The impact of an invasive weed *Tradescantia fluminensis* on native forest regeneration

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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 showed that *Tradescantia* biomass increased logistically with available light, to a maximum at 10–15% full light. The maximum *Tradescantia* biomass was greater at the wetter site (819 g m^{-2}) than at the comparatively dry site (695 g m^{-2}).

3. Native forest seedling species richness and abundance decreased 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 attributed this to decreasing light levels beneath *Tradescantia*. Under approximately 500 g m^{-2} of *Tradescantia* (*c.* 100% weed cover), available light was reduced to < 1% full light.

4. The compositions of the extant vegetation, seed rain and seed bank were 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* appeared to be the least tolerant, its LD50 (the biomass of *Tradescantia* at which its abundance is reduced to 50% of the maximum) being approximately 12 g m^{-2}, whereas *Dysoxylum spectabile* was the most tolerant, with an LD50 of 40 g m^{-2}.

6. *Dysoxylum spectabile* germination and early seedling establishment could 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 g m^{-2} (70–90% cover).

7. We predicted 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 light, forest restoration, seed bank, seed rain, seedling emergence, weed biomass.

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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;

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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 *Tradescantia albiflora*; R. Faden, personal communication) is a ground-smothering perennial herb native to South America (Esler 1978) that has invaded forest remnants in New Zealand (Kelly & Skipworth 1984), eastern Australia (Dunphy 1991) and Florida (Wunderlund 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 1984). *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 1984). 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. Finally, 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 north-west of the site (National Institute of Water & 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 north of both sites (National Institute of Water & Atmospheric Research 2000).

At each site, three 20 × 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 × 20-m² 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^{-1}). Ground cover other than *Tradescantia* comprised litter, bare soil, ferns, woody seedlings and grasses. Vegetation cover was estimated visually 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 (R. Standish, personal observation). *Alectryon excelsus*, *Beilschmiedia tawa* and *Melicytus ramiflorus* dominate the upper canopy in the non-*Tradescantia* plots, while only *Alectryon excelsus* comprises more than 10% of any layer in the *Tradescantia* plots. *Podocarpus totara* also occurs 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 subcanopy 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 *Beilschmiedia tawa* and *Laurelia novae-zelandiae*, with a subcanopy of *Melicytus ramiflorus*, particularly in *Tradescantia* plots, and *Dysoxylum spectabile*, with some *Hedycarya arborea*. *Macropiper 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 subcanopy 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 subcanopy comprises *Dysoxylum spectabile* and *Melicytus ramiflorus*. The understorey includes *Coprosma rhamnoides* and *Pennantia corymbosa* in *Tradescantia* plots and *Coprosma rhamnoides*, *Geniostoma ligustrifolium* and *Macropiper 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 × 20-m plot ($n = 18$ per site). Funnels were emptied every 30 ± 1 days for 12 months, from December 1997 to November 1998. *Dysoxylum 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 × 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 5·4 cm diameter. These samples were combined for each 50 × 50-cm subplot, and stored at 4 °C for *c.* 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 °C to 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-m² 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-m² quadrats. At each study site we selected six or seven 25 × 10-m or 50 × 10-m plots,

depending on the extent of *Tradescantia* infestation. These plots were usually separate from, but occasionally overlapped, the 20 × 20-m plots mentioned previously. Ten and 20 0·25-m² quadrats were randomly placed within the 250-m² and 500-m² plots, respectively. So as not to flatten the *Tradescantia*, we used a 0·5 × 0·5-m metal quadrat positioned on a set of 0·50-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 *Dysoxylum spectabile* seedlings in 0–526 g m⁻² *Tradescantia*, for 20 months beginning 2 August 1998.

LIGHT MEASUREMENT

At Denton's Bush (28 July–4 August 1998) and Kirkwell Bush (28 August–4 September 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; Li-Cor Inc., Lincoln, NB) attached to a Campbell data logger (CR21X datalogger; Campbell Scientific, Logan, UT), set up to record full sunlight. Adjacent to the sensor, two replicate booklets were exposed to each of 15 light integrals, ranging from 15 min 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) = $-2.22 + (0.63 \times$ 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-m² 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 ≤ 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 two-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 1. 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).

