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ORIGINAL ARTICLE

Colonization and decomposition of leaf litter by ligninolytic fungi in *Acacia mangium* plantations and adjacent secondary forests

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Abstract Colonization of leaf litter by ligninolytic fungi and relationships between mass loss and chemical qualities of surface leaf litter were examined in *Acacia mangium* plantations and adjacent secondary forests in southern Sumatra Island, Indonesia. Leaves were collected from eight *A. mangium* plantations of different ages and three secondary forests. Partly decomposed leaves beneath the surface leaf litter were used to measure the bleached area which indicated colonization by ligninolytic fungi. Surface leaf litter was used to measure initial chemical content and subjected to the pure culture decomposition test. The bleached area was greater in secondary forests than in *A. mangium* plantations. Nitrogen content was higher in all the *A. mangium* plantations than in the secondary forests, and acid unhydrolyzable residue (AUR) content was generally higher in the *A. mangium* plantations than in the secondary forests. The bleached area of leaf litter was negatively correlated with nitrogen content of surface leaf litter at all sites, indicating an inhibition of the colonization by ligninolytic fungi of leaves with higher nitrogen content. In a pure culture decomposition test inoculating a ligninolytic fungus to surface leaf litter, mass loss of leaves was negatively correlated with AUR content of surface leaf litter. Mass loss of leaves and AUR was not significantly related to nitrogen content. These results suggested that higher nitrogen content in *A. mangium* leaf litter had a negative effect by colonization of ligninolytic fungi, but the effect of high N in *A. mangium* leaf litter on the decomposition of leaf litter and AUR remained unsolved.

Keywords *Acacia mangium* · Bleach · Decomposition · Ligninolytic fungi · Nitrogen

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Introduction

Acacia mangium is a legume tree that is symbiotic with rhizobia and has an ability to fix atmospheric nitrogen (N). Because of its rapid growth and high quality timber production, *A. mangium* has been commonly planted in tropical regions. *Acacia mangium* produces N-rich leaves (Tilki and Fisher 1998; Akinnifesi et al. 2002) leading to changes in soil N dynamics in plantations. For example, Yamashita et al. (2008) reported that soil acidity was higher in *A. mangium* plantations compared with grasslands, in relation to the base cation loss from the soil profile associated with high leaching of nitrate anions (Binkley and Giardina 1997). Arai et al. (2008) and Konda et al. (2008, 2010) reported that N_2O emission from forest soil was greater in an *A. mangium* plantation than in secondary, intact, or selectively cut forests.

Such changes in soil N status in *A. mangium* plantations can influence the colonization and decomposition of leaf

litter by litter-decomposing fungi that play central role in decomposition process in soils. Previous studies have demonstrated that excess N supply can reduce the abundance and activity of fungi associated with the decomposition of recalcitrant compounds such as acid unhydrolyzable residue (AUR) (Reid 1991; Osono 2007). Thus, it is hypothesized that the colonization and decomposition of *A. mangium* leaf litter by ligninolytic fungi are suppressed as a result of high N content. Although a negative or positive relationship between N deposition and decomposition rate of leaf litter has been suggested in other tree species, climate zones, and laboratory experiments (Fog 1988; Berg and Matzner 1997; Knorr et al. 2005; Hobbie 2008), a few studies have examined the decomposition process of leaf litter in *A. mangium* plantations (Xiong et al. 2008; Kunhamu et al. 2009). Moreover, to our knowledge, no studies have evaluated the effects of high N status of *A. mangium* leaf litter on the fungal colonization and AUR decomposition.

The colonization of leaf litter by ligninolytic fungi results in the occurrence of bleached portions on the leaf surface (Osono 2007). The content of recalcitrant compounds is generally lower in a bleached leaf area than in adjacent non-bleached areas of the same leaf due to the decomposition by ligninolytic fungi (Osono and Takeda 2001; Koide and Osono 2003; Koide et al. 2005). Therefore, measurement of the bleached area on the surface of *A. mangium* leaf litter will be useful for evaluating the colonization of leaf litter by ligninolytic fungi. Comparing the bleached area of leaf litter in *A. mangium* plantations with that in adjacent forests of non-N-fixing trees will provide insights into the possible effects of excess N availability on the colonization of leaf litter by ligninolytic fungi.

