Decomposition dynamics of invasive alligator weed compared with native sedges in a Northland lake

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Abstract: Invasive weeds have been shown to alter ecosystem processes such as decomposition and nutrient cycling. However, little is known about the effects of introduced biocontrol agents on these processes. This study examined the effects of alligator weed (*Alternanthera philoxeroides*) and its biocontrol agent, the alligator weed flea beetle (*Agasicles hygrophila*), on nutrient cycling in a northern New Zealand lake. Alligator weed litter decomposed significantly faster than either of two native sedge species (*Schoenoplectus tabernaemontani, Isolepis prolifer)* in a litterbag experiment. In addition, the presence of the alligator weed flea beetle resulted in large amounts of decaying alligator weed litter entering the lake in early summer. Both the timing and magnitude of this litter input were uncharacteristic of seasonal biomass dynamics of the native sedges. Combined with alligator weed's rapid decomposition, this indicates altered patterns of nutrient cycling at the lake, with potential flow-on effects including facilitation of further weed invasion.

Keywords: *Agasicles hygrophila*; *Alternanthera philoxeroides*; biological control; ecosystem processes; flea beetle; invasive species; non-target effects

Introduction

Invasive weeds potentially affect ecosystem processes such as decomposition and nutrient cycling. Nutrient cycling may be altered when weeds' growing seasons and patterns of resource use differ from those of native vegetation. Invasive plant species often share traits such as rapid growth rates, high tissue nutrient concentrations and high specific leaf area (Allison & Vitousek 2004). For example, Gamba grass (*Andropogon gayanus* Kunth) decreased the seasonal availability of nitrate in invaded Australian savannas (Rossiter et al. 2004).

Invasive weeds may also alter nutrient cycling by changing decomposition dynamics. Those characteristics listed above represent a trade-off of low structural or chemical defences in favour of rapid growth (Cornelissen et al. 1999). If a plant species evolves to have less defended tissues, they are likely to break down more rapidly. Thus, litter decomposition rates vary between plant species with differing chemical constituents (Boulton & Boon 1991). Substances such as lignin and cellulose are highly resistant to degradation (Rowland & Roberts 1994). Conversely, high levels of nitrogen and phosphorus may elevate initial decomposition rates, as these nutrients often limit microbial growth (Berg & McClaugherty 2003).

In contrast to the high-productivity, rapid-nutrient-cycling strategy common among invasive plants, many non-invasive plants, particularly evergreen species, employ a more resource conservative strategy, producing resistant, longer lived leaves that break down more slowly following senescence (Cornelissen et al. 1999). For instance, several invasive species had high photosynthetic rates and leaf nitrogen concentrations, and decomposed rapidly compared with native Hawaiian plant species (Matson 1990; Allison & Vitousek 2004).

Weed invasion may alter environmental factors, such as moisture, temperature and habitat availability. By influencing the activity of decomposers this may alter decomposition rates in general, not just of the invasive litter. Lindsay and French (2004) attributed elevated decomposition rates beneath bitou bush (*Chrysanthemoides monilifera* ssp. *rotundata* (L.) T. Norl.) compared with native shrubs in Australian coastal sand dunes to altered microclimatic conditions.

While the effects of invasive plants themselves on nutrient cycling have received some attention, there has been little investigation of the role of biological control agents in altering ecosystem processes (Denslow & D'Antonio 2005). Instead, research into non-target impacts of weed biocontrol has generally centred on feeding on non-target host species, or interactions (direct or indirect) with other invertebrate species (Paynter et al. 2004; Louda et al. 2005). However, where biocontrol agents alter patterns of growth and senescence, they potentially affect ecosystem processes such as nutrient cycling. Given that most biocontrol achieves pest reduction rather than total eradication, pest and control agent continue to co-exist thus permanently altering the system.

