ELSEVIER

Forest Ecology and Management 144 (2001) 275–286

Forest Ecology and Management

www.elsevier.com/locate/foreco

Composition, structure, light attenuation and nutrient content of the understorey vegetation in a *Eucalyptus sieberi* regrowth stand 6 years after thinning and fertilisation

J. Bauhus[a,*], I. Aubin[a,b], C. Messier[b], M. Connell[c]

[a]*Department of Forestry, Australian National University, Canberra ACT 0200, Australia*
[b]*Groupe de recherche en écologie forestière interuniversitaire (GREFI), Dep. des sciences biologiques, Université du Québec à Montréal, C.P. 8888, succ. centre-ville, Montreal, Qc H3C 3P8, Canada*
[c]*CSIRO Forestry and Forest Products, PO Box E4008, Kingston ACT 2604, Australia*

Received 20 August 1999; accepted 21 March 2000

Abstract

In this study, we investigated the effects of commercial thinning and fertiliser application 6 years after treatment on the structure, composition, and nutrient concentrations of understorey vegetation in a *Eucalyptus sieberi* regrowth forest in East Gippsland. The stand was thinned at age 26 years , reducing the basal area by ca. 50% and lowering the stocking from ca. 1350 to ca. 250 stems ha^{-1}. Whereas the species diversity and richness of the understorey were not significantly affected by the treatments, thinning promoted the abundance of herbaceous species, and fertilisation increased the proportion of ground ferns such as *Pteridium esculentum*. Fertilisation with 100 kg N ha^{-1} and 100 kg P ha^{-1} decreased the foliage N concentration in *Tetrarrhena juncea* and *Gonocarpus teucrioides*, and increased the foliage P concentrations in four of the five most frequent species. This suggested that the understorey was more limited by P than by N. The photosynthetically active radiation above the understorey was 41% of that in the open in thinned stands and 32–34% in unthinned stands, showing that 6 years after thinning the canopy density had not yet returned to pre-treatment levels. However, light attenuation within the understorey did not differ among treatments, confirming that the understorey cover had not increased in response to increased light and nutrient availability.

The small changes in the understorey may be attributed to the fact that light and nutrients are not the major factors limiting its development, and that most species are well adapted to disturbance.

Keywords: Thinning; Fertilisation; Understorey composition; Eucalypt forest; Light attenuation

1. Introduction

The vast majority of plant species in most forest ecosystem occurs in the understorey (Ellenberg, 1986; Halpern and Spiess, 1995). In eucalypt forests, the understorey can play a particularly important role in the cycling and conservation of nutrients (Adams and Attiwill, 1984; O'Connell and Grove, 1996). The understorey structure is also an important determinant of ground-living mammal abundance (Cork and Catling, 1996), and it may be an important component of the aesthetics of forests. Forest understoreys and their diversity are related to the silvicultural manipulations of forests (e.g. Thomas et al., 1999).

* Corresponding author. Tel.: +61-2-6249-2748; fax: 61-2-6249-0746.
E-mail address: juergen.bauhus@anu.edu.au (J. Bauhus).

0378-1127/01/$ – see front matter
PII: S0378-1127(00)00403-5

The management of Australia's native eucalypt forests has traditionally been extensive (Dargavel, 1995; Florence, 1996), and past silvicultural practices have concentrated on the regeneration, fire management, and conservation of habitat and other environmental values. However, recent and prospective reductions of the forest resource available for timber production have led to the intensification of silvicultural practices in some regrowth forests close to markets. The aims of intensified silvicultural practices such as thinning and fertilisation are to enhance forest productivity in terms of quantity and quality of forest products, and to shorten the rotation length (Raison et al., 1995; Brown, 1997). Intensification of native forest management, however, may not be widely accepted if it impacts significantly on forest biodiversity and other non-timber forest values.

Silvicultural practices, such as thinning and fertilisation, have a direct influence on tree canopy cover (Stoneman et al., 1997) and, therefore, on the quantity and quality of light reaching the understorey (Cutini et al., 1998), and on the competition between trees and understorey for water and nutrients (Riegel et al., 1995; West and Osler, 1995). In addition, a portion of the understorey will be directly disturbed through heavy equipment and the deposition of harvesting slash. Perturbations imposed by these treatments may affect biological and chemical soil properties (Morris and Boerner, 1998), and diversity and structure of the understorey vegetation, and may also facilitate the establishment of weed species (Luken et al., 1997).

Previous thinning studies have documented the positive growth response of the tree component of eucalypt regrowth forests to intensified management practices (Kerruish and Rawlins, 1991; Brown, 1997; Connell et al., 1997; Stoneman et al., 1997) and some research has demonstrated the potential for increased groundwater recharge following thinning (e.g. Stoneman, 1993), but relatively little is known about the effects of intensive silviculture on understorey floristics or fauna biodiversity in eucalypt forests (e.g. Grove, 1988; Kutt, 1994; Liangmin et al., 1996). Vegetation surveys conducted within 1–3 years following thinning operations in East Gippsland provided no evidence for species elimination, but it was shown that the vegetation structure had substantially changed (Kutt et al., unpublished). However, for Douglas fir stands, Thomas et al. (1999) showed that the understorey was significantly affected by precommercial thinning and fertilisation in the longer term. After 12–16 years understorey cover was highest in stands with lowest density, and fertilisation with urea decreased species diversity. The understorey response to thinning of eucalypt forests in the longer term has not been documented. Possible effects on the understorey might be an increase in cover as more resources, light, nutrients, and water, become available through thinning and fertilisation. Increased resources, however, might reduce the plant diversity, as some species favoured by the manipulations may outcompete others (Tilman, 1982).

