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Forest Ecology and Management 181 (2003) 339–355

Forest Ecology and Management

www.elsevier.com/locate/foreco

Nitrogen-fixation by *Acacia dealbata* and changes in soil properties 5 years after mechanical disturbance or slash-burning following timber harvest

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Received 15 August 2002; received in revised form 12 October 2002; accepted 17 December 2002

Abstract

Logging followed by slash-burning can result in large losses of Nitrogen from an ecosystem. *Acacia dealbata* (silver wattle) is the main N-fixing plant in *Eucalyptus regnans* (mountain ash) forest in Victoria, but its potential N-fixing capacity is uncertain. Losses of N and changes in other soil properties as a result of logging and slash-burning and inputs of N through N-fixation by *A. dealbata* were quantified in mountain ash forest near Tanjil Bren, Victoria. The study was based on four logging coupes harvested in 1988 (two burnt following harvest and two disturbed mechanically) and three areas of unlogged, 55-year-old regrowth. There was a 19% increase in concentration of potentially available N and a 48% increase in available P on burnt coupes relative to unburnt coupes, but a 12% decrease in total N and a 17% decrease in organic carbon. These differences were consistent with N and C being lost through burning and with an increase in fertility of surface soil due to the ash-bed effect. Wattles increased concentrations of potentially available N, total N and organic C and reduced bulk density of soil, but did not effect the amount of total N in soil. However, significant differences between the natural abundance of ^{15}N in *A. dealbata* and *E. regnans* and a significant inverse relationship between stocking of silver wattle and $\delta(^{15}N)$ in soil indicated that N-fixation by *A. dealbata* trees had added substantial amounts of N to both vegetation and soil. At a stocking of 2500 stems ha^{-1} *A. dealbata* was estimated to contribute 40 kg ha^{-1} per year to total N in soil and 10 kg ha^{-1} per year to total N in vegetation through N-fixation over the first 5 years. This rate of N-fixation (50 kg ha^{-1} per year) is sufficient to replace an estimated loss of 430 kg N ha^{-1} due to timber harvesting and burning in 9 years.

Keywords: Nitrogen-fixation; *Acacia dealbata*; Slash-burning

1. Introduction

Logging operations remove nutrients held in the wood and bark of trees taken from the forest. Slash-burning causes nutrient loss through volatilization and particulate convection during the fire (e.g. Raison, 1980), and erosion and leaching of the ash-bed afterwards (e.g. Smith, 1970). Mechanical disturbance of the soil during timber harvesting or site preparation causes less initial loss of nutrients than burning, but there may be substantial redistribution of nutrients. Unless the inputs of these and other nutrients over a logging rotation are sufficient to replace the amounts lost, there will be a net reduction in the availability of N to plants over the long term.

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0378-1127/$ – see front matter
doi:10.1016/S0378-1127(03)00006-9

Attiwill (1984) estimated total gains and losses of N in a high-rainfall eucalyptus forest harvested on a 100-year rotation. Losses due to removal of timber and bark during harvest are 300 kg N ha^{-1}, while losses from the vegetation and soil due to burning of slash are 530 kg ha^{-1}. A further 50 kg N ha^{-1} is lost by leaching. Thus, a total of 880 kg N ha^{-1} is lost during harvesting and burning of the forest. Over 100 years, Attiwill (1984) estimated that 300 kg N ha^{-1} is replaced through rainfall and a further 150 kg N ha^{-1} is replaced through asymbiotic N-fixation by blue–green algae in the soil. Thus the balance that must be replaced by symbiotic N-fixation over a rotation is 430 kg N ha^{-1}.

Acacia spp. occur in the understoreys in many Australian ecosystems. Fast-growing trees such as *Acacia dealbata* (silver wattle) and the closely related *Acacia mearnsii* (black wattle) have been recognized as being important in balancing N losses due to timber harvesting in natural ecosystems and in reducing the need for fertilizer application in plantations (Baker and Attiwill, 1981).

A. dealbata occurs naturally in south-eastern Australia from Tasmania to northern New South Wales at altitudes ranging from 50 to 1000 m, and across a wide range of soil types and rainfall (600–1000 mm). However, the largest specimens occur in tall open forests (>30 m tall with a projected foliage cover of 30–70%, Specht, 1970) of *Eucalyptus regnans* (mountain ash), on deep well drained soils in moist mountain valleys, and where annual rainfall exceeds 1000 mm. *A. dealbata* occurs as a secondary tree in these forests, reaching heights of 25–28 m.

E. regnans forests are adapted to regenerating naturally after being destroyed by wildfire (Ashton and Attiwill, 1994). Both *E. regnans* and *A. dealbata* regenerate in profusion from seed after fire or logging, growing rapidly (1–1.5 m per year) and competing strongly with each other. *A. dealbata* is often considered to be an undesirable species reducing the growth of the economically more important *E. regnans*.

A number of studies have attempted to quantify the amount of nitrogen-fixed by wattles in natural environments, ranging from semi-arid to tall open forests, in Australia (Adams and Attiwill, 1984b; Hamilton et al., 1993; Hansen et al., 1987; Lawrie, 1981; Langkamp et al., 1979; Monk et al., 1981). The only estimate of the rate of nitrogen-fixation by *A. dealbata* in the field is 12–32 kg ha^{-1} per year for 2-year-old trees in tall open-forests (Adams and Attiwill, 1984b). At this rate, net losses of N due to clearfelling and burning would be replaced through N-fixation by *A. dealbata* over 14–36 years. However, the estimate was based on the acetylene reduction assay, which has significant errors (Minchin and Witty, 1989). Furthermore, rates of N-fixation undoubtedly vary considerably with site productivity, numbers of wattles and tree age. Thus, it is difficult to extrapolate these rates of N-fixation over time and across large areas.

The aims of this study were to (a) compare the effects of timber harvesting and site preparation (mechanical disturbance versus slash-burning) on soil nutrient concentrations and contents, and (b) determine the amount of N added to soil and vegetation through N-fixation by *A. dealbata* trees 5 years after harvest.

2. Method

2.1. Study areas and experimental sites

The study area was located near Tanjil Bren, 150 km east of Melbourne in the central highlands of Victoria. It was based on four cutting areas (coupes) on Ballantynes Spur (37°50.3′S, 146°09.3′E; altitude 640–840 m) that were harvested in summer 1987/1988 and three areas of unlogged mountain ash (*E. regnans*) forest that regenerated after bushfires in 1939 (‘unlogged forest’). Two of the coupes were burned (‘burnt coupes’) and two were mechanically disturbed (‘unburnt coupes’) in autumn after harvest. The four coupes formed part of the Silvicultural Systems Project established, using a random block design, by the Center for Forest Tree Technology in the Department of Natural Resources and Environment, Victoria (Squire, 1987). Climate, soils and vegetation in the study area and methods of timber harvesting and site preparation used on the coupes are described by Rab (1996). In the unlogged forest on Ballantynes, five plots were established adjacent to the burnt and unburnt coupes on similar soils and topography to those on the coupes. The other areas of unlogged forest included Rabbit Patch, 20 km to the north (37°48.0′S, 146°04.1′E; altitude 700–730 m) and East Tanjil, 10 km to the east (37°50.8′S, 146°11.7′E; altitude 520–560 m) of the main experiment. All plots in both logged and unlogged areas were on similar terrain (moderately steep hills with slopes varying from 5 to 20°) and soil (red gradational, 1.5–3 m deep over granitic parent material, Northcote et al., 1975).

