitrogen nutrition of *Tradescantia fluminensis*, a problem weed in New Zealand native forest remnants." New Zealand Journal of Ecology **19**(1): 35-46.

May, B. M. (1987). "Immature stages of Curculionoidea (Coleoptera): Rearing records 1964-1986." New Zealand Entomologist **9**: 44-56.

McCune, B. and J. B. Grace (2002). Analysis of Ecological Communities. Gleneden Beach, MjM Software Design.

McKinney, M. L. (1999). "Biotic homogenization: a few winners replacing many losers in the next mass extinction." Trends in Ecology & Evolution **14**(11): 450-453.

McLean, J. A. and D. C. Jones (2006). "Beetle diversity in forest and pastoral areas, Whangamata, Coromandel Peninsula." New Zealand Natural Sciences **31**(25-42).

Memmott, J., S. V. Fowler, et al. (2000). "The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats." Acta Oecologica **21**(3): 213-222.

Menzel, F., R. L. Kitching, et al. (2004). "Host specificity or habitat structure? - The epicortical beetle assemblages in an Australian suptropical rainforest." European Journal of Entomology **101**: 251-259.

Milbau, A., I. Nijs, et al. (2003). "Disentangling invasiveness and invasibility during invasion in synthesized grassland communities." New Phytologist **159**: 657-667.

Miller, A. L. and R. P. Duncan (2004). "The impact of exotic weed competition on a rare New Zealand outcrop herb, *Pachycladon cheesemanii* (Brassicaceae)." New Zealand Journal of Ecology **28**(1): 113-124.

Mitchell, C. E., A. A. Agrawal, et al. (2006). "Biotic interactions and plant invasions." Ecology letters **9**: 726-740.

Mitchell, D. S. (1978). Aquatic weeds in Australian waters. Canberra, Australian Government Publishing Service.

Moon, G. (2004). The Reed field guide to New Zealand birds. Auckland, Reed Books.

Morrison, J. A. (2002). "Wetland vegetation before and after experimental purple loosestrife removal." Wetlands **22**(1): 159-169.

Mudalige, R. G. and D. J. Longstreth (2006). "Effects of salinity on photosynthetic characteristics in photomixotrophic cell-suspension cultures from *Alternanthera philoxeroides*." Plant Cell, Tissue and Organ Culture **84**: 301-308.

Nachtrieb, J. G., M. J. Grodowitz, et al. (2007). An integrated approach to invasive plant management: biocontrol and native plant interactions. XII International Symposium on the Biological Control of Weeds, La Grande Motte, France.

Naeem, S. (2000). "Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors." Oikos **91**(1): 97-108.

Niell, R. S., P. F. Brussard, et al. (2007). "Butterfly community composition and oak woodland vegetation response to rural residential development." Landscape and Urban Planning **81**: 235-245.

Niemela, J., M. Koivula, et al. (2007). "The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests." Journal of Insect Conservation **11**: 5-18.

Nitterus, K., M. Astrom, et al. (2007). "Commercial harvest of logging residue in clear-cuts affects the diversity and community composition of ground beetles (Coleoptera: Carabidae)." Scandinavian Journal of Forest Research **22**: 231-240.

Northland Regional Council (2005). Annual Monitoring Report 2004-2005.

O'Dowd, D. J., P. T. Green, et al. (2003). "Invasional 'meltdown' on an oceanic island." Ecology Letters **6**: 812-817.

Ogle, C. C., G. La Cock, D, et al. (2000). "Impact of an exotic vine *Clematis vitalba* (F. Ranunculaceae) and of control measures on plant biodiversity in indigenous forest, Taihape, New Zealand." Austral Ecology **25**: 539-551.

Okada, K. A., S. I. Alonso, et al. (1985). "Un citotipo hexaploide de *Alternanthera philoxeroides* como nueva maleza en el partido de Balcarce, provincia de Buenos Aires." Revista de Investigaciones Agropecuarias **20**(2): 37-53.

Olden, J. D. (2004). "Ecological and evolutionary consequences of biotic homogenization." Trends in Ecology & Evolution **19**(1): 18-24.

Page, A. R. and K. L. Lacey (2006). Economic impact assessment of Australian weed biological control CRC for Australian Weed Management Technical Series Number 10.

Pan, X., Y. Geng, et al. (2006). "The influence of abiotic stress and phenotypic plasticity on the distribution of invasive *Alternanthera philoxeroides* along a riparian zone." Acta Oecologica **30**: 333-341.

Parker, I. M., D. Simberloff, et al. (1999). "Impact: toward a framework for understanding the ecological effects of invaders." Biological Invasions **1**: 3-19.