Alligator weed (*Alternanthera philoxeroides* (Mart.) Griseb.: Amaranthaceae) is a herbaceous, stoloniferous perennial that grows either as a rooted emergent aquatic weed or in damp terrestrial sites. Widely established in Northland and Auckland, especially around the Kaipara Harbour, it is spreading in the Waikato and Bay of Plenty regions (Environment Waikato Biosecurity Group 2005). Alligator weed reproduction in New Zealand is entirely from vegetative fragments (both roots and shoots), and dispersal is frequently human mediated (Julien 1995; Sainty et al. 1998). Alligator weed has widely documented impacts on pasture, cropping, recreational water use and flood control (Julien 1995), but little is known of its impacts in natural ecosystems in New Zealand or elsewhere. Aquatic alligator weed is characterised by rapid growth in spring, forming a dense mat of vegetation. As a fleshy herb, alligator weed's architecture differs markedly from native sedge and rush species occurring in the same elevation zone in northern New Zealand lakes. Further, alligator weed's chemical composition was expected to differ markedly from that of native sedge species, based on the much greater apparent 'toughness' of sedge vegetation, an attribute linked to high levels of substances retarding decomposition, such as lignin and cellulose (Graça & Zimmer 2005).

An introduced biocontrol agent, the alligator weed flea beetle (*Agasicles hygrophila* Selman & Vogt: Chrysomelidae), is present at aquatic alligator weed infestations throughout Northland, Auckland, and Waikato but has not been recorded at Bay of Plenty infestations (C. Winks, W. Mead pers. comms), and is predicted to have a more restricted potential distribution than alligator weed (Julien et al. 1995; Stewart et al. 1999). Both adults and juveniles defoliate the plant, and larvae pupate within stems, achieving substantial control of alligator weed in still bodies of water such as lakes (Philip et al. 1988). 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 et al. 2000). In contrast, terrestrial or uncontrolled aquatic alligator weed reaches peak biomass in summer, followed by winter senescence (Julien et al. 1992; Liu et al. 2004). Stem survival is high in both aquatic and terrestrial habitats in the absence of control, and erect stems collapse at the end of the growing season into a prostrate mat from which new season stems are produced (Julien et al. 1992; Liu et al. 2004).

This study investigated the following four hypotheses: (1) that annual patterns of biomass fluctuation and litter input would differ between alligator weed and native sedge species; (2) that alligator weed litter would decompose more rapidly than that of native sedge species, regardless of vegetation cover; (3) that litter beneath alligator weed would decompose more rapidly than that beneath native sedge species, regardless of litter type; and (4) that litter would decompose more rapidly in litterbags to which macroinvertebrate decomposers had access than in bags from which macroinvertebrates were excluded.

Methods

Study site

Decomposition dynamics were investigated in marginal vegetation at Lake Rotokawau, on the Karikari Peninsula, Northland, New Zealand (34°52' S, 173°19' E). Lake Rotokawau is 21.3 ha in area, shallow, with an iron-pan base (Champion et al. 2005). The alligator weed flea beetle is present on alligator weed throughout this site, resulting in the characteristic dieback pattern associated with flea beetle herbivory.

The surrounding catchment is predominately in animal pasture. Swans and other birds are abundant at the lake. As a result of nutrient inputs from these sources, Lake Rotokawau is classified as hypertrophic by Northland Regional Council (2005). This is the highest trophic level in the council's monitoring system, denoting levels exceeding 96 mg m^{-3} for total phosphorous, and 1558 mg m^{-3} for total nitrogen.

Vegetation at Lake Rotokawau is characterised by small-scale patchiness, with individual patches strongly dominated by a single plant species, be it alligator weed or a native species. Two native sedge species (*Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla and *Isolepis prolifer* (Rottb.) R.Br.) were selected to compare with alligator weed, as there is likely to be some difference between litter of any two species. Both are common at the site and similar ecosystems. Both are perennial and reproduce from seed. *S. tabernaemontani* grows to 1–2 m tall, with stiff, erect culms, and creeping rhizomes (Johnson & Brooke 1998). *I. prolifer* forms short dense stands, with soft culms 0.25–0.6 m long, and often proliferates, forming offset plants from culm ends (Johnson & Brooke 1998). Five replicate patches of alligator weed and each sedge species were selected, interspersed around the lake perimeter.

Biomass

Above-ground biomass was harvested monthly, removing all vegetation from a quadrat (0.25 × 0.25 m) in each replicate patch (five biomass samples per plant species per month). Due to the extractive sampling, a new, randomly selected quadrat was sampled in each patch each month. All visible *Agasicles hygrophila* (adults and juveniles) were counted and removed from excised vegetation. Vegetation was oven-dried at 70°C for 24 h.

Litter

Litter of the two sedges was kept separate, as combining litter from different species may alter decomposition rates (Swan & Palmer 2004), and the patchy nature of the site reduces the likelihood of co-decomposition.

