

Interactions between herbivores, vegetation and eucalypt tree seedlings in a plantation forestry environment

Kirsten le Mar¹ and Clare McArthur^{1,2,3}

¹ Cooperative Research Centre for Sustainable Production Forestry and the School of Zoology, University of Tasmania, Private Bag 5, Hobart, Tasmania 7001, Australia

²Email: claremc@usyd.edu.au

³School of Biological Sciences, Heydon-Laurence Building (A08), The University of Sydney 2006, Australia

Revised manuscript received 27 July 2005

Summary

Non-lethal management methods for reducing mammal browsing damage to *Eucalyptus* seedlings during plantation establishment are currently being investigated in Tasmania, Australia. One method is use of selective retention of non-seedling vegetation in plantations. To assess its potential, information is needed on how herbivores use such vegetation and whether it has positive or negative effects on browsing and growth of commercial tree seedlings. We quantified the populations of five mammalian herbivore species in and around a spot-herbicide *E. nitens* plantation during its establishment. We also investigated several aspects of the interactions between those mammalian herbivores, insect herbivores, tree seedlings and non-seedling vegetation. We found that overall population densities were high for red-bellied pademelons (*Thylogale billardierii*) and red-necked wallabies (*Macropus rufogriseus rufogriseus*), but very low for common brushtail possums (*Trichosurus vulpecula*), common wombats (*Vombatus ursinus*) and the introduced European rabbit (*Oryctolagus cuniculus*). Population densities of the five mammalian species did not change in response to planting *E. nitens* seedlings. Dominant vegetation in the plantation was grass, then forbs and non-grass monocots. Herbivores ate a large proportion of available plantation vegetation in unfenced plots. Mammal browsing had little effect on survival of *E. nitens* seedlings 15 weeks after planting, but significantly reduced their growth. In unfenced plots, insects, mainly *Heteronyx* spp., caused twice as much damage to seedlings as browsing mammals. The absence of mammalian browsing in fenced plots, which resulted in high grass cover, was associated with reduced insect damage to seedlings.

Keywords: browsing damage; population density; assessment; growth; mortality; marsupial; macropod; wallaby; pademelon; possum; *Eucalyptus nitens*; Tasmania; Australia

Introduction

Foliage loss during plantation establishment of commercial *Eucalyptus nitens* and *E. globulus* tree seedlings by browsing mammals is a significant cost to the Tasmanian forestry industry (Wardlaw and de Little 2000). Damage is attributed to three native species: red-bellied pademelon (*Thylogale billardierii*), red-

necked wallaby (*Macropus rufogriseus rufogriseus*), common brushtail possum (*Trichosurus vulpecula fuliginosus*) and to the introduced European rabbit (*Oryctolagus cuniculus*) (Gilbert 1961; Cremer 1969; Statham 1983; O'Reilly and McArthur 1997; Bulinski and McArthur 2000). Defoliation by insects, notably adults of *Heteronyx dimidiata* and *H. crinitus*, is also a problem concurrent with mammal browsing in some areas of Tasmania (Wardlaw and de Little 2000).

Current methods for managing mammal browsing include poisoning with '1080' (sodium monofluoroacetate) and/or shooting to reduce animal numbers. These lethal methods are socially and politically controversial due to questions of animal welfare and because three of the four species targeted by these operations are native. Non-lethal alternatives for reducing browsing damage to tree seedlings are therefore being investigated.

Managing browsing by reducing animal numbers assumes fewer animals will result in less damage. However, while mammal browsing damage is, on average, lower on poisoned than unpoisoned plantations (Bulinski 1999), the relationship between damage and abundance of the two macropod species (*T. billardierii* and *M. r. rufogriseus*) is not straightforward (Bulinski and McArthur 2003; Pietrzykowski *et al.* 2003). This is due in part to the influence of other non-seedling vegetation on browsing of tree seedlings by these species. For example, both cover and height of bracken (*Pteridium esculentum*) correlate negatively with severity of browsing damage to seedlings, while the inverse relationship has been demonstrated with grasses (e.g. *Poa* spp.) (Bulinski and McArthur 2003; Pietrzykowski *et al.* 2003). This suggests that selective retention of some types of vegetation in plantations has potential in non-lethal management of browsing damage.

Four components need to be considered in using vegetation for managing browsing. They are: non-seedling vegetation, tree seedlings, mammalian herbivores and defoliating insects. Important aspects or interactions between these components include the extent to which mammalian herbivores consume and alter the biomass/composition of non-seedling vegetation; the indirect influence of this consumption on defoliation of tree seedlings by both mammalian and insect herbivores; and the net effect of the above factors on tree seedling growth.

The main objective of this study was to explore some relationships between mammalian herbivores, vegetation and tree seedlings during establishment of an *E. nitens* plantation. Although our focus was on the plantation, we also quantified use of surrounding habitats by herbivores to place results in the context of the broader forestry environment. We also examined the indirect influence of mammalian herbivores on insect defoliation of tree seedlings, through their effect on plantation vegetation.

Specific questions addressed were:

- What were the population densities of mammalian herbivore species in an *E. nitens* plantation and surrounding habitats during establishment?
- Did herbivore densities change in response to planting of *E. nitens* seedlings?
- How did mammalian herbivores affect the biomass and composition of vegetation in the plantation during establishment?

- How did mammal browsing damage to *E. nitens* seedlings compare with insect damage?
- How did mammal and insect damage affect seedling growth?

While pademelons, wallabies, possums and rabbits are the main contributors to browsing damage within plantations (see above), we also included common wombats (*Vombatus ursinus*) in our study because they occurred at the site and so could potentially consume and influence non-seedling vegetation.

Study area

The study area was located in North Forest Product's (NFP, now Gunns Ltd) 'Surrey Hills' Tree-farm in north-western Tasmania (41°28'S, 145°48'E). Five habitats dominated the site (Fig. 1, Table 1), from greatest to least area: (i) older plantations of *E. nitens* (5–7 y old, 5 m tall); (ii) native forest (rainforest and