The regeneration on the burnt and unburnt coupes was 5 years old when soil was sampled, and the unlogged forest was 54–55 years old. Silver wattle was the only species of wattle on the sites on Ballantynes Spur, but hickory wattle (*Acacia obliquinervia*) occurred also at East Tanjil and Rabbit Patch. Mountain ash was the dominant eucalypt, with scattered mountain grey gum (*E. cypellocarpa*).

A random block design was used to select plots on the burnt and unburnt coupes. In each coupe, three blocks were established, each block containing three plots (4 m × 4 m) with either low, medium or high stocking of silver wattle. In the unlogged forest on Ballantynes Spur, a similar design was used in which blocks were located in five different areas surrounding the four coupes. In each block, three plots (10 m × 10 m) were established, again with either low, medium or high stocking of silver wattle. In the unlogged forest at East Tanjil and Rabbit Patch, 12 plots of 10 m × 10 m were laid out on a 50 m × 50 m grid.

2.2. Soil sampling

Sub-samples of soil were collected from two depths in each plot (unlogged forest: 10 sub-samples at 0–10 cm; burnt and unburnt coupes: 16 sub-samples at 0–5 and 5–10 cm) and bulked for each depth. This gave two duplicate bulked samples per plot in the unlogged forest and two duplicate bulked samples per plot for each depth in the 1988 regrowth. Moisture content and bulk density were determined for each bulked duplicate sample. Part of each sample was stored at 0 °C for 1 week and passed through a 2 mm sieve (field moist soil) and the other part was air-dried and ground to pass through a 0.2 mm sieve (air-dried soil).

2.3. Vegetation sampling

Diameters of all silver wattle and mountain ash in each plot were measured. On the burnt and unburnt coupes the competitive position of each tree was assessed (dominant or suppressed) and the heights of the tallest silver wattle and tallest mountain ash measured.

The tallest mountain ash and tallest wattle on each plot in the 1988 regrowth were felled and divided into trunk (to 20 mm diameter), branches (>6 mm diameter) and leaves and twigs (<6 mm diameter). The stem of each tree was sawn into 1 m sections, weighed and discs were sawn from the base of the stump and from the top end of each section. Branch, leaf and twig components were weighed and sampled. The samples of each component dried at 80 °C for 1 week and the dry mass of each component calculated. The branch and trunk samples were then chipped. All material of each sample was coarsely ground and a sub-sample from each sample was finely ground (<0.2 mm).

Total biomass of the above-ground silver wattle was determined from the fitted relationship between cross-sectional area and biomass of the felled trees. The same method was used to calculate the above-ground N content of silver wattle.

2.4. Chemical analysis

Total N in air-dried soil was analyzed as NH_4-N after digestion in H_2SO_4 with 0.4% selenium (Bremner and Mulvaney, 1984). Potentially available N was extracted by boiling field moist soil in 1 M KCl for 60 min (Whitehead, 1981) and analyzed as NH_4-N and NO_3-N. Available P was extracted using Bray and Kurtz no. 2 extraction (Jackson, 1958). A Technicon Auto Analyzer (Technicon Instruments, 1977a,b) was used for all analyses of N and P. Organic C was analyzed as Walkley-Black C (Hesse, 1971). Bulk density and concentrations and contents of nutrients in soil from 0 to 10 cm on unburnt and burnt coupes were calculated as weighted averages for the two depths (0–5 and 5–10 cm).

Total N in vegetation samples was analyzed as NH_4-N after digestion in H_2SO_4 with 0.4% selenium and H_2O_2 (Bremner and Mulvaney, 1984).

2.5. ^{15}N Analysis

Soil and vegetation samples were prepared and analyzed using the method described by Unkovich et al. (1993a). From each sample, an amount of material estimated to contain 1.2 mg N was digested in H_2SO_4 with a catalyst (K_2SO_4, $CuSO_4$ and Se). Digests were then distilled with 20 ml NaOH and 50 ml of the distillate was collected using 2 ml boric acid as a trap for ammonia. The distillates were then titrated against 0.025 M H_2SO_4 for the quantitative determination of N concentration. Two drops of 5 M H_2SO_4 were added to each distillate before reduction by heating. The reduced distillates were transferred to 5 ml glass vials and evaporated at 60 °C until dry.

Samples were analyzed for ^{15}N content using a VG Isogas mass spectrometer (Sira 10) standardized against $(NH_4)_2SO_4$ with an ^{15}N abundance of 0.3662 at.% after reacting with lithium hyperbromite in an evacuated chamber and removing unreacted bromine, CO_2 and water by freezing. The abundance of ^{15}N in the N_2 gas released was analyzed using a mass spectrometer.

2.6. Calculations

The difference between the ratio of atoms of ^{15}N:^{14}N in soil or plant samples (R_{sample}) and that in a standard such as air ($R_{standard}$) is expressed in terms of $\delta(^{15}N)$ in parts per 1000:

$$\delta(^{15}\mathrm{N}) = \frac{R_{\mathrm{sample}} - R_{\mathrm{standard}}}{R_{\mathrm{standard}}} \times 1000$$

In the ^{15}N natural abundance method the term at.% (i.e. atoms of ^{15}N relative to the total number of N atoms) is substituted for R. Although at.% is theoretically lower than R, the value for $\delta(^{15}N)$ is effectively the same provided that concentrations of ^{15}N are low (Shearer and Kohl, 1986).

The general formula for determining the proportion of N in plants that is acquired through N_2 fixation (P) is:

$$P = \frac{\delta(^{15}\mathrm{N}_{\mathrm{reference\ plant}}) - \delta(^{15}\mathrm{N}_{\mathrm{legume}})}{\delta(^{15}\mathrm{N}_{\mathrm{reference\ plant}}) - \beta} \times 100$$

where β is the $\delta(^{15}N)$ value for legumes grown with air as their only source of N. The best estimate for β in *Acacia* spp. is −1.3 in above-ground components of plants grown for 6–7 months (Stock et al., 1995) and is within the range of −1.0 to −1.9 reported for other plants (Domenach et al., 1989; Mariotti et al., 1992; Shearer et al., 1983). The total amount of N-fixed is thus the proportion of N obtained through fixation multiplied by the total amount of N in the plant. The amount of N in the soil derived from fixation can be calculated in the same way, by comparing the mean $\delta(^{15}N)$ values for soil from plots with no wattles with those from plots with wattles:

$$P = \frac{\delta(^{15}\mathrm{N}_{\mathrm{soil\ with\ no\ wattles}}) - \delta(^{15}\mathrm{N}_{\mathrm{soil\ with\ wattles}})}{\delta(^{15}\mathrm{N}_{\mathrm{soil\ with\ no\ wattles}}) - \beta} \times 100$$

$\delta(^{15}N)$ of soil with no wattles was assumed to equal that of soil from low stocking of wattle. The value for β is assumed to be the same because the N in the soil derived from N-fixation was originally plant material. The total amount of N-fixed is calculated by multiplying P by the content of N in the soil.

