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Modeling the effects of tree species and temperature on soil's extracellular enzyme activity in 78-year-old tree plantations

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Abstract. Forest plantations have been widely used as an effective measure for increasing soil carbon (C) and nitrogen (N) stocks and soil enzyme activities play a key role in soil C and N losses during decomposition of soil organic matter. However, few studies have been carried out to elucidate the mechanisms for the differences in soil C and N cycling by different tree species in response to climate warming. Here, we measured the responses of soil's extracellular enzyme activity (EEA) to a gradient of temperatures using incubation methods in 78-year-old forest plantations with different tree species. Based on a soil enzyme kinetics model, we established a new statistical model to investigate the effects of temperature and tree species on soil EEA. In addition, we established a soil–enzyme–C/N model to investigate how temperature and tree species influence soil C/N contents over time without considering plant C inputs. These extracellular enzymes included C acquisition enzymes (β-glucosidase, BG), N acquisition enzymes (*N*-acetylglucosaminidase, NAG; leucine aminopeptidase, LAP) and phosphorus acquisition enzymes (acid phosphatases). The results showed that temperature and tree species significantly influenced all soil EEA and *Eucalyptus* had higher soil EEA than coniferous tree species. Modeling showed that *Eucalyptus* had larger soil C losses but had longer soil C residence time than the coniferous tree species over time. The differences in the residual soil C and N contents between *Eucalyptus* and coniferous tree species, as well as between slash pine (*Pinus elliottii* Engelm. var. *elliottii*) and hoop pine (*Araucaria cunninghamii* Ait), become larger and larger over time. On the other hand, the modeling results help explain why exotic slash pine can grow faster, as it has longer residual soil N residence time than native coniferous tree species like hoop pine and kauri pine (*Agathis robusta* C. Moore). Our results will be helpful for understanding the mechanisms of soil C and N cycling by different tree species, which will have implications for forest management.

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1 Introduction

Global mean temperature is predicted to increase by 1.8–4.0 °C by the end of this century as a result of anthropogenic activities that increase carbon dioxide (CO_2) in the atmosphere (IPCC, 2013). Soil stocks large amounts of carbon (C) in terrestrial ecosystems, at least four times greater than that of the global stocks of C in the atmosphere and living plants (Jobbágy and Jackson, 2000). Minor losses of C via decomposition of soil organic matter (SOM) can cause positive feedback to atmospheric CO_2 concentrations and global temperature (IPCC, 2013). In return, climate warming has been shown to increase plant growth and decomposition of SOM (Davidson and Janssens, 2006; Wu et al., 2011), which can profoundly alter soil C and nitrogen (N) cycling (Luo, 2007).

Establishing forest plantations has been accepted as an effective measure for increasing soil C stocks and mitigating atmospheric CO_2 in national budgets (Vesterdal et al., 2013). Afforestation with different tree species have been found to enhance soil C stocks (Berthrong et al., 2009), with large differences in soil C sequestration under different tree species (Vesterdal et al., 2013). Until now, however, the underlying mechanisms for the differences in soil C and N contents under different tree species remain unclear (Hobbie, 2015). Alongside C and N inputs via litter decomposition and root exudation by different tree species, C and N losses via SOM decomposition are important for soil C and N cycling. During the decomposition of SOM, soil's extracellular enzyme activities (EEA) represent the rate limiting step of decomposition, marking the conversion of SOM into dissolved organic C and N, which is then metabolized by microbial decomposers (Schimel and Bennett, 2004; Caldwell, 2005; Bengtson and Bengtsson, 2007; Conant et al., 2011). Given the importance of soil EEA, a soil C/N model that incorporates soil EEA is a useful measure for investigating the effect of tree species on soil C and N cycling, which may improve our understanding of the mechanisms underlying differences in soil C and N contents under different tree species.

Previous work has shown that in a variety of ecosystems, the enzymatic activities associated with decomposition differ, depending upon the substrate (Sinsabaugh et al., 2002). Additionally, single-species tree plantations can lead to differences in labile soil C and N contents, which act as substrate for soil EEA (Lovett et al., 2004; Lu et al., 2012; Hobbie, 2015). Generally, microbes in warmer soils tend to produce fewer extracellular enzymes that are involved in C and nutrient cycling (Allison, 2005), since soil EEA increases with increasing incubation temperature (Koch et al., 2007). However, there are only a handful of studies that have measured the responses of soil's EEA to warming under different tree species (Allison et al., 2010; Kardol et al., 2010). To predict how soil C and N contents are likely to respond to warming as a future climate scenario under different tree species, it is necessary to establish a new soil–enzyme–C/N model that includes incubation temperature to investigate the effects of warming on soil C and N dynamics.

