

Foliar fibre predicts diet selection by invasive Red Deer *Cervus elaphus scoticus* in a temperate New Zealand forest

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Summary

1. There is much interest in how herbivores interact with plant communities, but the association between foliar traits and the feeding behaviour of invading browsing mammals has not been explored in this context.
2. We investigated whether eight foliar traits predicted the preferences of invasive Red Deer for 21 woody plant species in lowland forest in southern New Zealand.
3. The four models with substantial support for predicting variation in two indices of diet selection all included one or more traits related to foliar fibre (acid detergent fibre; acid detergent cellulose; acid detergent lignin). In all models the coefficients were negative, indicating that as the concentrations of foliar fibre increased, the preference of deer for foliage decreased.
4. Our results thus link the feeding behaviour of Red Deer with previously demonstrated shifts in the composition of New Zealand forests towards understorey species and leaf litter with high concentrations of foliar fibre.

Key-words: biological invasions, browsing, chemical defence, herbivory, plant traits

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Introduction

A general (but not universal, McNaughton 1985) response to an increase in the abundance of browsing mammals is a reduction in the abundance of the most palatable ('preferred') species and an increase in the abundance of the least palatable ('avoided') species (Augustine & McNaughton 1998; Wardle *et al.* 2001; Wardle & Bardgett 2004). These browser-induced shifts in plant community composition can alter litter quality and litter decomposition rates (Pastor *et al.* 1988, 1993; Wardle *et al.* 2001; Wardle, Bonner & Barker 2002), and alter carbon and nitrogen storage (Tracy & Frank 1998; Wardle *et al.* 2001; Olofsson, Stark & Oksanen 2004).

As plant species that are preferred by herbivores often have different ecophysiological traits to those that are avoided (Coley, Bryant & Chapin 1985; Grime 2001), plant traits could be useful predictors of the responses of plant communities to changes in the abundance of herbivores (Vesk, Leishman & Westoby 2004). For example, fibre content of leaves, and concentrations of lignins and polyphenols, are negatively correlated with palatability to invertebrate herbivores, and with below-ground decomposition rate (Grime *et al.* 1996; Wardle *et al.* 1998; Cornelissen *et al.* 1999).

The nutritional value of foliage to mammalian herbivores is typically expressed as digestible energy or digestible protein: these are the nutritional factors most commonly limiting browsing mammals (Robbins 1993). However, leaves can have a variety of chemical and morphological factors that can modify their attractiveness to herbivores. There are three general classes of chemical factor (Cooper, Owen-Smith & Bryant 1988): (1) nutrients such as N (a crude index of protein is $6.25 \times N$; Robbins 1993) and P, a major constituent of bone; (2) fibre, which includes cellulose, hemicellulose and lignin, the latter of which is indigestible to ungulates and reduces the proportion of potentially digestible fibre in forage (Robbins 1993); (3) secondary metabolites, a wide range of compounds that are toxic or reduce the availability of nutrients. A major suite of secondary metabolites are the phenolics, which include condensed tannins – these act primarily by binding with proteins and other macromolecules, precipitating cellular proteins and inactivating digestive enzymes (Robbins *et al.* 1987; Robbins 1993). Morphological traits that can affect the palatability of plants to herbivores include tree and branch size (Hartley *et al.* 1997); specific leaf area (SLA, Shipley *et al.* 1999; Pérez-Harguindeguy *et al.* 2003); tensile strength (Bond, Lee & Craine 2004); and spines (Belovsky *et al.* 1991).

Although cafeteria-style trials have shown that some secondary metabolites can reduce the feeding efficiency of browsing mammals (e.g. terpenes; Vourc'h *et al.* 2002),

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we know of only two published studies that have investigated the effects of foliar traits on the palatability of a large sample of plant species from a community to a browsing mammal. Cooper *et al.* (1988) suggested that the acceptability of 14 species of plants to hand-reared Kudus (*Tragelaphus strepsiceros*) and Impalas (*Aepyceros melampus*) was not related to any single chemical factor, but rather to the difference between the concentrations of protein and condensed tannins. Tixier *et al.* (1997) described how seven tame Roe Deer (*Capreolus capreolus*) feeding in an oak-beech woodland in France preferred a relatively small number of the available species, and that these preferences were negatively correlated with fibre content.

Many species of browsing mammal established in New Zealand between the 1770s and 1920s, with Red Deer (*Cervus elaphus scoticus* Lönnberg) now the most widespread (Challies 1990). Because browsing mammals were previously absent, there has been special interest in the effects of these species on forest ecosystems. Numerous enclosure studies have demonstrated that introduced ungulates have modified the distribution and abundance of species in the 'browse layer' (assumed to be ≤ 200 cm for Red Deer, Nugent, Fraser & Sweetapple 1997) in New Zealand, with unpalatable ferns and monocotyledonous species increasing and the palatable broadleaved species declining (Wardle *et al.* 2001 and references therein). Comparisons of ecosystem processes inside and outside 30 long-term exclosures throughout New Zealand also revealed that ungulates can alter soil C and N storage, but these effects were more spatially variable than above-ground effects (Wardle *et al.* 2001). Wardle *et al.* (2002) demonstrated that the foliage of understorey species that declined in abundance following the invasion of New Zealand forests by deer contained less fibre than those that had increased in abundance, and that fibre concentration was negatively correlated with the rate at which leaf litter decomposed.

The objective of this study was therefore to examine the relationships between foliar traits and diet selection by invasive Red Deer in a heterogeneous forest landscape in New Zealand. This was achieved by estimating the relative preferences of Red Deer for plant species within the browse tier, and then examining which of eight foliar traits best predicted those preferences. In doing this we also examined spatial variation in the availability of food to Red Deer in the study area.