2.7. Analysis of results

Significance of the effects of stocking class of wattle and site preparation on soil nutrients and bulk density were tested with a General Linear Model (Genstat) using a nested design to remove variation due to coupe and block. Relationships between stocking or basal area of dominant or total wattles and soil nutrients and bulk density were tested by adding these variables to the models as covariates in place of stocking class of wattle and in simple linear regressions. The probability level used to determine significance was $P < 0.050$. Least square differences (L.S.D.) and 95% confidence limits for means were calculated using results from the models with the lowest mean square error and most normally distributed residuals.

3. Results

3.1. Stocking of *A. dealbata* on burnt and unburnt coupes and 1939 regrowth

There was no significant difference between stocking of dominant wattles or total basal area of wattles on unburnt and burnt coupes, but basal area of dominant wattles was significantly greater on unburnt coupes (Table 1). The number of dominant wattles at high stocking was more than double that at medium stocking at 4 years. Between the fourth and fifth years, stocking of dominant wattles decreased by an average 14% through gradual suppression of previously

Table 1
Stocking and basal area of *A. dealbata* trees and bulk density and concentrations and contents of organic C, available P, potentially available N, total N and ratio of C:N in soil (0–10 cm) for areas with low moderate and high stocking of *A. dealbata* in unlogged forest and on unburnt and burnt coupes

Stocking class of wattles	Silver wattle			Soil								
	Stocking (stems ha^{-1})	Basal area (m^2 ha^{-1})	Bulk density (t m^{-3})	Potentially available N		Total N		Organic C		C:N	Available P	
				(ppm)	(kg ha^{-1})	(%)	(kg ha^{-1})	(%)	(t ha^{-1})		(ppm)	(kg ha^{-1})
Unlogged forest surrounding coupes at Ballantyne Spur												
Low	5 a	0.2 a	0.371	64 a	24.1 a	0.80 a	2920	11.8	42.5	14.7	7.1	2.57
Medium	83 a	5.1 a	0.359	65 a	22.8 a	0.86 ab	3030	12.8	44.2	14.9	7.2	2.45
High	259 b	22.7 b	0.330	100 b	31.9 b	1.00 b	3170	13.3	42.8	13.5	6.3	2.04
L.S.D.	124	10.1	0.067	27	7.3	0.18	350	2.2	3.6	1.4	1.7	0.57
Mean	116	9.4	0.353	76	26.3	0.89	3040	12.6	43.2	14.4	6.9	2.35
L.S.D. (for comparison with unburnt and burnt coupes)	38	3.6	0.065	13	4.0	0.11	410	1.8	5.7	1.5	2.8	1.29
Coupes at Ballantyne Spur												
Low	210 a	1.3 a	0.525 a	52.3 a	27.2 a	0.52 a	2660	7.8	40.0	15.2	8.5	4.34
Medium	2450 b	5.5 b	0.489 ab	65.8 b	31.4 b	0.58 ab	2770	8.3	39.5	14.4	6.7	3.41
High	5420 c	15.4 c	0.457 b	65.8 b	29.5 ab	0.61 b	2690	9.0	39.9	14.9	7.5	3.44
L.S.D.	810	2.4	0.054	9.8	3.0	0.08	350	1.4	4.9	1.0	2.5	1.15
Main effects of site preparation of coupes												
Unburnt	2670	9.7 a	0.458 a	59.1	26.8 a	0.64 a	2870 a	9.7 a	43.5 a	15.2	6.6 a	3.04 a
Burnt	2570	5.1 b	0.523 b	63.5	32.0 b	0.50 b	2540 b	7.0 b	36.1 b	14.5	8.6 b	4.48 b
L.S.D.	770	2.3	0.051	9.2	2.9	0.07	330	1.3	4.6	1.0	2.4	1.09
Mean	2690	7.4	0.490	61	29.4	0.57	2710	8.4	39.8	14.8	7.6	3.73
L.S.D.	470	1.4	0.031	5.6	1.7	0.04	200	0.8	2.8	0.6	1.5	0.66

L.S.D.: least square differences; and letters signify significant differences between means.

dominant wattles, as a result of inter- and intra-species competition.

In unlogged forest adjacent to the burnt and unburnt coupes, stocking of wattle varied from 5 stems ha^{-1} on plots with low stocking to 259 stems ha^{-1} on plots with high stocking (Table 1). Average basal area of wattle was 2.2 m^2 ha^{-1} at East Tanjil, 3.9 m^2 ha^{-1} at Rabbit Patch and 5.1 m^2 ha^{-1} on plots with medium stocking on Ballantynes Spur.

3.2. The effect of site preparation on soil properties

Bulk density of soil was significantly (12%) less on unburnt coupes than on burnt coupes and was 33% less in unlogged forest on Ballantynes Spur than on unburnt coupes (Table 1).

The amount (kg ha^{-1}) of potentially available N in soil was significantly (19%) greater on unburnt coupes than on burnt coupes and the average amount of potentially available N in unlogged forest was the same as that on unburnt coupes. Concentrations and contents of available P were 31 and 48% greater, respectively, on burnt coupes compared with unburnt coupes. Average content of available P on burnt coupes was 90% greater than that from surrounding unlogged forest.

Contents and concentrations of both total N and organic C in soil followed similar patterns. Content of total N was 12% (330 kg ha^{-1}) less and content of organic C was 17% (7.5 t ha^{-1}) less on burnt coupes compared with unburnt coupes (Table 1). Average contents of total N and total C in unlogged forest were significantly greater than those in burnt coupes, but not significantly different in those of soil on unburnt coupes. The difference between the amount of total N and organic C in soil from unlogged forest and the adjacent burnt coupes indicated that there was 500 kg ha^{-1} (16%) less total N and 7.1 t ha^{-1} (16%) less organic C, 5 years after logging and slash-burning. Because C and N were both affected to a similar degree by burning, C:N ratios were not influenced by site preparation or regrowth age, averaging 14.7 across all sites.