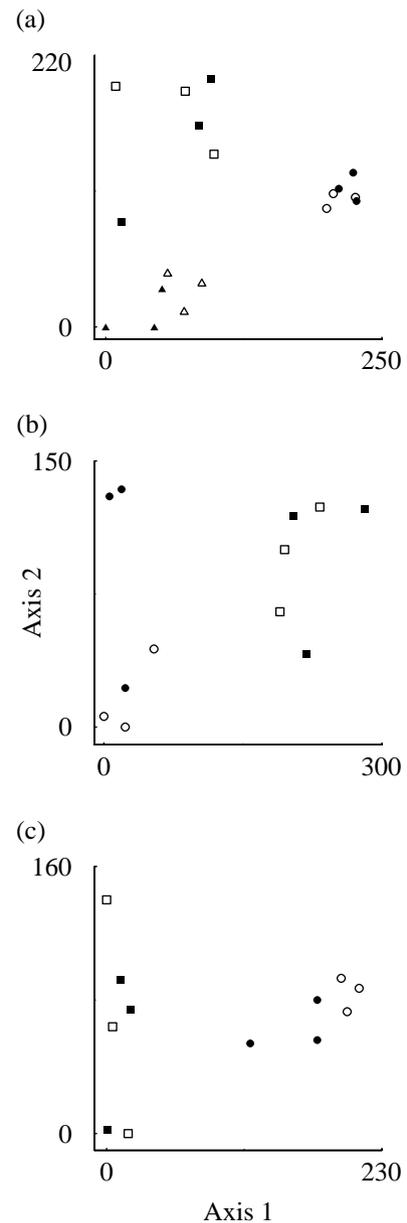The seed rain at Rangitawa Bush and Denton's Bush consisted of mostly bird-dispersed native species

Fig. 1. DCA ordination diagrams of plots based on (a) extant vegetation excluding ground cover; (b) seed rain; (c) seed bank data. Squares = Rangitawa Bush; circles = Denton's Bush; triangles = Kirkwell Bush; open symbols represent non-*Tradescantia* plots; 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; (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; 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; $A < 0$ 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 m²)	0·48	0·06
Seed rain	R, D	NT (6); T (6)	Plot (400 m²)	0·22	0·16
Seed bank	R, D	NT (6); T (6)	Plot (400 m²)	−0·07	0·84

Table 2. Seed rain and seed bank of *Tradescantia* (T) and non-*Tradescantia* (NT) plots at two sites (number. of seeds summed across nine 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; 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

(Table 2), and a majority of species were 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 differed 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 *Melicytus 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)].

RESPONSE OF *TRADESCANTIA* TO LIGHT

Tradescantia biomass increased 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 reached its maximum, 819 g m^{-2}, at about 10% full light at the wetter Denton's Bush, and 695 g m^{-2} at about 15% full light at the drier Kirkwell Bush. Forest interior light levels explained 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).
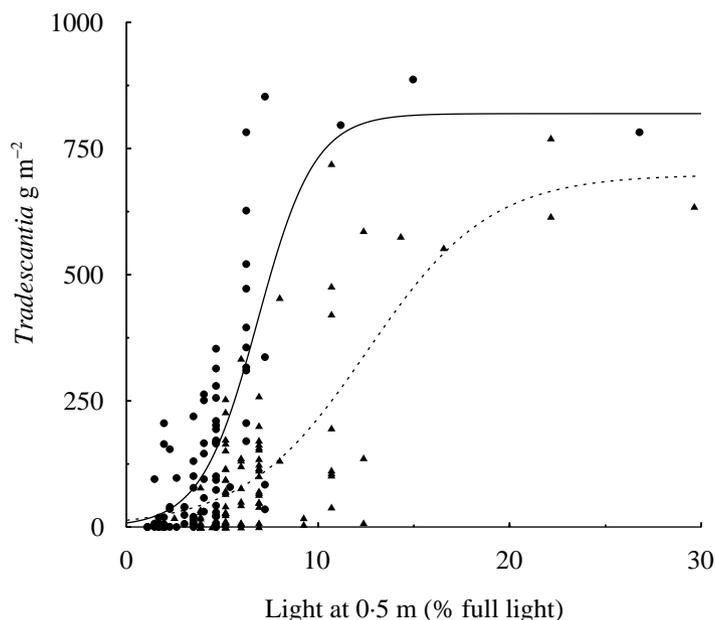
Fig. 2. The relationship of *Tradescantia* biomass to above-ground light levels at Denton's Bush (circles) and Kirkwell Bush (triangles), $n = 91$ and 94, respectively. Data fitted with a logistic regression: $y = ABe^{(Cx)}/A - B + Be^{(Cx)}$; where $y = $ *Tradescantia* biomass (gm^{-2}), $x = $ light at 0·5 m (% 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).