Litter was not oven-dried, to avoid affecting subsequent microbial activity (Boulton & Boon 1991). Fresh litter was air-dried for 3 weeks to a constant weight. Subsamples were oven-dried at 70°C for 24 h for oven-dried mass, and the difference used to convert air-dried weights of litterbags to oven-dried weights. Litterbags were individually weighed and numbered, filled with 2.5 ± 0.06 g of air-dried litter, sealed and reweighed. Litterbags were individually sealed in ziplock bags for transportation.

To investigate whether vegetation cover influenced decomposition rates, litter of all three species was placed 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. Bags were placed at the base of vegetation, where litter might naturally settle. The dense floating mats of *Isolepis prolifer* meant that in these patches bags were further up the water column than under the other two species. All bags were submersed at time of placement, though some intermittent exposure occurred during the experiment due to dropping water levels. Two different litterbag 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, while the large-mesh bags were made of 4-mm-mesh nylon.

Litterbags were placed in the field in December, to coincide with the beginning of alligator weed litter input resulting from herbivory by the biocontrol agent. Five replicate bags of each treatment were removed after each of 3, 5 and 10 weeks. Therefore under alligator weed cover we had 3 litter types × 5 patches × 2 mesh sizes × 3 removal dates. Under each sedge we had 2 litter types × 5 patches × 2 mesh sizes × 3 removal dates. Thus the experiment totaled 210 litterbags. Bags were sealed in individual ziplock bags and returned to a laboratory, had mud removed, then were oven-dried at 70°C for 24 h, determining final dry weight.

Nitrogen, phosphorus, potassium, fibre, cellulose and lignin contents of fresh leaves were analysed by the Landcare Research Environmental Chemistry Laboratory, Palmerston North. Nitrogen, phosphorus and potassium contents were obtained using a modified semi-micro Kjeldahl method (Blakemore et al. 1987), while fibre, cellulose and lignin were obtained using the acid-detergent fibre – sulphuric acid procedure (Rowland & Roberts 1994). All chemical results are expressed as percentages of litter oven-dried at 105°C.

Environmental measurements

Rapidly dropping lake levels exposed many thermometers set to record water temperatures. However, spot water temperature readings were conducted between 0900 and 1000 hours at both the start and finish of the decomposition experiment, in conjunction with dissolved oxygen measurements, using a Mettler Toledo MO128 meter. This was done in December, prior to alligator weed dieback, at the five replicate patches of each vegetation type, and again in March, when substantial amounts of alligator weed were decomposing. In March 10 replicate patches of each vegetation type were tested, as analyses from December indicated that five replicates might not detect potential differences. Minimum and maximum air temperatures were measured monthly from January 2006 at 0.1–0.2 m above water level, in four of the five replicate plots of each vegetation type.

Ten replicate water samples were taken from each vegetation type in December and March. Total nitrogen and phosphorus in the water were determined by persulphate digestion (Hosomi & Sudo 1986) by the Landcare Research Environmental Chemistry Laboratory, Palmerston North. Water depth was measured bimonthly in each of the five replicate patches of each vegetation type.

Analyses

Due to the unbalanced design, two-way ANOVAS tested for differences among litter types or dates within each cover type, and among cover types or dates within each litter type, followed by Tukey's pair-wise comparisons. Where unequal variances could not be overcome by transformation, alpha was lowered to 0.001 for both Levene's test and effects testing (Underwood 1981). The Levene's test p-value for alligator weed litter data was too small to allow a lower alpha level to be used. However, we can trust in the non-significance of the interaction term (Underwood 1981). Games–Howell post hoc analyses were performed for independently significant effect terms, as these do not assume equal variances. Environmental data were analysed using one- or two-way ANOVAS as appropriate. All analyses were performed in R v. 2.0.1 (Ihaka & Gentleman 1996).

Results

Biomass

Alligator weed above-ground biomass peaked in November in 2005 and December in 2006 (Fig. 1). Annual peak biomass varied considerably, being 0.7 kg m^{-2} in 2005 compared with 1.7 kg m^{-2} in 2006, although an earlier peak in 2005 may have occurred prior to sampling beginning. Alligator weed biomass declined as biocontrol numbers began to increase, with beetle abundance following weed biomass with a lag. Weed biomass was lowest in March and stayed low throughout autumn and winter, increasing again in spring. The rapid peak and trough biomass-cycle exhibited by alligator weed equated to a drop of 1.5 kg m^{-2} in biomass over the three months from December 2006 to March 2007.

