

Effects of forest thinning on soil-plant carbon and nitrogen dynamics

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Abstract

Aims *Corymbia* spp. (previously included in the genus *Eucalyptus*) are common species in sub/tropical Australia and produce high quality timber and round logs. Thinning of native forests helps to preserve native tree species and is more sustainable than replacing native forest stands with mono-species plantations to produce timber. This study aimed to explore the effects of native

forest thinning on soil-plant carbon (C) and nitrogen (N) dynamics in two experimental sites, Esk (5 years post-thinning) and Herberton (7 years post-thinning), situated in Queensland, Australia.

Methods The two sites had different thinning regimes. The final stocking rates varied between 75 and 200 stems ha⁻¹ at Esk and between 250 and 400 stems ha⁻¹ at Herberton. The thinned plots were compared to un-thinned plots. Soil samples were collected to measure labile C and N. Leaf samples were collected from *C. variegata* and *C. citriodora* in Esk and Herberton respectively.

Results Thinning did not change soil total C, total N, $\delta^{15}\text{N}$ and inorganic N at either Esk or Herberton. However, at Esk, intensive thinning resulted in decreases in water soluble total N (WSTN). Foliar $\delta^{13}\text{C}$ did not vary with respect to thinning whereas foliar $\delta^{15}\text{N}$ values were more enriched in thinned areas than those of un-thinned plots. The stepwise linear regression indicated that both foliar total N and $\delta^{15}\text{N}$ were explained mainly by soil TN and WSTN.

Conclusions Thinning did not change soil C and N most likely due to the retention of thinned materials on site and their incorporation into soil. Foliar $\delta^{13}\text{C}$ was not thinning-dependent due to homeostatic maintenance of the ratio of intercellular to ambient CO₂ concentrations during photosynthesis. In our study, soil N was not a limiting factor for foliar N, however, foliar N was mainly driven by WSTN which may foreshadow a possible N limitation in severely thinned plots in the long term. We conclude that forest thinning does not decrease soil C

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and N availability in native *Corymbia* forests for several years post-thinning if the thinned materials are retained on site.

Keywords Stable isotopes · Inorganic nitrogen · *Corymbia* spp. · *Eucalyptus* spp. · Farm forestry · Water soluble total N and C

Introduction

The protection of forest biodiversity maintains ecosystem function and productivity (Erskine et al. 2006; Piotto 2008). Privately-owned native forest management, or ‘farm forestry’, is practiced to bring over-stocked and genetically impoverished forests back to productivity and is far more sustainable than replacing native forest stands with mono-species plantations to produce timber (Paul et al. 2013). Increasing spacing through thinning in plantations or forests has been shown to increase individual plant growth (Briggs et al. 2000; Henskens et al. 2001; Bai et al. 2013). Improved plant growth post-thinning is a direct response to increased nutrient availability including nitrogen (N), phosphorus and potassium as well as decreased competition for available resources (Briggs et al. 2000; Thibodeau et al. 2000; Zhang et al. 2006). Improved tree growth has been reported for periods over three decades post-thinning (Zhang et al. 2006). Despite improved tree growth, it is uncertain how thinning affects carbon (C) and N cycling post-thinning and how this will be in turn translated in foliar C and N contents.

Nitrogen dynamics have been closely coupled with C cycling (Bai et al. 2015a, 2015b), and different studies suggest that enhanced N availability results in increased C sequestration in both plant biomass and soil (Högberg 2007; Xu et al. 2009). Soil and foliar C and N isotope compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) have been used to investigate long-term C and N cycling in different soil-plant systems including plantations, forests, revegetated areas and agricultural lands (Xu et al. 2000; Bai et al. 2013; Nottingham et al. 2015; Reverchon et al. 2015). The study of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ provides valuable long-term information on environmental conditions, water and nutrient availability, and management practices in different ecosystems (Ogaya and

Peñuelas 2008; Cernusak et al. 2009; Mullaney et al. 2015; Xu et al. 2015). Foliar $\delta^{13}\text{C}$ reflects long-term plant water-use efficiency because water regulates stomatal closure which influences $^{13}\text{CO}_2$ discrimination of photosynthesis (Farquhar et al. 1989). Photosynthesis is additionally controlled by N and light availability (Meir et al. 2007; Osunkoya et al. 2010; Ma et al. 2015). Enriched soil ^{15}N signals may indicate N losses or acceleration in N transformations as a result of increased microbial activities (Högberg 1997; Kleinebecker et al. 2013). Foliar $\delta^{15}\text{N}$ values in turn reflect soil N dynamics as non-legume species assimilate soil available N (Kähmen et al. 2008).

Australian members of the Myrtaceae family, such as *Eucalyptus* and *Corymbia*, produce an exceptional timber and constitute a high proportion of plantation trees in sub/tropical areas worldwide due to their high adaptability to harsh conditions and to their fast growth (Santos et al. 2004). In sub-tropical Australia, forests types are usually tall open forests dominated by *Eucalyptus* spp. and *Corymbia* spp. and are managed to preserve these native species to sustain timber production (Lee 2007; Johnson et al. 2009). Tree growth response to spacing in plantations worldwide has been well documented (Henskens et al. 2001; Alcorn et al. 2007; Vande Walle et al. 2007). However studies on tree response to different thinning regimes in managed native forests are scant. In a complementary study, we investigated the effects of different thinning regimes on plant growth at two sites located in sub-tropical Australia, 1 and 3 years post-thinning (Bai et al. 2013). Our results indicated that the thinning of native forests to stocking rates ranging from 50 to 200 stems ha^{-1} improved tree growth significantly compared to un-thinned plots (Bai et al. 2013).

