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# Invasion by a perennial herb increases decomposition rate and alters nutrient availability in warm temperate lowland forest remnants

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## Abstract

We determined the impact of the invasive herb, *Tradescantia fluminensis* Vell., on litter decomposition and nutrient availability in a remnant of New Zealand lowland podocarp–broadleaf forest. Using litter bags, we found that litter beneath mats of *Tradescantia* decomposed at almost twice the rate of litter placed outside the mat. Values of $k$ (decomposition quotient) were 9.44 ± 0.42 yrs for litter placed beneath *Tradescantia* and 5.42 ± 0.42 yrs for litter placed in native, non-*Tradescantia* plots. The impact of *Tradescantia* on decomposition was evident through the smaller forest floor mass in *Tradescantia* plots (2.65 ± 1.05 t ha$^{-1}$) compared with non-*Tradescantia* plots (5.05 ± 1.05 t ha$^{-1}$), despite similar quantities of annual leaf litterfall into *Tradescantia* plots (6.85 ± 0.85 t ha$^{-1}$ yr$^{-1}$) and non-*Tradescantia* plots (7.45 ± 1.05 t ha$^{-1}$ yr$^{-1}$). Moreover, there was increased plant nitrate available, as captured on resin bags, in *Tradescantia* plots (25.77 ± 8.32 cmol(−)/kg resin) compared with non-*Tradescantia* plots (9.55 ± 3.72 cmol(−)/kg resin). Finally, the annual nutrient uptake by *Tradescantia* represented a large proportion of nutrients in litterfall (41% N, 61% P, 23% Ca, 46% Mg and 83% K), exceeded the nutrient content of the forest floor (except Ca), but was a small proportion of the topsoil nutrient pools. Taken together, our results show that *Tradescantia* increases litter decomposition and alters nutrient availability, effects that could influence the long-term viability of the majority of podocarp–broadleaf forest remnants affected with *Tradescantia* in New Zealand. These impacts are likely mostly due to *Tradescantia*'s vegetation structure (i.e., tall, dense mats) and associated microclimate, compared with native ground covers.

*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*, is nitrogen-rich and decomposes easily compared with native litter in primary succession forest in Hawaii, leading to increased soil nutrients beneath the exotics

(Matson 1990). Conversely, invasive pines decrease rates of decomposition through addition of resistant litter (Versfeld and van Wilgen 1986), which may impact on 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* Vell. (Commelinaceae) (also known as *T. albiflora*; R. Faden, pers. comm.) is a perennial herb native to South America (Esler 1978), which has invaded forest remnants in New Zealand (Kelly and Skipworth 1984), eastern Australia (Dunphy 1991) and Florida (Wunderlund 1998). In New Zealand, most lowland forest remnants of the North Island and northern South Island have been subjected to anthropogenic disturbances (Timmins and Williams 1991), which have resulted in increased light levels in the forest interior which have favoured the invasion and biomass accumulation of *T. fluminensis* (hereafter *Tradescantia*) (Kelly and Skipworth 1984; Standish et al. 2001). *Tradescantia* does not invade undisturbed forest, but if the forest canopy is restored and light levels decrease, it can persist in the deep shade (down to 1.4% of full light; Adamson et al. 1991) typical of closed-canopy New Zealand podocarp forests (Ebbett and Ogden 1998). Under canopy gaps and at forest edges, high biomass mats of *Tradescantia* appear to remain indefinitely.

High biomass *Tradescantia* mats comprise a mass of thin (2–3-mm diameter), interlaced leafy shoots up to 60-cm tall. The lower, leafless stems are held to the forest floor by abundant fine roots that also form at aerial nodes within the mat. *Tradescantia* traps leaf litterfall and its roots penetrate the leaf litter and humus layers immediately below the mat. *Tradescantia* replaces native ground cover species and prevents the regeneration of woody seedlings (Esler 1978; Kelly and Skipworth 1984; Standish et al. 2001) that might otherwise provide competition for nutrients. Lastly, it can accumulate nitrogen (Maule et al. 1995). Therefore, *Tradescantia* could potentially affect the rate of litter decomposition by altering the microclimate (i.e., temperature and humidity), leaf litter chemistry and the composition of the decomposer community.