Parsons, W. T. and E. G. Cuthbertson (1992). Noxious Weeds of Australia. Melbourne, Inkata Press.

Paynter, Q. (2006). "Evaluating the impact of biological control against *Mimosa pigra* in Australia: Comparing litterfall before and after the introduction of biological control agents." Biological Control **38**: 166-173.

Paynter, Q. E., S. V. Fowler, et al. (2004). "Safety in New Zealand weed biocontrol: A nationwide survey for impacts on non-target plants." New Zealand Plant Protection **57**: 102-107.

Pearson, D. E., K. S. McKelvey, et al. (2000). "Non-target effects of an introduced biological control agent on deer mouse ecology." Oecologia **122**: 121-128.

Pederson, T. M. (1967). "Studies in South American Amaranthaceae." Darwinia **14**: 430-462.

Pemberton, R. W. (2000). "Predictable risk to native plants in weed biological control." Oecologia **125**: 489-494.

Perry, L. G. and S. M. Galatowitsch (2004). "The influence of light availability on competition between *Phalaris arundinacea* and a native wetland sedge." Plant Ecology **170**(1): 73-81.

Philip, B. A., C. J. Winks, et al. (1988). Current status of biological control of Alligator Weed in New Zealand. 41st New Zealand Weed and Pest Control Conference.

Pimental, D., L. Lach, et al. (2000). "Environmental and Economic Costs of Nonindigenous Species in the United States." BioScience **50**(1): 53-65.

Pomella, A. W. V., R. W. Barreto, et al. (2007). "*Nimbya alternantherae* a potential biocontrol agent for alligatorweed, *Alternanthera philoxeroides*." Biocontrol **52**: 271-288.

Prentis, P. J., E. M. White, et al. (2007). "Can hybridization cause local extinction: a case for demographic swamping of the Australian native *Senecio pinnatifolius* by the invasive *Senecio madagascariensis*?" New Phytologist **176**(4): 902-912.

Prescott, C. E. (2005). "Do rates of litter decomposition tell us anything we really need to know?" Forest Ecology and Management **220`**: 66-74.

Pysek, P. and K. Prach (1994). How Important are Rivers for Supporting Plant Invasions? Ecology and Management of Invasive Riverside Plants. L. C. de Waal, L. E. Child, P. M. Wade and J. H. Brock. Chichester, John Wiley and Sons Ltd**:** 19-26.

Quimby, P. C. and S. H. KAY (1977). "Hypoxic Quiescence in Alligatorweed." Physiologia Plantarum **40**: 163-168.

Quinn, J. M., I. K. G. Boothroyd, et al. (2004). "Riparian buffers mitigate effects of pine plantation logging on New Zealand streams 2. Invertebrate communities." Forest Ecology & Management **191**(1-3): 129-146.

Reid, V. A. (1998). The Impact of Weeds on Threatened Plants. Science and Research Internal Report No. 164. Wellington, Department of Conservation.

Roberts, L. I. N., C. J. Winks, et al. (1984a). Biological control of Alligator weed: report for the period July 1980 - April 1984. Internal report, Entomology Division, DSIR.

Roberts, L. I. N., C. J. Winks, et al. (1984b). Progress of Biological Control of Alligator Weed in New Zealand. 37th New Zealand Weed and Pest Control Conference.

Rogers, H. H. and D. E. Davis (1971). Nutrient absorption from sewage effluent by aquatic weeds. 24th Southern Weed Society Conference.

Rossiter, N., S. Setterfield, et al. (2004). Exotic grass invasion in the tropical savanna of northern Australia: ecosystem consequences. 14th Australian Weeds Conference, Wagga Wagga, Weed Society of New South Wales.

Rowland, A. P. and J. D. Roberts (1994). "Lignin and cellulose fractionation in decomposition studies using acid-detergent fibre methods." Communications in soil science and plant analysis **25**(3-4): 269-277.

Rypstra, A. L., P. E. Carter, et al. (1999). "Architectural features of agricultural habitats and their impact on the spider inhabitants." The Journal of Arachnology **27**: 371-377.

Sainty, G., G. McCorkelle, et al. (1998). "Control and spread of Alligator Weed *Alternanthera philoxeroides* (Mart.) Griseb., in Australia: lessons for other regions." Wetlands Ecology and Management **5**: 195-201.

Saitoh, T., K. Seiwa, et al. (2002). "Importance of physiological integration of dwarf bamboo to persistence in forest understorey: a field experiment." Journal of Ecology **90**: 78-85.