The objectives of the study, reported here, were to investigate changes in the structure, composition, and nutrient concentrations of understorey vegetation 6 years after thinning and fertilisation of a *Eucalyptus sieberi* regrowth forest in East Gippsland.

Our hypothesis were that (a) thinning and fertilisation increases the cover of understorey, and (b) fertilisation decreases the species diversity of the understorey.

2. Material and methods

2.1. Study site

The study site was a 32-year-old, even-aged regrowth stand of silvertop ash (*Eucalyptus sieberi*) which regenerated after a wildfire. The site is located at Boggy Creek in East Gippsland, Victoria Silvertop ash forms dry-to-moist sclerophyll forest communities in the coastal areas of southern New South Wales and eastern Victoria. This forest type is generally found on nutrient-poor soil (Costermans, 1983; Raison et al., 1995). The understorey is generally sparse and sclerophyllous (Costermans, 1983). Annual precipitation at the nearest meteorological station (Cabbage Tree Creek) averages 1084 mm and is distributed evenly throughout the year (Connell and Raison, 1996).

The silvicultural manipulations consisted of commercial thinning and various combinations of fertiliser application. The treatments used in this study were: (a) control (no thinning, no fertilisation); (b) thinned (commercial thinning with coppice control); (c) fertilised (unthinned and fertilised); and (d) thinned and fertilised (commercial thinning with coppice control and fertilisation). Commercial thinning was carried out in February 1992, when the stand was 26 years old. 'Outrows', 4.5 m wide access tracks, were used for extraction and felling of trees in the 'bays', which were at least 12 m wide between the outrows. Felling of trees was carried out using a crawler-based grapple harvester, and logs were transported with a rubber-tyred forwarder. The thinning operations aimed to reduce the basal area by ≈50%, but not below a basal area of 21 m^2 ha^{-1} (Sebire and Fagg, 1997). The stand was thinned from below by removing all of the suppressed and intermediate trees. This reduced the initial stocking of ca. 1350 stems ha^{-1} to a relatively even distribution of ≈250 stems ha^{-1}. Stems in non-merchantable dimensions were felled to waste. Coppice shoots were removed periodically from all stumps in all treatments. The fertiliser was applied by hand in grid cells overlaying treated plots in August and September 1992. The equivalent of 100 kg N as ammonium-sulphate and 100 kg P ha^{-1} as single superphosphate was applied. All treatments were replicated three times in a randomised block design; plot size was either 0.123 ha (35 m×35 m) or 0.09 ha (30 m×30 m) (Connell and Raison, 1996). The distances between plots ranged from 20 to 80 m. In November 1996, 4.8 years after the treatments were imposed, the tree heights were similar in all treatments, whereas the basal area was still substantially lower in the thinned treatments (Table 1).

In order to evaluate the effects of thinning on ground cover, light above the understorey and the floristic composition immediately following the operation, three plots were established in an area thinned 6 months before and located close to the main study site. This stand was thinned according to the same prescriptions as the main study site (Sebire and Fagg, 1997). The sampling at these plots was carried out in the same way as for plots at the main study site. Plot surveys, sampling of understorey foliage, and light measurements as describe below were carried out in March 1998.

2.2. Floristic and ground-cover survey

In order to assess the cover of understorey species, five circular sub-plots of 14 m^2 were sampled at each replicate plot. These five sub-plots were located on two transects diagonally crossing the square treatment plots. The percent cover of vascular understorey species was estimated in classes of <1, 1–5, 5–25, 25–50, 50–75, and 75–100%. Class midpoints were used for the aggregation of data. Bryophytes, fungi and lichen were not included in the survey. Trees forming the dominant canopy and overhanging the survey plots were also not included in the assessment of vegetation cover.

In order to assess whether the distribution of harvesting slash, wood and bark, or soil disturbance may have influenced the vegetation cover, an assessment of the ground conditions was carried out parallel to the assessment of vegetation cover. Ground conditions were recorded in the same classes as vegetation cover for the following three types: wood, bark and litter, and bare ground.

Table 1
Average tree height and basal area of the different treatments measured in November 1996, (n=3)[a]

Treatment	Tree height[b] (m)	Basal area[b] (m^2/ha)
Control	29.0 (0.6)	36.6 (4.7)
Thinned	30.5 (1.7)	25.4 (1.0)
Fertilised	29.0 (0.6)	32.7 (3.1)
Thinned and fertilised	31.9 (1.4)	25.8 (2.1)

[a] Coppice was controlled in all treatments.
[b] Standard error of mean is provided in parentheses.

2.3. Structure of understorey vegetation and light pattern

For assessing treatment effects on the light climate above, and within, the understorey vegetation, light attenuation patterns were determined at nine quadrats of 1 m^2 placed at equal distances along a diagonal transect across the treatment plots. The percentage of above-canopy photosynthetic photon flux density (% PPFD) was measured at the centre of each quadrat, at four different heights:

1. at 5 cm above the forest floor;
2. at 50 cm;
3. at 100 cm; and
4. above the understorey vegetation (up to 3 m).

All light measurements were made under completely overcast sky conditions following the method proposed by Messier and Puttonen (1995) and validated by Parent and Messier (1996). The photosynthetic photon flux density (PPFD 400–700 nm) was measured using an Li-190 point quantum sensor (LI-COR, Lincoln, NE). The quantum sensor is designed to measure radiation incident on a flat plane. Percent PPFD was calculated as the ratio between the instantaneous measurement made with the Li-190 in the understorey and a simultaneous measurement taken by a second Li-190 sensor linked to an Li-1000 datalogger located in a nearby open area to record above-canopy PPFD.