We sought to determine the impact of *Tradescantia* on litter decomposition and nutrient availability. We estimated the comparative decomposition rates of *Tradescantia* and *Melicytus ramiflorus* litters experimentally using litter bags. *M. ramiflorus*, a native tree common to the study sites, was selected in the absence of an abundant native ground cover. We also estimated decomposition rates indirectly, using measurements of annual leaf litterfall and forest floor mass in *Tradescantia*-affected and non-affected areas of two lowland forest remnants. To assess the impact of *Tradescantia* on nutrient availability, we compared available nitrogen and phosphorous in the soil using ion exchange resin (IER) bags in *Tradescantia*-affected and non-affected areas. Finally, we estimated nutrient uptake by *Tradescantia*, based on annual aboveground production and foliar nutrient levels of *Tradescantia*, and compared it with nutrient return by canopy litterfall in these *Tradescantia*-affected forest remnants.

## Materials and methods

### *Study sites*

The study sites were two remnants of lowland podocarp–broadleaf forest 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 is approximately 1176 mm and mean annual temperature is 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 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). Soils at Denton's Bush are 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 is well drained. Soils at Rangitawa Bush are classified as Argillic Perch-gley pallic derived from loess, and the soil type is Marton silt loam. Drainage at the site varies from imperfect to poor. In June 1998, 2 soil cores were collected at each site, and cut into four layers: 0–7.5, 7.5–15, 15–22.5 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 methods of Blakemore et al. (1987). Anaerobic mineralisable

*Table 1.* Soil properties of Denton's Bush and Rangitawa Bush. 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 |

nitrogen was determined as described in Keeney (1982). These soil properties are described in Table 1.

At each site, three 20 × 20 m plots were selected so that *Tradescantia* covered greater than 75% of the forest floor within the plots. These plots were near to the forest edge, i.e., minimum distance to the forest edge ranged from 4 to 20 m. Adjacent to each *Tradescantia* plot, a 20 × 20 m plot was selected where *Tradescantia* did not occur or was insignificant (<5% cover of forest floor), usually further into the forest remnant, i.e., minimum distance to the forest edge ranged from 7 to 62 m. Vegetation cover was visually estimated at 0.3–2, 2–5, 5–12 and >12 m above the ground within each plot ($n = 6$ plots/site) following the 'recce' method of Allen (1992). Plant nomenclature follows Allan (1961) and Healy and Edgar (1980), unless given at first mention.

Denton's Bush had sparse cover in the sub-canopy and understorey layers, as a result of stock grazing and possum (*Trichosurus vulpecula*) browsing before 1988 (M. Lutz, pers. comm.). *Tradescantia* has been established for *c.* 12 yrs (M. Lutz, pers. comm.). The forest canopy was comprised mainly of *Beilschmiedia tawa* and *Laurelia novae-zelandiae*. The sub-canopy was dominated by the native trees *M. ramiflorus*, particularly in *Tradescantia* plots, *Dysoxylum spectabile* and *Hedycarya arborea*. The native shrub *Macropiper excelsum* dominated the understorey, particularly in non-*Tradescantia* plots (Table 2). Canopy cover, summed for layers excluding the 0.3–2 m layer, was 157 ± 10% (SE) for *Tradescantia* plots and 210 ± 7% (SE) for non-*Tradescantia* plots. Ground cover species other than *Tradescantia* included ferns and woody seedlings. Ferns ranged from 1% to 2% cover in *Tradescantia* plots and 2% to 17% cover in non-*Tradescantia* plots. Woody seedlings ranged from 0% to 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.). *Tradescantia* has been established for at least 16 yrs (Ogle and Lovelock 1989). *Alectryon excelsus*, *B. tawa* and *M. ramiflorus* dominated the upper canopy in the non-*Tradescantia* plots, while only *A. excelsus* 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 species other than *Tradescantia* included ferns, woody seedlings and grasses. Ferns and grasses ranged from 1% to 5% cover in *Tradescantia* plots and 5% to 12% cover in non-*Tradescantia* plots. Woody seedlings ranged from 0% to 1% cover in *Tradescantia* plots and 0% to 4% cover in non-*Tradescantia* plots.