Methods

STUDY AREA

We conducted our study in the Waitutu Ecological Region of Fiordland National Park on the southern coast of South Island, New Zealand ($46^{\circ}4'S$, $167^{\circ}2'E$; Fig. 1). Annual rainfall varies from 1600 to 2400 mm, and the mean January and July temperatures are 12 and 5 °C, respectively (Ward 1988). The Waitutu Ecological Region contains a chronosequence of 13 marine ter-

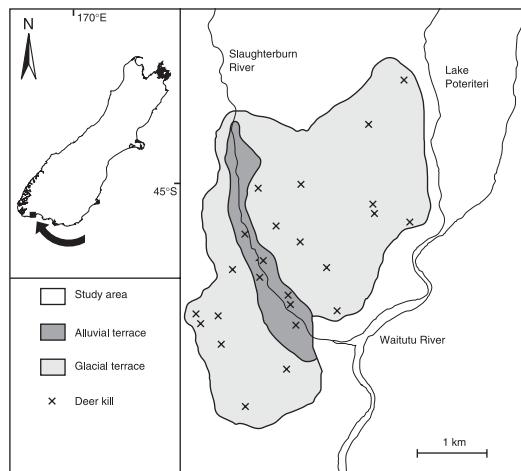


Fig. 1. Location of study area, southern South Island, New Zealand.

races that arose during the repeated cycles of glacial and interglacial periods during the Quaternary (Ward 1988). We focused on a 916 ha area of the chronosequence characterized by terraces of two ages (Fig. 1). Recent 'alluvial' terraces, formed less than 10 000 years ago, constituted 105 ha of the study area. Floods deposit silt on these terraces in most years, making these the most fertile of the terraces in the chronosequence (Wardle, Walker & Bardgett 2004; Coomes *et al.* 2005). The dominant canopy species on this terrace are *Nothofagus menziesii* and *Weinmannia racemosa*, with scattered emergents of *Dacrydium cupressinum* and *Dacrycarpus dacrydioides*. Subcanopy trees include *Melicytus ramiflorus* and *Schefflera digitata*. The understorey usually has a dense cover of ferns, including the tree ferns *Dicksonia squarrosa* and *Cyathea smithii*, and Crown Fern (*Blechnum discolor*) (Mark *et al.* 1988; Coomes *et al.* 2005). Plant nomenclature follows the New Zealand Plant Names database (Allan Herbarium 2000).

'Glacial' terraces are 80 000 years old, are less fertile and less well drained than the alluvial terraces (Coomes *et al.* 2005), and constituted the remaining 811 ha of the study area. The dominant canopy species on the glacial terraces are *D. cupressinum*, *Metrosideros umbellata*, *W. racemosa*, *N. menziesii*, and *Nothofagus solandri* var. *cliffortioides*. These forests have an understorey of *Coprosma foetidissima*, tree ferns and Crown Fern (Coomes *et al.* 2005). Red deer were introduced within ≈ 50 km of the study area in 1901 and 1904, and were common throughout the Waitutu Ecological Region by the late 1940s (Holloway 1950).

ESTIMATING RED DEER DIET

Two hunters systematically stalked the study area during 4–13 January 2002 and attempted to shoot all deer encountered. Each hunter had a trained indicator dog and stalked independently.

As most of the deer were using the alluvial terrace at night, the hunters typically stalked the alluvial terraces at dawn and tracked deer to the glacial terrace, where they were shot. The hunters shot a total of 24 deer: one hunter killed 13 and the other 11 deer. The location of each shot deer was recorded with a global positioning system (GPS, Garmin eTrex, Garmin International Inc., Olathe, KS, USA). The lower jaw of each deer was removed for subsequent ageing using the cementum annuli method (Fraser & Sweetapple 1993).

The rumen contents of each deer were stored in separate plastic bags and frozen within 4 h. In the laboratory each of the defrosted rumen samples was thoroughly mixed, and a subsample of 50 g was washed over a 5·6 mm sieve and sorted macroscopically following Nugent *et al.* (1997).

Previous work has indicated that a 5·6 mm sieve is a reasonable compromise between sorting time and the accuracy of the estimated diet of deer in New Zealand forests (Nugent & Challies 1988; Nugent 1990; Nugent *et al.* 1997). The sorted material, including the unidentified component, was then oven-dried (60 °C, 48 h) and weighed ($\pm 0\cdot5$ g). The proportion of each plant species in the diet of a deer was thus estimated using dry weight (DW).

ESTIMATING FORAGE AVAILABILITY

We estimated standing biomass using the method of Nugent (1990) immediately after stalking ended. The DW of available forage in the two terrace types was estimated by harvesting all potentially edible material within 2·0 m of ground level on 292 randomly located plots; 75 plots were on the recent alluvial terrace and 217 on the glacial terrace (Fig. 1). We used a stratified random sampling design because casual observation indicated that species preferred by deer in other New Zealand forests (Forsyth *et al.* 2002) were much more abundant on the alluvial terrace compared with the glacial terrace. Also there was a greater diversity of tree species on the alluvial terrace relative to the glacial terrace (Mark *et al.* 1988; Coomes *et al.* 2005), and having more plots per unit area would increase our probability of sampling these species.

We used a GPS to navigate to the 3·14 m² plots. All green foliage, small twigs, lichen and fungi from within each plot were harvested by hand, following Nugent *et al.* (1997). Bryophytes were present on a small number of plots, but were not included in the study because previous work had shown this group to be a minor component of deer diet in New Zealand forests ($\leq 3\%$ DW; Nugent & Challies 1988; Nugent 1990; Nugent *et al.* 1997; see Results). The wet weight of each species in each plot was recorded ($\pm 0\cdot5$ g) and a subsample stored in a plastic bag and frozen within 10 h of collection. The subsamples were oven-dried (60 °C, 48 h) in the laboratory and DW subsequently calculated for each species on each plot. Our total estimates of forage availability were corrected for

the stratified random sampling design following Cochran (1977).

ESTIMATING RED DEER DIET SELECTION

There are many ways to estimate diet selection (Manly *et al.* 2002). We used two indices to estimate diet selection by Red Deer in the Waitutu Ecological Region. We first used a modified form of Ivlev's index of electivity (I , Loehle & Rittenhouse 1982):

$$\hat{I}_i = \frac{u_i - \pi_i}{u_i + \pi_i}, \quad (\text{eqn 1})$$

where i denotes the i th species; u_i is the proportion of species i in the diet of deer; and π_i is the proportion of species i available to deer. This method has previously been used to estimate diet selection by White-tailed Deer (Nugent & Challies 1988), Fallow Deer (Nugent 1990) and Red Deer (Nugent *et al.* 1997) in New Zealand forests. I ranges from -1 (for species available but not ingested; 'avoided') to +1 (for species ingested but not sampled; 'preferred'). Following Nugent (1990), I was estimated for species that constituted $>0\cdot2\%$ of the diet and $>0\cdot1\%$ availability. However, we also estimated I for one species (*Peraxilla colensoi*) that was not sampled on plots but was present in 18 rumens in large amounts (a mean 25% of the DW biomass of woody species).