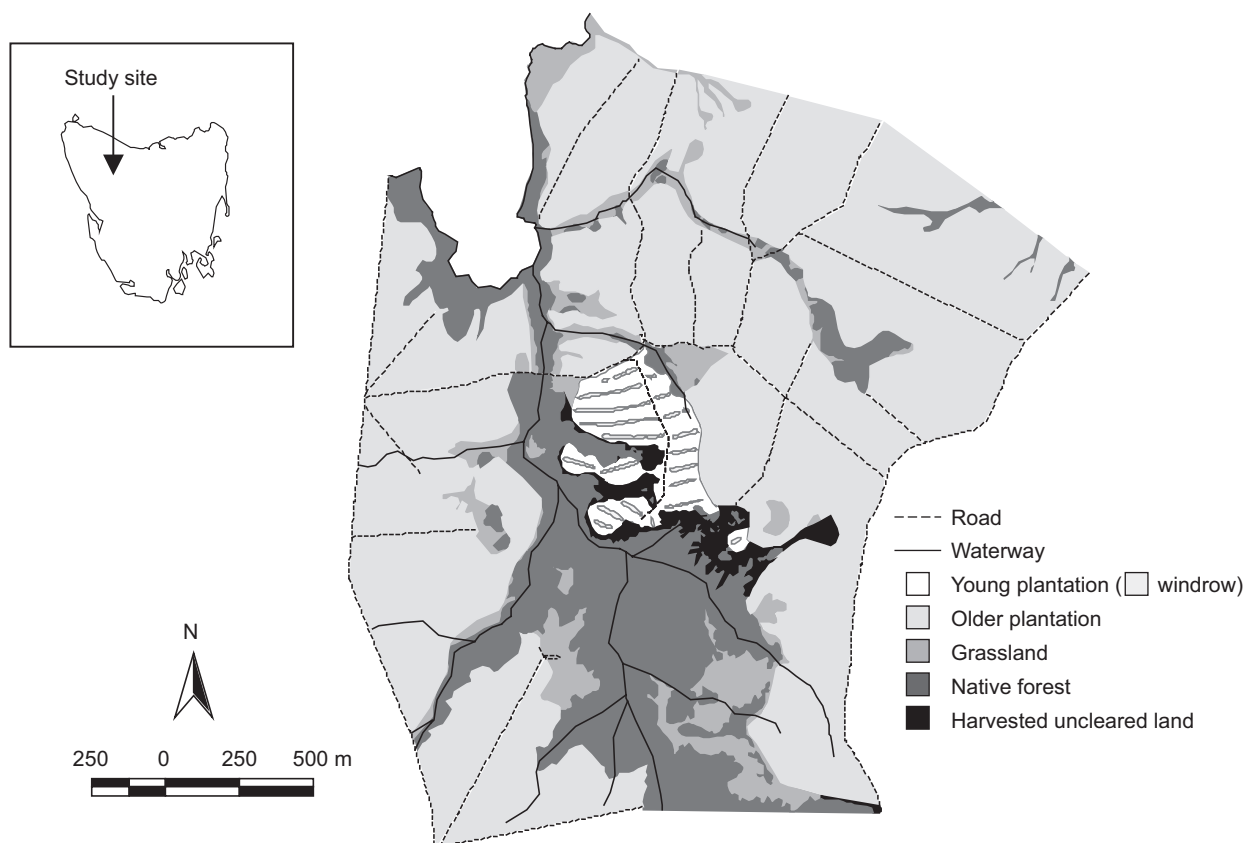


Figure 1. A map of the study site (428 ha) in north-western Tasmania showing the distribution of the five main habitat types: young plantation, older plantation, grassland, harvested uncleared land and native forest

Table 1. Descriptive statistics of the area, number and size of habitat patches within the study site (428 ha) in north-western Tasmania

Habitat	Habitat area			Patches within habitat		
	ha	% of site	No.	Mean size (ha)	Median size (ha)	Range (ha)
Young plantation	18	4.2	2	9	n.a.	2.0–16.0
Harvested land	8	1.8	4	1.9	1.2	0.3–4.9
Grassland	38	8.9	21	1.8	0.9	0.1–10.8
Native forest	89	20.8	33	2.7	0.2	<0.1–64.8
Older plantation	275	64.3	4	68.3	44.0	1.6–183.8

wet eucalypt forest); (iii) grassland; (iv) a prepared forestry plantation site with relatively high weed cover, planted with *E. nitens* tree seedlings during the study (hereafter referred to as 'young plantation'); and (v) harvested uncleared land (scrub and fallen vegetation).

The young plantation was the focus of the study. It was selectively logged some time before clearing in March 1996 and *E. nitens* seedlings (height 13–15 cm, 1100 ha⁻¹) were planted in November 1997. Seedlings were spot-herbicide within a 0.5 m radius with Roundup® (glyphosate) within one week of planting and were fertilised (100 g of Pivot® fertiliser (18N:20P:0K)) six weeks after planting. The potential for a full complement of weedy vegetation was provided by applying the herbicide as a spot treatment rather than broadcasting. Staff from NFP performed all forestry operations.

Methods

Population surveys and densities of mammalian herbivores

We used nocturnal line-transect sampling to estimate herbivore densities during eight sampling periods between May 1997 and March 1998. Each sampling period consisted of spotlighting on six nights, 2–3 nights apart, over 17 days. Sampling methods are described in detail elsewhere (le Mar *et al.* 2001). In brief, 84 permanent transect lines were located within four habitats: 30 in older plantation, 20 in native forest, 10 in grassland and 24 on the young plantation. We did not survey harvested uncleared land because visibility was extremely restricted (often < 1 m) due to dense vegetation cover. Transect lines were surveyed at night by a two-person team walking in single file at 1 km h⁻¹, using a 100 W spotlight. Both ground and canopy were searched for animals. Perpendicular distances to sighted animals were recorded using established distance categories marked by wooden stakes and reflectors (le Mar *et al.* 2001). Data collection began one hour after sunset and was completed within six hours.

When there were sufficient sightings to produce valid sighting histograms (Buckland *et al.* 1993), line-transect methodology (Buckland *et al.* 1993) and the software program DISTANCE (Laake *et al.* 1994) were used to calculate densities of the two macropod species for each habitat, during each sampling period (le Mar *et al.* 2001). Data were analysed for individuals rather than clusters (Buckland *et al.* 1993) as individuals of both species are essentially solitary (Strahan 1991). Akaike's Information Criterion was used to select the best of four candidate line-transect models (key function/adjustment: uniform/cosine, uniform/polynomial, half-normal/hermite and hazard-rate/cosine) (Buckland *et al.* 1993).

Buckland *et al.* (1993) recommend 60–80 sightings to accurately estimate the sightability parameter. This sample size was not achieved during individual sampling periods for the five species in any habitat. Consequently, this parameter was calculated from data pooled over time for each species in each habitat type, on the assumption that variation in sightability across time was likely to be insignificant relative to variation between species and habitats. Where too few sightings were obtained to produce valid sighting histograms, strip-transect analysis was used to estimate the density of a species (le Mar 2002).

At each sampling period, population density for each species in each habitat was calculated as the number of individuals per hectare, using transect as the unit of replication. Overall population density (\hat{D}_T) for each species was then calculated from the densities for the four habitats, averaged over time, and the proportion of habitat available (from Table 1, excluding harvested uncleared land) as:

$$\hat{D}_T = \Sigma[\hat{D}_i i(A_i/A)] \quad \text{and} \quad \text{se} = \sqrt{[\Sigma\{(A_i/A)^2 \text{var}(\hat{D}_i)\}]}$$

where \hat{D}_i is the mean density in habitat *i*, se is its standard error, A_i is the area of habitat *i* and *A* is the area of the study site.

Biomass density for each species was calculated as overall population density multiplied by average body mass. Possum body mass was obtained from trapped animals used in a telemetry study (le Mar 2002). Body mass estimates for pademelons, wallabies, wombats and rabbits were taken from Strahan (1991).

Effect of mammalian herbivores on non-seedling plantation vegetation

Two treatments (fenced and unfenced) were used to measure consumption of vegetation by mammalian herbivores in the young plantation. Unfenced plots were accessible to all mammalian herbivores while fenced plots excluded all except possums. Both plot treatments were accessible to insects. A third treatment (fenced plus netting roof) was used to exclude all herbivores, but as the roof appeared to change the microclimate within the plot, confounding results (le Mar 2002), it is not considered here. It was not possible to have treatments targeting each ground-dwelling species separately. Fifteen plots per treatment were set up between February and March 1997, about eight months before tree seedlings were planted on the young plantation. Plots measured 6 m × 8 m and were randomly located on a 50-m grid. Treatment type was also randomly allotted to each plot. Unfenced plots were marked using wire 'pig-tails' and surveyors tape. Fenced plots were constructed using steel fence posts and wire poultry netting (1.8 m high, 1 mm gauge, 50 mm spacing). Fences were about 1.3 m high and netting at the bottom of each fence was buried to a depth of 0.2 m to prevent burrowing animals from accessing plots. Although possums can readily climb fence netting, wooden ramps were attached to fences to enhance access to the plots.