Liu (1992) measured soil nutrients on one of the unburnt and one of the burnt coupes in 1988 and 1990 (Table 2). As it might be expected, concentrations of available P decreased on the burnt coupe between 1990 and 1994 (when the samples in this study were taken) and concentrations of organic C did not change with time on either burnt or unburnt coupes. In contrast, concentrations of potentially available N increased on burnt coupes but not on unburnt coupes and total N increased by 40 and 20% on burnt coupes and unburnt coupes, respectively. These increases suggest that both potentially available N and total N in soil were increased through N-fixation.

The abundance of ^{15}N in soil was significantly less on burnt coupes (2.6‰) than on unburnt coupes (3.1‰, Table 3). Abundance of ^{15}N was significantly less in unlogged forest (1.9‰, data not shown) than on either burnt or unburnt coupes, indicating that disturbance from logging resulted in losses of the more mobile ^{14}N through volatilization and leaching, thereby increasing the abundance of ^{15}N.

3.3. Effect of stocking of A. dealbata on soil properties

Concentrations and contents of potentially available N in unlogged forest were significantly greater (56 and 33%, respectively) for high stocking of wattle compared with low stocking (Table 1). However, there was no significant difference in either the concentration or

Table 2
Comparison between concentrations of potentially available N, available P (Bray and Kurtz), total N and organic carbon in soil measured by Liu (1992) in 1988 and 1990 and again in the current study in 1994 burnt and unburnt coupes

	Potentially available N (mg kg^{-1})			Available P (mg kg^{-1})		Total N (%)		Organic C (%)	
	1988	1990	1994	1990	1994	1990	1994	1990	1994
Unburnt coupe	68	69	59	3.1	4.8	0.50	0.60	9.0	9.1
Burnt coupe	142	53	79	29.0	9.4	0.41	0.56	7.1	7.9

Potentially available N is equal to the sum of inorganic N and potentially mineralisable N.

Table 3
Means and standard errors for N content and $\delta(^{15}N)$ of *A. dealbata*, $\delta(^{15}N)$ of reference trees (*E. regnans*), percentage and total amount of N in *A. dealbata* derived from N-fixation, content of total N, $\delta(^{15}N)$, percentage and total amount of N derived from N-fixation in soil and total amount of N in soil and *A. dealbata* derived from N-fixation for low, moderate and high stocking of *A. dealbata* on burnt and unburnt coupes

Stocking class of wattles	N in silver wattle trees					N in soil				Total N-fixed in silver wattle + soil (kg ha^{-1})
	N content (kg ha^{-1})	$\delta(^{15}N)$ (‰)	$\delta(^{15}N)$ of reference (‰)	N-fixed		N content (kg ha^{-1})	$\delta(^{15}N)$ (‰)	N-fixed		
				(%)	(kg ha^{-1})			(%)	(kg ha^{-1})	
Unburnt coupes										
Low	19 a	−1.13	−0.44	80	11 a	2900	3.37 b	0.0 a	0 a	11 a
Moderate	94 b	−0.86	−0.17	61	56 b	2910	3.11 b	4.7 a	135 a	190 ab
High	228 c	−0.66	−0.20	42	134 c	2800	2.83b	10.9ab	295 ab	430 b
Burnt coupes										
Low	13 a	−0.63	−0.65	66	7 a	2410	3.06 b	0.0 a	0 a	10 a
Moderate	73 b	−0.56	0.06	46	43 b	2620	2.62 a b	9.2 ab	266 ab	309 ab
High	172 c	−0.61	0.43	60	102 c	2590	2.15 a	18.9 b	589 b	690 b
L.S.D.	53	0.62	0.60	28	29	570	0.58	13.5	385	379
Main effect of wattle stocking										
Low	16 a	−0.88	0.10	70	9 a	2660	3.22 b	0.0 a	0 a	9 a
Moderate	84 b	−0.71	−0.06	53	49 b	2770	2.87 b	7.0 ab	201 ab	250 b
High	200 c	−0.63	0.12	53	118 c	2690	2.49 a	14.9 b	442 b	560 b
L.S.D.	38	0.45	0.42	21	20	350	0.36	8.3	235	231
Main effect of coupe site preparation										
Unburnt	114 b	−0.88	−0.27 a	60	67	2870 a	3.10 a	5.2	143	210
Burnt	86 a	−0.60	0.38 b	58	51	2540 b	2.61 b	9.4	285	336
L.S.D.	31	0.35	0.35	16	17	330	0.33	7.8	222	219

L.S.D.: least square differences; and letters beside means indicate significant differences between means.

content of total N in soil or in the natural abundance of ^{15}N. Thus, it was not possible to estimate the contribution of N-fixation to total soil N in unlogged forest. There was no difference in bulk density, nor in the concentration and content of organic carbon or available P under the different stocking classes of wattle, nor were relationships between number or basal area of wattle and these properties significant.

On the burnt and unburnt coupes, bulk density of soil was significantly (13%) less for high stocking of wattle than for low stocking. Although there was no significant difference in concentration or content of organic carbon in soil for different classes of wattle stocking, there was a significant relationship between concentration of organic carbon and basal area of dominant wattles ($R^2 = 0.11, P = 0.021$). With variation due to site preparation and block accounted for, the significance of this relationship increased ($R^2 = 0.14$, $P = 0.011$).

There was no significant difference in concentration or content of available P for different classes of wattle stocking or relationship between available P and stocking or basal area of wattle.

Wattles increased concentrations of potentially available and total N in soil on burnt and unburnt coupes. Concentrations of potentially available N and total N were significantly (26 and 17%, respectively) greater for high stocking (Table 1). There was also a significant relationship between concentration of total N and number of dominant wattles, with the number of dominant wattles at 5 years explaining 19% of variation of total N in soil (Fig. 1, $P = 0.027$). After accounting for differences due to site preparation and block, the amount of variation explained by wattle number remained the same but the significance of the relationship increased ($P = 0.007$). However, wattles did not significantly increase contents of potentially available N and total N.