Many forest thinning studies have investigated soil respiration as well as C and N dynamics post thinning and revealed a range of responses (Briggs et al. 2000; Kaye et al. 2005; Tang et al. 2005; Moore et al. 2006; Cheng et al. 2014, 2015). However, studies investigating C and N dynamics in both soils and plants post-thinning are relatively rare. Hence, the extent to which forest thinning alters C and N cycling in both soil and plant remains uncertain. Our study aimed to investigate mechanisms involved in C and N dynamics of both soils and plants at two *Corymbia* spp. dominated forests located in subtropical and tropical Australia, 5 and 7 years post-thinning.

Methods

Site description

The two experimental sites were situated at Esk (27° 14' S 152° 23' E) and Herberton (17° 27' S 45° 25' E), located in south-east and north-east Queensland, Australia. Esk is located approximately 200 km south of Gympie. The Esk site was categorised as open forest dominated by *Corymbia variegata* (F. Muell.) K.D. Hill & L.A.S. Johnson (spotted gum), *C. intermedia* (R.T. Baker) K.D. Hill & L.A.S. Johnson (red bloodwood) and other *Eucalyptus* spp. with an understorey of *Acacia* spp. and whipstick *Lophostemon confertus* (R. Br.) Peter G. Wilson & J.T. Waterh. The annual precipitation at Esk varied between 600 mm and 1400 mm from 2008 to 2014 (Fig. 1a). Throughout the sample collection period at Esk for the current study, the monthly rainfall varied between 7 mm and 190 mm (Fig. 1b).

The Herberton site is located in the Atherton tablelands approximately 100 km south-west of Cairns. The vegetation class was open forest with remnant vegetation dominated by *C. citriodora* K.D. Hill & L.A.S. Johnson (lemon-scented spotted gum) followed by *Eucalyptus argillacea* W. Fitzg. (Northern grey box) and other *Eucalyptus* spp. Herberton received annual rainfall within a range of 800 mm to 1800 mm in the years following the thinning (from 2007 to 2014) (Fig. 1a). At Herberton site during the sample collection in 2014, the monthly rainfall varied between 0 mm and 350 mm (Fig. 1b).

Experimental design and treatments

At Esk, a randomised complete block design with three replications was established in 2008. The plot areas were 70 m × 70 m (0.49 ha). The sample collections were undertaken in the centre of the plots. The treatments included thinning to a final stocking rate of 75 stems ha⁻¹ (11.5 m × 11.5 m of spacing); 120 stems ha⁻¹ (9 m × 9 m of spacing); and 200 stems ha⁻¹ (7.5 m × 7.5 m of spacing). The un-thinned plots contained a stocking rate of approximately 1150 stems ha⁻¹. The thinned materials were not removed from the thinned plots and were left on site to be decomposed.

At the Herberton site, the thinning commenced in 2007. We established a randomised complete block design with three replications for thinned areas. However, the un-thinned plots were established with six

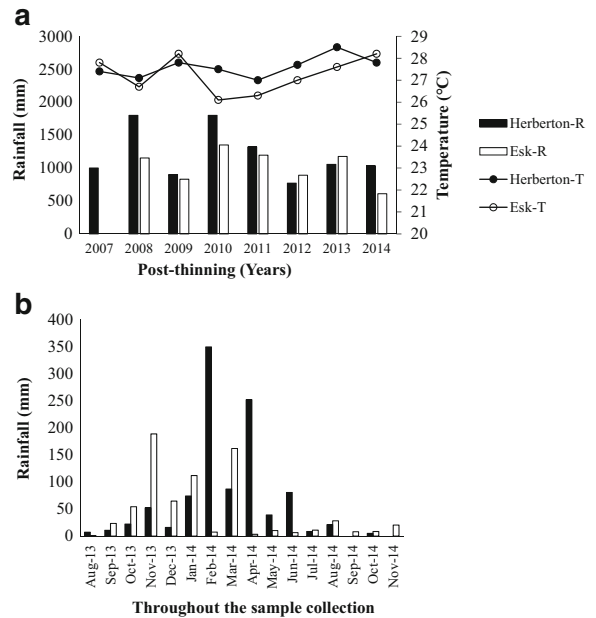


Fig. 1 Mean annual rainfall and mean annual maximum daily temperature at the experimental sites between 2007 and 2014, years following the thinning (a), mean monthly rainfall at the experimental sites throughout the sample collection (b), data extracted from Bureau of Methodology on-line database. Black column; rainfall (R) in Herberton, white column; rainfall in Esk, close circles; temperature (T) in Herberton and open circles; temperature (T) in Esk

replications to undertake more intensive sample collection due to high variability in tree density in the un-thinned areas. The plots were chosen in a circle with a surface area of 0.49 ha. Despite the fact that the plots were square at Esk and circular in Herberton, the plots had the same surface area and the sample collections were undertaken in the centre of the plots. The treatments included thinning to a final stocking rate of: 250 stems ha⁻¹; and 400 stems ha⁻¹. The un-thinned plots contained a stocking rate of up to 700 stems ha⁻¹. The thinned materials were not removed from the thinned plots and were left on site to be decomposed.

The thinned materials were not removed from thinned plots at either experimental sites because no viable commercial market existed in Australia for such products at the time. The thinned stems were not appropriate for fencing as they were not durable enough and/or they had poor form (e.g. bent or small). The thinned species were also not suitable for paper pulp. Nonetheless, the thinned materials could be used as bio-fuel, which is also a limited use due to the cost of transport and the distance between forests and the bio-fuel premises.