The purposes of the present study were to investigate the colonization and decomposition of *A. mangium* leaf litter by ligninolytic fungi and to examine whether higher N content in *A. mangium* leaf litter that was compared to leaf litter of non-N-fixing tree would have an inhibitory effect on the appearance of the bleached portion on the leaf litter and would also have an inhibitory effect on the decomposition of the leaf litter by a pure culture decomposition test. Samples were collected from eight *A. mangium* plantations of different ages (0–17 years old) located in southern Sumatra Island, Indonesia. Colonization by ligninolytic fungi was evaluated as the area of the bleached portions on the surface of leaf litter collected from the forest floor. The chemical properties of surface leaf litter were analyzed, and the effects of the properties on fungal decomposition were evaluated with a bioassay under pure culture conditions, using a ligninolytic fungus *T. versicolor* as an agent of decomposition. The data from *A. mangium* plantations were compared with those from three adjacent forests of non-N-fixing trees (one regenerating coppice of *Schima wallichii* and two mature secondary forests) to examine the possible effect of high N content in *A. mangium* leaf litter on the colonization and decomposition by ligninolytic fungi.

Materials and methods

Study site

Study sites were located in the southern part of Sumatra Island, Indonesia (3°52′S, 103°58′E). The mean annual temperature and annual precipitation of the area in 2004 were 29°C and 2,520 mm, respectively (Yamashita et al. 2008). A total of 11 forest stands were chosen from three regions, Sodong, Gemawang, and Merbau, for the present study. The distances from Sodong to Gemawang, from Sodong to Merbau and from Gemawang to Merbau were 33, 6 and 28 km, respectively. The stands included eight *A. mangium* plantations of different ages (0-, 3- and 5-year-old stands in the Sodong region and the Gemawang region, and 8- and 17-year-old stands in the Sodong region), and three secondary forests (a secondary regenerating stand of *S. wallichii* in the Sodong region, and two mature secondary forests in the Sodong and Merbau regions) (Table 1). The original vegetation in the 0-year-old *A. mangium* plantations was 7-year-old *A. mangium* which were cut 1–6 months prior to leaf litter collection. The planting interval of *A. mangium* in 3- and 5-year-old plantations was 3 m × 3 m (1,089 trees/ha), and was 2 m × 4 m (1,250 trees/ha) in an 8-year-old plantation. The mean DBH in 3-year-old *A. mangium* plantations was 12.1–13.5 cm, that in 5-year-old plantations was 13.7–16.0 cm, and that in secondary forests was 17.3–19.0 cm. No DBH data were available for 8- and 17-year-old *A. mangium* plantations or for *S. wallichii* regeneration. The mean canopy height in 3-year-old plantations was 13.3–17.0 m, that in 5-year-old plantations was 18.8–20.1 m, that in 8-year-old plantation was 24–25 m, and that in secondary forests was 17.5–18.9 m. No height data were available in 17-year-old plantation or in *S. wallichii* regeneration. *A. mangium* is fast-growing pioneer species, and the canopy is already closed even in 3-year-old plantations. Tree families in the secondary forests included Moraceae, Fabaceae, Myrtaceae, Proteaceae, Dipterocarpaceae, and Lecythidaceae. Fabaceae, the only family that has N-fixing ability, accounted 7.8% of the total number of stems in the secondary forests. Thus, we regarded the leaf litter in the secondary forests as being derived from non-N-fixing trees for the sake of simplicity.