Vegetation data were collected on seven occasions; four before planting tree seedlings and three after planting. Sampling intervals were the same as used for collecting spotlighting data, although it was not possible to collect data at sampling period 2 due to heavy snow cover.

Vegetation was described as seven categories: (i) grasses, (ii) forbs, (iii) shrubs, (iv) trees, (v) non-grass monocots (rushes, irises and orchids), (vi) moss, lichen and fungi and (vii) ferns. Many specimens could not be identified beyond genus as they were cropped by herbivores and/or were lacking reproductive structures. Data were collected for plant matter that was considered potential food available to animals. Partially dried-off grasses and dried grasses with seedheads were included (Jarman 1994), but dead vegetation within other categories was not.

Vegetation within plots was sub-sampled, using four haphazardly selected quadrats (1 m × 1 m) per plot. To avoid destructive sampling, data collection within each quadrat included a visual estimate of percent cover of vegetation, vegetation height and proportional biomass of each plant category. Height was taken as the highest point where vegetation intercepted the ruler at (usually 20) randomly allocated points within a quadrat. Vegetation that had been clipped in preparation for herbiciding, or had been sprayed with herbicide, was not measured. We estimated an index of total biomass using the average plot height multiplied by percent cover. It was further partitioned using the proportional biomass estimates for the seven plant categories. A previous study (Sprent 1997) had confirmed this method as being at least as accurate as the dry-weight-rank method (Mannetje and Haydock 1963) compared with destructive sampling.

To estimate biomass of the two major vegetation classes (grass and forbs) removed by foraging herbivores over time, the difference in biomass indices between fenced and unfenced treatments and the proportions that these values represented of potentially available (fenced) biomass were graphed. In reality, differences in biomass and species composition between fenced and unfenced plots reflect effects of both herbivory and subsequent plant succession, but it was not possible to separate these two factors within the present study.

Mortality, defoliation levels and growth of tree seedlings

Six seedlings were planted per vegetation plot, three trees in two adjacent rows, as part of the normal process of planting the entire plantation. Data were collected for plot seedlings on four occasions: (i) on the day of planting (spring); and (ii) 2.5 weeks (summer); (iii) 9 weeks (summer); and (iv) 15 weeks (autumn) after planting. Sampling intervals ii–iv were the same as sampling periods 6–8 for the spotlighting and vegetation studies.

At each sampling period, individual seedlings were classified as 'live' or 'dead'. Dead seedlings included plants that had been pulled out of the ground or were missing. Seedlings that appeared dead from transplant shock were recorded as a separate group, but were included in total mortality. No further information was collected for dead seedlings. Defoliation was measured as a visual estimate of the percentage of a seedling's biomass that had been removed through mammal or insect browsing, recorded for all live seedlings, and quantified using a seven-point scale: Score 0 = 0%, 1 = 1–9%, 2 = 10–29%, 3 = 30–49%, 4 = 50–69%, 5 = 70–89%, 6 = 90–100%. Scores were converted to mid-point percentage values for each class for analyses and were plotted over time. The number of leaders was counted for each seedling, and seedling height (± 0.5 cm) was measured from the base of the stem to the highest point of stem or foliage in the vertical plane.

Statistical analyses

Densities of each herbivore species on the young plantation were compared immediately before and after planting of *E. nitens* seedlings (sampling periods 5 and 6) with the Wilcoxon signed rank test using the univariate procedure (Proc Univariate) (SAS Institute Inc. 1990).

The effect of fence treatment on vegetation over time was analysed with a repeated measures general linear model (SAS Institute

Inc. 1989). Results for height and cover essentially followed that of biomass since the latter was derived from the former. Only biomass results are presented here. The unit of replication was the plot, using the average of the four sampled quadrats per plot to avoid pseudoreplication. Data were log transformed after checking for normal distribution and heteroscedasticity of variance using Proc Univariate (SAS Institute Inc. 1990; Zar 1996). Tests for sphericity applied to orthogonal components were used to determine the appropriate analyses for the within-subjects factor (time) and the interaction involving this factor (time × treatment). As the test for sphericity was very significant ($P < 0.01$), a MANOVA with Pillai's Trace was used (Johnson and Field 1993; Rao 1998). Where repeated measures tests showed significant results, comparisons between treatments were made within several individual sampling periods of interest. The effect of fence treatment on each vegetation category by the end of the study (sampling period 8) was analysed with a general linear model (SAS Institute Inc. 1989) for the two most dominant vegetation categories (grass and forbs; both square-root transformed) and with the non-parametric Kruskal–Wallis test (SAS Institute Inc. 1989) for the five other vegetation categories.

The effect of fence treatment on defoliation was tested using the average midpoint values across the three sampling periods after planting, with plot as the unit of replication. For mammal browsing, the Kruskal–Wallis analysis was used due to strong heterogeneity of variance. For insect defoliation, a one-way ANOVA using the general linear model procedure (Proc Glim) (SAS Institute Inc. 1989) was used with log transformed data. Insect and mammal defoliation in unfenced plots were compared using Proc Univariate (SAS Institute Inc. 1990). The effect of fence treatment on change in height of seedlings between planting and 15 weeks after planting was tested using Proc Glim (SAS Institute Inc. 1989). Least-squares means \pm standard error are used throughout.

Results

Population densities of mammalian herbivores

Pademelons followed by wallabies dominated the study area on both a numerical and biomass basis; possums, wombats and rabbits were present in very low densities (Table 2). Overall densities of the five herbivore species appeared relatively stable throughout the study period (Table 3).

When the two most abundant species, pademelons and wallabies, are considered by habitat type (Fig. 2), densities were generally high in open habitats (young plantation and grassland), and low in closed habitats (older plantation and native forest). Data for possums, wombats and rabbits are not shown, as densities were extremely low.

There were no significant differences in densities of the five species on the young plantation before and after planting *E. nitens* seedlings (Wilcoxon signed rank tests: pademelon $P = 0.44$ (Fig. 2); wallaby $P = 0.14$ (Fig. 2); possum $P > 0.99$; wombat $P = 0.95$ and rabbit $P > 0.99$).

Table 2. Mean nocturnal density (animals ha⁻¹ ± s.e.) of each species within each habitat, overall density and biomass density (kg ha⁻¹) throughout the entire 428 ha study site, using data from May 1997–March 1998 (sampling periods 1–8)

	Young plantation	Grassland	Older plantation	Native forest	Overall density	Biomass density
Pademelon	8.66 ± 1.21*	4.91 ± 1.24*	0.86 ± 0.21*	0.36 ± 0.13	1.46 ± 0.75	7.93
Wallaby	1.96 ± 0.39*	1.37 ± 0.55*	0.07 ± 0.04	0.04 ± 0.03	0.26 ± 0.22	4.41
Possum	0.10 ± 0.04	0.13 ± 0.05	0.01 ± 0.01	0.07 ± 0.04	0.04 ± 0.07	0.16
Wombat	0.64 ± 0.13*	0.21 ± 0.07	0.03 ± 0.02	0.00 ± 0.00	0.06 ± 0.08	1.66
Rabbit	0.10 ± 0.03	0.04 ± 0.03	0.01 ± 0.01	0.00 ± 0.00	0.02 ± 0.06	0.03

* calculated using line-transect analysis.