Sample collections

The sample collection strategies were similar at both sites. All the sample collections within one site were done on the same time. At the Esk site, both soil and leaf sample collections were undertaken in November 2013 and March 2014 (60 and 64 months, over 5 years post-thinning – before and after the wet season, respectively). At Herberton, the soil and leaf samples were collected in February and November 2014 (84 and 91 months, over 7 years post-thinning –after and before the wet season, respectively). Sampling dates were chosen based on the rainfall pattern in Esk and Herberton to be undertaken at the beginning and end of wet season.

Soil sample collections and analyses

Soil samples were collected at five points chosen randomly within the plots to a depth of 5 cm. The soil samples were collected using an auger with a 64-mm internal diameter. Soil samples collected from the same plots were bulked and mixed to provide one homogenised sample at each plot. Soil samples were then sieved (2 mm) when field moist in the laboratory and air dried before analysis.

A sub-sample of each soil sample was oven dried (50 °C) to a constant weight and ground to a fine powder (Rocklabs™ ring grinder). Approximately 20 mg were transferred into 8 mm × 5 mm tin capsules for total C (TC), total N (TN), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis using an isotope ratio mass spectrometer (GV Isoprime, Manchester, UK).

To measure water soluble organic C (WSOC) and water soluble total N (WSTN), 5 g soil were added to 35 ml deionised water, then shaken by an end-over-end shaker for 5 min followed by centrifuging at 10,000 rpm for 10 min. The suspension was filtered through a Whatman 42 filter paper followed by filtering through a 33 mm Millex syringe-driven 0.45 μm filter. The concentration of filtered solution was measured using a Shimadzu TOC-VCSH/CSN TOC/N analyser.

Soil inorganic N content ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$) was measured after shaking 5 g soil with 40 ml 2 M KCl by an end-over-end shaker for 60 min followed by a 10 min centrifugation at 4000 rpm and filtration through a Whatman 42 filter paper. The $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ concentrations were then determined using a SmartChem 200, Discrete Chemistry Analyser (DCA).

Foliar sample collections and analyses

Leaf samples were collected from *C. variegata* and *C. citriodora* in Esk and Herberton respectively. The species chosen for this study were the dominant species in the corresponding experimental sites. The outside middle canopy branches were targeted using a Big Shot slingshot. Five fully expanded leaves were collected from fallen branches. The leaf samples were oven dried at 50 °C to a constant weight and ground to a fine powder by a Rocklabs™ ring grinder. Approximately 4 mg of homogenised powder were transferred into 8 mm × 5 mm tin capsules to analyse foliar TC, TN, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using an isotope ratio mass spectrometer (GV Isoprime, Manchester, UK).

Statistical analysis

Thinning regimes differed at the two experimental sites, hence, we performed a repeated measures ANOVA at each site to detect significant difference among thinning treatments, sampling time and their interaction followed by Tukey test where significant differences were detected to compare treatments and sampling times of soil and foliar C and N contents. All data were tested for normality using Shapiro Wilk normality test and for homogeneity of variance using Levene's test. A stepwise regression using a linear model was then performed to determine which soil variables best explained foliar C and N contents. SPSS 21 software was used for all above statistical analyses. A linear regression was performed between soil WSTN and $\delta^{15}\text{N}$ as well as soil WSTN and foliar $\delta^{15}\text{N}$ pooling all data from both sites to find a general trend. Linear regression was performed in XLSTAT 15.1.

Results

Soil C and N pools

Esk

Total C and TN did not differ significantly among thinning treatments and there was no interaction between thinning and sampling time (Table 1). TC varied between 1.93 % and 3.18 % at this site and TN varied between 0.079 % and 0.160 %. Soil $\delta^{15}\text{N}$ did not vary either among treatments but it was significantly

influenced by the sampling time, being significantly higher at the beginning of the wet season than at the end in the 100 stems ha⁻¹ (Table 1).

No changes were detected in WSOC with respect to the thinning treatment whereas WSTN was significantly influenced by thinning (Table 1). In month 60, WSTN was significantly lower in 75 stems ha⁻¹ compared to 100 stems ha⁻¹ whereas in month 64, WSTN in 75 stems ha⁻¹ was significantly lower than that of other treatments including the un-thinned areas (Table 2). Both WSOC and WSTN were significantly responsive to the sampling time (Table 1). WSOC only increased in un-thinned plots from month 60 to month 64 whereas WSTN increased significantly in 75, 200 stems ha⁻¹ and un-thinned plots from month 60 to month 64 post-thinning (Table 2).

Neither NH₄⁺-N nor NO₃⁻-N were influenced by thinning treatments, however, these variables changed significantly over the sampling time (Table 1). In general, NH₄⁺-N increased from month 60 to 64 but the increased NH₄⁺-N was significant only in 200 stems ha⁻¹ and un-thinned (Table 2). In contrast, soil NO₃⁻-N decreased from month 60 to month 64 but the decrease was significant only in 75 stems ha⁻¹, 100 stems ha⁻¹ and un-thinned plots (Table 2).

Herberton

At Herberton, soil TC and TN did not differ at different thinning treatments at either sampling point (Tables 1 and 2). There was also no significant change for soil TC and TN between sampling times (Tables 1 and 2). Soil TC varied between 1.71 % and 5.04 % regardless of thinning treatment and sampling time (Table 2). Soil TN also varied between 0.146 % and 0.290 % regardless of

thinning treatment and sampling time (Table 2). No significant differences in soil δ¹⁵N were observed with respect to both thinning treatments and sampling time (Table 1).

