



# Nitrogen and carbon cycling associated with litterfall production in monoculture teak and mixed species teak and flueggea stands

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## Abstract

**Purpose** High demand for teak (*Tectona grandis* L.f.), a species of economic importance, was the reason Solomon Islands experienced a surge in community-wide planting of monoculture teak stands in the last two decades. Mixed species planting of teak and flueggea (*Flueggea flexuosa* Muell. Arg.) was introduced to overcome the reluctance of growers to thin their stands. However, there is lack of information on the effect of changing from monoculture to mixed species plantings on the cycling of nutrients especially carbon (C) and nitrogen (N).

**Materials and methods** This study assessed litter quantity and quality, total C (TC), total N (TN), C:N ratio and C and N isotope compositions ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) over 18 months at two sites (Ringgi and Poitete). The treatments included teak planted at 833 stems per hectare (sph) (T1), teak planted in rows with two rows of flueggea at 833 sph (T2), 625 sph (T3) and 416 sph (T4), and teak planted in alternating rows with flueggea at 833 sph (T5).

**Results and discussion** Treatment 1 (T1) produced significantly higher total litter than T4 at Ringgi. However, based on individual tree litterfall production, teak in T4 (lowest stocking rate) at both trials produced higher litter per tree than the teak in T3, T2, T5 and T1 while there was no significant difference with litter production of flueggea. An enrichment of litter  $\delta^{15}\text{N}$  was observed over time in either species, which suggested an increased N loss and transformations in both experimental sites. When comparing each treatment and using individual tree productivity, T4 significantly produced and returned higher litter TC and TN than T3, T2, T5 and T1.

**Conclusions** Overall, individual tree productivity demonstrated that mixed species stands had a significant potential for cycling higher rates of C and N than monoculture teak stands. Therefore, establishment of mixed species stands, especially T4 and T3, was recommended as a practical measure to address the widely experienced problem of reluctance by growers to thin high value

trees while preserving the balance of C and N inputs into the ground.

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**Keywords** C:N ratio · C and N isotope compositions · *Flueggea flexuosa* · Mixed species · Monoculture · *Tectona grandis*

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## 1 Introduction

Mixed species plantations are being introduced worldwide in order to counteract the negative effects of monoculture plantations (Forrester et al. 2006; Reverchon et al. 2015; Bai et al. 2017b; Vigulu et al. 2018). Mixed species plantations have shown to enhance biodiversity and to improve soil fertility through a reduction in plant competition for nutrients and an increase in soil carbon (C) and nitrogen (N) contents (Montagnini 2000; Balieiro et al. 2008; Vigulu et al. 2017). In addition, mixed species plantations may increase above

ground biomass accumulation and the concentrations of soil available nutrients due to the acceleration of litter decomposition compared with those of monoculture plantations (Binkley et al. 1992; Forrester et al. 2006; Polyakova and Billor 2007). Litter production is one of the major pathways to return organic matter from plants to the soil surface (Veneklaas 1991; Bubb et al. 1998; Oladoye et al. 2010). However, the quantity and quality of litterfall fractions vary with different factors including plant species, plant age, spacing regimes, management practices and soil nutrient availability (Polglase and Attiwill 1992; Bubb et al. 1998; Rothe and Binkley 2001). Nutrient availability from litterfall decomposition is further controlled by climate, litterfall physico-chemical properties (e.g. lignin content, other phenolic compounds, lignin/N ratio, C:N ratios, physical leaf toughness and physical leaf surface barriers) and the community of decomposer organisms (Attiwill and Adams 1993; Bubb et al. 1998; Lorenzen et al. 2007). Any change in tree cover, for example, through the establishment of mixed species plantations, is therefore likely to influence the dynamics of nutrient cycling associated with litter production and decomposition.

Teak plantations are accounted for over 4 million hectares worldwide (Fernández-Moya et al. 2014). The increased demand for teak (*Tectona grandis* L.f.) due to its excellent wood quality and wide range of end-uses has resulted in increased areas of teak monoculture plantations (Jha 2003; Fofana et al. 2008; Mutanal et al. 2009; Sharma et al. 2011). Teak plantations have also been used to rehabilitate the rainforest areas degraded by logging. In Solomon Islands, mixed species stands of teak and flueggea (*Flueggea flexuosa* Muell. Arg.) have been developed to overcome the reluctance of growers to thin pure teak stands (Vigulu et al. 2017, 2018). Our previous works have shown that interplanting teak with flueggea could enhance soil C and N stocks and potentially reduce N losses, thereby promoting a more efficient use of N resources and keeping competition for N at a minimum between both species (Reverchon et al. 2015; Vigulu et al. 2017). However, little is known regarding how the transition from monoculture to mixed species systems affects litter quantity and quality, particularly in terms of litter C and N concentrations.

Litter C and N concentrations are some of the main driving factors affecting litter decomposition, which in turn determines C and N return to soil (Zhang et al. 2008). Both leaf and litter C:N ratio and C and N isotope compositions ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) have been used as reliable indicators to investigate long-term C and N cycling in different ecosystems (Zhang et al. 2008; Tutua et al. 2014; Nguyen et al. 2017). Whilst foliar and litter  $\delta^{15}\text{N}$  unravels N cycling in the system,  $\delta^{13}\text{C}$  provides insights in plant photosynthesis and water relations (Högberg et al. 1993; Johannisson and Högberg 1994; Tutua et al. 2014; Bai et al. 2017a). The litter C and N cycling in the tropics have been mostly investigated on natural forests (Vitousek and Sanford 1986; Hermansah et al. 2002; Yang

et al. 2005) and plantations outside of the Pacific region (Bernhard-Reversat 1996; Ma et al. 2007; Oladoye et al. 2010), or both (Ashagrie and Zech 2013). However, teak litterfall studies have been conducted in monoculture plantations in South Asia (Sharma and Pande 1989; Pande et al. 2002; Jha 2003; Takahashi et al. 2012), Africa (Egunjobi 1974), and Latin America (Kraenzel et al. 2003). Considering the potential of establishing mixed species plantations for maintaining soil quality and wood production (Reverchon et al. 2015; Vigulu et al. 2018), it is critical to determine the contribution of the litter produced in these mixed species systems in terms of C and N cycling, in order to incorporate these findings into improved plantation management practices. The current study thus aimed to gain an understanding of the litterfall production and litter C and N dynamics in mixed species plantations where teak was interplanted with flueggea in different spacing regimes, and to compare litterfall nutrient dynamics with those of teak grown in monoculture plantations.