Table 3. Overall nocturnal densities (mean + s.e.) of pademelons, wallabies, possums, rabbits and wombats throughout the entire 428 ha study area for each sampling period over 11 months

Species	May 1997 autumn	June/July 1997 winter	August 1997 winter	Sept/Oct 1997 spring	Oct/Nov 1997 spring	Nov/Dec 1997 summer	January 1998 summer	Feb/Mar 1998 autumn
Pademelon	0.68 ± 1.26	1.94 ± 10.55	1.34 ± 3.33	2.55 ± 6.52	1.36 ± 0.99	1.48 ± 1.59	1.16 ± 2.09	1.12 ± 2.30
Wallaby	0.16 ± 0.04	0.07 ± 0.01	0.19 ± 0.09	0.17 ± 0.03	0.40 ± 0.34	0.49 ± 0.89	0.21 ± 0.05	0.41 ± 0.62
Possum	0.05 ± 0.02	0.00 ± 0.00	0.02 ± 0.00	0.02 ± 0.01	0.03 ± 0.00	0.07 ± 0.03	0.09 ± 0.17	0.03 ± 0.01
Wombat	0.03 ± 0.00	0.01 ± 0.00	0.04 ± 0.01	0.15 ± 0.18	0.14 ± 0.17	0.06 ± 0.01	0.11 ± 0.17	0.05 ± 0.01
Rabbit	0.07 ± 0.16	0.02 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

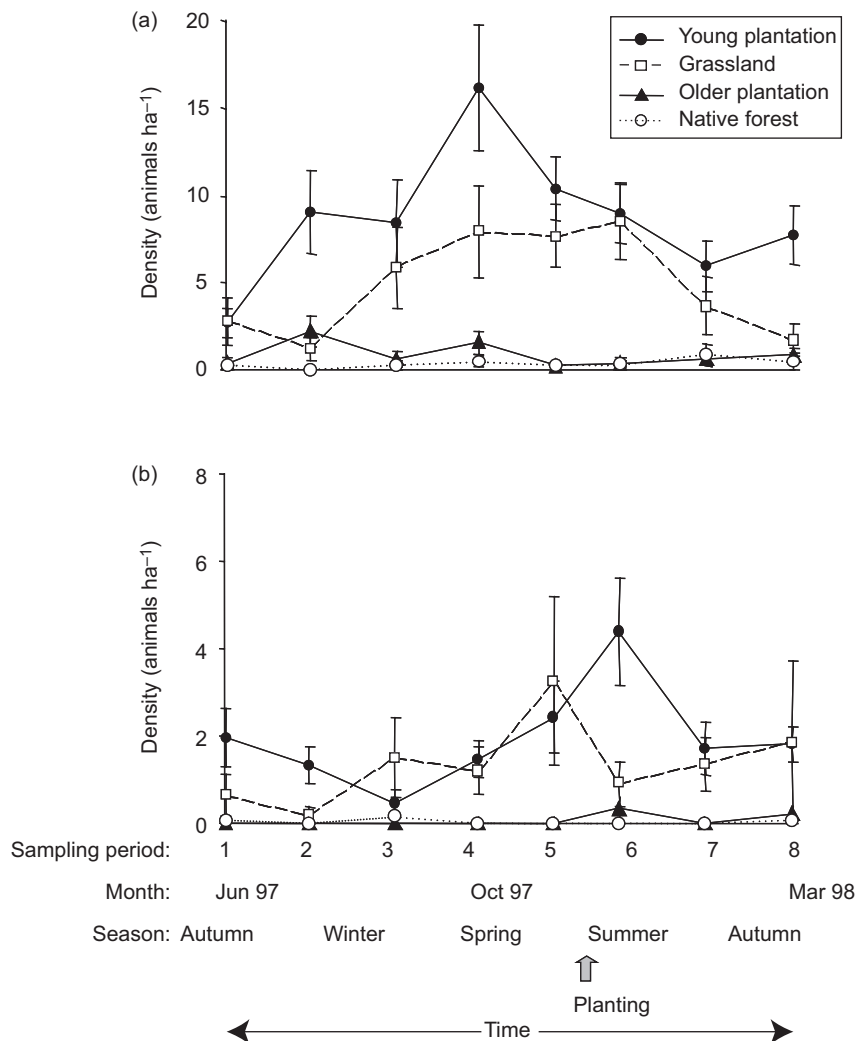


Figure 2. Nocturnal densities (mean ± s.e.) of (a) pademelons and (b) wallabies within the four habitats over the 11-month study. Grey arrow shows time of planting of commercial tree seedlings.

Effect of mammalian herbivores on non-seedling plantation vegetation

There was a significant treatment effect ($F_{1,28} = 40.67$, $P < 0.01$), time effect ($F_{6,23} = 59.69$, Pillai's Trace = 0.9397, $P < 0.01$) and time \times treatment effect ($F_{6,23} = 11.47$, Pillai's Trace = 0.7495, $P < 0.01$) on the total biomass index. Initially there was no difference between fenced and unfenced plots (Fig. 3), but in sampling periods 3–8, the biomass index was significantly higher in fenced than unfenced plots (all P values < 0.01) (Fig. 3). By the end of summer (sampling period 7), the biomass index was almost six times greater in the fenced than unfenced treatment.

Of the seven vegetation categories, five occurred in both fenced and unfenced treatments, but biomass varied considerably over time (Table 4). Trees were absent from unfenced and ferns were absent from fenced plots (Table 4). In both fenced and unfenced treatments, grass was dominant (75% of the total biomass) followed by forbs (20%) then non-grass monocots (3%) and shrubs (1%). Biomass of grasses, forbs and non-grass monocots was significantly greater in fenced than unfenced plots by the end of the study (sampling period 8) ($F_{1,28} = 22.82$, $P < 0.01$; $F_{1,28} = 20.93$, $P < 0.01$; $\chi^2_1 = 11.43$, $P < 0.01$ respectively). No difference was detected for the remaining four vegetation categories (shrubs $\chi^2_1 = 2.70$, $P = 0.10$; moss/lichen/fungi $\chi^2_1 = 0.31$, $P = 0.58$, trees (mostly native *E. delegatensis* and *Nothofagus cunninghamii* seedlings) $\chi^2_1 = 0.27$, $P = 0.60$; ferns $\chi^2_1 = 1.00$, $P = 0.32$), which were present in very low quantities.

Tall grass dominated fenced plots, and although still dominant in unfenced plots, was clipped to the ground as a result of herbivore grazing. Comparing fenced with unfenced data, the proportion of grass eaten was relatively low initially (56% in sampling

period 1), increased to a maximum of 90% in sampling period 4 then remained high (Fig. 4). Consumption of forbs was consistently high, even when present in very low biomass (70% eaten initially and up to 87% in summer). Herbivores continued to consume vegetation after tree seedlings were planted.