*Table 2.* Average % contribution of woody species (≥ 5% cover) to all layers of vegetation in non-*Tradescantia* and *Tradescantia* plots expressed as percentage of mean total cover ($n = 3$). *M. ramiflorus* and *M. excelsusm* are mesophyllous and the remaining species are sclerophyllous.

| | Non-*Tradescantia* | *Tradescantia* |
|---|---|---|
| Denton's Bush | | |
| *Beilschemiedia tawa* | 15 | 13 |
| *Laurelia novae-zelandiae* | 7 | 3 |
| *Dysoxylum spectabile* | 20 | 19 |
| *Melicytus ramiflorus* | 4 | 15 |
| *Hedycarya arborea* | 1 | 4 |
| *Macropiper excelsum* | 38 | 26 |
| Remaining | 15 | 20 |
| Rangitawa Bush | | |
| *Beilschmiedia tawa* | 18 | 5 |
| *Alectryon excelsus* | 9 | 29 |
| *Podocarpus totara* | 1 | 5 |
| *Melicytus ramiflorus* | 17 | 4 |
| *Macropiper excelsum* | 24 | 23 |
| Remaining | 31 | 34 |

### *Litterfall*

Litterfall was collected in circular funnels 0.1 m in area and 0.3 m deep, which were constructed from nylon shade cloth (0.5 mm mesh) erected at 1 m above ground level. Three funnels were randomly placed in each plot.

Traps were emptied approximately every 30 days for 12 months, from December 1997 to November 1998. Collected 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'). The litterfall of species with $> 5\%$ cover was identified (by RJS and PAW independently) according to green leaf texture (by feel): 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* plots at both sites. Leaf litterfall data were natural log transformed, and a $\ln(x + 1)$ transformation was used for twig litterfall data.

### *Forest floor mass and decomposition quotient*

Forest floor material, including recently fallen litter and decomposing organic matter above the mineral soil, was collected in March and September 1998, from three 0.5 × 0.5 m quadrats adjacent to litterfall traps within each *Tradescantia* and non-*Tradescantia* plot at both sites ($n = 2$ sites × 6 plots × 3 quadrats × 2 collections = 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, the biomass of litter components was determined. A two-factor repeated measures ANOVA was used to test differences among the forest floor mass (plot means) of *Tradescantia* and non-*Tradescantia* plots at both sites. Data were natural log transformed for analyses.

The decomposition quotient (Olson 1963), the proportion of litter decomposed annually, was calculated as:

$$k_L = I/X,$$

where $I$ is the mean annual litterfall and $X$ is the mean forest floor mass. Calculation of the $k_L$ quotient assumes simple exponential breakdown of litter in which the surface accumulation oscillates around some 'steady-state' value (Olson 1963). Decomposition quotients were calculated for litter of *Tradescantia* and non-*Tradescantia* plots at both sites.

### *Litter decomposition in litter bags*

Litter decomposition was examined at Denton's Bush using the litter bag technique (Falconer et al. 1933). *Tradescantia* and *M. ramiflorus* were compared for litter decomposition in *Tradescantia* and non-*Tradescantia* plots, and at different levels (see below). Fresh leaf material collected as litter, was not available in sufficient quantity, due to rapid litter turnover of these species. Leaves and shoots of *Tradescantia* were collected from three separate mats and senescing *M. ramiflorus* leaves were collected from the lower branches of more than 30 spatially separated trees. Fresh material was mixed and oven-dried before placement in 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 resprouted when removed from the oven after eight days. A sample of each litter type was retained for nutrient analyses. Litter bags ($n = 120$ total) were $10 \times 20$ cm, made from nylon mesh (mesh size = 1 mm) and closed with staples. The actual dry biomass of bagged litter was determined by drying (80 °C for 2 days) 10 supplementary samples of each litter type, which was $2.25 \pm 0.09$ g of *Tradescantia* litter (approximately equal amounts of shoot and leaf material) and $2.24 \pm 0.09$ g of *M. ramiflorus* litter.

Litter bags were placed in each of the following treatments: non-*Tradescantia* plots beneath the litter on the mineral soil (hereafter 'soil level'); *Tradescantia* plots at soil level; *Tradescantia* plots suspended within the weed mat and resting on the leafless stems ($\sim$10 cm above soil level); and non-*Tradescantia* plots suspended 10 cm above soil level (hereafter 'mat level'). Soil level bags were anchored with wire pegs and mat level bags were suspended vertically on wire frames.

A design was produced with SAS Proc Optex (SAS/QC Release 6.12, 1996) based on a 5 × 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 1 of the 6 plots, 3 *Tradescantia* and 3 non-*Tradescantia*; each containing 20 bag sites, 2 m apart, in a 5 × 4 grid. Bags were placed in the sites on 27 February 1998, and one bag of each litter type/treatment combination was harvested from each plot ($n$ = 3 replicates) 30, 60, 100, 120 and 150 days later. Upon collection in the field, litter bags were washed to remove soil and dried (80 °C for 2 days) before their mass was determined.