## 2 Materials and methods

### 2.1 Site description

The study was located at Ringgi (8° 05' 16.33" S and 157° 08' 46.62" E) and Poitete (7° 52' 34.39" S and 157° 07' 46.78" E) on Kolombangara Island, Western Province, Solomon Islands. Both trials were planted in April 2009 on land formerly covered with regenerated secondary forests and located on Oxisol soil (Hansell and Wall 1975). Ringgi and Poitete scientific trials are situated at the coastal region at an altitude of 84 m and 27 m a.s.l., where the slope is flat for Ringgi and slightly undulating for Poitete. The climate is humid tropical, and temperature is consistent all year with a yearly mean of 28 °C. Ringgi has a monthly rainfall range of 229–396 mm and Poitete 220–367 mm (Electronic Supplementary Material – ESM - Fig. S1). Although the rainfall is fairly evenly distributed throughout the year, there is often a drier period around August and September and wetter period between December and March for both sites. Soil physical and chemical properties are presented in Table 1.

### 2.2 Experimental design

Each trial was established on a 2 ha area and consisted of the same randomised complete block design with five treatments and four blocks, allowing for spatial variation across both trial sites. The trials were established to examine optimal spacing for teak and flueggea in a mixed species system and compare with monoculture teak. There were five treatments, characterised by species ratio and stems per hectare (sph) or

**Table 1** Soil physical and chemical properties for Ringgi and Poitete trial sites at two depths of 0–10 cm and 10–20 cm

	Ringgi site		Poitete site	
	0–10 cm	10–20 cm	0–10 cm	10–20 cm
Soil properties				
Bulk density (g cm <sup>-3</sup> )	0.82	0.82	0.80	0.82
pH	4.8	4.8	5.1	4.8
Cation exchange capacity (cmol(+) kg <sup>-1</sup> )	12.0	7.0	13	11
Total carbon (TC) (%)	6.23	4.30	6.75	5.35
Total nitrogen (TN) (%)	0.73	0.48	0.76	0.58
$\delta^{13}\text{C}$ (‰)	-27.10	-26.57	-27.25	-26.99
$\delta^{15}\text{N}$ (‰)	7.37	8.30	6.96	7.52

planting spacing (Table 2). In each plot, there were six planting rows with eight trees. Each plot was buffered by the 1st and the 6th lines and the 1st and the 8th trees of each line. Each plot had a total of 24 measured trees of which T1 had 100% teak; T2, T3 and T4 had 33% teak, and 67% flueggea with different tree spacing regimes and T5 contained 50% teak and 50% flueggea (Table 2). The undergrowth was rich with a shrub layer and herbaceous community. During the study period, two pruning operations were conducted at the Ringgi trial, and only one was conducted at the Poitete trial. Both trials were treated with manual clear weeding annually.

### 2.3 Litterfall sampling and plant growth

Litterfall was sampled using litter traps between March 2011 and September 2012 when plantation was between age 2 and 3½ years (over 18 consecutive months). The litter samples were collected monthly during the period of study. Each trial had a total of 60 litter traps (15 litter traps per block). Each treatment had three litter traps positioned at random locations at the mid-way point between lines. Traps were made of wooden squares holding nets made from shade cloth and mounted on wooden stakes 1 m above the forest floor. Each trap had a catchment area of 0.50 m<sup>2</sup> (0.71 m × 0.71 m) with a 30-cm depth. Over the study period, 99% of the litterfall were leaves, and therefore, only leaf litterfall production was studied. Leaf litter collected from each trap in each treatment were separated by species, pooled into two paper bags and oven dried at 60 °C to constant weight, and weighed separately. Dried leaf litterfall samples were ground to a fine homogenous powder using Puck and ring

mill (Rocklabs, New Zealand) and samples stored in sterile, airtight containers until elemental analysis. Tree growth was assessed at the end of litterfall study at both experimental sites and is presented in Table S1 (ESM).

### 2.4 Chemical analysis

Approximately, 9 mg of leaf litterfall homogenised powder were weighed into tin capsules and analysed for total C (TC), total N (TN), and C and N isotope composition ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) using an Isoprime isotope ratio mass spectrometer (Cheshire, UK) with a Europa Elemental Analyser GSL (Cheshire, UK). All analyses were carried out at Griffith University, Nathan, Queensland.

### 2.5 Data calculation and statistical analysis

Total litter collected over the study period for each treatment was divided by the total number of months and by the area of litter traps to determine the monthly mean production (expressed in kg ha<sup>-1</sup> month<sup>-1</sup>). Annual production per treatment was then calculated by multiplying the monthly litterfall production by 12. The monthly litterfall C and N contents for each treatment were obtained by multiplying the total carbon (TC) and total nitrogen (TN) concentrations with the monthly total litter biomass for each treatment. The annual inputs of C and N to the plantation floor for each treatment were determined by total annual litter production × % of C or N (Tutua et al. 2008). Potential return to soil of TC and TN of teak and flueggea within species and across treatments were compared using individual tree TC and TN production.

**Table 2** Detail of different treatments replicated in four blocks at the Ringgi and Poitete experimental sites

Treatment	Species	Species ratio	Planting space	Stems per hectare (sph)
1	Teak	1:0	4 m × 3 m	833
2	Teak and flueggea	1:2	4 m × 3 m	833
3	Teak and flueggea	1:2	4 m × 4 m	625
4	Teak and flueggea	1:2	4 m × 6 m	416
5	Teak and flueggea	1:1	4 m × 3 m	833

As treatment effect was not significant on the chemical parameters of litterfall from both species at both sites, the data of litterfall TC, TN,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of all treatments were pooled to detect potential differences over the study period. Therefore, the data were further analysed by one-way repeated measures analysis of variance (ANOVA) followed by a Bonferroni correction where significant differences were detected to compare sampling months. One-way ANOVA was used to detect differences among treatments in total litter production, annual leaf litter production and annual leaf litter TC and TN followed by post hoc Tukey's HSD test when the treatments were significantly different at  $P < 0.05$ . Normality of variables was tested using Shapiro–Wilk test, and homogeneity of variance was tested with Levene's test. If not stated otherwise, all reported values are given as the mean  $\pm$  standard error. The SPSS Statistics 22 software was used for statistical analyses.

### 3 Results

#### 3.1 Litterfall production

The annual litterfall ( $\text{Mg ha}^{-1} \text{ year}^{-1}$ ) production was not significantly different among T1, T2, T3 and T5 treatments at Ringgi trial, though T1 was significantly higher than T4 (Fig. 1a). There was no significant difference in litterfall

production among the treatments at the Poitete trial (Fig. 1b). Litter fell throughout the year with higher rates in the wet season than that of drier season, this seasonal effect being more pronounced in Poitete (Fig. 2).