Mortality, defoliation levels and growth of tree seedlings

By the end of the study, seedling mortality was high but did not differ between the two treatments: fenced = 25.6% \pm 5.8; unfenced = 26.7% \pm 4.2. As expected, browsing by mammal was effectively prevented in the fenced plots. Defoliation in unfenced plots was 15.8% (\pm 2.9), which was significantly higher than 0.0% (s.e. 2.9) in fenced plots over the 15 weeks following planting ($\chi^2 = 16.464$, $df = 1$, $P < 0.01$; Fig. 5). Browsing damage by possums was not recorded in fenced plots until 15 weeks after planting, when a single plot was visited (1% of trees affected; $< 1\%$ biomass removed). At 15 weeks, 6.0% of live seedlings within fenced plots and 12.1% of live seedlings in unfenced plots had multiple leaders.

In the unfenced plots, defoliation by mammals (15.8% \pm 2.9) was less than defoliation by insects (36.5% \pm 4.8) ($t = 2.45$, $n = 15$, $P = 0.03$), which was greater in unfenced than fenced plots (36.5% \pm 4.8 and 24.4% \pm 4.8 respectively; $F_{1,28} = 4.18$, $P = 0.05$; Fig. 5).

At planting, seedlings were 15.6 cm (\pm 0.5) and 13.6 cm (\pm 0.7) in fenced and unfenced plots respectively. After 15 weeks, seedlings were 24.7 cm (\pm 1.5) and 15.5 cm (\pm 1.3) in fenced and unfenced plots respectively. Seedling height growth was significantly greater in fenced than unfenced plots (increase in height: fenced 9.0 cm (\pm 1.4); unfenced 1.9 cm (\pm 1.4); $F_{1,28} = 12.31$, $P < 0.01$).

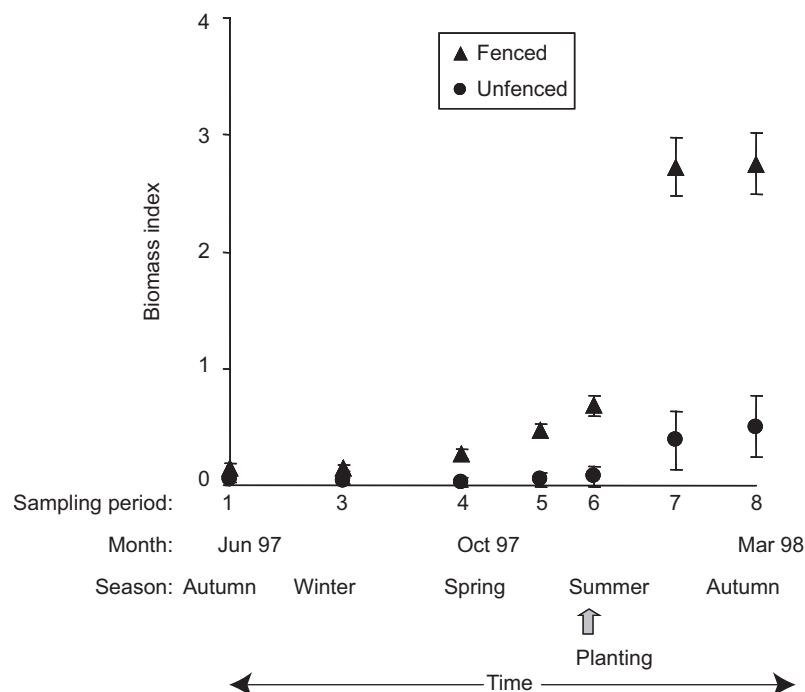


Figure 3. Biomass indices (mean \pm s.e.) of vegetation within fenced and unfenced plots, over time on the young plantation. Grey arrow shows time of planting of commercial *E. nitens* tree seedlings

Table 4. Biomass indices of the seven vegetation categories within fenced and unfenced plots (average ± s.e.) over time in the young plantation. Note that commercial *E. nitens* seedlings are not included in the tree category. Sampling periods 5 and 6 were immediately before and after planting of the *E. nitens* seedlings.

Treatment	Sampling period	Date	Season	Grass	Forb	Non-grass monocot	Shrub	Moss/lichen/fungi	Tree	Fern
Fenced	1	May 97	Autumn	1.19 ± 0.40	0.20 ± 0.06	0.05 ± 0.03	0.01 ± 0.01	0.03 ± 0.02	0.00 ± 0.00	0.00 ± 0.00
	3	Jul 97	Winter	1.35 ± 0.33	0.08 ± 0.02	0.04 ± 0.02	0.01 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
	4	Oct 97	Spring	2.39 ± 0.52	0.26 ± 0.04	0.04 ± 0.03	0.03 ± 0.01	0.03 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
	5	Nov 97	Spring	4.03 ± 0.77	0.51 ± 0.12	0.08 ± 0.04	0.05 ± 0.02	0.05 ± 0.03	0.00 ± 0.00	0.00 ± 0.00
	6	Dec 97	Summer	5.97 ± 1.09	0.67 ± 0.16	0.09 ± 0.05	0.06 ± 0.03	0.01 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	7	Jan 98	Summer	21.25 ± 3.23	4.55 ± 1.09	0.92 ± 0.36	0.51 ± 0.21	0.03 ± 0.02	0.01 ± 0.01	0.00 ± 0.00
	8	Mar 98	Autumn	21.35 ± 3.49	4.12 ± 0.86	1.26 ± 0.84	0.56 ± 0.26	0.05 ± 0.03	0.06 ± 0.06	0.00 ± 0.00
	Unfenced	1	May 97	Autumn	0.52 ± 0.29	0.06 ± 0.02	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.01	0.00 ± 0.00
3		Jul 97	Winter	0.39 ± 0.30	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
4		Oct 97	Spring	0.24 ± 0.11	0.03 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
5		Nov 97	Spring	0.37 ± 0.15	0.11 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
6		Dec 97	Summer	0.64 ± 0.24	0.12 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
7		Jan 98	Summer	2.63 ± 0.75	1.15 ± 0.34	0.01 ± 0.01	0.06 ± 0.04	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
8		Mar 98	Autumn	4.12 ± 1.30	0.76 ± 0.20	0.03 ± 0.02	0.12 ± 0.05	0.01 ± 0.00	0.00 ± 0.00	0.01 ± 0.01