Current soil organic C models can reproduce changes in C dynamics on various scales under most conditions (Todd-Brown et al., 2013). However, this is not the case in highly variable environments, which may require more models that are mechanistic and that include enzyme activities (Lawrence et al., 2009; Allison et al., 2010; Li et al., 2010). A few studies have explicitly incorporated enzyme activity into their models and have demonstrated the potential of this factor to improve

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predictions of changes in soil C and N contents in dynamic systems (Shimel and Weintraub, 2003; Lawrence et al., 2009; Davidson et al., 2012). Here, we selected a long term tree plantation which was established on a former banana (*Musa acuminata* Colla) farm in subtropical Australia. As these tree plantations were developed from the same soil material, we assume that the current differences in soil properties and litter C/N contents are a 'black box' and are mainly derived from the effects of tree species. We therefore simplified soil–enzyme–C/N model to consider the effects of both tree species and incubation temperature, although we acknowledge that soil properties such as pH and soil moisture content are important factors influencing soil EEA (Caldwell, 2005; Allison et al., 2010; Kardol et al., 2010). On the other hand, the enzymatic performance of microbial communities from different tree plantations was explored in a short-term incubation experiment along a laboratory temperature gradient.

The objective of this study was to investigate the mechanism(s) underlying the differences in soil C and N contents under different tree species in a 78-year-old forest plantation in subtropical Australia by combining soil EEA assays and a model of the effects of tree species on soil EEA in response to a gradient of incubation temperatures. We hypothesized that tree species and incubation temperature would greatly affect soil EEA, as they influence the soil substrate where the enzyme activities take place.

2 Materials and methods

2.1 Experimental site

We selected a 78-year-old forest plantation with different tree species which was established in 1935 on a site that was originally a banana farm. The forest plantation site is located at Cooloola, Tin Can Bay, Southeast Queensland, Australia (25°56′49″S, 153°5′27″E). The altitude is 43 m above sea level with a mean annual rainfall of 1287 mm. Winter temperatures range from 7°C to 23°C over June to August and summer temperatures range from 18°C to 30°C over December to February (Lu et al., 2012). Four tree species were selected, including an exotic coniferous species (slash pine (*Pinus elliottii* Engelm. Var. elliottii)) and two native conifer species (hoop pine (*Araucaria cunninghamii* Ait) and kauri pine (*Agathis robusta* C. Moore)), as well as a *Eucalyptus* species (*Eucalyptus grandis* W Hill ex Maiden). All of them were planted adjacently on a broad, gently undulating plain with a gentle slope of less than 5°. The plot size of each tree species was 1.087, 0.308, 0.428 and 0.60 ha, respectively (Lu et al., 2012). Four subplots of 10 m × 20 m in each tree plantation were randomly selected for soil sampling, resulting in a total of 16 subplots. The thicknesses of the litter and fermentation layers were 5–6 cm and 1–2 cm for slash pine, respectively, whereas the corresponding values were 4–5 cm and 1–2 cm for the hoop pine and kauri pine plots. The *Eucalyptus* plot had a thicker litter layer of 8–10 cm and a similarly thick fermentation layer of 1–2 cm.

2.2 Soil sampling and measurement of soil physiochemical properties

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Soil samples were collected in August 2013 using diagonal sampling pattern (i.e., one point at each corner and one in the center of each plot) using a soil auger (8-cm in diameter) at 0–10 cm depth within each plot. The soil cores were immediately mixed thoroughly and kept in a cooler (4 ^{o}C). After passing the samples through a 2-mm sieve to remove roots and stones, the soil samples were stored at 4 ^{o}C prior to analysis. Part of each fresh sample was stored at 4^{o}C for analysis of soil moisture, pH, and extractable organic C (EOC) and N (EON) (Zhou et al., 2017). The other parts were air-dried and stored at room temperature for soil soluble organic C and N analysis using hot water extraction, and for soil total C and N analysis after being finely ground. Soil moisture content was determined after samples were oven-dried at 105^{o}C overnight. The particle size of these soils was dominated by the sand fraction (~96%). All soil biochemical properties are shown in Table 1.

2.3 Measurements of soil enzyme activities

The activity of extracellular enzymes involved in C, N and phosphorus (P) cycling was measured. These enzymes included C acquisition enzymes (β-glucosidase, BG), N acquisition enzymes (*N*-acetylglucosaminidase, NAG; leucine aminopeptidase, LAP) and P acquisition enzymes (acid phosphatases). BG catalyzes one of the steps of cellulose degradation, NAG is involved in chitin and fungal cell wall breakdown, LAP breaks down the polypeptides involved in the mineralization of N from the substrates with polypeptides, and phosphatase is involved in the release of inorganic P. Enzyme activities were assayed spectrophotometrically using *para*-nitrophenol linked substrates (Verchot and Borelli, 2005; Sinsabaugh et al., 2009; Zhou et al., 2013). Briefly, moist field soil (1 g) was suspended in 4 mL of a 0.05 mol/L sodium acetate buffer (pH 6.5 for acid phosphatase, pH 5.0 for all other enzymes). After the substrates (1 mL) were added to Erlenmeyer flasks with the soil solution, the flasks were incubated in the dark at a gradient of temperatures (4, 15, 20, 25, 30 and 37 ^{o}C). The duration of incubation depended upon the optimal temperature for each enzyme: 1 h for BG and acid phosphastase, 3 h for NAG and 5 h for LAP at 20, 25, 30 and 37^{o}C; but 1.5 h for BG and 5 h for NAG and 8 h for LAP at 4^{o}C and 15^{o}C. After incubation, 1 M NaOH (4 mL) was added to quench the reaction in the flasks. Enzyme activities were expressed as mg *para*-nitrophenol formed per g dry soil per h.