In order to relate light transmission to vegetation cover, the percent vegetation cover was visually estimated in strata of 50 cm in height at these 1 m^2 plots. This stratification resulted in six layers, beginning from the forest floor to above understorey vegetation (0–50, 50–100, 100–150, 150–200, 200–250, and >250 cm). In these small plots, the percent cover was recorded in classes of 5% for plant guilds identified in the understorey. The understorey plant guilds comprised grasses, vines, ground ferns, herbs, woody shrubs, sedges, and tree regeneration. The total cover recorded for a quadrat was the sum of the percent cover in all strata in that quadrat.

2.4. Nutrient status of understorey vegetation

The foliage of selected understorey plants was analysed for N and P to assess the effects of fertilisation and thinning on the nutrient status of the understorey. Foliage was collected from the five most frequent species which also represented most of the vegetation guilds. These species were bracken fern (*Pteridium esculentum*), wiregrass (*Tetrarrhena juncea*), narrow-leaf bush-pea (*Pultanea mollis*), handsome flat-pea (*Platylobium formosum*), and *Gonocarpus teucrioides*, a herbaceous species. *P. mollis* and *P. formosum* are leguminous shrubs. The collection in March 1998 was carried out at a time when the foliage of all species was fully developed.

Three foliage samples of each species were collected within each replicate plot. Samples were oven-dried at 45°C for 3 days. To reduce the number of analyses, one of the three samples was split and distributed into the remaining two samples. This produced six foliage samples for every species and treatment. Prior to analysis, the samples were finely ground and digested in concentrated sulphuric acid and peroxide. Total N and P concentrations in digests were determined colorimetrically in a continuous flow system.

2.5. Data analysis

Treatment effects on the cover of understorey vegetation were assessed for both individual plant species, and vegetation guilds. One-way and two-way ANOVA were performed for the total cover only, not for individual strata, because the strata do not represent independent samples within the vegetation profile.

The mean percent cover by understorey species was calculated for each replicate. Treatment effects on species composition were assessed using two-way ANOVA. The mean relative dominance value was calculated for each species in the following way:

$$P_i = \frac{\%C_i}{\Sigma\%C_\mathrm{q}} \quad (1)$$

where the relative dominance (P_i) of a species i is the percent cover of this species (% C_i) divided by the total cover of all species found in the survey plot (C_q).

In order to assess whether thinning and fertilisation may have affected understorey composition, a diversity index and the evenness (equitability) were calculated for each plot. The Shannon–Weaver species diversity index (H') (Whittaker, 1972) was calculated as:

$$H' = -\sum_{i=1}^{n} P_i^* \ln P_i \quad (2)$$

To calculate the diversity of understorey guilds, the relative dominance (P_i) of a guild was calculated from the relative cover of the guild.

The evenness (J) was calculated as:

$$J = \frac{H'}{\ln S} \quad (3)$$

where S is the species richness or the number of species found in the plot.

Spearman correlations were used to test relationships between the relative dominance (P_i) of species. Treatment effects on diversity, evenness and richness were assessed using two-way ANOVA. Natural logarithmic transformations were used when data did not meet the requirements of homogeneity of variances or normality of residuals for parametric analysis. All analysis were done in Systat 7.0 (Systat, 1997).

3. Results

3.1. Light attenuation by the forest canopy and understorey vegetation

The percentage of above canopy photosynthetic photon flux density (% PPFD) above the understorey and above the forest floor were higher in thinned than in unthinned stands, suggesting that the canopy density of thinned stands had not yet reverted to pre-thinning levels 6 years after thinning (Table 2). In comparison, the relative light level beneath the canopy of the recently thinned stand was 64%, suggesting that the canopy of the stand thinned 6 years ago is slowly closing, since it is now transmitting only around 40% light.

Fertilisation had no effect on the percent PPFD above and beneath the understorey. Light transmission through the understorey strata was not influenced by thinning or by fertilisation, indicating that the capacity for understorey light interception had not changed. Treatment differences in light levels at various heights in the understorey were caused by differences in tree canopy density, not in understorey density.

Linear regression analysis showed that basal area of the plots explained only 45% of the variation in relative PPFD above the understorey (p=0.003).

3.2. Ground cover

There were no significant differences in the proportion of ground exposed to mineral soil or covered by wood or bark and litter between the different treatments (data not shown). This may in part be due to the high spatial heterogeneity of ground conditions and also the low levels of slash left after the thinning operation. The survey of ground conditions suggested that re-establishment of understorey vegetation through seed germination and resprouting was not impeded by thick layers of slash.

3.3. Understorey vegetation structure, species richness and diversity

The majority of vegetation cover was found below 50 cm in height (Fig. 1). The lowest stratum was dominated by grasses in all treatments. The percentage cover of vines and tree seedlings is insignificant in all treatments. The percentage of sedges is negligible in all treatments except in the thinned and unfertilised stands. Ground ferns dominated the 50–100 cm stratum in the fertilised treatments.

Significant changes in the floristic composition were restricted to only two guilds (Table 3). Thinning increased the percent cover of herbs, and fertilisation increased the abundance of ground ferns, in particular *Pteridium esculentum*. Total understorey percent cover was not different among the treatments.

A total of 51 vascular native plant species was found, but no weeds. The species richness observed

Table 2
The average percent of above-canopy photosynthetic photon flux density (%PPFD) at four different heights in, and above, the understorey vegetation for the different treatments (n=3)[a] (The ANOVA was performed on data from 5 cm height and above the understorey vegetation and for light transmission through understorey)

Treatments[b]	Control	Thinned[c]	Fertilised[c]	Thinned and fertilised[c]
Height (cm)				
5	23 (3) b	28 (3) a	19 (3) b	27 (1) a
50	28 (2)	38 (4)	27 (3)	34 (6)
100	31 (2)	41 (3)	32 (3)	38 (4)
Above understorey	32 (3) b	41 (3) a	34 (3) b	41 (3) a
Understorey light transmission (%)	71 (5)	68 (6)	56 (8)	66 (4)

[a] Standard error of mean is provided in parentheses.
[b] Treatments were only compared at the lowest stratum, above the understorey, and for light transmission through the understorey, because intermediate layers are not independent.
[c] Treatments sharing the same letter for a given height were not significantly different at p<0.05 (ANOVA and Post-hoc Tukey test).