Neither WSOC nor WSTN showed significant differences among thinning treatments regardless of sampling times (Tables 1 and 2). However, both WSOC and WSTN changed significantly from month 84 to 91 post-thinning (Tables 1 and 2). WSOC significantly decreased in 400 stems ha⁻¹ and un-thinned plots from month 84 to month 91 post-thinning (Table 2). WSTN also decreased only in 250 stems ha⁻¹ and un-thinned plots from month 84 to month 91 post-thinning (Table 3). Neither NH₄⁺-N nor NO₃⁻-N showed any significant change regardless of both thinning treatment and sampling time (Tables 1 and 2).

Foliar C and N content

Esk

Foliar TC and TN showed no significant differences regardless of the thinning (Table 3). However, there were significant changes for foliar TC and TN between the sampling times. Foliar TC decreased from month 60 to month 64 post-thinning in all plots including the un-thinned plots (Table 4). A decrease in foliar TN was also observed in thinned plots but not in un-thinned plots from month 60 to month 64 post-thinning (Table 4).

No significant differences of foliar δ¹³C with respect to thinning and sampling time were detected (Tables 3 and 4). Foliar δ¹⁵N was significantly higher in 100 stems ha⁻¹ compared to that of un-thinned plots and no differences in foliar δ¹⁵N were observed among 75 stems ha⁻¹, 200 stems ha⁻¹ and un-thinned plots at

Table 1 Probability of a two-way ANOVA for soil properties in a farm forestry practice located at Esk and Herberton

Soil	TC (%)	TN (%)	δ ¹⁵ N (‰)	WSOC (μg g ⁻¹)	WSTN (μg g ⁻¹)	NH ₄ ⁺ -N (μg g ⁻¹)	NO ₃ ⁻ -N (μg g ⁻¹)
Esk site							
Sampling time	0.784	0.516	0.037	0.001	<i>P</i> < 0.001	0.004	0.023
Thinning	0.527	0.444	0.357	0.166	0.028	0.470	0.871
Sampling time × Thinning	0.976	0.797	0.741	0.877	0.285	0.617	0.752
Herberton site							
Sampling time	0.078	0.736	0.419	<i>P</i> < 0.001	<i>P</i> < 0.001	0.052	0.389
Thinning	0.357	0.176	0.306	0.277	0.300	0.808	0.097
Sampling time × Thinning	0.971	0.838	0.288	0.675	0.218	0.906	0.815

Table 2 Soil total C (TC), total N (TN), C:N ratio, N isotope composition ($\delta^{15}\text{N}$), water soluble organic C (WSOC), water soluble total N (WSTN), $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ at Esk and Herberton measured on two sampling times. Means followed with

different letters show a significant difference at $P < 0.05$ at each sampling time. Values in bold cases represent significant differences between sampling time ($P < 0.05$). Mean standard errors are presented in the brackets

Soil – Esk site	TC (%)		TN (%)		$\delta^{15}\text{N}$ (‰)			
	Month 60	Month 64	Month 60	Month 64	Month 60	Month 64	Month 60	Month 64
Stocking rates								
75 (stems ha^{-1})	2.29 (0.5)	1.93 (0.5)	0.113 (0.03)	0.079 (0.01)	4.00 (0.7)	2.97 (0.3)		
100 (stems ha^{-1})	3.18 (0.9)	2.97 (0.8)	0.160 (0.03)	0.124 (0.02)	3.50 (0.7)	1.73 (0.7)		
200 (stems ha^{-1})	2.75 (0.4)	2.56 (0.3)	0.116 (0.01)	0.120 (0.01)	3.36 (0.4)	3.05 (0.9)		
Un-thinned	2.77 (0.7)	2.99 (0.8)	0.130 (0.03)	0.138 (0.04)	3.00 (0.5)	1.75 (0.9)		
	WSOC ($\mu\text{g g}^{-1}$)		WSTN ($\mu\text{g g}^{-1}$)		$\text{NH}_4^+\text{-N}$ ($\mu\text{g g}^{-1}$)		$\text{NO}_3^-\text{-N}$ ($\mu\text{g g}^{-1}$)	
	Month 60	Month 64	Month 60	Month 64	Month 60	Month 64	Month 60	Month 64
75 (stems ha^{-1})	181 (28)	299 (27)	9.09 (1.6)b	15.3 (1.1)b	6.99 (1.8)	11.4 (0.5)	11.5 (2.1)	8.43 (0.1)
100 (stems ha^{-1})	263 (35)	346 (61)	15.3 (1.3)a	20.6 (0.7)a	9.29 (2.5)	14.6 (2.2)	12.4 (2.2)	8.63 (0.3)
200 (stems ha^{-1})	196 (4.8)	298 (24)	10.8 (1.6)ab	21.2 (2.4)a	6.18 (0.4)	18.7 (5.0)	9.65 (0.4)	8.89 (0.3)
Un-thinned	243 (35)	390 (65)	11.3 (2.1)ab	22.6 (2.4)a	9.31 (2.1)	20.0 (6.0)	12.2 (3.2)	8.42 (0.1)
Soil – Herberton site								
	TC (%)		TN (%)		$\delta^{15}\text{N}$ (‰)			
	Month 84	Month 91	Month 84	Month 91	Month 84	Month 91	Month 84	Month 91
250 (stems ha^{-1})	3.46 (1.3)	1.71 (0.8)	0.206 (0.06)	0.165 (0.6)	3.23 (0.2)	3.13 (0.7)		
400 (stems ha^{-1})	5.04 (1.5)	3.64 (0.8)	0.263 (0.07)	0.290 (0.6)	2.97 (0.3)	2.90 (0.7)		
Un-thinned	4.75 (1.1)	2.29 (0.6)	0.181 (0.05)	0.146 (0.04)	2.01 (0.2)	3.05 (0.4)		
	WSOC ($\mu\text{g g}^{-1}$)		WSTN ($\mu\text{g g}^{-1}$)		$\text{NH}_4^+\text{-N}$ ($\mu\text{g g}^{-1}$)		$\text{NO}_3^-\text{-N}$ ($\mu\text{g g}^{-1}$)	
	Month 84	Month 91	Month 84	Month 91	Month 84	Month 91	Month 84	Month 91
250 (stems ha^{-1})	443 (113)	208 (41)	28.5 (2.7)	9.84 (3)	9.80 (1.5)	5.98 (2)	9.48 (0.5)	9.78 (0.9)
400 (stems ha^{-1})	674 (130)	272 (41)	21.2 (3.1)	13.7 (3)	10.0 (1.7)	7.86 (2)	9.49 (0.6)	10.5 (0.9)
Un-thinned	523 (101)	189 (29)	20.0 (2.4)	9.50 (2)	10.1 (1.3)	7.37 (1)	8.41 (0.5)	8.61 (0.6)