3.4 Statistical analyses

We first transformed the enzyme activity data using a natural logarithm. As the enzyme activity data for each plot were not independent along a gradient of temperatures, we established a new statistical model, **Model 1**, to investigate the effects of tree species, incubation temperature and their interaction on soil EEA. **Model 1** is shown as follows:

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$$EEA_{it} = \exp\{\beta_0 + (\beta_1 + X_{1it} \times \beta_{1sp} + X_{2it} \times \beta_{1hp} + X_{3it} \times \beta_{1kp}) \times T + (X_{1it} \times \beta_{2sp} + X_{2it} \times \beta_{2hp} + X_{3it} \times \beta_{2kp}) + \varepsilon_{it}\}$$

$$X_{1it} = \begin{cases} 1 \text{ if the } i^{th} \text{ tree is slash pine,} \\ 0 \text{ otherwise,} \end{cases}$$

$$X_{2it} = \begin{cases} 1 \text{ if the } i^{th} \text{ tree is hoop pine,} \\ 0 \text{ otherwise,} \end{cases}$$

$$X_{3it} = \begin{cases} 1 \text{ if the } i^{th} \text{ tree is kauri pine,} \\ 0 \text{ otherwise,} \end{cases}$$

where EEA_{it} indicates the soil's extracellular enzyme activity; i=1, 2, …, 16 is the plot number; T is the temperature (4, 15, 20, 25, 30 and 37°C); X_{1it}, X_{2it} and X_{3it} indicate the effects of tree species; β_0 is a constant; β_1 is the temperature coefficient; β_{1sp}, β_{1hp}, β_{1kp}, β_{2sp}, β_{2hp} and β_{2kp} are the slash pine, hoop pine and kauri pine coefficients, respectively, with temperature and without temperature; and ε_{it} is the normal distribution with a 0 mean and σ^2_{ε} variance. We ran all these enzyme activity data in Model 1 and the *F*-test results of the effects of temperature and tree species on soil EEA are presented Table 2.

Table 2 shows that the interactions between incubation temperature and tree species were not significant. We also ran a comparison of performance of Model 1 and Model 2 using Akaike information criterion and Bayesian information criterion (Table S1). Both results show that **Model 2** is better than **Model 1**, so we further updated **Model 1** to create **Model 2**, as shown below:

$$EEA_{it} = \exp\{\beta_0 + \beta_1 \times T + (X_{1it} \times \beta_{2sp} + X_{2it} \times \beta_{2hp} + X_{3it} \times \beta_{2kp}) + \varepsilon_{it}\}. \quad (2)$$

All the parameters in **Model 2** have been described in **Model 1**. We ran all these enzyme activity data in Model 2 and the *F*-test results are shown in Table 3.

As we assumed that the differences in soil properties and litter C/N contents under different tree species are the effects of tree species, we established a new soil–enzyme–C/N model to consider the effects of both tree species and incubation temperature without considering other soil properties and litter C inputs derived from tree species. In other words, we considered changes in soil properties and C inputs to be a 'black box' within the overall effects of tree species, all of which influenced soil EEA.

According to a previous soil enzyme kinetics model (**Model 3**) (Allison et al., 2010), we established the dynamic total C model (**Model 4**) as shown below:

$$d_{TC}/d_t = -K \times EEA \quad (3)$$

with the boundary conditions t = time = 0, $TC = TC_0$, and $TC > 0$, where the function of enzyme activities is:

$$EEA(\text{T, Tree, TC}) = \exp\{\beta_0 + \beta_1 \times T + (X_{1it} \times \beta_{2sp} + X_{2it} \times \beta_{2hp} + X_{3it} \times \beta_{2kp}) + \beta_3 \times \text{TC}\}; \quad (4)$$

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The analytical solution of differential equations (5) is shown below:

$$TC = -1/\beta_3 \times \log\{\beta_3 \times \exp\{\beta_0 + \beta_1 \times T + (X_{1it} \times \beta_{2sp} + X_{2it} \times \beta_{2hp} + X_{3it} \times \beta_{2kp}) + \log(K) \times t + \exp\{-\beta_3 \times TC_0\}\}\}. \quad (5)$$

where K is the unit conversion coefficient when $t = 0$ and $TC = TC_0$.

