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ARTICLE

Competition for nitrogen between trees in a mixed-species plantation in the Solomon Islands

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ABSTRACT

As part of an ACIAR project aiming at improving community forestry in Solomon Islands, mixed-species plantations were established to assess the feasibility of inter-planting teak (*Tectona grandis* L. f.) and flueggea (*Flueggea flexuosa* Muell. Arg). Flueggea is a native hardwood used for timber and fence construction, and early removal of flueggea from a mixed-species stand could have a similar silvicultural outcome to thinning a single-species stand of teak. Using ^{15}N-labelled ammonium sulphate, we investigated the competition for nitrogen (N) between the two species. The ^{15}N-labelled tracer was applied to the soil surface of plots containing pairs of trees, one of each species, in 2-year-old and 4-year-old mixed-species stands, after the pairs of trees were isolated from the rest of the stand by an impermeable membrane. After 12–18 months, the isolated trees were measured and harvested, and each tree component (roots, stem, branch and foliage) was weighed and analysed for total N and ^{15}N enrichment. There was no significant difference in the amounts of ^{15}N between teak and flueggea components at either age, suggesting equal uptake of added ^{15}N-labelled tracer by both species. The ^{15}N amount was greater in stem followed by root, foliage and branch for teak and branch followed by stem, root and foliage for flueggea. About 42% and 55% of the applied ^{15}N tracer were recovered in the 2-year and 4-year plots respectively, suggesting that higher uptake occurs with well-established root structure and that N losses decreased following canopy closure. The amount of total nitrogen was not significantly different between teak and flueggea components at age 2 and 4 years, and may indicate equal access to growth resources, and similar allocation. Although teak had significantly greater stem growth (height, basal area and volume) than flueggea in the 4-year plots, ^{15}N uptake were similar to flueggea, which may mean that competition for growth resources was still minimal or that access to the resources was equal and growth rates differed between species.

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Introduction

A greater interest in the benefits of mixed-species systems has resulted in an increase in mixed-species plantings being established over recent decades (Olsthoorn et al. 1999). Mixed-species plantations are expected to maintain soil fertility by reducing plant competition for nutrients and increasing soil carbon (C) and nitrogen (N) pools (Lang et al. 2014; Reverchon et al. 2015). However, empirical studies addressing nutrient cycling and nutritional interactions among different components of these mixed-species systems are still scarce (Nair & Souvannavong 2000; Rothe & Binkley 2001; Balieiro et al. 2008).

The study of nitrogen (N) dynamics in plants has been conducted using ^{15}N-labelled plant materials (Blumfield et al. 2004; Versini et al. 2016) and ^{15}N-labelled solutions (Barea et al. 1989; Blumfield & Xu 2006) to examine N uptake, N movement and competition between plants. Nitrogen uptake studies can provide insights into ecological and physiological processes such as litter decomposition or N assimilation (Dijkstra et al. 2003; Xu et al. 2009; Ibell et al. 2013). In terms of nutrient cycling, quantifying biomass and nutrient allocation in different tree and plant components is helpful for estimating tree nutrient uptake, and nutrient removal through harvesting, in a forest ecosystem. Quantifying above-ground biomass over time is important for evaluating forest ecosystem productivity, and nutrient and carbon cycling. Although a lot of information is available in the literature regarding nutrient-cycling dynamics in different forest ecosystems and plantations, less information is available with respect to mixed-species systems (Zeugin et al. 2010; Lang et al. 2014).

In the Solomon Islands, teak (*Tectona grandis* L. f.) is a commercially important exotic hardwood species usually grown in mono-species systems, mainly for export as round logs. Flueggea (*Flueggea flexuosa* Muell. Arg), on the other hand, is a local native lowland forest hardwood species much in demand for traditional timber houses and fence construction. Growing teak in mixed species stands with flueggea was seen as a way to address the reluctance of growers to thin mono-species stands of teak. Reluctance to thin (due to the perceived high value of each teak tree) is the greatest barrier to correct silvicultural management of smallholder plantations (Blumfield & Reverchon 2013). The principle behind the approach of growing flueggea with teak was that growers would remove the flueggea for personal use, effectively thinning the teak to final stocking rate.

As part of an ACIAR project aimed at improving community forestry in the Solomon Islands, and prior to introducing this

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mixed-species system into local communities, trials were established to understand the nature of the competition for available resources between teak and flueggea (Blumfield et al. 2013). The objective of this study was to examine the interactions between teak and flueggea with respect to competition for N and to determine N uptake and movement in both species. The uptake of N and allocation of N to biomass components by teak and flueggea of different ages were examined using a ^{15}N-labelled tracer and mass balance technique to assess ^{15}N recovery in an enclosed soil-plant system.