month 64 post-thinning (Fig. 2a). Foliar $\delta^{15}\text{N}$ significantly increased in all plots from month 60 to month 64 post-thinning (Fig. 2a).

Herberton

Foliar TC was significantly higher in all treatments at month 84 than in month 91 (Table 4). Foliar TN significantly varied with respect to thinning and sampling time and there was a significant interaction between thinning and sampling time (Table 3). At month 84, both 250 stems ha^{-1} and 400 stems ha^{-1} had significantly higher TN than un-thinned plots (Table 4). At month 93, however, no significant difference in foliar TN was found among all treatments (Table 4). Foliar TN in 250 stems ha^{-1} and 400 stems ha^{-1} significantly decreased between month 84 and month 91 post-thinning (Table 4).

No significant difference in foliar $\delta^{13}\text{C}$ among treatments was observed in either sampling time (Table 4). However, foliar $\delta^{13}\text{C}$ increased in all plots from month 84 to 91 post-thinning (Table 4). Foliar $\delta^{15}\text{N}$ was significantly higher in 250 stems ha^{-1} and 400 stems ha^{-1} compared to un-thinned plots at either sampling time (Fig. 2b). Foliar $\delta^{15}\text{N}$ values decreased significantly in all plots from month 84 to month 91 post-thinning (Fig. 2b).

Relationship between soil and foliar C and N content

Relationship between foliar TC, TN, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with soil C and N were examined using a stepwise regression. At Esk, soil WSTN and TN explained 71 % of variation in foliar TC (Table 5). WSTN was the sole significant factor explaining foliar TN and $\delta^{15}\text{N}$ (57 % and 36 % respectively; Table 5). At Herberton,

Table 3 Probability of a two-way ANOVA for foliar properties of *Corymbia variegata* at Esk and *C. citriodora* at Herberton

	TC (%)	TN (%)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Leaf – Esk site				
Sampling time	$P < 0.0001$	$P < 0.0001$	0.235	$P < 0.0001$
Thinning	0.816	0.975	0.365	0.016
Sampling time \times Thinning	0.741	0.177	0.066	0.837
Leaf – Herberton site				
Sampling time	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
Thinning	0.409	$P < 0.0001$	0.907	$P < 0.0001$
Sampling time \times Thinning	0.918	$P < 0.0001$	0.365	0.200

both WSTN and NO_3^- -N explained 66 % of variation in foliar TC (Table 5). At Herberton, whilst both soil WSTN and TN explained 55 % of variation in foliar TN, WSTN was the only variable explaining 47 % of variation in foliar $\delta^{15}\text{N}$ (Table 5). In general, WSTN explained variations of both soil and foliar $\delta^{15}\text{N}$ ($P < 0.05$; 13 % and 42 %, respectively) (Fig. 3 a, b).

Discussion

In general, thinning did not affect soil TC, TN, NH_4^+ -N and NO_3^- -N, at neither Esk (5 years post-thinning) nor Herberton (7 years post-thinning). Both increased and decreased N availability have been reported after thinning in different thinning regimes (Grady and Hart 2006; Baena et al. 2013; Overby and Hart 2016). For example, a decreased rate of N mineralisation was

observed up to 15 years following thinning in a ponderosa pine forest in Southwestern America due to decreased organic matter inputs (Grady and Hart 2006) whereas Kaye et al. (2005) reported an increased N availability after thinning in the same ponderosa pine forest. An increase in soil mineral C and in N mineralisation was also observed by Overby and Hart (2016) 6 month post-thinning, most likely due to incorporation of organic matter into the soil after thinning. However, both mineral C and mineral N returned to their initial levels one year following thinning (Overby and Hart 2016). Recently, increased nutrient availability due to thinning has been reported to be lessened in the longer term (Ganzlin et al. 2016). The mechanisms through which this attenuation of N dynamics could take place have been attributed to the decrease of mineralisation-immobilisation flushes that occur immediately after thinning, to N losses through leaching,

Table 4 Foliar total C (TC), total N (TN) and C isotope composition ($\delta^{13}\text{C}$) of *Corymbia variegata* at Esk; and *C. citriodora* at Herberton at different stocking measured on two sampling times. Means followed with different letters show a significant difference

