

Resistance and resilience of New Zealand tree species to browsing

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Summary

1. A prominent idea in the literature on plant–herbivore interactions is that fast-growing species have low resistance but high resilience to herbivory. In other words, fast-growing species are selectively eaten by herbivores but recover quickly following damage. Many studies have challenged the generality of this theory, but little attention has been paid to plant species that have evolved in the absence of major groups of herbivores. Here we analyse whether this resistance-resilience trade-off applies to New Zealand woody species, which evolved without exposure to mammalian herbivores until their introduction in 19th century.

2. We simulated deer browse by clipping saplings of 12 tree species to varying extents (0, 20, 40, 80 and 100% of leaf-bearing branches removed), and quantified the shoot growth, diameter growth and survival of these saplings. The time taken to regrow the removed branches was generally slow, but varied among species. For example, species took between 0.5 and 3 years to recover from removal of 60% of branches. It was the inherently fast-growing species that recovered most quickly. Some species had stimulated shoot growth at moderate levels of clipping (40–60%) but this effect had relatively little effect on recovery time compared with differences in potential growth rates of species.

3. Diameter growth rate fell linearly with increased clipping intensity for all 12 species, and there was no indication of recovery 2 years after the treatment. We speculate that saplings invested in rebuilding their canopies following clipping, and that few resources were left over for diameter growth.

4. Few saplings died as a result of clipping, except when 100% of leaf-bearing shoots were removed, in which case five species died in substantial numbers (> 15%), including all three conifers in the study.

5. Previous work has shown that the most palatable species (i.e. those with low resistance) have leaves with low fibre content. We find that these species are relatively fast growing and recover most rapidly from simulated browsing (i.e. are highly resilient). This provides some support for a resistance-resilience trade-off related to potential growth rates.

6. Deer invasion in New Zealand was associated with the loss of short soft-leaved tree species from the browse layer. Our study suggests that the most palatable species have the potential to grow fast and may be in a relatively strong position to recover if deer are eradicated.

Key-words: herbivory, invasive species, plant growth, plant–herbivore interactions, red deer, simulated browsing

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Introduction

A central theory of plant–herbivore interactions is that inherently slow-growing species are highly resistant to herbivory (Bryant *et al.* 1983; Coley *et al.* 1985; Herms & Mattson 1992; Fineblum & Rausher 1995). The basis for this theory is that investment in defence constrains plants to slower growth rates as a finite pool of assimilate must be shared between these two demands, or, alternatively, that slow-growing plants have a greater incentive for investment in defence as their tissues are typically long lived and costly to replace (Coley *et al.* 1985). A second theory is that slow growth rate is associated with weak capacity to recover after damage, perhaps through an inability to increase photosynthetic rates or reduced investment in storage organs (Maschinski & Whitham 1989; Herms & Mattson 1992), and consequently that there is a trade-off between resistance and resilience. The strategy favoured depends on the ecological circumstances of the plant; high resource availability, strong competition and low or infrequent herbivore pressure generally favouring resilience over resistance (Herms & Mattson 1992; Grime 2001). However, the validity of these simple assumed relationships has been questioned (Rosenthal & Kotanen 1994; Mauricio *et al.* 1997; Almeida-Cortez *et al.* 1999; Strauss & Agrawal 1999; de Jong & van der Meijden 2000; Hawkes & Sullivan 2001; Stamp 2003). For example, resistance may not trade off against growth rate when the nutrients required for construction of defensive compounds are not the factors limiting growth (Mole 1994). Also resilience might come at the expense of growth rate, rather than being positively associated with growth rate, if resources must be diverted to storage organs that fuel re-growth (Chapin *et al.* 1990; Bond & Midgley 2001). Thus, empirical investigations are required to clarify whether growth, resistance and resilience are correlated in communities that lacked large mammalian herbivores.

A resistance-resilience trade-off could have important implications for the responses of plants to invasive herbivores. The composition and structure of plant communities on remote islands have been transformed by mammalian herbivores that were introduced by sailors and by early European settlers (Thomson 1922; Cooper & Millener 1993), and it is well known that plant species differ in the extent to which they are preferred by mammalian invaders. For example, some New Zealand plants are heavily browsed by introduced deer whereas many others are avoided (e.g. Forsyth *et al.* 2002), perhaps as a result of pre-existing adaptations to infertile soils, native herbivores and pathogens (e.g. McGlone & Clarkson 1993; Grime *et al.* 1996; Hoffland *et al.* 1996). What is less well understood is whether New Zealand woody species also recover at different rates from mammalian herbivore damage, and whether the recovery rates are correlated with palatability (i.e. whether there is a resistance-resilience trade-off).

Here, we present a simulated browsing experiment on saplings of 12 common native New Zealand tree and tall shrub species growing *in situ* in field conditions. The study aims to explore the resilience of these species to damage by introduced deer. The specific aims of the study were to test the following hypotheses: (a) that fast-growing species are most resilient to browsing damage; (b) that fast-growing species are least resistant to browsing; and (c) that there is a trade-off in resistance and resilience among species (see Table 1). Our work builds on a study of red deer feeding preferences by Forsyth *et al.* (2005), which was based on a comparison of the abundance of plants in the guts of deer shot in a lowland rain forest with the availability of those plants in the browse layer. The study by Forsyth *et al.* (2005) provides us with measures of resistance to deer browsing which we compare with our measurements of sapling potential growth rates and resilience to test hypotheses (b) and (c).