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 these data followed a negative exponential curve over time (Figure 1). A generalised linear model (GLM) with a log link, normal errors and a zero intercept, was applied to ensure the decay curve passed through 100% dry weight remaining at time, $t = 0$ (McCullagh and Nelder 1989). The GLM was fitted using SAS Proc Genmod (SAS/STAT release 6.12 1996).

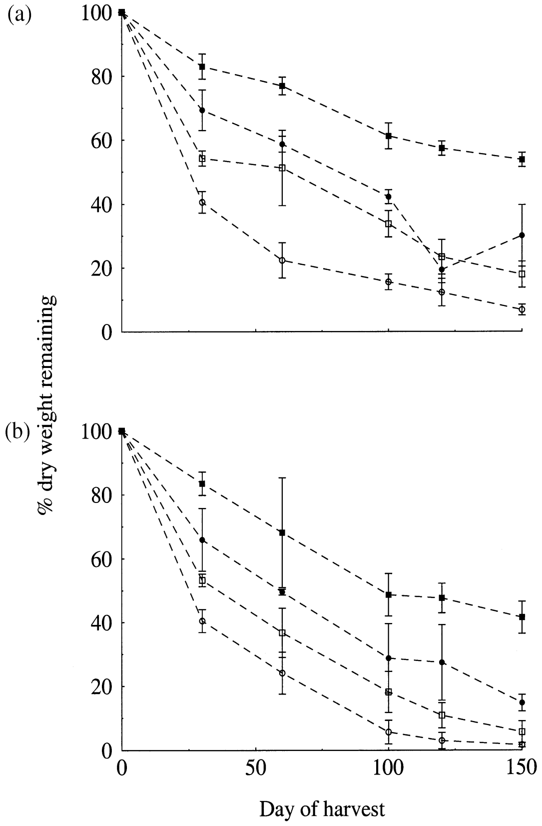

*Figure 1.* Decomposition (mean ± SE) of bagged *Tradescantia* leaf and shoot litter (a) and *M. ramiflorus* leaf litter (b) in Denton's Bush over 150 days of study. Treatments are as follows: non-*Tradescantia* plots at mat level (■); *Tradescantia* plots at mat level (●); non-*Tradescantia* plots at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

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). Values of $k$ and their standard errors were derived from the model (fitted with significant terms only) using the equation:

$$\log(\text{proportion dry weight remaining}) = k \times \text{time (days)}$$

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 chemistry*

Litterfall, forest floor material and litterbag material were oven-dried and ground (0.5 mm). Nitrogen, phosphorous, potassium, calcium and magnesium content (Blakemore et al. 1987) was determined for: (1) subsamples of litterfall from bulked seasonal (Nov.–Jan.; Feb.–Apr.; May–Jul. and Aug.–Oct.) samples from all *Tradescantia* and non-*Tradescantia* plots at each site ($n = 4$ seasons × 2 plot types × 2 sites); (2) bulked samples of the September (randomly selected) forest floor material from each plot and site (sub-sampled for fine, coarse and *Tradescantia* litter ($n = 10$)) and (3) subsamples of *M. ramiflorus* and *Tradescantia* litter from litter bags before decomposition ($n = 2$).

In addition, for the Nov.–Jan. litterfall samples from *Tradescantia* and non-*Tradescantia* plots at each site and bagged *M. ramiflorus* and *Tradescantia* litter ($n = 2$), determinations were made of the quantity of total phenolics, condensed tannins, acid–detergent fibre, $\alpha$-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 methods 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 IER bag method (Binkley and Matson 1983). Three nylon IER bags containing about 5 g of 'Duolite' (MB6113) mixed-bed resin (BDH, Ltd) were buried in each plot, at a depth of 5 cm in mineral soil. The assay lasted from 19 March 1999 to 31 March 2000. Upon removal, each bag was extracted with 100 ml of 2M KCl. All bags except one were recovered. $NH_4^+$–N and $NO_3^-$–N were determined by autoanalyser procedures and inorganic P with the Murphy and Riley (1962) reagent (Blakemore et al. 1987). A nested ANOVA on untransformed ($NO_3^-$–N) and log transformed ($NH_4^+$–N and inorganic P) data were used to test for differences in available nutrients in *Tradescantia* and non-*Tradescantia* plots.