Salter, M. G., K. A. Franklin, et al. (2003). "Gating of the rapid shade-avoidance response by the circadian clock in plants." Nature **426**: 680-683.

Samways, M. J., P. M. Caldwell, et al. (1996). "Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa." Agriculture Ecosystems & Environment **59**: 19-32.

Sax, D. F. (2002). "Equal diversity in disparate species assemblages: a comparison of native and exotic woodlands in California." Global Ecology and Biogeography Letters **11**: 49-57.

Scarsbrook, E. and D. E. Davis (1971). "Effect of sewage effluent on growth of five vascular aquatic species." Hyacinth Control Journal **9**: 26-30.

Schooler, S., Z. Baron, et al. (2006). "Effect of simulated and actual herbivory on alligator weed, *Alternanthera philoxeroides*, growth and reproduction." Biological Control **36**: 74-79.

Schooler, S., C. Clech-Goods, et al. (2006). "Ecological studies to assess the efficacy of biological control on populations of alligator weed and lippia." Australian Journal of Entomology **45**: 272-275.

Schooler, S., A. Yeates, et al. (2006). "Herbivory, mowing and herbicides differently affect production and nutrient allocation of *Alternanthera philoxeroides*." Aquatic Botany **86**(1): 62-68.

Shaw, R. H. (2003). Biological control of invasive weeds in the UK: opportunities and challenges. Plant Invasions: Ecological Threats and Management

Solutions. L. E. Child, J. H. Brock, G. Brunduet al. Leiden, The Netherlands, Backhuys Publishers**:** 337-354.

Shen, J., M. Shen, et al. (2005). "Effect of environmental factors on shoot emergence and vegetative growth of alligatorweed (*Alternanthera philoxeroides*)." Weed Science **53**: 471-478.

Sheppard, A. W., R. H. Shaw, et al. (2006). "Top 20 environmental weeds for classical biological control in Europe: a review of opportunities, regulations and other barriers to adoption." Weed Research **46**: 93-117.

Siemann, E., D. Tilman, et al. (1998). "Experimental tests of the dependence of arthropod diversity on plant diversity." The American Naturalist **152**(5): 738-750.

Simberloff, D. and B. Von Holle (1999). "Positive interactions of non-indigenous species: invasional meltdown?" Biological Invasions **1**: 21-32.

Sinden, J., R. Jones, et al. (2004). The economic impact of weeds in Australia. CRC for Australian Weed Management. Technical Series Number 8.

Southwood, T. R. E. and P. A. Henderson (2000). Ecological Methods. Oxford, Blackwell Science Ltd.

Standish, R. (2004). "Impact of an invasive clonal herb on epigaeic invertebrates in forest remnants in New Zealand." Biological Conservation **116**: 49-58.

Standish, R. J. (2002). "Experimenting with methods to control *Tradescantia fluminensis*, an invasive weed of native forest remnants in New Zealand." New Zealand Journal of Ecology **26**(2): 161-170.

Standish, R. J., A. W. Robertson, et al. (2001). "The impact of an invasive weed *Tradescantia fluminensis* on native forest regeneration." Journal of Applied Ecology. 38(6) **38**(6): 1253-1263.

Standish, R. J., P. A. Williams, et al. (2004). "Invasion by a perennial herb increases decomposition rate and alters nutrient availability in warm temperate lowland forest remnants." Biological Invasions **6**(1): 71-81.

Statistics New Zealand. (2005, 14 April 2005).   Retrieved 8 August, 2005, from http://www.stats.govt.nz/schools-corner/secondary/information/economic-issues-growth.htm.

Stewart, C. A. (1996). The effect of temperature on the biology and population ecology of *Agasicles hygrophila* (Coleoptera: Chrysomelidae), a biological control agent of alligator weed (*Alternanthera philoxeroides*). Canterbury, New Zealand, Lincoln University.

Stewart, C. A., R. B. Chapman, et al. (2000). "Growth of alligator weed (*Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae)) and population development of *Agasicles hygrophila* Selman & Vogt (Coleoptera:

Chrysomelidae) in northern New Zealand." Plant Protection Quarterly **15**(3): 95-101.

Stewart, C. A., R. M. Emberson, et al. (1996). Temperature effects on the alligator weed flea beetle, *Agasicles hygrophila* (Coleoptera: Chrysomelidae): implications for biological control in New Zealand. IX International Symposium on Biological Control of Weeds. V. C. Moran and J. H. Hoffman. Stellenbosch, South Africa**:** 393-398.

Stoner, J., R. Adams, et al. (2004). Exotic grass fuel in south eastern Australia. Proceedings of the Fourteenth Australian Weeds Conference, Wagga Wagga, NSW, Weed Society of New South Wales.