Similarly, when we consider the relationship between total soil N (TN) and enzyme activities, we get a similar analytical solution of differential Equation (6) as shown below:

$$TN = -1/\beta_3 \times \log\{\beta_3 \times \exp\{\beta_0 + \beta_1 \times T + (X_{1it} \times \beta_{2sp} + X_{2it} \times \beta_{2hp} + X_{3it} \times \beta_{2kp}) + \log(K) \times t + \exp\{-\beta_3 \times TN_0\}\}\}, \quad (6)$$

where K is the unit conversion coefficient when $t = 0$ and $TN = TN_0$.

Using Equation 5, we calculated the total soil C decomposition over time and compared the residual soil C contents over time among the tree species for different enzyme activities. As the three coniferous tree species showed similar soil C decomposition patterns across time, we only calculated the responses of the residual soil C contents to different temperatures under slash pine and *Eucalyptus*. The model parameters of Equation 5 for different enzyme activities under different tree species are shown in Table S2.

Similarly, using Equation 6, we calculated the total soil N decomposition over time and compared the residual soil N contents among the tree species for different enzyme activities. On the basis of the residual soil C and N contents over time, we finally calculated the ratios of the residual soil C and N contents among the tree species over time. The model parameters of Equation 6 for different enzyme activities under different tree species are shown in Table S3.

3 Results

Tree species and temperature significantly affected soil BG, NAG, LAP and acid phosphatase ($P < 0.05$) (Table 2). However, there was no significant effect of the interaction between tree species and temperature on the activity of these enzymes. In general, *Eucalyptus* had higher soil EEA than the other tree species along a temperature gradient (Fig. 1), followed by native coniferous species (kauri pine and hoop pine), whereas exotic conifer species (slash pine) had the lowest soil enzyme activity, except for NAG enzyme activity (Fig. 1).

The decreasing trends for residual soil C contents over time under different tree species were similar for all enzyme activities (Fig. 2). In general, *Eucalyptus* had the highest soil enzyme activity, followed by slash pine, hoop pine and kauri pine. Notably, *Eucalyptus* had the longest soil C residence time, almost double that of hoop pine and kauri pine; slash pine had a longer soil C residence time than the other two coniferous species (Table S4).

Temperature significantly influenced soil C decomposition, indicating that slash pine and *Eucalyptus* had shorter soil C residence times at higher temperatures than at lower temperatures (Fig. 3). At a given temperature, *Eucalyptus* had greater soil C losses, but had higher remaining soil C contents than slash pine (Fig. 3).

We also calculated the ratios of residual soil C contents between *Eucalyptus* and slash pine, between *Eucalyptus* and hoop pine, between *Eucalyptus* and kauri pine, and between slash pine and hoop pine. All of them exhibited consistent and similar patterns and increased with time (Fig. 4).

The decreasing trends for soil N contents under different tree species over time for NAG and LAP showed similar patterns (Fig. 5). *Eucalyptus* had the highest soil EEA, but had the longest decomposition time, almost double that of the other coniferous species. This is because *Eucalyptus* had a relatively flatter slope across time than the other tree species. For NAG, at a given time, *Eucalyptus* had the highest residual soil N contents, followed by (in decreasing order) kauri pine, slash pine and hoop pine. For LAP, at a given time, *Eucalyptus* had the highest residual soil N contents, followed by (in decreasing order) slash pine, hoop pine and kauri pine. The ratios of residual soil N contents between *Eucalyptus* and slash pine for NAG increased with time; similar patterns of the ratios of residual soil N contents between *Eucalyptus* and slash pine over time were seen for LAP (Fig. 6 and Table S5).

4 Discussion

As we expected, in this study we found that different tree species and incubation temperatures had significant impacts on soil EEA and soil physicochemical properties (Fig. 1, Tables 1 and 2). *Eucalyptus* had the highest soil EEA, which corresponded to higher soil moisture content and total C and N contents, and lower C:N ratios than the other coniferous species (Tables 1 and 2). It is well known that soil's EEA may be regulated by the soil's biochemical properties via the influence on soil microbial community and abundance (Ushio et al., 2010). In turn, soil enzyme activity plays a central role in mediating soil C and N cycling, which can result in soil C and N losses (Shimel and Weintraub, 2003; Drake et al., 2013). Given the critical role of extracellular enzymes in soil organic C decomposition and nutrient cycling, predicting soil enzyme activity in dynamic environments is challenging because of our limited understanding of enzyme production, residence time and turnover (Wallenstein and Weintraub, 2008), which is an important constraint in understanding the feedback between climate change and biogeochemical cycles (Todd-Brown et al., 2013).