We next used a method that accounts for individual variation in diet selection, and for the fact that the availability of resources was estimated rather than censused (Manly *et al.* 2002). In the Manly index, the selection ratio (w) for the j th deer and the i th resource can be estimated as:

$$\hat{w}_{ij} = \frac{u_{ij}}{\hat{\pi}_i u_{+j}}, \quad (\text{eqn 2})$$

where u_{ij} is the number of category i resources used by deer j ; $\hat{\pi}_i$ is the estimated proportion of the resources available in category i ; and u_{+j} is the number of resource units used by deer j . The selection ratio for the sample of deer was then averaged as:

$$\hat{w}_i = \frac{\sum_{j=1}^n \hat{w}_{ij}}{n}, \quad (\text{eqn 3})$$

where n was the number of deer sampled. A useful way of interpreting selection ratios is to standardize them (B_i) so that they add to 1:

$$B_i = \frac{\hat{w}_i}{\left(\sum_{i=1}^1 \hat{w}_j \right)}. \quad (\text{eqn 4})$$

As we were interested only in browse species, we ignored other components of the diet in our analyses. The dominant types of forage thus excluded were introduced grasses (mean 28·0% of deer diet by DW) and unidentified woody (4·4%) and fern (3·1%) stems.

FOLIAR TRAITS

Fresh leaves were collected from species belonging to one of four plant groups: angiosperm trees, angiosperm shrubs, conifer trees or ferns. Data are presented for each of these four groups. Four individuals of each species were randomly sampled on both alluvial and glacial terraces during the forage availability work. SLA was determined on fresh leaves using a leaf-area meter (LiCor Area Meter Li-3100, Lincoln, NE, USA) following Poorter & de Jong (1999). Material was oven-dried (60 °C, 48 h) and total N and phosphorus were determined using the acid digest and colorimetric methods (Blakemore, Searle & Daly 1987). We used the acid detergent method (Rowland & Roberts 1994) to estimate percentage acid detergent fibre (ADF), percentage acid detergent cellulose (ADC), and percentage acid detergent lignin (ADL). Estimates of percentage condensed tannins used the vanillin method of Broadhurst & Jones (1978). Total phenolics were estimated using the method of Price & Butler (1977). Because samples of *P. colensoi* were not collected from within the study area in January 2002, samples were collected in February 2004 and the foliar traits were estimated as for the other species.

STATISTICAL ANALYSES

Intraspecific differences in foliar traits between the two terraces were examined using general linear models (GLM). It was necessary to average foliar traits across the two terraces for analyses of foliar traits and diet selection because deer were utilizing both terraces. Differences in foliar traits among the four plant groups were examined using GLMs.

The distribution of I was strongly skewed towards both maximum (+1) and minimum (-1) values. To model these data, we transformed values of I to an ordinal rank. We constructed three categories: 1 (eaten less than expected from its availability; avoided) = -1·00 to -0·75; 2 (eaten in approximate proportion to its availability) = -0·74 to +0·74; 3 (eaten more than expected from its availability; preferred) = +0·75 to +1·00. Manly's index (\hat{B}) was best described by a negative binomial distribution.

Our aim was to identify which foliar traits best explained variation in I and \hat{B} . As models including

multiple individual foliar traits can be confounded if foliar traits are intercorrelated, we also used ordination to summarize each species according to the eight foliar traits in combination. Foliar trait data were first standardized to have a mean of 0 and a variance of 1 using PROC Standard in SAS ver. 8.0 (SAS Institute 1997). A factor analysis (PROC Factor in SAS ver. 8.0) was then used to summarize among-species variation in the standardized foliar trait data. We assessed the correlations between the ordination scores for each species on the first two axes with each of the individual foliar traits. Variation in I was modelled using proportional odds models (PROC LOGISTIC in SAS). All models satisfied the proportional odds assumption (Guisan & Harrell 2000). Variation in \hat{B} was modelled using generalized linear models (PROC GENMOD in SAS) with a log link and negative binomial error.

These regression models formed the basis of 13 candidate models (Table 1). We also included Cooper *et al.*'s (1988) 'best model' [preference is a consequence of the difference between protein (indexed by N; Robbins 1993) and condensed tannins] in our candidate set. We examined how each of our 13 candidate models predicted variation in each index. For each index we used the small-sample unbiased Akaike's information criterion (AIC_c) and Akaike's weight (w_i) to identify which models were best supported by the data (Burnham & Anderson 2002). The best model has the smallest AIC_c , and models within two AIC_c units of the best model are considered to have 'substantial support' (Burnham & Anderson 2002). The goodness of fit for all models with substantial support was determined using log-likelihood ratios relative to a null model (Guisan & Harrell 2000). Model coefficients (± 1 SE) are also presented for those models with substantial support.

Results

FORAGE AVAILABILITY

On both alluvial and glacial terraces, available forage was dominated by the ferns *B. discolor*, *Blechnum procerum* and *C. smithii*: together these three species constituted 85% of the total available biomass (Table 2). In terms of biomass available to deer per unit area, ferns were

Table 1. Thirteen candidate models for explaining variation in the preferences of Red Deer for plant species in Waitutu Ecological Region, New Zealand

Model number	Foliar predictors	Justification
1	None (null model)	Deer preferences are not related to foliar traits
2–9	Each foliar trait individually†	Deer are responding to a single foliar trait
10	Factor analysis axis 1	Deer respond to suites of foliar traits
11	Factor analysis axis 2	Deer respond to suites of foliar traits
12	6·25 N – condensed tannins	Ungulates select species based on difference between total protein and total tannins (Cooper <i>et al.</i> 1988)
13	Full model	Deer respond to all foliar traits

†Traits: acid detergent cellulose, fibre, lignin; phosphorus; nitrogen; phenolics; tannins; specific leaf area.

Table 2. Forage availability, use and selection by Red Deer in the Waitutu Ecological Region, New Zealand. Each of the 21 species is classified according to growth form. Both use and availability are presented as percentage of total dry mass of those species

