The ecological impact and control of an invasive weed *Tradescantia fluminensis* in lowland forest remnants.

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For Kim and Shirley
my first teachers

A passenger's guide to New Zealand trees
(heading south on Highway 1)

Cabbage trees
like slender ladies
dancing on old, worn carpet,
holding pom poms
that have seen better days

Showy pohutukawa
every summer, crowns its
old, mutton-like trunk,
with splashes of mardi-gras red

Pinus radiata
lined up like
candles on a cake
or tourists on the top deck
of the Cook Straight ferry

The forest remnant
like an old photograph left to fade
and tatty about the edges
        Among the weary veterans
        a pukatea stands proud
        draped in a kiekie cloak
        Tradescantia about its feet,
                ready to receive
                the fat pigeons in clean singlets
                who are sure to visit.

Tradescantia-affected Monro's Bush, Manawatu.

Abstract

While there is a general awareness of the global march of invasive weeds, there are relatively few studies which measure the ecological impact of these species on the systems they invade. *Tradescantia fluminensis* Vell. is an invasive weed of canopy-depleted native forest remnants in New Zealand where it carpets the ground and prevents regeneration. In three lowland forest remnants in the lower North Island I measured the ecological impact of *Tradescantia* by comparison of affected and non-affected areas of forest. In addition, I evaluated three methods for control of Tradescantia in two heavily infested forest remnants in the lower North Island.

The impact of *Tradescantia* on native forest regeneration is evident by the decreasing native forest seedling species richness and abundance with increasing *Tradescantia* biomass. Forest regeneration was prevented because of decreasing light levels beneath *Tradescantia.* The compositions of the extant vegetation, seed rain and seed bank are consistent with this interpretation. Seedlings of some native species were more tolerant of *Tradescantia* than others, though the growth to emergence of even the most tolerant species was compromised in dense *Tradescantia.*

While shading of native plants by invasive weeds is a well-studied phenomenon, comparatively little is known about the effects of weeds on ecosystem processes. Tradescantia increases litter decomposition and alters nutrient cycling by modifying the litter quality and microclimate within these forest remnants. The annual uptake of nutrients by *Tradescantia* was a significant amount of the nutrient inputs via litterfall, which (with the exception of Ca) exceeded the amounts of these nutrients held within the forest litter layer, but was only a small amount of these nutrients held within the topsoil.

It is likely that the microclimate within *Tradescantia* that promotes increased litter decomposition also affects invertebrate communities. Epigaeic invertebrates were sampled using pitfall traps. RTU richness was lower in *Tradescantia* plots compared with non-*Tradescantia* plots, though not statistically significant. Two-way indicator species and detrended correspondence analyses separated *Tradescantia* and non-*Tradescantia* plots within sites. Overall, impacts of *Tradescantia* were apparent despite large differences in invertebrate assemblages among sites. The possible biological consequences of the community and ecosystem impacts outlined in this and the preceding two paragraphs are discussed.

A reduction of *Tradescantia* biomass to ~80 gm^{-2} (~40% cover) is compatible with native forest regeneration. Chemical and manual control methods had limited success in controlling *Tradescantia*, whereas artificial shading significantly reduced its biomass after 17 months. Native sub-canopy trees were planted into *Tradescantia* to achieve natural shading over large areas of forest, but were too young to assess whether or not they will overshade the *Tradescantia*. My research supports the theory that management needs to target the attributes of these forest systems that make them invasible rather than *Tradescantia*, otherwise they remain invasible to other weeds. Therefore, an integration of targeted control and tree planting to improve canopy cover is suggested as a means to arrest the decline of *Tradescantia*-affected forest remnants.

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Arrangement of this thesis

The data chapters of this thesis have been written as stand-alone manuscripts for publication in refereed journals. Inevitably this has led to some repetition of the material and variation in the format among chapters. Each manuscript is set in the style required by the target journal. Where appropriate, manuscripts are co-authored. Alastair Robertson and Peter Williams contributed significant intellectual input and practical input regarding data capture to Chapters 1 & 2. Alastair also made a substantial contribution to the data analysis, including the suggestion of the statistical techniques employed in Chapter 1. Neal Scott contributed 'ecosystems expertise' to Chapter 2. Specifically, he suggested the resin bag study and provided a technician to do the nutrient assays required. Duncan Hedderley is the Statistician who helped design and analyse the litter decomposition study (Chapter 2). Ian Stringer co-supervised and played a significant role in obtaining funding for some of the research. However, in all cases I am senior author, which indicates the major scientific contribution to the study, and the primary role in writing the manuscript.

Chapter 1. Standish, R.J., Robertson, A.W. and Williams, P.A. 2001. The impact of an invasive weed *Tradescantia fluminensis* on native forest regeneration. Journal of Applied Ecology 38 (6): 1253–1263.

Chapter 2. Standish, R.J., Williams, P.A., Robertson, A.W., Scott, N.A. and Hedderley, D.I. (submitted) Invasion by *Tradescantia fluminensis* increases decomposition rate and alters nutrient cycling in New Zealand lowland forest remnants. Biological Invasions.

Chapter 3. Standish, R.J. (submitted) Impact of an invasive clonal herb on epigaeic invertebrates in forest remnants in New Zealand. Biological Conservation.

Chapter 4. Standish, R.J. (accepted) Experimenting with methods to control *Tradescantia fluminensis*. New Zealand Journal of Ecology.

Appendix 1 is a report I prepared on behalf of Landcare Research for the Department of Conservation.

Appendix 1. Standish, R.J., 2001. Prospects for biological control of *Tradescantia fluminensis* Vell. (Commelinaceae). DOC Science Internal Series #9. Department of Conservation, Wellington, 25p.

General introduction

Weed impacts

While there is a general awareness of the global march of invasive weeds, there are relatively few studies which measure the ecological impact of these species on the systems they invade.

The potential impacts of a weed on community and ecosystem properties are numerous and varied (Walker & Smith, 1997), and most likely to occur when the invader is ecologically distinct from the native species they replace (Walker & Smith, 1997; Woods, 1997). For example, as a nitrogen fixer, the fayatree *Myrica faya* has a novel method of resource aquistion compared with the native Hawaiian species, which has allowed it to invade and dominate the low nutrient volcanic soils of Hawaii and also primary succession (Vitousek & Walker, 1989). The invasion of African fynbos by *Acacia* and *Hakea* species has lead to an increased density and biomass of vegetation that increases the fire hazard of invaded compared with non-invaded stands (Versfeld & van Wilgen, 1986). This system is one of the few for which information is available on the impacts to fauna, a comparison of the ant assemblages of pure fynbos and fynbos invaded by *Acacia saligna* revealed differences in ant species composition and abundance, which was decreased in invaded fynbos (French & Major, 2001). A weed that is not so ecologically different to the native vegetation it replaces is bitou bush *Chrysanthemoides monilifera* that has invaded coastal golden wattle *Acacia longifolia* habitat along the temperate east coast of Australia (Weiss & Noble, 1984). Bitou bush has had minimal impacts on bird (French & Zubovic, 1997) and invertebrate assemblages (French & Eardley, 1997).

Measuring impact

A difficulty inherent in measuring and demonstrating weed impacts is the confounding influence of unnatural (i.e., anthropogenic) disturbances that are usually associated with the establishment of the weed, although this is not always the case (e.g., *M. faya*, *C. monilifera*). If anthropogenic disturbance is identified as a likely precusor to invasion then its confounding influence can be overcome by the use of: weed addition/ removal experiments, where the same sites are compared before and after manipulation; or time- sequence studies that follow the invasion process (Adair & Groves, 1998). More frequently however, a number of sites that are similar in all aspects other than the presence/ absence of the weed, are selected for comparison (e.g., French & Major, 2001). Each approach has advantages and disadvantages, an obvious disadvantage of weed addition is the risk of it spreading, whereas a multi-site comparison is often the most rapid and the most practical assessment available (Adair & Groves, 1998).

Management implications

A detailed knowledge of a weed's impact can determine the appropriate cause of action for conservation managers, especially if a negative impact has been assumed but not measured. There are numerous examples where an impact has been assumed in order to rank the weeds of conservation land in New Zealand and so to prioritise weed control efforts (Owen, 1997). For management of individual weeds, it is especially useful to know the level of control required for protection of native species. Such 'ecological damage thresholds' have been estimated for invasive wasps in New Zealand beech forest, which have provided conservation managers with a clear guideline about the level of control required for protection of some key native invertebrate species (Beggs & Rees, 1999). This information is often lacking in weed control programmes.

Tradescantia

Tradescantia fluminensis Vell. (syn. *T. albiflora*) is native to South America (Esler, 1978), and has naturalised in New Zealand (Kelly & Skipworth, 1984a), eastern Australia (Dunphy, 1991), Spain (Landcare Research, 1998), Russia (Tolkach et al., 1990) and the south-eastern USA (Farr et al., 1989; Wunderlin, 1998). Within its native range, *Tradescantia* is considered an agricultural weed (Dos Santos & De Araujo, 1971 cited in Kelly & Skipworth, 1984a; Robert Barreto, pers. comm.).

Tradescantia was first introduced to New Zealand in 1910 by a Manawatu farmer (Kelly & Skipworth, 1984a), and was recorded as being naturalised in Awanui, Northland, soon after (Carse, 1916). While it is not known to set seed in New Zealand (Healy & Edgar, 1980), *Tradescantia* has dispersed widely by the spread of fragments dumped in forest remnants as garden refuse, or naturally via streams (Esler, 1978). Livestock and road machinery have also been known to disperse fragments (Ogle & Lovelock, 1989; Department of Conservation, 1998). Fragments as small as one cm can successfully establish new plants (Kelly & Skipworth, 1984a).

The distribution of *Tradescantia* within New Zealand is restricted by its intolerance of frost (Bannister, 1986), and arguably, by its reliance on streams, people or animals to disperse. The absence of *Tradescantia* from large tracts of forest may be due to either of these limitations. In most cases, *Tradescantia* invades lowland forest remnants that have been modified by one or more of the following: drainage, selective logging, cattle and possum grazing. Once introduced to a site, available light is an important factor limiting the spread and biomass accumulation of *Tradescantia* (Kelly & Skipworth, 1984a; Maule et al., 1995) as is substrate (Smale & Gardner, 1999) and soil fertility (Ogle & Lovelock, 1989). In addition, there is some evidence that it is drought sensitive (pers. obs.), which may limit its biomass accumulation, or perhaps its ability to establish (e.g., in the eastern Wairarapa (Howell et al. 2000)). Currently, the distribution of *Tradescantia* on conservation lands spans most of the North Island (including offshore islands) except for the central region, and in the South Island its distribution extends from the northern-most tip south along the west coast to Haast (Fig. 1). *Tradescantia* is also common outside of conservation lands (e.g., suburban gardens), and continues to invade new sites (Owen, 1997).

The aims of this thesis are to measure the ecological impact of *Tradescantia* in New Zealand and evaluate methods for its control. Three of four data chapters focus on measuring the impact of *Tradescantia*, using a variation of the multi-site comparison approach. I compared infested and non-infested plots (blocked design) within sites which meant that, at least for comparisons within sites, potentially confounding influences were controlled for (e.g., disturbance histories). I used two to three sites to assess the impact of *Tradescantia* within lowland forest remnants generally. As the approach to measuring impact was largely comparative, each chapter measures variables other than *Tradescantia* which may account for the outcome (e.g., seed supply – which, if reduced, could account for a lack of seedlings in *Tradescantia*) or uses more than one approach to measure impact (e.g., direct and indirect

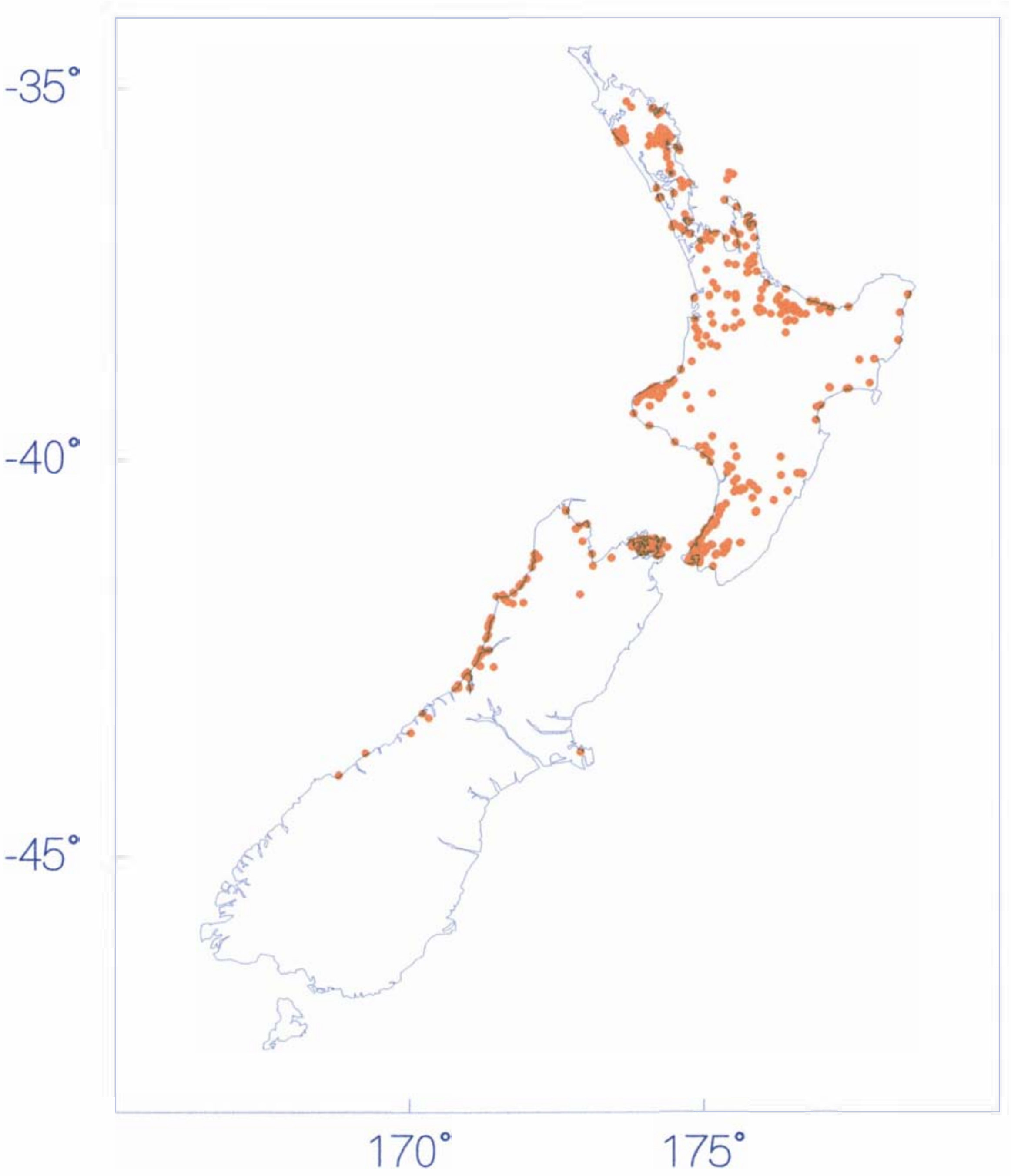


Figure 1. Distribution of *Tradescantia fluminensis* on conservation lands in New Zealand. Data supplied by Te Papa Atawhai, Department of Conservation, 2001.

measures of the effect of *Tradescantia* on litter decomposition). As these study sites were small and *Tradescantia* tended to occur at the forest edges, particular attention was paid to unravelling the potentially confounding influences of edge effects (Saunders et al., 1991; Murcia, 1995), e.g., reduced canopy cover at forest edges could result in reduced litterfall relative to forest interior which could account for a reduced crop of standing litter beneath *Tradescantia*.

I used an experimental approach to evaluate three methods for the control of *Tradescantia* in two heavily infested forest remnants (Chapter 4) and used the threshold level for regeneration of native species derived from Chapter 1 as a guide for success. As a fourth option, I reviewed the potential for biological control of *Tradescantia* in New Zealand (Appendix 1).

Chapter 1: The impact of an invasive weed *Tradescantia fluminensis* on native forest regeneration.

Kohekohe *Dysoxylum spectabile* in *Tradescantia* at Denton's Bush, Otaki.

Summary

1. *Tradescantia fluminensis* is an invasive weed of New Zealand, eastern Australia and Florida, where it carpets the ground in canopy-depleted native forest remnants and prevents regeneration. The aim of our study was to determine the *Tradescantia* biomass levels at which this occurs.

2. At two podocarp/broad-leaved forest remnants in New Zealand, we show that *Tradescantia* biomass increases logistically with available light, to a maximum at 10–15% full light. The maximum *Tradescantia* biomass was greater at the wetter site (819 gm^{-2}) than at the comparatively dry site (695 gm^{-2}).

3. Native forest seedling species richness and abundance decreases exponentially with increasing *Tradescantia* biomass, for example, from 3.4 and 81.5 m^{-2} respectively in the absence of the weed, to 0.37 and 6.28 m^{-2} at maximum *Tradescantia* biomass. We attribute this to decreasing light levels beneath *Tradescantia.* Under approximately 500 gm^{-2} of *Tradescantia* (~100% weed cover), available light is reduced to <1% full light.

4. The compositions of the extant vegetation, seed rain and the seed bank are consistent with our interpretation that light availability drives the differences in seedling species richness and abundance between *Tradescantia* and non-*Tradescantia* habitats.

5. We estimated the response of seedlings of six commonly occurring native woody species to *Tradescantia* biomass. *Macropiper excelsum* appears to be the least tolerant: its "LD50" (the biomass of *Tradescantia* at which its abundance is reduced to 50% of the maximum) is approximately 12 gm^{-2}, whereas *Dysoxylum spectabile* is the most tolerant with an LD50 of 40 gm^{-2}.

6. *D. spectabile* germination and early seedling establishment can occur in dense *Tradescantia*, but the probability of survival over 20 months decreased logistically with increasing *Tradescantia* biomass. The probability of survival at 100% weed cover was 6% compared with 84% for seedlings in non-*Tradescantia* habitat. We estimated that emergence above the weed occurs only where cover of *Tradescantia* is <200 gm^{-2} (70–90% cover).

7. We predict that increases in native species richness and abundance will accumulate with increasing suppression of the weed. Imposing shade by planting trees to improve the canopy cover is a potentially useful tool for restoration of *Tradescantia*-affected forest remnants.

Key-words: Forest restoration, forest light, seed bank, seed rain, seedling emergence, weed biomass.

Introduction

The potential effects of invasive weeds on plant communities include a reduction in the abundance and species richness of native plants, often leading to changes in the physical structure of the community (Smith 1994; Mullett & Simmons 1995; Holmes & Cowling 1997; review by Woods 1997; Roques, O'Connor & Watkinson 2001). Competition for light is often cited as being the primary mechanism for change following weed invasion, resulting in shading of native plants by invasive shrubs (Hobbs & Mooney 1986; Woods 1993; Smith 1994; Mullett & Simmons 1995; Holmes & Cowling 1997; Hutchinson & Vankat 1997), ferns (Walker 1994) and vines (Thomas 1980; Baars & Kelly 1996).

Tradescantia fluminensis Vell. (Commelinaceae) (also known as *T. albiflora*; R. Faden, personal communication) is a ground-smothering perennial herb native to South America (Esler 1978), which has invaded forest remnants in New Zealand (Kelly & Skipworth 1984a), eastern Australia (Dunphy 1991) and Florida (Wunderlin 1998). In New Zealand, the degraded state of most lowland forest remnants of the North Island and northern South Island (Timmins & Williams 1991) has resulted in increased forest interior light levels favourable for invasion and biomass accumulation of *Tradescantia* (Kelly & Skipworth 1984a). *Tradescantia* frequently dominates the ground cover within these forest remnants where canopy cover is reduced, and at the forest margins, preventing native forest regeneration by shading seedlings (Kelly & Skipworth 1984a). In contrast, under shaded conditions typical of a closed-canopy forest, *Tradescantia* does not attain high biomass, or prevent seedling emergence.

The aims of our study were to determine the relationship between *Tradescantia* biomass and available light, and the subsequent impact of shading by *Tradescantia* on seedling emergence within forest remnants in southern North Island, New Zealand. As seed supply directly affects seedling emergence, we examined the extant vegetation, annual seed rain and the seed bank of *Tradescantia*-affected and non-affected areas of forest. Lastly, we estimated the tolerance of individual forest species to increasing *Tradescantia* biomass. Ultimately, our study aimed to determine the *Tradescantia* biomass levels at which native forest regeneration is prevented.

Study sites

The main study sites were three lowland podocarp/broad-leaved forest remnants in the lower North Island, New Zealand, Rangitawa Bush (12.4 ha) on an old river terrace (40°06.0′ S, 175°27.6′ E; 100 m a.s.l.); Kirkwell Bush No. 4 (14.0 ha) on an old river terrace (40°47.8′ S, 175°10.3′ E; 40 m a.s.l.); and Denton's Bush (2.0 ha) on a flood plain (40°48.0′ S, 175°11.4′ E; 20 m a.s.l.). Mean annual rainfall for Rangitawa Bush is approximately 1046 mm and mean annual temperature is approximately 13 °C, recorded at Marton climate station, 4 km NW of the site (National Institute of Water and Atmospheric Research 2000). Mean annual rainfall for Kirkwell Bush and Denton's Bush is approximately 1176 mm and mean annual temperature is approximately 13 °C, recorded at Levin climate station, 18 km N of both sites (National Institute of Water and Atmospheric Research 2000).

At each site, three 20 m × 20 m plots were selected in areas of greatest *Tradescantia* infestation (> 75% cover at Rangitawa Bush and Denton's Bush, > 88% cover at Kirkwell Bush) and, adjacent to each, a 20 m × 20 m plot was selected where *Tradescantia* did not occur or was relatively sparse (< 5% cover at Rangitawa Bush and Denton's Bush, < 16% cover at Kirkwell Bush) (*n*= 6 plots/ site). Ground cover other than *Tradescantia* comprised litter, bare soil, ferns, woody seedlings and grasses. Vegetation cover was visually estimated at 0.3–2 m, 2–5 m, 5–12 m, and > 12 m above the ground within each plot. Plant nomenclature follows Allan (1961), Moore & Edgar (1970), Healy & Edgar (1980), Connor & Edgar (1987) and Webb, Sykes & Garnock-Jones (1988).

Rangitawa Bush has large canopy gaps, a result of selective logging in the late 19th and early 20th centuries (personal observation). *Alectryon excelsus*, *Beilschmiedia tawa* and *Melicytus ramiflorus* dominate the upper canopy in the non-*Tradescantia* plots, while only *A. excelsus*

comprises more than 10 % of any layer in the *Tradescantia* plots. *Podocarpus totara* also occur occasionally at canopy level, as well as *Kunzea ericoides* in non-*Tradescantia* plots. *Macropiper excelsum* dominates the understorey, with some *Coprosma areolata*.
Denton's Bush has a relatively intact canopy, but sparse sub-canopy and understorey layers, as a result of stock grazing and possum *Trichosurus vulpecula* Kerr browsing before 1988 (M. Lutz, personal communication). The forest canopy mainly comprises *B. tawa* and *Laurelia novae-zelandiae*, with a sub-canopy of *M. ramiflorus*, particularly in *Tradescantia* plots, and *D. spectabile*, with some *Hedycarya arborea*. *M. excelsum* dominates the understorey, particularly in non-*Tradescantia* plots.

Kirkwell Bush has regenerated, after forest clearance for farming, in the last 100 years and has a short-statured, even-aged canopy and a sub-canopy punctuated by gaps that are probably a consequence of stock grazing before 1984 (B. Empson, personal communication). Stock damage is also evident in the understorey. The forest canopy is exclusively *Podocarpus totara*. The sub-canopy comprises *D. spectabile* and *M. ramiflorus*. The understorey includes *Coprosma rhamnoides* and *Pennantia corymbosa* in *Tradescantia* plots and *C. rhamnoides*, *Geniostoma ligustrifolium* and *M. excelsum* in non-*Tradescantia* plots.

Materials and methods

SEED RAIN

At Denton's Bush and Rangitawa Bush, seed rain was collected in funnels of 0.38 m diameter, constructed from heavy nylon shade cloth (0.5 mm mesh) tied at the bottom for access. Funnels were attached to three stakes at 1 m above ground level. Three funnels were set up in each 20 m × 20 m plot ($n = 18$ per site). Funnels were emptied every 30 ± 1 days for 12 months, from December 1997 to November 1998. *D. spectabile* seed output varies widely between years (A. Dijkgraaf, personal communication), so we collected seed again in June and July 1999 to target this species. Funnels were accessible to seed predators, and there was evidence of rat *Rattus rattus* L. predation of *Rhopalostylis sapida* seed at Denton's Bush. After harvest, seeds were dried at 30°C for 2 days, identified and counted.

SEED BANK

To exclude seed rain, a 50 cm × 50 cm piece of perforated black plastic was secured over ground cleared of vegetation and litter, adjacent to each seed funnel in *Tradescantia* and non-*Tradescantia* plots ($n = 18$ per site), at Denton's Bush and Rangitawa Bush. Plastic squares were left in place from February 1998 to March 1999. In March 1999, eight soil samples were collected from beneath the plastic squares, to a depth of 2.5 cm using a soil corer of diameter 5.4 cm. These samples were combined for each 50 cm × 50 cm sub-plot, and stored at 4 °C for ~19 days to stimulate germination (Fountain & Outred 1991).

Each soil sample was spread over a 2:1 river sand:zeolite mix to a depth of <1 cm in seed germination trays. A control tray containing 2:1 river sand:zeolite mix was set up to test for contaminant seed within the glasshouse. Samples were watered regularly and temperature in the glasshouse ranged from 2–38 °C (winter and summer maximums were 28 °C and 38 °C respectively). Native germinants were recorded as they appeared, for 45 weeks. Unidentified seedlings were transferred to pots to mature. Seeds germinating from these samples were assumed to have remained dormant in the soil seed bank for at least 13 months and so were part of the persistent soil seed bank.

ESTIMATING *TRADESCANTIA* BIOMASS

In 23, 0.25 m^2 quadrats at three sites with a range of *Tradescantia* biomass levels—Denton's Bush, Monro's Bush (40° 23.3' S, 175° 36.7' E) and Massey University Campus (40° 23.0' S, 175° 37.1' E)—we measured percentage cover (assessed visually) and standing height of five randomly selected *Tradescantia* stems, measured to the base of the uppermost leaf (± 10 mm). We harvested all the *Tradescantia* (including roots) from each quadrat and oven dried it at 80 °C for 2 days for biomass determination. Later, we determined the relationship between *Tradescantia* biomass (gm^{-2}) and the percentage cover of *Tradescantia* multiplied by the mean standing height (mm) of five random *Tradescantia* stems. This derived parameter (x) was a good predictor of *Tradescantia* biomass (y), $y = 0.014x$ ($R^2 = 0.66$, $F_{1,22} = 42.63$, $P < 0.0001$) when the line was forced through zero.

FIELD SURVEY

In June 1998 at Denton's Bush and Kirkwell Bush, and in January 1999 at Rangitawa Bush, we estimated the biomass of *Tradescantia* (using the predictor as above) and abundance together with the height of native woody seedlings in 0.25 m^2 quadrats. At each study site we selected six or seven 25 m × 10 m or 50 m × 10 m plots, depending on the extent of *Tradescantia* infestation. These plots were usually separate from, but occasionally overlapped, the 20 m × 20 m plots mentioned previously. Ten and twenty 0.25 m^2 quadrats were randomly placed within the 250 m^2 and 500 m^2 plots respectively. So as not to flatten the *Tradescantia*, we used a 0.5 m × 0.5 m metal quadrat positioned on a set of 0.5 m legs. Within each we recorded percentage cover of ferns and grasses; the height (± 10 mm) of all native woody seedlings with at least two true leaves; and *Tradescantia* biomass. Lastly, at Denton's Bush, we measured the survival and growth of 35 *D. spectabile* seedlings in 0–526 gm^{-2} *Tradescantia*, for 20 months beginning 2 Aug 1998.

LIGHT MEASUREMENT

At Denton's Bush (28 July – 4 Aug 1998) and Kirkwell Bush (28 Aug – 4 Sept 1998), we made integrated measurements of incident radiation using simple, photosensitive paper light meters (Friend 1961). The light meters were calibrated using a Li-Cor quantum light sensor (Licor 190SA quantum sensor from Li-Cor Inc, Lincoln, Nebraska 68504, USA) attached to a Campbell data logger (CR21X datalogger from Campbell Scientific, Logan Utah 84321, USA), set up to record full sunlight. Adjacent to the sensor, two replicate booklets were exposed to each of 15 light integrals, ranging from 15 minutes to 1 week in length. The meter scores were regressed against the cumulative light received by the quantum light sensor. The predicted line, log cumulative light received (micromol photons m^{-2} s^{-1}) = -2.22 + (0.63 × number of papers exposed), was a good fit ($R^2 = 0.93$, $F_{1,30} = 383.69$, $P < 0.001$).

At Denton's Bush and Kirkwell Bush, we fastened light meters to 0.5 m wooden stakes in the centre of each 0.25 m^2 quadrat surveyed to record light available to *Tradescantia*, and anchored meters to the ground with two metal pegs, <10 cm north of the wooden stake, to record light available to seedlings. Simultaneous readings in an adjacent open field at both sites were used to express light availability as a percentage of full light.

STATISTICAL ANALYSES

Detrended correspondence analyses (DCA) of canopy cover and abundance data were used to explore differences in the extant vegetation (excluding ground covers), seed rain and seed bank of *Tradescantia* and non-*Tradescantia* plots. DCA was chosen because of its improved performance with heterogeneous data relative to other ordination techniques (Hill & Gauch 1980). Blocked multi-response permutation procedure (MRBP; Mielke 1984) was used to test for differences in the extant vegetation (excluding ground covers), seed rain and seed bank of *Tradescantia* and non-*Tradescantia* plots. Rare species (i.e. those with $\leq 5\%$ cover or that occurred ≤ 5 times) were excluded from these data sets, and abundance data were summed across traps for each plot and transformed to log $(x + 1)$ before analyses. This reduced the impact of both rare and very abundant species on the DCA result. These analyses were done using PC-ORD (McCune & Mefford 1999). We used a 2-factor ANOVA to test for differences in quantity of seed rain and seed bank between *Tradescantia* and non-*Tradescantia* habitats (log $(x + 1)$ transformed).

We fitted a logistic model to the response of *Tradescantia* to light levels at 0.5 m using SYSTAT (SPSS Inc. 1996). We fitted a line to the response of *Tradescantia* to light levels $<$ 5% at 0.5 m to calculate its light compensation point (i.e. where *Tradescantia* biomass = zero). For each site, the relationship of light availability at ground level, and of native woody seedling abundance and species richness to *Tradescantia* biomass was fitted to over-dispersed Poisson models, due to the abundance of quadrats with no or few seedlings. To allow for the clumping of seedlings evident in the data, we used the quasi-likelihood method of S-PLUS 4.5 (Mathsoft 1995) which allowed the dispersion parameter to vary from one. We also used this method for the model of light availability at ground level. In addition, seedlings of native tree and shrub species were modelled if they occurred in >20% of quadrats surveyed at each site. Our initial models tested for an effect of ground covers other than *Tradescantia* by fitting their combined cover as a covariate. In all cases, the effect of ground covers on native seedling abundance was positive, suggesting non-*Tradescantia* ground covers did not displace native seedlings, and the effect was dropped from the final model. Final Poisson models included a plot (block) effect.