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. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$

Site	Dependent variable	% var. exp. plot	% var. exp. *Tradescantia*	Slope ± SE	Prediction at $x = 0$ g m^{-2}	Prediction at $x = 250$ g m^{-2}	Prediction at $x = 500$ g m^{-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	1·60	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	3·40	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	3·30	1·71

IMPACT OF *TRADESCANTIA* AT THE FOREST FLOOR

An increase in *Tradescantia* biomass was associated with a rapid decrease in light availability at ground level (Fig. 3a). Under approximately 500 g m^{-2} of *Tradescantia* (which roughly equates to 100% weed cover at these sites), light levels were 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 decreased rapidly with increasing *Tradescantia* biomass and decreasing light at ground level (Fig. 3 and 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 3). 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 reflected 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
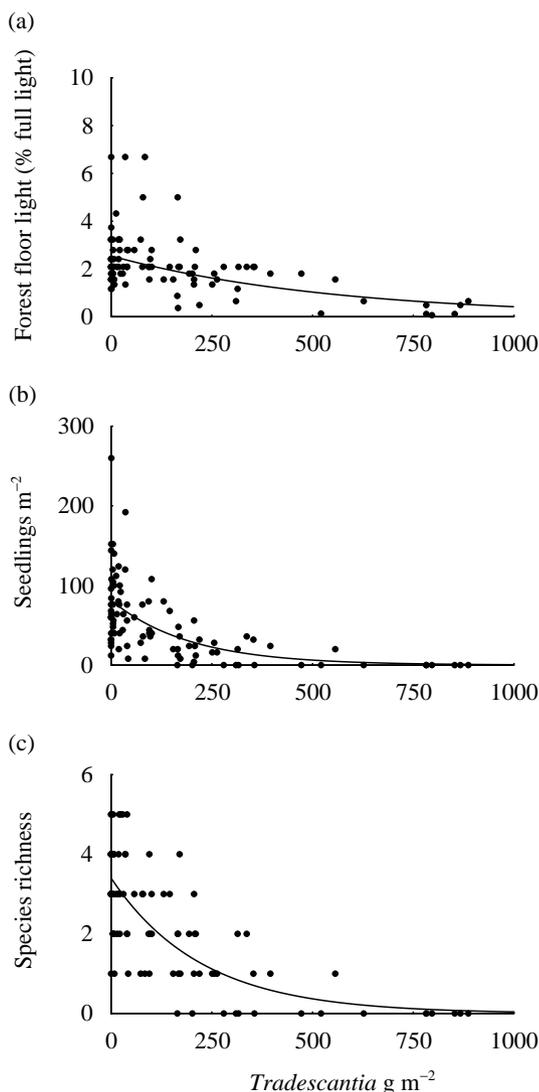
(a)

(b)

(c)

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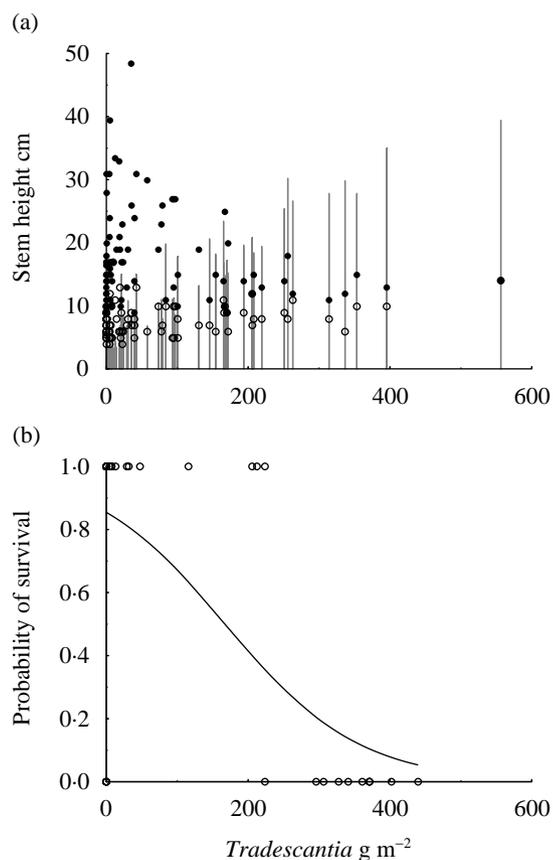