Materials and methods

Site description

The trials were conducted at Ringgi, on the island of Kolombangara (8°05′16.33′′S and 157°08′46.62′′ E, 84 m asl), Western Province, Solomon Islands. Trial plots were established on land formerly covered with regenerated secondary forests, on Oxisol soil (Hansell & Wall 1975). Ringgi has a monthly rainfall range of 229–396 mm, with a humid tropical climate and consistent temperature through the year, with a yearly mean of 28°C. Although the rainfall is fairly evenly distributed throughout the year, there is often a drier period around August and September and a wetter period between December and March. Soil physical and chemical properties are presented in Table 1.

Experimental design and N tracer experiment

Our ^{15}N-labelled tracer study investigated N uptake and movement in teak and flueggea growing in enclosed systems, in 2-year-old and 4-year-old mixed-species stands planted at 4 m × 3 m spacing. Four isolation plots (plots 1–4) were established in August 2011 when the first mixed-species trial, planted in April 2009, was 2.5 years old. Four other isolation plots (plots 5–8) were established in February 2012 when the second mixed-species trial, planted in November 2011, was 3 months old. Each isolation plot contained one teak and one flueggea tree and enclosed a total soil volume of 14.40 m^3 (Fig. 1). The plots were isolated by excavating a trench to a depth of 60 cm and installing a barrier of double-layered building-grade plastic film. The trenches were then firmly back-filled. Plots were thus isolated laterally from adjacent soil, but were not isolated from the soil beneath them or from the atmosphere. The barriers were placed at the midpoint between the trees in the plot and adjacent trees outside the plot, and represented the maximum free area available to the trees. Following the method described by Blumfield and Xu (2006), a tracer containing ^{15}N-labelled ammonium sulphate in solution was applied to all plots at a rate of 0.825 kg N ha^{-1} with 10.24 atom% ^{15}N. The mean natural abundance ^{15}N of soil on both sites is 0.3690‰ (0–10 cm) and 0.3693‰ (10–20 cm). Each plot surface was divided into eight blocks, and the same amount of solution applied to ensure an even coverage of each plot.

Table 1. Soil physical and chemical properties of the two mixed- species trials at Ringgi

Soil physical and chemical properties	2-year plots		4-year plots	
	0–10 cm	10–20 cm	0–10 cm	10–20 cm
Bulk density (g cm^{-3})	0.82	0.82	0.82	0.82
pH	4.8	4.8	4.8	4.8
Cation exchange capacity (cmol$^+$ kg^{-1})	12.0	7.0	12.0	7.0
Total carbon (%)	7.57	4.30	6.23	4.30
Total nitrogen (%)	0.75	0.44	0.73	0.48

Bulk density, pH and CEC were extracted from Hansell and Wall (1975) report and confirmed by an unpublished internal report from Kolombangara Forest Products Limited on the same sites. Total carbon and total nitrogen were determined using an Isoprime isotope ratio mass spectrometer (Cheshire, UK) linked to a Europa Elemental Analyser GSL (Cheshire, UK) by this study.

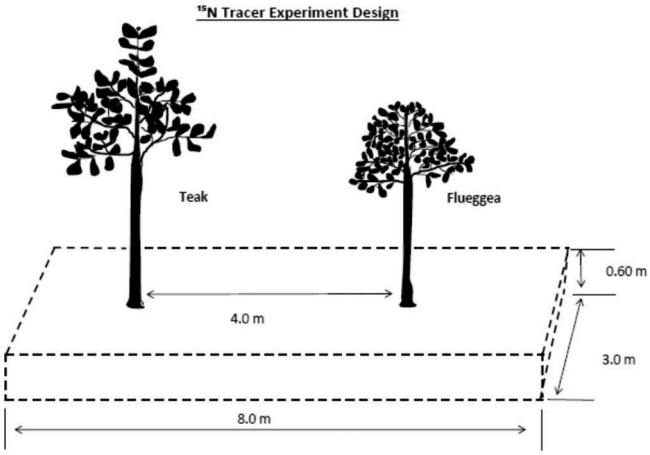

Figure 1. Schematic design of a ^{15}N tracer isolation plot

Plots 1–4 were sampled for a period of 18 months and the age of the trees at final excavation was 4 years; these will be referred to as the 4-year plots. The 4-year plots had an undergrowth of grass and shrubs. Plots 5–8 were sampled for 12 months and the age of the trees at final excavation was 2 years; these will be referred to as the 2-year plots. The 2-year plots had an undergrowth of grass and crops (bean, capsicum, peanut, potato and taro) during the tree-growth period, but potato and taro were the only crops growing when the excavation work was undertaken. Four teak and four flueggea trees in areas adjacent to the isolation plots within the mixed-species stand were selected for foliar sampling over the study period and were treated as control trees.