Table 1 Hypothesized relationships between potential growth rate, resistance and resilience of woody plants to simulated browsing. The hypotheses were tested by measuring the responses of 12 New Zealand tree species to simulated browsing, in terms of shoot and diameter growth, and correlating these responses with growth and resistance measurements. The potential growth rate of a species is defined as the growth rate of unclipped saplings that are growing in well-lit conditions

| Hypotheses | How the hypotheses are tested |
|---|--|
| Fast-growing species are most resilient to deer browse damage | (a) The average times taken for species to recover the branches/leaves removed in the clipping treatment are calculated. These recovery times are correlated with potential shoot growth rates. (b) Diameter growth rates of clipped saplings are correlated with potential diameter growth rates. (c) Percentage mortality of species when severely clipped is negatively correlated with potential growth rates. |
| Slow-growing species are most resistant to deer browse damage | Resistance to damage has been quantified for each species using the Ivlev's electivity index (I), which compares plant frequency in animal gut with frequency in the browse layer (Forsyth <i>et al.</i> 2005). Potential growth rates are correlated with $-I$. |
| Resistance trades off against resilience | Shoot recovery times are correlated with Ivlev's electivity indices. |

Methods

BACKGROUND INFORMATION ON DEER INVASION

Red deer (*Cervus elaphus scoticus*) were introduced into New Zealand from the UK in the mid 18th century, and now occupy much of the 6.5 million ha of indigenous forest (Fraser *et al.* 2000). Density increased rapidly in the two to three decades following colonization of a new area (Challies 1990) and the deer-preferred species of plant were quickly eliminated from accessible sites (e.g. Mark & Baylis 1975). When given the choice, deer feed on short-tree species in New Zealand that are associated with forest margins, disturbed sites and nutrient-rich gulleys: 17 of the 23 most preferred species fit into this category (Nugent *et al.* 2001). Deer populations remained at peak density for approximately 5–10 years, but during this phase the population sizes of animals declined, apparently due to a reduced availability of food, with animals feeding on species not previously eaten (Challies 1990). The national deer population is currently about 10% of its peak in the 1950s, thanks partly to intensive hunting for recreational, commercial and conservation purposes (Nugent & Fraser 1993). However, there are concerns that forests are not recovering following this reduction in browsing pressure (Coomes *et al.* 2003; Coomes *et al.* 2006) and that deer numbers are on the increase once again.

SIMULATED BROWSING EXPERIMENT

The study species comprised three evergreen conifers, eight evergreen woody dicots and one deciduous woody dicot (Table 2), selected because they are common components of South Island lowland rain forests and were known to vary in palatability to introduced herbivores (Forsyth *et al.* 2002). All plants were growing in regenerating mixed beech/conifer forest that was

selectively logged in the early 1980s, in the Rowallan Forest, Southland, New Zealand (2082975 E, 5437950 N). This area was chosen because deer numbers are very low, owing to intensive recreational hunting, and as a result the site provided undamaged specimens of the highly palatable species. We do not have information on the soils, but similar forests situated about 20 km to the West were found to be underlain by highly P-deficient soils (Coomes *et al.* 2005).

Saplings between 15 and 300 cm tall, corresponding to the height of the browse tier, were eligible to be included in the study. Eight to 10 saplings of each species were assigned to each of six clipping treatments, giving 48–60 samples per species. Clipping treatments were imposed in January, February and March of 2002, by using secateurs to remove fixed percentages of leaves and their associated branches from each plant (0, 20%, 40%, 60%, 80% or 100%), using a tape measure to estimate lengths and to select where to clip. For example, when 100% of leaves were removed, the branches were cut just below the nodes of the oldest leaves on the branches, and when 40% of leaves were removed, that amount was clipped off each first order lateral branch and the apical branch of the plant. These treatments are severe in comparison to those used in many previous studies of simulated ungulate browsing, which have removed varying fractions of only the current year's growth (e.g. Campa *et al.* 1992; Canham *et al.* 1994), but were thought appropriate as such levels of consumption are commonly observed on deer-palatable species in New Zealand forests (J. N. Bee, unpublished data). Branch length was removed as fixed percentages rather than absolute amounts in order to keep the relative intensity of clipping invariant with plant size. Other studies have tried to accurately reproduce deer browse by, for instance, using deer jaws to cut the branches and applying saliva to the cuts: the simplicity of our browsing treatment was necessitated by the large-scale cross-species comparisons that we were making (cf. Baldwin 1990).

Table 2 Diameter and shoot growth of unclipped plants and mortality of all plants of 12 woody plant species (C = conifer)

| Species | Acronym | Type | Diameter growth (mm year ⁻¹) | Shoot growth (%) | Mortality (%) |
|-----------------------------------|---------|------------|--|------------------|---------------|
| <i>Fuchsia excorticata</i> | Fuext | Small tree | 3.64 | 100 | 4 |
| <i>Nothofagus solandri</i> * | Notcli | Tall tree | 1.40 | – | 6 |
| <i>Griselinia littoralis</i> | Grilit | Small tree | 1.27 | 28 | 2 |
| <i>Nothofagus menziesii</i> | Notmen | Tall tree | 1.23 | 44 | 0 |
| <i>Raukawa simplex</i> | Psesim | Small tree | 1.20 | 40 | 20 |
| <i>Weinmannia racemosa</i> | Weirac | Tall tree | 1.17 | 33 | 0 |
| <i>Coprosma foetidissima</i> | Copfoe | Tall shrub | 0.98 | 38 | 19 |
| <i>Dacrydium cupressinum</i> (C) | Daccup | Tall tree | 0.97 | – | 6 |
| <i>Podocarpus hallii</i> (C) | Podhal | Tall tree | 0.85 | 23 | 15 |
| <i>Metrosideros umbellata</i> | Metumb | Tall tree | 0.71 | 29 | 15 |
| <i>Pseudowintera colourata</i> | Psecol | Small tree | 0.51 | 15 | 0 |
| <i>Prumnopitys ferruginea</i> (C) | Prufer | Tall tree | 0.47 | 8 | 20 |
| Mean (± SE) | | | 1.20 ± 0.24 | 36 ± 8 | 8.9 ± 2.4 |

*var. *cliffortioides*.

Names from the Allan Herbarium (2000).

Saplings were selected from a wide range of light environments as limited sapling availability prevented us from selecting within a narrow range of light environments. Light levels were quantified from HEMI-PHOT images taken using a digital camera (Nikon Cool-Pix, 1.3 Megapixel resolution) immediately above the top of each sapling and analysed using GLA software (Frazer *et al.* 1999). Light intensities are reported as the percentage of above-canopy direct plus diffused light that reaches each sapling.