Results

EXTANT VEGETATION, SEED RAIN AND SEED BANK

There was clear separation among sites, based on the composition of the extant vegetation (Fig. 1a). Of 38 species in total, 31 occurred at Rangitawa Bush, 20 at Denton's Bush and 16 at Kirkwell Bush. Six species were present at all three sites. There was some grouping of *Tradescantia* and non-*Tradescantia* plots at Kirkwell Bush, but not at the other two sites. Overall, *Tradescantia* and non-*Tradescantia* plots did not consistently differ in extant vegetation (Table 1).

The seed rain at Rangitawa Bush and Denton's Bush consists of mostly bird dispersed, native species (Table 2), and a majority of species are represented in the extant vegetation. Adventive species were common to both *Tradescantia* and non-*Tradescantia* plots. The seed rain of each site was distinct from the other (Fig. 1b). At Denton's Bush, there was some separation of *Tradescantia* plots B and C from the other plots, but overall, the seed rain of *Tradescantia* and non-*Tradescantia* plots was similar in composition (Table 1), and there were no differences in the abundance of seed between *Tradescantia* and non-*Tradescantia* plots ($F_{1,8} = 0.65$, $P = 0.44$ (habitat) and $F_{1,8} = 0.58$, $P = 0.47$ (site)). However, the rank order of seed rain abundance for some species common as seedlings at these sites differs between *Tradescantia* and non-*Tradescantia* plots (Table 2).

There was considerably less seed in the germinable seed bank, representing fewer species, compared with the seed rain (Table 2). Of the species present in the seed bank, 40% were not represented in the seed rain and 75% of these were not represented in the extant vegetation. There was a clear distinction between sites (Fig. 1c). There was some separation of *Tradescantia* and non-*Tradescantia* plots at Denton's Bush, mainly due to the larger store of *M. ramiflorus* in *Tradescantia* plots (Table 2), but overall, there was no significant difference in the amount of germinable seed stored in *Tradescantia* and non-*Tradescantia* plots ($F_{1,8} = 0.60$, $P = 0.46$ (habitat) and $F_{1,8} = 4.56$, $P = 0.07$ (site)).

Fig. 1. DCA ordination diagrams of plots based on : a) extant vegetation excluding ground cover; b) seed rain; and c) seed bank data. ■ = Rangitawa Bush, ● = Denton's Bush, ▲ = Kirkwell Bush, open symbols represent non-*Tradescantia* plots and closed symbols represent *Tradescantia* plots. Cumulative R^2 for the correlations between ordination distances and distances in the original n-dimensional space, for axes 1–3: a) 0.24, 0.57, 0.64; b) 0.72, 0.73, 0.74; and c) 0.56, 0.69, 0.73.

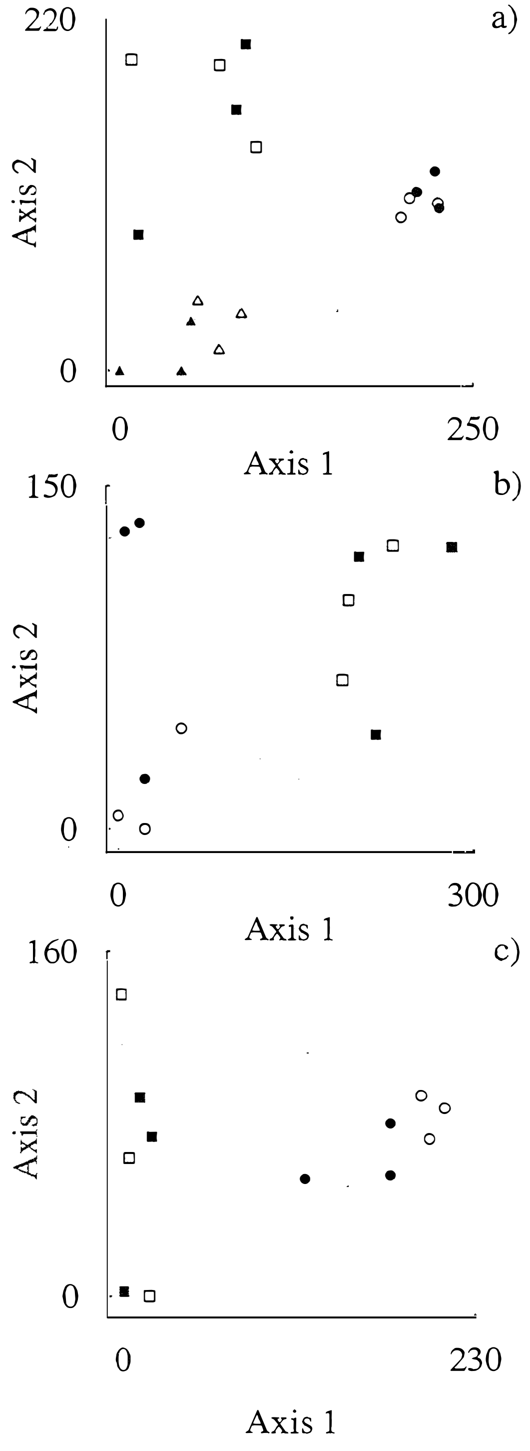


Table 1. Results of blocked multi-response permutation procedures (MRBP) for vegetation, seed rain and seed bank of *Tradescantia* (T) and non-*Tradescantia* (NT) plots. R = Rangitawa Bush, D = Denton's Bush and K = Kirkwell Bush. $A = 1$ - (observed delta/ expected delta). $A = 1$ when all items are identical within groups (delta = 0), $A = 0$ when heterogeneity within groups equals expectation by chance, and $A < 0$ with more heterogeneity within groups than expected by chance. P = probability of smaller or equal delta

Data	Sites	Groups (n)	Sampling unit	A	P
Vegetation	R, D, K	NT (9); T (9)	plot (400 m^2)	0.48	0.06
Seed rain	R, D	NT (6); T (6)	plot (400 m^2)	0.22	0.16
Seed bank	R, D	NT (6); T (6)	plot (400 m^2)	-0.07	0.84

RESPONSE OF *TRADESCANTIA* TO LIGHT

Tradescantia biomass increases logistically with increasing forest interior light levels (Fig. 2). The light compensation point for *Tradescantia* was 1.31% (for sites combined: adjusted-$R^2 = 0.18$, $F_{1,89} = 20.65$, $P < 0.001$). *Tradescantia* biomass reaches maximum, 819 gm^{-2}, at about 10% full light at the wetter Denton's Bush, and 695 gm^{-2} at about 15% full light at the drier Kirkwell Bush. Forest interior light levels explain 65.7% (Denton's Bush) and 60% (Kirkwell Bush) of the variation in *Tradescantia* biomass as described by the logistic models ($F_{3,88} = 97.84$, $P < 0.001$ and $F_{3,91} = 84.19$, $P < 0.001$ respectively).

IMPACT OF *TRADESCANTIA* AT THE FOREST FLOOR

An increase in *Tradescantia* biomass is associated with a rapid decrease in light availability at ground level (Fig. 3a). Under approximately 500 gm^{-2} of *Tradescantia* (which roughly equates to 100% weed cover at these sites), light levels are reduced to 1–2% full light (Table 3). Over-dispersed Poisson models explained 43% and 62% of total variation in light availability at ground level at Denton's Bush and Kirkwell Bush respectively, and increasing *Tradescantia* biomass explained a significant amount of the total variation (Table 3). Seedling abundance and species richness decrease rapidly with increasing *Tradescantia* biomass and decreasing light at ground level (Fig. 3; Table 3). An over-dispersed Poisson model explained 17% of total variation in seedling abundance and 17% of total variation in seedling species richness at Rangitawa Bush, and 63% of the total variation in seedling species richness and 59% of the total variation in seedling abundance at Denton's Bush.

Table 2. Seed rain and seed bank of *Tradescantia* (T) and non-*Tradescantia* (NT) plots at two sites (No. of seeds summed across 9 traps/ soil samples). Species marked with * are adventive. Rare species (i.e. those whose seeds occurred ≤ 5 times) are not listed. Dispersal modes indicated in parentheses, bird dispersal categories after Clout & Hay (1989), bb = birds with gape >1 cm (mostly kereru *Hemiphaga novaeseelandiae*), b = birds with gape < 1 cm and, w = wind.

Species	Rangitawa Bush				Denton's Bush			
	Seed Rain		Seed Bank		Seed Rain		Seed Bank	
	NT	T	NT	T	NT	T	NT	T
Alectryon excelsus (b)	15	246	-	-	-	1	-	-
Beilschmiedia tawa (bb)	14	5	-	-	35	15	-	-
Carpodetus serratus (b)	-	-	8	7	-	-	-	2
Coprosma hybrid	-	-	1	-	-	-	6	1
Cordyline australis (b)	26	13	53	44	1	2	-	-
Dysoxylum spectabile (bb)	-	-	-	-	68	181	-	-
Fuchsia excorticata (b)	-	-	-	-	-	-	12	6
Geniostoma rupestre (w)	-	149	-	-	-	-	-	-
Hedycarya arborea (b)	19	1	-	-	3	14	-	-
**Ilex aquifolium* (b)	20	5	-	-	-	1	-	-
Kunzea ericoides (w)	-	-	18	1	-	-	-	-
Laurelia novae-zelandiae (w)	44	31	-	-	1078	507	-	-
Macropiper excelsum (b)	79	48	13	5	6	23	1	1
Melicope ternata (w)	4	77	-	-	-	-	-	-
Melicytus micranthus (b)	-	-	-	-	-	13	-	-
Melicytus ramiflorus (b)	8	6	11	20	4	957	19	57
Muehlenbeckia australis (b)	632	51	2	7	-	-	-	-
Paratrophis sp. (w)	4	6	-	-	-	-	-	-
Parsonsia heterophylla (b)	371	12	-	-	7	1	-	-
Pennantia corymbosa (b)	3	8	-	-	1	-	-	-
**Phytolacca octandra* (b)	-	-	-	-	34	23	-	-
Pittosporum eugenioides (b)	3	3	-	-	-	-	-	-
Pittosporum tenuifolium (b)	22	6	-	-	-	-	-	-
Podocarpus totara (b)	220	48	-	-	8	6	-	-
Pseudopanax arboreus (b)	7	-	-	-	1	3	-	-
Rhopalostylis sapida (b)	-	-	-	-	3	16	-	1
**Solanum pseudocapsicum* (b)	-	-	-	-	-	15	-	-
Including rare species:								
TOTAL	1499	717	107	89	1262	1784	38	69
Mean density ± SE (m^{-2})	1666 ± 279	797 ± 315	649 ± 219	540 ± 158	1402 ± 448	1982 ± 971	230 ± 77	418 ± 128
Species richness	22	19	8	8	21	21	4	7

Fig. 2. The relationship of *Tradescantia* biomass to above ground light levels at Denton's Bush (●) and Kirkwell Bush (▲), $n = 91$ and 94 respectively. Data fitted with a logistic regression: $y = ABe^{(Cx)} / A - B + Be^{(Cx)}$; where y = *Tradescantia* biomass (gm^{-2}); x = light at 0.5m (% full light); $A = 819.15$, $B = 8.02$, $C = 0.67$ (Denton's Bush, solid line) and; $A = 698.35$, $B = 13.38$, $C = 0.31$ (Kirkwell Bush, dashed line).

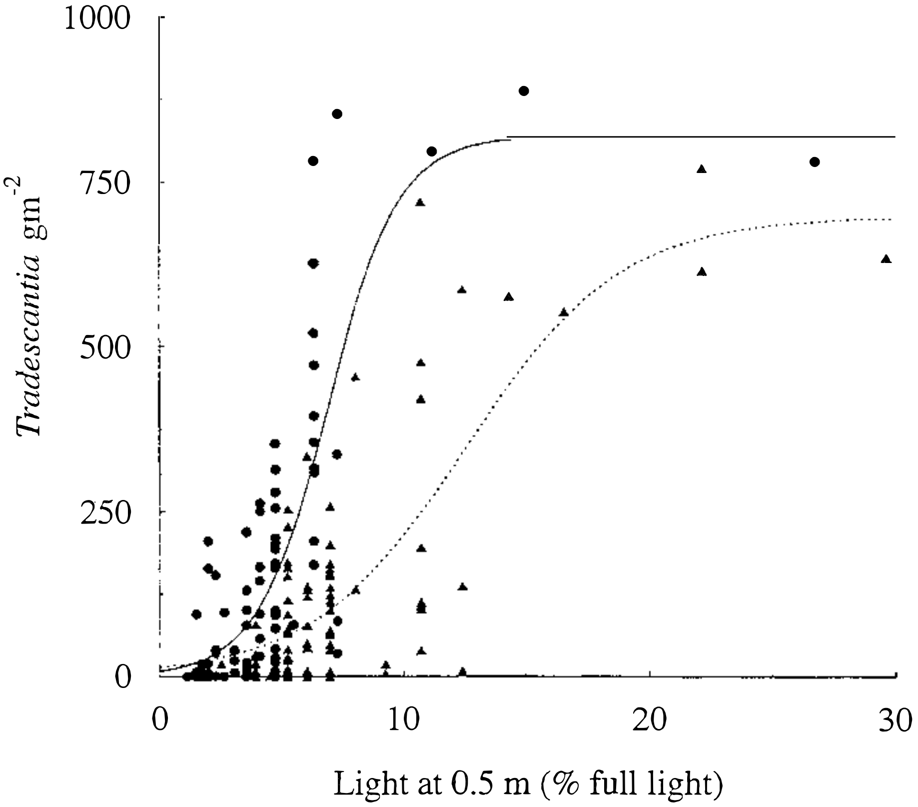


Fig. 3. Response to increasing *Tradescantia* biomass: a) light at ground level, b) native seedling abundance and c) seedling species richness at Denton's Bush ($n = 96$). Data fitted with over-dispersed Poisson models (Table 3).

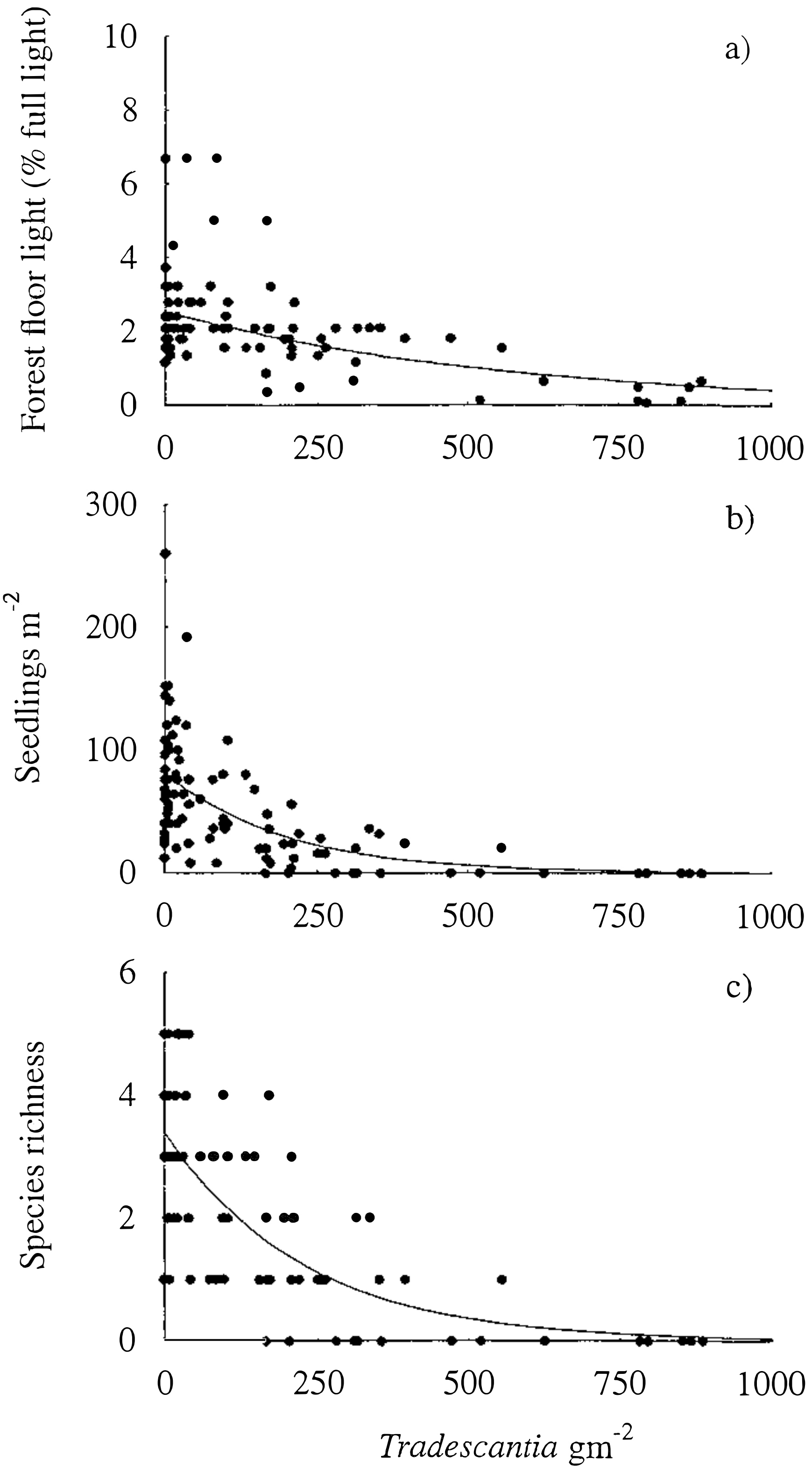


Table 3. Summary of the modelled response of light availability at ground level, and native tree and shrub seedling species richness and abundance to *Tradescantia* biomass at three sites. Model: $y = e^{(a+bx)}$; where x = *Tradescantia* biomass. *** = $P<0.001$; ** = $P<0.01$ and; * = $P<0.05$.

Site	Dependent variable	% Var. exp. plot	% Var. exp. *Tradescantia*	Slope ± SE	Prediction at $x = 0$ gm^{-2}	Prediction at x = 250 gm^{-2}	Prediction at x = 500 gm^{-2}
Rangitawa Bush	Species richness	11.8**	4.7**	-0.016 ± 0.006	1.08	0.41	0.15
	Abundance	6.9	9.5***	-0.029 ± 0.010	9.66	1.6	0.26
Denton's Bush	Light at ground	17.1***	25.4***	-0.007 ± 0.001	3%	2%	1%
	Species richness	11.9***	50.7***	-0.018 ± 0.002	3.4	1.12	0.37
	Abundance	24.3***	35.1***	-0.0205 ± 0.003	81.48	22.63	6.28
Kirkwell Bush	Light at ground	57.5***	4.5**	-0.007 ± 0.002	4%	2%	2%
	Species richness	35.9***	0.4	-0.004 ± 0.005	0.45	0.34	0.26
	Abundance	18.5*	1.8	-0.010 ± 0.009	6.36	3.3	1.71

The majority of variation was explained by increasing *Tradescantia* biomass (Table 3). Increasing *Tradescantia* biomass did not explain a significant amount of variation in the over-dispersed Poisson models of seedling species richness or seedling abundance at Kirkwell Bush, whereas the plot effect was significant. This result reflects the skewed distribution of dense *Tradescantia* at this site (i.e. high *Tradescantia* biomass was restricted to one surveyed plot), which reduced the power to detect a significant negative response to *Tradescantia*, as the plot/ high *Tradescantia* biomass effects were confounded.

SEEDLING RESPONSE TO *TRADESCANTIA*

The over-dispersed Poisson models of each species response to *Tradescantia*, including a plot effect, explained between 12 and 60% of the variation in seedling abundance (Table 4). While the abundance of each species declined with increasing *Tradescantia* biomass, the grade of response varied, e.g. the abundance of *M. excelsum* declined sharply with an increase in *Tradescantia* biomass, whereas *D. spectabile* persisted at 100% *Tradescantia* cover (500 gm^{-2}) (Table 4). Species with large intercepts, indicating high abundance in the absence of *Tradescantia*, showed a better fit to the model than species with small intercepts, indicating relatively low abundance in the absence of *Tradescantia*. However, there is no relationship between intercept and slope values among species, indicating that species abundance in the absence of *Tradescantia* does not predict its sensitivity to *Tradescantia* (adjusted-R^2 = -0.17, $F_{1,7} = 0.0006$, $P = 0.98$). Increasing *Tradescantia* biomass had a significant effect in the models of all seedling species abundance patterns at all sites except for *D. spectabile* at Kirkwell Bush. The variance in seedling abundance explained by plot was greater than that explained by an increasing gradient of *Tradescantia* biomass, for all species other than *M. excelsum* (Table 4). Again, this result reflects the high variation in *Tradescantia* biomass among plots.

D. SPECTABILE EMERGENCE IN *TRADESCANTIA*

At Denton's Bush, maximum *D. spectabile* height decreases with increasing *Tradescantia*, while minimum *D. spectabile* height does not alter (Fig. 4a). In less than 200 gm^{-2} of *Tradescantia* (70–90% cover), a majority of quadrats contained *D. spectabile* seedlings taller than the surrounding *Tradescantia* stems. On the other hand, in greater than 200 gm^{-2} of

Table 4. Summary of the modelled response of individual species to increasing *Tradescantia* biomass at three sites. Model: $y = e^{(a+bx)}$; where y = seedling abundance per m^2 and x = *Tradescantia* biomass. *** = $P<0.001$; ** = $P<0.01$ and; * = $P<0.05$. Percentage of total seedling abundance per site, at that biomass, is shown in parentheses. LD50 = *Tradescantia* biomass at which the seedling abundance is reduced to 50% of maximum (i.e. in the absence of *Tradescantia*), not estimated for *D. spectabile* at Kirkwell Bush as increasing *Tradescantia* biomass did not explain a significant amount of variation in the model.

Site	Dependent variable	% Var. exp. plot	% Var. exp. *Tradescantia*	Slope ± SE	Prediction at x = 0 gm^{-2}	Prediction at x = 500 gm^{-2}	LD50 gm^{-2}
Rangitawa Bush	*Alectryon excelsus*	11.8*	4.1*	-0.023 ± 0.012	2.80 (29%)	0.16 (61%)	30.43
	Macropiper excelsum	0.9	11.0**	-0.050 ± 0.023	4.23 (44%)	0.01 (3%)	13.75
Denton's Bush	*Dysoxylum spectabile*	26.1***	19.3***	-0.017 ± 0.004	48.40 (59%)	5.57 (89%)	40.12
	Hedycarya arborea	35.4***	11.3***	-0.040 ± 0.015	7.61 (9%)	0.05 (1%)	17.13
	Laurelia novae-zelandiae	18.3**	13.8***	-0.021 ± 0.008	6.66 (8%)	0.48 (8%)	32.99
	Macropiper excelsum	22.9***	37.3***	-0.069 ± 0.015	5.22 (6%)	0	10.02
Kirkwell Bush	*Alectryon excelsus*	25.4***	3.7*	-0.023 ± 0.012	3.24 (51%)	0.19 (11%)	30.43
	Dysoxylum spectabile	27.2**	0.2	-0.004 ± 0.012	0.78 (12%)	0.48 (28%)	-
	Melicytus ramiflorus	36.8***	3.9*	-0.025 ± 0.013	0.13 (2%)	0.01 (<1%)	27.95

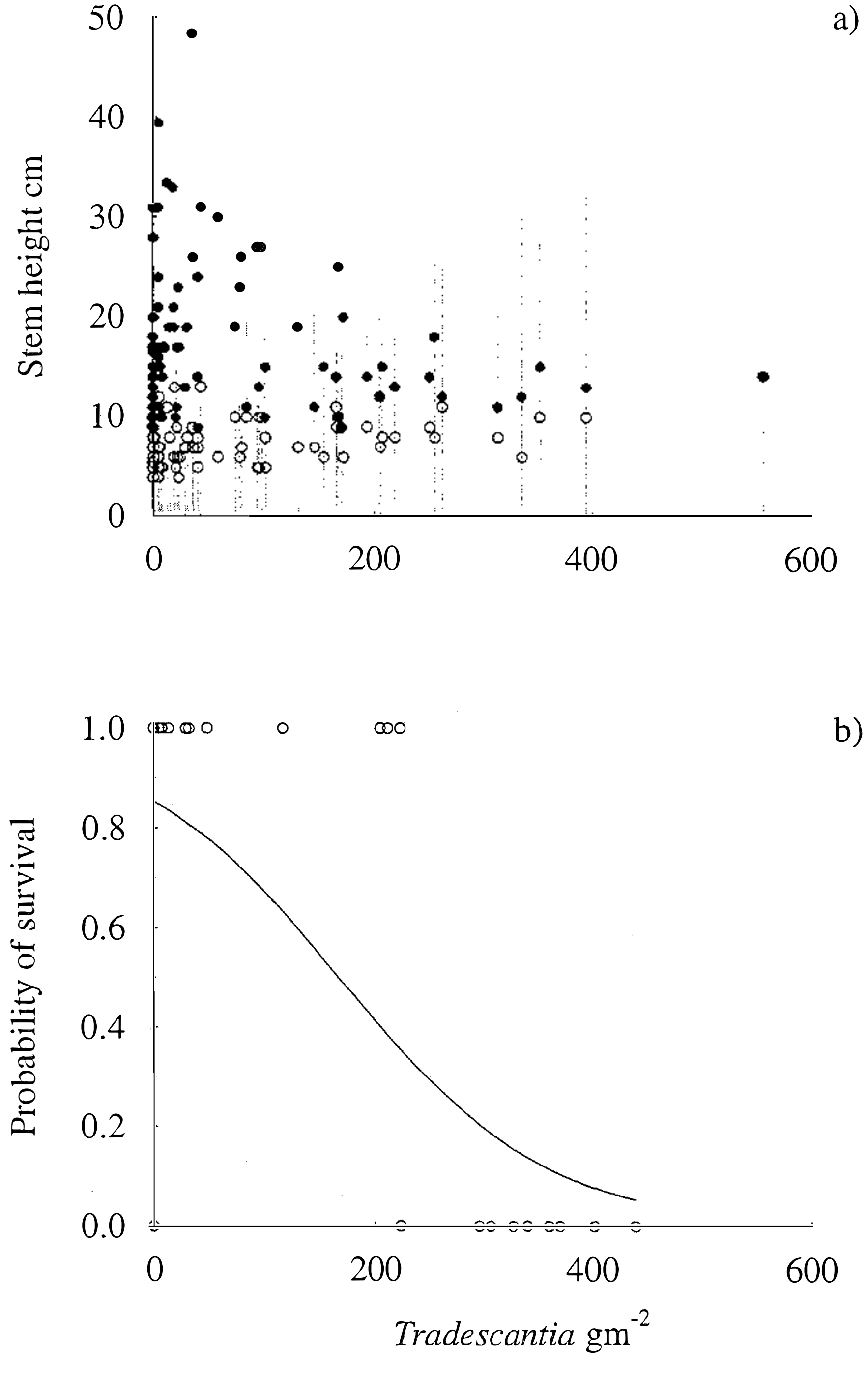
Tradescantia, the tallest *D. spectabile* are smaller than the surrounding stems of *Tradescantia* (Fig. 4a). The survival of tagged seedlings in *Tradescantia* above 200 gm^{-2} was very low (Fig. 4b). The logistic regression was highly significant ($F_{1,34} = 15.67$, $P < 0.0001$), and fitting survival probability to *Tradescantia* biomass explained 33% of the variance in *D. spectabile* seedling survival. The probability of survival dropped from 84% at 0 gm^{-2} to 39% at 200 gm^{-2} and 7% at 400 gm^{-2}. Despite this, there was no correlation between *Tradescantia* biomass and seedling relative growth rate ($R^2 = -0.05$, $F_{1,18} = 0.11$, $P = 0.75$). However, few seedlings survived at high *Tradescantia* biomass ($n = 4$ at >50 gm^{-2}), so there was little power to detect the effect of high *Tradescantia* biomass on seedling growth rate.

Discussion

Light availability is clearly important in determining the extent of *Tradescantia* infestation (Kelly & Skipworth 1984; Maule *et al.* 1995; this study). The dramatic decrease in the species richness and abundance of native seedlings can be attributed to an increase in *Tradescantia* biomass and a consequent decrease in light availability. The disparity in seedling abundance and species richness between *Tradescantia*-affected and non-affected habitats was not explicable by a consistent difference in seed supply either from the seed rain or the seed bank. The differences in seed rain between two *Tradescantia* plots and the remaining plots at Denton's Bush was driven by species uncommon (i.e. *Melicytus ramiflorus* and *Rhopalostylis sapida*) or absent (i.e. *M. micranthus*) as seedlings. Moreover, the seed rain of the species common as seedlings was greater into *Tradescantia* compared with non-*Tradescantia* plots, with the exception of *Laurelia novae-zelandiae* and *Macropiper excelsum* at Rangitawa Bush. *Alectryon excelsus* presents a striking case, for it was the main contributor to seed rain into *Tradescantia* plots, but seedling recruitment was less than 1% of seed rain. Conversely, *A. excelsus* ranked 10th in seed rain abundance for non-*Tradescantia* plots, and seedling recruitment was 33% of seed rain. It is difficult however, to assess the generality of these results as extreme spatial and temporal heterogeneity typically characterise seed rain and seed bank data (Enright & Cameron 1988; Burrows 1994; Sem & Enright 1996).

Ultimately, invasion by *Tradescantia* is likely to result in changes to the composition of the

Fig. 4. a) Minimum (○) and maximum (●) height of *D. spectabile* seedlings and the mean height of *Tradescantia* stems (vertical lines), in relation to *Tradescantia* biomass at Denton's Bush ($n = 83$); b) Logistic regression model of survival probability for *D. spectabile* seedlings at Denton's Bush, 2 Aug 1998–31 Mar 2000 ($n = 35$), $y = e^{(1.77-0.011x)}/(1+e^{(1.77-0.011x)})$.



native plant community. We predict *M. excelsum,* the only shrub among the group which is dominated by canopy trees, to be the most sensitive to increases in *Tradescantia* biomass, and *Dysoxylum spectabile* the least sensitive. Therefore, *Tradescantia*-affected forest would probably comprise more *D. spectabile* and less *M. excelsum* than non-affected forest. The remaining species comprise a group 'moderately' tolerant to *Tradescantia*, from approximately least to most tolerant these were: *Hedycarya arborea* < *Melicytus ramiflorus* < *Alectryon excelsus* < *Laurelia novae-zelandiae.* The response of *A. excelsus* and *M. excelsum* to *Tradescantia* was consistent between sites. The local extinction of these 'moderately tolerant' species would depend on the extent of *Tradescantia* infestation. We did not measure the tolerance of any native ground covers, though it appears that invasion by *Tradescantia* can result in their local extinction (Esler 1978; Polly & West 1996).