In contrast, *Isolepis prolifer* above-ground biomass peaked in late summer/autumn when alligator weed biomass was at its lowest, and varied by 0.85 kg m^{-2} over an entire year. *Schoenoplectus tabernaemontani* showed a more similar pattern to 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, dropping by only 0.38 kg m^{-2} between December 2006 and March 2007.

Litterbags

Bag mesh size was not significant in any comparisons. Data for both mesh sizes were combined in all further analyses.

Alligator weed litter decomposed 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 *Schoenoplectus tabernaemontani* not losing this much litter over the entire experiment (Fig. 2a). Mean litter loss beneath alligator weed differed with both removal date and litter species independently (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 *Isolepis prolifer* litter loss intermediate between the two ($P < 0.001$ in all pair-wise comparisons).

Litter decomposing beneath *Schoenoplectus 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 loss from *S. tabernaemontani* bags ($P < 0.001$ in all pair-wise comparisons; Fig. 2b). *S. tabernaemontani* litter loss differed among all removal dates, indicating sustained litter breakdown over the course of the experiment ($P < 0.01$ in all pair-wise comparisons). In contrast, alligator weed litter loss did not differ between any removal dates. Over 70% of alligator litter was lost within the first three weeks, with decomposition subsequently slowing to non-significant levels.

Litter decomposing beneath *Isolepis prolifer* also showed an interaction between removal date and litter type ($F_{2,45} = 5.16$, $P < 0.01$; Fig. 2c). Alligator weed litter loss after 3 weeks' decomposition was less than that at either 5 or 10 weeks' decomposition ($P < 0.05$ and < 0.001 respectively). However, there was no difference in alligator weed litter loss between weeks 5 and 10, indicating that decomposition had slowed by this stage. *I. prolifer* litter did not differ between removal dates. Five *I. prolifer* bags were not recovered at week 10, reducing the number of replicates for this treatment to five. In addition, *I. prolifer* reproduces vegetatively from the ends of culms, and neighbouring plants had grown vigorously into some litterbags. This made determination of the original litter difficult. These two factors may explain 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.

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 (Fig. 3). Litter loss was greater under *Schoenoplectus tabernaemontani* than under either alligator weed or *Isolepis prolifer* ($P < 0.01$ and 0.001 respectively), with no difference between alligator weed and *I. prolifer*.

Schoenoplectus tabernaemontani litter loss was also affected by both vegetation cover type and removal date independently (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.