Samples were collected in September 2007. Ten quadrats (20 cm × 20 cm) were set on the forest floor along a 9-m line transect at 1-m intervals inside each site, which

Table 1 Stand age (in years), initial chemical content in surface leaf litter (mg g^{-1}), bleached area of partly decomposed leaves on the forest floor (% total leaf area), mass and AUR loss (% original mass) of surface leaf litter and AUR caused in the pure culture by *Trametes versicolor*

Forest type	Region	Site abbr.	Stand age	Chemical content of surface leaf litter		Bleached area	Pure culture decomposition test	
				AUR	Nitrogen		Mass loss	AUR loss
Plantations								
Acacia mangium	Gemawang	G0	0	519.7	27.9	nd	16.2 ± 1.2 d	13.7
	Sodong	S0	0	420.5	32.7	nd	21.3 ± 0.8 abcd	18.5
	Gemawang	G3	3	458.8	18.9	7.6 ± 1.2 bc	22.4 ± 1.4 abc	19.6
	Sodong	S3	3	490.8	19.9	10.9 ± 1.2 bc	20.2 ± 1.6 abcd	17.5
	Gemawang	G5	5	497.5	20.1	7.8 ± 0.8 bc	21.0 ± 0.8 abcd	20.8
	Sodong	S5	5	517.2	20.5	8.2 ± 0.9 bc	19.8 ± 0.8 bcd	16.1
	Sodong	S8	8	515.6	20.1	4.7 ± 1.4 c	16.6 ± 0.2 cd	12.4
	Sodong	S17	17	489.7	21.4	7.4 ± 1.0 bc	19.0 ± 1.4 bcd	12.6
Secondary forests								
Schima wallichii regeneration	Sodong	Sw	nd	407.0	16.3	13.0 ± 1.6 b	25.8 ± 0.8 a	26.9
Mature forest	Sodong	FS	nd	431.7	15.0	10.7 ± 0.8 bc	22.5 ± 2.0 ab	25.0
	Merbau	FM	nd	460.7	13.1	27.1 ± 2.8 a	6.7 ± 1.1 e	11.7

Values are means ± SE ($n = 10$ for bleach area, $n = 4$ for mass loss). Values that do not share a common letter are significantly different at the 5% level by Tukey's HSD test

nd Not determined

was about 1–1.5 ha in size. Surface leaf litter accumulated on the surface of the forest floor was collected within the quadrats and used for chemical analysis and pure culture decomposition tests. Partly decomposed leaves that had undergone decomposition but more than half the original leaf area remained were collected from beneath the surface leaf litter and were used for leaf area measurement. Numbers of partly decomposed leaves that we collected ranged from 20 to 97 pieces in each quadrat and totalled 389–548 pieces in each site. The collected leaves only included those of the respective species in the *A. mangium* plantations and the *S. wallichii* regeneration because they were pure stands, but we did not distinguish individual tree species in the mature secondary forests. Partly decomposed leaves were not collected at two 0-year-old *A. mangium* plantations because no bleached leaves were seen there.

Chemical analyses

Surface leaf litter from 10 quadrats was combined to make one sample for each forest stand and oven-dried at 40°C for 1 week. Surface leaf litter was then ground in a laboratory mill to pass through a 0.5-mm screen and used for chemical analysis. The AUR content in the samples was estimated by gravimetry, according to a standardized method using hot sulfuric acid digestion (King and Heath 1967). Samples were extracted with alcohol-benzene at room temperature (15–20°C), and the residue was treated with 72% (v/v) sulfuric acid for 2 h at room temperature with occasional stirring. The mixture was diluted with distilled water to furnish a 2.5% sulfuric acid solution and autoclaved at 120°C for 60 min. After cooling, the residue was filtered and washed with water through a porous crucible (G4), dried at 105°C, and weighed as AUR. Total N content was measured by automatic gas chromatography (Sumigraph NC-900 NC analyzer; Sumitomo Chemical, Osaka, Japan). The methods are described in detail elsewhere (Osono and Takeda 2005). Throughout this paper, we use AUR to refer to the final residual fraction remaining after proximate analysis. AUR fraction contains a mixture of organic compounds in various proportions, including condensed tannins, phenolic compounds, carboxylic compounds, alkyl compounds such as cutins, and true lignin (Preston et al. 1997).