Wattles significantly reduced natural abundance of ^{15}N in soil from unburnt and burnt coupes (Table 3). Weighted average $\delta(^{15}N)$ of soil from 0 to 10 cm decreased from 3.22‰ for low stocking of wattle to 2.87‰ for medium stocking and 2.49‰ for high stocking. This decrease was evidence of accumulation of atmospherically derived N, indicating that N-fixation by *A. dealbata* is contributing significantly to the total N pool in the soil. Natural abundance of ^{15}N was significantly less at 0–5 cm (2.66‰) than at 5–10 cm (3.06‰). However, the effect of wattle stocking was significant for both soil depths (0–5 and 5–10 cm), showing that the differences were not due simply to the effect of decomposing *A. dealbata* foliage, depleted

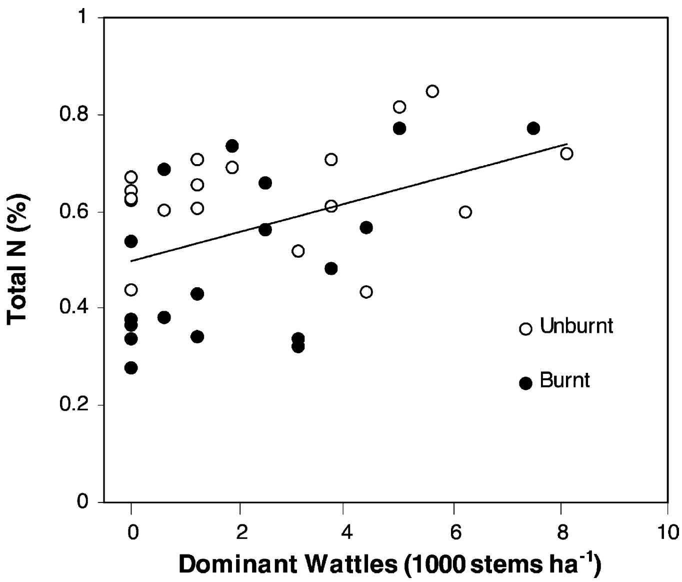

Fig. 1. Relationship between number of dominant *A. dealbata* at 5 years and concentration of total N in soil on burnt and unburnt coupes ($R^2 = 0.188$).

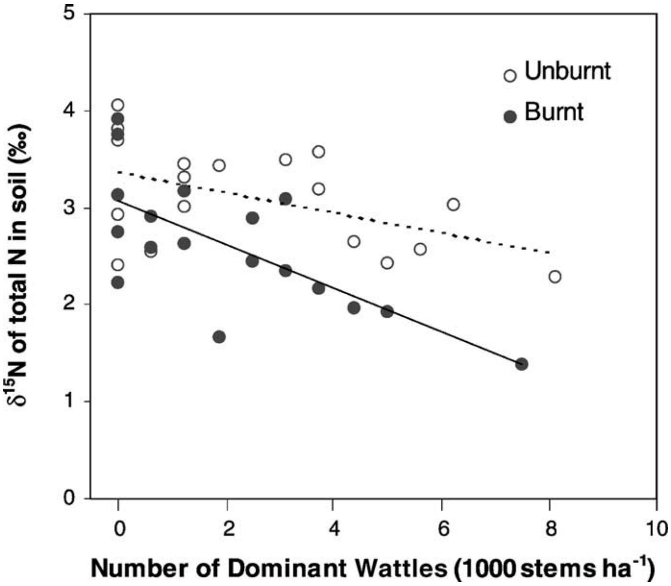

Fig. 2. Relationship between number of dominant *A. dealbata* at 5 years and natural abundance of ^{15}N in top 10 cm of soil burnt and unburnt coupes ($R^2 = 0.246$ (unburnt), $R^2 = 0.490$ (burnt)).

in ^{15}N, on the soil surface, which may have influenced the abundance of ^{15}N in the 0–5 cm samples.

There were significant relationships between $\delta(^{15}\mathrm{N})$ in soil and number of dominant *A. dealbata*, total number of wattles and basal area of wattles in 1988 regrowth. The relationship between δ^{15}N of soil and of dominant wattles expressed as 000's of stems ha^{-1} (W) at 5 years (Fig. 2) was:

- burnt coupes

$$\delta(^{15}\mathrm{N})\,(‰) = -0.225\,(\pm 0.075) \times W + 3.08\,(\pm 0.28),\quad r^2 = 0.49$$

- unburnt coupes

$$\delta(^{15}\mathrm{N})\,(‰) = -0.105\,(\pm 0.075) \times W + 3.38\,(\pm 0.28),\quad r^2 = 0.25$$

The relationship was stronger and significantly more negative on burnt coupes than on unburnt coupes.

Assuming an isotopic discrimination factor of −1.3‰ for *A. dealbata*, the proportion of N in soil derived from N-fixation over 5 years was 7% (equivalent to 200 kg N ha^{-1}) at medium stocking and 15% (equivalent to 440 kg N ha^{-1}) at high stocking (Table 3). These amounts equate to rates of 40 kg ha^{-1} per year of N at medium stocking and 88 kg ha^{-1} per year of N at high stocking of *A. dealbata*.

There were significant relationships between the estimated amount of soil N derived from N-fixation and number of dominant *A. dealbata*, total number of wattles and basal area of wattles in 1988 regrowth. The relationship between total N in soil derived from N-fixation and number of dominant wattles at 4 years (Fig. 3, 95% confidence limits in brackets) was:

$$\text{soil N derived from N-fixation}\,(\mathrm{kg\,ha^{-1}}) = 80.9\,(\pm 28.3) \times \text{dominant wattles} \times (1000\,\text{stems ha}^{-1}),\quad r^2 = 0.33$$

There was no significant difference between the slope of this relationship or average amount of soil N derived from N-fixation on burnt coupes compared with unburnt coupes, because the increased proportion of soil N derived from N-fixation on burnt coupes tended to be balanced by the lower N content of soil on those coupes.

3.4. N derived from fixation in A. dealbata in 1988 regrowth

Abundance of ^{15}N was significantly lower in *A. dealbata* (−0.72‰) than in *E. regnans* (0.07‰).

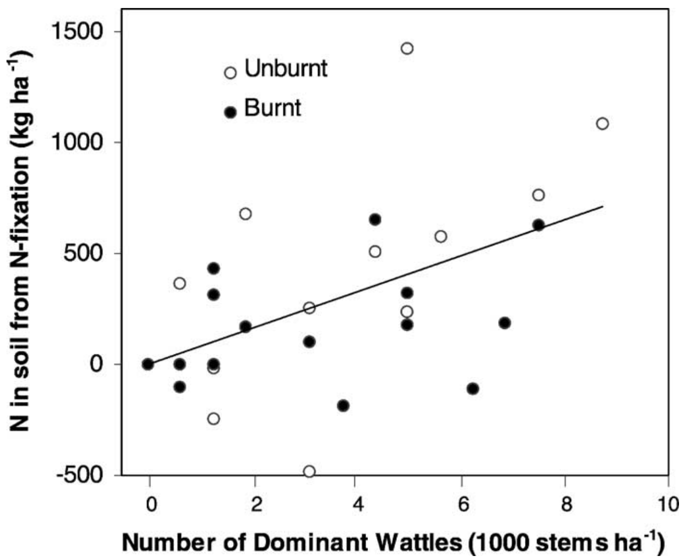

Fig. 3. Relationship between the amount of N in soil derived from N-fixation over 5 years and number of dominant wattles at 4 years ($R^2 = 0.326$).

There were significant differences between $\delta(^{15}N)$ in leaves, branches and stems of both species, with ^{15}N most abundant in foliage, and least abundant in branches of *A. dealbata* and stems of *E. regnans* (Fig. 4). Although there were significant differences between abundance of ^{15}N in vegetation from different coupes, the relative difference between *A. dealbata* and *E. regnans* stayed the same.