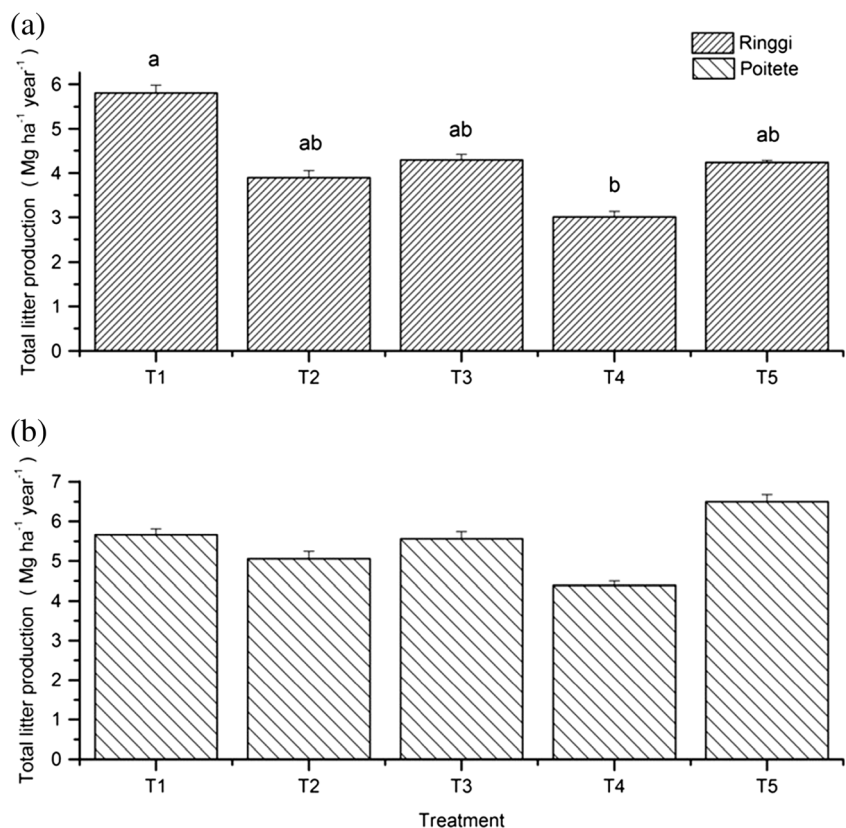
At the species level, no significant difference in litterfall production was observed among the different treatments at Ringgi for either teak or flueggea (Fig. 3a, b). At Poitete, however, teak litterfall production was significantly higher in T4 than that of T1 and there was no significant difference in flueggea litter production among the treatments (Fig. 3c, d).

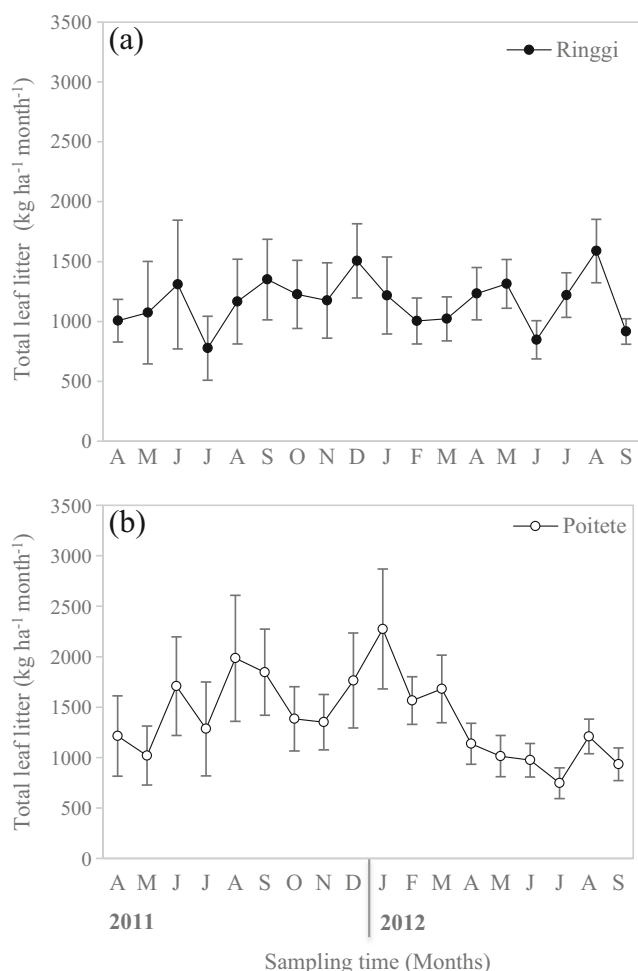
#### 3.2 Leaf litter TC and TN, and C:N ratio

The monthly mean of teak litterfall TC in either trial (Ringgi and Poitete) was significantly higher in December 2011, January 2012 and February 2012 than those of other sampling months (Fig. 4a). Flueggea litterfall TC was significantly higher in December 2011, January 2012, February 2012 and June 2012 compared with those of other sampling months in Ringgi (Fig. 4a). Flueggea litterfall TC in June 2012 was significantly lower than all sampling months with exception observed in August 2011 at Poitete (Fig. 4b).

Monthly litterfall TN was significantly higher in August 2011, February 2012 and June 2012 than in March 2011 for teak, whereas flueggea TN was significantly higher in August 2011 than that of March 2011 and December 2011 at Ringgi

**Fig. 1** Annual total production of leaf litter by treatment at (a) Ringgi and (b) Poitete. Different lowercase letters represent significant differences among treatments at  $P < 0.05$





**Fig. 2** Mean monthly leaf litterfall ( $\text{kg ha}^{-1}$ ) from April 2011 to September 2012 at Ringgi (a) and Poitete (b)

(Fig. 4c). Monthly litterfall TN was significantly higher in December 2011, January 2012, February 2012 and June 2012 than that in March 2011 for teak at Poitete (Fig. 4d). Flueggea had significantly higher litterfall TN in December 2011, January 2012 and March 2012 than in March 2011 at Poitete (Fig. 4d). Over the study period, monthly mean C:N ratio was significantly higher for teak in March 2011 in either trial than those of August 2011 and June 2012 (Fig. 4e, d). The C:N ratio of flueggea was significantly higher in March 2011 than that in August 2011 and June 2012 in Ringgi (Fig. 4e). The C:N ratio of flueggea did not differ among sampling months at Poitete (Fig. 4f).

### 3.3 Leaf litter $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

There was no significant difference in litter  $\delta^{13}\text{C}$  of teak among sampling months over the study period at Ringgi (Fig. 5a). Litterfall  $\delta^{13}\text{C}$  for flueggea significantly decreased after August 2011 at Ringgi (Fig. 5a). Litter  $\delta^{13}\text{C}$  of teak was significantly higher in December 2011

compared with that in February 2012 at Poitete (Fig. 5b). At Ringgi, the litterfall  $\delta^{15}\text{N}$  of teak and flueggea was significantly higher in February 2012 than that in March 2011 (Fig. 5c). At Poitete, teak showed higher litter  $\delta^{15}\text{N}$  values in December 2011 and February 2012 whereas flueggea higher litter  $\delta^{15}\text{N}$  values were observed only in December 2011 compared with other sampling months (Fig. 5d).