Leaf area measurement

Partly decomposed leaves were pressed between broad papers and oven-dried at 40°C for 1 week, then photocopied and scanned with a scanner (Epson GT-8000). The area of the bleached portions, where the color of the leaf litter was defined as being clearly paler than the surrounding leaf area by the software, and the total leaf area were measured by image analysis performed on a Windows computer using image software (v.4.0.3, Windows version of NIH image; Scion). For each sample that was collected

from a quadrat, the bleached area was defined as the proportion of the total leaf area and expressed as a percentage to the total leaf area. The mean value of the bleached area was calculated for each forest stand.

Pure culture decomposition test

Surface leaf litter was cut into pieces 1 cm in width and preserved in a PVC bag until the experiment started. The leaves (300 mg) were sterilized by exposure to ethylene oxide gas at 60°C for 6 h. The sterilized litter was placed on the surface of Petri dishes (9 cm diameter) containing 20 ml of 2% agar. *Trametes versicolor* is a white rot fungus of wood possessing an ability to decompose recalcitrant compounds such as AUR. The strain IFO30340 used in the present study was the one that was registered in Institute of Fermentation, Osaka (IFO), Osaka, Japan, and had been used as a standard for the decomposition test of timber under Japanese Industrial Standards (JIS). Moreover, the strain had been repeatedly used in bioassays of leaf litter decomposition (Osono et al. 2003; Osono and Takeda 2006; Osono 2010). Thus, we used this strain in the pure culture decomposition test in the present study. The inoculum was cut from the margin of the previously inoculated Petri dishes on 2% malt-extracted agar [malt extract 2% and agar 2% (w/v)] with a sterile cork borer (6 mm diameter) and placed on the agar adjacent to the litter, one plug per plate. The plates were incubated for 12 weeks at 25°C in darkness. The plates were sealed firmly with laboratory film during incubation so that moisture did not limit decomposition on the agar. After incubation, the leaves were retrieved, oven-dried at 40°C for 1 week, and weighed. The undecomposed initial litter was also sterilized, oven-dried at 40°C for 1 week, and weighed to determine the original mass. Four plates were prepared for each forest stand, and four uninoculated plates served as a control. Mass loss of leaves was determined as a percentage of the original mass, taking the mass loss of control litter into consideration. Duplicated samples of surface leaf litter after the incubation were combined to make one sample per forest stand and were also analyzed for AUR content with the method as above. Mass loss of AUR was determined as a percentage of the original AUR amount, taking the mass loss of AUR of control litter into consideration.

Data analysis

Welch's t test was used to test differences in the chemical properties of surface leaf litter and bleached area of partly decomposed leaf litter between *A. mangium* plantations and secondary forest. One-way analysis of variation (ANOVA) was used to test differences in the bleached area and mass loss of leaf litter among forest stands. Tukey's honestly significant difference (HSD) test was used for multiple comparisons of means. ANOVA and Tukey's HSD were performed with SPSS for Windows v.10.0.5 (SPSS, Chicago, IL, USA). Pearson's correlation coefficients were calculated for linear relationships among forest age, chemical contents of surface leaf litter, bleached leaf area, mass loss and AUR loss of surface leaf litter caused by *T. versicolor* for *A. mangium* plantations and for all forest stands.

Results

Chemical compositions

Initial AUR contents were significantly (t test, $P < 0.05$) greater in surface leaf litter from the *A. mangium* plantations (420.5–519.7 mg g^{-1}) than in the secondary forests (407.0–460.7 mg g^{-1}) (Table 1). Initial N contents were significantly (t test, $P < 0.01$) greater in surface leaf litter from the *A. mangium* plantations (18.9–32.7 mg g^{-1}) than in the secondary forests (13.1–16.3 mg g^{-1}) (Table 1). The age of *A. mangium* plantations was not significantly ($P > 0.05$) correlated with the initial AUR ($n = 8$, $r = 0.255$) or N ($n = 8$, $r = 0.457$) contents of newly shed leaves.