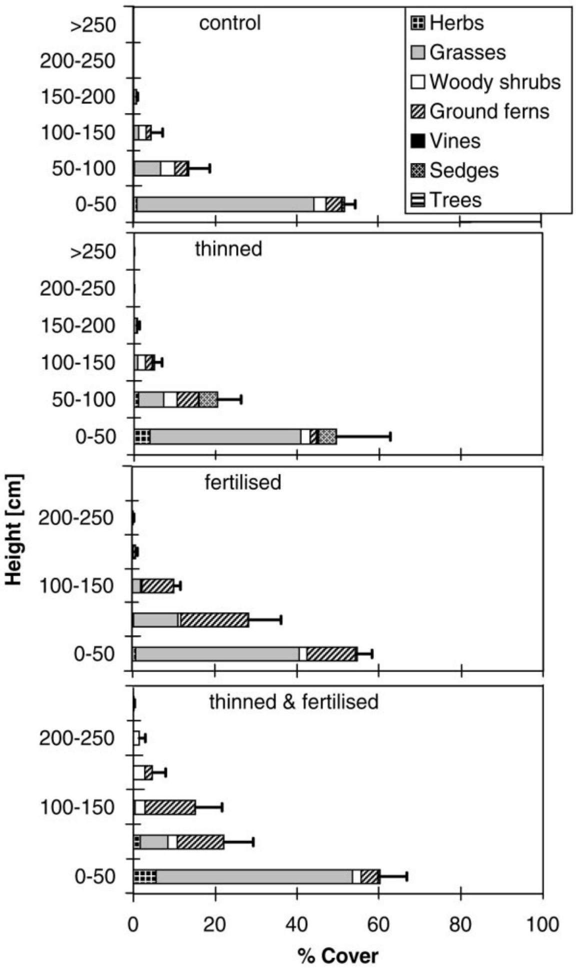

Fig. 1. Percent cover of understorey vegetation guilds in thinned, fertilised and untreated regrowth stands (determined in 1 m^2 plots). Bars indicate the standard deviation of the cover of all vegetation in a stratum.

in different treatments indicates that not all species occurred in all treatments (Table 4). Wiregrass, *Tetrarrhena juncea*, was the dominant understorey species across all treatments (Table 5). The relative importance of the most frequently observed species is provided in Table 5.

The treatments affected the percent cover and the relative importance value only in a few species. Although the relative-importance value of *Pultanea mollis* was not different between treatments (Table 5), the percent cover of this species was significantly higher in thinned and fertilised plots than in plots that were either thinned or fertilised only. The percent cover of *Pteridium esculentum* was higher in thinned and fertilised plots than in the control and the thinned plots. Cover of another ground fern, *Sticherus lobatus*, was higher in the fertilised and unthinned plots than in all other treatments. The percent ground cover of the herb *Lepidosperma urophyllum* in the thinning treatment was significantly lower than in fertiliser treatments. Thinning increased the percent cover and the relative importance of the herb *Gonocarpus teucrioides*. *Leptospermum scoparium* occurred only in the unthinned and fertilised treatment.

Neither fertilisation, nor thinning, nor the combination of these treatments significantly changed the species richness, species and plant guild diversity, and evenness of the understorey vegetation (Table 4). The species evenness in the understorey was relatively low, indicating thereby that it was dominated by a few species such as *Tetrarrhena juncea* and *Pteridium esculentum*. The distribution of guilds was more equitable.

Table 3
Percent cover by vegetation guilds for each treatment (n=3) as determined in surveys of 14 m^2 plots[a]

Treatments	Control[b]	Thinned[b]	Fertilised[b]	Thinned and fertilised[b]
Herbs	0.8 (0.3) b	5.0 (0.9) a	1.1 (0.2) b	7.3 (1.2) a
Grasses	51.1 (7.7)	44.0 (21.2)	52.6 (5.9)	55.1 (9.0)
Woody shrubs	8.9 (1.4)	8.0 (2.5)	3.3 (0.3)	11.3 (6.5)
Ground ferns	8.0 (3.2) b	8.4 (4.5) b	36.4 (6.3) a	29.5 (13.7) a
Vines	0.4 (0.2)	1.0 (0.9)	0.2 (0.2)	0.2 (0.1)
Sedges	0.8 (0.6)	9.1 (4.9)	0.4 (0.4)	0.4 (0.4)
Trees	0.0	0.2 (0.2)	0.0	0.0
Total cover	67.8 (10.6)	74 (20.0)	91.6 (8.8)	101.8 (21.1)

[a] Standard error of mean is provided in brackets.
[b] Treatments sharing the same letter for a given understorey guild were not significantly different at $p<0.05$ (ANOVA and Post-hoc Tukey test).

Table 4
Diversity measures for the understorey vegetation in all treatments[a]

Treatment	Species diversity	Guild diversity	Species evenness	Guild evenness	Species richness
Control	1.52	0.96	0.215	0.808	32
Thinned	1.54	1.21	0.239	0.593	28
Fertilised	1.23	1.18	0.187	0.668	27
Thinned and fertilised	1.53	1.06	0.231	0.651	28

[a] Diversity was calculated as the Shannon–Weaver index.