Foliar and litterfall sampling

Foliar samples were taken from each plot at 6, 12 and 18 months after the application of ^{15}N-labelled tracer in the 4-year plots and at 6 and 12 months after application in the 2-year plots. Foliar samples of each species were taken from upper branches and second or third order of leaves and packed in labelled paper bags. Additional samples of mature leaves and old leaves (middle and lower leaves from shoots) were taken from both trees in each plot at final harvest. Young leaves were not sampled.

Litterfall was collected monthly over a 12-month period after the application of ^{15}N-labelled tracer in the 4-year plots. Over the 12-month litterfall collection period, dead branches and twigs did not fall into the traps and litterfall was therefore composed of leaves. The leaves were collected and separated into labelled paper bags by species. There was no significant litterfall production in the 2-year plots and therefore collection was not done.

Foliar and litterfall samples were dried at 60°C to constant mass and each the dried mass of each sample was then determined. Dried litterfall samples were ground to a fine homogenous powder using a Puck and ring mill (Rocklabs, New Zealand) and sub-samples stored in sterile, airtight

containers. Cross-contamination of ^{15}N between samples was prevented by thoroughly washing the grinding vessel under running warm water between grinding operations.

Grasses and shrubs growing in the 4-year plots and crops and grass growing in the 2-year plots were also harvested to assess the mass balance of the ^{15}N-labelled tracer. Sub-samples were oven-dried at 60°C to constant mass, and subjected to the same analytical process as the foliar and litter samples.

Measurement of above- and below-ground biomass

Three replicates of the 2-year plot and four replicates of the 4-year plots were manually excavated 12 and 18 months respectively after application of ^{15}N-labelled ammonium application. A flueggea in Plot 7 (2-year plots) died during the study period and this plot was therefore excluded from the analysis. Before felling of the trees, diameter at breast height over bark (DBHOB) and crown radius were measured. When felled, each tree's total fall height, crown height (from ground level to the first living branch) and crown length (first branch to crown tip) were measured.

Each stem was cut into 1 m sections for ease of weighing, and stump and roots were excavated. Three stem discs were sampled from each tree at 20 cm above ground, at the middle of the stem length (2.5 and 5.5 m for teak of 2 and 4 years, and 1.5 and 3.5 m for flueggea of 2 and 4 years, respectively) and at 5 m below the tip of each tree's stem. Eighteen leaves of flueggea and nine leaves of teak were sampled from three top branches exposed to sunlight, from the middle of the middle branches, and from the base of bottom branches (labelled top, middle and bottom). Tree parts were separated into foliage, branches, stem wood and roots, and fresh weight determined in the field. Each teak and flueggea biomass component was sub-sampled and processed for elemental analysis as above. A 5–10 mm disc was taken from each of the stem sections, dried to constant weight and ground to a fine, homogenised powder. Branches of teak and flueggea were not sampled from the 4-year plots for both species.

Soil sampling

Soil sampling took place at the same time as tree excavation, that is, 12 and 18 months following ^{15}N-labelled tracer applications at the 2- and 4-year plots. Before excavation of the trees, three transects were demarcated at equal distance from each other, parallel to the longest side of each plot. Soil samples were taken from four cores at equal distance from each other along each transect at depths of 0–10 and 10–20 cm. The four soil samples from the same depth in each transect were kept separate and used to examine if surface flow had affected the distribution of the ^{15}N-labelled tracer application over time. The soil samples for each transect and depth of each plot were air dried for at least three weeks, sieved (<2 mm) and processed in the same way as the foliar and litter samples.

Chemical analyses

About 6 mg of roots, stem wood, branch, foliage and crop, 9 mg of litterfall, and 16 mg of soil homogenised powder were weighed and analysed on an Isoprime isotope ratio mass spectrometer (Cheshire, UK) linked to a Europa Elemental Analyser GSL (Cheshire, UK). Samples were analysed for total N (TN) and ^{15}N as reported previously (Ibell et al. 2013). Results for ^{15}N were expressed as enrichment over the background abundance. All analyses were carried out at Griffith University, Nathan, Queensland.