4.1 Mechanisms for the differences in soil C and N contents between *Eucalyptus* and coniferous trees

We modeled the responses of residual soil C contents to enzyme activity over time (Fig. 2). The results clearly show that *Eucalyptus* had a longer soil C residence time and slower turnover rates for all enzyme activities than coniferous tree species, even though similar patterns can be seen when soil enzyme activities under slash pine and *Eucalyptus* respond to different temperatures (Fig. 3). The lower soil C turnover rate under *Eucalyptus* could be caused by lower soil pH, which was supported by significantly negative correlations between soil organic C and soil pH ($r = -0.58$, $P < 0.001$).

Eucalyptus had a longer mean soil N residence time for LAP and slower soil N turnover rates than the other tree species (Fig. 5 and Table S5). Unlike NAG, which is involved in chitin and fungal cell wall breakdown in the short term, LAP can break down polypeptides in the long term and is involved in the mineralization of N from the substrates with polypeptides (Sinsabaugh et al., 2002; Weand et al., 2010). The longer mean soil N residence time could be another reason for the higher soil C contents seen under *Eucalyptus*, as higher N contents may support plant growth and, in turn, increase soil C stocks.

4.2 Mechanisms for differences in soil C and N contents between exotic and native pine species

There is much controversy about the effects of exotic tree species on soil C and N cycling (Hobbie, 2015). Here, our modeling results show that slash pine (an exotic tree species) had a longer soil C residence time and lower soil C loss rates than the native hoop pine and kauri pine for all enzymes (Fig. 2 and Table S4), and it had a longer soil N residence time and lower N loss rates for LAP (Fig. 5 and Table S5). All these results indicated that slash pine has higher residual N contents across time, which may enhance available N contents for tree growth by extending the soil C and N residence time.

4.3 Ratios of residual soil C and N contents between tree species

Global C models usually use a specific parameter to describe soil C decomposition (Todd-Brown et al., 2013). Some of them can simulate microbial decomposition through a new soil biogeochemistry model (Davidson et al., 2012; Steinweg et al., 2012; Wieder et al., 2013). However, the mechanisms of the dynamics of soil C and N contents under different tree species and the mechanisms of the different decomposition times between sites with different soil fertility are still unclear (Hobbie, 2015). Here, we found that the more fertile soil seen under *Eucalyptus*, which had higher soil C and N contents, lost more soil C and N, as it had higher C- and N-related enzyme activity. However, as soil under *Eucalyptus* had a longer remaining soil C and N residence time than the less fertile soil under coniferous tree species with lower soil C and N contents, the differences in the residual soil C and N contents between *Eucalyptus* and coniferous tree species became larger and larger with time (see Figs. 4 and 6). Similarly, the differences in residual soil C and N contents among coniferous tree species became larger and larger with time as well. These results are helpful for understanding soil C and N cycling in tree plantations.

5 Conclusions

Both tree species and temperature significantly affected soil EEA. Our modeling analysis clearly shows that though *Eucalyptus* had higher soil EEA activities, it had a longer residual soil C and N residence time. Furthermore, the differences in soil C and N contents between *Eucalyptus* and coniferous tree species, as well as between slash pine and hoop pine, became larger and larger with decomposition time, which is in contrast to what we expected. On the other hand, our results

help to explain why exotic slash pine can grow faster than the other species studied, as it had a longer residual soil N residence time than native coniferous tree species like hoop pine and kauri pine. Soil extracellular enzyme assays in combination with statistical modeling, are powerful tools for exploring the mechanisms of soil C and N cycling by different tree species. Our results can provide useful information for local forest management.

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Table 1. Soil biochemical properties in 78-year-old forest plantations with different tree species.

Properties	Slash pine	Hoop pine	Kauri pine	*Eucalyptus*
Moisture (%)	4.26±0.22b	3.11±0.53b	3.09±0.67b	7.69±1.66a
pH	4.58±0.03b	5.64±0.22a	6.01±0.23a	4.49±0.04b
Total C (Mg ha^{-1})	7.36±0.57b	5.69±0.73b	5.07±0.75b	13.88±2.22a
Total N (kg ha^{-1})	232±22b	245±23b	239±33b	462±71a
C:N	31.8±0.7a	23.1±1.3b	21.2±0.7b	29.8±0.6a
EOC (mg kg^{-1})	340±41b	341±31b	360±30b	625±77a
EON (mg kg^{-1})	14.7±2.9b	18.4±1.9ab	23.1±1.5a	22.4±1.8a
EOC:EON	24.17±1.81a	18.79±1.48b	15.66±0.87b	27.64±1.64a

C, carbon; N, nitrogen; EOC, extractable organic C; EON, extractable organic N

Different letters in the same row indicate significant differences at $P<0.05$ among tree species.

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Table 2. *F*-test results showing the effects of tree species and temperature on soil's extracellular enzyme activity in 78-year-old forest plantations with different tree species with Model 1.

	BG	NAG	LAP	AP
Temperature (T)	586.39***	493.56***	84.93***	477.71***
Tree species	23.44**	5.25*	5.41*	35.46**
T × tree species	0.15	0.39	7.02	0.01

*, ** and *** indicate significant differences at $P<0.05$, $P<0.01$ and $P<0.001$, respectively.