The possession of a large seed is thought to increase the chance of successful tree and shrub establishment in vegetation comprising perennial herbs, primarily because a large seed confers seedling shade tolerance (Grime & Jeffrey 1965; Grime 1979; Leishman & Westoby 1994; Walters & Reich 2000). However, other studies have found little relationship between seed mass and seedling shade tolerance (Augspurger 1984; Grubb & Metcalfe 1996). The seed weights (oven dry) of the species presented in Table 4, are as follows: *D. spectabile* (288 mg; this study) > *H. arborea* (171 mg; Wardle 1991) > *A. excelsus* (165 mg; Williams & Karl 1996) >> *L. novae-zelandiae* (12 mg; Wardle 1991) > *M. excelsum* (2.4 mg; this study) > *M. ramiflorus* (0.7 mg; Wardle 1991). *D. spectabile* is the most tolerant of *Tradescantia* and has the heaviest seed, and *M. excelsum* is the least tolerant of *Tradescantia* and has a low seed weight. Within these two extremes there is no relationship between seed weight and relative tolerance to *Tradescantia.*

A degree of shade tolerance is generally necessary for tree species to survive in New Zealand lowland forest communities (Pook 1979; Wardle 1991). Seeds of *D. spectabile* will germinate and continue to grow in the dark for at least 18 weeks (Court & Mitchell 1988). Clearly, this attribute enables *D. spectabile* to germinate and persist, at least initially, in dense *Tradescantia*, although, *D. spectabile* seedling survival suggests that seedling emergence only occurs in sparse (<200 gm^{-2}) *Tradescantia. H. arborea* seeds will germinate in the dark

(Burrows 1995a) and it is 'truly shade-tolerant' because it can reach maturity beneath a tall forest canopy (Wardle 1991). *L. novae-zelandiae* is also 'truly shade-tolerant' (Wardle 1991). *M. ramiflorus* will germinate in the dark (Burrows 1995b) and its seedlings are relatively shade tolerant (Williams & Buxton 1989). The degrees of shade tolerance possessed by these three trees explain their relative tolerance of *Tradescantia*. *M. excelsum* seeds will germinate in the dark (Burrows 1995b), but its apparent intolerance of *Tradescantia* suggests lower seedling shade tolerance than the other species.

The development of a large biomass, such as that seen in shading plants, will often result in decreased soil nutrient availability (Grime 1979). At high biomass, *Tradescantia* carpets the forest floor, allowing it to penetrate a large volume of topsoil with its fine roots, and so has an opportunity to sequester nutrients at the forest floor and, to its further advantage, has the ability to store nitrogen (Maule *et al.* 1995). Despite this, we found soil nitrate availability to be greater in *Tradescantia*-affected than non-affected plots within one of these forest remnants, reflecting a faster decomposition of litterfall (Chapter 2). We do not know whether *Tradescantia* sequesters these nutrients at a cost to native seedlings, but the high fertility of these sites (Chapter 2) and of *Tradescantia*-affected sites generally (Ogle & Lovelock 1989), may reduce competition for nutrients.

MANAGEMENT IMPLICATIONS

Significantly, seedling abundance does not 'protect' a species from the threat of local extinction in *Tradescantia*-affected forest remnants. Ultimately, the survival of a species will be driven by its ability to tolerate *Tradescantia*, which in turn will determine the long-term species composition of these forest remnants. The impact of *Tradescantia* on species composition is evident in the understorey at Denton's Bush and Kirkwell Bush, where *M. excelsum* abundance is reduced in *Tradescantia*-affected relative to non-affected areas. *Tradescantia* has been established at these sites for ~12 and ~16 years respectively (M. Lutz & B. Empson, personal communication).

Seedling recruitment of canopy species is largely dependent on bird-dispersed seed rain, the majority of species germinating within one year. In these forest remnants, the species that do maintain a seed bank are early successional types (i.e. *Cordyline australis*, *Kunzea ericoides*) as well as *Carpodetus serratus* and *Fuchsia excorticata* ('gap colonisers'; Ogden 1985), whereas late successional trees are poorly represented. These trends characterise New Zealand forests (Enright & Cameron 1988; Partridge 1989; Sem & Enright 1996) and other forests generally (Thompson 1978; Hopkins & Graham 1983; Enright 1985). The altered vegetation structure in *Tradescantia*-affected areas of forest, such as a lack of tall canopy trees at Rangitawa Bush and a sparse sub-canopy at Denton's Bush, could affect bird foraging patterns (Fitzgerald, Robertson & Whitaker 1989; Spurr, Warburton & Drew 1992), but the similarity of seed rain between *Tradescantia* and non-*Tradescantia* areas suggests otherwise.

Tradescantia's real impact occurs at high light levels. Therefore, a reduction in the biomass of *Tradescantia* by shading should lead to an increase in the abundance and species richness of forest seedlings. For long-term benefits, imposing shade, i.e. 1.3 to 5% full light (Adamson *et al.* 1991; this study), by closely planting canopy-forming trees, is a potentially useful tool for restoration of *Tradescantia*-affected forest remnants (Kelly & Skipworth 1984a; this study). Research into the practicality of this restoration tool is ongoing.

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Chapter 2: Invasion by *Tradescantia fluminensis* increases decomposition rate and alters nutrient cycling in New Zealand lowland forest remnants.

Litter bags beneath non-*Tradescantia* (top) and *Tradescantia* (bottom) habitats at Denton's Bush, Otaki.

Abstract

The biggest ecological threat posed by plant invaders is the alteration of ecosystem-level properties. We determined the impact of the ground smothering weed, *Tradescantia fluminensis* Vell., on litter decomposition and nutrient cycling in a New Zealand lowland podocarp-broadleaf forest remnant. Using litter bags, we found that litter beneath mats of *Tradescantia* decomposed at almost twice the rate of litter placed outside the mat. K values were 9.44 ± 0.42 yrs for litter placed beneath the mat of *Tradescantia* and 5.42 ± 0.42 yrs for litter placed in native habitat. The impact of *Tradescantia* on decomposition was evident through the reduced litter layers in *Tradescantia*-affected areas (2.65 ± 1.05 t ha^{-1}) relative to non-affected areas (5.05 ± 1.05 t ha^{-1}), despite similar quantities of leaf litterfall, 6.85 ± 0.85 t ha^{-1} yr^{-1} into *Tradescantia* habitat and 7.45 ± 1.05 t ha^{-1} yr^{-1}into non-*Tradescantia* habitat. Moreover, there was increased plant available IER (ion exchange resin) estimated nitrate in *Tradescantia*-affected (25.77 ± 8.32 cmol(-)/ kg resin) relative to non-affected (9.55 ± 3.72 cmol(-)/ kg resin) areas of forest. Finally, the annual uptake of nutrients by *Tradescantia* was a significant amount of the nutrient inputs via litterfall (41% N, 61% P, 23% Ca, 46% Mg and 83% K), which exceeded the amounts of these nutrients held within the forest litter layer (except Ca) but was only a small amount of these nutrients held within the topsoil. Taken together, our results show that *Tradescantia* increases litter decomposition and alters nutrient cycling, which could influence the long-term viability of a majority of podocarp-broadleaf forest remnants affected with *Tradescantia* in New Zealand.

Keywords: Litterfall, litter bag decomposition, litter layer, soil nutrients, weed impacts

Abbreviations: IER = ion exchange resin, NT = Non-*Tradescantia*, T = *Tradescantia*

Introduction

Invasive weeds can alter ecosystem function by changing disturbance frequency or intensity (D'Antonio and Vitousek 1992; Fensham et al. 1994; Smith 1994; Mullet and Simmons 1995), altering trophic structure (Cross 1982; Hobbs and Mooney 1986; Braithwaite et al. 1989) and changing resource availability (Vivrette and Muller 1977; Vitousek and Walker 1989; Boswell and Espie 1998). The litter of two exotics, *Buddeleja asiatica* and *Myrica faya*, decomposes more rapidly than native litter in primary succession forest in Hawaii, leading to increased soil nutrients beneath the exotics (Matson 1990). Conversely, invasive pines have been shown to decrease rates of decomposition through addition of recalcitrant litter (Versfeld and van Wilgen 1986), which presumably impacts nutrient availability. Invasion of barberry (*Berberis thunbergii*) and wiregrass (*Microstegium vimineum*) lead to increased and decreased rates of decomposition respectively in New Jersey hardwood forests, both resulting in higher nitrification rates in the soil than in soils beneath adjacent patches of native shrub (Ehrenfeld et al. 2001).

Tradescantia fluminensis (Commelinaceae) (also known as *T. albiflora*; R. Faden, pers. comm.) is a ground-smothering perennial herb native to South America (Esler 1978), which has invaded forest remnants in New Zealand (Kelly and Skipworth 1984a), eastern Australia (Dunphy 1991) and Florida (Wunderlin 1998). In New Zealand, the degraded state of most lowland forest remnants of the North Island and northern South Island (Timmins and Williams 1991) has resulted in increased forest interior light levels favourable for invasion and biomass accumulation of *T. fluminensis* (hereafter referred to as *Tradescantia*) (Kelly and Skipworth 1984a). Even if the forest canopy is restored and light levels decrease, *Tradescantia* can grow in partial shade (down to 1.4 % of full light; Adamson et al. 1991) typical of closed-canopy New Zealand podocarp forests (Ebbett and Ogden 1998). In this manner, *Tradescantia* can persist in closed-canopy forest and increase in biomass when forest interior light levels increase following canopy disturbance (Kelly and Skipworth 1984a). Under canopy gaps and at forest edges, swards of high biomass *Tradescantia* appear to remain indefinitely.

Tradescantia could potentially effect the rate of litter decomposition by altering the microclimate (i.e., temperature and humidity), litter quality, and the composition of the decomposer community. Furthermore, *Tradescantia* has features that may allow it to exploit nutrients at the forest floor, and so alter nutrient availability for forest species. *Tradescantia* inhibits the growth, and eventually smothers, native ground cover and seedlings (Esler 1978; Kelly and Skipworth 1984a) that might otherwise compete with it for nutrients. *Tradescantia* accumulates litter, and penetrates a large volume of top soil with a finely reticulated root system. Lastly, it has the ability to accumulate a store of nitrogen for later use (Maule et al. 1995).

The aim of our study was to determine the impact of *Tradescantia* on litter decomposition and nutrient cycling. We estimated the decomposition rates of *Tradescantia* and *M. ramiflorus* litters, selected as bioassays, experimentally using litter bags. We also estimated decomposition rates indirectly, using measurements of annual leaf litterfall and leaf litter layers in *Tradescantia*-affected and non-affected areas of two lowland forest remnants. To assess the impact of *Tradescantia* on nutrient cycling, we compared the amount of nitrogen and phosphorous available in the soil using ion exchange resin bags in *Tradescantia* affected and non-affected areas. We also estimated nutrient uptake by *Tradescantia*, based on annual aboveground production and foliar nutrient levels of *Tradescantia*, and compared it to nutrient return by litterfall in these *Tradescantia*-affected forest remnants.

Materials and methods

Study sites

The study sites were two lowland podocarp-broadleaf forest remnants in the lower North Island, New Zealand: Denton's Bush (2 ha) on a flood plain (40°48′ S, 175°11.4′ E; 20 m a.s.l.) and Rangitawa Bush (12.4 ha) on an old river terrace (40°06′ S, 175°27.6′ E, 100 m a.s.l.). Mean annual rainfall for Denton's Bush was approximately 1176 mm and mean annual temperature was approximately 13 °C, recorded at Levin climate station, 18 km N of the site (National Institute of Water and Atmospheric Research 2000). Mean annual rainfall for Rangitawa Bush was approximately 1046 mm and mean annual temperature was approximately 13 °C, recorded at Marton climate station, 4 km NW of the site (National Institute of Water and Atmospheric Research 2000). Soils at Denton's Bush were classified as Typic Fluvial of recent alluvial origin, and the soil type Rangitikei clay/silt loam overlaying rounded greywacke gravels at 0.8–1 m. The site was well drained. Soils at Rangitawa Bush were classified as Argillic Perch-gley pallic of loess origin, and the soil type Marton silt loam. Drainage at the site varied from imperfect to poor. In June 1998, two soil cores were collected at each site ($n = 4$), and cut into four horizons: 0–7.5 cm, 7.5–15 cm, 15–22.5 cm and 22.5–30 cm. For each horizon, soil pH (in water), total carbon, total nitrogen and exchangeable cations (i.e., calcium, magnesium, potassium and sodium) were determined using the methodology of Blakemore et al. (1987). Anaerobic mineralisable nitrogen was determined as described in Keeney (1982). These soil properties are described in Table 1.

At each site, three 20 m × 20 m plots were selected in areas of greatest *Tradescantia* infestation (> 75% cover), near to the forest edge (i.e., minimum distance to the forest edge ranged from 4–20 m). Adjacent to each *Tradescantia* plot, a 20 m × 20 m plot was selected where *Tradescantia* did not occur or was insignificant (< 5% cover), usually further into the forest remnant (i.e., minimum distance to the forest edge ranged from 7–62 m). Vegetation cover was visually estimated at 0.3–2 m, 2–5 m, 5–12 m, and > 12 m above the ground within each plot ($n = 6$ plots/ site). Plant nomenclature follows Allan (1961) and Healy and Edgar (1980), unless given at first mention.

Table 1. Soil properties of two *Tradescantia*-affected lowland podocarp/broad-leaved forest remnants. Soil nutrients and exchangeable cations are mean (± SE) t ha^{-1}, $n = 4$.

Soil depth (cm)	pH	Total C	Total N	C: N	Anaerobic N	Ca	Mg	K
0–7.5	5.5 ± 0.2	41.4 ± 5.1	2.8 ± 0.4	14	0.07 ± 0.02	1.40 ± 0.28	0.30 ± 0.03	0.18 ± 0.04
7.5–15	5.5 ± 0.3	27.6 ± 2.6	2.0 ± 0.2	14	0.04 ± 0.07	1.03 ± 0.23	0.26 ± 0.04	0.16 ± 0.05
15–22.5	5.4 ± 0.3	22.5 ± 3.0	1.5 ± 0.3	15	0.02 ± 0.05	0.86 ± 0.26	0.23 ± 0.04	0.14 ± 0.05
22.5–30	5.4 ± 0.3	16.4 ± 2.1	1.0 ± 0.2	16	0.06 ± 0.03	0.74 ± 0.27	0.22 ± 0.04	0.13 ± 0.06

Denton's Bush had sparse sub-canopy and understorey layers, as a result of stock grazing and possum (*Trichosurus vulpecula*) browsing prior to 1988 (M. Lutz, pers. comm.). The forest canopy mainly comprised *Beilschmiedia tawa* and *Laurelia novae-zelandiae*. The sub-canopy was dominated by *Melicytus ramiflorus*, particularly in *Tradescantia* plots, and *Dysoxylum spectabile*, with some *Hedycarya arborea*. *Macropiper excelsum* dominated the understorey, particularly in non-*Tradescantia* plots (Table 2). Summed canopy cover, excluding the 0.3–2 m layer, was 157 ± 10% (SE) for *Tradescantia* plots and 210 ± 7% (SE) for non-*Tradescantia* plots. Ground cover other than *Tradescantia*, litter or bare soil was provided by ferns and woody seedlings. Ferns ranged from 1–2% cover in *Tradescantia* plots and 2–17% cover in non-*Tradescantia* plots. Woody seedlings ranged from 0–4% cover in

Tradescantia plots and 4–16% cover in non-*Tradescantia* plots.

Rangitawa Bush has large canopy gaps, a result of selective logging in the late 19th and early 20th centuries (B. Rolston, pers. comm.). *Alectryon excelsus*, *B. tawa* and *M. ramiflorus* dominated the upper canopy in the non-*Tradescantia* plots, while only the first species comprised more than 10% of any layer in the *Tradescantia* plots. *Podocarpus totara* also occurred occasionally at canopy level, as well as *Kunzea ericoides* (A.Rich) J. Thompson in non-*Tradescantia* plots. *M. excelsum* dominated the understorey, with some *Coprosma areolata* (Table 2). Summed canopy cover, excluding the 0.3–2 m layer, was 194 ± 6% (SE) for *Tradescantia* plots and 213 ± 5% (SE) for non-*Tradescantia* plots. Ground cover other than *Tradescantia*, litter or bare soil, was provided by ferns, woody seedlings and grasses. Ferns and grasses ranged from 1–5% cover in *Tradescantia* plots and 5–12% cover in non-*Tradescantia* plots. Woody seedlings ranged from 0–1% cover in *Tradescantia* plots and 0–4% cover in non-*Tradescantia* plots.

Litterfall

Litterfall was collected in circular funnels 0.38 m in diameter and 0.3 m deep, which were constructed from heavy nylon shade cloth (0.5 mm mesh) tied at the bottom for access. Funnels were attached to three stakes at 1 m above ground level, three funnels were set up in each plot (n= 18 per site). Traps were emptied every 30 ± 1 days for 12 months, from December 1997 to November 1998. Litter was oven-dried at 80°C for 2 days, and sorted into species-specific leaf litter (>5 mm), flowers, litter <5 mm (collectively referred to as 'leaf litter') and woody material (referred to as 'twig litter'). Dominant (>5% cover) species' litterfall was classified according to the texture of their leaves: mesophyllous (soft): *M. ramiflorus* and *M. excelsum*; sclerophyllous (hard): remaining species. After sorting, each litter component was weighed. A two-factor repeated measures ANOVA was used to test differences in litterfall (plot means) of *Tradescantia* and non-*Tradescantia* habitat at both sites. Leaf litterfall data were natural log transformed for analyses, and a $\ln(x + 1)$ transformation was used for twig litterfall data.

The litter layer and decomposition quotient

The litter layer, including recently fallen litterfall and decomposing organic matter above the mineral soil, was collected in March and September 1998, from three 0.25 m^2 quadrats adjacent to litterfall traps within each *Tradescantia* and non-*Tradescantia* plot at both sites (n= 72). Samples were oven-dried at 80 °C for 2 days and sorted into species-specific leaf litter (>5 mm), flowers, litter <5 mm (collectively referred to as 'leaf litter') and woody material (referred to as 'twig litter'). After sorting, all litter components were weighed. A two-factor repeated measures ANOVA was used to test differences among the litter layer (plot means) of *Tradescantia* and non-*Tradescantia* habitat at both sites. Data were natural log transformed for analyses.

Table 2. Average % contribution of dominant (≥5% cover) woody species to all layers of vegetation in non-*Tradescantia* and *Tradescantia* plots and their annual leaf litterfall, expressed as percentage of mean total cover and sum total leaf litterfall respectively (n = 3). Excluding *Kunzea ericoides* and *Coprosma areolata* at Rangitawa Bush as litterfall not estimated for these species.

Woody species	non-*Tradescantia*		*Tradescantia*	
Denton's Bush	Vegetation	Litterfall	Vegetation	Litterfall
Beilschemiedia tawa	15	20	13	12
Laurelia novae-zelandiae	7	19	3	14
Dysoxylum spectabile	20	12	19	8
Melicytus ramiflorus	4	<1	15	21
Hedycarya arborea	1	0	4	<1
Macropiper excelsum	38	<1	26	<1
Remaining	15	48	20	44
Woody species	non-*Tradescantia*		*Tradescantia*	
Rangitawa Bush	Vegetation	Litterfall	Vegetation	Litterfall
Beilschmiedia tawa	18	19	5	12
Alectryon excelsus	9	8	29	15
Podocarpus totara	1	<1	5	4
Melicytus ramiflorus	17	7	4	2
Macropiper excelsum	24	2	23	3
Remaining	31	64	34	64

The decomposition quotient (Olson, 1963) estimates the proportion of litter decomposed in one year and is calculated by the equation:

$$k_L = I / X,$$

where I is the mean annual litter input to the forest floor and X is the mean mass of the litter layer. Calculation of the k_L quotient is based on the assumptions of simple exponential breakdown of litter in conditions where the amount accumulated on the soil surface oscillates around some 'steady-state' value (Olson, 1963). Decomposition quotients were calculated for litter of *Tradescantia* and non-*Tradescantia* habitats at both sites, using the above data.

Decomposition of litter in bags

Litter decomposition was studied at Denton's Bush using the litter bag technique (Falconer et al. 1933). *Tradescantia* and *M. ramiflorus*, a native tree common to Denton's Bush and Rangitawa Bush, were selected as bioassays to compare the decomposition of their litter in *Tradescantia* and non-*Tradescantia* habitats, and at different levels (see below). We did not use a mixed species litter as the species composition of leaf litterfall varies between *Tradescantia* and non-*Tradescantia* plots, and also seasonally. Fresh leaf material was collected from the site as senescent or dead material was not available in sufficient quantity, due to rapid litter turnover of these species. Leaves and shoots of *Tradescantia* were collected from three separate swards, and older *M. ramiflorus* leaves were collected from the lower branches of over 30 spatially separated trees. Fresh material was oven-dried prior to placement in the litter bags, at 30°C for 15 days and 45°C for 1 day (*Tradescantia*) and at 30°C for 4–8 days (*M. ramiflorus*). *Tradescantia* was oven-dried for longer and finally at a higher temperature than *M. ramiflorus* as it contained more moisture, and it re-sprouted when removed from the oven after eight days. A sample of each litter type was set aside for nutrient analyses. Litter bags (n = 120) were 10 cm × 20 cm, made from nylon mesh (mesh size = 1mm) and closed with staples. The actual dry weight of litter bagged was determined by drying 10 supplementary samples of each litter type at 80°C for 2 days, which was 2.25 ± 0.09 g of *Tradescantia* litter (approx. equal amounts of shoot and leaf material) and 2.24 ± 0.09 g and *M. ramiflorus* litter.

Tradescantia swards are comprised of densely packed vertical leafy shoots (>60 cm) over a layer of older, leafless shoots with roots at the nodes, lying horizontally (~10 cm, the 'lattice'). Litter bags were placed in each of the following treatments: non-*Tradescantia* habitat at ground level; *Tradescantia* habitat at ground level; *Tradescantia* habitat at lattice level; and non-*Tradescantia* habitat at lattice level. A design was produced with SAS Proc Optex (SAS/ QC Release 6.12, 1996) based on a 5 x 5 Latin Square with one row dropped, which attempted to balance harvest times against treatments, rows and columns within each plot. Bags were placed in one of six plots (three *Tradescantia* and three non-*Tradescantia*) containing 20 bag sites, 2 m apart, in a 5 x 4 grid. We set the bags in place on February 27, 1998, and harvested one of each litter type/ treatment combination from each plot ($n = 3$ replicates) 30, 60, 100, 120 and 150 days later. Wire pegs were used to anchor ground level bags, and wire frames held litter bags vertically within the leafy shoots, atop the lattice layer of *Tradescantia*. Ground level bags were buried in the litter layer and/or *Tradescantia*. Immediately after harvest, the litter bags were washed under running tap water to remove soil and foreign debris, and dried at 80°C for 2 days for dry weight determination.

Initially we tested for statistical differences in the rates of decomposition between replicates and replicate × time × treatment interactions for *Tradescantia* and *M. ramiflorus* litter. None of these tests was significant and we proceeded with a test of the treatment effects. Inspection of the data (% dry weight of litter remaining at each harvest time per treatment/ litter-type combination) indicated that, as expected, these data followed a negative exponential curve over time. The absolute variation around each curve remained roughly constant over the course of the study suggesting that a simple regression of the log of % dry weight remaining over time (plus interactions with habitat, level and litter-type) would not be appropriate. A more suitable model was applied–a Generalised Linear Model (GLM) with a log link, normal errors and a zero intercept, to ensure the curve passed through 100% dry weight remaining at time = 0 (McCullagh and Nelder 1989). The GLM was fitted using SAS Proc Genmod (SAS/ STAT release 6.12 1996).

Assuming that the rate of litter decomposition conforms to a negative exponential relationship, the K parameter is a measure of the average loss rate over the sampling period (Olson 1963). K values and their standard errors were derived from the model (fitted with significant terms only). The time (t) to decay to 1% of original dry weight was calculated from the equation:

$$t\ (99\%\ \text{decay}) = \log_e (0.01)/ (-K)$$

Litter nutrients and quality

Leaf litter samples harvested from the litter traps, the litter layer and the litter bags were milled to a powder. Nitrogen, phosphorous, potassium, calcium and magnesium analyses (Blakemore et al. 1987) were carried out on: sub-samples of litter from bulked seasonal (Nov–Jan; Feb–Apr; May–Jul and Aug–Oct) litterfall from all *Tradescantia* and non-*Tradescantia* plots at each site (n = 16); September litter layer samples from each habitat and site (sub-sampled for fine, coarse and *Tradescantia* litter (n = 10)); and sub-samples of *M. ramiflorus* and *Tradescantia* litter from litter bags prior to decomposition (n = 2).

In addition, for the Nov–Jan litterfall samples from each habitat and site (n = 4) and bagged *M. ramiflorus* and *Tradescantia* litter (n = 2), determinations were made of the quantity of total phenolics, condensed tannins, acid-detergent fibre, α-cellulose and ADF-lignin. Total phenolics and condensed tannins were determined colorimetrically (Price and Butler 1977; Broadhurst and Jones 1978) after extraction from the plant material with 50% acetone. The remaining fractions were determined following the methodology of Rowland and Roberts (1994). Samples were not corrected for ash content. A carbon value of 45% by dry weight was used in C:element ratio calculations.

Soil nutrient availability

We determined available nitrate, ammonium and phosphate in the soil at Denton's Bush using the ion exchange resin (IER) bag method (Binkley and Matson 1983). Three IER bags were buried in each plot (n = 18), at a depth of 5 cm, below the forest floor/ mineral soil interface. The assay lasted from 19 March 1999 through 31 March 2000. All bags except one were recovered. A nested ANOVA on untransformed (NO_3) and log transformed (NH_4 and PO_4) data were used to test for differences in available nutrients in *Tradescantia* and non-*Tradescantia* plots.

Tradescantia aboveground production

Three 0.25 m^2 sub-plots per 20 m × 20 m plot were located at each site, and five non-bifurcating and flowerless *Tradescantia* stems were double tagged within each sub-plot. The first tag was placed three internodes from the growing tip (internode > 0.5 cm) and the second, distally, three internodes from the last green leaf (towards growing tip). The following were recorded every two months for one year (April 1998–March 1999): stem length (± 0.1 cm) between the tip and tag 1; stem length between tag 1 and tag 2; the number of internodes between the tip and tag 1; leaf loss or leaf browning since last measurement using tag 2 as a guide (internode decay). From these measurements we determined: 1. Internode growth relative to decay at each site; 2. The mean annual relative growth rate (RGR) for each sub-plot and site. RGR [stem length (final–initial/ initial) × 100%] was calculated using stem growth between Tag 1 and the tip only, as stem growth between tags was insignificant (usually <1 cm). To estimate *Tradescantia* aboveground production we multiplied RGR by mean *Tradescantia* biomass estimates for each site (Chapter 1).

Results

Litterfall

Leaf litter formed 84.8 ± 1.1% (n = 216 samples, summed across traps and months) of the total litterfall at Denton's Bush, and 84.2 ± 1.0% (n = 216 samples, summed across traps and months) at Rangitawa Bush. Leaf litterfall reflected vegetation composition except for *K. ericoides*, *P. totara* (litterfall underestimated because of small leaf size) and *M. excelsum* (Table 2). At Denton's Bush, mesophyllous species made little contribution to the litterfall of non-*Tradescantia* plots (<1% combined), whereas for *Tradescantia* plots, *M. ramiflorus* was a significant contributor (21%). Mesophyllous and sclerophyllous species contributed similarly to the litterfall of non-*Tradescantia* plots and *Tradescantia* plots at Rangitawa Bush (Table 2). Leaf litterfall mass did not differ between habitats or sites (Table 3; $F_{1,9} = 0.87$, $P = 0.38$ (habitat); $F_{1,9} = 0.29$, $P = 0.60$ (site)), although leaf litterfall was greater at Denton's Bush during June–September, and Rangitawa Bush during November–May and October ($F_{11,99} = 9.23$, $P < 0.001$ (month × site)). Twig fall mass did not differ between habitats or sites (Table 3; $F_{1,9} = 2.70$, $P = 0.14$ (habitat); $F_{1,9} = 3.91$, $P = 0.08$ (site)).

The litter layer and decomposition quotient

The litter layer mass was greater in non-*Tradescantia* than in *Tradescantia* habitat at both sites (Table 3; $F_{1,9} = 37.32$, $P < 0.001$ (habitat); $F_{1,9} = 30.27$, $P < 0.001$ (site)). *Tradescantia* litter represents a small percentage of the leaf litter layer (2.5 % and 1.6 % at Denton's Bush and Rangitawa Bush respectively). There was no difference in the mass of the twig component of the litter layer between habitats or sites (Table 3; $F_{1,9} = 4.84$, $P = 0.06$ (habitat); $F_{1,9} = 1.98$, $P = 0.19$ (site)).

Table 3. Litterfall (t ha^{-1} yr^{-1}) and litter layer (t ha^{-1}) of two *Tradescantia*-affected lowland podocarp/broad-leaved forest remnants (mean ± SE, n= 9). T = *Tradescantia* and NT = non-*Tradescantia*. Decomposition quotients (k_L) calculated by dividing the mean annual litter/ twig fall by the mean litter/ twig layer.