At the time of clipping, the two orthogonal measurements of trunk diameter were taken for each plant, at 10 cm from the ground, using callipers (resolution ± 0.05 mm) and measurement points were marked with white paint. Repeat measurements were made after 12 and 24 months, and annual growth increment was calculated by subtraction of the previous year's measurement. New shoot production was assessed 1 year after clipping for 10 of the 12 species in which that year's new growth could be clearly distinguished from old growth by its pale colouration and softer tissue. The large size of most saplings made it impractical to score each whole plant for new growth, so four primary branches were subsampled at random from each plant. For the small-leaved species with numerous leaves, the total length of new shoots was measured on each subsampled branch, and shoot growth was calculated as a percentage of the original length of leaf-bearing branches (i.e. distances of stems from the oldest leaves to the apices). For the larger-leaved species, the number of new leaves was counted and growth was calculated as a percentage of original leaf number. No measurements of shoot growth were made on the two species for which we could not distinguish new growth from old at the time of resampling.

Mortality was recorded 1 and 2 years after clipping. Saplings with dried, brittle stems and no obvious living tissue were classified as dead.

STATISTICAL ANALYSIS OF SIMULATED BROWSING EXPERIMENT

Stem diameter growth was modelled separately for each species using a Michaelis–Menten function of light (Pacala *et al.* 1994; Finzi & Canham 2000):

$$G = \frac{a}{1 + b/L} + \epsilon \quad \text{eqn 1}$$

where G is annual diameter growth increment averaged over the 2 years of the study (mm year^{-1}), L is light intensity (estimated by hemispherical photography), and a and b are coefficients estimated by regression: a is the light-saturated growth rate and b the light intensity at which half of the light-saturated growth rate is reached, and ϵ is the residual error. This model was fitted for each species using the *gnlr* routine in R version 2.1.0 (R Foundation 2005), using Gaussian errors to model ϵ . We excluded from the analyses nine outliers that we strongly suspected to have resulted from recording errors (1.5% of samples).

Next, six alternative models based on eqn 1 were then fitted for each species by the same methods. These models ask whether sapling growth depends on initial plant size and on the intensity of clipping by examining whether the light-saturated growth rate a in eqn 1 varies with these variables (Table 3). We then selected the 'best' model from this set by comparing their Akaike information criteria for small samples (AICc), which was calculated for each model as:

Table 3 Comparison of the statistical support for six candidate models describing the effects of clipping, light availability and plant size on stem diameter growth (mm year^{-1}) and shoot growth (% year) of New Zealand tree species. Model 1 predicts that growth (G) is unaffected by light, clipping or plant size. Model 2 predicts that saplings respond non-linearly to light (see text for details), and models 3–6 are modifications of this basic function to accommodate the effects of clipping (C , %) and initial sapling diameter (D , mm). The lower case letters in the functions represent coefficients that were estimated by maximum likelihood methods. The statistical support for each model is given by its AICc values (summed across species): the model with the lowest AICc is most strongly supported, and is shown in bold

| Description | Function | Explanation | AICc Diameter | AICc Shoot | Model ID |
|---------------------------|---------------------------|---|------------------|---------------|-------------|
| Null model | $G = c$ | Growth independent of light, size and clipping | 1149.3 | 4810.9 | 1 |
| Basic model | $G = \frac{a * L}{L + b}$ | Growth is a Michaelis-Menten function of light (L). a = light-saturated growth rate, b = half light-saturated growth rate | 1071.1 | 4789.8 | 2 |
| Plant size effects | $a = aD$ | Light-saturated growth is a linear function of plant size | 1120.8 | 4967.5 | 3 |
| | $a = aD^x$ | Light-saturated growth is a power function of plant size | 1075.7 | 4846.6 | 4 |
| Linear clipping effects | $a = a_0 + a_1C$ | Light-saturated growth rate linearly related to clipping | 896.6 | 4776.5 | 5 |
| Quadratic clipping effect | $a = a + a_1C + a_2C_2$ | Light-saturated growth is a quadratic function of clipping | 914.8 | 4765.3 | 6 |

$$\text{AICc} = -2 \log L + 2K(n/(n - K - 1)) \quad \text{eqn 2}$$

where K is the number of parameters and n the number of samples. Following Burnham & Anderson (2002), we ranked the candidate models from best to worst fitting based on their AICc values (the best fitting model has the smallest AICc value). We calculated a Δ_i value for each model as the difference between the AICc value for each model and the AICc value of the best-fitting model (i.e. the best-fitting model has a Δ_i value of 0). Burnham & Anderson (2002) provide some rules of thumb for assessing the relative merit of models in a candidate set: models with $\Delta_i < 2$ have substantial support, models with $\Delta_i > 10$ have virtually no support, while models with Δ_i values in the range 2–10 have marginal support. The whole percentage of shoot growth (as the percentage of the size of the branches before clipping) was analysed by the same method.

MEASURES OF RESISTANCE AND RESILIENCE

Three different measures of resilience were calculated (Table 1), and compared with measures of resistance to damage by introduced deer. The resistance data were taken from a recent paper that compared the amount of leaves consumed by deer (i.e. appearing in the guts of culled animals) with the amounts available in the browse layer (Forsyth *et al.* 2005). In that study, available forage was assessed by destructive sampling of browse-layer vegetation within 292 plots of 3.14 m² situated at a study site around 20 km to the west of Rowallan Forest, and the food selected by the deer was assessed by examining the types of gut contents of 24 culled animals. These data were used to calculate a modified form of Ivlev's index of electivity (Loehle & Rittenhouse 1982), which is given by $I = (\mu_i - \pi_i)/(\mu_i + \pi_i)$ where i denotes the i th species, μ_i is the proportion of species i in the diet of deer, and π_i is the proportion of species i available to deer. The value of I ranges from -1 (avoided) to $+1$ (highly preferred) and we give $-I$ as our

measure of resistance. Ivlev's index provides an objective measure of resistance, because it is based on comparing gut contents with environmental availability, and this contrasts with traditional approaches that define resistance in terms of traits associated with defence, such as secondary compound content, silicon and thorniness. *Fuchsia excorticata* was missing from that study but present in ours: it is undoubtedly one of the most highly preferred species in New Zealand (Forsyth *et al.* 2002), so was assigned the same value of Ivlev's index as the most selected species in the deer-gut study, which was *Griselinia littoralis*. Correlations between measures of resistance, resilience and maximum growth rate were tested using Spearman's rank correlation test. For all the analyses, statistical significance was assessed at $\alpha = 0.05$.