BG, β-glucosidase; NAG, *N*-acetylglucosaminidase; LAP, leucine aminopeptidase; AP, acid phosphatase

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Table 3. *F*-test results showing the effects of tree species and temperature on soil's extracellular enzyme activity with Model 2.

	BG	NAG	LAP	AP
Temperature	603.35***	533.38***	134.92***	502.63***
Tree species	24.12**	6.16*	7.37**	37.91**

*, ** and *** indicate significant differences at $P<0.05$, $P<0.01$ and $P<0.001$, respectively.

BG, β-glucosidase; NAG, *N*-acetylglucosaminidase; LAP, leucine aminopeptidase; AP, acid phosphatase

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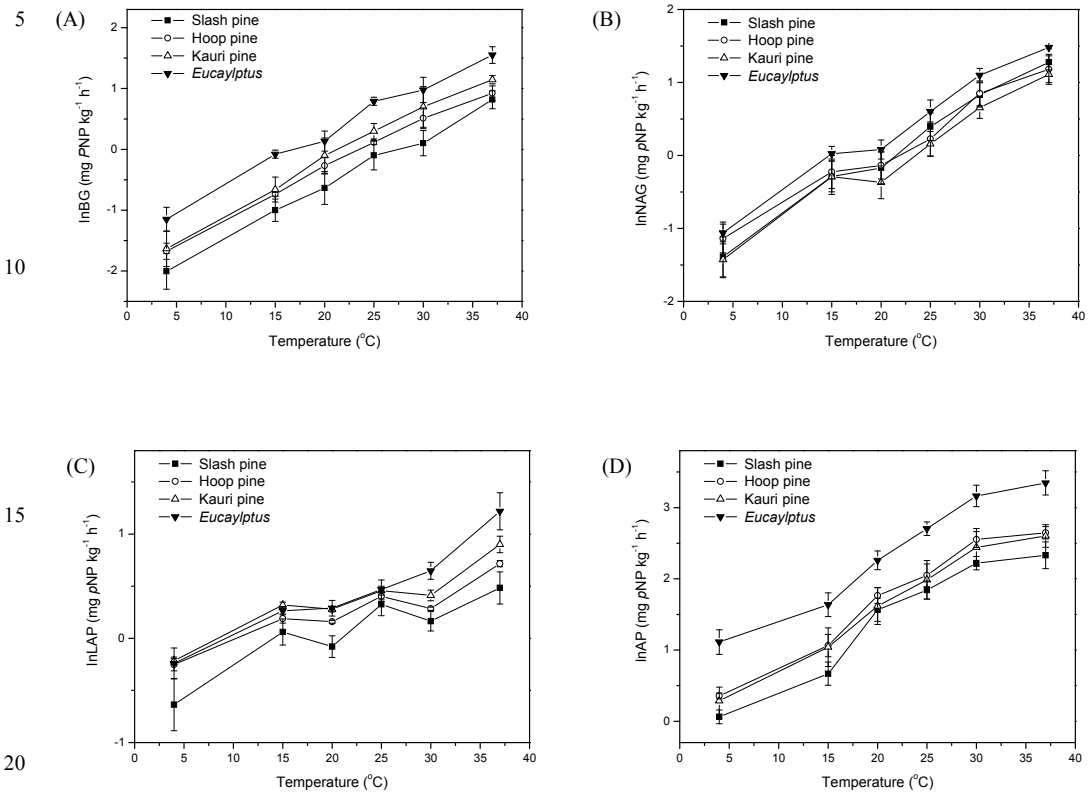

Figure 1. Extracellular enzyme activity in the soil along a gradient of temperatures under different tree species. BG, β-glucosidase; NAG, *N*-acetylglucosaminidase; LAP, leucine aminopeptidase; AP, acid phosphatase; *p*NP, *para*-nitrophenol.