Plant species	Used by deer		Available to deer (%)			Selection		
	%	N	Alluvial	Glacial	Total†	\hat{I}_i	\hat{w}_i	\hat{B}_j
Ferns								
<i>Blechnum colensoi</i>	0·0	0	0·0	0·1	0·1	-1·00	0	0·000
<i>Blechnum discolor</i>	0·3	2	13·9	41·0	54·9	-0·99	2	0·003
<i>Blechnum procerum</i>	0·0	0	2·9	23·0	25·9	-1·00	0	0·000
<i>Cyathea smithii</i>	0·0	1	3·8	1·4	5·1	-0·99	0	<0·001
<i>Dicksonia squarrosa</i>	0·7	4	0·2	1·5	1·8	-0·44	5	0·007
<i>Polystichum vestitum</i>	0·0	1	0·3	0·0	0·3	-0·90	0	<0·001
Conifer trees								
<i>Dacrydium cupressinum</i>	1·0	4	0·1	0·2	0·3	0·54	8	0·010
<i>Podocarpus hallii</i>	0·0	2	0·0	1·4	1·4	-0·96	0	<0·001
<i>Prumnopitys ferruginea</i>	0·0	0	0·0	0·2	0·3	-1·00	0	0·000
Angiosperm trees								
<i>Carpodetus serratus</i>	4·2	14	0·1	0·1	0·1	0·94	34	0·042
<i>Griselinia littoralis</i>	33·7	23	0·1	0·5	0·6	0·97	274	0·337
<i>Metrosideros umbellata</i>	0·0	0	0·1	0·5	0·6	-1·00	0	0·000
<i>Nothofagus menziesii</i>	4·3	22	0·6	0·8	1·4	0·50	35	0·043
<i>Nothofagus solandri</i> var. <i>cliffortioides</i>	1·0	11	0·4	1·5	1·9	-0·33	8	0·010
<i>Pseudopanax crassifolius</i>	6·3	9	0·1	0·5	0·1	0·97	51	0·063
<i>Pseudopanax simplex</i>	1·6	7	0·0	0·1	0·1	0·87	13	0·016
<i>Pseudowintera colorata</i>	0·0	0	0·7	1·8	2·5	-1·00	0	0·000
<i>Weinmannia racemosa</i>	20·2	21	0·3	0·9	1·2	0·88	164	0·202
Angiosperm shrubs								
<i>Coprosma foetidissima</i>	1·8	7	0·0	0·1	0·1	0·88	14	0·018
<i>Cyathodes juniperina</i>	0·0	0	0·0	1·2	1·2	-1·00	0	0·000
<i>Peraxilla colensoi</i>	25·1	18	0·0	0·0	0·0	1·00	203	0·250
Total†	100·0	24			100·0			1·000

†Due to rounding, totals sometimes differ slightly from the sums of rows and columns shown. N is the number of deer rumens that the species was recorded in. 'Alluvial' and 'glacial' are the contributions of those two terraces to the total availability. \hat{I}_i is Ivlev's electivity index; \hat{w}_i is Manly's index; \hat{B}_j is a standardized selection ratio (see text). Plant names follow Allan Herbarium (2000).

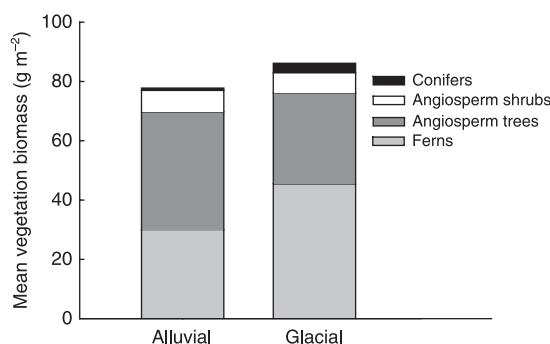


Fig. 2. Mean available biomass (standing vegetation <2 m and litter) of the four plant growth forms on the two terraces.

more abundant on the glacial terrace than on the alluvial terrace (Fig. 2). Although there was little biomass available to deer from the three conifer tree species (Table 2), there was more on the glacial compared with the alluvial terrace (Fig. 2). Of the nine angiosperm trees considered, all but two (*M. umbellata* and *Neomyrtus pedunculata*) were, after correcting for the different areas of the terraces, either more or similarly abundant on the alluvial relative to the glacial terrace (Table 2). Of the three angiosperm shrubs, only

Cyathodes juniperina was less abundant on the alluvial terrace relative to the glacial terrace.

RED DEER DIET AND DIET PREFERENCES

Twelve male and 12 female Red Deer were shot throughout the study area (Fig. 1). The estimated median ages for males and females were 25 months (range 1–54) and 37 months (range 13–61), respectively.

A total of 38 genera and 44 species were recorded in the 24 rumens. However, three species formed the bulk of the browse component of the diet (Table 2): *Griselinia littoralis* (34%), *P. colensoi* (25%) and *W. racemosa* (20%). Bryophytes were recorded in seven of the 24 rumens and comprised only 0·03% of the diet. Ivlev's and Manly's indices indicated similar diet preferences for most species (Table 2). Species with a low \hat{I} (approaching -1·0) also had a low \hat{w} (approaching 0) and \hat{B} (approaching 0: avoided, Manly *et al.* 2002); species with a high \hat{I} (approaching 1·0) also had a high \hat{w} and \hat{B} (approaching 0·3: preferred). Note that \hat{w} does not have an upper limit (is very large for highly preferred items in some situations; Manly *et al.* 2002). A simple way to interpret these data is by the standardized selection ratio (B_j), which is the estimated probability that species

i would be the next one selected if all of the species were presented in equal abundance (Manly *et al.* 2002). Hence *G. littoralis*, *P. colensoi* and *W. racemosa* were all similarly highly preferred, and the three *Blechnum* spp., *C. smithii*, *C. juniperina*, *M. umbellata*, *Podocarpus hallii*, *Prumnopitys ferruginea* and *Pseudowintera colorata* were all similarly avoided. The other species occupied a continuum between the extremes of preferred and avoided.

Whereas all but one (*D. squarrosa*) of the six ferns and one (*D. cupressinum*) of the three conifers were avoided, seven of the 12 angiosperms were preferred, two were eaten in proportion to their availability, and three were avoided (Table 2). Of the seven preferred angiosperms, one was a tree (*W. racemosa*) and six were shrubs, one of which was a hemiparasitic mistletoe (*P. colensoi*) not recorded on any of the 292 plots sampling forage availability. The DW biomass available to deer per unit area was greater on the alluvial compared with the glacial terrace for all the preferred angiosperms (except for *P. colensoi*). Conversely, the DW biomasses of the two avoided angiosperms were both higher per unit area on the glacial terrace.

Across all four plant groups, there was a general relationship between the available biomass of a species and its use by deer (Fig. 3). The most abundant species were all strongly avoided, and the most preferred species were the least abundant. However, there was a continuum between these two extremes.