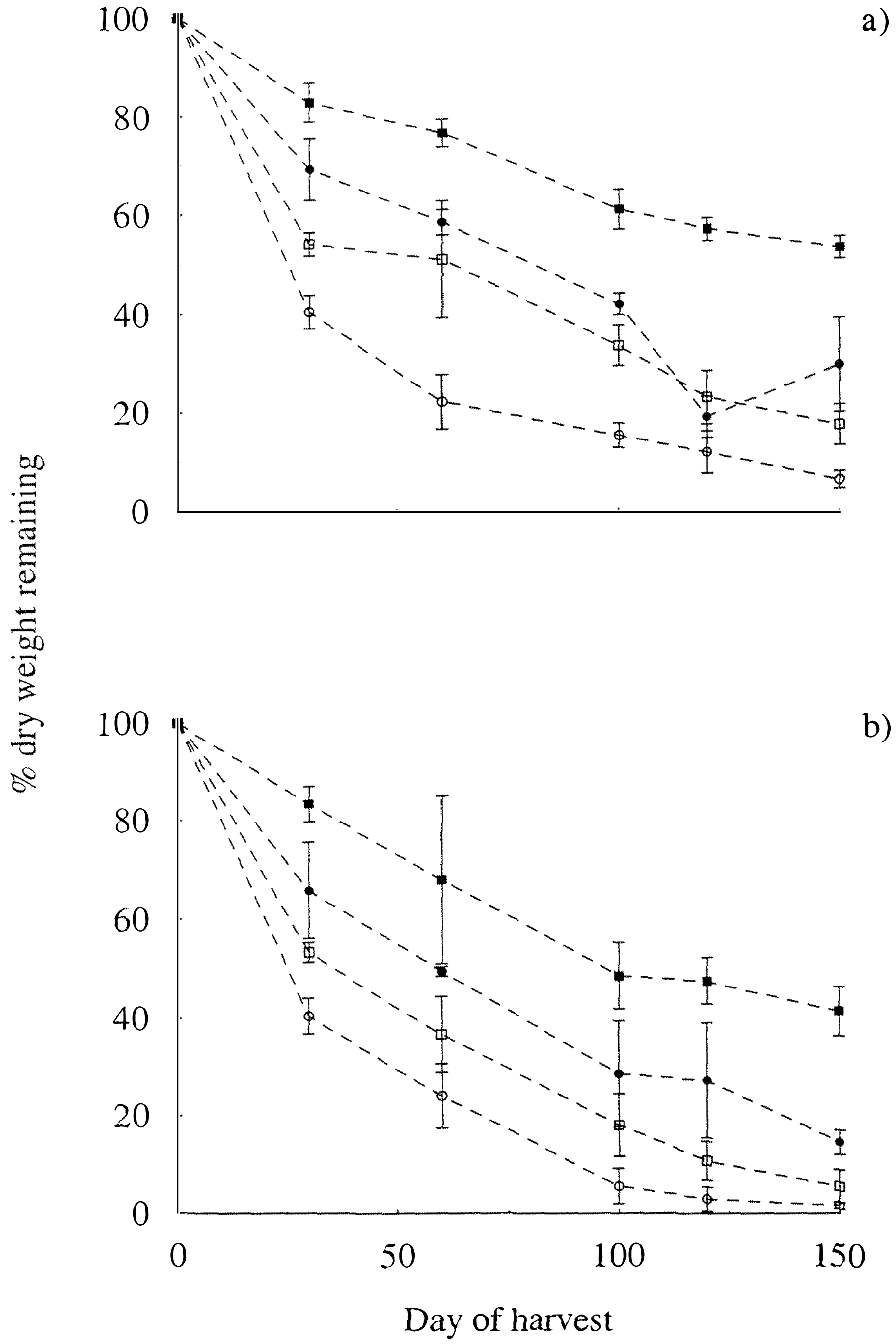
Site	Habitat	Leaf litterfall (t ha^{-1} yr^{-1})	Leaf litter layer (t ha^{-1})	k_L (leaf)	Twig fall (t ha^{-1} yr^{-1})	Twig litter layer (t ha^{-1})	k_L (twig)
Denton's	T	6.0 ± 0.5	1.6 ± 0.3	3.8	1.0 ± 0.2	1.7 ± 0.4	0.6
Bush	NT	6.4 ± 0.5	4.0 ± 0.4	1.6	1.8 ± 0.4	4.5 ± 0.9	0.4
Rangitawa	T	7.7 ± 0.6	3.7 ± 0.3	2.1	2.6 ± 0.7	3.6 ± 0.9	0.7
Bush	NT	8.5 ± 0.6	6.1 ± 0.6	1.4	1.9 ± 0.3	4.4 ± 0.5	0.4

The indirect measures of leaf litter decomposition (k_L) indicated that it is more rapid in *Tradescantia* than non-*Tradescantia* habitat (Table 3). Decomposition appeared to be faster at Denton's Bush than at Rangitawa Bush. Decomposition quotients are >1, which indicates leaf litter turnover occurs in less than 1 year in these forest habitats (Table 3).

Decomposition of litter in bags

The relative rates of litter decay were the same for bagged *Tradescantia* and *M. ramiflorus* litter across treatments (Fig. 1). Bagged litter decomposed faster in *Tradescantia* habitat at ground level than at the same level in non-*Tradescantia* habitat, and litter decomposed more rapidly in the *Tradescantia* lattice than at the same height in non-*Tradescantia* habitat. The rate of litter decomposition in the *Tradescantia* lattice was similar to that at ground level in non-*Tradescantia* habitat (Fig. 1).

Figure 1. Decomposition (mean ± SE) of bagged *Tradescantia* leaf and shoot litter (a) and *M. ramiflorus* leaf litter (b) in Denton's Bush over 150 days of study. Treatments are as follows: non-*Tradescantia* habitat at lattice level (■); *Tradescantia* habitat at lattice level (●); non-*Tradescantia* habitat at ground level (□); and *Tradescantia* habitat at ground level (○).



The GLM accounted for 98.2% of the total variation in the data (Table 4). The overall effect of time was most important, but the time × level and time × habitat terms indicate significant differences in the rate of decay between ground and lattice level, and between habitats (see also Fig. 1). The small but significant time × habitat × level interaction indicates that the differences in decomposition rates between levels were less marked in *Tradescantia* than non-*Tradescantia* habitats. The time × litter interaction indicates that *M. ramiflorus* litter decomposed more quickly than *Tradescantia* litter. Decomposition rates, based on just the significant terms of the GLM, are given in Table 5.

Litter nutrients and quality

Of the *Tradescantia* and non-*Tradescantia* (mixed species) components of the litter layer, *Tradescantia* litter contained greater amounts of all nutrients (Table 6). The non-*Tradescantia* component of the litter layer was leached of K, Ca and Mg relative to litterfall (Table 6). Bagged litter used in the decomposition study contained greater amounts of all nutrients (*Tradescantia*: 2.72 g/ 100g N, 0.43 g/ 100g P, 4.04 g/ 100g K, 2.32 g/ 100g Ca, 0.92 g/ 100g Mg; and *M. ramiflorus*: 2.53 g/ 100g N, 0.24 g/ 100g P, 3.80 g/ 100g K, 1.67 g/ 100g Ca, 0.39 g/ 100g Mg) except for Ca in *M. ramiflorus*, than was held in the litter layer (Table 6). Note that bagged *Tradescantia* contained greater amounts of all nutrients than bagged *M. ramiflorus*. *Tradescantia* and *M. ramiflorus* litters had lower C:N ratios, and lower concentrations of condensed tannins, total phenolics, fibre and lignin than canopy litter (Table 7). In addition, they were mesophyllous, while the majority of the canopy species were sclerophyllous. While *M. ramiflorus* and *Tradescantia* were similar in litter quality, *M. ramiflorus* litter had more ADF-lignin and less $\propto$-cellulose than *Tradescantia* litter (Table 7).

Soil nutrient availability

There were increased levels of IER estimated available nitrate ($F_{1,11} = 99.51$, $P < 0.001$ (treatment); $F_{4,11} = 27.25$, $P < 0.001$ (plot (treatment))), and similar levels of ammonium ($F_{1,11} = 0.27$, $P = 0.62$ (treatment); $F_{4,11} = 3.61$, $P = 0.04$ (plot (treatment))) and phosphate ($F_{1,11} = 1.30$, $P = 0.28$ (treatment); $F_{4,11} = 2.38$, $P = 0.12$ (plot (treatment))), in the soil of *Tradescantia* plots relative to non-*Tradescantia* plots (Fig.2).

Table 4. Proportion of variation explained (= % deviance) by each term in the GLM. *** = $P<0.001$; * = $P<0.05$; ND = not determined since the model has no intercept term.

Term	% Total deviance
Time	91.5^{ND}
Time × habitat	1.8***
Time × level	4.4***
Time × habitat × level	0.1*
Time × litter	0.3***
Time × litter × habitat	0
Time × litter × level	0.1
Time × litter × habitat × level	0
Residual	1.8

Table 5. K values, standard errors and decay times (to 99% of original) for each litter type/ treatment combination placed in Denton's Bush for 150 days (derived from the GLM fitted with significant terms only). Treatment codes are as follows: TGL = *Tradescantia* habitat at ground-level; TLL = *Tradescantia* habitat lattice-level; NTGL = non-*Tradescantia* habitat at ground-level and NTLL = non-*Tradescantia* habitat lattice-level.

Litter type	Treatment	K value (yrs^{-1})	SE	Decay time 99% (yrs)
Tradescantia	TGL	9.02	0.66	0.51
M. ramiflorus	TGL	9.86	0.66	0.47
Tradescantia	TLL	3.58	0.22	1.29
M. ramiflorus	TLL	4.42	0.22	1.04
Tradescantia	NTGL	5	0.33	0.92
M. ramiflorus	NTGL	5.84	0.33	0.79
Tradescantia	NTLL	1.61	0.18	2.87
M. ramiflorus	NTLL	2.45	0.18	1.88

Tradescantia production

Total annual aboveground *Tradescantia* growth exceeded decay at both sites. At Denton's Bush, annual sub-plot mean RGR values range from 48–137%, and the annual site mean (± SE) was 73 ± 5%. At Rangitawa Bush, annual sub-plot mean RGR values range from 34–78%, and the annual site mean (± SE) was 51 ± 2%. Relative growth rate peaked during the December–January period at Denton's Bush, and the October–November period at Rangitawa Bush. Growth was less than decay during April–May at Denton's Bush and December–March at Rangitawa Bush. *Tradescantia* aboveground production was estimated to be 1.28 t ha^{-1} yr^{-1} at Denton's Bush, and 0.64 t ha^{-1} yr^{-1} at Rangitawa Bush.

Table 6. The mean (± SE) concentrations (g/ 100g) of nutrients in litter at Denton's Bush and Rangitawa Bush.

Litter	N	P	K	Ca	Mg
Litterfall	1.43 ± 0.09	0.15 ± 0.01	1.05 ± 0.19	2.13 ± 0.15	0.43 ± 0.07
Litter layer					
Non-*Tradescantia*	1.66 ± 0.08	0.15 ± 0.01	0.33 ± 0.05	1.99 ± 0.07	0.33 ± 0.04
Tradescantia	2.3 ± 0.29	0.23 ± 0.07	1.24 ± 0.43	2.08 ± 0.24	0.51 ± 0.05

Table 7. Litter quality of leaf litterfall at two sites and bagged litter prior to decomposition. Carbon compounds are mean (± SE) concentrations (g/ 100g).

Litter	C: N	Condensed tannins	Total phenolics	Fibre	∝-Cellulose	ADF-lignin	Lignin : N
Litterfall	31	1.7 ± 0.1	2.7 ± 0.5	45 ± 1.9	19 ± 1.2	24.3 ± 2.7	17
Tradescantia	17	0.5	0.7	32.7	29	3.6	1.3
M. ramiflorus	18	0.2	1	31.1	23.3	7.7	3

We have estimated the annual uptake of nutrients by *Tradescantia* (i.e., annual aboveground production × % nutrient content of *Tradescantia* litter at 0 days), and compared this with the nutrients returned annually through litterfall by forest trees (i.e., annual litterfall (Table 3) × % nutrient content of litterfall (Table 6)) and the amounts held within the forest litter layer (i.e., [forest litter layer (Table 3) × % nutrient content of forest litter layer (Table 6)] + [*Tradescantia* litter layer × % nutrient content of *Tradescantia* litter layer (Table 6)]). The annual uptake of nutrients by *Tradescantia* was a significant amount of the nutrient inputs via litterfall (41% N, 61% P, 23% Ca, 46% Mg and 83% K; Table 8), which exceeded the amounts of these nutrients held within the forest litter layer (except Ca) (Table 8) but was only a small amount of these nutrients held within the topsoil (Table 1), even assuming only a small portion of this pool is available to plants.

Figure 2. Available nutrients in *Tradescantia* (T) and non-*Tradescantia* (NT) soils at Denton's Bush. Values are means ± SE (*n* = 3) determined by IER bag method.

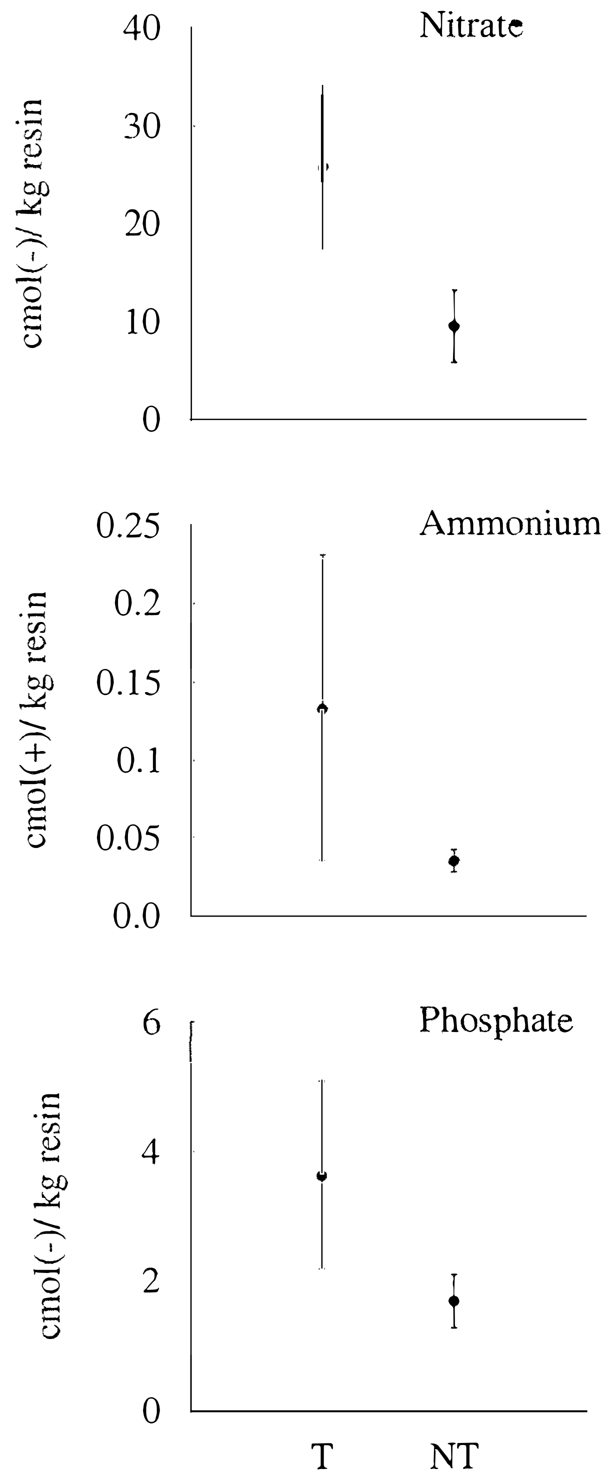


Table 8. The estimated annual uptake of nutrients by *Tradescantia* compared with the nutrients returned annually through litterfall by forest trees, and the amount held within the forest litter layer. Calculations are based on figures in Tables 3 and 6, see text for details. Soil nutrients are given in Table 1.

Nutrient	*Tradescantia* uptake (t ha^{-1} yr^{-1})	Litterfall input (t ha^{-1} yr^{-1})	Litter layer (t ha^{-1})
N	0.035	0.086	0.027
P	0.006	0.009	0.002
Ca	0.03	0.128	0.032
Mg	0.012	0.026	0.005
K	0.052	0.063	0.006

Discussion

Our results demonstrate that *Tradescantia* increased the rates of litter decomposition and altered nutrient cycling. Rapid litter turnover beneath swards of *Tradescantia* was evident by the increased decomposition rates of bagged litter and by the reduced litter layer in *Tradescantia* areas relative to non-*Tradescantia* areas of forest, despite similar quantities of litterfall entering both habitats. Soil nitrate availability (IER estimated) was increased under mats of *Tradescantia* relative to non-*Tradescantia* areas of forest. The annual uptake of nutrients by *Tradescantia* exceeded the amounts of these nutrients held within the forest litter layer (N, P, K, Mg, not Ca) but was only a small amount of these nutrients held within the topsoil. We don't know whether *Tradescantia* sequesters nutrients at a cost to native plants, but the high fertility of these sites suggests that nutrients are not limiting.

The soils of these lowland forest remnants are fertile, as suggested by comparison with soil nutrient levels of other New Zealand forests (New Zealand Soil Bureau 1968). Generally, *L. novae-zelandinae* and *D. spectabile* are indicative of wet fertile soils and *P. totara* and *B. tawa* occur on drier fertile soils (Wardle 1991). In addition, nutrient return by litterfall has been shown to relate directly to available soil nutrients (Vitousek 1982; Vitousek and Sanford 1986). Forests on moderately fertile soils generally return more litter at higher nutrient concentrations than do forests on less fertile soils (Vitousek and Sanford 1986). The N-P-Ca use efficiency (dry mass of litterfall produced per unit of nutrient) of these forests suggests high nutrient availability compared with world forests (Vitousek 1982).

The estimated mean annual leaf litterfall values, 6.85 ± 0.85 t ha^{-1} into *Tradescantia* habitat and 7.45 ± 1.05 t ha^{-1} into non-*Tradescantia* habitat, are similar to annual leaf litterfall of warm temperate broad-leaved evergreen forests generally (6.5 t ha^{-1}, Vogt et al. 1986). Conversely, the litter layers, 2.65 ± 1.05 t ha^{-1} in *Tradescantia* habitat and 5.05 ± 1.05 t ha^{-1} in non-*Tradescantia* habitat, are both lower than litter layers of warm temperate broad-leaved evergreen forests generally (19.2 t ha^{-1}, Vogt et al. 1986). Our indirect measures of leaf litter turnover times (k_L = 1.4 to 3.8) are high relative to those in warm temperate broad-leaved evergreen forests, and even tropical broad-leaved evergreen forests generally (k_L = 0.34 and 0.42 respectively, Vogt et al. 1986), although k_L values as high as four are reported for some tropical forests (Olson 1963). These comparisons indicate that the study sites are highly productive, and that litter is broken down rapidly, especially where *Tradescantia* occurs.

Tradescantia has the potential to influence all three factors which determine the rate of litter decomposition, namely litter quality, climate (temperature and moisture) and composition of the decomposer community (Heal et al. 1997). In general, the attributes of litter quality that affect decay rate are N content, and C:N and lignin:N ratios (Melillo et al. 1982). There are three issues to discuss regarding litter quality. Firstly, *Tradescantia* litter contained more nitrogen, had lower C:N and lignin: N ratios than the mixed-species leaf litterfall, which probably contributed to its faster decomposition. Secondly, *M. ramiflorus* litter was of similar quality to *Tradescantia* litter which partly explains why our K values, estimated using the bioassays, are greater than our estimates of k_L, which were based on the mixed-species canopy leaf litter. Also, the use of single-species litter bags probably influenced associated decomposers and so affected estimated decay rates (Blair et al., 1990). Thirdly, the relative contributions of sclerophyllous and mesophyllous species to the leaf litterfall into *Tradescantia* and non-*Tradescantia* habitats may have affected faster decay rates in *Tradescantia*, at least at Denton's Bush. The degree of sclerophylly characterises the physical quality of litter which reflects chemical parameters e.g., ADF fibre, lignin (Palm and Rowland 1997). This character does not explain why decomposition was faster in

Tradescantia at Rangitawa Bush, where the contributions of mesophyllous and sclerophyllous species to the leaf litterfall of *Tradescantia* and non-*Tradescantia* habitats was similar.

We have some anecdotal evidence to suggest that soil moisture is greater under mats of *Tradescantia* than under leaf litter (Standish, unpubl. data), which could explain the increased rates of decomposition under *Tradescantia*. Collembola and Acarina abundance was greater within *Tradescantia* habitat than in non-*Tradescantia* habitat at this site (Chapter 3). Collembola are thought to act as catalysts in the breakdown of organic matter and in the cycling of plant nutrients through their feeding and other activities (Greenslade 1991), and similarly, soil-dwelling Acarina perform an essential role in the breakdown of organic matter (Forster & Forster 1973). Although Collembola were observed to colonise lattice level bags within *Tradescantia*, the activity of these and other decomposing organisms is likely to be greater within the forest floor/ mineral soil interface than above the soil surface, which probably explains why decomposition occurred more rapidly at ground level than at lattice level.

Tradescantia invades areas with reduced canopy cover, such as forest edges. Canopy cover was reduced in *Tradescantia* plots relative to non-*Tradescantia* plots, but surprisingly did not result in reduced litterfall. Also associated with forest edges is an altered microclimate (i.e., light exposure, wind exposure, precipitation, and temperature and moisture of air and soil) relative to the forest interior (Saunders et al. 1991), which could potentially alter the processes of litter decomposition and nutrient cycling accordingly (Murcia 1995). Edge effects on microclimate extend at least 40 to 50 m into New Zealand podocarp-broadleaf forest remnants (Young and Mitchell 1994; Davies-Colley et al. 2000), which means that remnants < 9 ha in area are dominated by edge microclimate conditions (Young and Mitchell 1991). Our *Tradescantia* and non-*Tradescantia* plots were located within 40 to 50 m of the forest edge, except for one non-*Tradescantia* plot at Denton's Bush, a site which would be regarded as 'all edge'. Therefore, the edge effects on microclimate were similar in *Tradescantia* and non-*Tradescantia* plots, and do not explain the increased rates of decomposition beneath mats of *Tradescantia*.

Vitousek (1990) suggests that plant invaders are likely to be more successful on more fertile soils compared to sites with lower soil fertility, and this appears to be the case for *Tradescantia* in New Zealand (Ogle and Lovelock 1989). Our calculations estimate *Tradescantia* aboveground production (0.64–1.28 t ha^{-1} yr^{-1}) to be up to 20% of forest litter production, which represents a considerable addition of groundcover biomass to these forests as native groundcover is sparse. Furthermore, annual growth exceeded decay at both sites, which indicates that biomass is accumulating still. Maule et al. (1995) report similar growth rates in a sward of *Tradescantia* at similar equilibrium biomass in a mixed *M. ramiflorus* remnant at Akaroa (southern New Zealand) despite there being more light available in some areas of the Akaroa forest. In a forest remnant in the Manawatu (New Zealand), average *Tradescantia* production (regrowth estimated after removal) was ~3 t ha^{-1} yr^{-1} (Kelly and Skipworth 1984a).

There was a great deal of variation in the amount of plant available IER nutrients in *Tradescantia* plots, relative to that in non-*Tradescantia* plots. Perhaps this variation reflects the stage of invasion, whereby a newly established plant absorbs more nutrients than a plant established for a longer time (Maule et al. 1991). With increased replication of IER bags, perhaps controlling for sward age, microclimate and light availability, the effects of *Tradescantia* on nutrient cycling would become clearer.

This paper documents the impact of *Tradescantia* on litter decomposition rates and nutrient cycling. We don't know whether *Tradescantia* sequesters nutrients at a cost to native plants, although the different rooting zones occupied by *Tradescantia* and the majority of forest trees may allow for co-existence. Furthermore, podocarps are mycotrophic (Baylis 1969) which may enable them to access nutrients that are unavailable to *Tradescantia*, particularly phosphorous. Lastly, the high fertility of these sites and of *Tradescantia*-affected sites generally (Ogle and Lovelock 1989), may reduce competition for nutrients (Grubb 1994).

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Chapter 3: Impact of an invasive clonal herb on epigaeic invertebrates in forest remnants in New Zealand.

Coleoptera: Staphylinidae: Microsilphinae: *Microsilpha* sp.
Strongly associated with non-*Tradescantia* habitat.

Abstract

This study determines the impact of an invasive herbaceous weed *Tradescantia fluminensis* on invertebrates within three lowland forest remnants in New Zealand. Epigaeic invertebrates were sampled within three *Tradescantia*-infested plots and three non-infested plots at each of three sites using pitfall traps. The abundance of invertebrates was reduced in *Tradescantia* plots compared with non-*Tradescantia* plots if Collembola and Acarina, the two most abundant and variable orders, are excluded (647 ± 123 (mean ± SE) compared with 1153 ± 370), though this difference is not statistically significant. There was no difference if they were included (3897 ± 2530 compared with 2505 ± 1095). Five of the 23 orders collected were sorted into recognisable taxonomic units (RTUs). RTU richness was lower in *Tradescantia* plots compared with non-*Tradescantia* plots (39.7 ± 5.5 compared with 51.7 ± 8.9) though there was weak statistical support for this difference. Two-way indicator species and detrended correspondence analyses clearly separated *Tradescantia* and non-*Tradescantia* plots within sites when based on RTUs, but not when based on orders/ families. Overall, impacts of *Tradescantia* were apparent despite large differences in invertebrate assemblages among sites. The impact of *Tradescantia* could be a result of the weed's tall, dense vegetation structure and associated microclimate, relative to native ground covers.

Keywords: Weed impacts, *Tradescantia fluminensis*, pitfall trap, invasive weed, invertebrate assemblages, forest remnants, New Zealand.

1. Introduction

An increasing number of studies have demonstrated that where invasive exotic plant species have replaced native vegetation, there is an impact on native invertebrate assemblages (e.g., Breytenbach, 1986; Samways et al., 1996; French and Eardley, 1997; French and Major, 2001), although there are exceptions (Hedge and Kriwoken, 2000). The size of impact may vary with the degree of change to the vegetation structure. For example, a comparison of the litter invertebrate assemblages of exotic *Chrysanthemoides monilifera* shrubland and native heathland of similar structure (i.e., height, canopy and leaf litter cover) revealed minimal impacts (French and Eardley, 1997), whereas a comparison of native grasslands invaded by exotic shrubs and trees with non-invaded native grasslands in South Africa indicated significant differences in the composition of the invertebrate species assemblages (Samways et al., 1996).

Tradescantia fluminensis (Commelinaceae) (syn. *T. albiflora*; R. Faden, pers. comm.) is a ground-smothering perennial herb native to South America (Esler, 1978). It has replaced native ground cover in forest remnants in New Zealand (Kelly and Skipworth, 1984a), eastern Australia (Dunphy, 1991) and Florida (Wunderlin, 1998). In New Zealand, there are several reasons why *Tradescantia* invasion could impact on invertebrate communities. First, *Tradescantia* forms a dense layer of vegetation more than 60 cm tall, contrasting with native ground covers, which are smaller statured and sparsely distributed among the leaf litter (Chapter 2). Second, *Tradescantia* produces a litter that decomposes more readily than the leaf litter of the mixed-species forests it invades, and increases the rate of litter decomposition and alters nutrient cycling relative to non-affected areas of forest (Chapter 2). Third, soil moisture is greater under mats of *Tradescantia* than under leaf litter (Standish, unpublished data). Last, invasion by *Tradescantia* is associated with a decrease in abundance and species richness of native forest seedlings (Chapter 1). This decrease in floral diversity has been correlated with a decrease in the diversity of Malaise-trapped beetles and fungus gnats (Toft et al., 2001).

This study complements that by Toft et al. (2001), which investigated the impact of *Tradescantia* on beetles and fungus gnats sampled above ground level using Malaise traps, and that by Yeates and Williams (2001), which documents the impact of *Tradescantia* on soil microfauna. I focussed on the epigaeic invertebrate communities by using pitfall traps to sample the same three lowland forest remnants in the lower North Island, New Zealand, within the same experimental plots and at the same time as Toft et al. (2001).

2. Methods

2.1 Study sites

Three *Tradescantia*-affected lowland podocarp/ broadleaved forest remnants in the lower North Island, New Zealand, were chosen for study. These were Rangitawa Bush (12.4 ha) on an old river terrace (40°06.0′ S, 175°27.6′ E; 100 m asl); Denton's Bush (2.0 ha) on a flood plain (40°48.0′ S, 175°11.4′ E; 20 m asl) and; Kirkwell Bush #4 (14.0 ha) on an old river terrace (40°47.8′ S, 175°10.3′ E; 40 m asl). Mean annual temperature for all three sites is 13° C, while mean annual rainfall is 1050 mm (Rangitawa Bush) and 1220 mm (Denton's Bush and Kirkwell Bush #4; NIWA, 2000). The study sites are described in detail in Chapter 1. A locality map for the study sites can be found in Toft et al. (2001).

At each site, three 20 m x 20 m plots were selected in areas of greatest *Tradescantia* infestation and, adjacent to each, a 20 m x 20 m plot was selected where *Tradescantia* did not occur or was insignificant (*n*= 6 plots/ site; Table 1). Though plots with *Tradescantia* were located closer to the forest edge, all plots were within 50 m of the forest edge or located within sites that were dominated by edge microclimate conditions (i.e., Denton's Bush) (Young and Mitchell, 1994). Ground cover, other than *Tradescantia*, comprised leaf litter, woody seedlings, ferns, grasses and bare ground. Total plant groundcover ranged from 10% for Rangitawa Bush non-*Tradescantia* plots to 95% for Kirkwell Bush *Tradescantia* plots (Table 1). Canopy cover, estimated visually for each of four height classes (*Tradescantia* and vegetation < 30 cm excluded) and then summed to give a total % cover value, was less for *Tradescantia* plots than for non-*Tradescantia* plots (Table 1). A dead wood index [i.e., logs (linear m ha^{-1}) + standing dead (m^2 ha^{-1})] ranged from 0 at Kirkwell Bush, to 94 for a non-*Tradescantia* plot at Rangitawa Bush (Table 1). Detrended correspondence analysis (DCA) and a blocked multi-response permutation procedure (MRBP; Mielke, 1984) of canopy cover (excluding ground covers) showed a clear separation of sites, but no clear separation of *Tradescantia* and non-*Tradescantia* plots (Chapter 1).

Table 1. Mean (± SE) percentage groundcover, percentage canopy cover summed across height classes and dead wood at the three study sites (*n*= 3 plots). R= Rangitawa Bush, D= Denton's Bush, K= Kirkwell Bush, T= *Tradescantia* and NT = non-*Tradescantia.*

Groundcover	RNT	RT	DNT	DT	KNT	KT
Tradescantia	1.2 ± 1.2	83.7 ± 4.3	1.3 ± 1.1	79.7 ± 4.7	11.5 ± 4.0	93.7 ± 3.0
Woody seedlings	1.2 ± 1.2	0.2 ± 0.2	35.3 ± 19.8	2.3 ± 1.2	6.3 ± 4.7	0.5 ± 0.0
Ferns and grasses	7.3 ± 2.1	2.7 ± 1.0	9.7 ± 3.4	0.8 ± 0.3	7.8 ± 5.0	0.7 ± 0.2
Leaf litter	83.7 ± 4.3	11.5 ± 4.0	55.5 ± 26.3	10.3 ± 5.2	50.3 ± 12.3	1.5 ± 1.0
Bare ground	0	0	0	1.2 ± 1.2	23.0 ± 7.5	0
Canopy cover	213 ± 5	194 ± 6	210 ± 7	157 ± 10	115 ± 56	61 ± 17
Dead wood index	51.8 ± 21.6	25.3 ± 19.6	11.5 ± 3.5	38.7 ± 14.1	0	0

2.2 Sampling

Pitfall traps were used to sample epigaeic invertebrates. Dense *Tradescantia* is likely to impede the movement of some invertebrates and so reduce pitfall trap catch compared with non-*Tradescantia* habitat (Greenslade, 1964; Melbourne, 1999), but pitfall traps are generally regarded as the best available method for sampling different vegetations (Samways et al., 1996; Crisp et al., 1998) and for allowing for adequate replication (cf. behavioural extractors). Two pitfall traps were sunk within each 20 m x 20 m plot, one 5 m north and one 5 m south of the centre point. The traps were similar to those of Moeed and Meads (1985) except a tin cover was added to keep out the rain and also to prevent litter falling in and providing a means for the invertebrates to escape. The tin cover sat on two stones and was held down with a piece of wire. Gault's solution (Walker and Crosby, 1988) was used as a preservative, and the traps were emptied weekly for four weeks from December 1, 1997.