Data analysis

Data analysis followed the method used by Rowe et al. (2001) and Ibell et al. (2013). Briefly, dry weight conversion factors were obtained for each tree component of teak and flueggea at both ages. Teak and flueggea TN, ^{15}N-labelled tracer uptake, and ^{15}N allocation in each tree part were calculated for each age. The ^{15}N recovery was determined using the mass balance technique (Blumfield & Xu 2006). The amount of ^{15}N in each plant component was calculated as follows:

$$^{15}\text{N content (g)} = \text{biomass (g)} \times \text{N concentration (\%)} \times \text{atom \% } ^{15}\text{N},$$

where atom % ^{15}N is calculated as excess over the background natural abundance. Recovery of added N was calculated as follows:

$$\text{Recovery of added } ^{15}\text{N(\%)} = (^{15}\text{N recovered (g)}/ ^{15}\text{N applied (g)}) \times 100,$$

where ^{15}N applied was also calculated as excess over the background natural abundance.

Monthly and annual litterfall production was calculated for each species. The monthly litterfall TN and ^{15}N content (kg) were obtained for each species, and the annual inputs of TN and ^{15}N to the forest floor were determined for each species by multiplying annual litter biomass with the mean TN and ^{15}N.

The SPSS Statistics 22 software was used for statistical analyses. Normality of variables was tested using Shapiro-Wilk test and homogeneity of variance was tested with Levene's test. The data were further analysed using multiple univariate ANOVA and Tukey post hoc test, where necessary, to investigate pairwise significant differences in plant and litter biomass and in TN and ^{15}N contents within species components and between species

Results

Tree growth and biomass

The mean height of teak was significantly greater than flueggea in both age groups (Table 2). However, there was a difference in DBH between the species only in the 4-year plots when teak was significantly greater than flueggea. Teak had significantly greater basal area (BA) and volume than flueggea in the 4-year plots, although neither was significantly different in the 2-year plots. There was no significant difference in crown radius and crown height between teak and flueggea at either age. Teak had significantly greater crown depth than flueggea in the 4-year plots but no significant difference was observed in the 2-year plots (Table 2). Teak had significantly greater mean annual increment (MAI) of tree height and of DBH than flueggea in the 4-year plots, and had significantly greater MAI of tree height in the 2-year plots (data not shown).

There was no significant difference in dry mass of foliage, branch, stem and root between teak and flueggea in the 2-year plots (Table 3). However, teak had significantly greater

Table 2. Growth characteristics of destructively sampled teak and flueggea

	2-year plots		4-year plots	
Growth parameter	Teak	Flueggea	Teak	Flueggea
Tree height (m)	8.39 ± 0.20[a]	4.76 ± 0.71[b]	15.6 ± 0.88[a]	11.8 ± 0.55[b]
Diameter at breast height (DBHOB) (cm)	8.47 ± 1.57[a]	5.40 ± 0.95[a]	19.4 ± 1.04[a]	12.7 ± 0.58[b]
Basal area (BA) (m^2/tree) *	0.006 ± 0.002[a]	0.002 ± 0.001[a]	0.029 ± 0.003[a]	0.013 ± 0.001[b]
Volume (m^3/tree) **	0.025 ± 0.01[a]	0.006 ± 0.002[a]	0.235 ± 0.04[a]	0.076 ± 0.01[b]
Crown height (m)	4.37 ± 1.28[a]	1.57 ± 0.07[a]	6.07 ± 0.09[a]	6.20 ± 0.41[a]
Crown radius (m)	1.11 ± 0.53[a]	2.03 ± 0.26[a]	3.33 ± 0.32[a]	2.70 ± 0.22[a]
Crown depth (m)	4.02 ± 1.31[a]	3.19 ± 0.64[a]	9.56 ± 0.93[a]	5.58 ± 0.78[b]

Tabulated values are mean ± SE. Values followed by the same lower-case letter within rows under each age are not significantly different at $P < 0.05$ (Tukey post-hoc test).
* Basal area (BA) = $(DBHOB/200)^2 \times \pi$
** Volume = BA x Tree height x 0.5

Table 3. Above- and below-ground biomass dry matter of teak and flueggea

	2-year plots		4-year plots	
Biomass components	Teak	Flueggea	Teak	Flueggea
Foliage (kg)	2.76 ± 1.06[a]	2.15 ± 0.67[a]	10.84 ± 1.02[a]	10.46 ± 1.05[a]
Branch (kg)	1.90 ± 1.54[a]	2.33 ± 0.93[a]	16.25 ± 1.24[a]	14.13 ± 1.97[a]
Stem (kg)	8.72 ± 1.90[a]	4.43 ± 1.58[a]	67.6 ± 10.78[a]	42.76 ± 5.04[b]
Root (kg)	3.76 ± 0.89[a]	2.66 ± 0.92[a]	29.32 ± 3.90[a]	20.62 ± 1.91[a]

Tabulated values are mean ± SE. Values followed by the same lower-case letter within rows under each age are not significantly different at $P < 0.05$ (Tukey post-hoc test).

stem biomass than flueggea in the 4-year plots, although there was no significant difference in foliage, branch and root biomass.