FOLIAR TRAITS

Across all plant groups, the only differences in foliar traits (mean \pm SE) between the two terraces were P (GLM: $F_{1,32} = 16.76$, $P = 0.0003$, alluvial terrace $0.19 \pm 0.02\%$, glacial terrace $0.09 \pm 0.01\%$) and SLA (GLM: $F_{1,32} = 9.06$, $P = 0.005$, alluvial terrace $215 \pm 22 \text{ cm g}^{-1}$, glacial terrace $130 \pm 18.2 \text{ cm g}^{-1}$). After combining the data from both terraces, there were significant differences in some foliar traits among the four plant groups. Foliar N concentrations varied more than twofold across the four plant groups (GLM: $F_{3,17} = 3.89$, $P = 0.03$) with higher concentrations in ferns ($1.51 \pm 0.16\%$) relative to angiosperm trees ($0.90 \pm 0.12\%$). Foliar P concentrations varied threefold among the four plant groups (GLM: $F_{3,17} = 4.05$, $P = 0.02$) with significantly higher concentrations in ferns ($0.18 \pm 0.02\%$) relative to both

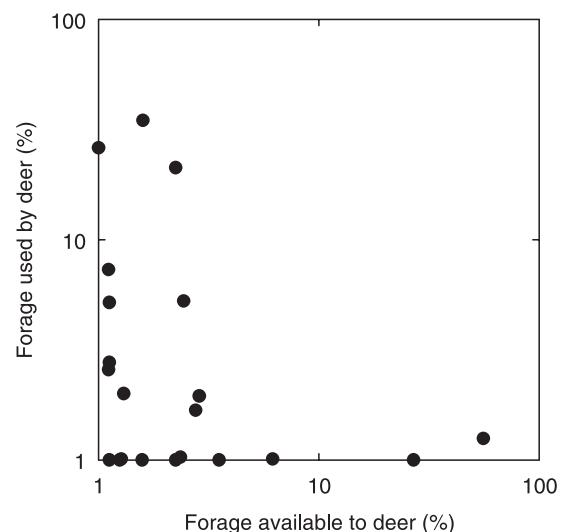


Fig. 3. Relationship between available and used vegetation. Note that both axes are on a log scale.

angiosperm trees ($0.10 \pm 0.02\%$) and conifers ($0.06 \pm 0.04\%$). Foliar ADC varied 1.5-fold among the four plant groups (GLM: $F_{3,17} = 4.20$, $P = 0.02$) with higher concentrations in ferns ($32.7 \pm 2.2\%$) relative to angiosperm trees ($23.4 \pm 1.7\%$). Foliar ADF varied 1.5-fold among the four plant groups with higher concentrations in ferns ($63.4 \pm 3.3\%$) relative to angiosperm trees ($43.8 \pm 2.5\%$), conifers ($44.6 \pm 5.7\%$) and shrubs ($47.5 \pm 4.6\%$) (GLM: $F_{3,17} = 5.56$, $P = 0.05$). Foliar tannins, ADL, phenolics and SLA did not differ significantly among the four plant groups (GLM: $P > 0.05$ in all instances).

Foliar traits were strongly intercorrelated, indicating that differences among species were driven by suites of foliar traits rather than by individual traits (Table 3). The first two axes from the factor analysis accounted for $>70\%$ of total variation in the eight foliar traits (Table 4). The first axis described variation in foliar nutrients and chemical defences, while the second related to variation in the concentrations of foliar fibre (ADF, ADC and ADL).

WHICH FOLIAR TRAITS PREDICT DIET SELECTION BY RED DEER?

The model including only ADF best explained variation in the diet preferences of deer estimated using Ivlev's

Table 3. Correlations among eight foliar traits ($N = 21$)

Trait	Nitrogen	Phosphorus	ADF	ADC	ADL	Tannins	Phenolics
Phosphorus	0.86***						
ADF	0.32	0.41					
ADC	0.01	0.13	0.76***				
ADL	0.42	0.42	0.76***	0.17			
Tannins	-0.54*	-0.47*	0.21	0.18	0.18		
Phenolics	-0.55*	-0.47*	-0.08	-0.04	-0.04	0.78***	
SLA	0.66**	0.57**	0.05	0.05	-0.02	-0.56**	-0.38

ADF, ADF, ADL = acid detergent cellulose, fibre, lignin; SLA = specific leaf area.

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

Table 4. Summary of factor analysis using eight foliar traits from 21 species. The eigenvalue and the percentage of total variation explained are provided for the first two axes of the factor analysis. The correlation between each of the eight foliar traits and the species' scores for each of the factor analysis axes are presented

Trait	Factor analysis axis (eigenvalue, % of total variation explained)	
	Axis 1 (3·50, 44%)	Axis 2 (2·31, 29%)
ADC	0·18	0·68***
ADF	0·43	0·89***
ADL	0·41	0·70***
Phenolics	-0·71***	0·33
Phosphorus	0·89***	0·09
Nitrogen	0·92***	-0·02
SLA	0·72***	-0·28
Tannins	-0·67***	0·62**

ADC, ADF, ADL = acid detergent cellulose, fibre, lignin;
SLA = specific leaf area.

* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.

index (Table 5). A likelihood ratio test also indicated that fibre was a significant variable in predicting \hat{I}_i ($\chi^2 = 12·81$, df = 1, $P = 0·0003$). The coefficient for ADF in that model was $-0·17 \pm 0·06$ ($R^2 = 0·46$). Hence, as the concentration of foliar ADF increased, the preference of deer for that species decreased. The second factor analysis axis also had substantial support (Table 5). A likelihood ratio test also indicated that this factor analysis axis was a significant variable in predicting \hat{I}_i ($\chi^2 = 11·49$, df = 1, $P = 0·0007$). The coefficient for the factor analysis axis was $-1·79 \pm 0·65$ ($R^2 = 0·42$). The other 11 candidate models all had $\Delta_i \geq 5·2$, indicating that they had almost no support (Burnham & Anderson 2002).

Two models had substantial support for explaining variation in the diet preferences of deer estimated using

Manly's index (Table 6). The model containing only ADC had the most support, and a likelihood ratio test also indicated that cellulose was a significant variable in predicting \hat{B}_i ($\chi^2 = 7·01$, df = 1, $P = 0·008$). The coefficient for ADC in that model was $-0·26 \pm 0·09$ ($R^2 = 0·16$), indicating that as the concentration of foliar cellulose increased, the preference of deer for that species decreased. The model containing ADF also had substantial support (Table 6), and a likelihood ratio test also indicated that fibre was a significant variable in predicting \hat{B}_i ($\chi^2 = 5·67$, df = 1, $P = 0·02$). ADF in this model had a similar coefficient to that estimated for Ivlev's index ($-0·126 \pm 0·048$, $R^2 = 0·22$). Again, as the concentration of foliar fibre increased, the preference of deer for that species decreased.