Invertebrates were initially sorted to Order except for insect larvae, which were grouped as such. The Coleoptera were further classified into families. The Coleoptera, Araneae, Hemiptera, Homoptera and Formicidae were further sorted into recognisable taxonomic units (RTUs). Recognisable taxonomic units are a cost-effective surrogate for species and their use does not generally compromise scientific accuracy (Oliver and Beattie, 1996). The taxa sorted to RTU were selected with reference to Moeed and Meads (1985) (i.e., abundant in pitfall traps within similar forest type) and/ or because they had obvious morphological characteristics that were useful for classification. Abundant Coleopteran RTUs associated with either *Tradescantia* or non-*Tradescantia* were identified to species (R. Leschen, New Zealand Arthropod Collection; R. Harris, Landcare Research). Beetle nomenclature follows Klimaszewski and Watt (1997). Beetles were also classified into functional groups (i.e., detritivores, herbivores and predators) at the family or subfamily level with reference to Hutcheson (1996), Klimaszewski and Watt (1997) and Didham et al. (1998) (Appendix 2).

2.3 Statistical analyses

I used a mixed model ANOVA (site = random, habitat = fixed) to test for differences in abundance and RTU richness between *Tradescantia* and non-*Tradescantia* plots. Abundance data were log transformed before analysis.

Two-way indicator species analysis (TWINSPAN; Hill, 1979; Gauch and Whittaker, 1981) and detrended correspondence analysis (DCA; Hill and Gauch, 1980) were used to explore differences in the invertebrate assemblages sampled in *Tradescantia* and non-*Tradescantia* plots. Both techniques use the composition of taxa, but offer different features. TWINSPAN arranges groups into a hierarchy, whereas DCA arranges groups along ordination axes. TWINSPAN provides indicator taxa at each division of the hierarchy and DCA does not force association among groups. Relative to other ordination techniques, DCA has improved performance with heterogeneous data (Hill and Gauch, 1980). The blocked multi-response permutation procedure (MRBP; Mielke, 1984) was used to test for differences in the invertebrate community of *Tradescantia* and non-*Tradescantia* plots blocked by site. Data were pooled across weeks ($n = 4$) and traps ($n = 2$) for each plot. Insect larvae and rare taxa (i.e., those that occurred <5 times) were excluded from these data sets. Raw data were grouped into abundance classes for TWINSPAN (i.e., cut levels are 0, 2, 5, 10 and 20 individuals) or transformed to $[\log (x + 1)]$ before DCA and MRBP, which reduced the impact of very abundant species on the result. These analyses were done on orders/ families and RTUs for the sub-set of taxa sorted to this level, using PC-ORD (McCune and Mefford, 1999). I used correlations and overlays to aid interpretation of the DCA on RTUs using the variables listed in Table 1 (seedlings, ferns and grasses were summed to give a percentage ground cover other than *Tradescantia*), excluding percentage leaf litter cover, which was highly correlated with *Tradescantia* cover.

3. Results

3.1 Invertebrate abundance and RTU richness

A total of 18986 individuals were collected and classified into 23 orders, and five of these were classified into 147 RTUs (Table 2; Appendix 2). There was no difference in the number of invertebrates trapped in *Tradescantia* and non-*Tradescantia* plots (Fig. 1a; $F_{1,2} = 0.49$, $P = 0.56$). If Collembola and Acarina, the two most abundant orders that displayed highly variable trap catches, are excluded, there is weak support for a decrease in the number of invertebrates trapped in *Tradescantia* compared with non-*Tradescantia* plots (Fig. 1a; $F_{1,2} = 7.19$, $P = 0.12$).

There was weak statistical support for the decreased RTU richness of *Tradescantia* plots compared with non-*Tradescantia* plots (Fig. 1b; $F_{1,2} = 6.36$, $P = 0.13$), which in part could be attributed to a lack of statistical power to detect a difference. RTU richness of *Tradescantia* plots compared with non-*Tradescantia* plots was consistently lower across orders: Coleoptera: 50: 61; Araneae 23: 30; Homoptera: 5: 9; Hemiptera 4: 6 and Formicidae: 4:5 (Fig. 1b). Denton's Bush was the most species rich site — 83 RTUs were identified, 59 in non-*Tradescantia* plots and 49 in *Tradescantia* plots. Seventy-nine RTUs were identified at Rangitawa Bush, 62 in non-*Tradescantia* and 40 in *Tradescantia* plots; and 52 RTUs were identified at Kirkwell's Bush, 34 in non-*Tradescantia* and 30 in *Tradescantia* plots (Fig. 1b).

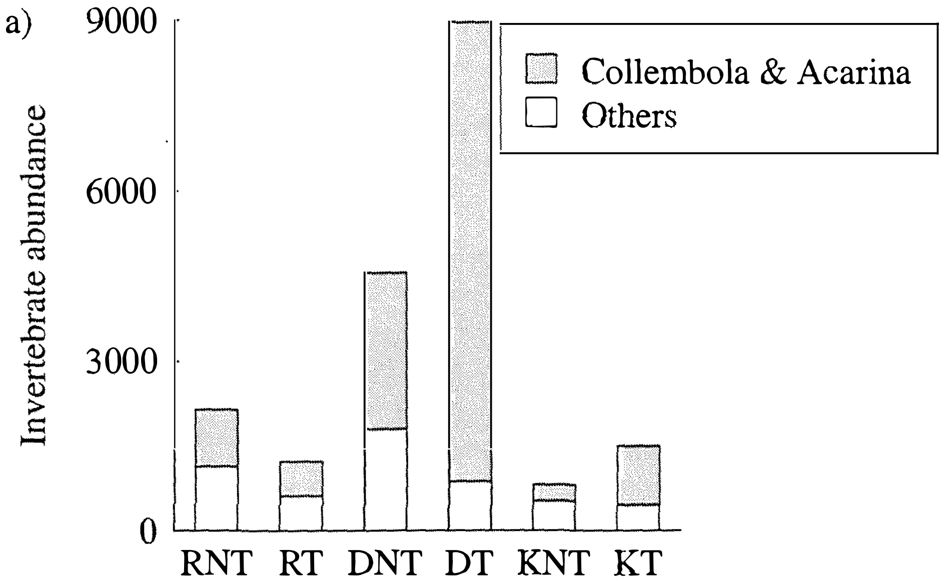
Table 2. Invertebrate orders and families sampled within the three study sites using pitfall traps. Taxa are placed in rank order of abundance and the number of RTUs identified are indicated for taxa sorted to this level. Beetle RTUs are listed in Appendix 2 (page 138).

Taxon	Taxon	Taxon	Taxon
Collembola	Coleoptera cont'	Coleoptera cont'	Hemiptera (8)
Acarina	Corticariidae (5)	Anobiidae (1)	Opiliones
Coleoptera	Coccinellidae (1)	Scraptiidae (1)	Pseudoscorpiones
Leiodidae (9)	Hydrophilidae (1)	Clambidae (1)	Isopoda
Staphylinidae (14)	Corylophidae (1)	Diptera	Meinertellidae
Scarabaeidae (2)	Nitidulidae (3)	Hymenoptera	Lepidoptera
Carabidae (5)	Mycetophagidae (2)	Formicidae (5)	Gastropoda
Ptiliidae (2)	Endomychidae (1)	Non-Formicidae	Chilopoda
Scydmaenidae (1)	Trogossitidae (1)	Homoptera (11)	Orthoptera
Zopheridae (7)	Unknown (1)	Diplopoda	Oligochaeta
Curculionidae (16)	Cerambycidae (1)	Amphipoda	Thysanura
Cerylonidae (2)	Chrysomelidae (1)	Thysanoptera	Plecoptera
Cryptophagidae (2)	Anthribidae (1)	Araneae (41)	Siphonaptera

3.2 *Beetle guilds*

There were more detritivorous beetles in non-*Tradescantia* plots than in *Tradescantia* plots, though this difference was not statistically significant because of the differences among sites and the lack of power to detect a difference (Table 3). There was no difference in numbers of herbivorous or predacious beetles between plots, but again, variation among sites (Table 3).

Fig. 1. Total abundance of pitfall trap invertebrates (a) and RTU richness for sub-sample of invertebrates sorted to this level (b) in *Tradescantia* and non-*Tradescantia* plots at three sites. R= Rangitawa Bush, D= Denton's Bush, K= Kirkwell Bush, T= *Tradescantia* plot, NT= non-*Tradescantia* plot. Note log scale on y-axis for (a).



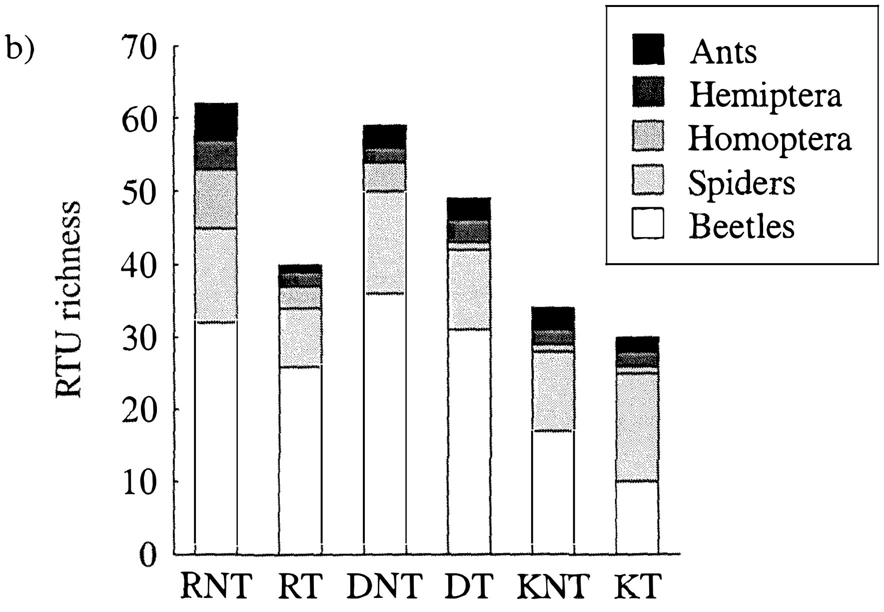


Table 3. The abundance of beetles classified into functional groups. *F* and *P* values are for mixed model ANOVAs, d.f.= 1, 2, interaction= Habitat × site. R= Rangitawa Bush, D= Denton's Bush, K= Kirkwell Bush, T= *Tradescantia* plot, NT= non-*Tradescantia* plot.

Functional	Abundance						*F* value		*P* value
group	RNT	RT	DNT	DT	KNT	KT	Habitat	Interaction	
Predators	22	31	148	84	59	14	1.80	1.70	1.06
Herbivores	39	53	26	11	1	1	0.02	0.03	0.75
Detritivores	30	10	779	64	206	58	11.63	0.90	0.07

3.3 *TWINSPAN classifications and DCA ordinations*

The TWINSPAN classification showed that, within sites, there was separation of *Tradescantia* plots and non-*Tradescantia* plots when based on RTUs but not when based solely on orders/ families (Fig. 2). Similarly, within sites plots of the same habitat type were more closely associated in the ordination of RTUs compared with that of orders/ families (Fig. 3). For the ordination of RTUs, percentage bare ground explained most of the variation along axis 1 (37%) but this merely reflects the skewed distribution of this variable (i.e., incidence of bare ground largely restricted to Kirkwell Bush non-*Tradescantia* plots; Table 1). Percentage *Tradescantia* cover, percentage ground cover other than *Tradescantia*, and percentage dead wood, explained 21%, 28% and 14% of the variation along axis 1 respectively. Percentage *Tradescantia* cover explained 21% of the variation along axis 2, and the remaining variables together explained <4% variation (Fig. 3b, Table 1).

3.4 *Blocked multi-response permutation procedure*

The results of the MRBP indicated that there were not distinct *Tradescantia* and non-*Tradescantia* community assemblages but rather that differences between *Tradescantia* and non-*Tradescantia* plots were site specific, for ordinal/ familial data: A= 0.29 and P= 0.07; or for RTU data: A= 0.26 and P= 0.07; where $A = 1 -$ (observed delta/ expected delta). $A = 1$ when all items are identical within groups (delta = 0), $A = 0$ when heterogeneity within groups equals expectation by chance, $A < 0$ with more heterogeneity within groups than expected by chance, and P = probability of smaller or equal delta.

Fig. 2a. TWINSPAN dendrogram of orders/ families. R= Rangitawa Bush, D= Denton's Bush, K= Kirkwell Bush, NT= non-*Tradescantia* plot, T= *Tradescantia* plot and a, b and c refer to replicate plots. Eigenvalues and indicator taxa for each division are indicated.

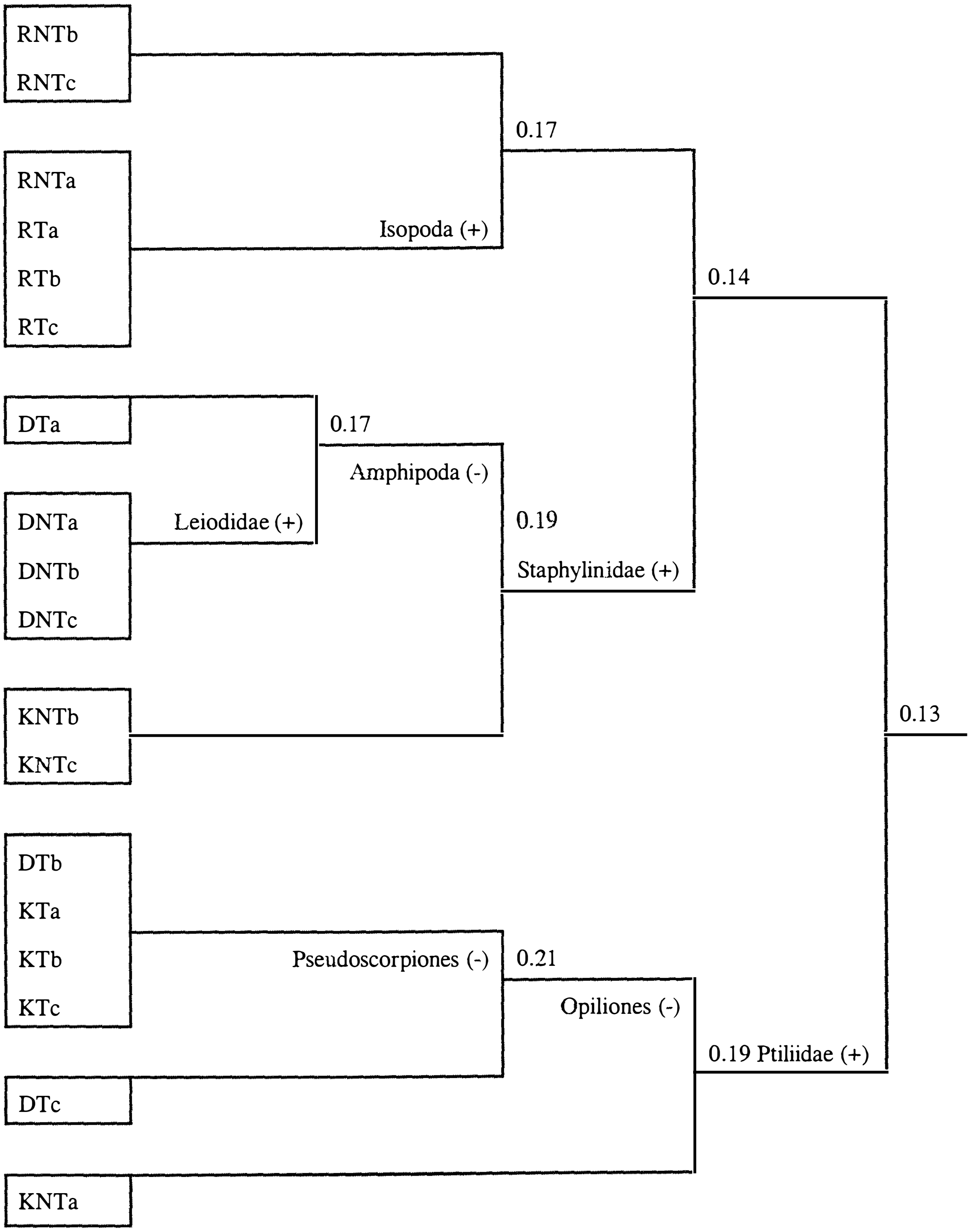
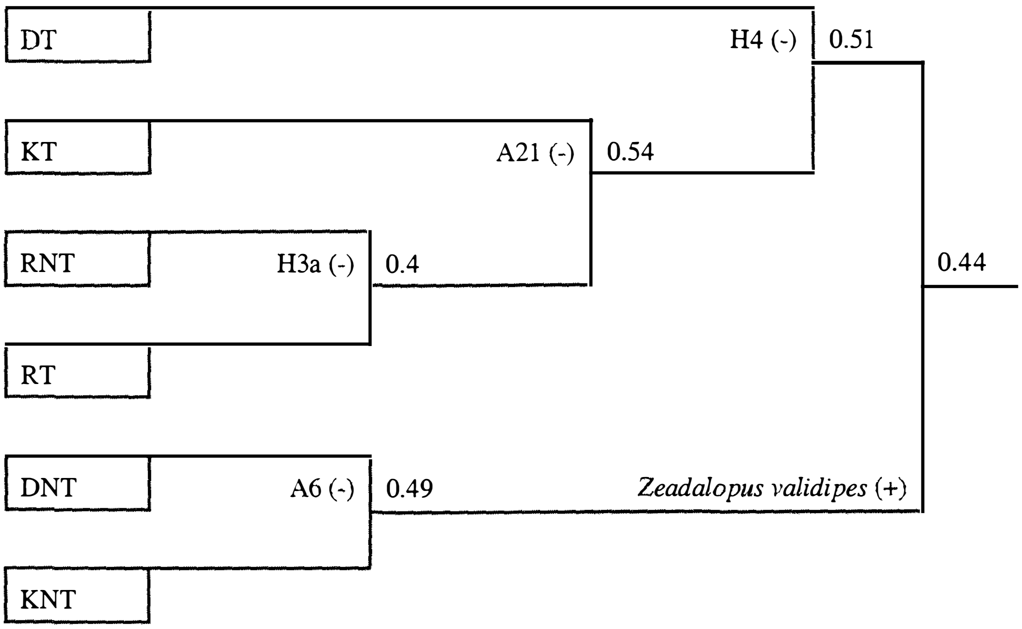


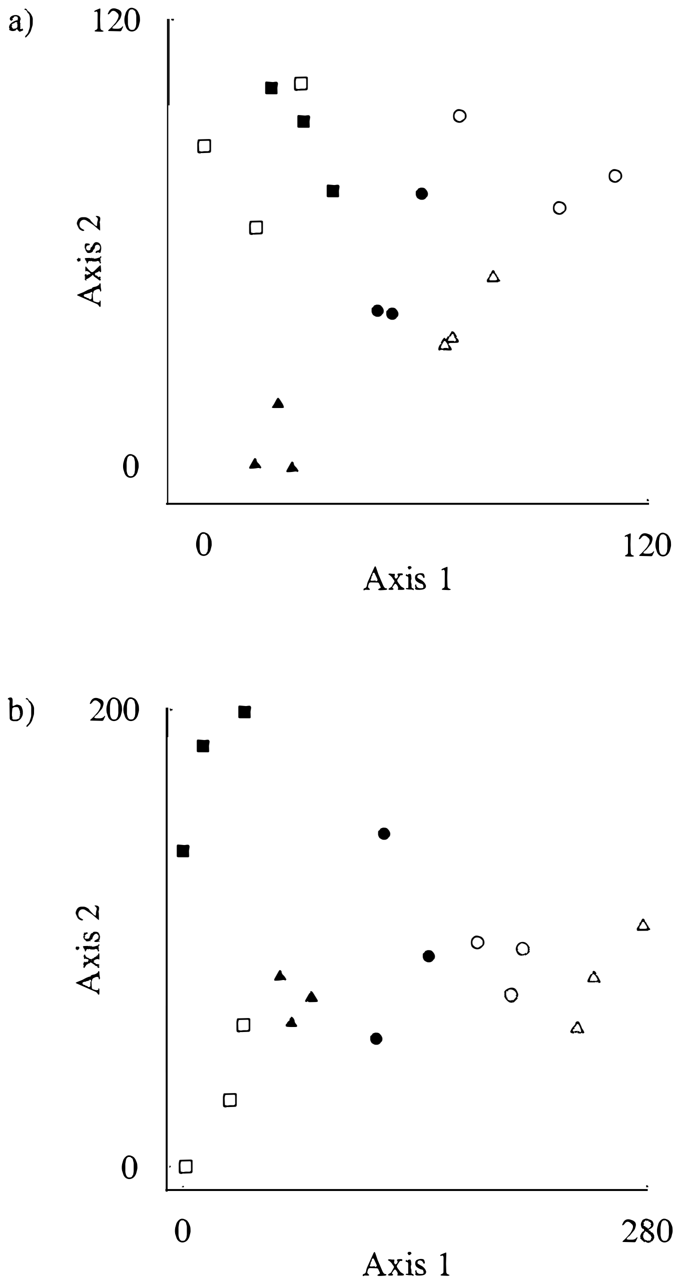
Fig. 2b. TWINSPAN dendrogram of RTUs. R= Rangitawa Bush, D= Denton's Bush, K= Kirkwell Bush, NT= 3 non-*Tradescantia* plots, T= 3 *Tradescantia* plots. Eigenvalues and indicator taxa for each division are indicated. H4= unidentified hemipteran listed in Table 2; H3a= unidentified homopeteran listed in Table 2; A21 and A6 are unidentified Araneae.



3.5 *Habitat associations: indicator taxa*

Excluding rare groups (i.e., those represented by <5 individuals), there were three orders/ families associated with *Tradescantia* or non-*Tradescantia* habitat. There were no Orthoptera trapped in *Tradescantia* plots and 11 trapped in non-*Tradescantia* plots (none were caught at Denton's Bush). The Leiodidae (Coleoptera) were associated with non-*Tradescantia* plots, *n*= 921 were trapped in non-*Tradescantia* compared with *n*= 8 in *Tradescantia.* The Zopheridae (Coleoptera) were associated with *Tradescantia* plots, *n*= 29 in *Tradescantia* compared with *n*= 6 in non-*Tradescantia.* These habitat associations were consistent among sites and detected for more than one RTU within the Coleopteran families. Leiodidae and Ptiliidae (Coleoptera) were TWINSPAN indicator taxa for division of *Tradescantia* and non-*Tradescantia* plots (Fig. 2a), although the Ptiliidae were represented by only one RTU.

Fig. 3. DCA ordination diagrams of plots based on invertebrates sampled using pitfall traps: a) orders/ families and; b) RTUs. ■ = Rangitawa Bush, ● = Denton's Bush, ▲ = Kirkwell Bush, open symbols represent non-*Tradescantia* plots and closed symbols represent *Tradescantia* plots. Cumulative R^2 for the correlations between ordination distances and distances in the original n-dimensional space, for axes 1–3: a) 0.26, 0.49, 0.54; b) 0.20, 0.39, 0.43.



Excluding rare RTUs, 13 RTUs were unique to, or predominantly associated with, non-*Tradescantia* plots at one or more sites (seven of these were represented by >10 individuals; Table 4) and eight RTUs were unique to, or predominantly associated with, *Tradescantia* plots at one or more sites (four of these were represented by >10 individuals; Table 4). Three of the RTUs listed in Table 4 are TWINSPAN indicator taxa for division of *Tradescantia* and non-*Tradescantia* plots (Fig. 2b).

Table 4. RTUs represented by more than 10 individuals associated with either *Tradescantia* or non-*Tradescantia* habitats at three lowland forest remnants. D= Denton's Bush, K= Kirkwell Bush, R= Rangitawa Bush, NT = non-*Tradescantia* and T= *Tradescantia*. In brackets: D= detritivore, P= predator and U= unclassified.

Taxon	Species	RNT	DNT	KNT	RT	DT	KT
Coleoptera: Cryptophagidae	*Micrambina* sp. (D)	0	22	0	0	0	0
Coleoptera: Leiodidae	*Isocolon* sp. (D)	0	25	1	0	0	0
Coleoptera: Leiodidae	*Zeadalopus spinipes* Broun (D)	0	6	21	0	0	0
Coleoptera: Leiodidae	*Zeadalopus validipes* Daffner (D)	12	662	167	3	0	1
Coleoptera: Staphylinidae: Microsilphinae	*Microsilpha* spp. (P)	1	70	41	1	0	0
Hymenoptera: Formicidae	*Prolasius advena* (Smith) (P)	4	0	57	0	0	1
Homoptera	Not determined (U)	33	0	0	0	0	0
Coleoptera: Ptiliidae	*Notoptenidium* spp. (D)	0	5	3	0	9	52
Coleoptera: Zopheridae	*Pristoderus blakewelli* (Pascoe) (P)	0	0	0	2	9	0
Coleoptera: Carabidae	*Lecanomerus sharpi* (Csiki) (P)	1	0	0	11	0	0
Hemiptera	Not determined (U)	0	0	0	0	23	0

4. Discussion

Tradescantia has an impact on the active epigaeic invertebrates of the native lowland forest remnants that it invades. This impact was evident, though not statistically significant, by a decreased abundance (with Collembola and Acarina excluded) and RTU richness of invertebrates sampled in pitfall traps beneath *Tradescantia* compared with those sampled beneath non-*Tradescantia* habitat within three native forest remnants. Further, the invertebrate community composition of *Tradescantia*-infested areas of forest were different from non-infested areas at these sites. These impacts were apparent despite large differences in invertebrate assemblages among sites. An impact of *Tradescantia* was detected for the epigaeic invertebrate community beneath the weed, but not for beetles and fungus gnats sampled above the weed (Toft et al., 2001). *Tradescantia* had no impact on the abundance or species richness of soil nematodes, though individual nematode taxa were affected, as was rotifer abundance (Yeates and Williams, 2001).

The impact of *Tradescantia* was evident at the order and family levels. Orthoptera were not caught in *Tradescantia* plots, which may suggest that this habitat impeded their movement, though flying and crawling invertebrates of similar size to the Orthoptera were not similarly affected (e.g., Lepidoptera, Opiliones). Alternatively, they could have been seeking shelter beneath the pitfall trap covers in the relatively sunlit non-*Tradescantia* plots (R. Toft, pers. comm.). The fungal-feeding Leiodidae (Coleoptera) were associated with non-*Tradescantia* habitat, while the predacious Zopheridae (Coleoptera) were associated with *Tradescantia.* These associations may result from a requirement of particular foods, microclimate or refuge provided by one or other habitat.

In addition to the predacious Zopheridae, specifically *Pristoderus blakewelli*, the predator *Lecanomerus sharpi* (Coleoptera: Carabidae) was associated with *Tradescantia.* Similarly, the carnivorous snail *Powelliphanta traversi traversi* utilizes both *Tradescantia* and non-*Tradescantia* habitats — territories of snails fitted with transponders were as common in the weed as in native habitat, and juvenile snails appeared to be using *Tradescantia* as a refuge (Standish et al., 2001a). These observations are counter to the suggestion that predators are less able to colonise exotic patches of vegetation than herbivores or detritivores (Samways et al., 1996).

There were several Coleopteran detritivores among the species that responded to invasion by *Tradescantia.* All displayed a clear preference for native habitat, with the exception of *Notoptenidium* spp. belonging to the Ptiliidae that feed on a variety of fungal spores and hyphae (Klimaszewski and Watt, 1997), which may thrive in the moister *Tradescantia* habitat. Of those that preferred native habitat, the fungal-feeding leiodids have been mentioned, while cryptophagids feed on fungi hyphae, conidia and spores (Klimaszewski and

Watt, 1997). Fungal-feeding Aphelenchidae nematodes were also less abundant in *Tradescantia*-infested relative to non-infested areas at Rangitawa Bush and Denton's Bush (Yeates and Williams, 2001). Perhaps the fungal species preferred by these three taxa are absent from *Tradescantia* habitat. Increased rates of decomposition in *Tradescantia* habitat compared with non-*Tradescantia* habitat (Chapter 2) are not associated with either an increase in the abundance of beetle detritivores, or a consistent increase in the abundance of Collembola and Acarina (this study), or a change in the proportion of bacterial-feeding nematodes (Yeates and Williams, 2001).

Indigenous insect herbivores in general tend not to feed extensively on introduced plants (Breytenbach, 1986; Olckers and Hulley, 1991). This also appears to be the case for *Tradescantia* in New Zealand (Appendix 1), perhaps because it contains flavonoids (del Pero Martínez and Martínez, 1993) that may deter generalist feeders (Harborne and Williams, 2000). Herbivores did not feature among the RTUs affected by *Tradescantia*'s invasion, but herbivores were poorly represented among the taxa sorted to RTUs relative to the detritivores (i.e., majority of beetles) and predators (i.e., spiders, ants). The abundance of herbivorous beetles, represented by the Scarabaeidae, Curculionidae, Nitidulidae and Chrysomelidae families, did not vary between *Tradescantia* and non-*Tradescantia.* In contrast, herbivorous nematodes were the only feeding group of six to respond to invasion by *Tradescantia*, and their density was increased in *Tradescantia* compared with non-*Tradescantia* at Rangitawa Bush and Denton's Bush (Yeates and Williams, 2001).

It is clear from this study and others that consider the impacts of invasive weeds on invertebrates that: a) it is more usual to find an impact at species (RTU) level rather than family or higher taxonomic levels and; b) site characteristics are important in affecting the outcome (Samways et al., 1996; Toft et al., 2001; Yeates and Williams, 2001). Of the taxa sorted into RTUs, beetles were the most useful as indicators of the impact of *Tradescantia*, and their use allowed assessment for representatives of all trophic groups. Of the beetles identified to species by an expert, errors of identification (i.e., 'lumping') were detected for the RTUs belonging to the Staphylinidae and Ptiliidae families. Problems with the correct identification of staphylinids by non-experts has been highlighted previously (Oliver and Beattie, 1996).

At these study sites the invertebrate assemblages may have been additionally affected by processes associated with forest fragmentation (Didham, 1997), and suffered species losses as a result (Harris and Burns, 2000). Kirkwell Bush was a regenerated forest patch rather than a forest remnant like the other two sites, which may explain its lower species richness (see also Toft et al., 2001) as re-colonisation of flora and fauna may be ongoing (Harris and Burns, 2000). Beetle herbivores were almost entirely absent from this site. Rangitawa Bush was the least modified by stock grazing and possum (*Trichosurus vulpecula* Kerr) browsing, and floristically was the most diverse (Toft et al., 2001), yet Denton's Bush, which was the smallest site, with a history of stock grazing and possum browsing (Chapter 1), showed the greatest species richness.

One common effect of fragmentation on invertebrate communities is an influx of species from the neighbouring human-modified habitat, and this has been demonstrated most often for beetles (Didham, 1997). Adventive beetles from neighbouring pasture were sampled in Malaise traps within 50 m of the edge of native kahikatea forest fragments in New Zealand (Harris and Burns, 2000). It is surprising then that no adventive beetles were identified in this study (Kuschel, 1990; R. Harris, personal communication), which was confined to the forest edges.