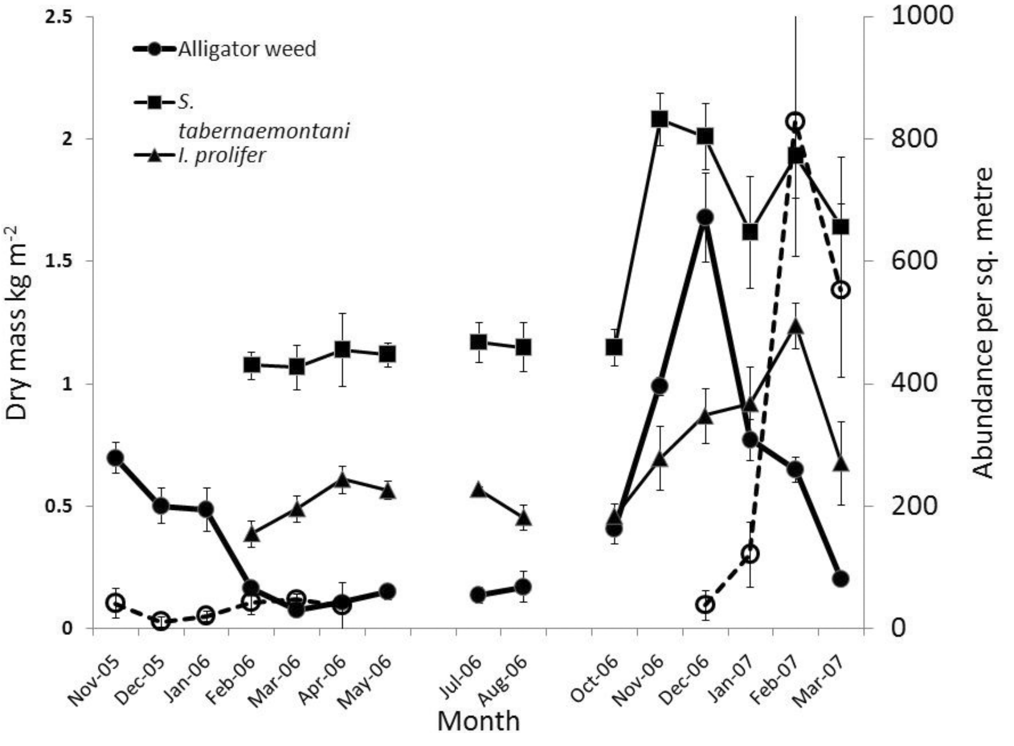

Figure 1. Seasonal variation in above-ground biomass of alligator weed (*Alternanthera philoxeroides*) and two co-occurring native sedge species (*Schoenoplectus tabernaemontani*, *Isolepis prolifer*) along with abundance of the biocontrol beetle *Agasicles hygrophila* on excised alligator weed. Means ± SE.

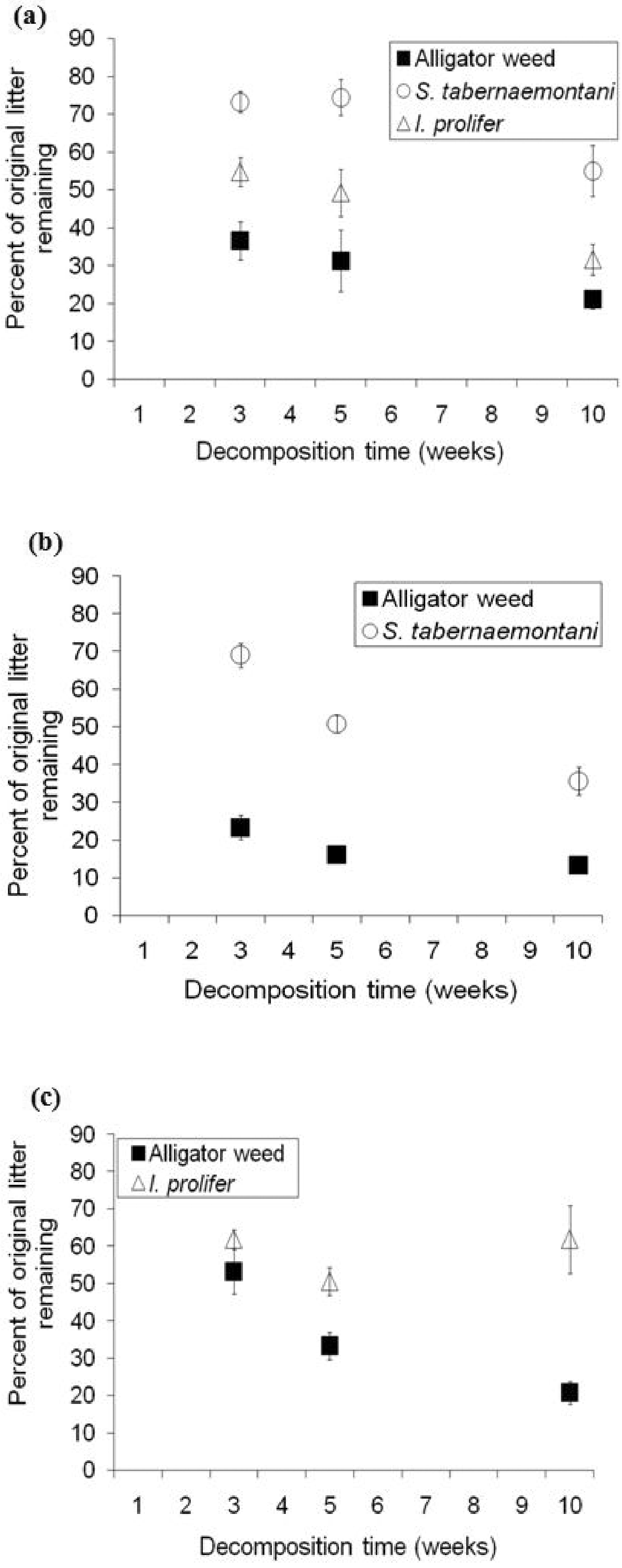

Figure 2. Litter remaining in litter bags following decomposition: (a) under alligator weed (*Alternanthera philoxeroides*) cover, (b) under *Schoenoplectus tabernaemontani* cover, (c) under *Isolepis prolifer* cover. Means ± SE, both bag mesh sizes combined.