Strauss, S. Y., C. O. Webb, et al. (2006). "Exotic taxa less related to native species are more invasive." PNAS **103**(15): 5841-5845.

Stuefer, J. F. and M. J. Hutchings (1994). "Environmental heterogeneity and clonal growth: a study of the capacity for reciprocal translocation in *Glechoma hederacea* L." Oecologia **100**: 302-308.

Swan, C. M. and M. A. Palmer (2004). "Leaf diversity alters litter breakdown in a Piedmont stream." Journal of the North American Benthological Society **23**(1): 15-28.

Taki, H. and P. G. Kevan (2007). "Does habitat loss affect the communities of plants and insects equally in plant-pollinator interactions? Preliminary findings." Biodiversity and Conservation **16**: 3147-3161.

Tan, W. Z., Q. J. Li, et al. (2002). "Biological control of alligatorweed (*Alternanthera philoxeroides*) with a *Fusarium* sp." BioControl **47**: 463-479.

Taylor, R. and I. Smith (1997). The State of New Zealand's Environment. Wellington, The Ministry for the Environment.

Templer, P., S. Findlay, et al. (1998). "Sediment chemistry associated with native and non-native emergent macrophytes of a Hudson River marsh ecosystem." Wetlands **18**(1): 70-78.

Thompson, R. M. and C. R. Townsend (2000). New Zealand's stream invertebrate communities: An international perspective. New Zealand stream invertebrates: ecology and implications for management. K. J. Collier and M. J. Winterbourn. Christchurch, New Zealand Limnological Society**:** 53-74.

Timmins, S. M. and I. W. Mackenzie (1995). Weeds in New Zealand Protected Natural Areas Database. Wellington, Department of Conservation.

Toft, R. J., R. J. Harris, et al. (2001). "Impacts of the weed *Tradescantia fluminensis* on insect communities in fragmented forests in New Zealand." Biological Conservation **102**(1): 31-46.

Toft, R. J., R. J. Harris, et al. (2001). "Impacts of the weed *Tradescantia fluminensis* on insect communities in fragmented forests in New Zealand." Biological Conservation **102**: 31-46.

Tolonen, K. T., H. Hamalainen, et al. (2003). "Body size and substrate association of littoral insects in relation to vegetation structure." Hydrobiologia **499**: 179-190.

Topp, W., H. Kappes, et al. (2008). "Response of ground-dwelling beetle (Coleoptera) assemblages to giant knotweed (*Reynoutria* spp.) invasion." Biological Invasions **10**(4): 381 - 390.

U.S Army Corps of Engineers. (2007, October 15 2007). "*Schoenoplectus tabernaemontani* (K. C. Gmel.) Palla (Great or Soft-Stem Bulrush)." Retrieved October 25 2007, from http://el.erdc.usace.army.mil/aqua/apis/plants/html/schoenop.html.

Underwood, A. J. (1981). "Techniques of analysis of variance in experimental marine biology and ecology." Oceanography and Marine Biology Annual Review **19**: 513–605.

van Ruijven, J. (2003). "Diversity reduces invasibility in experimental plant communities: the role of plant species." Ecology Letters **6**(10): 910-918.

Vandergast, A. G. and R. G. Gillespie (2004). "Effects of Natural Forest Fragmentation on a Hawaiian Spider Community." Community and Ecosystem Ecology **33**(5): 1296-1305.

Veblen, T. T. and G. H. Stewart (1982). "The effects of introduced wild animals on New Zealand forests." Annals of the Association of American Geographers **72**(3): 372-397.

Vila, M., J. L. Maron, et al. (2005). "Evidence for the enemy release hypothesis in *Hypericum perforatum*." Oecologia **142**(3): 474-479.

Vitousek, P. M. and L. R. Walker (1989). "Biological Invasion by *Myrica Faya* in Hawai'i: Plant Demography, Nitrogen Fixation, Ecosystem Effects." Ecological Monographs **59**(3): 247-265.

Vogt, G. B. (1973). Exploration for Natural Enemies of Alligator Weed and Related Plants in South America. Aquatic Plant Control Program Technical Report 3. Biological Control of Alligator Weed. E. O. Gangstad, R. A. J. Scott and R. G. Cason. Vicksburg, Mississippi, U. S Army Engineer.

Vogt, G. B., P. C. Quimby, et al. (1992). Effects of Weather on the Biological Control of Alligator Weed in the Lower Mississippi Valley Region, 1973-83, U.S. Department of Agriculture Technical Bulletin 1766.