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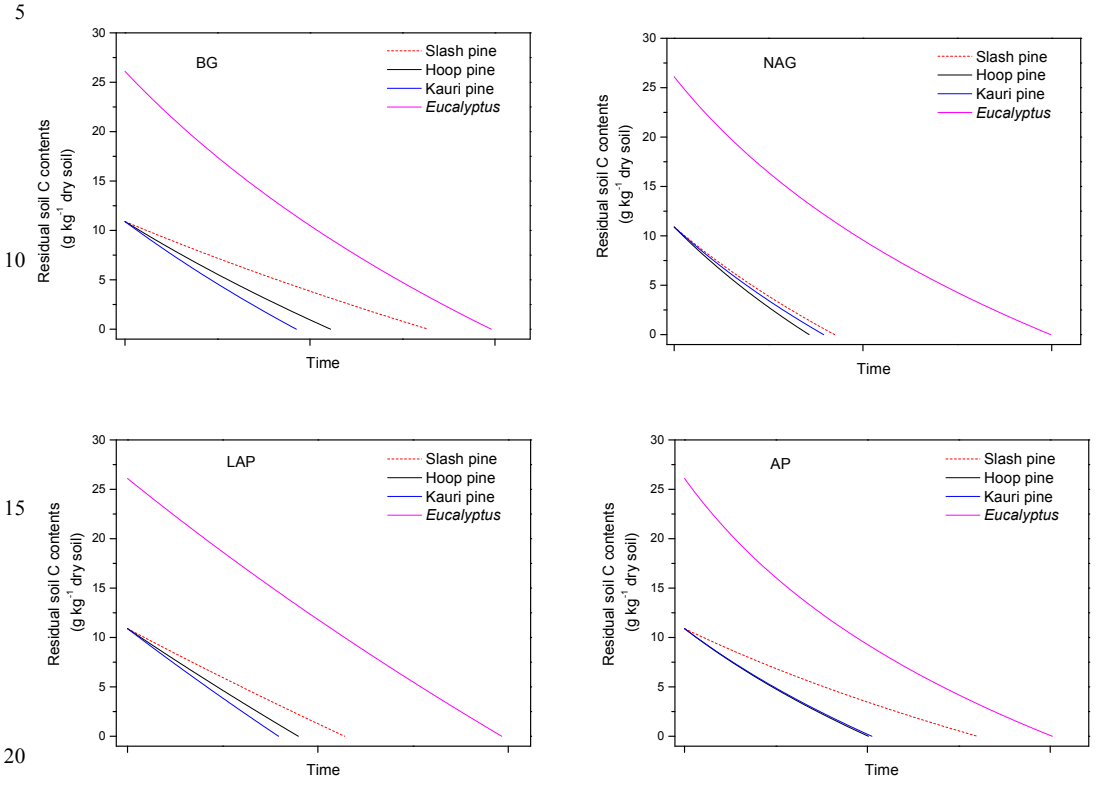

Figure 2. Residual soil C contents under different tree species across time with β-glucosidase (BG), *N*-acetylglucosaminidase (NAG), leucine aminopeptidase (LAP) and acid phosphatase (AP) at 25°C. The total soil C decomposition over time was calculated via Equation 5 and the residual soil C contents over time was compared for different enzyme activities among the tree species.

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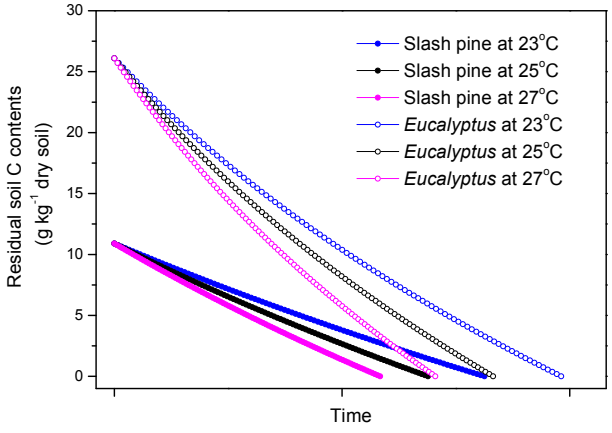

Figure 3. Residual soil C contents with β-glucosidase at 23°C, 25°C and 27°C under slash pine and *Eucalyptus* over time. The total soil C decomposition over time was calculated via Equation 5 and the residual soil C contents over time was compared for different enzyme activities among the tree species.

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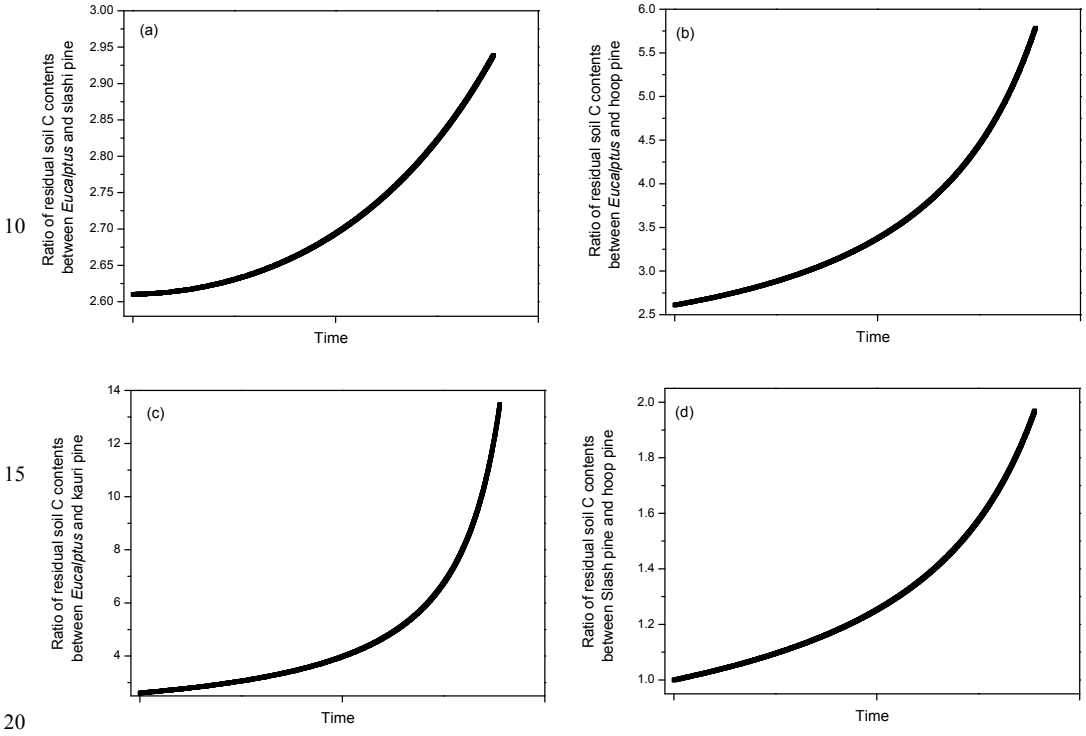