Table 5
Mean relative importance value, P_i (%), of the most frequent understorey species for each treatment[a]

Understorey species	Control[b]	Thinned[b]	Fertilised[b]	Thinned and fertilised[b]
Pultanea mollis	2.8 (1.1)	1.3 (0.7)	1.2 (0.8)	5.6 (2.6)
Platilobium formosum	4.5 (1.3)	4.5 (1.8)	2.6 (0.7)	2.1 (1.0)
Pteridium esculentum	9.0 (1.7)	7.1 (1.7)	7.3 (3.3)	21.7 (5.9)
Tetrarrhena juncea	62.5 (4.2)	50.5 (6.1)	57.8 (3.5)	48.4 (4.2)
Gonocarpus teucrioides	1.6 (0.4) a	8.4 (2.6) b	1.1 (0.4) a	8.9 (2.5) b

[a] Standard error of mean is provided in parentheses.
[b] Treatments sharing the same letter for a given species were not significantly different at $p<0.05$ (ANOVA and Post-hoc Tukey test).

The presence of *Tetrarrhena juncea* was negatively correlated with the importance value of *Gonocarpus teucriodes* ($r=-0.79$, $p=0.002$), indicating that these two species may respond differently to treatments or compete for similar niches. The relative importance of *Tetrarrhena juncea* was also negatively correlated with the Shannon–Weaver diversity index ($r=-0.71$, $p=0.01$), and with evenness ($r=-0.85$, $p=0.001$), suggesting that the diversity is lower in understorey communities in which *Tetrarrhena juncea* assumes higher importance.

3.4. Understorey foliage nutrient status

Thinning had no effect on foliar P concentrations in the five most frequent species (Table 6), whereas it

Table 6
Foliar nitrogen (mg g^{-1}) and phosphorus (mg kg^{-1}) concentration in five understorey species in regrowth *Eucalyptus sieberi* forest which were thinned, fertilised, thinned and fertilised or remained untreated; $n=3$[a]

Treatments	Control[b]	Thinned[b]	Fertilised[b]	Thinned and fertilised[b]
N (mg g^{-1})				
Pultanea mollis	15.02 (0.62)	14.90 (0.39)	16.13 (0.33)	15.60 (0.50)
Platilobium formosum	11.86 (0.53)	12.34 (0.46)	12.54 (0.38)	10.42 (0.42)
Pteridium esculentum	11.81 (0.39) a	10.38 (0.40) b	10.74 (0.33) ab	11.10 (0.31) ab
Tetrarrhena juncea	5.63 (0.34) a	6.45 (0.29) ab	3.96 (0.25) c	4.79 (0.23) bc
Gonocarpus teucrioides	9.69 (0.62) a	9.61 (0.25) a	7.42 (0.23) b	8.49 (0.35) ab
P (mg kg^{-1})				
Pultanea mollis	326 (18.4) a	358 (20.1) a	520 (30.0) b	461 (22.9) b
Platilobium formosum	206 (16.9)	279 (22.3)	351 (31.2)	239 (28.8)
Pteridium esculentum	672 (38.3) a	650 (49.5) a	934 (47.0) ab	1086 (131.5) b
Tetrarrhena juncea	166 (26.3) a	217 (18.5) ab	386 (47.2) c	354 (58.1) b
Gonocarpus teucrioides	219 (21.3) a	304 (37.1) a	670 (80.9) b	741 (157.9) b

[a] Standard error of mean is provided in parentheses.
[b] Treatments sharing the same letter for a given plant species were not significantly different at $p<0.05$, ANOVA and Post-hoc Tukey test.

slightly decreased foliar N concentrations in one species, *Pteridium esculentum*. Fertilisation, however, decreased the N concentration in *Tetrarrhena juncea* and *Gonocarpus teucrioides*, though it increased the P concentrations in *Pultanea mollis*, *Tetrarrhena juncea*, and *Gonocarpus teucrioides*. In *Pteridium esculentum*, foliar P concentrations were significantly higher in the thinned and fertilised treatment. Interactions were significant for foliar N concentrations in *Pteridium esculentum* and *Platilobium formosum*, and for P concentrations in *Platilobium formosum*.

4. Discussion

Based on our findings both the hypotheses are rejected. The increase of understorey cover following thinning and fertilisation was not significant. Neither the understorey species diversity, nor the guild diversity were significantly affected by the treatments.

The light levels above the understorey were at the lower end of values that have been reported for other native eucalypt forests. These differences may result from the use of different techniques (Lieffers et al., 1999). Values for relative light intensity found in the literature were 47% in a mature tall open *E. regnans* forest (Ashton, 1976), 45% in open forest of *E. intermedia*, 35% in tall open *E. grandis* forest (Turton and Duff, 1992), 49–56% in dry open *E. rossii*/*E. macrorhyncha* forest, and 30–41% in tall open *E. maculata*/*E. gummifera* forests (Anderson, 1981). These values are consistently higher than those measured in northern hemisphere conifer and hardwood forests, where they may range from 0.5 to 15% (Canham et al., 1990; Brown and Parker, 1994; Messier et al., 1998). The comparatively high light transmission of eucalypt canopies is consistent with the open nature of these forests with little or no interlocking of crowns and pendulous leaves.

Thinning operations had opened up the canopy, providing more light to the understorey. Shortly after a commercial thinning, we measured 64% of above-canopy PPFD above the understorey vegetation in an adjacent regrowth stand. This has decreased to $\approx$40% of above-canopy PPFD 6 years after thinning, but it was still significantly higher than in the control plots. The recovery of the canopy can be explained by an expansion of individual tree crowns and also an increase in specific leaf area in both the thinned and fertilised treatments (Connell and Raison, 1996).