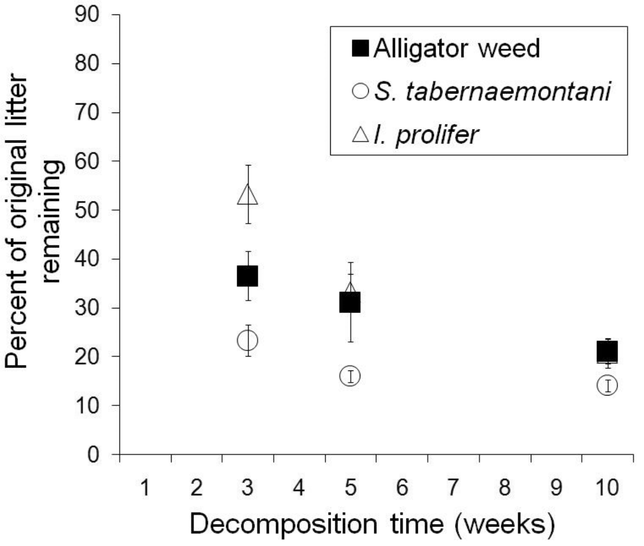

Figure 3. Litter of alligator weed (*Alternanthera philoxeroides*) remaining under different vegetation cover types following decomposition. Means ± SE, both bag mesh sizes combined.

Litter chemistry

Fresh alligator weed litter had proportionally less fibre and cellulose than both *Schoenoplectus tabernaemontani* and *Isolepis prolifer* (Table 1). Lignin levels were similar between fresh alligator weed and *S. tabernaemontani*, both somewhat higher than those in fresh *I. prolifer* litter. Fresh alligator weed litter had proportionately higher nitrogen, phosphorus and potassium than *S. tabernaemontani* litter, but was more similar to *I. prolifer*, particularly in nitrogen and phosphorus (Table 1).

In November 2005, alligator weed covered an estimated 1681.6 m^2 at Lake Rotokawau (I. Bassett, unpubl. data). 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 litterbags (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 could be expected for other nutrients (Table 2).

Environmental analyses

Dissolved oxygen varied with vegetation type (Table 3), being lower in water sampled beneath *Isolepis prolifer*, than either *Schoenoplectus tabernaemontani* or alligator weed.

Nitrogen and phosphorus also differed between vegetation types (Table 3). Water from *Schoenoplectus tabernaemontani* sites contained less nitrogen than from either alligator weed or *Isolepis prolifer* sites, and less phosphorus than from alligator weed sites. Sampling date did not affect nitrogen, phosphorus or dissolved oxygen (P = 0.62, 0.87 and 0.24 respectively; Table 3). However, while not significant, phosphorus in water beneath alligator weed increased following dieback, contrasting with the trend under both native sedge species. Water temperature was lower in *I. prolifer* patches than in either alligator weed or *S. tabernaemontani* patches in March (Table 4). There were no differences in water temperature in

Table 1. Chemical composition of fresh litters. All values expressed as percent of total dry mass. Values are based on a single sample.

Litter species	Fibre	Cellulose	Lignin	Nitrogen	Phosphorus	Potassium
Alligator weed (*Alternanthera philoxeroides*)	25.0	20.3	4.1	2.1	0.29	5.2
Schoenoplectus tabernaemontani	42.8	37.2	4.9	1.0	0.12	1.8
Isolepis prolifer	27.5	25.1	1.6	2.7	0.28	3.4

Table 2. Estimated nutrient inputs from alligator weed (*Alternanthera philoxeroides*) 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 per whole lake	kg m^{-2}	kg per whole lake
Nitrogen	0.01	16.8	0.03	51.2
Phosphorus	0.002	2.6	0.004	7.1
Potassium	0.03	46.4	0.08	126.8

Table 3. Effect of vegetation type and sampling month on water chemistry. Vegetation type but not sampling month affected each variable in two-way ANOVAs. Within month, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Values with the same letter are not significant at $P < 0.05$.