(a)

(b)

Fig. 4. (a) Minimum (open circles) and maximum (filled circles) height of *Dysoxylum 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 *Dysoxylum spectabile* seedlings at Denton's Bush, 2 August 1998 to 31 March 2000 (*n* = 35), $y = e^{(1.77-0.011x)}/(1 + e^{(1.77-0.011x)})$.

species declined with increasing *Tradescantia* biomass, the grade of response varied, e.g. the abundance of *Macropiper excelsum* declined sharply with an increase in *Tradescantia* biomass, whereas *Dysoxylum spectabile*

persisted at 100% *Tradescantia* cover (500 g m^{-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 was no relationship between intercept and slope values among species, indicating that species abundance in the absence of *Tradescantia* did not predict

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; *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 *Dysoxylum 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 $x = 0$ g m^{-2}	Prediction at $x = 500$ g m^{-2}	LD50 g m^{-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

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 *Dysoxylum 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 *Macropiper excelsum* (Table 4). Again, this result reflected the high variation in *Tradescantia* biomass among plots.

DYSOXYLUM SPECTABILE EMERGENCE IN *TRADESCANTIA*

At Denton's Bush, maximum *Dysoxylum spectabile* height decreased with increasing *Tradescantia*, while minimum *Dysoxylum spectabile* height did not alter (Fig. 4a). In less than 200 g m^{-2} of *Tradescantia* (70–90% cover), a majority of quadrats contained *Dysoxylum spectabile* seedlings taller than the surrounding *Tradescantia* stems. On the other hand, in greater than 200 g m^{-2} of *Tradescantia*, the tallest *Dysoxylum spectabile* were smaller than the surrounding stems of *Tradescantia* (Fig. 4a). The survival of tagged seedlings in *Tradescantia* above 200 g m^{-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 *Dysoxylum spectabile* seedling survival. The probability of survival dropped from 84% at 0 g m^{-2} to 39% at 200 g m^{-2} and 7% at 400 g m^{-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 g m^{-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. *Melicytus 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, *Alectryon 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 characterize 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 native plant community. We predict *Macropiper excelsum*, the only shrub among the group that 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 *Dysoxylum spectabile* and less *Macropiper 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 *Alectryon excelsus* and *Macropiper 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, although 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: *Dysoxylum spectabile* (288 mg; this study) > *Hedycarya arborea* (171 mg; Wardle 1991) > *Alectryon excelsus* (165 mg; Williams & Karl 1996) ≫ *Laurelia novae-zelandiae* (12 mg; Wardle 1991) > *Macropiper excelsum* (2·4 mg; this study) > *Melicytus ramiflorus* (0·7 mg; Wardle 1991). *Dysoxylum spectabile* is the most tolerant of *Tradescantia* and has the heaviest seed, and *Macropiper 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 *Dysoxylum spectabile* will germinate and continue to grow in the dark for at least 18 weeks (Court & Mitchell 1988). Clearly, this attribute enables *Dysoxylum spectabile* to germinate and persist, at least initially, in dense *Tradescantia*, although *Dysoxylum spectabile* seedling survival suggests that seedling emergence only occurs

in sparse (< 200 g m^{-2}) *Tradescantia*. *Hedycarya 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). *Laurelia novae-zelandiae* is also truly shade-tolerant (Wardle 1991). *Melicytus 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*. *Macropiper 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 (R. Standish, unpublished data). We do not know whether *Tradescantia* sequesters these nutrients at a cost to native seedlings, but the high fertility of these sites (R. Standish, unpublished data) 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 *Macropiper excelsum* abundance is reduced in *Tradescantia*-affected relative to non-affected areas. *Tradescantia* has been established at these sites for *c.* 12 and *c.* 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 1 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 colonizers; Ogden 1985), whereas late successional trees are poorly represented. These trends characterize 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. 1·3–5% 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 1984; this study). Research into the practicality of this restoration tool is ongoing.

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