Results

RESILIENCE IN SHOOT AND DIAMETER GROWTH

Potential growth rate (i.e. the light-saturated growth rate of unclipped saplings estimated from our regression models) varied greatly among species: there was a seven-fold difference in potential diameter growth and a nine-fold difference in potential shoot growth between the fastest and slowest growing species. Potential shoot and diameter growth rates were positively correlated across species ($\rho = 0.56$, $P < 0.0001$). Shoot and diameter growth were nonlinearly related to light intensity (Fig. 1, model 2 vs. model 1 in Table 3). In contrast, neither shoot nor diameter growth was related to plant size (models 3 and 4 vs. model 2 in Table 3), perhaps because the range of sizes was limited.

Diameter growth decreased with clipping intensity for all 14 species in the study (Fig. 2). In the cases of the two fastest-growing species, *Fuchsia excorticata* and *Nothofagus menziesii*, the relationship between clipping and growth was curvilinear (the effect of clipping

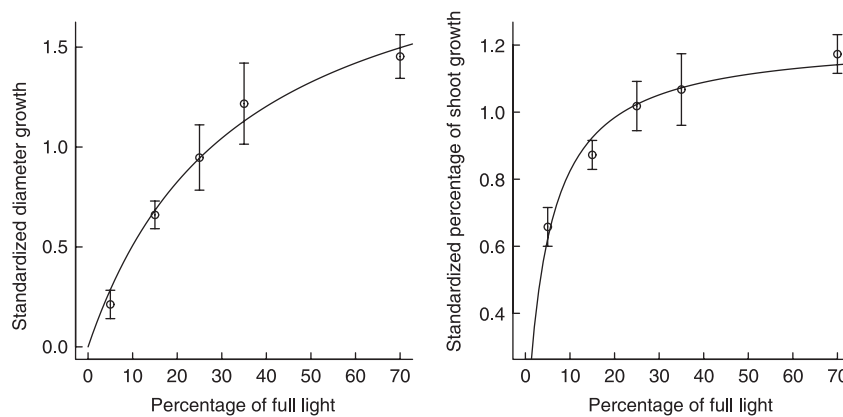


Fig. 1 Light response curves for (a) diameter growth and (b) percentage shoot growth for New Zealand tree species. The growth rate of each sapling was scaled by the average growth rate of the species to give standardized growth rates and the means (\pm SEM) within light-intensity bins are shown, and Michaelis–Menten functions were fitted to data (model 2).

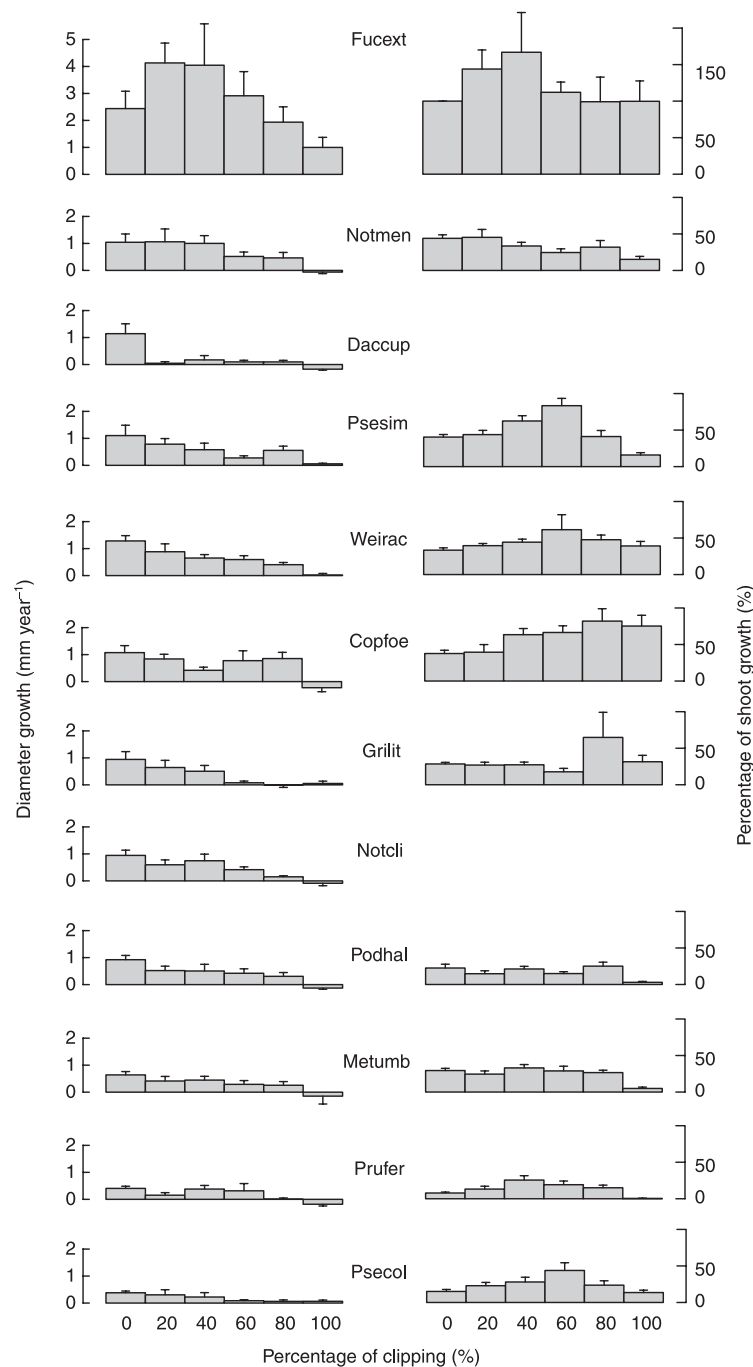


Fig. 2 Mean diameter and shoot growth (± 1 SEM) of saplings of 12 tree species from New Zealand (for acronyms see Table 2), in response to clipping of leaf-bearing branches (0–100% removed).

was modelled with a quadratic function; Table 4). These species would appear to have recovered from relatively minor damage because growth rates in the 20% and 40% clipping treatments are similar to, or exceed, the growth rates of the control plants. However, neither of these species had recovered from the 80 and 100% clipping treatments. In the cases of the other 12 species, there was a linear decrease in growth with clipping (Table 2). Therefore, none of these species showed any signs of recovering from simulated browsing. The growth rates in the 100% clipping treatment were similarly low for all species (Fig. 3a, Table 2).