Figure 4. Ratios of residual soil C contents between *Eucalyptus* and slash pine (a), between *Eucalyptus* and hoop pine (b), between *Eucalyptus* and kauri pine (c) and between slash pine and hoop pine (d) with β-glucosidase across time.

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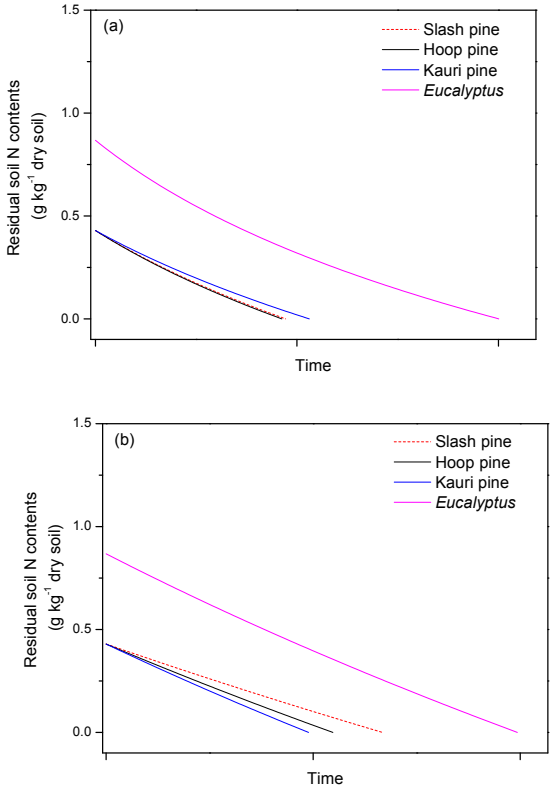

Figure 5. Residual soil N contents under different tree species with *N*-acetylglucosaminidase (a) and leucine aminopeptidase (b) across time. The total soil N decomposition over time was calculated via Equation 6 and the residual soil N contents over time was compared for different enzyme activities among the tree species.

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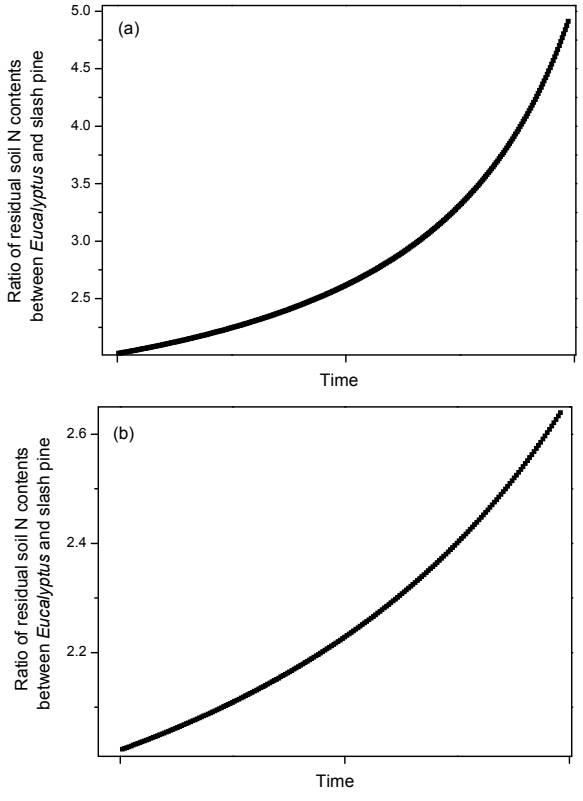

Figure 6. Ratios of residual soil N contents between *Eucalyptus* and slash pine for *N*-acetylglucosaminidase (a) and leucine aminopeptidase (b) across time.