### Tradescantia *aboveground production*

Three 0.5 × 0.5 m sub-plots per 20 × 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 values were recorded every 2 months from April 1998 to 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 senescence since last measurement using tag 2 as a guide (internode decay). From these measurements we determined: (1) internode growth compared with 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 (Standish et al. 2001). RGR is a good estimate of production because there is no consolidation of older biomass. Apical growth is balanced by basal decay, i.e., the vertical leafy stem grades into a horizontal stem, the end of which is decaying (Kelly and Skipworth 1984; Maule et al. 1995).

## 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. Mesophyllous and sclerophyllous species contributed similar percentage cover in non-*Tradescantia* plots and *Tradescantia* plots at Denton's Bush; whereas, at Rangitawa Bush, mesophyllous species contributed more to vegetation cover in non-*Tradescantia* plots than in *Tradescantia* plots (Table 2). Leaf litterfall mass did not differ between non-*Tradescantia* and *Tradescantia* plots or sites (Table 3; $F_{1,8} = 0.08$, $P = 0.78$ (NT/T); $F_{1,8} = 0.02$, $P = 0.88$ (site); $F_{1,8} = 0$, $P = 0.99$ (NT/T × site)). Likewise, twig fall mass did not differ between non-*Tradescantia* and *Tradescantia* plots or sites (Table 3; $F_{1,8} = 3.50$, $P = 0.10$ (NT/T); $F_{1,8} = 0.45$, $P = 0.52$ (site); $F_{1,8} = 1.95$, $P = 0.20$ (NT/T × site)).

### *Forest floor mass and decomposition quotient*

The forest floor leaf mass was greater in non-*Tradescantia* than in *Tradescantia* plots at both sites (Table 3; $F_{1,8} = 16.62$, $P = 0.004$ (NT/T); $F_{1,8} = 0.02$, $P = 0.90$ (site); $F_{1,8} = 3.84$, $P = 0.09$ (NT/T × site)). *Tradescantia* litter represented a small percentage of the forest floor mass (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 forest floor material between plots or sites (Table 3;

*Table 3.* Litterfall (t ha$^{-1}$ yr$^{-1}$) and forest floor mass (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 as explained in text.

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

$F_{1,8} = 3.65$, $P = 0.09$ (NT/T); $F_{1,8} = 0.54$, $P = 0.48$ (site); $F_{1,8} = 1.58$, $P = 0.24$ (NT/T × site)).

Leaf litter decomposition ($k_L$) is more rapid in *Tradescantia* than non-*Tradescantia* plots (Table 3). Decomposition appeared to be faster at Denton's Bush than at Rangitawa Bush. Decomposition quotients are >1, which indicates that leaf litter turnover occurs in less than 1 yr in these forest plots (Table 3).

### *Litterbag decomposition*

The relative rates of litter decay were the same for bagged *Tradescantia* and *M. ramiflorus* litter across treatments (Figures 1a, b). Bagged litter decomposed more rapidly in *Tradescantia* plots at soil level than at the same level in non-*Tradescantia* plots, and litter decomposed more rapidly at mat level in *Tradescantia* than at the same height in non-*Tradescantia* plots. The rate of litter decomposition at mat level in *Tradescantia* was similar to that at soil level in non-*Tradescantia* plots (Figures 1a, b).

The factors in the GLM accounted for 98.2% of the total variation in the data. The overall effect of time was most important (explained 91.5% of variation, $P$ not determined since the model has no intercept term) but the time × level (explained 4.4% of variation, $P < 0.001$) and time × plot (explained 1.8% of variation, $P < 0.001$) terms indicate significant differences in the rate of decay between soil and mat levels, and between *Tradescantia* and non-*Tradescantia* plots (see also Figures 1a, b). The small but significant time × plot × level interaction (explained 0.1% of variation, $P < 0.05$) indicates that the differences in decomposition rates between levels were less marked in *Tradescantia* than non-*Tradescantia* plots. The time × litter interaction (explained 0.3% of variation, $P < 0.001$) indicates that *M. ramiflorus* litter decomposed more rapidly than *Tradescantia* litter. Decomposition rates, just based on the significant terms of the GLM, are shown in Figure 2.