Bleached area

Mean values of the bleached area of partly decomposed leaves ranged from 4.7 ± 1.4 to $10.9 \pm 1.2\%$ in six *A. mangium* plantations and from 10.7 ± 0.8 to $27.1 \pm 2.8\%$ in three secondary forests (Table 1). There was no significant difference in the bleached area between *A. mangium* plantations and secondary forests (t test, $P > 0.05$). The bleached area of partly decomposed leaves from the secondary forest in the Merbau region was significantly (ANOVA, $P < 0.05$) greater than those in the other stands, and that in the secondary regeneration stand of *S. wallichii* was significantly (ANOVA, $P < 0.05$) greater than that in the 8-year-old *A. mangium* plantation in the Sodong region (Table 1). The bleached area of partly decomposed leaves was not significantly ($P > 0.05$) correlated with contents of initial AUR for all nine stands ($r = -0.404$) or for six *A. mangium* plantations ($r = -0.277$). The bleached area of partly decomposed leaves was significantly ($P < 0.05$) and negatively correlated with N content for all nine stands ($r = -0.814$) (Fig. 1a), whereas the correlation was not significant ($P > 0.05$) when examined for six *A. mangium* plantations ($r = -0.059$). Age of the *A. mangium* plantation was not significantly ($P > 0.05$, $n = 6$, $r = 0.366$) correlated with the bleached area of partly decomposed leaves.

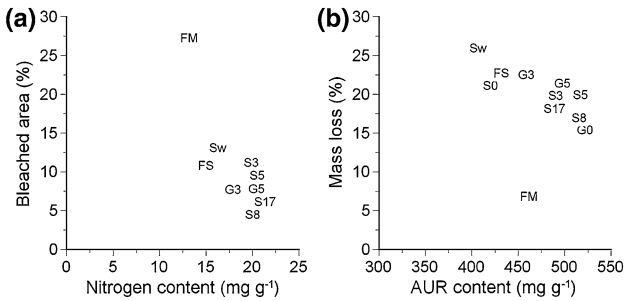

Fig. 1 Bleached area of partly decomposed leaves on the forest floor as a function of N content (**a**), and mass loss of surface leaf litter caused in the pure culture by *T. versicolor* as a function of initial AUR content (**b**) of surface leaf litter. Site abbreviations are listed in Table 1

Pure culture decomposition test

The mean values of mass loss of leaves caused by *T. versicolor* ranged from 16.6 ± 0.2 to 22.4 ± 1.4% for eight *A. mangium* plantations and from 6.7 ± 1.1 to 25.8 ± 0.8% for three secondary forests (Table 1). There was no significant difference (*t* test, $P > 0.05$) of mass loss between *A. mangium* plantations and secondary forests. The lowest values of mass loss of leaves were recorded for the secondary forest in the Merbau region and for the 0-year-old *A. mangium* plantation in the Gemawang region, whereas the highest values were recorded for the secondary regeneration of *S. wallichii* and the secondary forest in the Sodong region (Table 1). Mass loss of leaves was not significantly ($P > 0.05$) correlated with initial AUR content for all 11 stands ($r = -0.369$), but was significantly ($P < 0.01$) and negatively correlated with initial AUR content when the data of the secondary forest in the Merbau region were excluded from the analysis ($r = -0.845$, $n = 10$) (Fig. 1b). Mass loss of leaves was marginally significantly ($P = 0.055$) and negatively correlated with initial AUR content when examined for the eight *A. mangium* plantations ($r = -0.696$). Mass loss of leaves was not significantly ($P > 0.05$) correlated with N content for all 11 stands ($r = 0.157$) nor for the eight *A. mangium* stands ($r = -0.114$).