Using the assumed isotopic discrimination factor of −1.3‰, the average percentage of N in *A. dealbata* derived from N-fixation was 59 (±10)%. There was no significant difference in the percentage of N-fixed in

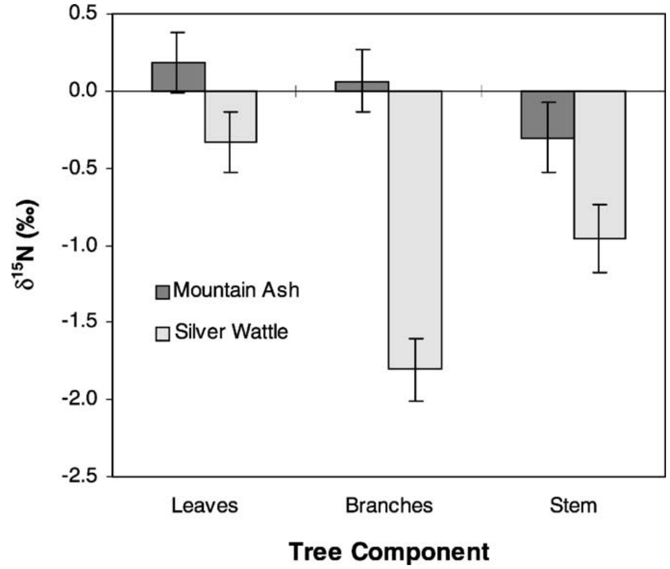

Fig. 4. $\delta(^{15}N)$ in leaves, branches and stems of *E. regnans* and *A. dealbata* trees. Error bars represent 95% confidence limits.

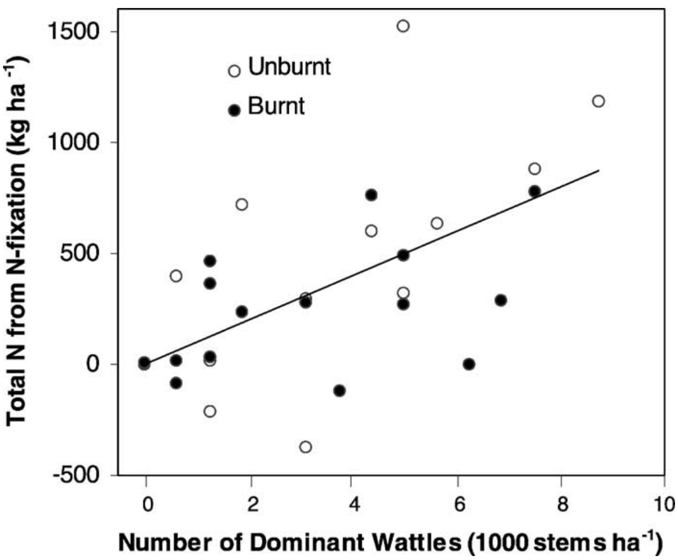

Fig. 5. Relationship between the amount of N in soil and vegetation derived from N-fixation over 5 years and the number dominant wattles at 4 years after harvest ($R^2 = 0.407$).

individual *A. dealbata* trees on burnt or unburnt coupes or for different stocking classes of wattle (Table 3). Total amounts of N derived from N-fixation in *A. dealbata* were 9 kg ha^{-1} at low stocking, 49 kg ha^{-1} at medium stocking and 118 kg ha^{-1} at high stocking.

The total amount of N derived from N-fixation in soil and *A. dealbata* over 5 years was 9 ($\pm$164) kg ha^{-1} at low stocking, 250 ($\pm$164) kg ha^{-1} at medium stocking and 560 ($\pm$164) kg ha^{-1} at high stocking of *A. dealbata*. These amounts are equivalent to annual rates of 112 ($\pm$33) kg ha^{-1} per year at high stocking and 50 ($\pm$33) kg N ha^{-1} per year at medium stocking.

The relationship between the number of dominant wattles at 4 years and the total amount of N derived from N-fixation on burnt and unburnt coupes over 5 years (Fig. 5, 95% confidence limits in brackets) was:

$$\text{total N derived from N-fixation (kg ha}^{-1}) = 99.6\,(\pm 28.1) \times \text{dominant wattles} \times (1000\,\text{s stem per ha}), \quad r^2 = 0.41$$

Again, there was no significant difference between the slope of the relationship on burnt and unburnt coupes.

Based on this relationship, the rate of N-fixation per tree is 20 ($\pm$5.6) g N per tree per year. Thus, the amount of N-fixed by *A. dealbata* trees is almost the same as the previous estimates, but the confidence limits are considerably smaller. The annual rate of N-fixation estimated in this manner is 108 ($\pm$30) kg N ha^{-1} per year at 5400 dominant stems ha^{-1} (equivalent to high stocking) and 50 ($\pm$14) kg ha^{-1} per year at 2500 stems ha^{-1} (equivalent to moderate stocking).

4. Discussion

4.1. Effects of site preparation on soil properties

The differences in nutrient concentrations and contents in the soil from burnt coupes and unlogged forest at Tanjil Bren are similar to findings in other studies. Reductions in total N and organic C concentrations and contents were similar to those reported by Ellis et al. (1982) and Rab (1996). Furthermore, differences in contents of total N (330 kg ha^{-1}) and organic C (7.5 t ha^{-1}) between burnt and unburnt coupes (from Table 1) were very close to those reported by Ellis and Graley (1983) for combustion of N (211 kg ha^{-1}) and C (7.36 t ha^{-1}) in soil during slash-burning.

However, the differences between the amounts of total N in soil in unlogged 54-year-old *E. regnans* forest and that from burnt coupes (500 kg N ha^{-1}) are less than the estimated total losses after logging burning (880 kg N ha^{-1}, Attiwill, 1984). This difference cannot be accounted for as a result of inputs through rainfall (15 kg), asymbiotic (6 kg) N-fixation over 5 years since harvesting and slash-burning and may reflect the substantial contribution of symbiotic N-fixation by *A. dealbata* to the N balance in the soil.

The increases in potentially available N and available P on burnt coupes are consistent with the ash-bed effect associated with burning. Increases in availability of N and P have been widely reported after drying and heating of soil in the laboratory (Chau, 1987; Chambers and Attiwill, 1994; Ashton and Kelliher, 1996) and after slash-burning in the field (Ellis et al., 1982; Weston and Attiwill, 1996; Smith, 1970). Mineral N and P in soil of *E. regnans* forest are rapidly immobilized in the soil by microorganisms after fire (Polglase et al., 1986; Weston and Attiwill, 1996) and are accumulated in regenerating vegetation (Adams and Attiwill, 1984a; Liu, 1992). The effects of fire on nutrient concentrations are normally limited to the first few years, with studies at 9 years (Humphreys and Lambert, 1965) and 25 years (Kraemer and Hermann, 1979) showing no difference between concentrations of N, P and organic matter in burned and unburned soils. However, increases in availability of nutrients in the soil may persist for up to three decades in highly productive forests (Kraemer and Hermann, 1979; Ellis et al., 1982; Ellis and Graley, 1983; Weston and Attiwill, 1990).