It is likely that the tall, dense structure of *Tradescantia*, providing a moist microclimate and an impenetrable thicket for some invertebrates, has more influence on the invertebrate community than its weediness *per se* (see also Samways and Moore, 1991). Nevertheless, the size of *Tradescantia*'s impact on epigaeic invertebrates appears incongruous with its degree of change to the vegetation structure. It appears greater than the impact on epigaeic invertebrates of *Acacia* spp., lantana *Lantana camara* and bugweed *Solanum mauritianum* invasion of native grasslands, assessed using similar measures of impact to this study (Samways et al., 1996), yet these invasive plants are considered to have 'effectively arborized a native grassland ecosystem' (M. Samways, pers. comm.).

While *Tradescantia* remains restricted to forest edges and beneath canopy gaps together with extensive areas of non-affected habitat, as it was at these study sites, there will be alternative native refuges and food sources. However, *Tradescantia* is widespread throughout northern New Zealand (Owen, 1997) and can become the dominant ground cover of forest remnants that it invades (pers. obs.). In these cases, the impact to invertebrate communities will be more profound and it is likely that they will suffer further species losses as a result.

Acknowledgements

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Chapter 4: Experimenting with methods to control *Tradescantia fluminensis.*

Shade house over *Tradescantia* at Monro's Bush, Manawatu.

Abstract: *Tradescantia fluminensis* Vell., commonly referred to as '*Tradescantia*', is an invasive weed of canopy-depleted forest remnants. Previous research suggests that a reduction of *Tradescantia* biomass to ~80 gm^{-2} (~40% cover) is compatible with native forest regeneration. I assessed herbicide application, hand weeding and artificial shading, as methods for the control of *Tradescantia* in two lowland podocarp/ broad-leaved forest remnants in the lower North Island. Hand weeding and herbicide spray, applied to separate experimental plots, did not prevent re-growth of *Tradescantia* after three successive treatments. Re-growth of *Tradescantia* and invasion of other weeds was positively related to light availability, which was increased in canopy-depleted areas, and negatively related to native forest regeneration measured two years after initial treatment. Artificial shading was the most effective method of control. The biomass of *Tradescantia* was significantly reduced in artificially shaded plots (2–5% full light; 81.3 ± 10.6 gm^{-2}), relative to non-shaded plots (15–27% full light; 597.6 ± 6.6 gm^{-2}; $t_4 = 17.38$, $P < 0.001$) after 17 months. Native sub-canopy trees were planted into *Tradescantia* to achieve natural shading over large areas of forest. After 2.5 years, 61% of the saplings planted have emerged from the surrounding *Tradescantia*.

Key words: hand weeding, herbicide, light availability, invasive weed, native forest regeneration, shade, triclopyr, weed control.

Introduction

Tradescantia fluminensis (Commelinaceae) is an invasive, ground-smothering perennial herb capable of preventing native forest regeneration by inhibiting the growth of seedlings (Kelly and Skipworth, 1984a; Chapter 1). A native of South America (Esler, 1978), it occurs in forest remnants in New Zealand (Kelly and Skipworth, 1984a), eastern Australia (Dunphy, 1991) and Florida (Wunderlin, 1998). In New Zealand, *Tradescantia* has spread through the dumping of rubbish and naturally via streams (Esler, 1978). Fragments as small as one cm in length can successfully establish new plants by vegetative reproduction (Kelly and Skipworth, 1984a). It has not been known to set seed in New Zealand (Healy and Edgar, 1980). Available light is the primary factor limiting the spread and biomass accumulation of

Tradescantia (Kelly and Skipworth, 1984a; Maule *et al.,* 1995; Chapter 1) which, in turn, determines its impact on native forest regeneration (Chapter 1). Its greatest impact occurs in parts of these forest remnants where canopy cover is reduced and at the forest margins as this is where it grows most vigorously.

Currently, chemical control by herbicides are considered the only practical means of controlling large infestations of *Tradescantia* (McCluggage, 1998; Tony McCluggage, *pers. comm.*; Chris Buddenhagen, *pers. comm.*). Manual means of weed removal are considered suitable for removal of small infestations (Porteous, 1993; Chris Buddenhagen, *pers. comm.*), if care is taken to remove every last piece. A combination of these removal methods has been used with success in a lowland podocarp/ broad-leaved forest remnant in Feilding (Manawatu), but has required repeated efforts to ensure continued control (Anon., 1995). An alternative method to suppress *Tradescantia*, that has been suggested but not trialed, is shading by artificial or natural means (*i.e.*, planting native species into damaged forest remnants to enhance natural vegetation cover) (Kelly and Skipworth, 1984a; Stockard, 1991; Maule *et al.,* 1995; Chapter 1). While native plantings have been used to restore degraded natural habitats (Ashby, 1987; Lamb, 1993; Saunders *et al.*, 1993; Reay and Norton, 1999; Yates *et al.*, 2000), their specific use for weed control within natural habitats is less common (Eliason and Allen, 1997; Swarbrick and Hart, 2000).

Previous work indicates that by decreasing *Tradescantia*, there will be an associated increase in the abundance and species' richness of native forest seedlings that regenerate (Chapter 1). The aims of this study were, firstly, to compare the success of herbicide application and hand weeding as methods for the control of *Tradescantia*, and to compare the native regeneration after weed removal by these methods. An advantage of chemical control is its cost-effectiveness, and a disadvantage its detrimental impact to native flora (e.g., Kelly and Skipworth, 1984b; Brown and Rees, 1995). Hand weeding is time consuming but probably has less impact on native flora. In heavily infested forest remnants, gaps left by manual or chemical removal of *Tradescantia* are likely to be filled by other invasive species (Hobbs and Mooney, 1993). The second aim of the study was to test shading as a method of control, so I artificially shaded *Tradescantia* in the field and measured its response. Conceivably, artificial shading would: require less follow-up treatment than chemical and manual control methods, reduce invasion of other weeds and have minimal impact on established native flora. However, it would be impractical for controlling large areas of weed. Therefore, with regard to imposing shade on the scale of a forest remnant, I planted native sub-canopy trees into swards of *Tradescantia* and measured their initial survival and growth.

Methods

Experiment 1. Herbicide application vs. hand weeding for *Tradescantia* control

The study site was a road-side forest remnant in Awahuri, lower North Island, New Zealand (40°14.9′ S, 175°32.5′ E). This small podocarp/ broad-leaved forest remnant on a flood plain (< 1 ha) was bordered on one side by farmland, and was separated, by road, from a larger (10 ha) forest remnant. The canopy was mainly titoki (*Alectryon excelsus*), mahoe (*M. ramiflorus*) and tawa (*Beilschmiedia tawa*), with a few emergent kahikatea (*Dacrycarpus dacrydioides* (A. Rich.) de Laub.). Kawakawa (*Macropiper excelsum*), supplejack (*Ripogonum scandens*) and small leaved shrubs [e.g. small-leaved milk tree (*Streblus heterophyllus* (Blume) Corner), long-leaved lacebark (*Hoheria sexstylosa*)] occurred at the understorey level. Plant nomenclature follows Allan (1961) and Moore and Edgar (1970) unless given at first mention. *Tradescantia* formed a carpet up to 90 cm thick throughout the forest remnant, and in the few patches where *Tradescantia* did not occur, ground cover was provided by litter and woody seedlings.

Where *Tradescantia* carpeted the ground, I established 30 contiguous, 5 × 10 m^2 experimental plots. To compare herbicide application and hand weeding for control of *Tradescantia*, and the effect season of initial removal had on control success, I split the plots into five blocks, then randomly assigned initial season of removal (summer or winter) to sets of three plots within each block. Treatment (herbicide application, hand weeding or non-treatment) was randomly assigned to plots within seasonal blocks for the first 15 plots and the same assignment repeated for the second 15 plots. So, there were five replicates of each treatment. The first summer herbicide treatment was applied on 26 February 1997 and re-applied to patches of re-growth on 24 July 1997 and 13 January 1998. Similarly, the first winter herbicide treatment was applied on 24 July 1997 and re-applied on 13 January 1998 and 31 August 1998. I used Grazon® herbicide (active constituent 600g/L triclopyr; Dalliance (NZ) Ltd, New Plymouth) on the basis of its successful control of *Tradescantia* in previous trials (Brown and Rees, 1995; McCluggage, 1998) and its wide use within the North Island for controlling *Tradescantia* (e.g., T. Guard, Wellington; J. Davis, Palmerston North; G. Scott, Manawatu; T. McCluggage, Northland), though it can kill native adult trees and their seedlings (Brown and Rees, 1995; G. Scott, *pers. comm.*; C. Buddenhagen, *pers. comm.*). The herbicide was applied, 100 ml per 15 L water, to the foliage using a knapsack, at a volume of 6–9 L per plot (or 1200–1800 L ha^{-1}), depending on the depth of the mat of *Tradescantia* within the plot. On the days of herbicide spraying, there was no cloud cover and minimal wind. The triclopyr residue in the soil, measured prior to herbicide treatment and at two, seven and twenty weeks post-treatment, had almost deteriorated by 20 weeks (Standish *et al.*, 2001b). For the initial hand weeding treatment (on 25 February 1997 and 23 July 1997), I rolled the *Tradescantia* up like a carpet (Porteous 1993) and collected the remaining fragments. Fragments of *Tradescantia* re-growth were collected from the hand weeded plots prior to treating the herbicide plots for the second and third time.

I designated the central 3 m × 8 m plot of each experimental plot for recording: % cover of *Tradescantia* (monthly or bi-monthly), % cover of other decolonizing weeds (monthly or bi-monthly) and survival of established native flora > 0.5 m (six monthly). This allowed for some interference of neighbouring treatments (e.g., spread of *Tradescantia* from non-treatment plots, herbicide drift) without affecting the data collected. The number and identity of all native seedlings with at least two true leaves was recorded in a 1 m × 8 m strip within each herbicide treated and hand weeded plot, two years after the initial treatment. In addition, I made integrated measurements of incident radiation using simple photosensitive paper light meters (Friend, 1961), which were calibrated as described in Chapter 1. I fastened the light meters on top of 0.5 m wooden stakes in the centre of each plot and left them for one week (15–22 March 1999). Simultaneous readings were taken in an adjacent open field to obtain estimates of full light for the period. Final light values are expressed as a percent of full light.

Experiment 2. Response of *Tradescantia* to artificial shading

The second study site was Monro's Bush (40°23.3′S, 175°36.7′E), a 2 ha lowland podocarp/broad-leaved forest remnant heavily infested with *Tradescantia* and described in Kelly and Skipworth (1984a). I set up three large shade houses to cover *Tradescantia* on 6 November 1998 and adjacent to each, an unshaded *Tradescantia* plot of similar area. Each shade house consisted of a horizontal metal frame 2.8 m x 2.8 m, supported by 1 m high legs at each corner, and a sloped roof with an apex of 2 m to prevent the accumulation of forest litter. The frame was covered in three layers of 70% shade cloth secured with plastic cable ties. Light levels were assessed using the light meters described above. Existing forest interior light levels were mostly between 7 and 16% full light, I aimed to decrease light levels to ~1% full light in the shade houses. However, at best, I achieved 2% full light by shading, up to 4 and 5% full light ($n = 2$ light meters per plot, recorded during 16–23 March 1999), which is similar to well-shaded areas of closed-canopy New Zealand podocarp forests (2–30% full light; Ebbett and Ogden, 1998). The light levels in the adjacent unshaded plots varied from 15–27% full light.

In each plot, I measured the growth (± 0.1 cm) of five non-bifurcating and flowerless *Tradescantia* stems over a period of six months. I laid a ladder across two saw-horses to access the tagged stems so as to prevent crushing the *Tradescantia* during measurement. A *Tradescantia* biomass estimate, using percent cover and standing height as predictors (Chapter 1), was taken prior to, and 17 months after, the initiation of the experiment.

Experiment 3. Planting into *Tradescantia*

I selected four shade tolerant tree species, karamu (*Coprosma robusta*), mahoe (*M. ramiflorus*), lowland ribbonwood (*Plagianthus regius* (Poet.) Hothr.) and long-leaved lacebark (*H. sexstylosa*), for planting into ground covered by dense *Tradescantia* at Monro's Bush. These species were selected because they were present in the understorey or sub-canopy at the site and available as 0.5 m saplings grown from locally sourced seed. I choose 0.5 m saplings as plants less than this in height are considered to be unlikely to survive in competition with *Tradescantia* (Esler, 1962). Karamu and mahoe are known for their fast growth rates and tolerance of most environments, and their fleshy fruits are attractive to birds which may promote forest regeneration (Porteous, 1993). Lowland ribbonwood and long-leaved lacebark are often used for revegetation in New Zealand (Bulloch, 1991; Stewart and Woods, 1991; P. van Essen, *pers. comm.*) and the former has a preference for fertile soils such as those at Monro's Bush (Ogle and Lovelock, 1989; Ravine, 1995). I cleared *Tradescantia* from an area 1 m in diameter around half of the saplings at the time of planting. Twenty saplings of each species were planted, in a completely randomized block design with respect to sapling species and clearing treatment, on 1 September 1997, with a 2 m spacing between each. There were ten blocks, blocks two, three and four were contiguous, as were blocks six and seven, and nine and ten, while the other blocks were between 4 m and 20 m from the next block. Survival and height of the saplings was measured at six months, one year, 1.5 years and 2.5 years, and herbivore damage (low = 10%, high = 90% and intermediate = 10–90%, of leaves damaged) was estimated after six months.

I determined the relative soil fertility and light availability at each of the planting sites. The soil fertility was measured by means of a bioassay in which brown top (*Agrostis capillaris* L.) was grown for a period of ~11 weeks on soil taken from each planting site. I selected this species for its ability to respond to a wide range of soil fertilities (Lee and Fenner, 1989). Three cores of soil (5.4 cm diameter × 8 cm depth) were collected from each planting site on 26 August 1997, and stored at 4°C until 28 August 1997 when they were sieved (using a 5 mm sieve), mixed, and placed into black plastic pots (10 × 10 × 10 cm). Brown top seed (0.7 g) was added to each, and the pots were randomly ordered on a table in a glasshouse. The pots were watered daily. On 14 November 1997 the grass shoots were harvested, then oven-dried and weighed. The yield (g) per soil sample was taken as a measure of the relative soil fertility of the planting sites. I used light meters (as for experiment 1, from 24 September –1 October 1997) to record light levels at the planting sites.

Statistical Analyses

For experiment 1, a repeated measures, fixed effects ANOVA was used to test for differences between hand weeding and herbicide application treatments, and the effect of season of treatment (SYSTAT, SPSS Inc., 1996). Data, % cover of *Tradescantia* at approximately six months after treatment and repeat treatments were applied, were log transformed ($x + 1$) prior to analysis and available light was included as a covariate. Non-treatment plots were excluded as *Tradescantia* cover remained unchanged at 100%.

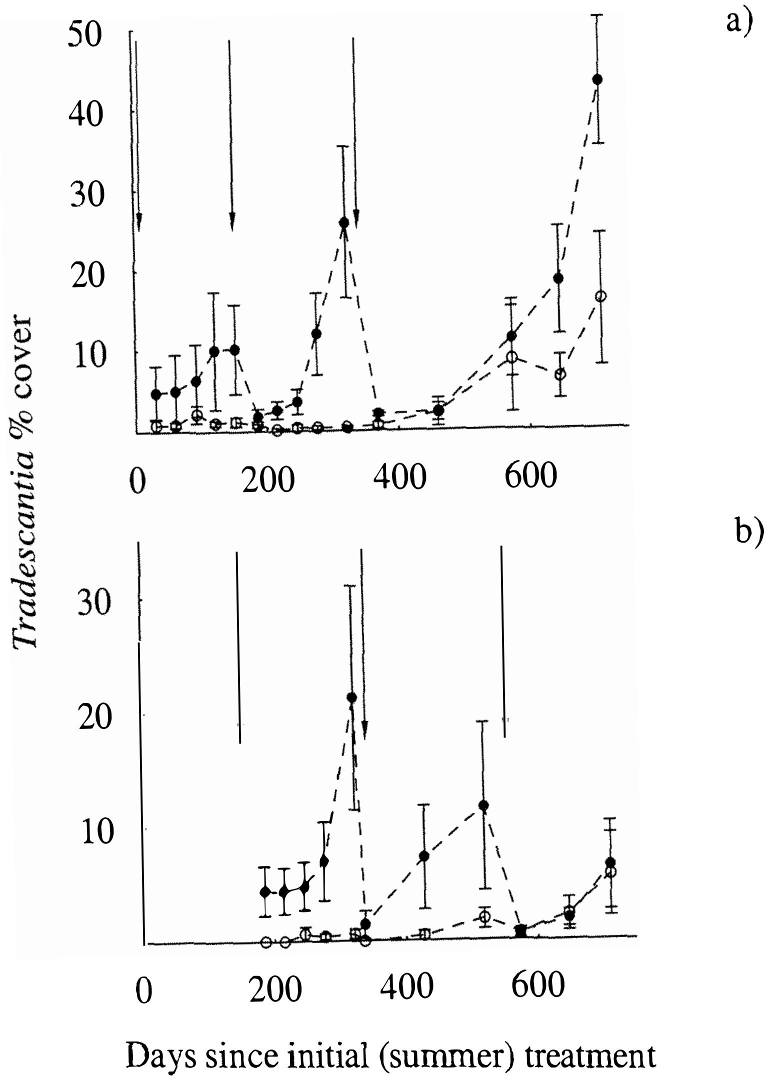
To determine the effect of shading on *Tradescantia*, I used a repeated measures ANOVA for growth data and, an independent, pooled variance t-test for *Tradescantia* biomass data. I used a repeated measures, fixed effects ANOVA to test for differences in the relative growth rate (RGR= {final height - initial height}/ initial height × 100%) of planted trees at six months, one year, 1.5 and 2.5 years after planting. Light availability, soil fertility and herbivore damage were included as covariates in the analysis. These data were log transformed prior to analysis. Tukey tests of pairwise means comparisons were used to determine significant differences in RGR measured at 2.5 yrs among the species/ treatment combinations.

Results

Experiment 1.

While herbicide application and hand weeding reduced the percent cover of *Tradescantia* from the initial 100% cover, removal was incomplete and remaining fragments continued to re-grow after each successive treatment (Fig. 1). Hand weeding was more successful than herbicide application for control of *Tradescantia* (Fig. 1), although the significant interaction term, time × treatment, indicated that the differences between treatments were less marked at time three (Table 1). Also, the interaction between time, treatment and season indicated that differences between treatments were less marked for winter plots than for summer plots. Overall, the season of treatment application did not effect the outcome of either control

Figure 1. Response of *Tradescantia* to herbicide application (filled symbols) and hand weeding (clear symbols) in summer (a) and winter (b). Values are means ± SE ($n = 5$ plots). Vertical arrows indicate three successive treatments. Cover in non-treatment plots (not shown) remained at 100% throughout.



methods used. *Tradescantia* percent cover increased with available light (Fig. 2a) and available light explained almost as much of the variation in *Tradescantia* re-growth as treatment did (Table 1). The percent cover of other colonizing weeds was also positively related to light (Fig. 2b).

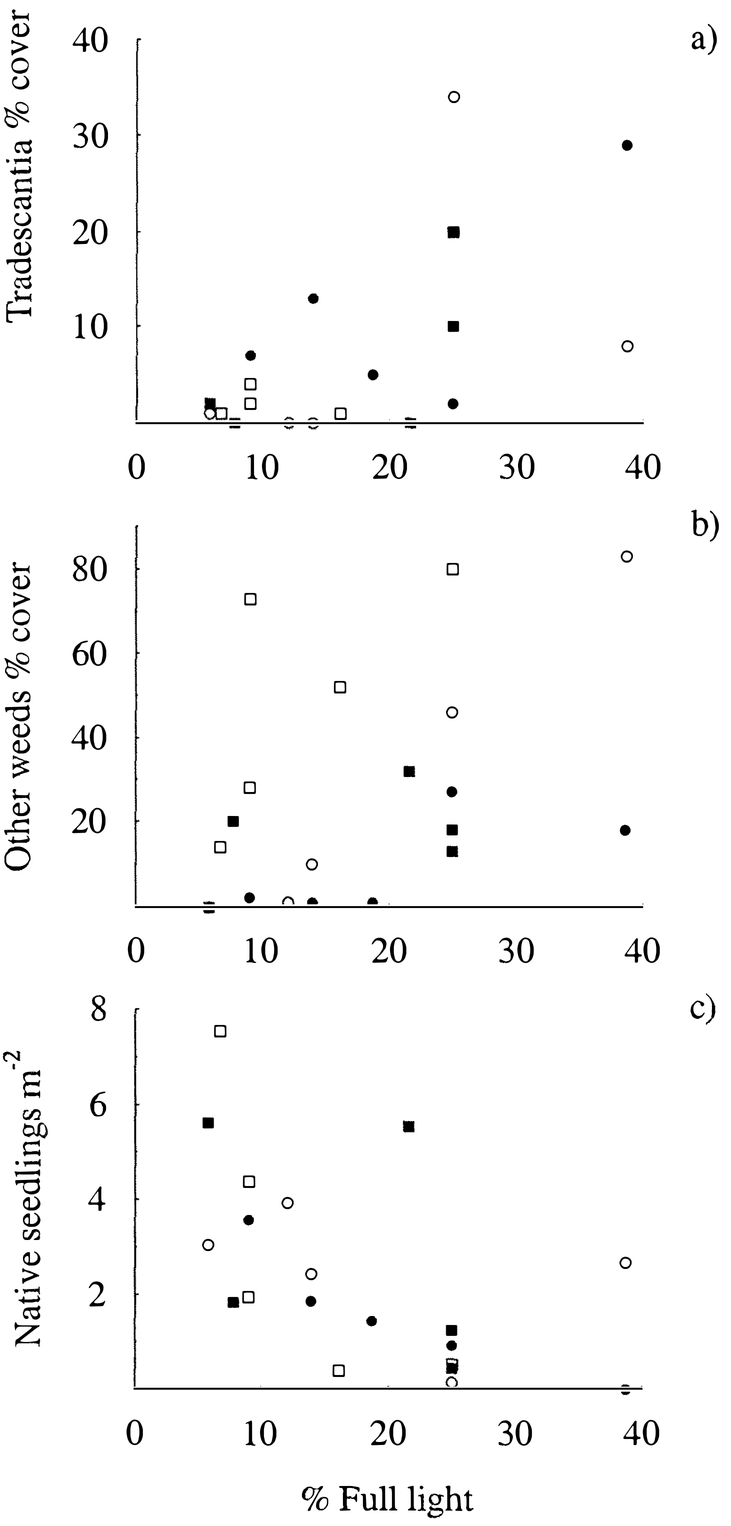
Table 1. Repeated measures ANOVA of the effect of herbicide application and hand weeding treatments, applied to experimental plots in summer and winter, on percentage cover of *Tradescantia* at Awahuri road-side remnant (n = five plots per treatment; experiment 1). Percent full light was a covariate. Huynh-Feldt Epsilon-P values quoted for within treatment tests.

Between subjects — Source	SS	DF	F	P
Treatment	17.82	1	16.75	0.001
Season	0.84	1	0.79	0.387
Treatment × season	0.85	1	0.8	0.386
Light	17.27	1	16.23	0.001
Error	15.96	15		
Within subjects — Source				
Tradescantia cover	0.97	2	0.8	0.459
Tradescantia cover × treatment	6.58	2	5.39	0.01
Tradescantia cover × season	2.11	2	1.73	0.195
Tradescantia cover × treatment × season	6.91	2	5.66	0.008
Tradescantia cover × light	0.82	2	0.67	0.52
Error	18.31	30		

The number of establish native plants >0.5 m in height that died during the 20 months after the initiation of the experiment were as follows: 13 (herbicide treated plots); 4 (hand-weeded plots) and 2 (non-treatment plots). All were saplings < 1m in height except for two trees in non-treatment plots.

Native regeneration (*i.e.*, seedling abundance) *decreased* with increasing light levels (Fig. 2c) because of the increasing cover of *Tradescantia* and other weeds (Figs 2a, b). There was no effect of *Tradescantia* control treatment or season of treatment on the abundance of native seedlings ($F_{1, 15}$ = 0.02, P = 0.901 (treatment); $F_{1, 15}$ = 0.02, P = 0.892 (season) and; $F_{1, 15}$ =

Figure 2. Relationship of available light to: % cover of *Tradescantia* (a), % cover of other weeds(b) and, abundance of native seedlings (c), two years after initial treatment (filled symbols = herbicide application, clear symbols = hand weeding, circles = summer application, squares = winter application) in experimental plots.



11.46, $P = 0.004$ (light)). Species richness of native seedlings was similarly unaffected ($F_{1, 15} = 0.001$, $P = 0.978$ (treatment); $F_{1, 15} = 1.16$, $P = 0.298$ (season) and $F_{1, 15} = 10.28$, $P = 0.006$ (light)). Across plots, there were 2.47 ± 0.46 (mean ± SE) seedlings per m^2, and species richness was 8.15 ± 0.67 (mean ± SE). *Macropiper excelsum* seedlings were the most abundant (57% of the total), followed by seedlings of *Cordyline australis* (11%) and *Plagianthus regius* (5%) (Table 2).

Table 2. Native seedlings regenerated 2 (summer) and 1.5 (winter) years after initial *Tradescantia* control. $N = \sum 5$ plots/ treatment.

Species	Herbicide treated plots		Hand-weeded plots	
	Summer	Winter	Summer	Winter
Macropiper excelsum	274	275	372	473
Cordyline australis	1	274	-	9
Plagianthus regius	5	8	66	47
Muehlenbeckia australis	11	35	11	36
Dacrycarpus dacrydioides	9	29	22	30
Melicytus ramiflorus	29	35	1	20
Passiflora tetrandra	11	22	22	27
Hedycarya arborea	19	6	9	45
Hoheria sexstylosa	4	-	50	-
Coprosma areolata	1	1	10	19
Alectryon excelsus	6	7	10	6
Pennantia corymbosa	4	2	19	-
Pittosporum crassifolium	6	7	1	11
Parsonsia heterophylla	1	14	1	-
Sophora microphylla	5	2	2	6
Prumnopitys taxifolia (D. Don) Laubenf.	1	8	1	-
Haloragis sp.	1	-	8	-
Melicope (*simplex*?)	-	-	-	7
Solanum aviculare	1	4	-	-
Sp. A	-	3	-	1
Ripogonum scandens	-	-	3	-
Coprosma sp.	-	2	1	-
Total	389	734	609	737

Experiment 2.

Shading had a significant effect on the growth of *Tradescantia* (Table 3; $F_{1,4} = 52.62$, $P = 0.002$ (treatment); $F_{1,4} = 23.35$, $P = 0.008$ (time) and; $F_{1,4} = 4.78$, $P = 0.094$ (time × treatment)). After 17 months in 95–98% shade, the biomass of *Tradescantia* was massively and significantly reduced (81.3 ± 10.6 gm^{-2}, equivalent to ~40% cover), relative to *Tradescantia* biomass in unshaded plots (597.6 ± 6.6 gm^{-2}, equivalent to 100% cover; $t_4 = 17.38$, $P < 0.001$).

Table 3. The effect of shading on the growth (cm/ day) of *Tradescantia* at Monro's Bush (experiment 2). Values are means ± SE, three and six months after the experiment was initiated (n = 3 plots).

Treatment	3 months	6 months
Shaded	0.10 ± 0.016	0.02 ± 0.004
Non-shaded	0.14 ± 0.049	0.19 ± 0.034

Experiment 3.

Overall, 61% of saplings planted into *Tradescantia* at Monro's Bush survived to 2.5 yrs (Table 4). Of the four species, mahoe had more, and karamu fewer, individuals remaining at 2.5 yrs ($Chi^2 = 8.58$, df = 3, $P < 0.05$) and clearing made no difference to the survival of the saplings ($Chi^2 = 1.32$, df = 1, $P = 0.25$). The mean ± SE, and maximum heights for each species (across cleared and non-cleared treatments) at 2.5 yrs were: karamu 2.33 ± 0.33 m, 4.0 m; mahoe 1.72 ± 0.12 m, 2.8 m; long-leaved lacebark 1.45 ± 0.14 m, 2.2 m and; ribbonwood 1.39 ± 0.77 m, 1.8 m. The species varied significantly in relative growth rates and karamu consistently scored the highest mean growth rate (Fig. 3 ; Table 5). Overall, the clearing treatment was not significant, although the interaction term indicated that some species showed better overall growth in cleared treatments (*i.e.*, long-leaved lacebark; Fig. 3) although this was not consistent over time (growth × treatment × species interaction). At 2.5 yrs the RGR of long-leaved lacebark in the cleared treatment was significantly greater than for any other species/ treatment combination except cleared ribbonwood (Tukey tests, P= 0.05). Available light and soil fertility significantly effected the growth of the saplings, while herbivore damage did not (Table 5). The individual species responses to light availability and soil fertility varied, karamu and long-leaved lacebark responded positively to increased light availability whereas there was no relationship between growth and light availability for mahoe and lowland ribbonwood. There were weak negative relationships between growth and soil fertility for karamu and lowland ribbonwood, and no relationship for mahoe and long-leaved lacebark.

Table 4. Number of surviving saplings 2.5 years after planting into *Tradescantia* at Monro's Bush (experiment 3). Ten saplings of each species were planted for both treatments.

Species	Cleared	Non-cleared
Karamu	4	4
Lowland ribbonwood	7	5
Mahoe	10	7
Long-leaved lacebark	6	6
TOTAL	27	22

Figure 3. The relative growth rates of four sapling species planted into cleared (clear symbols) and non-cleared (filled symbols) *Tradescantia* at Monro's Bush. Values are means (back-transformed) and 95% CIs. Note different scale on Y-axes.