Discussion

PREDICTORS OF DIET SELECTION

Our results demonstrate a community-level relationship between foliar fibre (ADF, ADC and ADL) and diet selection by invasive Red Deer: species with low foliar fibre tended to be preferred by Red Deer, and those with high foliar fibre tended to be avoided. We are unaware of any published studies that have investigated how the traits of a receiving plant community influence diet selection by an invasive mammalian herbivore. Two other studies have reported a negative relationship between the preferences of indigenous Cervidae for foliage and the fibre content of foliage. Danell *et al.* (1994) observed that the feeding preferences of reindeer (*Rangifer tarandus*) for nine plant taxa showed a strong negative relationship with ADF. Similarly, the preferences of tame Roe Deer for oak-woodland species had a negative relationship with ADF (Tixier *et al.* 1997). Acid detergent fibre is composed of cellulose, lignin and ash, with further sequential treatments destroying the cellulose (ADC) and lignin (ADL) components,

Table 5. Comparison of the 13 candidate models predicting variation in Ivlev's index (I) of diet selection to eight foliar traits ($N = 21$ species). Models with $\Delta_i \leq 2$ have substantial support (Burnham & Anderson 2002) and are shown in bold

Rank	Candidate model	K	AIC_c	Δ_i	w_i
1	Acid detergent fibre	3	39·6	0·0	0·63
2	Factor analysis axis 2	3	40·9	1·3	0·32
3	Acid detergent lignin	3	45·4	5·9	0·03
4	Intercept	3	49·6	10·1	0·00
5	Factor analysis axis 1	2	50·2	10·7	0·00
6	Tannins	3	51·0	11·4	0·00
7	Specific leaf area	3	52·1	12·6	0·00
8	Acid detergent cellulose	3	52·2	12·6	0·00
9	6·25 N – tannins (Cooper <i>et al.</i> 1988)	3	52·2	12·6	0·00
10	Nitrogen	3	52·4	12·8	0·00
11	Phenolics	3	52·4	12·8	0·00
12	Phosphorus	3	52·4	12·8	0·00
13	Full model	10	63·3	23·7	0·00

K = number of estimated parameters in the model. In a logistic model the error term is assumed and need not be included in K (Burnham & Anderson 2002). Δ_i = difference in AIC_c between best model (models with smallest value of AIC_c) and model i . w_i = Akaike's weight, which indicates the weight of evidence in favour of model i .

Table 6. Comparison of the 13 candidate models predicting variation in Manly's index (B) of diet selection to eight foliar traits ($N = 21$ species). Models with $\Delta_i \leq 2$ have substantial support (*sensu* Burnham & Anderson 2002) and are shown in bold

Rank	Candidate model	K	AIC_c	Δ_i	w_i
1	Acid detergent cellulose	3	-6301.9	0.0	0.51
2	Acid detergent fibre	3	-6300.5	1.3	0.26
3	Intercept	2	-6297.6	4.3	0.06
3	Factor analysis axis 2	3	-6296.7	5.1	0.04
5	Acid detergent lignin	3	-6295.6	6.2	0.02
6	Phosphorus	3	-6295.4	6.5	0.02
7	Specific leaf area	3	-6295.4	6.5	0.02
8	Nitrogen	3	-6295.1	6.7	0.02
9	Phenolics	3	-6295.0	6.9	0.02
10	Factor analysis axis 1	3	-6294.9	6.9	0.02
11	Tannins	3	-6294.9	7.0	0.02
12	6.25 N – tannins (Cooper <i>et al.</i> 1988)	4	-6291.8	10.0	0.00
13	Full model	9	-6283.7	18.2	0.00

K = number of estimated parameters in the model including 1 df for estimate of dispersion (Burnham & Anderson 2002).

Δ_i = difference in AIC_c between best model (models with smallest value of AIC_c) and model i . w_i = Akaike's weight, which indicates the weight of evidence in favour of model i .

respectively (Rowland & Roberts 1994). Cellulose cannot be digested by vertebrates without symbiotic gastrointestinal microflora, and lignin is largely indigestible (Robbins 1993). Our model selection procedure identified models containing ADF, ADC and ADL, or a factor analysis axis reflecting variation in these three variables, as the best predictors of the diet preferences of Red Deer based on both Ivlev's and Manly's indices (Tables 5 and 6). There was relatively little support ($w_i \leq 0.05$) for models containing other variables. Our results are therefore consistent with earlier studies suggesting that structural fibre is an important determinant of foliar palatability for both vertebrate and invertebrate herbivores (Cornelissen *et al.* 1999; Schädler *et al.* 2003).

Three species comprised 78% of the browse eaten by deer in our study area. Although previous studies have shown both *G. littoralis* and *W. racemosa* to be common in the diet of Red Deer (and other Cervidae) in New Zealand forests, *P. colensoi* has not been recorded as eaten by deer (Forsyth *et al.* 2002). Introduced grasses comprised a substantial proportion of the total diet (28%), and are known to be particularly attractive to Red Deer in summer (Challies 1990). Introduced grasses were only observed on small areas of the alluvial terrace regularly disturbed by flooding. The presence of introduced grasses would have increased the attractiveness of the alluvial terrace to deer relative to the glacial terrace.

Foliar fibre explained 46 and 16% of the variation in Ivlev's and Manly's indices of Red Deer diet selection, respectively. The unexplained variation can be attributed to at least four factors. First, the foliage of some species may have contained secondary metabolites that we did not measure, but which acted as important deterrents for deer (e.g. terpenes; Vourc'h *et al.* 2002). Second, plant morphological traits can decrease the rate at which foliage is removed by ungulates per unit time (Hartley *et al.* 1997; Shipley *et al.* 1999), and a

peculiarity of the New Zealand flora is the high frequency of the small-leaved tangle-branched growth form ('divaricate', Greenwood & Atkinson 1977). The divaricate growth form has been considered an adaptation to browsing by Moa (Greenwood & Atkinson 1977; Bond *et al.* 2004; but see Howell, Kelly & Turnbull 2002), and is likely to reduce the feeding efficiency of deer (*sensu* Owen-Smith 2002). Third, because both food availability and use were estimated with error, our indices also had error (Manly *et al.* 2002). Some of the 24 deer sampled would have had home ranges partially outside the study area, where food availability was not quantified. Apart from increasing sample sizes, we can see no way around this problem in a field study like this: the alternative to a field study is a cafeteria-style trial, but these are difficult when a large number of resources are to be compared (Manly *et al.* 2002). Fourth, all indices of diet selection are a simplification of a complex process (Hanley 1997). There are many indices with which to assess diet selection, and we attempted to assess the robustness of our results by using two indices (Manly *et al.* 2002). That similar models were selected for both indices indicates that our results are robust.