Leaf – Esk site	TC (%)		TN (%)		$\delta^{13}\text{C}$ (‰)	
	Month 60	Month 64	Month 60	Month 64	Month 60	Month 64
Stocking rates	Month 60	Month 64	Month 60	Month 64	Month 60	Month 64
75 (stems ha^{-1})	58.0(0.6)	48.1(0.6)	1.44(0.05)	1.18(0.05)	-28.6(0.25)	-28.9(0.25)
100 (stems ha^{-1})	58.0(0.6)	48.3(0.5)	1.46(0.05)	1.20(0.05)	-29.1(0.25)	-29.1(0.23)
200 (stems ha^{-1})	58.7(0.6)	48.6(0.6)	1.43(0.06)	1.20(0.05)	-29.2(0.26)	-29.1(0.25)
Un-thinned	58.6(0.6)	47.7(0.6)	1.34(0.05)	1.29(0.05)	-29.5(0.25)	-28.5(0.25)
Leaf – Herberton site						
	TC (%)		TN (%)		$\delta^{13}\text{C}$ (‰)	
	Month 84	Month 91	Month 84	Month 91	Month 84	Month 91
250 (stems ha^{-1})	44.0(0.4)	32.1(0.4)	2.43(0.10)a	1.36(0.10)	-29.8(0.20)	-28.5(0.20)
400 (stems ha^{-1})	43.6(0.4)	32.1(0.4)	2.13(0.10)b	1.32(0.10)	-29.5(0.20)	-28.7(0.20)
Un-thinned	44.3(0.3)	32.5(0.3)	1.41(0.08)c	1.22(0.08)	-29.5(0.16)	-28.7(0.17)

at $P < 0.05$ at each sampling time. Values in bold cases represent significant differences between sampling time ($P < 0.05$). Mean standard errors are presented in the brackets

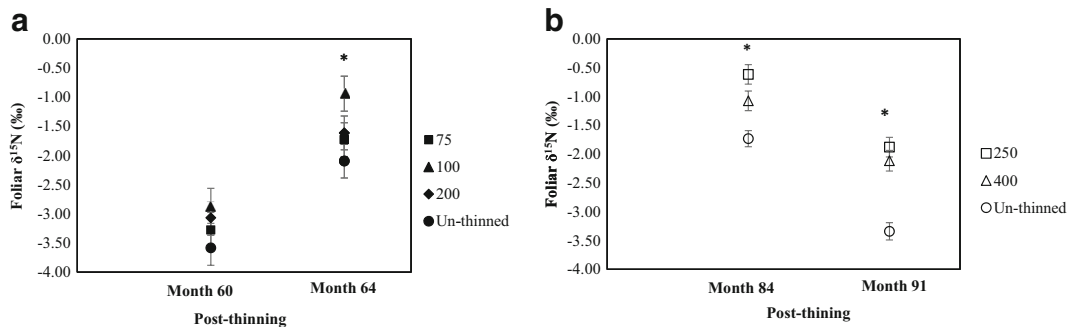


Fig. 2 Foliar N isotope composition ($\delta^{15}\text{N}$) of *Corymbia variegata* at Esk – close symbols (a); and *C. citriodora* at Herberton – open symbols (b) at different stocking measured on two sampling times. Stocking rates of 75 (stems ha^{-1}) – close rectangular, 100 (stems ha^{-1}) – close triangular, 200 (stems ha^{-1}) –

close diamond, un-thinned – close circle at Esk; and 250 (stems ha^{-1}) – open rectangular, 400 (stems ha^{-1}) – open triangular and un-thinned – open circle at Herberton. Asterisks indicate significances at $P < 0.05$

erosion, or denitrification, or to N adsorption by phenolic compounds (Hättenschwiler and Vitousek 2000; Dannenmann et al. 2006; Ganzlin et al. 2016).

At Herberton, the higher tree density in thinned areas than the one mentioned in Overby and Hart (2016) (116 stems ha^{-1}), as well as the lack of thinned material removal from the thinned plots, could explain the lack of thinning effects on soil C and N. At Esk, a severe thinning had been performed (75 stems ha^{-1}), however, lack of thinned material removal from the thinned plots may explain the absence of significant decreases in TC and TN in thinned areas compared to un-thinned areas. No effects of thinning on soil C and N were reported even three decades post-thinning which was partly associated

to leaving thinned materials on site (Nilsen and Strand 2008). However, those authors found a decrease in above ground C storage by increased thinning intensities which may suggest thinning may require over 30 years to affect soil C and N storage (Nilsen and Strand 2008).

Thinning has been shown to change plant cover composition with increased herbaceous species (Moore et al. 2006). Nitrogen mineralisation is a microbially mediated process which can be influenced by alteration of vegetation composition, time since thinning and other environmental factors, which may explain the contradictory results reported in different studies undertaken in the same experimental site (Kaye et al. 2005; Grady and Hart 2006; Overby and Hart 2016). Thinning may change soil organic layer C and N, due to the decrease in organic matter input but without affecting the mineral layer of soil C and N (Inagaki et al. 2011) which may additionally explain those contrasting findings.

Intensive thinning may limit N availability in long term which was supported by the lowest WSTN observed in the intensively thinned plots at the Esk. The soil WSTN mainly originates from organic matter inputs and is an important indicator of soil N availability (Huang and Schoenau 1998). However, soluble forms of soil N are also highly susceptible to leaching and lighter N (^{14}N) is more prone to be leached compared to heavier N (^{15}N), which leads to soil $\delta^{15}\text{N}$ enrichment (Högberg 1997). The negative relationship between soil WSTN and soil $\delta^{15}\text{N}$ observed in our data (Fig. 3a) further indicates a possible acceleration of leaching in intensively thinned plots.