### *Litter chemistry*

*Tradescantia* litter had higher nutrient concentrations than the non-*Tradescantia* (mixed species) litter (Table 4). The nitrogen use efficiency, i.e., dry mass of litterfall produced per unit of nitrogen (Vitousek 1982), calculated using data from Tables 3 and 4, was 75.8 at Denton's Bush and 64.9 at Rangitawa Bush. Bagged litter contained greater amounts of all nutrients (*Tradescantia*: 2.72 g/100 g N, 0.43 g/100 g P, 4.04 g/100 g K, 2.32 g/100 g Ca, 0.92 g/100 g Mg; and *M. ramiflorus*: 2.53 g/100 g N, 0.24 g/100 g P, 3.80 g/100 g K, 1.67 g/100 g Ca, 0.39 g/100 g Mg) except for Ca in *M. ramiflorus*, than the non-*Tradescantia* litter (Table 4). *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 5). In addition, the litter of *Tradescantia* and *M. ramiflorus* were mesophyllous, while the majority of the canopy species were sclerophyllous. While *M. ramiflorus* and *Tradescantia* were similar in litter chemistry, *M. ramiflorus* litter had more ADF-lignin and less $\alpha$-cellulose than *Tradescantia* litter (Table 5).

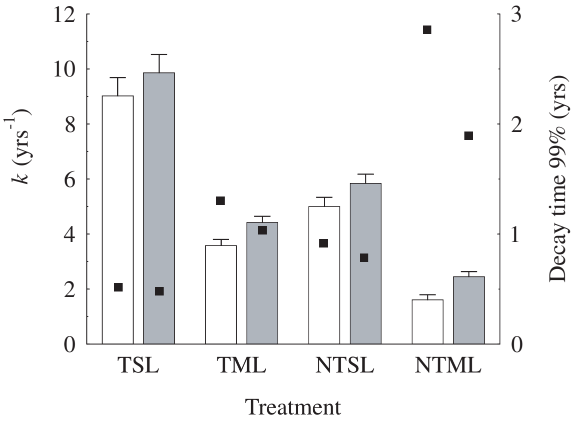

*Figure 2.* Values of $k$ (+ SE) for *Tradescantia* (white bars) and *M. ramiflorus* (grey bars) litters, and decay times (to 99% of original) (black squares), for each litter type/treatment combination placed in Denton's Bush for 150 days (derived from the GLM fitted with significant terms only). Treatment codes are: TSL = *Tradescantia* plots at soil level; TML = *Tradescantia* plots at mat level; NTSL = non-*Tradescantia* plots at soil level and NTML = non-*Tradescantia* plots at mat level.

### *Soil nutrient availability*

There were larger levels of available nitrate ($F_{1,11} = 99.51$, $P < 0.001$ (NT/T); $F_{4,11} = 27.25$, $P < 0.001$ (plot (NT/T))) in the soil of *Tradescantia* plots (25.77 ± 8.32 cmol(−)/kg resin) compared with non-*Tradescantia* plots (9.55 ± 3.72 cmol(−)/kg resin). There were similar levels of IER estimated available ammonium, 0.13 ± 0.10 cmol(+)/kg resin in *Tradescantia* and 0.04 ± 0.01 cmol(+)/kg resin in non-*Tradescantia* plots ($F_{1,11} = 0.27$, $P = 0.62$ (NT/T);

*Table 4.* The mean (± SE) concentrations (g/100 g) of nutrients in litter at Denton's Bush and Rangitawa Bush. Sample sizes are eight and four for litterfall and non-*Tradescantia* forest floor litter, respectively.

| Site | Litter | N | P | K | Ca | Mg |
|---|---|---|---|---|---|---|
| Denton's Bush | Litterfall | 1.32 ± 0.06 | 0.17 ± 0.01 | 1.29 ± 0.13 | 1.88 ± 0.09 | 0.33 ± 0.01 |
| | Forest floor | | | | | |
| | Non-*Tradescantia* | 1.67 ± 0.25 | 0.16 ± 0.02 | 0.37 ± 0.06 | 1.90 ± 0.12 | 0.28 ± 0.02 |
| | *Tradescantia* | 2.59 | 0.30 | 1.67 | 2.32 | 0.56 |
| Rangitawa Bush | Litterfall | 1.54 ± 0.07 | 0.13 ± 0.01 | 0.80 ± 0.09 | 2.37 ± 0.16 | 0.52 ± 0.05 |
| | Forest floor | | | | | |
| | Non-*Tradescantia* | 1.66 ± 0.14 | 0.13 ± 0.01 | 0.29 ± 0.09 | 2.06 ± 0.19 | 0.37 ± 0.05 |
| | *Tradescantia* | 2.01 | 0.16 | 0.81 | 1.83 | 0.46 |

*Table 5.* Chemistry of leaf litterfall at Denton's Bush (D) and Rangitawa Bush (R), and bagged litter prior to decomposition. Carbon compounds are mean (± SE, $n = 2$) concentrations (g/100 g).