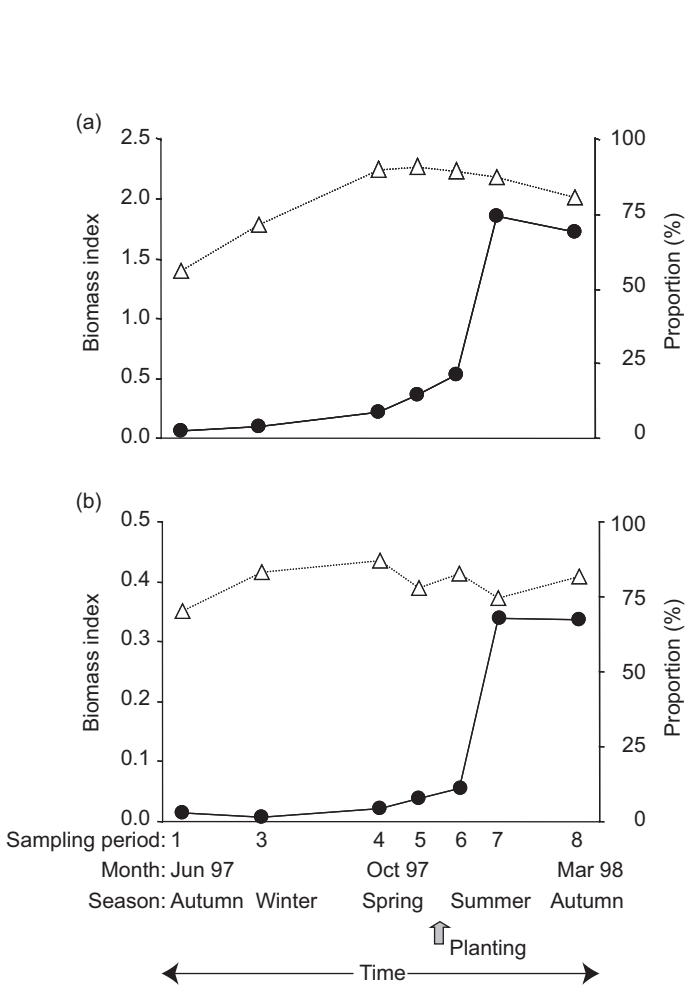


Figure 4. Biomass indices of (a) grasses and (b) forbs consumed by foraging herbivores (●), calculated as the difference in biomass between the fenced and unfenced plots; and the proportion of the available biomass that this represents (△), over time on the young plantation. Grey arrow shows time of planting of commercial tree seedlings

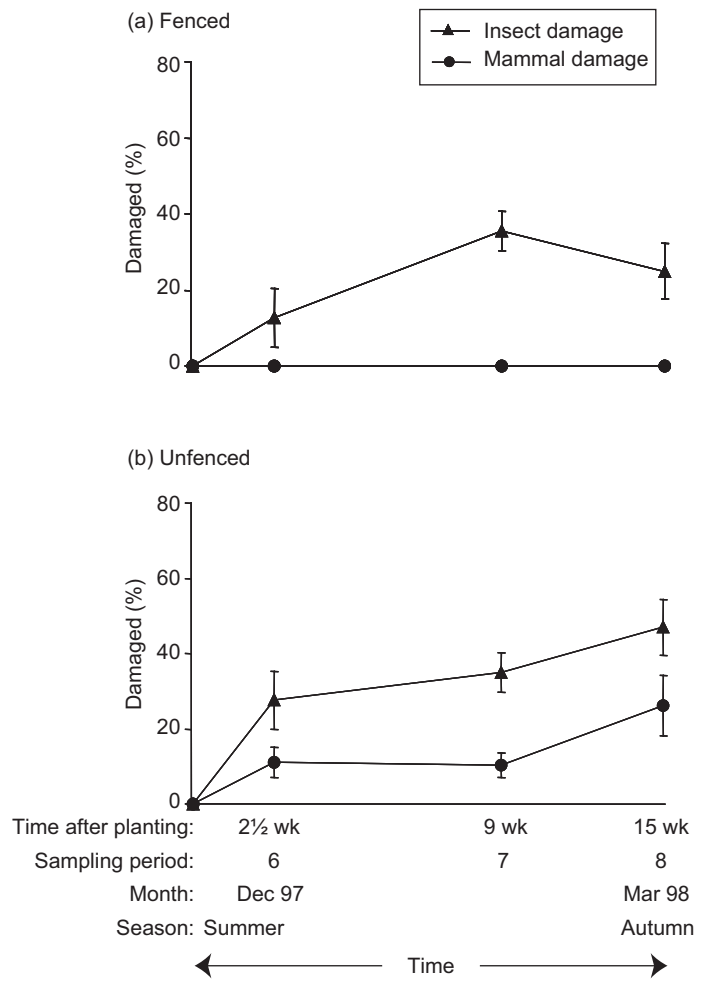


Figure 5. Foliage removed (% damaged; mean ± s.e.) by mammal and insect browsing to live *E. nitens* seedlings within (a) fenced and (b) unfenced plots over time on the young plantation

Discussion

Population densities of mammalian herbivores

The two macropod species were the most abundant herbivores in this plantation forestry environment. Pademelons were five times more abundant than wallabies, and wallaby density was an order of magnitude higher than those reported for possums, wombats and rabbits. At night, macropod densities were highest in both of the open habitats (young plantation and grassland), which reflected the abundance and diversity of grasses and forbs available in these habitats (1e Mar 2002).

Overall site population densities of the macropods were reasonably high. Density estimates are unavailable for native forest in Tasmania for comparison, but red-necked wallabies (*M. r. banksianus*) on mainland Australia range from 0.01–0.15 animals ha⁻¹ (Robertshaw and Harden 1986; Southwell *et al.* 1995) to 0.529 and 8.0 animals ha⁻¹ where native forest abuts pasture (Jarman *et al.* 1987; Southwell 1987). This latter value is similar to the local density of pademelons in the young plantation in our study and suggests that, in its current state, it is a high-quality environment for the species, consistent with our conclusion based on home range size (1e Mar *et al.* 2003).

Population densities for the other three species were all low relative to other regions within their distribution, suggesting that the environment was marginal for them. The overall possum population density (0.04 animals ha⁻¹) is an order of magnitude lower than others reported in Australia (Dunnet 1964; Hocking 1981; How and Hillcox 2000), which suggests that despite an apparent abundance of foliage for this folivore (Fitzgerald 1984; Kerle, 1984), either food, shelter such as den sites, or some other factor was limiting. The population density of wombats (0.06 animals ha⁻¹) is similar to that of a population defined as low density (<0.15 animals ha⁻¹) in Victoria, in contrast to a high reported density of 2–3 animals ha⁻¹ elsewhere in Victoria (Banks *et al.* 2002), and was concentrated in the open habitats as expected for this grazing herbivore (Barboza and Hume 1992). Similarly, the overall density of rabbits (0.02 animals ha⁻¹), again concentrated in the young plantation, was markedly lower than densities elsewhere. Densities of 25–50 rabbits ha⁻¹, for example, have been described as relatively low to moderate on mainland Australia (Croft *et al.* 2002).

The relative stability of populations over the duration of the study indicates that planting *E. nitens* seedlings did not attract animals into the study area as a whole, nor into the young plantation in particular. This result is not surprising given the small contribution that the tree seedlings made to the overall vegetation biomass on the plantation, which itself comprised only 4.2% of the study area; and the fact that the seedlings are not highly preferred, at least by pademelons (McArthur *et al.* 2000), which were the dominant herbivore.

Effect of mammalian herbivores on non-seedling plantation vegetation

Vegetation biomass was initially low, but increased rapidly from spring to summer. Feeding by herbivores had an enormous impact on the vegetation and most was eaten irrespective of abundance. The much higher levels of consumption of grasses and forbs in

the last two sampling periods of the study (sampling periods 6 and 7; Fig. 4) compared with previous periods reflect the greatly increased available biomass during the same periods (Fig. 3). Notably, increased densities of herbivores were not detected in the plantation, suggesting that the *per capita* foraging benefits were substantially greater during this summer/ autumn timeframe. From spring onwards (sampling period 4), the net reduction in biomass as a result of herbivory was between 82% and 90%. Taking into account both the feeding niches (Hume 1999) and the relative densities of the five species, we suggest that consumption of vegetation was largely due to foraging by macropods and wombats. The fact that forbs appeared to be strongly selected (high proportion eaten) even at low biomass may reflect the very high density of pademelons within this habitat and their preference for forbs (Sprent and McArthur 2002). Lack of a detected difference in biomass of the minor vegetation categories between fenced and unfenced plots suggests that these plant types were avoided by the herbivores. Alternatively, it may simply reflect a lack of resolution in our method of assessment.