LINKAGES BETWEEN DEER HERBIVORY, VEGETATION RESPONSES AND LITTER QUALITY AND DECOMPOSITION RATES

Numerous studies in New Zealand have described patterns of understorey vegetation change that reflect a systematic decline in the distribution and abundance of species identified in this (Table 2) and other studies (Forsyth *et al.* 2002) as preferred by introduced deer, and a concomitant increase in the distribution and abundance of species that are avoided by deer (Holloway 1950; Wardle *et al.* 2001; Coomes *et al.* 2003). If deer reduce the abundance of preferred plant species, then we would expect that preferred species will always be rare and avoided species may be common. There are

no long-term quantitative data on changes in species abundance in the Waitutu Ecological Region with which to test the prediction that deer browsing is responsible for the rarity of preferred species, but the pattern in Fig. 3 fits the prediction: deer avoided the most abundant species, and the species preferred by deer had low abundances.

Comparisons of vegetation inside and outside exclosures throughout New Zealand revealed that both the vegetation response and litter decomposition rates were strongly negatively correlated with foliar fibre (Wardle *et al.* 2001, 2002). Our results suggest a link between the feeding behaviour of introduced deer and long-term changes in understorey composition, litter quality and litter decomposition rates. The foliar fibre concentration of a species is negatively associated with the probability of deer removing foliage from that species (this study), and hence is negatively correlated with the long-term change in abundance of that species in the presence of deer (Wardle *et al.* 2001). Wardle *et al.* (2002) showed that the deer-induced shift in the understorey composition of New Zealand forests has led to poorer quality litters with lower decomposition rates.

Wardle *et al.* (2001) described spatially variable effects of ungulates on soil C and N storage. One possible reason for the variation is the heterogeneous distribution of preferred plant species in the landscape. In our study area, all the preferred species were more abundant, per unit area, on the alluvial terrace relative to the glacial terrace. Relative to the alluvial terrace, the glacial terrace is considerably more acidic and has higher C : N, C : P and N : P (Wardle *et al.* 2004; Coomes *et al.* 2005). As ungulates tend to maximize foraging time in areas of the landscape where preferred foods are most abundant (Wallis de Vries & Schippers 1994), their impacts on both above-ground and below-ground processes would probably be greatest in those areas. Most of the plant species preferred by Red Deer in the Waitutu Ecological Region are fast-growing and shade-intolerant angiosperms (Coomes *et al.* 2003) that grow on the most fertile and least waterlogged terrace. We therefore predict that the long-term effects of Red Deer will be greater on the alluvial terrace compared with the glacial terrace.

Conclusion

We have shown that foliar fibre was the best predictor of diet selection by invasive Red Deer in a lowland temperate New Zealand forest. Our study thus links the feeding behaviour of Red Deer with previously demonstrated changes in understorey composition, litter quality and decomposition rates.

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References

- Allan Herbarium (2000) *New Zealand Plant Names database: Ngé Tipu o Aotearoa – New Zealand plants*. Landcare Research, Lincoln, NZ. <http://nzflora.landcareresearch.co.nz>
- Augustine, D.J. & McNaughton, S.J. (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* **62**, 1165–1183.
- Belovsky, G.E., Schmitz, O.J., Slade, J.B. & Dawson, T.J. (1991) Effects of spines and thorns on Australian arid zone herbivores of different body masses. *Oecologia* **88**, 521–528.
- Blakemore, L.C., Searle, P.L. & Daly, B.K. (1987) *Methods for Chemical Analysis of Soils*. New Zealand Soil Bureau Scientific Report 80. Department of Scientific and Industrial Research, Wellington, NZ.
- Bond, W.J., Lee, W.G. & Craine, J.M. (2004) Plant structural defences against browsing birds: a legacy of New Zealand's extinct moas. *Oikos* **104**, 500–508.
- Broadhurst, R.B. & Jones, W.T. (1978) Analysis of condensed tannins using acidified vanillin. *Journal of the Science of Food and Agriculture* **29**, 788–794.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York, USA.
- Challies, C.N. (1990) Red deer. *The Handbook of New Zealand Mammals* (ed. C.M. King), pp. 436–458. Oxford University Press, Auckland, NZ.
- Cochran, W.G. (1977) *Sampling Techniques*, 3rd edn. John Wiley, New York, USA.
- Coley, P., Bryant, J.P. & Chapin, F.S. III (1985) Resource availability and plant antiherbivore defenses. *Science* **230**, 895–899.
- Coomes, D.A., Allen, R.B., Forsyth, D.M. & Lee, W.G. (2003) Factors preventing the recovery of New Zealand forests following control of invasive deer. *Conservation Biology* **17**, 450–459.
- Coomes, D.A., Allen, R.B., Canham, C.D. *et al.* (2005) The hare, the tortoise, and the crocodile: the ecology of angiosperm dominance, conifer persistence, and fern filtering. *Journal of Ecology* in press.
- Cooper, S.M., Owen-Smith, N. & Bryant, J.P. (1988) Foliage acceptability to browsing ruminants in relation to seasonal changes in the leaf chemistry of woody plants in a South Africa savanna. *Oecologia* **75**, 336–342.
- Cornelissen, J.H.C., Pérez-Harguindeguy, N., Díaz, S. *et al.* (1999) Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist* **143**, 191–200.
- Danell, K., Utsi, P.K., Palo, R.T. & Eriksson, O. (1994) Food plant selection by reindeer during winter in relation to plant quality. *Ecography* **17**, 153–158.
- Forsyth, D.M., Coomes, D.A., Nugent, G. & Hall, G.M.J. (2002) The diet and diet preferences of ungulates (Order: Artiodactyla) in New Zealand. *New Zealand Journal of Zoology* **29**, 323–343.