Species differed in their shoot-production response to clipping (Fig. 2b). Four species showed no response to clipping, one showed a linear decrease in growth with clipping, one showed a linear increase with clipping, and two species had quadratic response curves with peaks occurring in the mid-ranges of clipping intensity (Table 4, Fig. 3b). Thus, clipping stimulated the shoot growth of three species, but the majority of species were unaffected. Species that were fast growing when unclipped also tended to be fast growing when clipped: for example, there was a close correlation between the shoot growth rates at 0% and 40% ($\rho = 0.855$,

Table 4 Statistical tests of whether the growth of 12 species of New Zealand tree is unrelated to clipping intensity (Model 2), decreases or increases linearly with clipping intensity (Model 5) or is curvilinearly related to clipping intensity (Model 6). These candidate models were fitted to stem diameter growth (mm year^{-1}) and shoot growth (% year) data using maximum likelihood methods, and Akaike Information Criteria (AICc) values were calculated in order to compare the models (see Table 3 for further details). Within each row the model with the lowest AICc value is the most strongly supported statistically, and is shown in bold. N is the number of saplings sampled

| Species | <i>n</i> | Model 2 | Model 5 | Model 6 |
|------------------------|----------|---------------|---------------|---------------|
| Diameter growth | | | | |
| Copfoe | 55 | 107.67 | 101.19 | 103.32 |
| Daccup | 48 | 60.27 | 52.07 | 60.9 |
| Fuext | 39 | 169.6 | 165.18 | 164.28 |
| Grilit | 39 | 75.99 | 47.84 | 49.85 |
| Metumb | 48 | 57.79 | 55.05 | 57.22 |
| Notcli | 51 | 73.14 | 68.88 | 70.99 |
| Notmen | 50 | 125.69 | 123.99 | 123.76 |
| Podhal | 54 | 68.17 | 58.98 | 59.66 |
| Prufer | 54 | 33.19 | 32.63 | 34.3 |
| Psecol | 51 | 31.82 | 31.11 | 33.31 |
| Psesim | 47 | 60.75 | 47.07 | 49.42 |
| Weirac | 52 | 92.07 | 78.4 | 80.21 |
| Shoot growth | | | | |
| Copfoe | 51 | 513.43 | 503.3 | 505.66 |
| Fuext | 46 | 536.79 | 539.09 | 541.49 |
| Grilit | 48 | 496.84 | 497.59 | 499.97 |
| Metumb | 50 | 400.36 | 395.93 | 391.61 |
| Notmen | 56 | 504.25 | 495.5 | 497.83 |
| Podhal | 57 | 461.42 | 461.05 | 463.36 |
| Prufer | 53 | 432.42 | 433.35 | 426.68 |
| Psecol | 53 | 465.35 | 467.59 | 469.65 |
| Psesim | 50 | 479.88 | 482.17 | 482.65 |
| Weirac | 53 | 499.93 | 502.16 | 503.61 |

$P = 0.0031$). The time required for saplings to recover their former canopy size following clipping (in years) is approximately $(\% \text{ clipping})/(\% \text{ shoot growth})$. Recovery times varied greatly: *Fuchsia excorticata* is predicted to

take half a year to recover its original canopy size after 60% clipping, while *Prumnopitys ferruginea* is predicted to take more than 3 years to recover. The differences are even greater at 100% clipping, where the recovery time of *Prumnopitys ferruginea* is predicted to be more than 200 years, in comparison with 1 year for *Fuchsia excorticata*.

RESILIENCE AND MORTALITY RATES

Of the total of 609 saplings in the study, three died in the first year after clipping, and a further 48 died by the end of the second year. Mortality was unevenly spread across species (Table 1; $\chi^2 = 33.9$, d.f. = 11, $P = 0.0004$), and was high among the three conifer species. Mortality was largely restricted to the highest levels of clipping, with 86% of total mortality occurring within the 100% clipping class ($\chi^2 = 118.3$, d.f. = 5, $P < 0.0001$).

LINKS BETWEEN RESISTANCE, RESILIENCE AND POTENTIAL GROWTH RATES

The hypothesis that slow-growing species are better defended against herbivory was partially supported: we found that resistance to deer damage, $-I$, was significantly correlated with potential diameter growth rate (Fig. 4a; $\rho = -0.75$, $P = 0.0046$), but was not significantly correlated with potential shoot growth (Fig. 4b; $\rho = -0.55$, $P = 0.10$).

The hypothesis that fast-growing species would recover quickly from simulated browsing was supported for shoot growth but not for diameter growth. In the case of shoot growth, there was a negative correlation between potential growth rate and recovery time for all clipping intensities (the correlations at 40% and 100% clipping are shown in Fig. 4d,f). However, there was no correlation between potential diameter growth rate