Taking light transmission through the understorey as a measure of understorey density, fertilisation had not increased the density of understorey vegetation. Despite the increased quantities of light beneath the canopy of thinned stands, there was no increase in understorey cover. This finding is in contrast to studies in temperate and boreal forests in the northern hemisphere showing relatively close relationships between the tree canopy cover and understorey cover (Klinka et al., 1996; Messier et al., 1998). Kirkpatrick (1997) suggested that the openness of eucalypt canopies does not require the understorey to be shade-adapted, unless they grow beneath a dense second stratum, which was not the case at our study sites. The openness of undisturbed eucalypt canopies may be the reason why changes in the floristic composition as a result of increased light penetration following thinning were small. Our results indicate that light and nutrients are not the most limiting factors to the overall density and cover of understorey in these *E. sieberi* forests, unlike in other forest ecosystems, where the improvement of light or nutrient conditions may promote the growth of a dense understorey vegetation (Cannell and Grace, 1993; Aubin et al., 2000). It is difficult to explain the lack of a response in understorey cover, because thinning should have increased the water availability to the understorey. However, the opening of the canopy might have also increased transpiration rates of understorey plants. Different results may be obtained for thinning and fertilisation in eucalypt forests with wet sclerophyll or rainforest understoreys. Interestingly, Thomas et al. (1999) also found no clear relationship between the PPFD and understorey cover in fertilised and unfertilised Douglas fir stands thinned to three different densities. They suggested two potential reasons for this phenomenon, namely time lags in vegetation response, and the effects of physical disturbance during the thinning operation. Based on the results of the ground cover survey, the latter seems to be an unlikely explanation in our study.

The plant species richness observed at the study sites was similar to that reported by Loyn et al. (1983) for a similar forest type in East Gippsland. It has been observed that clearfelled sites in dry sclerophyll forests, with or without slash burning, are invaded by exotic vascular plant species (Loyn et al., 1983;

Dickinson and Kirkpatrick, 1987). Thinning of regrowth forests in our study, however, was not followed by invasion of exotic species. This may be explained by the lower degree of disturbance, in particular the limited area of exposed mineral soil, or the ability of the native vegetation to resprout quickly following disturbance. The site was located within a large contiguous forested area. Invasion may be more likely if thinned stands are in closer proximity to agricultural areas and weed propagules.

Based on vegetation surveys carried out shortly following thinning, Kutt et al. (unpublished) suggested that *E. sieberi* regrowth forests will have a structurally less complex understorey in the long term. Six years following thinning there were no significant differences in species richness, diversity and evenness between thinned and unthinned stands. This points to the importance of long-term monitoring of management impacts. It has often been observed that species diversity is highest a few years following disturbance (Loyn et al., 1983; Dickinson and Kirkpatrick, 1987; Attiwill, 1994). The peak in diversity at that stage of succession is generally explained by the overlapping occurrence of early successional and later successional species. The fact that thinning and fertilisation did not change species diversity indicates that these forestry operations did not significantly increase the availability of niches that could be occupied by species currently not present. Tilman et al. (1997) showed, for a grassland ecosystem, that the functional group component of diversity, similar to the diversity of plant guilds in our study, was more closely related to ecosystem properties and processes such as productivity and nutrient concentrations than the species component of diversity. In our study, there was no treatment effect on plant guild diversity, which may indicate that ecosystem processes in relation to the understorey remained largely unchanged.

The absence of management induced changes in species diversity and richness indicate that in this forest no particular species in the understorey was able to monopolise the increased resources, or the resources that were not added to outcompete other species. Although there were no treatment differences in diversity and richness, some species and plant guilds were affected by thinning. The increase in herb cover has also been reported shortly following thinning in *E. sieberi* regrowth stands in East Gippsland (Kutt et al., unpublished) suggesting that herbs, which usually occur in the lower strata of the understorey may be light limited in these forests. In the same study, it was found that *Tetrarrhena juncea* and *Pteridium esculentum* cover was lower after thinning (Kutt et al., unpublished). The absence of a thinning effect on these species in our study suggests that the decrease in cover of these two widespread species is only temporary. *Tetrarrhena juncea* was negatively correlated with plant diversity. Thus, management practices that influence the abundance of *Tetrarrhena juncea* have the potential to increase or decrease understorey diversity.

Fertilisation with 100 kg ha^{-1} N and P had no effect on understorey species richness, diversity and evenness 6 years following the application. However, the increase in ground fern abundance, in particular that of *Pteridium esculentum*, was paralleled by a significant increase in foliar P concentrations in that species. This indicates that some species might have been favoured by the increased resource supply. However, the increase in ground ferns did not result in higher light attenuation in the understorey, which may explain why there was no negative effect on other species in the fertilised and thinned and fertilised treatments.

It is interesting to note that the response of plant guilds to thinning and fertilisation in our study was very different from the response of those life-forms in a thinning and fertilisation trial in Douglas fir (Thomas et al., 1999). In their study, ground ferns showed a positive response to thinning, but a negative response to fertilisation. This included *Pteridium aquilinum*, a close relative to the most abundant ground fern at the field sites in our study. In contrast to our results, the cover of the herb layer was reduced by a light thinning, and graminoids responded positively to thinning (Thomas et al., 1999). This indicates that it will be very difficult to make any generalisations about the response of different plant life-forms to thinning and fertilisation across a range of forest ecosystem types.

The foliar nutrient concentrations of the investigated species were more affected by the P than by N application. Due to their capacity to fix atmospheric nitrogen, the response of legumes may be of particular importance for long-term site fertility. One of the two legumes studied in more detail, *Platilobium formosum*, was the only species of the five investigated that showed no increase in foliar P concentrations. Interestingly, 18 months after fertilisation, Connell and Raison (1996) had found a substantial increase in the P concentrations of leaves and twigs of *Platilobium formosum* at the same site. Their analysis showed that the increase in P concentrations was more pronounced in twigs than in leaves, which was also found by Grove (1990) for *Bossiaea laidlawiana*, an understorey legume in *Eucalyptus diversicolor* forests, in response to P fertilisation. Thus, the absence of a change in tissue concentration in *Platylobium formosum* in our study may have resulted from choosing leaves instead of twigs as the plant tissue for nutrient diagnosis.