The differences between abundance of ^{15}N in plant available N (as measured in the reference plant) and total N in soil on burnt and unburnt coupes are probably the result of isotopic discrimination against ^{15}N. It could be expected that burning would result in an increase in the abundance of ^{15}N at least in the inorganic fraction of soil N, due to the preferential loss of the more mobile ^{14}N during volatilization and leaching. The accumulation of ^{15}N in the more mobile plant available N pool on burnt coupes relative to unburnt coupes is evidence of these processes occurring. The contrasting depletion of ^{15}N in the total N pool on burnt coupes may be a result of incorporation of ash from vegetation depleted in ^{15}N into the soil during burning, while the lower abundance of ^{15}N in plant available N is probably a result of preferential uptake of ^{14}N from the soil, again due to its greater mobility. Other authors have reported similar decreases in abundance of ^{15}N in non-N-fixing plants relative to both mineral N and total N in soil (Feigin et al., 1974; Stock et al., 1995; Yoneyama et al., 1993).

4.2. Effect of *A. dealbata* on soil properties

The higher concentrations of potentially available N and total N under *A. dealbata* relative to *E. regnans* in 1988 regrowth and 1939 regrowth (Table 1) are consistent with results from other studies (Ellis and Graley, 1987; Weston, 1990). There are many reports of increased concentrations of total N in soil under acacias and other legumes (e.g. Bormann and DeBell, 1981; Turvey et al., 1983; Saka et al., 1994; Khanna, 1997). However, as with this study, variation in bulk density usually makes any increase in total N difficult to detect. Decreases in bulk density under wattles have been previously reported by Adams and Attiwill (1984a) and by Bormann and DeBell (1981) under *Alnus rubra*. As with this study these decreases were associated with increases in the concentration of organic carbon under legumes.

The effect of wattles in reducing bulk density and increasing organic matter in soil is an important result, as timber harvesting and other forest management practices generally increase bulk density and reduce organic matter. Thus, in addition to adding N to soil, the growth of *A. dealbata* may reverse other negative impacts of logging on soil properties.

The ^{15}N natural abundance technique is far more precise than the total N difference method. Rather than trying to detect relatively small increases in the large and highly variable pool of total soil N, it measures differences in the much smaller and more stable pool of ^{15}N (which typically makes up around 0.6–0.7% of the total soil N). Furthermore, the relative difference in abundance of ^{15}N differences is not influenced by variations in bulk density, reducing the potential for error in the estimates. The use of, and benefits associated with the ^{15}N natural abundance technique are discussed in detail by Shearer and Kohl (1986) and Peoples et al. (1991).

Although the addition of plant material, depleted in ^{15}N, to the soil has been discussed by a variety of authors (Binkley et al., 1985; Stock et al., 1995; Van

Kessel et al., 1994), this is the first study to use the dilution effect to estimate the increase in soil N as a result of N-fixation. The additions of 200 kg N ha^{-1} to soil under medium stocking of *A. dealbata* and 440 kg N ha^{-1} to that under high stocking of *A. dealbata* through N-fixation are three times greater than the amount of fixed N contained in the *A. dealbata* trees at 5 years and represent about 80% of the total amount of N-fixed. If the accumulation of fixed N in soil is ignored in calculating rates of N-fixation, total N-fixation will be underestimated.

Since there was no difference in ^{15}N abundance in soil under different stocking of *A. dealbata* in unlogged forest, the addition of fixed N to the soil reflects the input of N from regenerating *A. dealbata* through the decomposition of roots, leaves and woody material. At high stocking, the net input of N amounted to 540 kg N ha^{-1} over 5 years. The abundant and rapidly growing acacia regeneration would provide the source of this N. Liu (1992) showed that regeneration of *A. dealbata* contained up to 1 t N ha^{-1} above-ground, only 12 months after harvest and site preparation. By year 5, natural thinning as a result of intense competition had reduced the total N content above-ground in *A. dealbata* to 365 kg ha^{-1} in these same plots (May, 1999).

4.3. Natural abundance of ^{15}N in vegetation

The assumed isotopic discrimination factor of −1.3‰ for N-fixed in *A. dealbata* from Stock et al. (1995) is in the range for other N-fixing plants (−1.0‰ for *Casuarina equisetifolia*, Mariotti et al., 1992, to −1.9‰ for *Alnus glutinosa*, Domenach et al., 1989, excluding the values around zero for *Acacia alata*, *Acacia extensa* and *Acacia pulchella*, Hansen and Pate, 1987) (Table 4). Because $\delta(^{15}\mathrm{N})$ of *A. dealbata* and the reference plant (*E. regnans*) were both close to this figure, the proportion of N derived from N-fixation in *A. dealbata* is strongly influenced by its value. However, the figure of 59% of N in *A. dealbata* being derived from N-fixation is supported by a glasshouse study that indicated that N-fixation contributed 50–65% of total plant N for seedlings of *A. dealbata* grown in sand for 6 months (Smith, 1983). Furthermore, because the total amount of N-fixed was mainly influenced by the amount of N in soil derived from N-fixation (which was less influenced by the isotopic discrimination factor) the estimate of total fixation by *A. dealbata* over 5 years are considered to be accurate.

Table 4
Estimates of isotopic discrimination factors β for a number of N-fixing plants

Species	β	Reference
Acacia alata	0.2	Hansen and Pate (1987)
Acacia extensa	−0.3	
Acacia pulchella	0.1	
Acacia cyclops	−1.34	Stock et al. (1995)
Acacia saligna	−1.27	
Alnus incana	−1.8‰	Domenach et al. (1989)
Alnus glutinosa	−1.9‰	
Casuarina equisetifolia	−1.0‰	Mariotti et al. (1992)
Gliricidia sepium	−1.45‰	Ladha et al. (1993)
Prosopis glandulosa	−1.3‰	Shearer et al. (1983)

There were significant differences between $\delta(^{15}\mathrm{N})$ of leaves, branches and stems of both *A. dealbata* and *E. regnans*, indicating discrimination in favor of ^{15}N during translocation and incorporation of N into foliage. This effect contrasts with results from Zakra et al. (1993) who found that concentrations of ^{15}N in *Acacia mangium* and *A. auriculiformis* tended to be greatest in stems and new foliage and less concentrated in mature leaves. However, Shearer and Kohl (1986) noted that stems of woody plants are often depleted in ^{15}N relative to shoots and leaves. Van Kessel et al. (1994) reported differences in $\delta(^{15}\mathrm{N})$ of components of 6-year-old *Leucaena leucocephala* similar to those in the current study for *A. dealbata*, with $\delta(^{15}\mathrm{N})$ greatest in leaves, 0.7‰ less in stems and 1.4‰ less in branches.