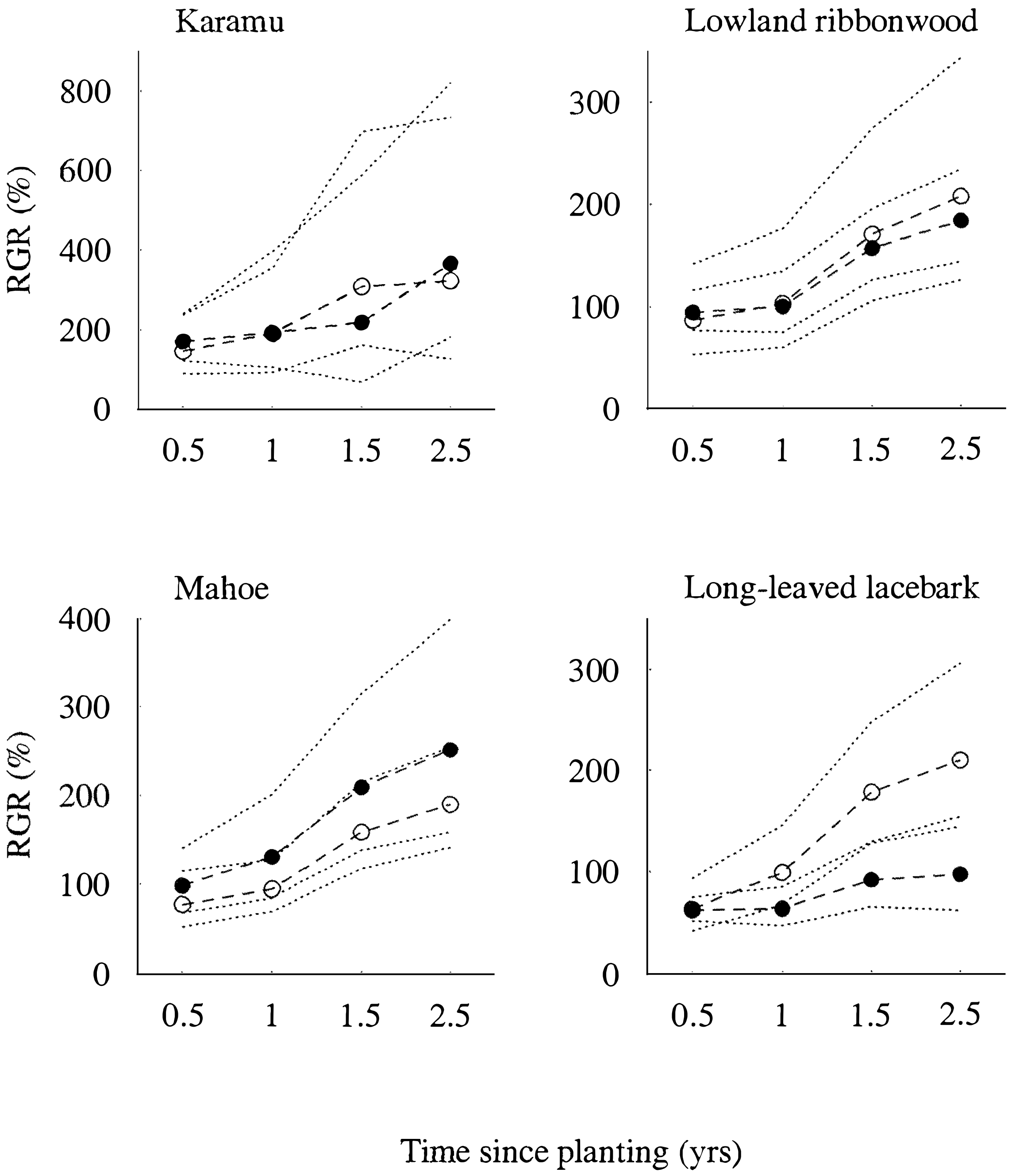


Table 5. Repeated measures ANOVA in the relative growth rate of four native tree species planted into cleared and non-cleared *Tradescantia* at Monro's Bush (experiment 3). Percent full light, soil fertility and insect herbivore damage were covariates. Huynh-Feldt Epsilon-*P* values quoted for within treatment tests.

Between subjects — Source	SS	DF	*F*	*P*
Species	13.18	3	9.2	<0.001
Treatment (cleared or non-cleared)	0.06	1	0.12	0.737
Species × treatment	5.13	3	3.58	0.023
Light	3.07	1	6.42	0.016
Soil fertility	2.39	1	5.01	0.031
Herbivore damage	1.15	1	2.4	0.129
Error	18.14	38		
Within subjects — Source				
Growth	0.59	3	5.14	0.002
Growth × species	0.6	9	1.75	0.085
Growth × treatment	0.64	3	5.65	0.001
Growth × species × treatment	1.01	9	2.95	0.004
Growth × light	0.08	3	0.66	0.577
Growth × soil fertility	0.004	3	0.04	0.991
Growth × herbivore damage	0.09	3	0.82	0.488
Error	4.32	114		

Discussion

The most effective method for sustained control of *Tradescantia*, without invasion of other weeds, was artificial shading. Efforts to control *Tradescantia* by repeated herbicide application and hand weeding at a second site resulted in the re-growth of *Tradescantia* and invasion by other weeds that appeared to hinder native forest regeneration. Re-growth of *Tradescantia* and invasion by other weeds was extreme in plots with extensive canopy damage (*i.e.*, increased available light). While it is too early to determine whether or not planted trees will overshadow *Tradescantia*, 61% of saplings were able to emerge clear of the *Tradescantia* sward within 2.5 yrs of planting, and release from *Tradescantia* at the time of planting made no difference to survival and growth within this period.

Grazon® effects native seedlings, yet native regeneration (in terms of seedling species richness and abundance) did not differ between herbicide treated and hand-weeded plots. Native seedlings first appeared in a hand-weeded plot two (winter plots) to three (summer plots) months after *Tradescantia*'s removal. Seedlings did not appear in herbicide treated plots until four (winter plots) to six (summer plots) months after the first application of Grazon®. The emergence of seedlings in herbicide treated plots roughly corresponded with the deterioration of triclopyr residues in the soil. The second and third applications of Grazon® to plots were patchy in comparison to the first blanket spray and so probably had less effect on the seedlings. While the repeated spray regime was designed to mimic that which reserve managers might follow, another option would have been to follow-up the initial spray treatment with manual removal so as to further reduce the risk of non-target effects.

Overall, the native species that emerged following the removal of *Tradescantia* were representative of those at the study site and/ or across the road at Kitchener Park (Esler and Greenwood, 1967). Despite its small size and poor condition, Awahuri road-side remnant has retained the capacity to regenerate on removal of *Tradescantia*. Conspicuous in their absence as seedlings were *Podocarpus totara*, tawa and the small-leaved milk tree. *Hedycarya arborea* and *Pittosporum crassifolium* were not present as mature specimens at the site or at Kitchener Park (Esler and Greenwood, 1967). Ferns are not expected to appear until quite a few years after the disturbance (*i.e.*, weed removal) (P. Williams, *pers. comm.*). The dominance of *Macropiper excelsum* seedlings reflected its dominance in the understorey at the study site. Experience at Kitchener Park indicates that ongoing monitoring and removal of *Tradescantia* is required for native seedlings to establish (Anon., 1995), at least until plants are 0.5 m high.

Imposing shade (2–5% full light) reduced *Tradescantia* biomass to ~80 gm^{-2} (~40% cover), which is compatible with the germination and establishment of some native seedlings (Chapter 1). Individual species can vary in their ability to tolerate *Tradescantia*, in a group of commonly occurring native woody species kohekohe (*Dysoxylum spectabile*) is the most tolerant, kawakawa the least tolerant, and pigeonwood (*Hedycarya arborea*), mahoe, titoki and pukatea (*Laurelia novae-zealandiae*) are moderately tolerant (Chapter 1). The ability to tolerate *Tradescantia* seems to relate to shade tolerance, and so other shade tolerant native seedlings should be able to germinate and establish in ~80 gm^{-2} of *Tradescantia* (~40% cover). Clearly, light demanding forest species will not establish under shade imposed to reduce *Tradescantia* biomass, but nor will they establish in high light environs (10–30% full light) affected by *Tradescantia* (Chapter 1).

Although karamu showed the fastest growth rates of the species trialed, its tendency to form spindly trees (its ability to respond to increased light, within the range 3–18% full light, is evidence of shade intolerance) which often fell over and became overgrown by *Tradescantia*, made it a unsatisfactory choice for this project. On the other hand, mahoe was a good choice because it tended to grow so as to become quite bushy, at 2.5 yrs it had started to shade the *Tradescantia* directly beneath it, and its survival was greatest. Neither mahoe or lowland ribbonwood showed a response to increased light (between 5–15% full light), although lowland ribbonwood is not as shade tolerant as mahoe (Williams and Buxton, 1989). Long-leaved lacebark showed an ability to respond to elevated light levels, within the range 5–16% full light, indicating that it is somewhat light demanding (*i.e.*, shade intolerant). At 2.5 yrs, long-leaved lacebark provided less shade than mahoe, but more than lowland ribbonwood.

The period between planting and canopy closure is likely to be dependent on site conditions (*e.g.*, soil fertility, light availability), the species planted and their rate of growth, the spacing of plants and aftercare (this study; Porteous, 1993). I estimate that it would take ~6 yrs for karamu to reach its mature height (5 m), based on the average annual height increment in the first 2.5 yrs, 0.72 m, which is greater than the annual height increment of 0.48 m for this species grown in the northern South Island, New Zealand (Wardle, 1991). The average annual height increment for mahoe was the same as that reported for this species grown in the northern South Island, New Zealand (Wardle, 1991), and at this rate I estimate it would take ~20 yrs to reach the sub-canopy (10 m). The average annual height increment for long-leaved lacebark was lower than that for lacebark (*H. populnea*) grown south of its natural range ($0.38 < 0.79$ cm yr^{-1}; Wardle, 1991) which suggests that this species is not responding well to conditions at this site. Based on its growth in the first 2.5 yrs, long-leaved lacebark will take

~14.5 yrs to reach its mature height (6 m). Similarly, lowland ribbonwood will take an estimated 40 yrs to reach the sub-canopy (15 m). Ultimately, grouping plantings beneath canopy gaps and minimizing space between plants, rather than the blocked design and 2 m spacing used in experiment 3, may facilitate faster growth and more effective canopy closure.

There are only a few successes controlling *Tradescantia* with current chemical and manual techniques (e.g., Kitchener Park, N.Z.; Anon., 1995; Wingham Brush, N.S.W.; Stockard *et al.*, 1985 and Stephens Island, N.Z.; Chris Buddenhagen, *pers. comm.*). There are numerous forest remnants throughout New Zealand that would benefit from *Tradescantia* control. This study is the first in New Zealand to document the response of the native plant community after removal of *Tradescantia*. Imposing shade is a novel approach for successful control of this persistent forest weed. It remains to be seen if trees planted into *Tradescantia* will overshadow the weed and allow native regeneration to proceed. The ultimate measure of success would be the regeneration of light demanding native seedlings in the absence of *Tradescantia*.

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Chapter 5: General Discussion

What makes Tradescantia *an invader?*

I use the term invader to mean a non-native 'species that establishes a new range in which it proliferates, spreads and persists to the detriment of the environment' (Mack et al. 2000). Weeds (i.e., flora naturalised beyond their native range) become invaders if they demonstrate an ecologically significant impact on the system they invade. *Tradescantia* has spread beyond its native range by human vectors (i.e., as an ornamental plant). Consequently, a lack of long-distance dispersal mechanisms has not prevented its spread.

Tradescantia possesses several 'weedy' attributes including vigorous vegetative reproduction and regeneration from fragments, brittleness and an ability to compete interspecifically by smothering growth (Baker, 1974). These attributes have been highlighted as being particularly important in 'the essentially closed communities of cool, damp climates' in contrast to 'drier, more open habitats' where 'r-selected attributes assume greater significance' (Thompson et al., 1995). Among the British flora there is a tendency for the naturalised species to possess larger leaves than the native species (Williamson & Fitter, 1996). *Tradescantia* has large leaves according to the classification used. No doubt these reproductive and morphological attributes are important in the establishment and spread phases of invasion identified by Williamson (1996). Vegetative growth ensures long-term persistence beyond these initial phases.

There are few invertebrate pests or diseases of *Tradescantia* in countries where it has naturalised (Appendix 1), a common and intuitive reason for the success of many introduced species (Pimm, 1989; Crawley et al., 1989). Also, *Tradescantia* is taxonomically distinct from native resident species (Appendix 1) which if equal to ecological distinctiveness, could explain some of its success as an invader (Williamson, 1996).

More specific reasons for *Tradescantia*'s success can be gained from consideration of the habitat in which it has been successful. Maule et al. (1995) proposed an invasion strategy for *Tradescantia* in New Zealand forest remnants, central to which is a physiology which enables rapid response to the availability of two key resources — light and nitrogen. Light and nitrogen availability increases following a disturbance, such as tree-fall, allowing

Tradescantia to rapidly invade the disturbed site. It grows rapidly in the increased light environment while accumulating a store of nitrogen in its tissues. Then, if the canopy gap is closed, *Tradescantia* can acclimatise to the reduced light availability and utilise its store of nitrogen (Maule et al., 1995).

It is feasible that one well-adapted genotype of *Tradescantia* exists in New Zealand. This has been suggested for invasive *Senecio madagascariensis* in Australia, which is found as a single ecotype and is associated with only pasture and ruderal habitats (Radford & Cousens, 2000). Similarly, invasive *Fallopian japonica* exists as one widespread clone in Britain (Hollingsworth & Bailey, 2000) and is associated with disturbed habitats (Child et al., 1998). If this is this case for *Tradescantia*, then its reproductive strategy is ideally suited for spread into similar habitats.

What makes these forest systems invasible?

It is important to assess *Tradescantia*'s ability as an invader in the context of the systems it invades (Pimm, 1989). *Tradescantia* is a weed of forest systems in New Zealand (Kelly & Skipworth, 1984a), eastern Australia (Dunphy, 1991) and Florida (Wunderlin, 1988). I will restrict my assessment of invasibility to New Zealand forest remnants.

The role of anthropogenic disturbance in rendering forests susceptible to invasion by *Tradescantia* cannot be underestimated (Hobbs, 1989, 1991; Lonsdale, 1999). Disturbance enhances invasibility as it increases the availability of a limiting resource for the invading species (Hobbs, 1989; Davis et al., 2000). In New Zealand, *Tradescantia* does not invade large tracts of closed-canopy forest, rather its success as an invader is limited to forest remnants that have been modified as a result of fragmentation, and perhaps selective logging, stock grazing and possum browsing. A direct result of these modifying processes has been to increase light availability within the forest, which is of primary importance to the successful invasion of *Tradescantia* (Chapter 1). Other factors associated with habitat disturbance, such as increased soil nitrogen, have also contributed (Maule et al. 1995; Ogle & Lovelock, 1989).

Disturbance also serves to remove competing vegetation (Grime, 1974, 1988; Hobbs, 1991). In the case of lowland podocarp-broadleaf forest remnants, cattle grazing and trampling has been particularly detrimental to native groundcover and understorey plants, sometimes leading to local extinction. If *Tradescantia* is introduced to a site that has not recovered from such disturbance then there is the potential for the invasion of unoccupied forest floor.

Propagule pressure, defined as the number of propagules arriving at a site (Williamson, 1996) is another important concept of invasion ecology (Bazzaz, 1986; Williamson & Fitter, 1996; Lonsdale, 1999). There is evidence that the probability of a species establishing is directly related to the number introduced — the deliberate introduction of birds into New Zealand is one example (Williamson, 1996). Human vectors have ensured a steady supply of propagules to New Zealand, and also its establishment and spread around New Zealand. Secondary dispersal via streams has also helped to maintain propagule pressure.

A discussion of the concept of invasibility would not be complete without consideration of the role of chance and timing (Crawley, 1989). The roles of these processes are evident throughout the invasion process (introduction, establishment, spread) and can determine the success or failure of the invading species. In New Zealand, chance has played a role in the dispersal of *Tradescantia* as it was, and is largely reliant on human vectors. Whereas the timing of its arrival was favourable for invasion as the disturbance necessary for its establishment had occurred or was still occurring.

The role of species attributes in determining invasibility

Dense *Tradescantia* out-competes native ground cover and forest floor seedlings (Chapter 1). In addition, it clearly responds to resource availability more rapidly than the resident species and/ or is a better competitor. Both concepts are important in determining invasibility (Lonsdale, 1999). It is notable that *Tradescantia* probably does not out-compete other ground covers and forest seedlings in its native forest environment.

The hypothesis that diverse communities are more resilient to invasion than less diverse communities (Elton, 1958) has been supported by empirical studies (Fox & Fox, 1986;

Tilman, 1997; Dukes, 2001) but there are exceptions (Timmins & Williams, 1991; Robinson et al., 1995; Lonsdale, 1999; Levine, 2000), perhaps because it is difficult to generalise across spatial scales and vegetation type (Stohlgren et al., 1999) and to account for other influencing factors (Rejmánek, 1989). Theory predicts that diverse communities use resources more completely than simple ones, and therefore are more resistant to invasion (Levine & D'Antonio, 1999). I do not have the data to test this hypothesis and it is difficult to assess the role of community diversity as a barrier to invasion in these forests that have presumably lost species due to past disturbances. However, I speculate that the low diversity of native groundcovers within modified podocarp-broadleaf forest remnants has expedited *Tradescantia*'s invasion.

How does Tradescantia *alter community and ecosystem properties?*

I have demonstrated that *Tradescantia* has an impact on native forest regeneration (Chapter 1) by direct evidence of decreasing native forest seedling species richness and abundance with increasing *Tradescantia* biomass. I provide supporting evidence that the compositions of the extant vegetation, seed rain and seed bank were not likely to be responsible for the reduced regeneration of forest species. Seedlings of some native species were more tolerant of *Tradescantia* than others, though the growth to emergence of even the most tolerant species was compromised in dense *Tradescantia*. Forest regeneration was prevented because of decreasing light levels beneath *Tradescantia*.

While shading of native plants by invasive weeds is a well-studied phenomenon (refer references Chapter 2), comparatively little is known about the effects of weeds on ecosystem processes. I determined the impact of *Tradescantia* on litter decomposition and nutrient cycling (Chapter 2). Leaf litter placed in bags beneath mats of *Tradescantia* decomposed at almost twice the rate of litter placed outside the mat. The impact of *Tradescantia* on decomposition was evident through the reduced litter layers in *Tradescantia*-affected areas relative to non-affected areas despite similar quantities of leaf litterfall into each habitat. Moreover, there was increased plant available nitrate in *Tradescantia*-affected relative to non-affected plots. Finally, the annual uptake of nutrients by *Tradescantia* was a significant amount of the nutrient inputs via litterfall, which (with the exception of Ca) exceeded the amounts of these nutrients held within the forest litter layer, but was only a small amount of these nutrients held within the topsoil. The litter quality and microclimate of *Tradescantia* are the likely mechanisms by which it alters these ecosystem properties.

It is likely that the microclimate within *Tradescantia* that promotes increased litter decomposition also affects invertebrate communities. Epigaeic invertebrates were sampled within three *Tradescantia*-infested plots and three non-infested plots at each of three sites using pitfall traps (Chapter 3). Five of the 23 orders collected were sorted into recognisable taxonomic units (RTUs). RTU richness was lower in *Tradescantia* plots compared with non-*Tradescantia* plots, though not statistically significant. Two-way indicator species and detrended correspondence analyses separated *Tradescantia* and non-*Tradescantia* plots within sites. Overall, impacts of *Tradescantia* were apparent despite large differences in invertebrate assemblages among sites.

Biological consequences of community and ecosystem change

It is difficult to predict many of the biological consequences of invasion by *Tradescantia* because of the complexity of above-ground and below-ground ecological interactions within the forest ecosystem. A simplified interaction web indicating the direct, measured effects and the potential follow-on effects is presented (Fig. 1). The text below explains some potential outcomes.

Tradescantia is potentially immortal within these forests whereas the life span of canopy trees extends 160 yrs (*Kunzea ericoides*); 200–400 yrs (*Beilschmiedia tawa*) (Wardle, 1991); ~400 yrs (*Podocarpus totara*; McSweeney, 1982). The full impact of *Tradescantia* has yet to be realised as it has been established for less than 100 years. Given its potential to persist, I predict that *Tradescantia*-affected forests will eventually become shorter in stature as a result of the tall-canopy species being unable to replace themselves. This trend is evident at Monro's Bush (Manawatu; photo pg. i) where *Tradescantia* has been established for >90 yrs, the tall-canopy dominants, pukatea *Laurelia novae-zealandiae* and tawa *B. tawa*, are not replacing themselves whereas the shorter-statured titoki *Alectryon excelsus*, mahoe *Melicytus ramiflorus*, *Coprosma grandifolia* and karaka *Corynocarpus laevigatus* are present in a full

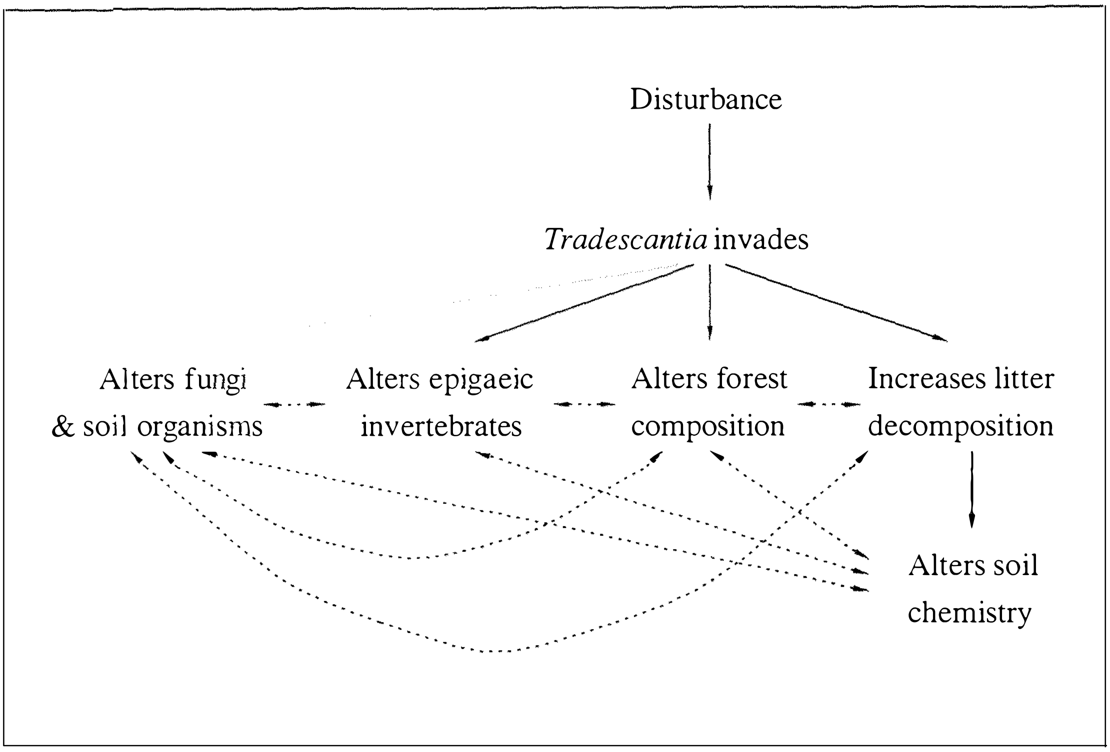

Figure 1. Conceptual model of the ecological impacts of *Tradescantia* in lowland forest remnants. Solid black line= impact demonstrated; solid grey line= potential impact; dashed line= potential indirect effects (not measured). The proposed mechanisms for these impacts include shading, and alterations to the microclimate and litter quality.

range of sizes (A. Robertson, unpub. data). I can be reasonably sure that the failure of pukatea and tawa to regenerate is due to *Tradescantia*, as other disturbances (e.g., selective logging, possum grazing) have long been mitigated, except perhaps for the continuing effects of drainage.

It is conceivable that *Tradescantia* could eventually become the dominant ground cover of fertile forest remnants such as Denton's Bush as it has at Monro's Bush where it has been established for a longer time. Clearly, the impact of *Tradescantia* on native flora and fauna, community and ecosystem processes, will increase with its increase in cover, to maximum in forest remnants where it has completely excluded native ground cover. Moreover, *Tradescantia* is likely to persist and continue to impact the affected forest remnant following the predicted conversion to a shorter-statured stand.

Changes in the species composition, such as those predicted for *Tradescantia*-affected forest, are likely to alter ecosystem processes through changes in the functional diversity of the species within the system (Chapin et al. 1997). An example of this might be that if the strongly mycotrophic podocarps (e.g., *Podocarpus totara*) were lost from the forest system, then the amount of phosphorous in the soil may decrease without the contribution of phosphorous-rich litter, and so increase competition among plants for this nutrient, which could affect further changes in species composition. Theory predicts that 'changes in species composition will affect the functioning of ecosystems most strongly when species differ in their effects on ecosystem processes or in their response to environmental change' (Chapin et al., 1997). So, the loss of mycotrophic podocarps may not result in the cascade of events just described if their functional role is fulfilled by other native plants resistant to *Tradescantia*'s invasion. In fact a majority of New Zealand native plants are mycotrophic (Wardle, 1991).

Loss of functional diversity need not be restricted to the plant species that are directly effected by *Tradescantia*. 'Trophic cascade' is a term that has been used to describe loss of species from a system that are indirectly effected by the invader via interactions across trophic levels (McDonald et al., 1989). Though difficult to prove, an example of this phenomenon could be the loss of certain bird species from these forests as a result of a lack of tall canopy trees suitable for perching in *Tradescantia*-affected forest (see Chapter 1). Similarly, certain fungal-feeding beetle species may have been lost because of a lack of a specific fungus that was parasitic on a plant that has been lost from *Tradescantia*-affected areas of forest (Chapter 3).

More generally, changes in the composition of the leaf litter will sequentially effect litter decomposition, soil chemistry and forest composition, so completing a feedback loop (Fig. 1). A consequence of *Tradescantia*'s impact on nutrient cycling could be reduced nutrient availability for resident native species but this has not been demonstrated and is unlikely given the high fertility of these forests (Chapter 3). The relative competitive abilities of these species could be altered though. Lastly, *Tradescantia* occupies and maintains a nutrient-rich environment suited to its own needs, and which is suited to invasion by other weeds in the event of its removal (Chapter 4).

Implications for management

Ecological succession is an ongoing process in all plant communities, even those with a long-term dominant species such as *Tradescantia* (Luken, 1997). The challenge for management is to prevent the successional trajectory leading to a short-statured forest. My research (Chapter 4) supports the theory that management needs to target the attributes of these forest systems that makes them invasible rather than the invasive species (Hobbs & Humphries, 1995; Luken, 1997; Mack et al., 2000). This involves having an understanding of the mechanisms of invasion. In the case of *Tradescantia* invasion of forest remnants, the mechanism is increased light availability bought about by past anthropogenic disturbance (Chapter 1). Therefore, management should focus on reducing light availability by improving canopy cover. Focusing on the forest system rather than the weed is especially pertinent for management of *Tradescantia*-affected sites as they are usually close to urban areas where there is a ready supply of weedy propagules to take the place of *Tradescantia* (Chapter 4).

Chemical and manual control methods will have limited success in controlling *Tradescantia* and preventing invasion of other weeds (Chapter 4). Biological control also targets the weed rather than the system but offers continuous action. Commitment and continuing diligence have been highlighted as important for effective invader control (Mack et al., 2000). The best approach may be "ecological control" (Groves, 1989, 1991) defined as 'the planned use of one or several methods of control when integrated with an understanding of the dynamics of the ecosystem in which the invasive plant occurs'. Ecological control of *Tradescantia* could involve an integration of biological control of *Tradescantia* and tree planting to improve canopy cover. In addition, 'armouring' the edge of forest remnants has been mooted as a potential means to reduce disturbance and improve canopy cover (P. Williams, pers. comm.). Such an approach might involve planting a buffer zone around the forest remnant, or at least about the edges exposed to prevailing winds (to reduce tree-fall).

Are there predictions for other forest weeds?

It is a relatively easy task to account for the invasion of *Tradescantia* into forest remnants in New Zealand. However, the attributes which make *Tradescantia* an invader are particular to its invasion of forest remnants in New Zealand. There are few, if any general attributes that identify plant invaders (Mack et al., 2000). In contrast, the attributes of the forest system that make it invasible for *Tradescantia* also make it susceptible to invasion by other weeds (Chapter 4). Therefore, in the context of New Zealand forest remnants, it is possible to make some prediction about future plant invaders. There are many weeds that could potentially become invasive (Owen, 1997). One in particular, Kahili ginger *Hedychium gardnerianum*, shares several traits with *Tradescantia*, including a smothering habit, vigorous vegetative reproduction and strong competitive ability (Byrne, 1992). It prevents native regeneration in forest margins of the Waitakere Ranges, Auckland (Byrne, 1992). The range of *H. gardnerianum* extends from North Auckland south to Gisborne in the North Island, and within the Nelson-Buller region in the South Island (Roy et al., 1998) where it could be having similar impacts.

References

Adair, R.J. & Groves, R.H. 1998. *Impact of environmental weeds on biodiversity: A review and development of a methodology.* Environment Australia, Canberra, Australia.

Adamson, H.Y., Chow, W.S., Anderson, J.M., Vesk, M. & Sutherland, M.W. 1991. Photosynthetic acclimation of *Tradescantia albiflora* to growth irradiance: morphological, ultrastructural and growth responses. *Physiologia Plantarum 82*: 353–359.

Allan, H.H. 1961. *Flora of New Zealand, Volume 1.* Government Printer, Wellington, NZ.

Anon. 1995. The battle for Kitchener Park. *New Zealand Geographic 26*: 9–12.

Ashby, W.C. 1987. Forests. *In*: Jordan III, W.R.; Gilpin, M.E. & Aber, J.D. (Eds) *Restoration ecology: a synthetic approach to ecological research*, pp. 89–108. Cambridge University Press, Cambridge, U.K.

Augspurger, C.K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology 72*: 777–795.

Baars, R. & Kelly, D. 1996. Survival and growth responses of native and introduced vines in New Zealand to light availability. *New Zealand Journal of Botany 34*: 389–400.

Baker, H.G. 1974. The evolution of weeds. *Annual Review of Ecology and Systematics 5*: 1–24.

Bannister, P. 1986. Winter frost resistance of leaves of some plants growing in Dunedin, New Zealand, in winter 1985. *New Zealand Journal of Botany 24*: 505–507.

Baylis, G.T.S. 1969. Mycorrhizal nodules and growth of podocarps in nitrogen-poor soil. *Nature 223*: 1385–1386.

Bazzaz, F.A. 1986. Life history of colonizing plants: Some demographic, genetic and physiological features. *In*: Mooney, H.A.; Drake, J.A. (Eds) *Ecology of biological invasions of North America and Hawaii*, pp. 96–110. Springer-Verlag, NY.

Beggs, J. & Rees, J. 1999. Restructuring of Lepidoptera communities by introduced *Vespula* wasps in a New Zealand beech forest. *Oecologia 119*: 565–571.

Binkley, D. & Matson, P. 1983. Ion exchange resin bag method for assessing forest soil nitrogen availability. *Soil Science Society of America Journal 47*: 1050–1052.

Blair, J.M., Parmelee, R.W. & Beare, M.H. 1990. Decay rates, nitrogen fluxes, and decomposer communities of single- and mixed-species foliar litter. *Ecology 71*: 1976–1985.

Blakemore, L.C., Searle, P.L. & Daly, B.K. 1987. Methods for chemical analysis of soils. *New Zealand Soil Bureau Scientific Report 80*, New Zealand Soil Bureau, Wellington, NZ, pp 1–103.

Boswell, C.C. & Espie, P.R. 1998. Uptake of moisture and nutrients by *Hieracium pilosella* and effects on soil in a dry sub-humid grassland. *New Zealand Journal of Agricultural Research 41*: 251–261.

Braithwaite, R.W., Lonsdale, W.M. & Esthbergs, J.A. 1989. Alien vegetation and native biota in tropical Australia: impact of *Mimosa pigra. Biological Conservation 48*: 189–210.

Breytenbach, G.J. 1986. Impacts of alien organisms on terrestrial communities with emphasis on communities of the south-western Cape. *In*: Macdonald, I.A.W.; Kruger, F.J. & Ferrar, A.A. (Eds) *The ecology and management of biological invasions in southern Africa*, pp. 229–238. Oxford University Press, Cape Town, South Africa.