The sample collection in this study was undertaken before and after the wet season. WSOC and WSTN were higher after the wet season compared to before

Table 5 Stepwise regression to identify driving factors explaining foliar C and N using soil variables, including soil TN, WSTN, $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ as independent parameters

Dependent	Independent	R ²	Probability
Esk site			
Foliar TC	WSTN	0.71	$P < 0.0001$
	TN		
Foliar TN	WSTN	0.57	0.004
Foliar $\delta^{15}\text{N}$	WSTN	0.36	0.002
Herberton site			
Foliar TC	WSTN	0.66	$P < 0.0001$
	$\text{NO}_3^-\text{-N}$		
Foliar $\delta^{13}\text{C}$	WSTN	0.41	0.001
Foliar TN	WSTN	0.55	$P < 0.0001$
	TN		
Foliar $\delta^{15}\text{N}$	WSTN	0.47	$P < 0.0001$

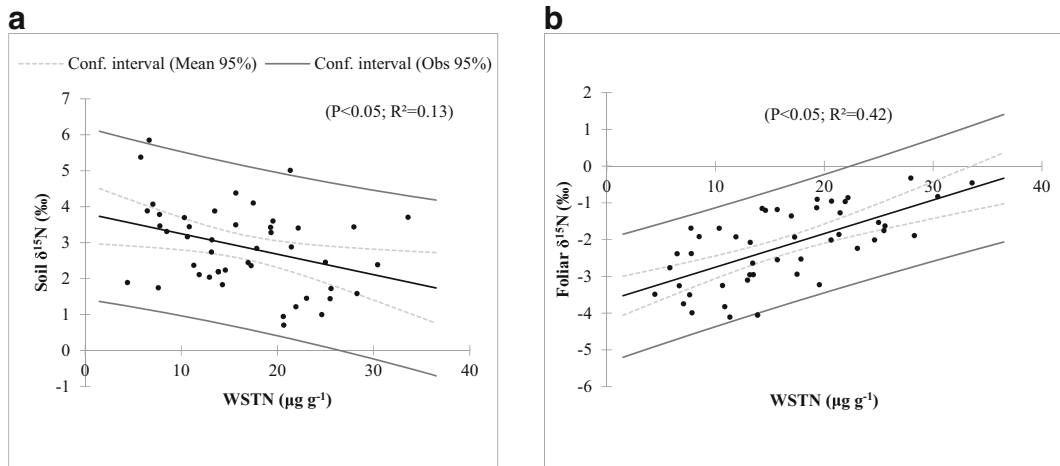


Fig. 3 Relationship between soil water soluble total nitrogen (WSTN) and soil N isotope composition ($\delta^{15}\text{N}$) (a) and between WSTN and foliar $\delta^{15}\text{N}$ (b)

wet season mainly in less intensively thinned areas and un-thinned plots. Soil organic C and N as well as microbial biomass C and N were investigated under thinning in both summer and autumn in two Mediterranean forests (Baena et al. 2013). There was a significant relationship between soil labile C and N and soil moisture, as soil labile C was higher in autumn than summer when temperature was also lower (Baena et al. 2013). Soil moisture is one of the main driving factors for microbial C and N transformations (Merilä et al. 2002). Increases and decreases of WSOC and WSTN at both sites in the current study concurred with the precipitation patterns. Despite the fact that WSOC and WSTN were responsive to precipitation patterns, soil TC and TN remained unaffected. We think that less intensively thinned and un-thinned plots may have resulted in increased organic inputs to temporally increase WSOC and WSTN. However, the inputs were not sufficiently high to change soil TC and TN.

In this study, foliar $\delta^{13}\text{C}$ was not tree density-dependent. Foliar $\delta^{13}\text{C}$ can change with water, light and resource availability. For example, foliar $\delta^{13}\text{C}$ is expected to increase due to increased water limitation (Qiu et al. 2013; Mullaney et al. 2015) as a consequence of increased stomatal closure leading to greater ^{13}C fixation in the carboxylation site (Farquhar et al. 1989). Lack of foliar $\delta^{13}\text{C}$ response to tree density has also been observed in other studies, suggesting that increased light intensity, water and N availability post-thinning may not be translated into an overall change in foliar $\delta^{13}\text{C}$ (Gebler et al. 2001; Fotelli et al. 2003; Skov et al. 2004; Inagaki et al. 2011). Our results are contradictory

with a study undertaken in overstory and understory trees of *E. marginata* post-thinning where increases in water availability and decreases in N availability led to decreased foliar $\delta^{13}\text{C}$ of *E. marginata* juveniles (Qiu et al. 2013). Those authors suggested that N limitation was affecting foliar $\delta^{13}\text{C}$ in *E. marginata* juveniles post-thinning, but also attributed this decrease in N availability to an extremely dry climate combined with their thinning experiment (Qiu et al. 2013).