### 3.4 Carbon and N return via litterfall

At Ringgi, T1 returned significantly greater C and N to the soil than all mixed species treatments (Fig. 6a, b). No significant differences among T2, T3 and T5 in N return to the soil were also observed (Fig. 6b). At Poitete, T5 contributed with a significantly greater return of C to the soil than those other treatments (Fig. 6c). Treatment 1 and T3 contributed with a significantly greater C return to the soil than T2 and T4 at Poitete (Fig. 6c). Treatment 5 returned significantly higher N to the soil than that of T2, T3 and T4 at Poitete (Fig. 6d). There was no significant difference between T1 and T5 in terms of N return to soil at Poitete (Fig. 6d). When taking into account individual tree productivity, C and N return to the soil significantly increased with increasing spacing in teak, and was greater at T4 than the other treatments, at either trial (Figs. 7 and 8). However, flueggea spacing did not influence C and N return to the soil (Figs. 7 and 8).

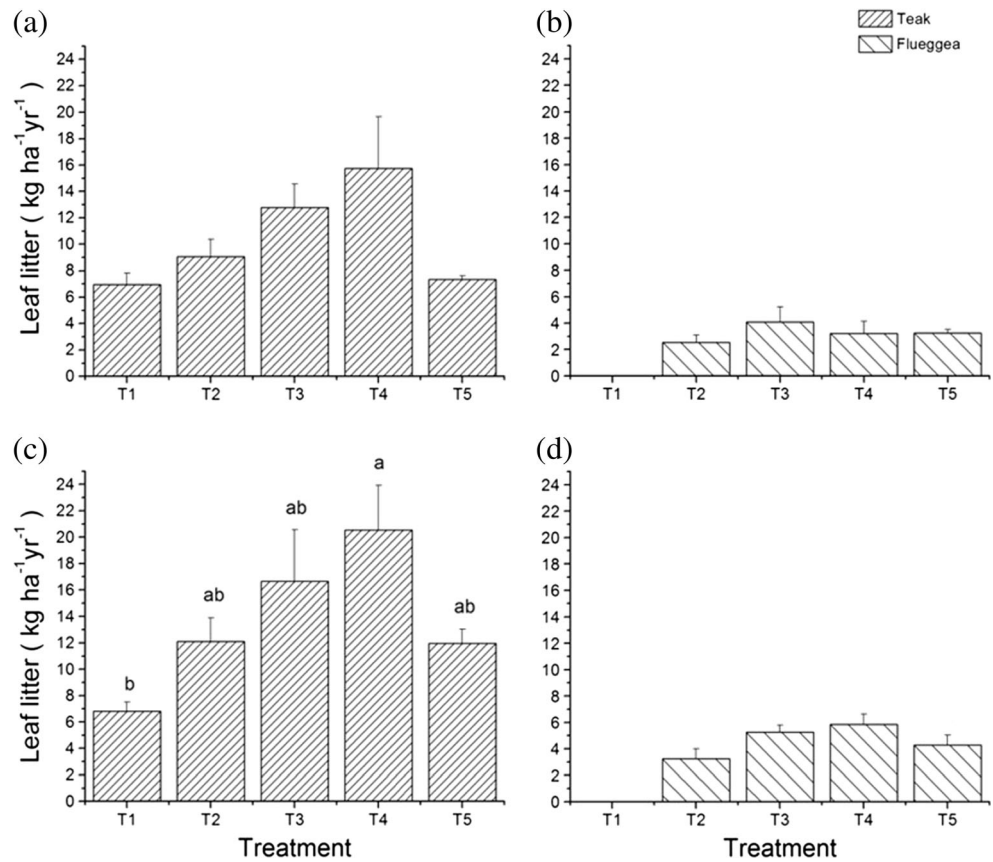
## 4 Discussion

### 4.1 Litterfall production

Mixed teak and flueggea plantings with increased spacing led to increased teak litter production per tree compared with monoculture teak plantation. Increased tree spacing has shown to increase biomass accumulation and crown development in trees (McClain et al. 1994) due to decreased competition for resources including light, nutrients and water (Bai et al. 2017a, b). Teak responded to available growing space around age 2 to 3 years by developing its crown horizontally and therefore increasing its crown size, which led to a higher litterfall production. In the higher density stands, teak tended to develop its crown vertically with a smaller crown to overcome early competition for light and therefore produced lower leaf mass. Our results showed that mixed stand of 416 sph (T4) had the potential to promote higher individual tree crown and litter production than single and mixed species stands of 833 sph.

Litter fell throughout the year with higher rates in the wetter season than that of the drier season, which was more pronounced in Poitete where only one pruning operation

**Fig. 3** Tree species mean annual leaf litter ( $\text{kg ha}^{-1} \text{ year}^{-1}$ ) production at different treatment at Ringgi (a, b) and Poitete (c, d). Different lowercase letters represent significant differences among treatments at  $P < 0.05$