Van Kessel et al. (1994) reported also that $\delta(^{15}\mathrm{N})$ of non-N-fixing understorey plants grown in association with N-fixing *Leucaena leucocephala*, decreased with time, approaching that of the N-fixing plant as material depleted in ^{15}N was cycled through litterfall and decomposition. There was no evidence in the current study that $\delta(^{15}\mathrm{N})$ of *E. regnans* was affected by increasing stocking of *A. dealbata* (Table 3), demonstrating that recycling of fixed N did not affect the results.

4.4. N-fixation by A. dealbata

N-fixation by *A. dealbata* added 250 kg N ha^{-1} at medium stocking and 540 kg N ha^{-1} at high stocking

Table 5
Published estimates of N-fixation by *Acacia* species in Australia and overseas

Species	Acetylene (nmol h^{-1} g^{-1})	N-fixation (mg per plant per year)	N-fixation (kg ha^{-1} per year)	Age (months)	Location	Method	Reference
Acacia alata	0.7	5.5	–	24	Field	Acetylene	Hansen et al. (1987)
Acacia dealbata	–	37	–	3	Glasshouse	Acetylene	Hopmans et al. (1983)
A. dealbata	20	–	–	7	Glasshouse	Acetylene	Shirrefs (1977)
A. dealbata	8	40	–	12	Glasshouse	Acetylene	Chau (1987)
A. dealbata	4.4	120	24	24	Field	Acetylene	Adams and Attiwill (1984b)
A. dealbata	–	20000	50	60	Field	^{15}N	This study
Acacia extensa	4.5	–	–	24	Field	Acetylene	Hansen et al. (1987)
Acacia holosericea	2200	11	–	11	Glasshouse	^{15}N enriched	Cornet et al. (1985)
Acacia mearnsii	3.0	53	0.7	24	Field	Acetylene	Lawrie (1981)
Acacia melanoxylon	11	<0.1	–	27	Field	^{15}N	Hamilton et al. (1993)
A. melanoxylon	2.5	38	<0.1	12	Field	Acetylene	Lawrie (1981)
Acacia mucronata		60		24	Field	Acetylene	Lawrie (1981)
Acacia parradoxa	1.6	60	<0.1	24	Field	Acetylene	Lawrie (1981)
A. parradoxa		26	<0.1	27	^{15}N	Acetylene	Hamilton et al. (1993)
Acacia pellita	20	11000	12	36	Field	Acetylene	Langkamp et al. (1979)
Acacia pulchella	11220	3000	2.2	48	Field	Acetylene	Monk et al. (1981)
A. pulchella	10	12	0.6	6	Field	Acetylene	Hingston et al. (1982)
A. pulchella	1.6	15	–	24	Field	Acetylene	Hansen et al. (1987)
Acacia verniciflua		8000	32	78	Field	Accumulation	Turvey et al. (1983)
Acacia spp.		7900	38	66	Field	Accumulation	Koch (1987)

Acetylene: acetylene reduction assay; ^{15}N: ^{15}N natural abundance method; ^{15}N enriched: ^{15}N enrichment method; accumulation: N accumulation method; '–' indicates data unavailable.

to soil and vegetation over 5 years. Thus, at high stocking, symbiotic N-fixation will more than compensate for the N deficit after timber harvesting and slash-burning (430 kg N ha^{-1}) and at medium stocking it will make up 58% of the deficit over this period. Even allowing for decreasing rates of N-fixation over time, as surviving *A. dealbata* trees are gradually suppressed by the faster growing *E. regnans*, the N balance will almost certainly be maintained over a 100-year rotation. However, forest management should aim to regenerate sufficient *A. dealbata* to ensure stocking of at least 2500 dominant stems ha^{-1} at 4 years.

The rate of N-fixation for medium stocking of 50 kg ha^{-1} per year is double that previously estimated for *A. dealbata* (Adams and Attiwill, 1984b) and is substantially greater than estimates by other authors for wattles in Australia (Table 5). However, the rate is the same as that measured in stands of red alder (*A. rubra*) in North America (50 kg N ha^{-1} per year, Bormann and DeBell, 1981), while at high stocking, the rate of 112 kg ha^{-1} per year is comparable to N-fixation rates of pasture legumes such as lupins (*Lupinus angustifolius*, 177 kg N ha^{-1}) and field pea (*Pisum sativum*, 144 N ha^{-1}, Unkovich et al., 1993b). The amount of N-fixed by individual trees (20 g N per year) is double the rate calculated for other acacia species of similar ages from other studies (Turvey et al., 1983; Koch, 1987). However, this figure would be lower if the change in stocking over time was taken into account. The relatively high rates of N-fixation estimated in this study may be explained by the high productivity of the sites, the density and rapid growth of regeneration following harvest and potential underestimation of N-fixation determined using other methods (Minchin and Witty, 1989).

A. dealbata can fix sufficient N to maintain the N pool over successive logging rotations in *E. regnans* forest. Indeed the relatively high concentrations of N in the soil and vegetation at Tanjil Bren show that it has clearly been doing so after regular wildfires over the past millennia. However, N-fixation rates are dependent on the stocking and rate of growth of *A. dealbata*. Further work is needed to determine whether the ballpark figure of 2500 stems ha^{-1} at 4 years is typical after timber harvesting and the impact of changing harvesting regimes, rotation lengths and management strategies on *A. dealbata* regeneration and nitrogen-fixation.

5. Conclusion

Logging and slash-burning in *E. regnans* forest at Tanjil Bren reduce the concentrations and contents of total N and organic matter in the soil, but increase the amounts of available N and P. Increasing stocking of wattle is associated with lower bulk density of soil and higher concentrations of total N, potentially available N and organic C. Although there was no difference in total N content of soil, differences in the abundance of ^{15}N showed that *A. dealbata* added significant amounts of nitrogen to the soil. At medium stocking (2500 stems ha^{-1} at 4 years) *A. dealbata* added 201 kg N ha^{-1} to soil through N-fixation and accumulated 49 kg N ha^{-1} in above-ground wattle biomass over 5 years. The total amount fixed was 250 or 50 kg ha^{-1} per year. Given that the total N deficit over a 100 year rotation of logging and slash-burning is about 430 kg ha^{-1}, N-fixation by *A. dealbata* will make up the deficit in 9 years provided this rate is maintained.

Acknowledgements

Funding for this work was provided by the Commonwealth Government of Australia through an Australian Post-graduate Research Award and by the Department of Natural Resources and Environment (DNRE). The authors also would like to thank staff of DNRE for assisting with experimental design and Phil Chalk and members of his group in the Department of Agriculture and Forestry, University of Melbourne for their help with carrying out the ^{15}N analyses.

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