| Litter | C : N | Condensed tannins | Total phenolics | Fibre | $\alpha$-Cellulose | ADF-lignin | Lignin : N |
|---|---|---|---|---|---|---|---|
| Litterfall–D | 34 | 1.70 ± 0.21 | 2.14 ± 0.66 | 43.08 ± 3.16 | 20.70 ± 1.45 | 20.92 ± 4.13 | 15.8 |
| Litterfall–R | 29 | 1.67 ± 0.06 | 3.26 ± 0.57 | 46.91 ± 2.07 | 17.20 ± 0.02 | 27.73 ± 1.62 | 18 |
| *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 |

$F_{4,11} = 3.61$, $P = 0.04$ (plot (NT/T))); and phosphate, 3.65 ± 1.45 cmol(−)/kg resin in *Tradescantia* and 1.68±0.41 cmol(−)/kg resin in non-*Tradescantia* plots ($F_{1,11} = 1.30$, $P = 0.28$ (NT/T); $F_{4,11} = 2.38$, $P = 0.12$ (plot (NT/T))). There was more variation in plant available nutrients in *Tradescantia* plots than in non-*Tradescantia* plots.

### Tradescantia *production*

Total annual aboveground *Tradescantia* growth at both sites exceeded decay. At Denton's Bush, annual sub-plot mean RGR values range from 48% to 137%, and the annual site mean (± SE) was 73 ± 5%. At Rangitawa Bush, annual sub-plot mean RGR values range from 34% to 78%, and the annual site mean (± SE) was 51 ± 2%. RGR peaked during Dec.–Jan. at Denton's Bush, and during Oct.–Nov. at Rangitawa Bush. Growth was less than decay during Apr.–May at Denton's Bush and Dec.–Mar. 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.

We estimated the annual uptake of nutrients by *Tradescantia* (i.e., annual aboveground production × % nutrient content of *Tradescantia* litter at 0 days). We compared this value with the nutrients returned annually through litterfall (i.e., annual litterfall (Table 3) × % nutrient content of litterfall (Table 4)) and the nutrient content of the forest floor (i.e., (forest floor mass (Table 3) × % nutrient content of forest floor (Table 4)) + (mass of *Tradescantia* litter in forest floor × % nutrient content of *Tradescantia* litter in forest floor (Table 4))). Annual uptake of nutrients by *Tradescantia* was large compared with litterfall nutrient inputs (41% N, 61% P, 23% Ca, 46% Mg and 83% K; Table 6). Annual nutrient uptake by *Tradescantia* was higher than the nutrient content of the forest floor (Table 6), but small compared with mineral soil nutrient pools (Table 1).

*Table 6.* The estimated annual uptake of nutrients by *Tradescantia* compared with the nutrients returned annually through litterfall by forest trees and the nutrient content of the forest floor. Calculations are based on the figures in Tables 3 and 4 (see text for details). Total soil nutrients are given in Table 1.

| Nutrient | *Tradescantia* uptake (t ha$^{-1}$ yr$^{-1}$) | Litterfall input (t ha$^{-1}$ yr$^{-1}$) | Forest floor (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 availability. Rapid litter turnover beneath *Tradescantia* was evident from the greater decomposition rates of bagged litter and by the reduced forest floor mass in *Tradescantia* plots compared with non-*Tradescantia* plots, despite similar quantities of litterfall entering both. Available nitrogen (nitrate) was higher under mats of *Tradescantia* compared with non-*Tradescantia* plots. Annual nutrient uptake by *Tradescantia* was higher than the nutrient content of the forest floor, but small compared with mineral soil nutrient pools. While it is clear that *Tradescantia* invasion alters ecosystems processes in these forests, further work is required to determine whether this invasion influences the native forest species.

*Tradescantia* invades areas with reduced canopy cover, such as forest edges. Canopy cover was lower in *Tradescantia* plots compared with 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) compared with the forest interior (Saunders et al. 1991), which could potentially alter litter decomposition and nutrient availability (Murcia 1995). Edge effects on microclimate extend at least 40–50 m into New Zealand podocarp–broadleaf forest remnants (Young and Mitchell 1994; Davies-Colley et al. 2000). Therefore, remnants $< 9$ ha in area are dominated by edge microclimate conditions (Young and Mitchell 1994). Our *Tradescantia* and non-*Tradescantia* plots were within 40–50 m of the forest edge or within sites that are 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*. Nevertheless, we cannot eliminate the possibility that the disturbed forest environment associated with *Tradescantia*’s invasion may have intensified the impacts we measured.