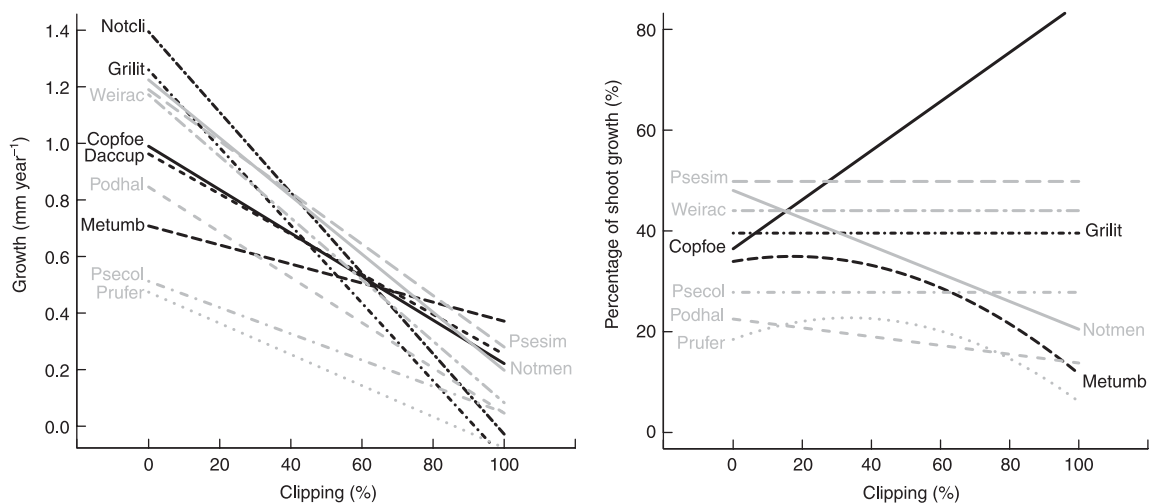


Fig. 3 Clipping response curves for (a) 12 tree species (for acronyms see Table 2) estimated from the best-fit radial growth model (model 5, Table 4) for the average light (25%), (b) 10 tree species from the best-fit percentage of shoot growth model (either model 7 represented as a quadratic line, model 5 represented as linear curve or model 2 represented by an horizontal line, Table 4). *Fuchsia excorticata* radial growth was too high to be represented on this figure; its slope for the clipping effect is -0.0063 mm per percentage clipped.

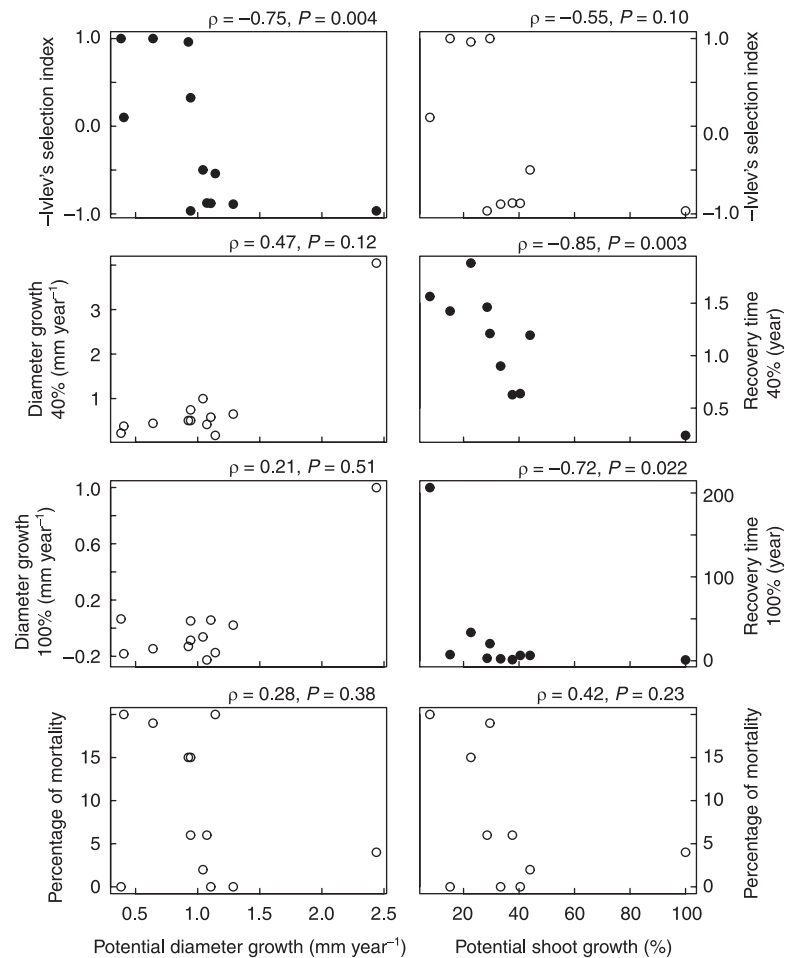


Fig. 4 Interspecific correlations between potential growth rate of saplings (diameter growth in first column and shoot growth in second column) and -Ivlev's index of palatability and shoot growth when 40% and 100% clipped and mortality (%) for woody species from New Zealand. Potential growth is the light-saturated growth rate of unclipped plants. Spearman's rank correlation coefficients, ρ , and statistical significances are provided (correlation with $P < 0.05$ indicated by filled circles).

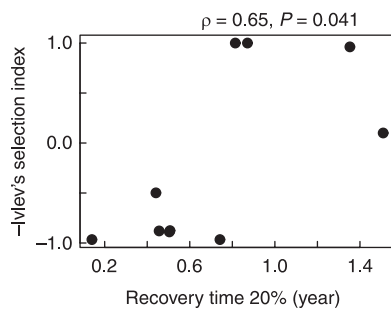


Fig. 5 Correlations between recovery time when 40% clipped with Ivlev's index of 10 New Zealand tree species. Spearman's rank correlation coefficients, ρ , and statistical significances are provided (correlation with $P < 0.05$ indicated by filled circles).

and diameter growth rates under the clipping treatments (the correlations at 40% and 100% clipping are shown in Fig. 4c,e). The diameter growth of all species was much less than that of the unclipped control plants, except in the case of *Fuchsia*. Therefore, the hypothesis that fast-growing species would recover their former diameter increments more rapidly than slower-growing species was rejected. The hypothesis that fast-growing species would have low mortality under severe clipping

treatments was also rejected: there was no correlations between potential growth and mortality, for either shoot or diameter growth (Fig. 4g,h).

Finally, the hypothesis that there is a trade-off between resistance and resilience was weakly supported. We found a significant correlation between recovery time following 20% clipping and Ivlev's electivity index (Fig. 5; $\rho = 0.65$, $P = 0.04$). However, correlations between $-I$ and recovery time were not statistically significant for any other clipping intensity; the P -values of the rank correlations ranged from 0.07 to 0.16.