Environmental variable	Month	Mean (SE)		
		^{1}Alligator weed	^{2}*S. tabernaemontani*	^{3}*I. prolifer*
Dissolved oxygen (%)	December	74.3 (3.7)^{a}	77.2 (4.7)^{a}	15.1 (2.5)^{b***}
	March	63.9 (13.1)^{a}	109.1 (8.4)^{a}	21.2 (14.1)^{b***}
Total nitrogen (mg L^{-1})	December	9.5 (3.2)^{a}	4.1 (0.9)^{b*}	9.0 (2.0)^{a}
	March	11.1 (2.7)^{a}	3.7 (0.4)^{b*}	10. 1 (3.0)^{a}
Total phosphorus (mg L^{-1})	December	1.5 (0.7)^{a}	0.3 (0.1)^{b*}	1.4 (0.5)^{a}
	March	1.9 (0.8)^{a}	0.2 (0.1)^{b*}	1.3 (0.5)^{a}

^{1}*Alternanthera philoxeroides,* ^{2}*Schoenoplectus,* ^{3}*Isolepis*

Table 4. Water and air temperatures for different vegetation types. Water temperatures are spot readings, while air temperatures are monthly values. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Values with the same letter are not significant at $P < 0.05$.

Environmental variable	Month	Mean (SE)		
		^{1}Alligator weed	^{2}*S. tabernaemontani*	^{3}*I. prolifer*
Water temperature (ºC)	December	20.7^{a} (0.7)	20.5^{a} (0.2)	19.4^{a} (0.2)
	March	24.4^{a} (0.3)	23.9a (0.3)	22.3^{b***} (0.2)
Minimum air temperature (ºC)	January	4.7^{a} (0.9)	10.7^{b**} (0.3)	4.7^{a} (1.2)
	July	0.3^{a} (0.3)	1.3^{a} (0.3)	0.3^{a} (0.3)
	September	2.3^{ab} (0.7)	3.8^{a} (0.7)	0.8^{b*} (0.3)
Maximum air temperature (ºC)	January	29.7^{a} (0.9)	30.3^{a} (0.9)	29.0^{a} (1.0)
	July	23.0^{a} (2.7)	22.3^{a} (0.7)	23.3^{a} (0.9)
	September	25.0^{a} (4.4)	24.4^{a} (1.7)	27.0^{a} (2.5)
Water depth (m)	January	0.21^{a} (0.03)	0.24^{a} (0.01)	0.25^{a} (0.06)
	July	0.67^{a} (0.03)	0.69^{a} (0.01)	0.70^{a} (0.05)

^{1}*Alternanthera philoxeroides,* ^{2}*Schoenoplectus,* ^{3}*Isolepis*

December (Table 4). Minimum air temperatures tended to be higher in *S. tabernaemontani* plots than in either *I. prolifer* or alligator weed plots, probably due to *S. tabernaemontani*'s tall structure, which would trap still air, thus retaining heat overnight (Table 4). No differences in maximum air temperature or water depth were detected between vegetation types (Table 4).

Discussion

Effect of litter type

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

Differences in decomposition rates between litter types relate in part to differences in chemical composition. Fresh alligator weed litter had higher nitrogen and phosphorous concentrations than *Schoenoplectus tabernaemontani*, along with lower fibre, cellulose and lignin levels, all of which have been linked to high decomposition rates in other plant species (Gonçalves et al. 2004). Gonçalves et al. (2004) found *Nymphaea ampla* Kotschy ex Casp. decomposed 26 times faster than *Typha domingensis* Pers., which they attributed to higher nitrogen and phosphorous levels in *N. ampla*, along with a lower percentage of cell wall fraction. Fresh *Isolepis prolifer* litter was intermediate between alligator weed and *S. tabernaemontani* in much of its chemical make-up, consistent with its intermediate decomposition rate.

Implications of alligator weed biomass dynamics

Alligator weed growth and decomposition is consistent with other invasive species with rapid growth rates, high leaf nutrient levels and fast decomposition combined in a high-productivity, rapid-nutrient-cycling strategy (Cornelissen et al. 1999; Allison & Vitousek 2004).

In addition to rapid decomposition, alligator weed exhibited a large litter input over a short space of time, contrasting with both sedge species, which showed smaller and more gradual seasonal changes in biomass. A large input of rapidly decomposing litter may result in a sharp peak of nutrients released in a manner uncharacteristic of pre-existing native vegetation. This has a range of potential consequences, 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 & Von Holle 1999; O'Dowd 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, but were not observed to the same extent at two nearby uninvaded lakes, despite these lakes having similarly high background nutrient levels (Northland Regional Council 2008; I. Bassett unpubl. data). 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* (L.f.) Royle and native aquatic plants reduced algal blooms in artificial ponds by reducing nutrient input from herbivory-induced leaf decomposition (Nachtrieb et al. 2008).