Mortality, defoliation levels and growth of tree seedlings

Tree seedling mortality was very high, irrespective of plot type, by the end of the study at 15 weeks after planting. Despite the high level of defoliation by herbivores (discussed below), this is unlikely to have contributed to mortality within this timeframe, as even severe browsing over six months does not correlate with seedling mortality (Bulinski 1999). Observations suggested that at least some of the mortality was due to transplant shock.

Seedlings were severely defoliated over the 15 weeks, but insect defoliation was more than twice as great as that caused by the abundant mammalian herbivores. Scarab beetles (*Heteronyx* sp.) were considered largely responsible for this damage: they were highly abundant at this time, were seen actively defoliating seedlings, and the pattern and timing of the insect defoliation measured at this site reflects the seasonal activity of scarab beetles (Wardlaw and de Little 2000). Defoliation by possums appeared to be minimal, although their impact may have been underestimated if they avoided using fenced vegetation plots. However, as possum density has been correlated with browsing damage across *E. nitens* plantation sites (Bulinski and McArthur 2003), results are consistent with the very low possum density.

Data collected over a longer period (8 months) showed that mammal browsing at this site was largely confined to the winter period, six months after seedlings were planted and beyond the time frame presented here (1e Mar 2002). Observations at that time showed that very little non-seedling vegetation in the plantation was then available to herbivores because most of the grasses had died off. Other studies have also reported a peak in browsing damage to commercial tree seedlings over winter, when alternative food was limited (Cremer 1969; Statham 1983; Coleman *et al.* 1997).

An interesting result was the greater insect defoliation in unfenced than fenced plots (36.5% cf. 24.4% respectively). This suggests an interaction between mammalian herbivores and the insects, as it is highly unlikely that the fencing itself would have reduced insect access (D. de Little, Gunns Ltd, *pers. comm.*). Although the nature of this interaction cannot be determined here, it is

possible that the large reduction in non-seedling vegetation in unfenced plots, as a result of the mammals, increased the vulnerability of the tree seedlings to insect defoliation. This could occur through reduced availability of alternative food or enhanced apparency of the seedlings. Apparency has been suggested to be important in affecting defoliation by other beetles such as the scarab *Popillia japonica* (Rowe and Potter 2000). However, as a similar proportion of seedlings was defoliated by insects in fenced and unfenced plots ($66.7\% \pm 7.3$, $60.0\% \pm 5.4$, respectively at 15 weeks (le Mar 2002)), a difference in apparency seems less plausible. Greater knowledge of the biology of the *Heteronyx* species is required to explain this.

Results from fenced and unfenced plots enable us to compare effects of insect defoliation vs. insect plus mammal defoliation on growth of seedlings, but we cannot directly determine how these compare with an absence of defoliators. We suggest that the level of insect defoliation alone in the fenced plots was probably sufficient to reduce growth, as 20–30% loss of foliage in a similar species (*E. globulus*) over ten weeks reduced height growth in a study elsewhere in Tasmania (Close *et al.* 2002). Either way, the combined effect of insect and mammal damage in the unfenced plots further reduced height growth, essentially preventing any growth at all. Thus, despite the fact that competition between vegetation and seedlings may have been greater in fenced than unfenced plots, since grasses are generally considered severe competitors with eucalypt seedlings (Adams *et al.* 2003), seedlings still grew more in fenced plots where defoliation was lower.

Management implications

Although this study only examined relationships between mammalian herbivores, vegetation and tree seedlings on a single newly established plantation and its surrounding habitats, our results are the first to provide some biological insight into this complex set of interactions. They demonstrated that the mammalian herbivores substantially reduced non-seedling vegetation biomass in the plantation. Whether this has any potential commercial benefit remains to be seen. Reduction in competition through reduced grass cover can enhance tree growth (Adams *et al.* 2003). It is not clear, however, whether reduced above-ground biomass from herbivory, as seen in our study, actually reduced overall competition with seedlings as there may have been similar below-ground competition for water or nutrients. Whatever the potential benefit of reduced vegetation biomass, it did not outweigh the direct cost of browsing on tree seedlings, as defoliation was greater and growth was less in unfenced than fenced seedlings. Further research is clearly needed to understand the interactions between herbivory and plant-plant competition, and to elucidate the costs and benefits of manipulating these interactions in plantation management.

Our results also demonstrate that high mammalian herbivore density does not necessarily result in severe browsing of tree seedlings, possibly because there was abundant alternative food in the plantation (grass and forbs), which was readily consumed. This conclusion appears to contradict a between-plantation study (Bulinski and McArthur 2003), in which the percentage of grass cover was positively correlated with browsing damage to tree seedlings. Although it is possible that damage levels would have been lower in our study in the absence of vegetation on the site,

it is equally plausible that conclusions drawn at one scale (between-plantations) cannot be extrapolated to other scales (a single plantation).

There is no quantitative published information available on levels of insect defoliation at establishment in the forestry system we examined. Our result that insect defoliation can be greater than that caused by mammalian herbivores is therefore significant for the forestry industry. It is particularly pertinent since infrequent monitoring may result in misidentification of defoliation as mammal damage, leading to an underestimation of the damage caused by insects during plantation establishment.

An important interaction highlighted by this study was the indirect effect of mammalian herbivory on tree seedling defoliation by insects. Exclusion of mammalian herbivores resulted in higher vegetation biomass, and this was associated with decreased insect defoliation to seedlings. This suggests a complex interaction between the two types of herbivores, the non-seedling vegetation and the tree seedlings. This relationship deserves further exploration, including a much greater understanding of the insects, in order to determine the costs and benefits of using vegetation as part of a management strategy at plantation establishment.

Acknowledgements

The Cooperative Research Centre for Sustainable Production Forestry provided funding for this study. We thank North Forest Products, Burnie (now Gunns Ltd) for financial and logistical support, and in particular, Ian Blanden, David de Little, Calton Frame and Lawrence White. Christine Mann, James Dick and Jeremy Wilson kindly provided aerial photos and produced maps from Gunns' GIS. Miles Lawler and Stuart Millen assisted with data collection. Colin Southwell, Glen McPherson and David Ratkowski provided statistical advice. K. le Mar was supported by an Australian Postgraduate Award and CRC-SPF scholarships.

References

- Adams, P.R., Beadle, C.L., Mendham, N.J. and Smethurst, P.J. (2003) The impact of timing and duration of grass control on growth of a young *Eucalyptus globulus* Labill. plantation. *New Forests* **26**, 147–165.
- Banks, S.C., Skerratt, L.F. and Taylor, A.C. (2002) Female dispersal and relatedness structure in common wombats (*Vombatus ursinus*). *Journal of Zoology* **256**, 389–399.
- Barboza, P.S. and Hume, I.D. (1992) Hindgut fermentation in the wombats: two marsupial grazers. *Journal of Comparative Physiology B* **162**, 561–566.
- Buckland, S.T., Anderson, D.R., Burnham, K.P. and Laake, J.L. (1993) *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall, London.
- Bulinski, J. (1999) A survey of mammalian browsing damage in Tasmanian eucalypt plantations. *Australian Forestry* **62**, 59–65.
- Bulinski, J. and McArthur, C. (2000) Spatial distribution of browsing damage and mammalian herbivores in Tasmanian eucalypt plantations. *Australian Forestry* **63**, 27–33.
- Bulinski, J. and McArthur, C. (2003) Identifying factors related to the severity of mammalian browsing damage in eucalypt plantations. *Forest Ecology and Management* **183**, 239–247.