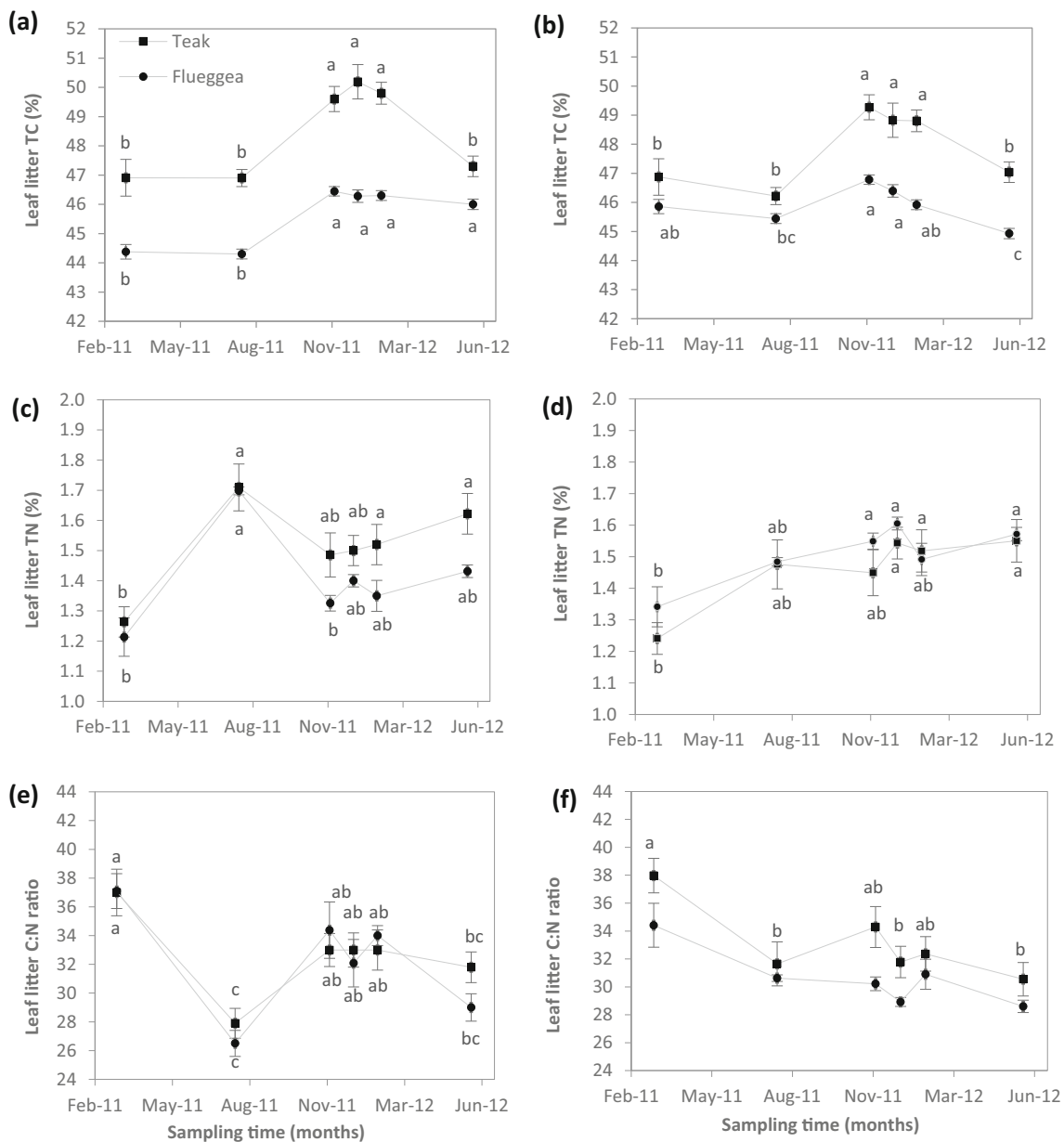


was conducted. Increased litterfall production during the wet season is comparable with other tropical species including Afara (*Terminalia superba* Engl. & Diels) and *Leucaena leucocephala* (Lam) (Ola-Adams and Egunjobi 1992; Oladoye et al. 2010). However, the peak of teak litterfall at wet season contrasts with the findings of other studies which have reported that teak litter peaks in the dry season as a result of desiccation or water stress (Egunjobi 1974; Ola-Adams and Egunjobi 1992). This highlights one of the differences between Solomon Island grown teak and many other teak producing countries. Teak is naturally deciduous and will defoliate completely in areas where there is a prolonged dry season such as Thailand (Blumfield et al. 2018). The fact that the peak of teak litterfall in our study was in the wetter season may relate to the high winds associated with the rainy (monsoon) season and diurnal temperature range (Ogunyebi et al. 2013). Teak has larger leaf surface area than flueggea and therefore was hit harder by the rainfall and wind, causing it to shed more leaves than flueggea. Leaf shedding is an adaptive response of trees to wind (Gardiner et al. 2016), which may be presented by teak and explain its greater contribution to litterfall than flueggea. As shown by Wilson (1980), leaf shape and vein distribution are also associated with wind tolerance in trees, which may be another explanation for flueggea to

present a lesser leaf loss compared with those of teak. Flueggea leaves may also be attached more tightly to the tree branches and thus less susceptible to wind than those of teak. Therefore, environmental factors and leaf characteristics, which have control over the onset of senescence and abscission process, must not be overlooked (Vitousek 1984; Ogunyebi et al. 2013). Site differences should also be taken into account, as different management practices were applied in Poitete and Ringgi. As mentioned before, pruning was carried out twice at Ringgi and once at Poitete. Leaf litterfall has been shown to decrease with increasing pruning intensity, as pruning reduces above-ground biomass (Andivia et al. 2013; Ssebulime et al. 2018).

#### 4.2 Litter C:N ratio

Overall, litter C:N ratios did not differ with respect to tree species and spacing regimes. However, litter C:N ratio was higher in the wet season than that of dry season, which was more pronounced at the Ringgi site compared with that of the Poitete site. The higher litter C:N ratio observed during the wet season may be attributed to foliar N leaching due to rainfall; although, previous reports showed that the N quantity lost through precipitation may be less than 0.6%

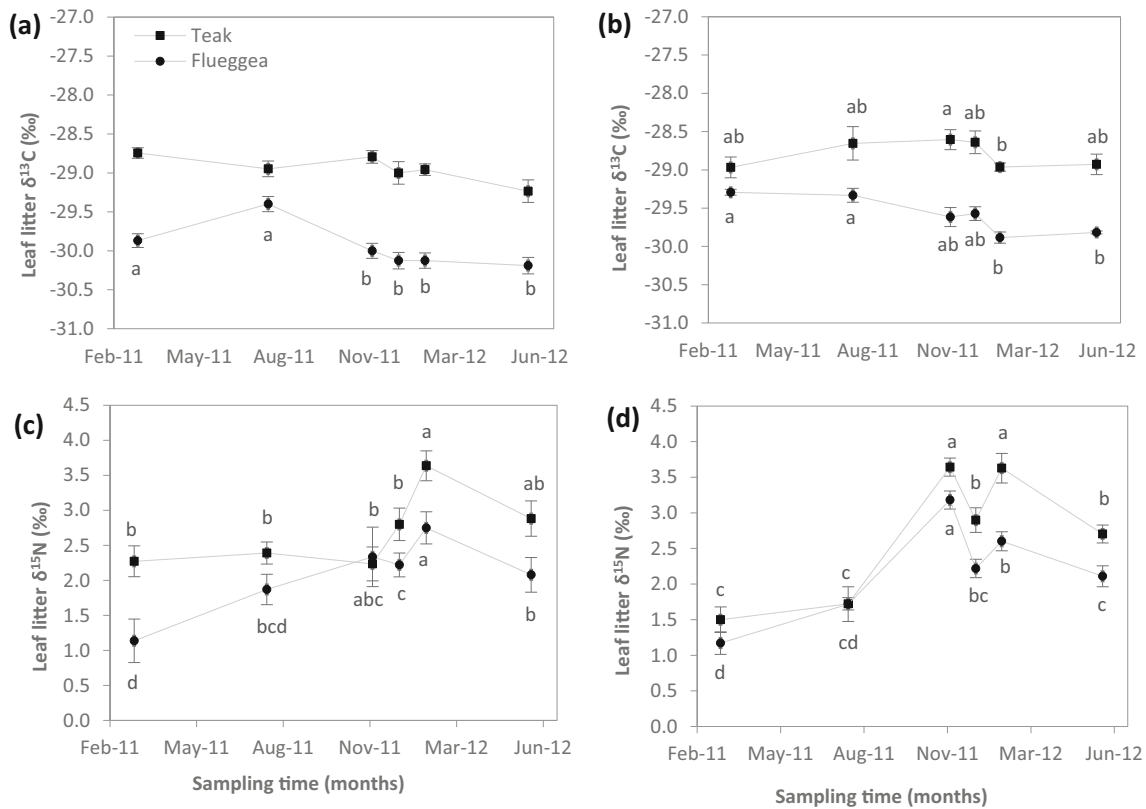


**Fig. 4** Leaf litter TC (%) at Ringgi (a), TC (%) at Poitete (b), TN (%) at Ringgi (c), TN (%) at Poitete (d), C:N ratio at Ringgi (e), and C:N ratio at Poitete (f) between March 2011 and June 2012 in teak (close rectangular)

and flueggea (close circle). The different lowercase letters represent significance among sampling time for each tree species at  $P < 0.05$