Given high nutrient levels are typical of other uninvaded lakes in the region (Northland Regional Council 2008), alligator weed decomposition may not be having a significant effect on ecosystem processes at this particular site. However, although more aggressive in nutrient-rich environments, alligator weed does tolerate low-nutrient environments better than other weeds such as water hyacinth (*Eichhornia crassipes*) and eurasian milfoil (*Myriophyllum spicatum* L.) (Rogers & Davis 1971). Where alligator weed does invade less nutrient rich waterways it may significantly alter nutrient cycling.

Role of the alligator weed flea beetle

Fluctuations in beetle abundance tracked behind weed biomass in a pattern similar to that predicted by models for simple predator–prey systems (Berryman 1992). The change in weed biomass dynamics caused by the beetle is important not only in the volume of litter decomposing, but also in the timing of litter input (rapid summer dieback rather than a summer biomass peak followed by winter senescence), with decomposition rates generally faster in summer due to warmer conditions.

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

Alternative pathways for nutrients

Nutrients released by alligator weed may have followed alternative pathways rather than direct decomposition. Similarly, various factors may have affected the accuracy of estimated biomass inputs. Due to reabsorption from dying leaves, natural litter may be poorer in nutrients than that used here (Berg & Laskowski 2005). However, insect herbivory can increase rates of 'greenfall', where green leaf fragments enter the system as litter. These tend to be higher in nitrogen and phosphorus than senescent leaves, thus accelerating decomposition rates (Fonte & Schowalter 2005). Furthermore, as the drop in alligator weed biomass results from 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, and some dispersal of beetles out of the system may occur. Factors governing nutrient release 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.

Vegetation cover type

All litters showed a pattern of most rapid decomposition beneath *Schoenoplectus tabernaemontani*. 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, litterbags set at the base of *Isolepis prolifer* mats dried out more often than those in *S. tabernaemontani* dominated areas. This is consistent with the trend elsewhere towards faster decomposition rates in humid or aquatic environments compared with dry terrestrial situations (Battle & Mihuc 2000; Lindsay & French 2004). While temperature data were limited, the data suggest that *S. tabernaemontani* patches may have been somewhat warmer, and *I. prolifer* patches somewhat cooler. Decomposition rates tend to be elevated in warmer environments, due to enhanced activity of microbial and invertebrate decomposers (Berg & McClaugherty 2003).

Schoenoplectus tabernaemontani culms often decompose considerably while still upright and largely emergent above water (I. Bassett pers. obs.), thus potentially decomposing more slowly than observed in this study due to drier conditions, and also reabsorbing a higher proportion of nutrients. Differences in decomposition rates particularly beneath alligator weed and *S. tabernaemontani* may therefore have been over-represented. As *Isolepis prolifer* forms such an impenetrable mat, litter is more likely to be retained amongst the vegetation, and slower decomposition observed under this plant therefore may be experienced under natural conditions as well. This mat structure, with considerable associated trapped organic matter, is also likely to have contributed to the very low dissolved oxygen levels recorded in *I. prolifer* plots.

As decomposition rates beneath the two native species differed substantially, 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 the invasive herb *Tradescantia fluminensis* Vell. as it did in non *T. fluminensis* infested plots, and this was attributed to altered microclimate (Standish et al. 2004). Similarly, elevated decomposition rates beneath bitou bush compared with native vegetation were attributed to changes in microclimate, including moisture (Lindsay & French 2004). This effect of microclimate 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.

Invertebrates

The lack of differences in decomposition between large- and small-mesh litterbags indicates macroinvertebrates did not play a dominant role in decomposition. Similar results have been found for litterbag experiments in other New Zealand swamp systems (Pegman & Ogden 2005, 2006). Similarly, microbes were the primary decomposers in stagnant backwater areas in Louisiana, with invertebrates more important in faster flowing riverine sites (Battle & Mihuc 2000).

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. However, the already degraded state of the study ecosystem may have masked potential effects of alligator weed on nutrient dynamics. The role of the biocontrol agent in promoting litter input highlights the potential not only of invasive species, but also of their biocontrol agents, to influence ecosystem processes such as nutrient cycling in invaded systems.

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