Tree biomass total N and ^{15}N

The N content was not significantly different between teak biomass components at either age (Table 4). In flueggea trees, however, N content was significantly greater in stem than in foliage in the 4-year plots, whereas no significant differences were detected between flueggea components in the 2-year plots. There was no significant difference in N content in foliage, branch, stem and root between teak and flueggea in the 2-year plots, or between foliage, stem and root in the 4-year plots.

The amount of ^{15}N was significantly greater in stem than in the root, branch and foliage of teak in the 2-year plots (Table 5). The amount of ^{15}N in stem of teak was significantly greater than in the root and foliage, while teak root contained significantly more ^{15}N than did the foliage in the 4-

Table 4. Above- and below-ground biomass N of teak and flueggea

	2-year plots		4-year plots	
Biomass components	Teak	Flueggea	Teak	Flueggea
Foliage (kg)	0.0079 ± 0.003[aA]	0.0044 ± 0.001[aA]	0.0341 ± 0.004[aA]	0.0255 ± 0.002[aB]
Branch (kg)	0.0056 ± 0.004[aA]	0.0115 ± 0.004[aA]		
Stem (kg)	0.0150 ± 0.003[aA]	0.0108 ± 0.004[aA]	0.0868 ± 0.02[aA]	0.0776 ± 0.01[aA]
Root (kg)	0.0148 ± 0.001[aA]	0.0103 ± 0.003[aA]	0.1597 ± 0.05[aA]	0.0473 ± 0.01[aAB]

Tabulated values are mean ± SE. Values followed by the same lower-case letter within rows under each age are not significantly different at $P < 0.05$ (Tukey post-hoc test). Values followed by the same upper-case (capital) letter within columns are not significantly different at $P < 0.05$ (Tukey post-hoc test).

Table 5. Mass of ^{15}N in above- and below-ground biomass of teak and flueggea

	2-year plots		4-year plots	
Biomass components	Teak	Flueggea	Teak	Flueggea
Foliage (g)	0.089 ± 0.02[aB]	0.086 ± 0.02[aA]	0.30 ± 0.05[aC]	0.44 ± 0.05[AbaB]
Branch (g)	0.036 ± 0.03[aB]	0.067 ± 0.03[aA]		
Stem (g)	0.63 ± 0.05[aA]	0.39 ± 0.11[aA]	1.90 ± 0.15[aA]	1.63 ± 0.26[AaaA]
Root (g)	0.18 ± 0.05[aB]	0.29 ± 0.18[aA]	0.91 ± 0.13[aB]	0.92 ± 0.36[aAB]

Tabulated values are mean ± SE. Amounts of ^{15}N are calculated as excess over the background natural abundance. Values followed by the same lower-case letter within rows under each age are not significantly different at $P < 0.05$ (Tukey post hoc test). Values followed by the same upper-case (capital) letter within columns are not significantly different at $P < 0.05$ (Tukey post-hoc test).

year plots. Similar results were also observed in flueggea where the stem contained significantly more ^{15}N compared with the foliage, while no differences in the amount of ^{15}N were found between flueggea foliage and root in the 4-year plots (Table 5). There were no significant differences found in the amount of ^{15}N between components of flueggea in the 2-year plots. No significant differences in amount of ^{15}N were detected between each teak and flueggea component at either age.

Litterfall TN and ^{15}N

There was no significant difference in monthly litterfall production or litterfall N content between teak and flueggea over the 12-month study period in the 4-year plots (Table 6). Approximately 0.049 and 0.037 mg of ^{15}N-labelled tracer was released monthly in litterfall by teak and flueggea over the period of 12-month litter measurement. About 16% and 36% of the applied ^{15}N-labelled tracer were released monthly in litterfall from teak and flueggea respectively.