(Chapin and Kedrowski 1983). We noted that most of the litter that shed around August at Ringgi were mostly green leaves that fell from mechanical damage caused by strong wind after pruning took place, when canopy was opened. Litter that fell from December to February during the wet season was a combination of mature and brown leaves. The Poitete trial was not pruned, and therefore, most litterfall

would be from senescing and abscission process. Foliar N concentrations have been reported to be higher in green leaves than in senescent litter due to the re-translocation of N from senescing leaves to the growing zone (Vitousek 1984). However, we did not find significant differences between the TN of green leaves and litterfall for both species. Therefore, the maturity of leaves in the shed litter was



**Fig. 5** Leaf litter  $\delta^{13}\text{C}$  (‰) at Ringgi (a),  $\delta^{13}\text{C}$  at Poitete (b),  $\delta^{15}\text{N}$  (‰) at Ringgi (c) and  $\delta^{15}\text{N}$  at Poitete (d) between March 2011 and June 2012 in teak (close rectangular) and flueggea (close circle). The different lowercase letters represent significance among sampling time at  $P < 0.05$

not a driving factor for this observation. A decreased litter TN and increased litter TC in the wet season were responsible for observed increases of litter C:N in the wet season. Increased photosynthesis (gas exchange) rates have been observed in wet season compared with dry season leading to increased C uptake in rainforest trees due to increased leaf area index (Goulden et al. 2004). Therefore, increased C uptake in the wet season could explain increased litter TC in the wet season leading to increased C:N ratio in our experiment.

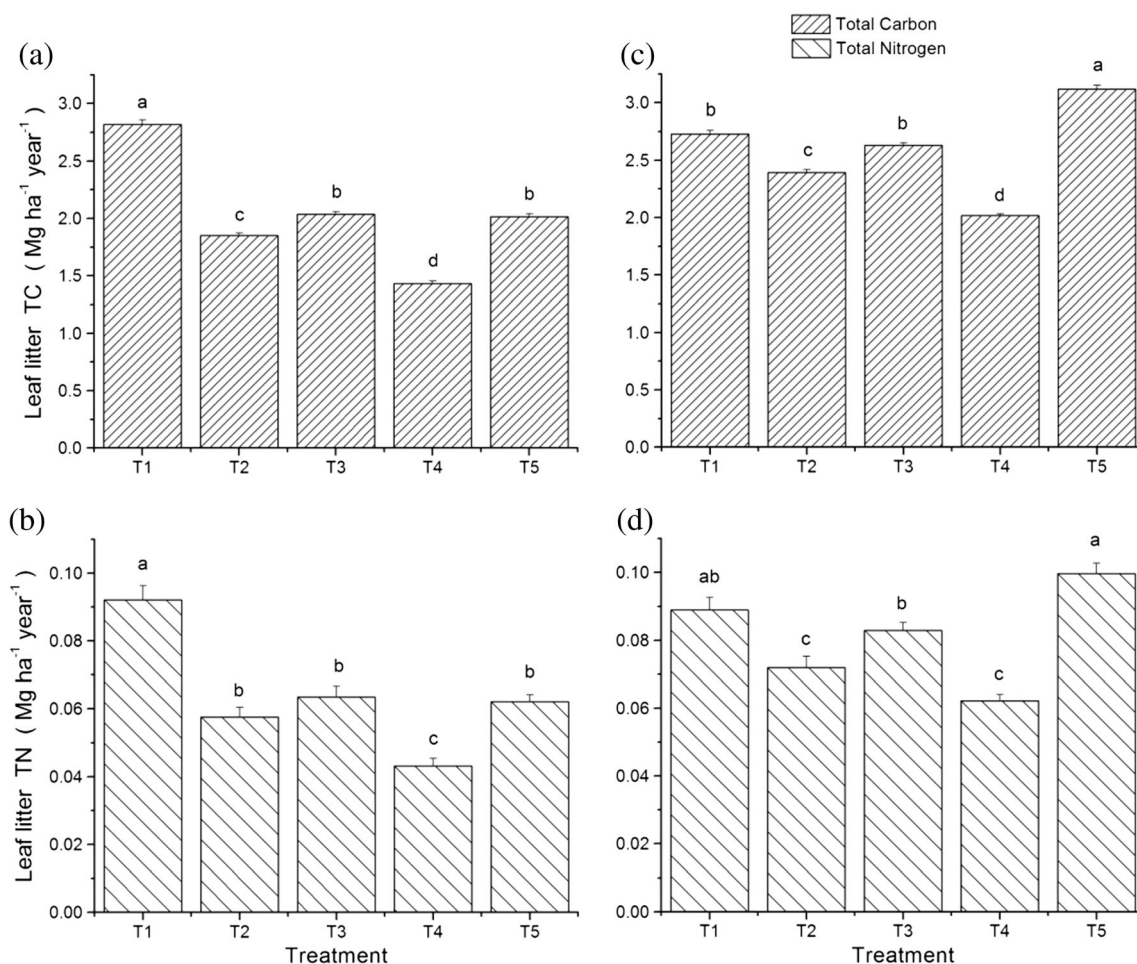
### 4.3 Litter $\delta^{13}\text{C}$

Despite growing in the same soils, teak had significantly greater litter  $\delta^{13}\text{C}$  than flueggea. Foliar  $\delta^{13}\text{C}$  differences between teak and flueggea could be explained through different mechanisms. For example, plant species have shown to possess different  $\delta^{13}\text{C}$  despite growing at the same site (Hogberg et al. 1995; Bassiri et al. 2003; Charles et al. 2011; Bai et al. 2017b). Some plant species may also not discriminate against  $^{13}\text{C}$  as strongly as others leading to increased foliar  $\delta^{13}\text{C}$  (DeLucia and

Schlesinger 1991; Arndt et al. 2000; Kristiansen et al. 2005; Huang et al. 2008; Ibell et al. 2013). Increased foliar  $\delta^{13}\text{C}$  also suggests an enhanced water use efficiency (Arndt et al. 2000). Higher teak litter  $\delta^{13}\text{C}$  compared with flueggea may indicate that teak has higher water use efficiency (WUE) than flueggea (DeLucia and Schlesinger 1991; Ometto et al. 2006), and teak may not discriminate against  $^{13}\text{C}$  as strongly as flueggea during photosynthesis (DeLucia and Schlesinger 1991; Arndt et al. 2000; Kristiansen et al. 2005; Huang et al. 2008; Ibell et al. 2013). Plants with shallow rooting systems have also shown a less conservative water-use strategy ( $\delta^{13}\text{C}$  becomes more negative) than those with deep rooting systems (Cullen et al. 2008). Soil moisture might be mostly available at the soil surface, benefiting flueggea which develops surface root network and forcing teak to engage to a higher WUE strategy because it has a deeper root network (Vigulu 2018).