Wagh, G. K., H. V. Ghate, et al. (1995). "First record of the alligator weed, *Alternanthera philoxeroides* (Mart.) Griseb. from Pune, Maharashtra." Journal of the Bombay Natural History Society **92**(1): 141-143.

Waipara, N. W., G. W. Bourdot, et al. (2006). "*Sclerotinia sclerotiorum* shows potential for controlling water lettuce, alligator weed and wandering jew." New Zealand Plant Protection **59**: 23-27.

Wang, B., W. Li, et al. (2005). "Genetic diversity of *Alternanthera philoxeroides* in China." Aquatic Botany **81**: 277-283.

Wardle, D. A. (2001). "Experimental demonstration that plant diversity reduces invasibility - evidence of a biological mechanism or a consequence of sampling effect?" Oikos **95**(1): 161-170.

Wardle, D. A., G. W. Yeates, et al. (2003). "The response of a three trophic level soil food web to the identity and diversity of plant species and functional groups." Oikos **102**(1): 45-56.

Watt, J. C. (1982). "New Zealand beetles." New Zealand Entomologist **7**: 213-221.

Weihe, P. E. (1997). "The effects of shading on competition between purple loosestrife and broad-leaved cattail." Aquatic Botany **59**(1-2): 127-138.

Werner, F. G. and D. S. Chandler (1995). Anthicidae (Insecta: Coleoptera). Fauna of New Zealand 34. Lincoln, Manaaki Whenua Press.

White, P. S. and S. T. A. Pickett (1985). Natural Disturbance and Patch Dynamics: An Introduction. The Ecology of Natural Disturbance and Patch Dynamics. S. T. A. Pickett and P. S. White. Orlando, Florida, Academic Press Inc**:** 3-13.

Wikum, D. A. and G. F. Shanholtzer (1978). "Application of the Braun-Blanquet Cover-Abundance Scale for Vegetation Analysis in Land Develpment Studies." Environmental Management **2**(4): 323-329.

Wilkie, L., G. Cassis, et al. (2007). "The effects on terrestrial arthropod communities of invasion of a coastal heath ecosystem by the exotic weed bitou bush (*Chrysanthemoides monilifera* ssp. *rotundata* L.)." Biological Invasions **9**: 477-498.

Williams, J. A. and C. West, J (2000). "Environmental weeds in Australia and New Zealand: issues and approaches to management." Austral Ecology **25**: 425-444.

Williamson, M. (1996). Biological Invasions. London, Chapman and Hall.

Williamson, M. H. and A. Fitter (1996). "The Characteristics of Successful Invaders." Biological Conservation 78 (1996) 163-170 **78**: 163-170.

Willis, A. J. and J. Memmott (2005). "The potential for indirect effects between a weed, one of its biocontrol agents and native herbivores: A food web approach." Biological Control **35**: 299-306.

Wilson, J. R. U., A. Yeates, et al. (2007). "Rapid response to shoot removal by the invasive wetland plant, alligator weed (*Alternanthera philoxeroides*)." Environmental and Experimental Biology **60**: 20-25.

Wilson, S. D. and J. W. Belcher (1989). "Plant and bird communities of native prairie and introduced Eurasian vegetation in Manitoba, Canada." Conservation Biology **3**(1): 39-44.

Winks, C. J., S. V. Fowler, et al. (2004). "Invertebrate fauna of boneseed, *Chrysanthemoides monilifera* ssp. *monilifera* (L.) T. Norl. (Asteraceae: Calenduleae), an invasive weed in New Zealand." New Zealand Entomologist **27**: 61-72.

Wissinger, S. A., A. R. McIntosh, et al. (2006). "Impacts of introduced brown and rainbow trout on benthic invertebrate communities in shallow New Zealand lakes." Freshwater Biology **51**: 2009-2028.

Xie, Y., H. Qin, et al. (2004). "Nutrient limitation to the decomposition of water hyacinth (*Eichhornia crassipes*)." Hydrobiologia **529**: 105-112.

Xu, C.-Y., W.-J. Zhang, et al. (2003). "Genetic diversity of alligator weed in China by RAPD analysis." Biodiversity & Conservation. **12**: 637-645.

Xu, K. Y. (2004). "The role of diversity and functional traits of species in community invasibility." Botanical Bulletin of Academia Sinica **45**(2): 149-157.

Ye, W. H., J. Li, et al. (2003). "Genetic uniformity of *Alternanthera philoxeroides* in South China." Weed Research **43**: 297-302.

Yeates, G. W. and P. A. Williams (2001). "Influence of three invasive weeds and site factors on soil microfauna in New Zealand." Pedobiologia **45**(4): 367-383.