The lack of foliar $\delta^{13}\text{C}$ response to tree density observed in our study may be explained through different mechanisms. For example, it has been shown that increased light interception and N availability may have a counteracting effect to increased water availability, because they generally tend to increase $\delta^{13}\text{C}$ by increasing the drawdown of CO_2 from the atmosphere to the sites of carboxylation (Cernusak et al. 2013). This acts in opposition to increased water availability, which tends to decrease the drawdown of CO_2 from the atmosphere to the carboxylation sites by allowing stomata to be more open. Additionally, homeostatic regulation of the ratio of intercellular CO_2 to ambient CO_2 concentrations during photosynthesis may also associate with a lack of foliar $\delta^{13}\text{C}$ response to tree density because homeostatic maintenance of gas exchange in plants adjusts carbon fixation at the carboxylation site for a given stomatal conductance (Wong et al. 1979; Skov et al. 2004; McDowell et al. 2006). Homeostatic maintenance is evident in anisohydric plants giving them an advantage over isohydric plants to cope with water limitation (McDowell and Allen 2015). Some *Eucalyptus* spp. have been shown to be anisohydric, maintaining higher

stomatal conductance under a given foliar water potential compared to isohydric species, which makes these species more tolerant to water limitation (Franks et al. 2007; McDowell et al. 2008). Hence, we think that although plants at Esk were experiencing a very dry year with 609 mm rainfall in 2014, the foliar $\delta^{13}\text{C}$ did not vary due to the fact that there might have been maintenance of a relatively constant ratio of intercellular to ambient CO_2 concentrations for photosynthesis, even while trees were experiencing water scarcity.

Foliar $\delta^{15}\text{N}$ tended to be more enriched in thinned plots compared to un-thinned plots. Foliar $\delta^{15}\text{N}$ indicates the condition of N at the moment of plant growth and is therefore linked to soil $\delta^{15}\text{N}$ (Ibell et al. 2013). Various mechanisms have been shown to influence leaf ^{15}N signatures. Firstly, when canopy density reduces after thinning, a higher N uptake would lead to higher ^{15}N fixation in leaves (Qiu et al. 2013). Secondly, an increase in foliar $\delta^{15}\text{N}$ indicates an acceleration of N transformation due to an increase in soil microbial activity and/or increased leaching (Garten 1993; Ibell et al. 2010; Reverchon et al. 2014). Soil microbial N transformation changes the ^{15}N signal of both $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ (Natalhoffer and Fry 1988). An enhanced leaching and N turnover in thinned areas are likely to occur in the long term due to the release of added biomass residues to the soil from thinned materials (Qiu et al. 2012). A positive relationship between soil N availability and enriched foliar $\delta^{15}\text{N}$ has also been observed after N fertilisation and understorey removal which was associated with enhanced mineralization and nitrification as well as increased leaching (Matsushima et al. 2012). This is consistent with the results from our regression analysis where WSTN, which is an indicator of fast N availability, explained 42 % of variation in foliar $\delta^{15}\text{N}$ (Fig. 3b). Thirdly, many tree species including *Eucalyptus* spp. have a strong mutualistic relationship with mycorrhizal fungi which additionally affect their N uptake (Horton et al. 2013). Isotopic fractionation occurs when N is transferred from mycorrhizal fungi to plants and mycorrhizal ^{15}N signals are more enriched than plants (Hobbie et al. 2000; Spriggs et al. 2003). It is possible that trees in un-thinned plots are more reliant upon mycorrhizal colonisation to overcome the competition leading to less enriched foliar ^{15}N signals in un-thinned plots compared to thinned plots. In addition, thinning has been shown to alter mycorrhizal fungal communities (Buée et al. 2005; Teste et al. 2012). We did not measure ^{15}N signal of soil inorganic N nor

mycorrhizal ^{15}N in this study, hence, the magnitude of their influence on foliar ^{15}N signals remains uncertain.

In our previous study, we found that there were no significant differences in tree growths in thinned plots at the Esk site (Bai et al. 2013). Therefore, decreased WSTN in intensively thinned plots (75 stems ha^{-1}) at Esk did not compromise plant growth probably due to lower competition for available N in severely thinned plots compared to other thinning regimes. However, it may imply a decrease in organic matter input in this site. Nitrogen utilisation efficiency has been reported to remain unaffected by thinning in a hinoki cypress plantation in Japan (Inagaki et al. 2011) despite a decrease in organic soil N content. However, those authors suggested that in the long-term, plant N uptake might be limited (Inagaki et al. 2011). While severe thinning may be the only practical and sustainable solution to improve the genetics of a native forest that has been progressively harvested of the best timber for generations, it also has implications for the soil organic matter. Thinning promotes understorey regeneration due to improved light and resource availability which compensates for part of the decreased organic matter inputs after thinning (Grady and Hart 2006; Moore et al. 2006). The current study also suggests leaving thinned organic matter in thinned plots further ensures preserving soil total C and N if high intensity thinning is required to be applied.

Conclusion

Soil and plant interactions following thinning have been studied and shown to improve tree growth due to increased nutrient and light availability as well as decreased competition (Giuggiola et al. 2015; Chase et al. 2016; Zhang et al. 2016). Farm forestry has also been revealed to be economically viable in areas receiving annual rainfall over 600 mm and if not replacing agricultural lands (Paul et al. 2013). However, the present study showed that soil TC and TN were not influenced by thinning most likely due to the fact that thinned materials had not been removed from the thinned plots and/or due to stimulation of understorey growth. Lack of significant differences in soil C and N with respect to thinning was also consistent with a lack of response of foliar TC and TN. Possible soil N limitation in the long term in intensively thinned plots was supported by decreased WSTN and increased foliar $\delta^{15}\text{N}$ which was an indication of increased leaching and N turnover. Lack of

foliar $\delta^{13}\text{C}$ response to tree density may be attributed to offsetting effects of increased light interception and N availability acting in opposition to effects of increased water availability, as well as homeostatic regulation of the ratio of intercellular CO_2 to ambient CO_2 concentrations during photosynthesis. Considering that tree growth was not influenced in intensively thinned plots compared to less intensively thinned plots (Bai et al. 2013), less intensive thinning may ensure longer term sustainability in the system compared to intensive thinning. If intensive thinning is required to be undertaken, incorporating thinning residues in soil helps to retain soil C and N.

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