Broadhurst, R.B. & Jones, W.T. 1978. Analysis of condensed tannins using acidfied vanillin. *Journal of the Science of Food and Agriculture 29*: 788–794.

Brown, D. & Rees, D. 1995. Control of *Tradescantia* on Stephens Island. *Ecological Management 3*: 6–9.

Bulloch, B.T. 1991. The native plant option for soil conservation. *In*: Smale, M.C.; Meurk, C.D. (Compilers) *Proceedings of a workshop on scientific issues in ecological restoration*, pp. 58–61. Landcare Research, N.Z.

Burrows, C.J. 1994. Seed trapping in Ahuriri Summit Bush, Port Hills, western Banks Peninsula, Canterbury, New Zealand. *New Zealand Journal of Botany 32*: 183–215.

Burrows, C.J. 1995a. Germination behaviour of the seeds of six New Zealand woody plant species. *New Zealand Journal of Botany 33*: 365–377.

Burrows, C.J. 1995b. Germination behaviour of seeds of the New Zealand species *Fuchsia excorticata, Griselinia littoralis, Macropiper excelsum* and *Melicytus ramiflorus. New Zealand Journal of Botany 33*: 131–140.

Byrne, J.H. 1992. *The invasion of wild ginger* (Hedychium gardnerianum) *into native forest in the Waitakere Ranges.* Unpublished Masters Thesis, University of Auckland, Auckland, NZ. 134 p.

Carse, H. 1916. Some further additions to the flora of Mangonui county. *Transactions of the New Zealand Institute 48*: 237–243.

Chapin (III), F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E. & Tilman, D. 1997. Biotic control over the functioning of ecosystems. *Science 277*: 500–504.

Child, L., Wade, M. & Wagner, M. 1998. Cost effective control of *Fallopia japonica* using combination treatments. *In*: Starfinger, U.; Edwards, K.; Kowarik, I.; Williamson, M. (Eds) *Plant invasions: ecological mechanisms and human responses*, pp. 143–154. Backhuys publishers, Leiden, The Netherlands.

Clout, M.N. & Hay, J.R. 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. *New Zealand Journal of Ecology 12*: 27–33.

Connor, H.E. & Edgar, E. 1987. Name changes in the indigenous New Zealand Flora, 1960–1986 and Nomina Nova IV, 1983–1986. *New Zealand Journal of Botany 25*: 115–170.

Court, A.J. & Mitchell, N.D. 1988. The germination ecology of *Dysoxylum spectabile* (Meliaceae). *New Zealand Journal of Botany 26*: 1–6.

Crawley, M.J. 1989. Chance and timing in biological invasions. *In*: Drake, J.A.; Mooney, H.A.; di Castri, F.; Groves, R.H.; Kruger, F.J.; Rejmánek, M.; Williamson, M. (Eds) *Biological Invasions: A global perspective*, pp. 407–423. John Wiley & Sons, NY.

Crawley, M.J., Harvey, P.H. & Purvis, A. 1989. Comparative ecology of the native and alien floras of the British Isles. *In*: Silvertown, J; Franco, M.; Harper, J.L. (Eds) *Plant life histories*, pp. 36–53. Cambridge University Press, UK.

Crisp, P.N., Dickinson, K.J.M. & Gibbs, G.W. 1998. Does native invertebrate diversity reflect native plant diversity? A case study from New Zealand and implications for conservation. *Biological Conservation 83*: 209–220.

Cronk, C.B. & Fuller, J.L. 1995. *Plant invaders: The threat to native ecosystems.* Chapman & Hall, London, UK.

Cross, J.R. 1982. The invasion and impact of *Rhododendron ponticum* in native Irish vegetation. *In*: White, J. (Ed) *Studies on Irish Vegetation*, pp 209-220. Royal Dublin Society, Dublin.

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

Davies-Colley, R.J., Payne, G.W. & van Elswijk, M. 2000. Microclimate gradients across a forest edge. *New Zealand Journal of Ecology 24*: 111–122.

Davis, M.A., Grime, J.P. & Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology 88*: 528–534.

del Pero Martínez, M.A. & Martínez, A.J. 1993. Flavonoid distribution in *Tradescantia. Biochemical Systematics and Ecology 21*: 255–265.

Department of Conservation 1998. *Garden Escapes: garden plants invading our bush.* Department of Conservation, Wellington, NZ.

Didham, R.K. 1997. An overview of invertebrate responses to forest fragmentation. *In*: Watt, A.D.; Stork, N.E. & Hunter, M.D. (Eds) *Forests and Insects*, pp. 303–320. Chapman and Hall, London, UK.

Didham, R.K., Hammond, P.M., Lawton, J.H., Eggleton, P. & Stork, N.E. 1998. Beetle species responses to tropical forest fragmentation. *Ecological Monographs 68*: 295–323.

Dukes, J.S. 2001. Biodiversity and invasibility in grassland microcosms. *Oecologia 126*: 563–568.

Dunphy, M. 1991. Rainforest weeds of the big scrub. In: Phillips, S. (Ed) *Rainforest remnants: proceedings of a workshop on rainforest rehabilitation*, pp. 85-93. NSW National Parks and Wildlife Service, Sydney, Australia.

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

Ehrenfeld, J.G., Kourtev, P. & Huang, W. 2001. Changes in soil functions following invasions of exotic understorey plants in deciduous forests. *Ecological Applications 11*: 1287–1300.

Eliason, S.A. & Allen, E.B. 1997. Exotic grass competition in suppressing native shrubland re-establishment. *Restoration Ecology 5*: 245–255.

Elton, C. 1958. *The ecology of invasions by animals and plants.* Methuen, London.

Enright, N.J. 1985. Existence of a soil seed bank under rainforest in New Guinea. *Australian Journal of Ecology 10*: 67–71.

Enright, N.J. & Cameron, E.K. 1988. The soil seed bank of a kauri (*Agathis australis*) forest remnant near Auckland, New Zealand. *New Zealand Journal of Botany 26*: 223–236.

Esler, A.E. 1962. The Banks Lecture: forest remnants of the Manawatu lowlands. *New Zealand Plants and Gardens 4*: 255–268.

Esler, A.E. & Greenwood, R.M. 1967. *Kitchener Park: plan for replanting.* Unpublished report to Feilding Borough Council, NZ, 21 p.

Esler, A.E. 1978. *Botany of the Manawatu.* Government Printer, Wellington, NZ.

Falconer, G.J., Wright, J.W. & Beall, H.W. 1933. The decomposition of certain types of fresh litter under field conditions. *American Journal of Botany 20*: 196–203.

Farr, D.F., Bills, G.F., Chamuris, G.P. & Rossman, A.Y. 1989. Fungi on plants and plant products in the United States. APS Press, St. Paul, Minnesota, USA.

Fensham, R.J., Fairfax, R.J. & Cannell, R.J. 1994. The invasion of *Lantana camara* L. in Forty Mile Scrub National Park, north Queensland. *Australian Journal of Ecology 19*: 297–305.

Fitzgerald, B.M., Robertson, H. & Whitaker, A.H. 1989. Vertical distribution of birds mist-netted in a mixed lowland forest in New Zealand. *Notornis 36*: 311–321.

Forster, R.R. & Forster, L.M. 1973. Spider relatives: the Mites, False Scorpions and Harvestmen. *In*: *New Zealand Spiders an introduction*, pp 51–66. Collins Bros. & Co. Ltd, Auckland, NZ.

Fountain, D.W. & Outred, H.A. 1991. Germination requirements of New Zealand native plants: a review. *New Zealand Journal of Botany 29*: 311–316.

Fox, M.D. & Fox, B.J. 1986. The susceptibility of natural communities to invasion. *In*: Groves, R.H.; Burdon, J.J. (Eds) *Ecology of biological invasions*, pp. 57–60. Cambridge University Press, Cambridge, UK.

French, K. & Eardley, K. 1997. The impact of weed infestations on litter invertebrates in coastal vegetation. *In*: Klomp, N.; Lunt, I. (Eds) *Frontiers in ecology: building the links*, pp. 89–102. Elsevier Science, Oxford, U.K.

French, K. & Major, R.E. 2001. Effect of an exotic *Acacia* (Fabaceae) on ant assemblages in South African fynbos. *Austral Ecology 26*: 303–310.

French, K. & Zubovic, A. 1997. Effect of the weed *Chrysanthemoides monilifera* (Bitou bush) on bird communities. *Wildlife Research 24*: 727–735.

Friend, D.T.C. 1961. A simple method of measuring integrated light values in the field. *Ecology 42*: 577–580.

Gauch, H.G. Jr. & Whittaker, R.H. 1981. Hierarchical classification of community data. *Journal of Ecology 69*: 135–152.

Greenslade, P.J. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology 33*: 301–310.

Greenslade, P.J. 1991. Collembola. *In*: Naumann, I.D.; Carne, P.B.; Lawerence, J.F.; Nielsen, E.S.; Spradberry, J.P.; Taylor, R.W.; Whitten, M.J.; Littlejohn, M.J. (Eds) *The insects of Australia. Volume 1*, pp 252–264. Melbourne University Press, Melbourne, Australia.

Grime, J.P. 1974. Vegetation classification by reference to strategies. *Nature 250*: 26–231.

Grime, J.P. 1979. *Plant strategies and vegetation processes*. John Wiley and Sons, Chichester, UK.

Grime, J.P. 1988. The C-S-R model of primary plant strategies: origins, implications, and tests. *In*: Gottlieb, L.D.; Jain, S.K.(Eds) *Plant Evolutionary Biology*, pp. 371–393. Chapman & Hall, London.

Grime, J.P. & Jeffery, D.W. 1965. Seedling establishment in vertical gradients of sunlight. *Journal of Ecology 53*: 621–642.

Groves, R.J. 1989. Ecological control of invasive terrestrial plants. *In*: Drake, J.A.; Mooney, H.A.; di Castri, F.; Groves, R.H.; Kruger, F.J.; Rejmánek, M.; Williamson, M. (Eds) *Biological Invasions: A global perspective*, pp. 437–461. John Wiley & Sons, NY.

Groves, R.J. 1991. Control of environmental weeds. *Plant Protection Quarterly 6*: 95–98.

Grubb, P.J. 1994. Root competition in soils of different fertility: a paradox resolved? *Phytocoenologia 24*: 495–505.

Grubb, P.J. & Metcalfe, D.J. 1996. Adaptation and inertia in the Australian tropical lowland rain-forest flora: contradictory trends in intergeneric and intrageneric comparisons of seed size in relation to light demand. *Functional Ecology 10*: 521–520.

Harborne, J.B. & Williams, C.A. 2000. Advances in flavonoid research since 1992: A review. *Phytochemistry 55*: 481–504.

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

Heal, O.W., Anderson, J.M. & Swift, M.J. 1997. Plant litter quality and decomposition: an historical overview. *In*: Cadisch, G.; Giller, K.E. (Eds) *Driven by nature: plant litter quality and decomposition*, pp 3–32. CABI Publishing, Oxon, UK.

Healy, A.J. & Edgar, E. 1980. *Flora of New Zealand, Volume III.* Government Printer, Wellington, NZ.

Hedge, P. & Kriwoken, L.K. 2000. Evidence for effects of *Spartina anglica* invasion on benthic macrofauna in Little Swanport estuary, Tasmania. *Australian Journal of Ecology 25*: 150–159.

Hill, M.O. 1979. *TWINSPAN–A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes.* Cornell University, Ithaca, NY.

Hill, M.O. & Gauch, H.G. Jr. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio 42*: 47–58.

Hobbs, R.J. 1989. The nature and effects of disturbance relative to invasions. *In*: Drake, J.A.; Mooney, H.A.; di Castri, F.; Groves, R.H.; Kruger, F.J.; Rejmánek, M.; Williamson, M. (Eds) *Biological Invasions: A global perspective*, pp. 389–407. John Wiley & Sons, NY.

Hobbs, R.J. 1991. Disturbance a precursor to weed invasion in native vegetation. *Plant Protection Quarterly 6*: 99–104.

Hobbs, R.J. & Humphries, S.E. 1995. An integrated approach to the ecology and management of plant invasions. *Conservation Biology 9*: 761–770.

Hobbs, R.J. & Mooney, H.A. 1986. Community changes following shrub invasion of grassland. *Oecologia 70*: 508–513.

Hobbs, R.J. & Mooney, H.A. 1993. Restoration ecology and invasions. *In*: Saunders, D.A.; Hobbs, R.J.; Ehrlich, P.R. (Eds) *Nature conservation 3: the reconstruction of fragmented ecosystems*, pp. 127–133. Surrey Beatty and Sons, Chipping Norton, N.S.W, Australia.

Hollingsworth, M.L.; Bailey, J.P. 2000. Evidence for massive clonal growth in the invasive weed *Fallopia japonica* (Japanese knotweed). *Botanical Journal of the Linnean Society 133*: 463–472.

Holmes, P.M. & Cowling, R.M. 1997. The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrublands. *Journal of Applied Ecology 34*: 317–332.

Hopkins, M.S. & Graham, A.W. 1983. The species composition of soil seed banks beneath lowland tropical rainforests in North Queensland, Australia. *Biotropica 15*: 90–99.

Howell, C., Hughes, P & Sawyer, J. 2000. *Pest plant atlas: Wellington Conservancy excluding the Chatham Islands.* Department of Conservation, Wellington, NZ.

Hutcheson, J.A. 1996. *Characterisation of insect communities of tawa forest in the Onaia Ecological Area using Malaise trapped beetles, and indications of influences including 1080 operations, on these communities.* Unpublished M.Phil. thesis, University of Waikato, Hamilton, NZ.

Hutchinson, T.F. & Vankat, J.L. 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. *Conservation Biology 11*: 1117–1124.

Keeney, D.R. 1982. Nitrogen availability indices. *In*: Page, A.L.; Miller, R.H.; Keeney, D.R. (eds) *Methods of soil analysis part 2: chemical and microbiological properties*, pp 711–733. American Society of Agronomy, Madison, Wisconsin.

Kelly, D. & Skipworth, J.P. 1984a. *Tradescantia fluminensis* in a Manawatu (New Zealand) forest: 1. Growth and effects on regeneration. *New Zealand Journal of Botany 22*: 393–397.

Kelly, D. & Skipworth, J.P. 1984b. *Tradescantia fluminensis* in a Manawatu (New Zealand) forest: II. Management by herbicides. *New Zealand Journal of Botany 22*: 399–402.

Klimaszewski, J. & Watt, J.C. 1997. *Coleoptera: Family-group review and keys to identification. Fauna of New Zealand No. 37.* Manaaki Whenua Press, Lincoln, NZ.

Kuschel, G. 1990. *Beetles in a suburban environment: a New Zealand case study.* Department of Scientific and Industrial Research, Auckland, NZ.

Lamb, D. 1993. Restoration of degraded forest ecosystems for nature conservation. *In*: Moritz, C.; Kikkawa, J. (Eds) *Conservation biology in Australia and Oceania*, pp. 101–114. Surrey Beatty and Sons, Chipping Norton, NSW, Australia.

Landcare Research 1998. *ALLWEEDS database.* Landcare Research, Lincoln, NZ (Acessed 11 December 1998).

Lee, W.G. & Fenner, M. 1989. Mineral nutrient allocation in seeds and shoots of twelve *Chionochloa* species in relation to soil fertility. *Journal of Ecology 77*: 704–716.

Leishman, M.R. & Westoby, M. 1994. The role of large seed size in shaded conditions: experimental evidence. *Functional Ecology 8*: 205–214.

Levine, J.M. 2000. Species diversity and biological invasions: Relating local process to community pattern. *Science 288*: 852–854.

Levine, J.M. & D'Antonio, C.M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos 87*: 15–26.

Lockwood, J.L., Simberloff, D.S., McKinney, M.L. & Von Holle, B. 2001. How many, and which, plants will invade natural areas? *Biological Invasions 3*: 1–8.

Lonsdale, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology 80*: 1522–1536.

Luken, J.O. 1997. Management of plant invasions: Implicating ecological succession. *In*: Luken, J.O.; Thieret, J.W. (Eds) *Assessment and management of plant invasions*, pp. 133–144. Springer-Verlag, NY.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications 10*: 689–710.

Mathsoft 1995. *S-PLUS 4.5. Guide to statistics.* Data Analysis Products Division, Mathsoft, Seattle, USA.

Matson, P. 1990. Plant-soil interactions in primary succession at Hawaii Volcanoes National Park. *Oecologia 85*: 241–246

Maule, H.G., Andrews, M., Morton, J.D., Jones, A.V. & Daly, G.T. 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*: 35–46.

McCluggage, T. 1998. Herbicide trials on *Tradescantia fluminensis. Conservation Advisory Science Notes No. 180.* Department of Conservation, Wellington, NZ.

McCullagh, P. & Nelder, J.A. 1989. *Generalised Linear Models.* Chapman and Hall, London, UK.

McCune, B. & Mefford, M.J. 1999. *PC-ORD. Multivariate analysis of ecological data, version 4.* MjM Software Design, Gleneden Beach, Oregon, USA.

McDonald, I.A.W., Lloyd, L.L., Usher, M.B. & Hamann, O. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. *In*: Drake, J.A.; Mooney, H.A.; di Castri, F.; Groves, R.H.; Kruger, F.J.; Rejmánek, M.; Williamson, M. (Eds) *Biological Invasions: A global perspective*, pp. 215–255. John Wiley & Sons, NY.

McSweeney, G.D. 1982. Matai/ totara flood plain forests in south Westland. *New Zealand Journal of Ecology 5*: 121–128.

Melbourne, B.A. 1999. Bias in the effect of habitat structure on pitfall traps: An experimental evaluation. *Australian Journal of Ecology 24*: 228–239.

Melillo, J.M., Aber, J.D. & Muratore, J.F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology 63*: 621–626.

Mielke, P.W. Jr. 1984. Meteorological applications of permutation techniques based on distance functions. In: Krishnaiah, P.R.; Sen, P.K. (Eds) *Handbook of Statistics Volume 4*, pp. 813–830. Elsevier Science Publishers, NY.

Moeed, A. & Meads, M. J. 1985. Seasonality of pitfall trapped invertebrates in three types of native forest, Orongorongo Valley, New Zealand. *New Zealand Journal of Zoology 12*: 17–53.

Moore, L.B. & Edgar, E. 1970. *Flora of New Zealand, Vol. II.* Government Printer, Wellington, NZ.

Mullett, T. & Simmons, D. 1995. Ecological impacts of the environmental weed sweet pittosporum (*Pittosporum undulatum* Vent.) in dry sclerophyll forest communities, Victoria. *Plant Protection Quarterly 10*: 131–138.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution 10*: 58–62.

National Institute of Water and Atmospheric Research 2000. *Summary reports of total rainfall and mean air temperature for Marton Climate Station, 1987–2000 and Levin Climate Station, 1990–2000.* National Institute of Water and Atmospheric Research, Wellington, NZ.

New Zealand Soil Bureau 1968. Soils of New Zealand. Part 3. *New Zealand Soil Bureau Bulletin 26 (3).*

Ogle, C. & Lovelock, B. 1989. *Methods for the control of wandering Jew (Tradescantia* fluminensis*) at "Rangitawa", Rangitikei District, and notes on other aspects of conserving this forest remnant.* Science and Research Internal Report No. 56, Department of Conservation, Wellington, NZ.

Ogden, J. 1985. An introduction to plant demography with special reference to New Zealand trees. *New Zealand Journal of Botany 23*: 751–772.

Olckers, T. & Hulley, P.E. 1991. Impoverished insect herbivore faunas on the exotic bugweed *Solanum mauritianum* Scop. relative to indigenous *Solanum* species in Natal/ KwaZulu and the Transkei. *Journal of the Entomological Society of Southern Africa 54*: 39–50.

Oliver, I. & Beattie, A.J. 1996. Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology 10*: 99–109.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology 44*: 322–332.

Owen, S.J. 1997. *Ecological weeds on conservation land in New Zealand: a database.* Department of Conservation, Wellington, NZ.

Palm, C.A. & Rowland, A.P. 1997. A minimum dataset for characterization of plant quality for decomposition. *In*: Cadisch, G.; Giller, K.E. (eds) *Driven by nature: plant litter quality and decomposition*, pp 379–392. CABI Publishing, Oxon, UK.

Partridge, T.R. 1989. Soil seed banks of secondary vegetation on the Port Hills and Banks Peninsula, Canterbury, New Zealand, and their role in succession. *New Zealand Journal of Botany 27*: 421–436.

Pimm, S.L. 1989. Theories of predicting success and impact of introduced species. *In*: Drake, J.A.; Mooney, H.A.; di Castri, F.; Groves, R.H.; Kruger, F.J.; Rejmánek, M.; Williamson, M. (Eds) *Biological Invasions: A global perspective*, pp. 351–368. John Wiley & Sons, NY.

Polly, B. & West, C. 1996. Kitchener Park then and now. *Wellington Botanical Society Bulletin 47*: 59–62.

Pook, E.W. 1979. Seedling growth in tanekaha (*Phyllocladus trichomanoides*): effects of shade and other seedling species. *New Zealand Journal of Forestry Science 9*: 193–200.

Porteous, T. 1993. *Native forest restoration: a practical guide for landowners.* Queen Elizabeth the Second National Trust, Wellington, NZ.

Price, M.L. & Butler, L.G. 1977. Rapid visual estimation and spectrophotometric determination of tannin content of sorghum grain. *Journal of Agricultural and Food Chemistry 25*: 1268–1273.

Radford, I.J.; Cousens, R.D. 2000. Invasiveness and comparitive life-history traits of exotic and indigenous *Senecio* species in Australia. Oecologica 125: 531–542.

Ravine, D.A. 1995. *Manawatu Plains Ecological District: Survey report for the Protected Natural Areas programme.* Department of Conservation, Wanganui, NZ.

Reay, S.D. & Norton, D.A. 1999. Assessing the success of restoration plantings in a temperate New Zealand forest. *Restoration Ecology 7*: 298–308.

Rejmánek, M. 1989. Invasibility of plant communities. *In*: Drake, J.A.; Mooney, H.A.; di Castri, F.; Groves, R.H.; Kruger, F.J.; Rejmánek, M.; Williamson, M. (Eds) *Biological Invasions: A global perspective*, pp. 369–388. John Wiley & Sons, NY.

Robinson, G.R., Quinn, J.F. & Stanton, M.I. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology 76*: 786–794.

Roy, B., Popay, I., Champion, P., James, T. & Rahman, A. 1998. An illustrated guide to common weeds of New Zealand. New Zealand Plant Protection Society, Canterbury, NZ.

Roques, K.G., O'Connor, T.G. & Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivore, rainfall and density dependence. *Journal of Applied Ecology 38*: 268–280.

Rowland, A.P. & Roberts, J.D. 1994. Lignin and cellulose fraction in decomposition studies using acid-detergent fibre methods. *Communications in Soil Science and Plant Analysis 25*: 269–277.

Samways, M.J. & Moore, S.D. 1991. Influence of exotic conifer patches on grasshopper (Orthoptera) assemblages in a grassland matrix at a recreational resort, Natal, South Africa. *Biological Conservation 57*: 117–137.

Samways, M.J., Caldwell, P.M. & Osborn, R. 1996. Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. *Agriculture, Ecosystems and Environment 59*: 19–32.

SAS/ QC and SAS/ STAT 1996. *Release 6.12 for Windows*. SAS Institute, North Carolina, USA.

Saunders, D.A., Hobbs, R.J. & Ehrlich, P.R. 1993. Reconstruction of fragmented ecosystems: problems and possibilities. *In*: Saunders, D.A.; Hobbs, R.J.; Ehrlich, P.R. (Eds) *Nature conservation 3: the reconstruction of fragmented ecosystems*, pp. 305–313. Surrey Beatty and Sons, Chipping Norton, NSW, Australia.

Saunders, D.A., Hobbs, R.J. & Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: A review. *Conservation Biology 5*: 18–32.

Sem, G. & Enright, N.J. 1996. The relationship between seed rain and the soil seed bank in a temperate rainforest stand near Auckland, New Zealand. *New Zealand Journal of Botany 34*: 215–226.

Smale, M.C. & Gardner, R.O. 1999. Survival of Mount Eden Bush, an urban forest remnant in Auckland, New Zealand. *Pacific Conservation Biology 5*: 83–93.

Smith, J.M.B. 1994. The changing ecological impact of broom (*Cytisus scoparius*) at Barrington Tops, New South Wales. *Plant Protection Quarterly 9*: 6–11.

SPSS Inc. 1996. *SYSTAT Version 6.0 for Windows*. SPSS Inc., Chicago, U.S.A.

Spurr, E.B., Warburton, B. & Drew, K.W. 1992. Bird abundance in different aged stands of rimu (*Dacrydium cupressinum*): implications for coupe-logging. *New Zealand Journal of Ecology 16*: 109–118.

Standish, R.J., Bennett, S.J. & Stringer, I.A.N. 2001a. *Habitat use of* Tradescantia fluminensis *by* Powelliphanta traversi. Department of Conservation Contract Report key output 5-236, investigation number 2153 (submitted), Wellington, NZ.

Standish, R.J.; Bennett, S.J. & Stringer, I.A.N. 2001b. *Effects of* Tradescantia fluminensis *removal on* Powelliphanta traversi *and other invertebrates.* Department of Conservation Contract Report key output 5-236, investigation number 2153 (submitted), Wellington, NZ.

Stewart, G.H. & Woods, D. 1991. A second generation at Matawai Park. *In*: Smale, M.C.; Meurk, C.D. (Compilers) *Proceedings of a workshop on scientific issues in ecological restoration*, pp. 62–63. Landcare Research, NZ.

Stockard, J. 1991. Rainforest rehabilitation at Wingham Brush. In: Phillips, S. (Ed) *Rainforest remnants: proceedings of a workshop on rainforest rehabilitation*, pp. 94–100. NSW National Parks and Wildlife Service, Sydney, Australia.

Stockard, J., Nicholson, B. & Williams, G. 1985. An assessment of a rainforest regeneration program at Wingham Brush, New South Wales. *The Victorian Naturalist 103*: 84–93.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs 69*: 25–46.

Swarbrick, J.T. & Hart, R. 2000. Environmental weeds of Christmas Island (Indian Ocean) and their management. *Plant Protection Quarterly 16*: 54–57.

Thomas, L.K. Jr. 1980. *The impact of three exotic plant species on a Potomac Island.* National Park Service Scientific Monograph, No. 13. US Department of Interior, Washington DC.

Thompson, K. 1978. The occurrence of buried viable seeds in relation to environmental gradients. *Journal of Biogeography 5*: 425–430.

Thompson, K., Hodgson, J.G. & Rich, T.C.G. 1995. Native and alien invasive plants: more of the same? *Ecography 18*: 390–402.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology 78*: 81–92.

Timmins, S.M. & Williams, P.A. 1991. Weed numbers in New Zealand's forest and scrub reserves. *New Zealand Journal of Ecology 15*: 153–162.

Toft, R.J., Harris, R.J. & Williams, P.A. 2001. Impacts of the weed *Tradescantia fluminensis* on insect communities in fragmented forests in New Zealand. *Biological Conservation 102*: 31–46.

Tolkach, V.F., Chuyan, A.Kh. & Krylov, A.V. 1990. Characterisation of a potyvirus isolated from *Tradescantia albiflora* in a southern locality of the Soviet Far East. *Byulleten' Glavnogo Botanicheskogo Sada 157*: 76–80 (abstract only).

Versfeld, D.B. & van Wilgen, B.W. 1986. Impact of woody aliens on ecosystem properties. *In*: Macdonald, I.A.W.; Kruger, F.J.; Ferrar, A.A. (Eds) *The ecology and management of biological invasions in southern Africa*, pp 239–246. Oxford Uni Press, Cape Town, South Africa.

Vitousek, P.M. 1982. Nutrient cycling and nutrient use efficiency. *American Naturalist 119*: 553–572.

Vitousek, P.M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos 57*: 7–13.

Vitousek, P.M. & Sanford, R.L. 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics 17*: 137–167.

Vitousek, P.M. & Walker, L.R. 1989. Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, and ecosystem effects. *Ecological Monographs 59*: 247–265.

Vivrette, N.J. & Muller, C.H. 1977. Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum*. *Ecological Monographs 47*: 301–318.

Vogt, K.A., Grier, C.C. & Vogt, D.J. 1986. Production, turnover, and nutrient dynamics of above- and below-ground detritus of world forests. *Advances in Ecological Research 15*: 303–377.

Walker, A.K. & Crosby, T.K. 1988. *The preparation and curation of insects*. DSIR Information Series No. 163, Department of Science and Industrial Research, Wellington, NZ.

Walker, L.R. 1994. Effects of fern thickets on woodland development on landslides in Puerto Rico. *Journal of Vegetation Science 5*: 525–532.

Walker, L.R. & Smith, S.D. 1997. Impacts of invasive plants on community and ecosystem properties. *In*: Luken, J.O.; Thieret, J.W. (Eds) *Assessment and management of plant invasions*, pp. 69–86. Springer, NY.

Walters, M.B. & Reich, P.B. 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology 81*: 1887–1901.

Wardle, P. 1991. *Vegetation of New Zealand.* Cambridge University Press, Cambridge, UK.

Webb, C.J., Sykes, W.R. & Garnock-Jones, P.J. 1988. *Flora of New Zealand, Vol IV.* Botany Division, Department of Scientific and Industrial Research, Christchurch, NZ.

Weiss, P.W. & Noble, I.R. 1984. Status of coastal dune communities invaded by *Chrysanthemoides monilifera. Australian Journal of Ecology 9*: 93–98.

Williams, P.A. & Buxton, R.P. 1989. Response to reduced irradiance of 15 species of native and adventive shrub and tree seedlings from eastern Canterbury. *New Zealand Journal of Ecology 12*: 95–101.

Williams, P.A. & Karl, B.J. 1996. Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. *New Zealand Journal of Ecology 20*: 127–145.

Williamson, M. 1996. *Biological Invasions.* Chapman & Hall, London.

Williamson, M.H. & Fitter, A. 1996. The characters of successful invaders. *Biological Conservation 78*: 163–170.

Woods, K.D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. *American Midland Naturalist 130*: 62–74.

Woods, K.D. 1997. Community response to plant invasion. *In*: Luken, J.O.; Thieret, J.W. (Eds) *Assessment and management of plant invasions*, pp. 56–68. Springer, NY.

Wunderlin, R.P. 1998. *Guide to the vascular plants of Florida.* University of Florida Press, Gainesville, Florida, USA.

Yates, C.J., Hobbs, R.J. & Atkins, L. 2000. Establishment of perennial shrub and tree species in degraded *Eucalyptus salmonophloia* (salmon gum) remnant woodlands: effects of restoration treatments. *Restoration Ecology 8*: 135–143.

Yeates, G.W. & Williams, P.A. 2001. Influence of three invasive weeds and site factors on soil microfauna in New Zealand. *Pedobiologia 45*: 367–383.

Young, A. & Mitchell, N. 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biological Conservation 67*: 63–72.