Both leguminous species that were investigated, *Platylobium formosum* and *Pultanea mollis*, were not negatively affected by fertilisation. Grove and Malajczuk (1992) found that P fertilisation of *Eucalyptus diversicolor* forests stimulated rates of nitrogen fixation by understorey legumes as well as their biomass production. Nitrogen fertilisation, however, decreased growth of legumes and increased growth of non-leguminous species. In our experimental design, we could not separate the effects of N and P.

5. Conclusion

The effects of thinning and fertiliser application on the structure and composition of the understorey in *E. sieberi* forests were small 6 years after the treatments, which may still be early in the secondary succession in these forests. Previous studies have shown that the understorey species occurring in these forests are well adapted to disturbances such as clearfelling and burning. The practices associated with intensive regrowth management might be regarded as a less intensive disturbance event, to which the understorey species are also well adapted. The absence of a significant change in understorey density and cover following thinning and fertilisation in our study indicates that other factors such as water may be more limiting to the understorey in these dry sclerophyll eucalypt forests. These findings are in contrast to studies from temperate and boreal forests, where the understorey is usually light limited. Our findings also show that individual plant species can be favoured or disadvantaged by the practice. This could be critical in the case of rare and endangered species. To assess the effects of repeated thinning and the possible combination of thinning and slash burning on biodiversity more comprehensively, further studies are needed.

Acknowledgements

This study was financially supported by CSIRO Forestry and Forest Products. Isabelle Aubin received a travel scholarship from the University of Québec at Montreal. Further assistance was provided by Stephen Henry and Allen Trumbull-Ward, Department of Natural Resources and Environment, and Mark Lutze, Centre for Forest Tree Technology, Victoria. Thanks to Doug Walsh for assisting with the field work, and to John Marsh for carrying out the nutrient analysis. We also thank Chris Beadle and Michael Battaglia for their helpful reviews of the manuscript.

References

Adams, M.A., Attiwill, P.M., 1984. Role of *Acacia* spp. in regenerating *Eucalyptus regnans* F. Muell. forest. I. Temporal changes in biomass and nutrient content. Aust. J. Bot. 32, 205–215.

Anderson, M.C., 1981. The geometry of leaf distribution in some south-eastern Australian forests. Agric. Meteorol. 25, 195–205.

Ashton, D.H., 1976. The development of even-aged stands of *Eucalyptus regnans* F. Muell. in Central Victoria. Aust. J. Bot. 24, 397–414.

Attiwill, P.M., 1994. Ecological disturbance and the conservative management of eucalypt forests in Australia. For. Ecol. Manage. 63, 301–346.

Aubin, I., Beaudet, M., Messier, C., 2000. Light extinction coefficients specific to the understory vegetation of the southern boreal forest, Quebec. Can J. For. Res. 30, 168–177.

Brown, G., 1997. Growth responses to thinning in eucalypt regrowth forests. Tasforest 9, 105–122.

Brown, M.J., Parker, G.G., 1994. Canopy light transmittance in a chronosequence of mixed species deciduous forests. Can. J. For. Res. 24, 1694–1703.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20, 620–631.

Cannell, M.G.R., Grace, J., 1993. Competition for light: detection, measurement and quantification. Can. J. For. Res. 23, 1969–1979.

Connell, M.J., Raison, J.R., 1996. Studies on spacing, thinning and fertilization in Silvertop Ash regrowth forests of East Gippsland. A report to the Department of Natural Resources and Environment, Victoria. CSIRO, Canberra, 107 pp.

Connell, M.J., Raison, J.R., Rawlins, W.H.M., 1997. Potential benefits of intensive management of even-aged regrowth eucalypt forests. In: Bachelard, E.P., Brown, A.G. (Eds.), Preparing for the 21st century. Proceedings of the 4th joint conference of the Institute of Foresters of Australia and the New Zealand Institute of Forestry. April 1997, Canberra, ACT, Australia, pp. 127–133.

Cork, S.J., Catling, P.C., 1996. Modelling distributions of arboreal and ground-dwelling mammals in relation to climate, nutrients, plant chemical defences and vegetation structure in the eucalypt forests of southeastern Australia. For. Ecol. Manage. 85, 163–175.

Costermans, L.F., 1983. Native trees and shrubs of south-eastern Australia. Rigby, Adelaide, 422 pp.

Cutini, A., Matteucci, G., Mugnozza, G.S., 1998. Estimation of leaf area index with the LI-COR LAI 2000 in deciduous forests. For. Ecol. Manage. 105, 55–65.

Dargavel, J., 1995. Fashioning Australia's Forests. Oxford University Press, 312 pp.

Dickinson, K.J.M., Kirkpatrick, J.B., 1987. The short-term effects of clearfelling and slash-burning on the richness, diversity and relative abundance of higher plant species in two types of eucalypt forest on dolerite in Tasmania. Aust. J. Bot. 35, 601–616.

Ellenberg, H., 1986. Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. Ulmer, Stuttgart, 989 pp.

Florence, R.G., 1996. Ecology and Silviculture of Eucalypt forests. CSIRO, Melbourne, 400 pp.

Grove, T.S., 1988. Growth responses of trees and understorey to applied nitrogen and phosphorus in Karri (*Eucalyptus diversicolor*) forest. For. Ecol. Manage. 23, 87–103.