- Fraser, K.W. & Sweetapple, P.J. (1993) *Assessing the Age and Condition of Deer from Jawbones*. Manaaki-Whenua Press, Lincoln, NZ.
- Greenwood, R.M. & Atkinson, I.A.E. (1977) Evolution of the divaricating plants in New Zealand in relation to moa browsing. *Proceedings of the New Zealand Ecological Society* **24**, 21–33.
- Grime, J.P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. Wiley, Chichester, UK.
- Grime, J.P., Cornelissen, J.H.C., Thompson, K. & Hodgson, J.G. (1996) Evidence of a causal connection between anti-herbivore defense and the decomposition rate of leaves. *Oikos* **77**, 489–494.
- Guisan, A. & Harrell, F.E. (2000) Ordinal response regression models in ecology. *Journal of Vegetation Science* **11**, 617–626.
- Hanley, T. (1997) A nutritional view of understanding and complexity in the problem of diet selection by deer (Cervidae). *Oikos* **79**, 209–218.
- Hartley, S.E., Iason, G.R., Duncan, A.J. & Hitchcock, D. (1997) Feeding behaviour of Red Deer (*Cervus elaphus*) offered Sitka Spruce seedlings (*Picea sitchensis*) grown under different light and nutrient regimes. *Functional Ecology* **11**, 348–357.
- Holloway, J.T. (1950) Deer and the forests of western Southland. *New Zealand Journal of Forestry* **6**, 123–137.
- Howell, C.J., Kelly, D. & Turnbull, M.H. (2002) Moa ghosts exorcised? New Zealand's divaricating shrubs avoid photo-inhibition. *Functional Ecology* **16**, 232–240.
- Loehle, C. & Rittenhouse, L.R. (1982) An analysis of forage preference indices. *Journal of Range Management* **35**, 316–319.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*, 2nd edn. Chapman & Hall, London.
- Mark, A.F., Greigh, G., Ward, C.M. & Wilson, J.B. (1988) Ecological studies of a marine terrace sequence in the Waitutu Ecological District of southern New Zealand. Part 1: The vegetation and soil patterns. *Journal of the Royal Society of New Zealand* **18**, 29–58.
- McNaughton, S.J. (1985) Ecology of a grazing system: the Serengeti. *Ecological Monographs* **55**, 259–294.
- Nugent, G. (1990) Forage availability and the diet of fallow deer (*Dama dama*) in the Blue Mountains, Otago. *New Zealand Journal of Ecology* **13**, 83–95.
- Nugent, G. & Challies, C.N. (1988) Diet and food preferences of white-tailed deer in north-eastern Stewart Island. *New Zealand Journal of Ecology* **11**, 61–71.
- Nugent, G., Fraser, W. & Sweetapple, P. (1997) *Comparison of Red Deer and Possum Diets and Impacts in Podocarp-Hardwood Forest, Waihaha Catchment, Pureora Conservation Park*. Science for Conservation 50. Department of Conservation, Wellington, NZ.
- Olofsson, J., Stark, S. & Oksanen, L. (2004) Reindeer influence on ecosystem processes in the tundra. *Oikos* **105**, 386–396.
- Owen-Smith, R.N. (2002) *Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments*. Cambridge University Press, Cambridge, UK.
- Pastor, J., Naiman, R.J., Dewey, B. & McInnes, P. (1988) Moose, microbes and the boreal forest. *Bioscience* **38**, 770–777.
- Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F. & Cohen, Y. (1993) Moose browsing and soil fertility of Isle Royale National Park. *Ecology* **74**, 467–480.
- Pérez-Harguindeguy, N., Diaz, S., Vendramini, F., Cornelissen, J.H., Gurvich, D.E. & Cabido, M. (2003) Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecology* **28**, 642–650.
- Poorter, H. & de Jong, R. (1999) A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist* **143**, 163–176.
- Price, M.L. & Butler, L.G. (1977) Rapid visual estimation of and spectrophotometric determination of tannin content of sorghum grain. *Journal of Agricultural and Food Chemistry* **25**, 1268–1273.
- Robbins, C.T. (1993) *Wildlife Feeding and Nutrition*, 2nd edn. Academic Press, San Diego, CA, USA.
- Robbins, C.T., Hanley, T.A., Hagerman, A.E., Hjeljord, O., Baker, D.L., Schwartz, C.C. & Mautz, W.W. (1987) Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* **68**, 98–107.
- Rowland, A.P. & Roberts, J.D. (1994) Lignin and cellulose fractionation in decomposition studies using acid detergent fibre methods. *Communications in Soil Science and Plant Analysis* **25**, 269–275.
- SAS Institute (1997) *SAS/STAT Software: Changes and Enhancements Through Release 6.12*. SAS Institute Inc, Cary, NC, USA.
- Schädler, M., Jung, G., Auge, H. & Brandl, R. (2003) Palatability, decomposition and insect herbivory: patterns in a successional old-field plant community. *Oikos* **103**, 121–132.
- Shipley, L.A., Illius, A.W., Danell, K., Hobbs, N.T. & Spalinger, D.E. (1999) Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimisation. *Oikos* **84**, 55–68.
- Tixier, H., Duncan, P., Scehovic, J., Yani, A., Gleizes, M. & Lila, M. (1997) Food selection by European roe deer (*Capreolus capreolus*): effects of plant chemistry, and consequences for the nutritional value of their diets. *Journal of Zoology, London* **242**, 229–245.
- Tracy, B.F. & Frank, D.A. (1998) Herbivore influence on soil microbial biomass and nitrogen mineralization in a northern grassland ecosystem: Yellowstone National Park. *Oecologia* **114**, 556–562.
- Vesk, P., Leishman, M.R. & Westoby, M. (2004) Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *Journal of Applied Ecology* **41**, 22–31.
- Vourc'h, G., de Garine-Wichatitsky, M., Labb  , A., Rosolowski, D., Martin, J.-L. & Fritz, H. (2002) Monoterpene effect on feeding choice by deer. *Journal of Chemical Ecology* **28**, 2411–2427.
- Wallis de Vries, M.F. & Schippers, P. (1994) Foraging in a landscape mosaic: selection for energy and minerals in free-ranging cattle. *Oecologia* **100**, 107–117.
- Ward, C.M. (1988) Marine terraces of the Waitutu district and their relation to the late Cenozoic tectonics of the southern Fiordland region, New Zealand. *Journal of the Royal Society of New Zealand* **18**, 1–28.
- Wardle, D.A. & Bardgett, R.D. (2004) Human-induced changes in large herbivorous mammal density: the consequences for decomposers. *Frontiers in Ecology and the Environment* **3**, 145–153.
- Wardle, D.A., Barker, G.M., Bonner, K.I. & Nicholson, K.S. (1998) Can comparative approaches based on ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *Journal of Ecology* **86**, 405–420.
- Wardle, D.A., Barker, G.M., Yeates, G.W., Bonner, K.I. & Ghani, A. (2001) Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecological Monographs* **71**, 587–614.
- Wardle, D.A., Bonner, K.I. & Barker, G.M. (2002) Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology* **16**, 585–595.
- Wardle, D.A., Walker, L.R. & Bardgett, R.D. (2004) Ecosystem properties and forest declines in contrasting long-term chronosequences. *Science* **305**, 509–513.