Studies also reported that tree height can influence  $\delta^{13}\text{C}$  concentrations as a result of changes in hydraulic conductivity, responsible for drawing in water through the roots and pulled up through the tree to the tips of all branches





**Fig. 6** Total leaf litter TC and TN (Mg ha<sup>-1</sup> year<sup>-1</sup>) for Ringgi (**a, b**) and Poitete (**c, d**). Different lowercase letters represent significant differences among treatments at  $P < 0.05$

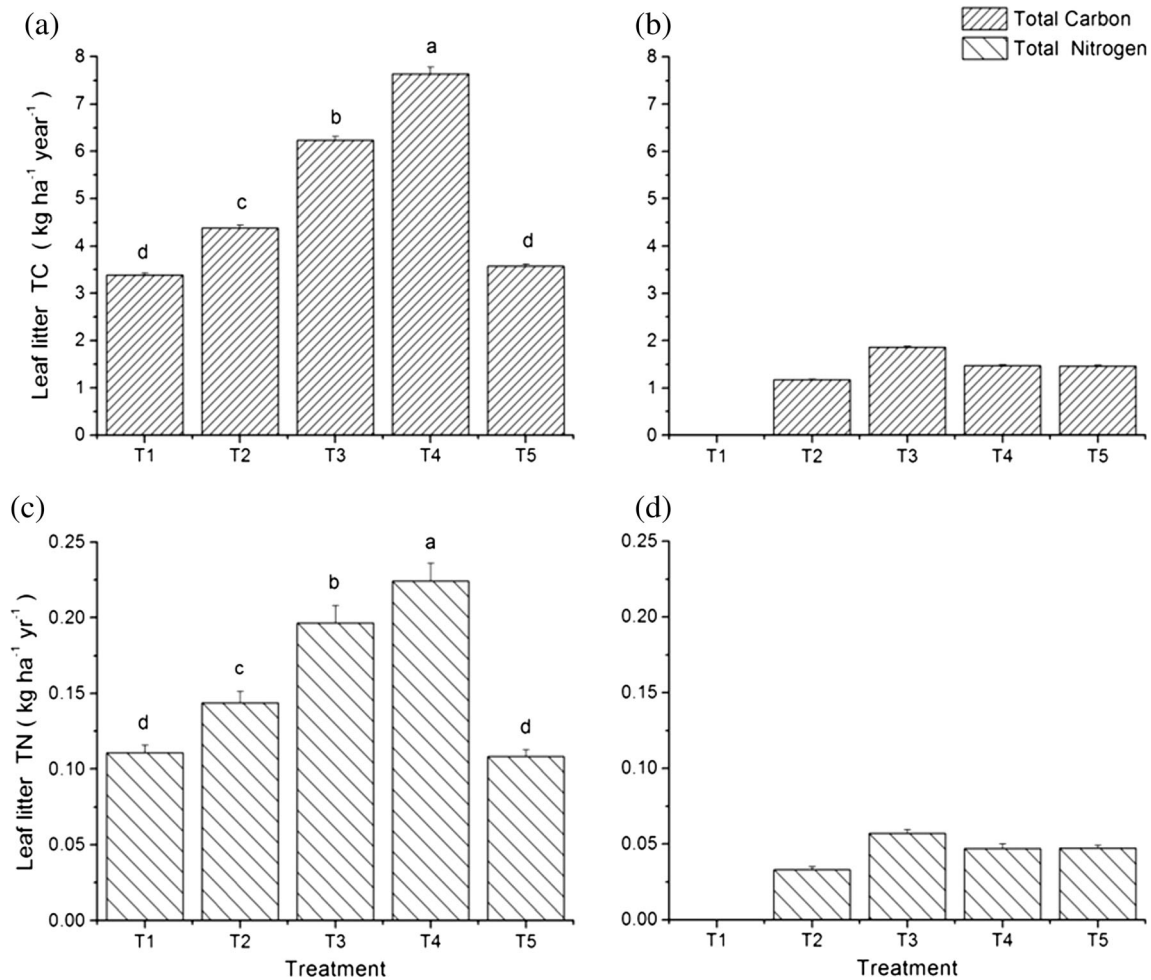
over time (McCarroll and Loader 2004; Ibell et al. 2013). Teak grew rapidly during its early growth and had a dominant canopy exposed to sunlight than flueggea (Vigulu et al. 2017). With greater leaf evaporative area, teak may use higher amounts of water for cooling as transpiration than in physiological processes such as photosynthesis and respiration (Kocher and Harris 2007). Higher requirement of water for transpiration may cause teak to experience water stress and develop higher WUE as indicated by less negative  $\delta^{13}\text{C}$  than flueggea as water potential and stomatal conductance decrease with height (Ibell et al. 2013).

#### 4.4 Litter $\delta^{15}\text{N}$

Whilst litter  $\delta^{15}\text{N}$  did not differ between two tree species, an increased litter  $\delta^{15}\text{N}$  was observed over the period of study in both species. Our complementary study using  $^{15}\text{N}$  tracer has also found no differences in litter  $\delta^{15}\text{N}$  of the both species which has been associated with lack of

competition for N in those plantations (Vigulu et al. 2017). Litter  $\delta^{15}\text{N}$  also reflects the soil  $\delta^{15}\text{N}$  which is, in turn, dependent upon the soil N source (Charles et al. 2011; Ibell et al. 2013) and reflects the isotopic composition of N that was acquired by plant roots over the entire rhizosphere (Mardegan et al. 2009; Charles et al. 2011). The general increase in litter  $\delta^{15}\text{N}$  over the study period may indicate that the tree roots were accessing soil N in deeper soil zone as  $\delta^{15}\text{N}$  increases with depth (Hogberg 1997; Rowe et al. 2001; Bustamante et al. 2004; Charles et al. 2011; Bai et al. 2015; Liu et al. 2019). Our data were consistent with those studies that have shown increases of plant root network coverage could lead to the increase of live leaf and litterfall  $\delta^{15}\text{N}$  over time (Mardegan et al. 2009; Charles et al. 2011).