Grove, T.S., 1990. Twig and foliar nutrient concentrations in relation to nitrogen and phosphorus supply in a eucalypt (*Eucalyptus diversicolor* F. Muell.) and an understorey legume (*Bossiaea laidlawiana* Tovey and Morris). Plant Soil 126, 265–275.

Grove, T.S., Malajczuk, N., 1992. Nodule production and nitrogen fixation (acetylene reduction) by an understorey legume (*Bossiaea laidlawiana*) in eucalypt forest. J. Ecol. 80, 303–314.

Halpern, C.B., Spiess, T.A., 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol. Appl. 5, 913–934.

Kerruish, C.M., Rawlins, W.H.M., 1991. The Young Eucalypt Report — Some Management Options for Australia's Regrowth Forests. CSIRO, Melbourne, 272 pp.

Kirkpatrick, J.B., 1997. Vascular plant-eucalypt interactions. In: Williams, J.E., Woinarski, J.C.Z. (Eds.), Eucalypt Ecology: Individuals to Ecosystems. Cambridge University Press, Cambridge, pp. 227–245.

Klinka, K., Cheng, H.Y.H., Wang, Q., de Montigny, L., 1996. Forest canopies and their influence on understorey vegetation in early seral stands on west Vancouver Island. Northwest Sci. 70, 193–200.

Kutt, A.S., 1994. Arboreal marsupials and nocturnal birds in thinned regrowth, unthinned regrowth and old lowland forest, unthinned regrowth and old lowland forest, East Gippsland, Victoria. Aust. For. 57, 123–130.

Kutt, A.S., Thompson, B., Trumbull-Ward, A., Henry, S., unpublished. Impacts of eucalypt regrowth thinning on flora and fauna values in lowland forest in East Gippsland. Report to Department of Conservation and Natural Resources, Orbost, Vic., 29 pp.

Loyn, R.H., Fagg, P.C., Piggin, J.E., Morton, A.G., Tolhurst, K.G., 1983. Changes in the composition of understorey vegetation after harvesting eucalypt for sawlogs and pulpwood in East Gippsland. Aust. J. Ecol. 8, 43–53.

Luken, J.O., Kuddes, L.M., Tholemeier, T.C., Haller, D.M., 1997. Comparative responses of *Lonicera maackii* (Amur Honeysuckle) and *Lindera benzoin* (Spicebush) to increased light. Am. Mid. Nat. 138, 331–343.

Liangmin, W., Attiwill, P.M., Adams, M.A., 1996. Fertilizer impacts on the understorey of a regenerating Mountain Ash (*Eucalyptus regnans* F. Muell.) forest, Vic. Aust. J. Ecol. 21, 459–463.

Lieffers, V.J., Messeir, C., Stadt, K.J., Gendron, F., Comeau, P.G., 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29, 796–811.

Messier, C., Puttonen, P., 1995. Spatial and temporal variations in the light environment of developing Scots pine stands: the basis for a quick and efficient method of characterizing light. Can. J. For. Res. 25, 343–354.

Messier, C., Parent, S., Bergeron, Y., 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forest. J. Veg. Sci. 9, 511–520.

Morris, S.J., Boerner, R.E.J., 1998. Interactive influences of silvicultural management and soil chemistry upon soil microbial abundance and nitrogen mineralization. For. Ecol. Manage. 103, 129–139.

O'Connell, A.M., Grove, T.S., 1996. Biomass production, nutrient uptake and nutrient cycling in the Jarrah (*Eucalyptus marginata*) and Karri (*Eucalyptus diversicolor*) forests of southwestern Australia. In: Attiwill, P.M., Adams, M.A. (Eds.), Nutrition of Eucalypts. CSIRO Publishing, Collingwood, Vic., pp. 155–189.

Parent, S., Messier, C., 1996. A simple and efficient method to estimate microsite light availability under a forest canopy. Can. J. For. Res. 26, 151–154.

Raison, J., Geary, P., Kerruish, B., Connell, M., Jacobsen, K., Roberts, E., Hescock, R., 1995. Opportunities for more productive management of regrowth eucalypt forests: a case study in the *E. sieberi* forests of East Gippsland. Research, Technology and Biological Resources, 32–37 pp.

Riegel, G.M., Miller, R.F., Krueger, W.C., 1995. The effects of above-ground and below-ground competition on understorey species composition in a *Pinus ponderosa* forest. For. Sci. 41, 864–889.

Sebire, I., Fagg, P., 1997. Thinning of mixed species regrowth. Department of Natural Resources and Environment, Vic. Native Forest Silviculture Guideline No. 14, 48 pp.

Stoneman, G.L., 1993. Hydrological response to thinning a small jarrah (*Eucalyptus marginata*) forest catchment. J. Hydrol. 150, 393–407.

Stoneman, G.L., Crombie, D.S., Whitford, K., Hingston, F.J., Giles, R., Portlock, C.C., Galbraith, J.H., Dimmock, G.M., 1997.

Growth and water relations of *Eucalyptus marginata* (Jarrah) stands in response to thinning and fertilization. Tree Physiol. 17, 267–274.

Systat, 1997. Systat 7.0, New Statistics. Systat Inc., Evanston.

Tilman, D., 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, MA, 296 pp.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. Science 277, 1300–1302.

Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A., Austin, K.A., 1999. Plant diversity in managed forests: understorey responses to thinning and fertilization. Ecol. Appl. 9, 864–879.

Turton, S.M., Duff, G.A., 1992. Light environment and floristic composition across an open forest–rainforest boundary in northeastern Queensland. Aust. J. Ecol. 17, 415–423.

West, P.W., Osler, G.H.R., 1995. Growth response to thinning and its relation to site resources in *Eucalyptus regnans*. Can. J. For. Res. 25, 69–80.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251.