- Close, D., McArthur, C., Pietrzykowski, E., Fitzgerald, H. and Paterson, S. (2002) *Field Browsing Resistance of Shining Gum and Tasmanian Blue Gum Seedlings Raised under Different Nutrient Regimes in the Nursery*. Cooperative Research Centre for Sustainable Production Forestry, Hobart, Tasmania, 96 pp.
- Coleman, J.D., Montague, T.L., Eason, C.T. and Statham H.L. (1997) *The Management of Problem Browsing and Grazing Mammals in Tasmania*. LC9596/106, Manaaki Whenua Landcare Research New Zealand Ltd, Lincoln, New Zealand.
- Cremer, K.W. (1969) Browsing of mountain ash regeneration by wallabies and possums in Tasmania. *Australian Forestry* **33**, 201–210.
- Croft, J.D., Fleming, P.J.S. and van de Ven, R. (2002) The impact of rabbits on a grazing system in eastern New South Wales. 1. Ground cover and pastures. *Australian Journal of Experimental Agriculture* **42**, 909–916.
- Dunnet, G.M. (1964) A field study of local populations of the brush-tailed possum *Trichosurus vulpecula* in eastern Australia. *Proceedings of the Zoological Society of London* **142**, 665–695.
- Fitzgerald, A.E. (1984) Diet of the possum (*Trichosurus vulpecula*) in three Tasmanian forest types and its relevance to the diet of possums in New Zealand forests. In: Smith, A.P. and Hume, I.D. (eds) *Possums and Gliders*. Australian Mammal Society, Sydney, pp. 137–143.
- Gilbert, J.M. (1961) The effects of browsing by native animals on the establishment of seedlings of *Eucalyptus regnans* in the Florentine Valley, Tasmania. *Australian Forestry* **25**, 116–121.
- Hocking, G.J. (1981) The population ecology of the brush-tailed possum, *Trichosurus vulpecula* (Kerr), in Tasmania. MSc thesis, University of Tasmania.
- How, R.A. and Hillcox, S.J. (2000) Brushtail possum, *Trichosurus vulpecula*, populations in south-western Australia: demography, diet and conservation status. *Wildlife Research* **27**, 81–89.
- Hume, I.D. (1999) *Marsupial Nutrition*. Cambridge University Press, Cambridge.
- Jarman, P.J. (1994) The eating of seedheads by species of Macropodidae. *Australian Mammalogy* **17**, 51–63.
- Jarman, P.J., Johnson, C.N., Southwell, C.J. and Stuart-Dick, R. (1987) Macropod studies at Wallaby Creek. I. The area and animals. *Australian Wildlife Research* **14**, 1–14.
- Johnson, C.R. and Field, C.A. (1993) Using fixed-effects model multivariate analysis of variance in marine biology and ecology. *Oceanography and Marine Biology Annual Review* **31**, 177–221.
- Kerle, J.A. (1984) Variations in the ecology of *Trichosurus*: its adaptive significance. In: Smith, A.P. and Hume, I.D. (eds) *Possums and Gliders*. Australian Mammal Society, Sydney, pp. 115–128.
- Laake, J.L., Buckland, S.T., Anderson, D.R. and Burnham, K.P. (1994) *Distance User's Guide Version 2.1*. Colorado Cooperative Fisheries and Wildlife Research Unit, Colorado State University, Colorado.
- le Mar, K. (2002) Spatial organisation and habitat selection patterns of three marsupial herbivores within a patchy forest environment. PhD thesis, University of Tasmania.
- le Mar, K., Southwell, C. and McArthur C. (2001) Evaluation of line transect sampling to estimate nocturnal densities of macropods in open and closed habitats. *Wildlife Research* **28**, 9–16.
- le Mar, K., McArthur, C. and Statham, M. (2003) Home ranges of sympatric red-necked wallabies, red-bellied pademelons and common brushtail possums in a temperate eucalypt forestry environment. *Australian Mammalogy* **25**, 183–191.
- McArthur, C., Goodwin, A. and Turner S. (2000) Preferences, selection and damage to seedlings under changing availability by two marsupial herbivores. *Forest Ecology and Management* **139**, 157–173.
- O'Reilly, J. and McArthur, C. (1997) Damage to and intake of plantation seedlings by captive European rabbits (*Oryctolagus cuniculus*). *Australian Forestry* **63**, 1–6.
- Pietrzykowski, E., McArthur, C., Fitzgerald, H. and Goodwin A.N. (2003) Influence of patch characteristics on browsing of tree seedlings by mammalian herbivores. *Journal of Applied Ecology* **40**, 458–469.
- Rao, P.V. (1998) *Statistical Research Methods in the Life Sciences*. Duxbury Press/Brooks/Cole/ITP, Belmont, California.
- Robertshaw, D.J. and Harden, R.H. (1986) The ecology of the dingo in north-eastern New South Wales IV. Prey selection by dingoes, and its effect on the major prey species, the swamp wallaby, *Wallabia bicolor* (Desmarest). *Australian Wildlife Research* **13**, 141–163.
- Rowe, W.J. and Potter D.A. (2000) Shading effects on susceptibility of *Rosa* spp. to defoliation by *Popillia japonica* (Coleoptera: Scarabaeidae). *Environmental Entomology* **29**, 502–508.
- SAS Institute Inc. (1989) *SAS/STAT User's Guide. Volume 2. Version 6*. SAS Institute, Cary, North Carolina.
- SAS Institute Inc. (1990) *SAS Procedures Guide*. SAS Institute, Cary, North Carolina.
- Southwell, C. (1987) Macropod studies at Wallaby Creek. II. Density and distribution of macropod species in relation to environmental variables. *Australian Wildlife Research* **14**, 15–33.
- Southwell, C.J., Weaver, K.E., Cairns, S.C., Pople, A.R., Gordon, A.N., Sheppard, N.W. and Broers, R. (1995) Abundance of macropods in north-eastern New South Wales, and the logistics of broad-scale ground surveys. *Wildlife Research* **22**, 757–766.
- Sprent, J. (1997) Food availability and diet of three marsupial herbivores. BSc (Hons.) thesis, University of Tasmania.
- Sprent, J. and McArthur, C. (2002) Diet and diet selection of two species in the macropodid browser-grazer continuum — do they eat what they 'should'? *Australian Journal of Zoology* **50**, 183–192.
- Statham, H.L. (1983) *Browsing Damage in Tasmanian Forest Areas and Effects of 1080 Poisoning*. Bulletin No. 7, Forestry Commission, Tasmania, Hobart, Australia.
- Strahan, R. (1991) *The Australian Museum Complete Book of Australian Mammals*. Cornstalk Publishing, Sydney.
- 't Mannetje, L. and Haydock, K.P. (1963) The dry-weight-rank method for the botanical analysis of pasture. *Journal of the British Grassland Society* **18**, 268–275.
- Wardlaw, T. and de Little, D. (2000) Tasmania. In: Elliott, H., McArthur, C., Floyd, R.B. and de Little, D. (eds) *Proceedings of a Workshop on Managing Pests of Eucalypt Plantations*. Cooperative Research Centre for Sustainable Production Forestry, Hobart, Australia, pp. 33–43.
- Zar, J.H. (1996) *Biostatistical Analysis*. Prentice-Hall International Inc., London.