An increase in litter  $\delta^{15}\text{N}$  in our study over time would also suggest an acceleration of N cycling rates at our study site. Increases in  $\delta^{15}\text{N}$  could be associated with different mechanisms, including increased potential for N losses through leaching, volatilization or microbial fractionations (Hogberg 1997; Reverchon et al. 2015). Leaching is associated with



**Fig. 7** Individual tree TC and TN (kg ha<sup>-1</sup> year<sup>-1</sup>) inputs of teak (**a, c**) and flueggea (**b, d**) litterfall to the forest floor at Ringgi trial. Different lowercase letters represent significant differences among treatments at

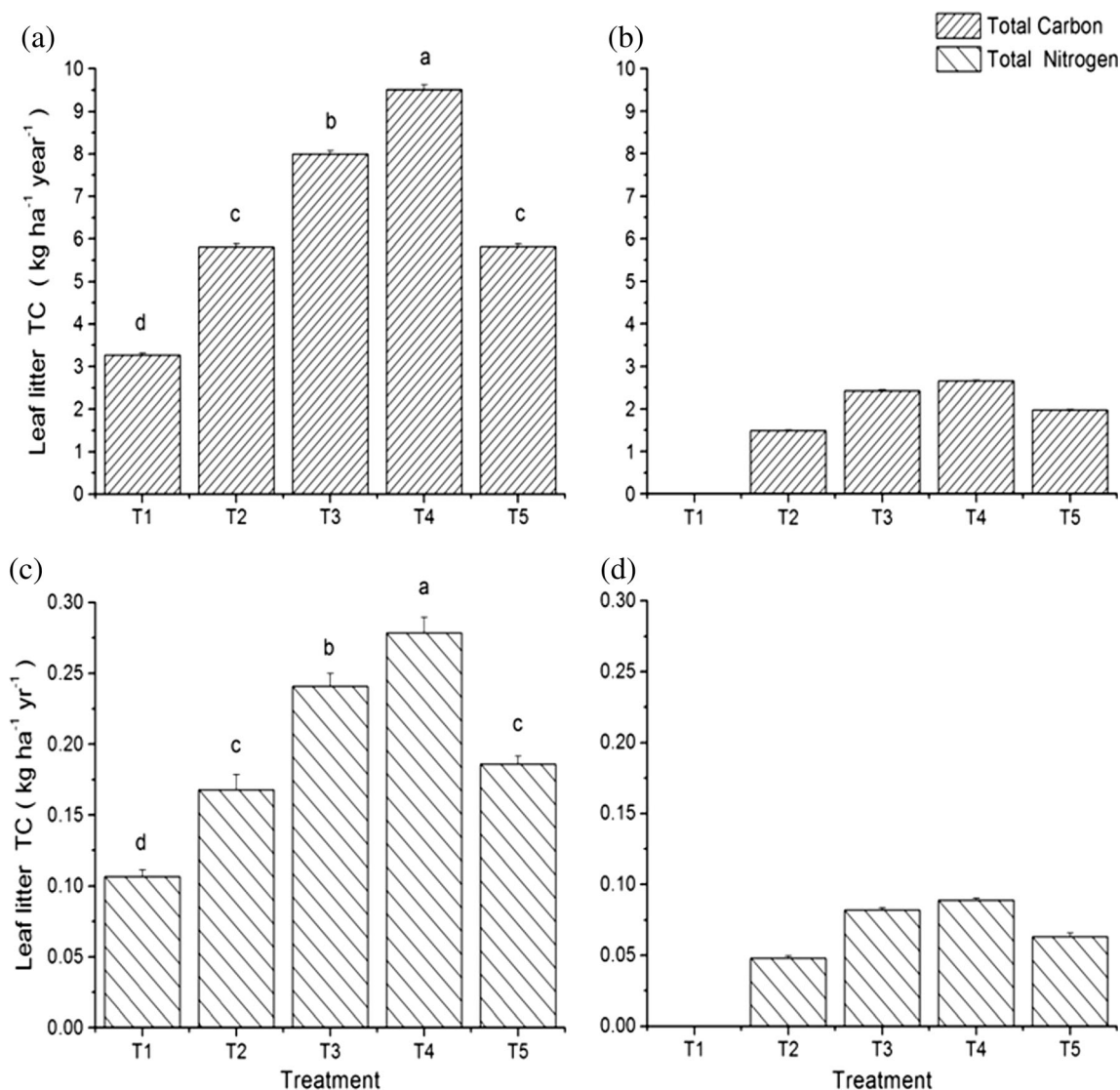
*P* < 0.05. Individual tree annual production was determined by dividing each treatment’s annual production by its tree density

heavy rainfall, and therefore, the significant variations of δ<sup>15</sup>N over time may reflect nitrate leaching towards the deeper soil layers, as shown by the increase of soil δ<sup>15</sup>N with depth (Matson et al. 1987; Hogberg 1997; Charles et al. 2011). Another possible explanation for the increase of δ<sup>15</sup>N with depth is the result of fractionation against <sup>15</sup>N during the mineralization of organic matter, leaving behind a decomposed organic matter with higher <sup>15</sup>N values (Hogberg 1997; Blumfield et al. 2004). At the ecosystem level, teak and flueggea litter with higher δ<sup>15</sup>N may indicate high N losses (Lajtha and Michener 1994), which is accompanied by relatively high rates of N cycling and transformation (Templer et al. 2007; Ibell et al. 2013).

### 4.5 Carbon and N inputs via leaf litter

Teak presented a greater contribution to C and N return through leaf litter than flueggea. However, the C and N returns of teak via leaf litter were density-dependent. The

decreased planting density stimulated individual tree canopy development and, as a result, individual tree input of C and N to the soil was significantly greater than those of higher density stands. Our results on TC return through teak leaf litter (1.5–2.75 Mg ha<sup>-1</sup> year<sup>-1</sup>) for both trials were lower than those stated in a study conducted in Thailand, where an estimation of 6.06 to 7.76 Mg C ha<sup>-1</sup> year<sup>-1</sup> was reported (Imvitthaya et al. 2011). The lower return of C in the present study as compared to reported elsewhere in the literature for tropical forests and plantations (Pregitzer and Euskirchen 2004; Imvitthaya et al. 2011) may be associated with differences in climatic conditions, and tree species density and composition. However, our annual result on teak litter TN from both trials (30–90 kg N ha<sup>-1</sup>) was within the ranges reported in other studies (Egunjobi 1974; Jha 2003). The differences in the C and N amount returned among the treatments of both trials were attributed to differences in total litter production and litter C and N concentrations.



**Fig. 8** Individual tree TC and TN ( $\text{kg ha}^{-1} \text{ year}^{-1}$ ) inputs of teak (a, c) and flueggea (b, d) litterfall to the forest floor at Poitete trial. Different lowercase letters represent significant differences among treatments at

$P < 0.05$ . Individual tree production was determined by dividing each treatment's annual production by its tree density

## 5 Conclusions

The present study determined the patterns of litterfall production, and C and N return for single and mixed stands of teak and flueggea. It was determined that local weather and thinning were partly responsible for the variations in litterfall production, and litter C and N concentrations and inputs to the forest floor. Single teak stands (T1) returned the highest C and N through total leaf litterfall while T4 returned the least. However, individual tree litter productivity and litter C and N returned to the soil were significantly greater at T4 and T3 than those of the other treatments. Our results indicated that mixed species systems, especially T3 and T4 with stocking rates of 625 and 416 sph, were sustainable alternatives to monoculture

teak plantations, as litter production and the return of C and N by individual teak trees to the soil may promote an increase in soil C and N stocks.

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