The nitrogen use efficiency of these forests suggests high soil nitrogen availability. Within and among tropical, temperate deciduous, coniferous, Mediterranean and fertilised ecosystems, there is a strong inverse relationship between nitrogen return by litterfall and nitrogen use efficiency, which probably relates to soil nitrogen availability (Vitousek 1982). Forests with relatively high nitrogen availability generally have a nitrogen-rich litterfall and a low nitrogen use efficiency (Vitousek 1982). Also, *L. novae-zelandinae* and *D. spectabile* are indicative of permanently wet fertile soils and *P. totara* and *B. tawa* occur on drier fertile soils (Wardle 1991).

Estimated values for mean annual leaf litterfall, $6.85 \pm 0.85\,\mathrm{t\,ha^{-1}}$ into *Tradescantia* plots and $7.45 \pm 1.05\,\mathrm{t\,ha^{-1}}$ into non-*Tradescantia* plots, are similar to annual leaf litterfall of warm temperate broad-leaved evergreen forests (mean $= 6.5\,\mathrm{t\,ha^{-1}}$, Vogt et al. 1986). Conversely, the forest floor mass, $2.65 \pm 1.05\,\mathrm{t\,ha^{-1}}$ in *Tradescantia* plots and $5.05 \pm 1.05\,\mathrm{t\,ha^{-1}}$ in non-*Tradescantia* plots, are both lower than the forest floor mass of other warm temperate broad-leaved evergreen forests (mean $= 19.2\,\mathrm{t\,ha^{-1}}$, Vogt et al. 1986). Our indirect measures of leaf litter turnover times ($k_{\mathrm{L}} = 1.4$–$3.8$) are high relative to values for other evergreen forests (range $= 0.015$–$4.0$, Olson 1963). These comparisons indicate that the study sites are highly productive, and that litter is broken down rapidly, especially where *Tradescantia* occurs.

*Tradescantia* can influence the three factors that determine litter decomposition rates: microclimate (temperature and moisture), composition of the decomposer community and litter quality (Heal et al. 1997). It is likely that the tall, dense mats of *Tradescantia* provide a microclimate that promotes rapid litter decomposition compared with that of native habitat where ground cover is mostly leaf litter. An alteration of microclimate is likely to affect the composition of the decomposer community, which may also promote rapid litter decomposition.

In general, the components of litter that affect decay rate are N content and C : N and lignin : N ratios (Melillo et al. 1982). *Tradescantia* litter contained more nitrogen, had lower C : N and lignin : N ratios than the mixed-species leaf litterfall; these features probably contributed to its faster decomposition. *M. ramiflorus* litter was more similar to that of *Tradescantia* than the mixed-species canopy leaf litter, which explains why our estimates of $k$ are greater than our estimates of $k_{\mathrm{L}}$. Also, the use of single-species litter bags probably influenced associated decomposers and so affected estimated decay rates (Blair et al. 1990). The relative contributions of sclerophyllous and mesophyllous species to the leaf litterfall in *Tradescantia* and non-*Tradescantia* plots does not explain why decomposition was more rapid in *Tradescantia* – the percentage cover of mesophyllous species was greater in non-*Tradescantia* plots at Rangitawa Bush. The degree of sclerophylly reflects chemical parameters, e.g., ADF fibre, lignin (Palm and Rowland 1997) and mesophyllous species decompose more easily.

Our calculations estimate *Tradescantia* above-ground production (0.64–1.28 $\mathrm{t\,ha^{-1}\,yr^{-1}}$) to be up to 20% of forest litter production, which represents a considerable addition of ground cover biomass to these forests as native ground cover is sparse. Furthermore, annual growth exceeded decay at both sites, which indicates that biomass is accumulating. 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 $\sim 3\,\mathrm{t\,ha^{-1}\,yr^{-1}}$ (Kelly and Skipworth 1984).

This paper documents the impact of *Tradescantia* on litter decomposition rates and nutrient availability in remnant podocarp forests in New Zealand. Whether nutrient uptake and storage by *Tradescantia* influences forest productivity or overall nutrient budgets in these forests require further investigation. Podocarps are mycotrophic (Baylis 1969) which may enable them to access nutrients that are unavailable to *Tradescantia*, particularly phosphorus. The high fertility of these sites and of *Tradescantia*-affected sites generally (Ogle and Lovelock 1989) may mitigate some of the effects of *Tradescantia* on ecosystem processes.

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