The values of mass loss of AUR caused by *T. versicolor* followed a similar trend to those of leaves, ranging from 12.4 to 20.8% for eight *A. mangium* plantations and from 11.7 to 26.9% for three secondary forests (Table 1). Mass loss of AUR was not significantly different (*t* test, $P > 0.05$) between *A. mangium* plantations and secondary forests. The lowest values of mass loss of AUR were recorded for the secondary forest in the Merbau region and for the 8-year-old *A. mangium* plantation, whereas the highest values were from the secondary regeneration of *S. wallichii* and the secondary forest in Sodong (Table 1). Mass loss of AUR was significantly ($P < 0.05$) correlated with initial content of AUR of surface leaf litter ($r = 0.680$). Mass loss of AUR of surface leaf litter was not significantly ($P > 0.05$) correlated with N content neither for all 11 stands ($r = 0.213$) nor for the eight *A. mangium* plantations ($r = 0.024$).

Discussion

The initial AUR and N contents of surface leaf litter of *A. mangium* in the present study (Table 1) were similar to those reported for legume trees (e.g., Ngoran et al. 2006; Siddique et al. 2008) and were relatively high when compared to those of non-legume tree species in other tropical forests (e.g., Aerts 1997; Kurokawa and Nakashizuka 2008).

The bleached area of partly decomposed leaves in *A. mangium* plantations (Table 1) was generally lower than those in other tropical forests, whereas those in the three secondary forests were at similar levels to those in other tropical forests (7.9–29.7%; Osono 2006). The smaller area of bleached area in *A. mangium* plantations and the negative relationship between the bleached area and N content (Fig. 1a) suggested that high N content could inhibit colonization by ligninolytic fungi. Previous studies showed that N could cause a biochemical suppression of AUR-degrading enzymes of fungi (Keyser et al. 1978; Fenn et al. 1981). This might have reduced competitiveness relative to other fungi and hence mycelial growth in *A. mangium* leaves. Similarly, Osono et al. (2002) reported that avian-derived N suppressed the colonization of ligninolytic fungi in coniferous litter in a temperate forest. Thus, the present study successfully demonstrated the inhibitory effect of high N content of *A. mangium* surface leaf litter on the appearance of the bleached area that represent colonization by ligninolytic fungi. The bleached area of *A. mangium* leaf litter was not significantly correlated with the stand age between 3 and 17 years where the canopies were closed, consistent with the results of Osono et al. (2008) reporting that the bleached area on salal leaf litter was not significantly different among forest stands of different ages (50–324 years) after canopy closure.

In contrast to the colonization of *A. mangium* leaves in the field, which was limited by N, the decomposition of the leaves by a ligninolytic fungus (*T. versicolor*) was limited by initial AUR content (Fig. 1b). Recalcitrant compounds in tree leaves categorized as AUR, such as lignin, have often been shown to limit the rate of decomposition in forest soils (e.g., Mellilo and Aber 1982; Osono and Takeda 2005). The factors causing the low rate of mass loss of leaves from the secondary forest in the Merbau region remained unclear, but might have been related to inhibitory

compounds in tree leaves included in the leaf mixture. The lack of a significant relationship between the mass loss of leaves and AUR and N content suggested that the growth and AUR decomposition by *T. versicolor* was not suppressed by N. It was unclear from the results of the present study whether N-rich leaves of *A. mangium* had inhibitory effects on the decomposition by other ligninolytic fungi, or whether fungi taking part in the decomposition of *A. mangium* leaves in the field could be adapted to the N-rich conditions of the leaves.

In conclusion, the present study has demonstrated that the colonization of *A. mangium* leaf litter by ligninolytic fungi was suppressed due to high N content, but the effect of high N in *A. mangium* leaf litter on the decomposition of leaf litter and AUR remained unsolved. Further studies will be necessary regarding the ligninolytic fungi associated with the bleaching of *A. mangium* leaves and the effect of N-rich conditions on the decomposition of the leaves by these fungi.

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