Tree ^{15}N recovery and total ^{15}N recovery in the soil-plant system

The ^{15}N recovery in teak stem, as a proportion of the applied ^{15}N, was significantly greater than in teak root, branch and foliage in the 2-year plots (Table 7). Recovery of ^{15}N in teak root was significantly greater than in teak branch and foliage in the 2-year plots, and was significantly greater than in teak foliage in the 4-year plots. There were no significant differences in ^{15}N recovery between biomass components of flueggea at either age. No significant difference in ^{15}N recovery was detected between components of teak and flueggea, despite the difference in biomass, in either the 2- or 4-year plots. Teak and flueggea had similar total recovery of ^{15}N recovery at both ages.

No significant differences were detected in the amount of ^{15}N recovered in terms of mass (Table 8) or proportion of the applied ^{15}N (Table 9) in the plant and soil compartments, for both periods of ^{15}N-labelled tracer application. The total amount of ^{15}N recovered in the soil was larger than the total amount of ^{15}N recovered in teak, flueggea and weed/shrub in both the 2-year and the 4-year plots. However, the proportion of ^{15}N recovered in the soil and in crops in the 2-

Table 6. Litterfall production, total nitrogen, and ^{15}N in the 12-month litterfall in 4-year plots

	Teak	Flueggea
Monthly litterfall (kg ha^{-1})	77.4 ± 14.10^{a}	52.8 ± 3.73^{a}
Total nitrogen (g)	1.3 ± 0.27^{a}	0.761 ± 0.07^{a}
^{15}N (mg)	0.587 ± 0.17^{a}	0.438 ± 0.12^{a}
^{15}N (% of applied)	0.0309 ± 0.0093^{a}	0.023 ± 0.01^{a}

Tabulated values are mean ± SE. Amounts of ^{15}N are calculated as excess over the background natural abundance. Values followed by the same lower-case letter within rows are not significantly different at $P < 0.05$ (Tukey post-hoc test).

Table 7. Recovery of applied ^{15}N from teak and flueggea biomass

	2-year plots 12 months following ^{15}N application		4-year plots 18 months following ^{15}N application	
Biomass components	Teak	Flueggea	Teak	Flueggea
Foliage (%)	0.14 ± 0.04^{aC}	0.094 ± 0.02^{aA}	0.50 ± 0.09^{aB}	0.60 ± 0.11^{aA}
Branch (%)	0.059 ± 0.04^{aC}	0.17 ± 0.07^{aA}		
Stem (%)	0.58 ± 0.04^{aA}	0.50 ± 0.16^{aA}	1.25 ± 0.04^{aAB}	1.57 ± 0.31^{aA}
Root (%)	0.38 ± 0.05^{aB}	0.61 ± 0.34^{aA}	2.55 ± 0.88^{aA}	1.08 ± 0.38^{aA}
Total (%)	1.159 ± 0.17^{Aa}	1.374 ± 0.59^{Aa}	4.30 ± 1.01^{a}	3.25 ± 0.80^{a}

Tabulated values are mean ± SE. Values followed by the same lower case letter within rows under each age are not significantly different at $P < 0.05$ (Tukey post-hoc test). Values followed by the same upper-case (capital) letter within columns are not significantly different at $P < 0.05$ (Tukey post-hoc test).

Table 8. Mass of ^{15}N in above- and below-ground biomass of teak and flueggea

	2-year plots		4-year plots	
Biomass components	Teak	Flueggea	Teak	Flueggea
Foliage (g)	0.089 ± 0.02^{aB}	0.086 ± 0.02^{aA}	0.30 ± 0.05^{aC}	0.44 ± 0.05^{aB}
Branch (g)	0.036 ± 0.03^{aB}	0.067 ± 0.03^{aA}		
Stem (g)	0.63 ± 0.05^{aA}	0.39 ± 0.11^{aA}	1.90 ± 0.15^{aA}	1.63 ± 0.26^{aA}
Root (g)	0.18 ± 0.05^{aB}	0.29 ± 0.18^{aA}	0.91 ± 0.13^{aB}	0.92 ± 0.36^{aABab}

Tabulated values are mean ± SE. Amounts of ^{15}N are calculated as excess over the background natural abundance. Values followed by the same lower-case letter within rows under each age are not significantly different at $P < 0.05$ (Tukey post-hoc test). Values followed by the same upper-case (capital) letter within columns are not significantly different at $P < 0.05$ (Tukey post-hoc test).