Discussion

RESILIENCE IN SHOOT AND DIAMETER GROWTH

New Zealand plants responded to simulated deer browse by resprouting from dormant buds and mobilizing stored reserves to create new shoots; these are inherent responses to disturbance that allow plants to recover from damage by fire, wind storms and so forth (Bellingham & Sparrow 2000; Bond & Midgley 2001), and coincidentally allow them to recover from damage

caused by herbivores with which they did not co-evolve. Although all of the study species resprouted, many of them recovered only slowly: diameter growth showed little indication of returning to pre-clipping levels even after 2 years, and the mean shoot recovery time for 60% clipped plants was almost 2 years. A slow rate of recovery was even more apparent in the diameter growth data: the growth increments of clipped plants were very much less than those of unclipped plants (except in the case of *Fuchsia*) in the 2 years after clipping. These low growth rates probably result from the slow recovery of shoots. If 60% of leaves were removed by clipping then photosynthetic capacity is reduced by 60% (or more, as only the older leaves remained). Thus, by the end of the second year some of the leaves had been replaced, but recovery in canopy area was slow and so photosynthetic capacity was still less than pre-clipping. In addition, it may be that saplings reallocated resources away from diameter growth and into shoot production following clipping, because recovering leaf area takes precedence over diameter growth. These results suggest that browsing may substantially reduce diameter growth for several years. Slow recovery was also found in another experimental study of resilience to deer browse of a New Zealand species, which reported that the effects of defoliation were evident 20 years after browsing in the alpine tussock grass *Chionochloa pallens* (Lee *et al.* 2000). Studies of the effects of culling possums (*Trichosurus vulpecula*), an arboreal marsupial introduced from Australia, have shown that vegetation recovery is sometimes slow. Intensive possum control halted the loss of foliage from eight tree species in a North Island study but did not result in recovery of the affected trees (Payton *et al.* 1997), while recent studies report that relatively fast-growing species (*Dysoxylum spectabile* and *Fuchsia excorticata*) sometimes recover rapidly from defoliation by possum (Pekelharing *et al.* 1998; Nugent *et al.* 2002).

Why was recovery slow in our study? It may simply be that the New Zealand tree species used in the study

had low potential growth rates compared with trees in other forests, and consequently take a long time to regain biomass lost through defoliation (Wardle 1991; McGlone *et al.* 2004). A review of recent sapling growth papers shows that the mean light-saturated radial growth rate of saplings in this study was almost half that reported in any of nine recent studies around the world (Table 5). Slow growth may be the result of nutrient-poor soils. Detailed chemical analyses of soils within the 20 km of our study reveal that the region has lower concentrations of soil nutrients than are found in equivalent areas in the northern hemisphere (Coomes *et al.* 2005). More generally, New Zealand soils are thought to be relatively nutrient poor (McGlone *et al.* 2004): the primary rocks are low in P and Ca (McLaren & Cameron 1996), loess soils contain little calcium and are difficult for roots to penetrate, and many soils are severely leached as a result of high rainfall (McGlone *et al.* 2004; Richardson *et al.* 2004; Wardle *et al.* 2004).

There are other possible explanations for the generally slow recovery of New Zealand trees. First, clipping may have removed a large proportion of the nutrient capital of the saplings. Recent research in the same field site shows that young leaves contain roughly 30% more N and 50% more P than second and third year leaves on the same branch, presumably because saplings reallocate nutrients in order to maximize carbon assimilation (Gaxiola *et al.*, in press). Because our clipping treatments removed the younger leaves and retained the older ones, the effect on whole-plant photosynthesis and nutrient status may be greater than the proportion clipped. Clipping also reduces the whole-plant demand for water and thereby reduces the need for sapwood production, so reduced diameter growth may have been a plastic response. Secondly, because the flora is predominantly evergreen it might perhaps be that trees do not store starch in winter to the same extent as deciduous species in northern temperate forests, so do not have sufficient stores of resources to rebound rapidly after damage; this speculation requires further

Table 5 Asymptotic diameter growth (mm year⁻¹) of 12 species from New Zealand with data collected using comparable methods in nine other locations. When other studies found significant size effects, we calculated diameter growth of 2-cm diameter stems, which are comparable in size with those in our study. The number of species in the study is given, and the mean, minimum and maximum growth rates of these species

| Location | Mean | Minimum | Maximum | <i>n</i> | References |
|---------------------------|------|---------|---------|----------|-------------------------------|
| South-western New Zealand | 1.2 | 0.5 | 3.6 | 12 | This study |
| Texas, USA | 2.5 | 1.1 | 4.4 | 7 | Lin <i>et al.</i> (2001) |
| British Columbia, Canada* | 2.8 | 0.7 | 15.1 | 26 | Wright <i>et al.</i> (2000) |
| France | 3.1 | 2.6 | 3.6 | 2 | Kunstler <i>et al.</i> (2005) |
| Southern China | 4.0 | 3.5 | 4.5 | 3 | Cao (2001) |
| Panama | 4.6 | 0.4 | 27.3 | 60 | Uriarte <i>et al.</i> (2004) |
| South-western Canada | 7.4 | 3.0 | 10.0 | 6 | Claveau <i>et al.</i> (2002) |
| North-eastern USA | 7.6 | 3.8 | 13.6 | 6 | Finzi & Canham (2000) |
| Himalayas (Bhutan) | 7.7 | 4.7 | 20.1 | 6 | Gratzer <i>et al.</i> (2004) |
| North-eastern USA | 7.9 | 5.0 | 10.6 | 10 | Pacala <i>et al.</i> (1994) |

*Summary statistics include measurements taken on the same species in various vegetation zones.

investigation. Thirdly, under natural disturbance regimes there might have been little incentive for plants to store up provisions in order to resprout strongly after disturbance (Bond & Midgley 2001), because natural disturbance events such as volcanic activity, windstorms, flooding, snow damage and earthquake-induced landslips occurred too infrequently and unpredictably for such investments to be beneficial (Grant 1963; Ogden & Stewart 1995; Wells *et al.* 2001). Finally, the avian herbivores with which New Zealand plants co-evolved had different feeding strategies to deer (Bond *et al.* 2004) so plants may have developed traits necessary to defend themselves against birds but not against mammalian herbivores. In particular, moas probably pecked off individual leaves rather than chewing off whole branches, and species with tiny leaves on divaricating branches may have been less susceptible to herbivory (Bond *et al.* 2004). However, the influence of avian herbivores on native species evolution is still a matter of much debate (Atkinson & Greenwood 1989; McGlone & Clarkson 1993), all focused on resistance rather than resilience.

RESILIENCE AND MORTALITY RATES

The species in our study were resilient to clipping in the sense that very few died, except when they were totally denuded of leaves. The question of whether such saplings would survive if repeatedly browsed has not been addressed by us, but the disappearance from the browse layer of many woody species (e.g. Wardle 1984) suggests that long-term exposure results in higher rates of mortality. The fact that New Zealand woody plants have the capacity to resprout after browsing damage is not especially surprising because many species of woody plant resprout when branches are snapped off by disturbance events such as windstorms (Bellingham & Sparrow 2000; Bond & Midgley 2001), and in some respects deer browsing is just another type of damage. In other parts of the world, specific adaptations such as storage organs from which to replace lost leaves and the capacity to raise photosynthetic rates following damage, enable species to tolerate low levels of herbivore damage without showing ill effects (Lee & Bazzaz 1980; Campa *et al.* 1992; Hjalten 1999). It is difficult to assess whether New Zealand trees are any less resilient than species with similar growth rates from other floras, as differences between studies in the intensity and timing of browsing treatments limit comparability (see Canham *et al.* 1994; see McLaren 1996; Rooke *et al.* 2004).

Clipping-induced mortality was particularly high among conifer species, which echoes findings from a global study that reported that conifers are generally unable to resprout after wind damage perhaps due to a lack of dormant meristems along the main stem (Everham & Brokaw 1996). For our species, a lack of meristems is unlikely to explain mortality as surviving plants of all species produced new leaves in the 100% clipping treatment. It may be that high rates of mortality

at the most severe level of clipping for five species resulted from insufficient reserves to tide plants over until they could produce enough new leaves to regain a positive carbon balance.

LINKS BETWEEN RESISTANCE, RESILIENCE AND POTENTIAL GROWTH RATE

The study species ranged greatly in resistance to damage by introduced deer, from those that were hardly ever browsed, such as the conifers *Podocarpus hallii* and *Dacrydium cupressinum*, to those that are hardly even seen in the browse layer because they are browsed so very heavily, such as the short trees *Fuchsia excorticata* and *Griselinia littoralis* (Wardle 1991). Our findings are broadly supportive of two well-known theories found in the literature on plant–herbivore interactions: (i) that the species which are least-resistant to herbivory are inherently fast growing (Bryant *et al.* 1983; Coley *et al.* 1985; Herms & Mattson 1992; Fineblum & Rausher 1995), and (ii) that there is a trade-off between resistance and resilience (Fig. 5; (Maschinski & Whitham 1989; Herms & Mattson 1992). The fast-growing species that were highly palatable and fast to recover were those with short-lived leaves and high photosynthetic rates (A. Gaxiola *et al.*, unpublished data), and relatively low fibre contents (Forsyth *et al.* 2005), and which are commonly associated with fertile soils (Wardle 1984; Coomes *et al.* 2003). The most likely explanation for these associations is that plants adapted to relatively fertile soils are inherently fast-growing and so have less incentive for investment in defence than slow-growing plants because their tissues are typically short lived and relatively cheap to replace (Coley *et al.* 1985). In the wider context, the majority of New Zealand species are unpalatable to introduced ungulates, even though there is no recent history of mammalian herbivore exposure (Forsyth *et al.* 2002; Coomes *et al.* 2003), and most of these species are slow growing and associated with nutrient-poor soils (McGlone *et al.* 2004), and have long-lived leaves with low nutritive value once mature (Bee 2004).

The trade-offs observed among the New Zealand species in our study are particularly intriguing in the light of many recent studies that have challenged the generality of these simplistic trade-offs (Rosenthal & Kotanen 1994; Mauricio *et al.* 1997; Almeida-Cortez *et al.* 1999; Strauss & Agrawal 1999; de Jong & van der Meijden 2000; Hawkes & Sullivan 2001; Stamp 2003). There seem to be many exceptions to the general rule. For example, a fast-growing plant might be highly resistant to deer browse if it contains a secondary compound that gives it a bitter taste or has a toxic effect. One intriguing possibility is that the trade-off is observed in New Zealand because plants lack specific defensive compounds that are widespread in plants associated within the native ranges of deer. A study of monoterpenes may be particularly worthwhile in New

Zealand, because these compounds are known to be repugnant to deer. Seedlings of the conifer *Thuja plicata* growing on an island off Canada that was isolated from deer throughout Holocene until their recent reintroduction, were found to have lower monoterpene concentrations than seedlings growing on the mainland, and be much more palatable to deer. Other studies have found that plants containing high concentrations of polyphenols may be unpalatable to deer (McCallion *et al.* 1982; Takarada *et al.* 2004), but this does not seem to be the case in New Zealand.

Conclusions

Our study indicates that slow growth and low resilience may hinder recovery of New Zealand forests. The saplings investigated by us, in the south of the country, were slower growing than those reported in nine other studies from around the world. The implication is that deer populations will need to be reduced to very low densities in this part of New Zealand in order to allow widespread recruitment of trees. Many previous studies have shown that palatable species are disappearing from the browse layer of New Zealand forests, even though they have the capacity to recover most rapidly from damage. Species such as *Fuchsia excorticata* and *Griselinia littoralis* are browsed in excess of their potential to recover (Wardle 1984), while unpalatable species, such as *Pseudowintera colourata*, are left untouched by deer and slowly spread over a decadal time scale (Wardle 1984; Coomes *et al.* 2003). However, residual populations of palatable species persist in locations inaccessible to deer, such as on the trunks of tree ferns, the clefts of large trees, on bluffs and on raised surfaces (e.g. Coomes *et al.* 2006), and these trees may provide opportunities for recovery under suitable conditions.

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