Table 9. Recovery of applied ^{15}N for plot components at 12 and 18 months

Plot component	12 months following ^{15}N application	18 months following ^{15}N application
Teak (%)	1.154 ± 0.07^{aB}	4.298 ± 0.98^{aB}
Flueggea (%)	1.380 ± 0.39^{aB}	3.247 ± 0.78^{aB}
Crop (%)	1.713 ± 0.47^{AB}	
Weed/shrub (%)	0.905 ± 0.57^{aB}	0.217 ± 0.16^{aB}
Soil 0–20 cm (%)	37.129 ± 16.60^{aA}	47.060 ± 13.39^{aA}
Total system (%)	42.281 ± 18.06^{a}	54.823 ± 17.38^{a}

Tabulated values are mean % ± SE %. Values followed by the same lower-case letter within rows are not significantly different at $P < 0.05$ (Tukey post-hoc test). Values followed by the same upper-case (capital) letter within columns are not significantly different at $P < 0.05$ (Tukey post-hoc test).

year plots were not significantly different (Table 9). Approximately 58% and 45% of the applied ^{15}N-labelled tracer were lost from the soil-plant system in the 2-year and 4-year plots respectively.

Discussion

Growth and biomass

The high rainfall, ample sunlight and fertile soils of the Solomon Islands give tree growers near perfect conditions, resulting in faster tree growth and shorter rotation lengths (Blumfield & Reverchon 2013). This was evident from the average total height and DBH of teak in both 2-year and 4-year plots in our study, which were greater than those reported for trees of a similar age grown in India (Kumar et al. 1998) or in Costa Rica (Pérez & Kanninen 2005).

Teak biomass growth was only significantly higher than that of flueggea in the 4-year plots, which indicates teak may begin developing stem biomass around that age. This is consistent with findings from other studies, which have shown that heartwood formation begins when the tree is between 4 and 6 years old for fast-growing plantation teak trees (Moya et al. 2014). The similarity of biomass of all tree components across species also indicates similar allocations of carbon and biomass in both species, and suggests that competition was at a minimum in our plots. Teak stem biomass reported in this study was much higher than the observed and predicted bole biomass reported for teak at aged 4 years in India (Sharma et al. 2011), growing in mono-species plantation under 1200 mm annual rainfall, which emphasises the favourable growth conditions existing for teak in the Solomon Islands.

TN content and ^{15}N content of plant and litterfall

The greatest amount of TN for teak was found in its roots, in both 2-year and 4-year plots. Flueggea had an allocation strategy which was slightly different from that of teak and changed with age, as the highest amount of TN was found for root and branches in the 2-year plots and foliage and roots in the 4-year plots. The lowest amounts of TN were found in the stem for both species at both ages. A lower concentration of TN in tree stem was also reported by Blumfield and Xu (2006) in hoop pine seedling stem and Zeller et al. (2001) in European beech. Changing amounts of TN in flueggea components over time may indicate prioritisation and allocation of N in the 4-year plots for canopy development for photosynthesis requirements (Zeller et al. 2001). Although TN concentrations among the components were different (data not shown), these differences were masked when expressed in mass units due to the differences in dry biomass between tree components.

The application and use of ^{15}N tracer made it possible to examine the uptake and partitioning of ^{15}N to the tree components and changes over time in both teak and flueggea. The total uptake of ^{15}N-labelled tracer was not significantly different between the two species, indicating that N competition within the system was minimal or insignificant in the first 4 years. Teak and flueggea allocated a higher proportion of the applied ^{15}N to their foliage, followed by the root, stem and branch, indicating allocation of N to the growing tissues for growth. The large N allocation to leaves is consistent with results found in other forest ecosystems (Zeller et al. 2001; Bloomfield et al. 2014) and reflects N investment in photosynthesis. However, when expressed in mass units, the highest ^{15}N content was found in stems and roots for both teak and flueggea at both ages, which indicates higher biomass allocation to their stems as TN concentration was lowest in the stem and branch (Buchmann et al. 1996). Significant increase in ^{15}N content in the stem in both species may be related to the role of the stem as a conduit between roots and shoots and to the importance of N for structural components (Dickson 1989; Blumfield & Xu 2006; Bloomfield et al. 2014).

The ^{15}N content of litterfall allowed us to follow N release rates. The amount of ^{15}N-labelled tracer in the litterfall was similar for both species and a similar amount was released to litterfall monthly. However, as teak sheds more leaves and has larger leaf surface area than flueggea, teak litterfall had a higher ^{15}N content than flueggea. Zeller et al. (2001) reported that less than 30% of litter ^{15}N incorporated in tree biomass returned to the soil as litterfall. Our study showed that about 16% and 36% of applied ^{15}N-labelled tracer was released in teak and flueggea leaf litterfall respectively, suggesting that greater litter N in teak was retained through translocation and used for growth. Teak uses higher N for its growth and therefore having flueggea in the mixed-species stand could ensure N cycling and maintenance of soil fertility (Reverchon et al. 2015).

Tracer recovery in tree, crop and soil pools

The recovery of the applied ^{15}N tracer was greatest in the stem for teak and in the root for flueggea in the 2-year plots. At age 4 years, ^{15}N recovery was greatest in the root for teak and the stem for flueggea. The changes in ^{15}N recovery between stem and root for teak between 2 and 4 years, and from root to stem for flueggea, demonstrated that

partitioning strategy for growth changed with age, possibly prompted by the emerging competition, phenological changes or aging of physiological tissues (Blumfield & Xu 2006). As trees age, their requirements change: they usually need less N to support growth, and tend to invest in more structural and storage materials (Fernández-Moya et al. 2013). Furthermore, as trees grow, they may compete for the available resources and, over time as above- and below-ground biomass develop, the bigger trees with wider crowns and longer roots would end up being the best competitors of growth resources. This was evident in our result as the ^{15}N recovery was greater at age 4 than at age 2, which may indicate that a better developed root structure (due to age) enabled higher nutrient uptake.

Soil was the main sink for ^{15}N, with 37% and 47% recovered in soil for 2-year and 4-year plots respectively, consistent with recent findings by Gurmesa et al. (2016) in a tropical forest of Southern China. The higher total ^{15}N recovery in the 4-year plots (55%) than in the 2-year plots (42%) may be due to better developed root structure in the 4-year plots that prevented leaching and promoted ^{15}N uptake. Canopy closure resulted in lower temperatures, reduced the direct fall of rain and increased forest floor biomass, which might have lessened the possibility both of denitrification and of leaching of ^{15}N. Denitrification is expected to be higher in under an open canopy with higher temperatures and the soil surface exposed to high rainfall and surface flow (Davidson et al. 1993; Bustamante et al. 2004). However, the total recovery of ^{15}N was lower than the recovery rates of approximately 75% found in other studies in tropical (Gurmesa et al. 2016) and temperate ecosystems (Templer et al. 2012). Few studies using ^{15}N labelling to analyse N cycling rates have been carried out in tropical forests, and more information is needed to unravel the mechanisms behind N retention and N loss in tropical ecosystems. The high cycling rates occurring under tropical settings may promote larger leaching rates and gaseous losses than those occurring under temperate conditions (Gurmesa et al. 2016).

The total amount of unaccounted ^{15}N tracer was greater (58%) in the 12-month experimental period with 2-year-old trees than in the 18-month experimental period with 4-year-old trees (45%). This may be explained by root development over time allowing trees to access ^{15}N lower down in the soil profile. The greater loss from the younger trees (2 years) than the older trees (4 years) may be partly attributable to denitrification (Pu et al. 2002). The ^{15}N tracer was applied to the younger trees under an open canopy and exposed to rain and sun, which would have led to a higher rate of denitrification and a longer period for this to occur (Xu et al. 1992, 2013). Further, in the 2-year plots, crops had been harvested and weeds were removed during crop maintenance, thus resulting in greater potential for ^{15}N loss. The proportion of applied ^{15}N that was recovered in food crops was not significantly different from that recovered in the soil, which may indicate higher uptake of ^{15}N into harvested crops. This is potentially the cause of the largest differences between ^{15}N recovery in the 2-year and 4-year plots, and is an important issue in agroforestry nutrient management. The N-use efficiency of species used in agroforestry systems should be considered in order to maintain soil fertility and design more sustainable management practices.

Conclusion

Teak and flueggea had similar uptake and allocation of nitrogen to biomass components, and allocated the highest proportion of applied ^{15}N to foliage, which reflects the investment of nitrogen in photosynthesis. Teak released approximately 16% of the applied ^{15}N monthly through leaf litterfall. Differences in recovery of ^{15}N between teak and flueggea were not significant in plots of either 2 or 4 years of age, which indicated similar rates of uptake at both ages. In the younger stand, crops had greater uptake of ^{15}N than teak and flueggea, and crop harvest and burning of weeds during maintenance may have contributed to higher losses of ^{15}N from the system, which has important implications for agroforestry systems. Although teak showed significantly greater growth than flueggea, ^{15}N uptake by teak was similar to flueggea, which may mean that competition in growth resources was minimal. This has important implications as canopy closure began at around age 4, and some flueggea were removed to avoid competition for light. The lack of below-ground competition for resources between the two species at this stage suggests that flueggea provides a compatible, mixed-species system for the growth of teak.

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