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Effects of understory removal and nitrogen fertilization on soil microbial communities in *Eucalyptus* plantations

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ABSTRACT

Understory removal and/or nitrogen fertilization are important forest management practices in forest plantations. Relative to overstory vegetation, understory vegetation is overlooked in forest ecosystems; and the effects of nitrogen fertilization on soil microbial communities are poorly understood. The objective of this study was to improve our knowledge of how understory removal and/or fertilization influence soil microbial communities. We conducted an experiment in which understory was removed or retained in plots with or without nitrogen fertilization in *eucalyptus* plantations; and we measured their effects on soil temperature, soil water content, and soil microbial communities (as indicated by phospholipid fatty acids). Understory removal increased soil temperature, decreased soil water content, decreased fungal biomass and decreased fungal to bacterial biomass (F:B) values. Additionally, fungal biomass correlated negatively with soil temperature. Nitrogen fertilization did not significantly affect soil temperature, soil water content, or soil microbial community. These findings suggest that the presence of understory is favorable for sustaining soil microclimates and acts as an important driver of soil microbial communities in *eucalyptus* plantations. Moreover, understory vegetations are important components and should not be removed from *eucalyptus* plantations.

1. Introduction

Traditionally, understory vegetation has been considered an inhibiting factor in forest ecosystems. Because understory plants compete with the overstory species for nutrients and water, understory vegetation is typically removed (Nambiar and Sands, 1993; Chang et al., 1996). Additionally, understory vegetation removal helps prevent fire, and favors seed germination and seedling growth of desirable species (Camprodon and Brotons, 2006). In their review of research on boreal forests, Nilsson and Wardle (2005) emphasized that the understory affects many ecological processes, e.g., tree seedling generation or ecosystem succession, litter decomposition, nutrient flow, and accumulation of soil nutrients. Recently, several studies explored the ecological functions of understory vegetations in humid subtropical China. For example, understory removal reduced fungal PLFAs and litter decomposition (Wu et al., 2011b; Liu et al., 2012; Zhao et al., 2012), reduced soil nematode and microarthropod densities (Zhao et al., 2011, 2012, 2013), impacted soil CO_2 and N_2O fluxes (Li et al., 2010, 2011; Wang et al., 2011; Wu et al., 2011a,b). Understory vegetation plays important roles in maintaining aboveground and belowground biota and biodiversity, microclimates, and ecosystem nutrient cycling. Collectively, these studies reveal the ecological function of understory vegetation in forest ecosystems of humid subtropical and tropical regions (Zhao et al., 2012).

Nitrogen fertilization is a common management practice of agroforestry. Meta-analysis results show that nitrogen fertilizer increases primary production in most situations worldwide (Elser et al., 2007). However, the effect of nitrogen fertilization on soil microbial communities is unclear. Many previous studies report that nitrogen fertilizers reduce soil microbial biomass (Smolander et al., 1994; Arnebrant et al., 1996; Fisk and Fahey, 2001; Lee and Jose, 2003; DeForest et al., 2004) and affect the composition of soil microbial communities (Bardgett et al., 1996; Belay et al., 2002; Marschner et al., 2003). On the contrary, other studies suggest that nitrogen fertilization has no significant effects (Wiemken et al., 2001; Mo et al., 2006, 2008) or has positive effects (Hart and Stark, 1997; Zhang and Zak, 1998) on microbial biomass. These conflicting results may be due to the differences in the initial status of the microbial communities, organic matter, soil nitrogen-saturation contents, and soil pH (Lee and Jose, 2003; Wallenstein et al.,

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2006). For example, nitrogen fertilization results in soil acidification and indirectly influences soil biota (Huhta et al., 1983; Lindberg and Persson, 2004; Wallenstein et al., 2006). Nitrogen fertilization decreases the soil microbial biomass in nitrogen-saturated soils, but not in nitrogen-unsaturated soils (Mo et al., 2006, 2008). Additionally, nitrogen fertilizers reduce some taxa of soil biota owing to toxicity or salinity effects (Lohm et al., 1977; Huhta et al., 1983).

Eucalyptus is a fast-growing species and demands copious amounts of water and nutrient supplies. In southern China, farmers usually apply large amounts of fertilizers before planting seedlings, and harvest the *eucalyptus* logs after 4–6 years. Most published studies report fertilizers improve the growth of *eucalyptus* in South Africa, Argentina, Portugal, southern China, Australia, southern Brazil (Herbert, 1990; Madeira and Pereira, 1990; Fox and Morrow, 1992; Pampolina et al., 2002; Xu et al., 2002; Graciano et al., 2006; Miranda et al., 2006; Laclau et al., 2009). However, studies rarely considered the effects of nitrogen fertilization on soil microbial communities of *eucalyptus* forests; and the results are conflicting (Hossain et al., 1995; Wang et al., 2008). For example, nitrogen fertilization had no significant effect on microbial biomass in a natural subalpine *Eucalyptus pauciflora* located near Canberra in Australia (Hossain et al., 1995). In contrast, nitrogen fertilization decreased microbial biomass in *Eucalyptus dunnii* plantations in southern China (Wang et al., 2008).

The research in the current study was conducted in experimental plantations in South China with distinct overstory (*eucalyptus* trees) and understory (grasses and shrubs) layers. The dominant understory plant in these plantations is *Dicranopteris dichotoma*, which often forms a dense understory. The objective of this study was to improve our knowledge of the effects of understory removal and/or fertilization on soil microbial communities. We hypothesized that: (1) understory removal would reduce resource input to soil subsequently changing soil microclimates, reducing microbial biomass and altering soil microbial community composition; and (2) nitrogen fertilization would increase primary production which will increase soil microbial biomass and affect soil microbial community.

2. Materials and methods

2.1. Site description

This study was conducted at the Heshan Hilly Land Interdisciplinary Experimental Station (112°50′E, 22°34′N), Chinese Academy of Sciences (CAS), Guangdong Province, China. The climate is subtropical monsoon with a distinct wet (from April to September) and dry season (from October to March). The mean annual temperature and precipitation are 21.7 °C and 1700 mm, respectively. The soil is an acrisol (FAO, 2006).

The experimental site consisted of three independent 4-year-old *Eucalyptus urophylla* plantations; each of three plantations occupied about 1 ha. The *eucalyptus* seedlings had been transplanted with a spacing of 3 × 2 m. The understory vegetation was dominated by *D. dichotoma*. Other common understory plants included *Miscanthus sinensis* and *Rhodomyrtus tomentosa*. The experiment was established in September 2009.

2.2. Experimental design

The experiment contained treatments representing a complete factorial combination of fertilizer and understory removal (a two-factor (2^2) design) to give a total of four treatments: no fertilizer and no understory removal as a control (CK), fertilization without understory removal (F), understory removal without fertilization (UR), and understory removal with fertilization (F + UR). A complete suite of treatments was established at each of three plantations for a total of 12 experimental units. Within a plantation, treatment combinations were arranged as a split plot design with fertilizer as main plots and understory removal as subplots. Main plots were 15 × 15 m and subplots were 5 × 5 m. Nitrogen was applied at 100 kg ha^{-1} yr^{-1}. N-fertilizer application to the pits (holes dug for fertilization) is a common practice in the processes of managing of *eucalyptus* monocultures in southern China. There are about 1650 trees in each 1 ha plantation. Therefore, for the F and F + UR treatments, 173 g of NH_4NO_3 (equal to 60.6 g of N) was allocated to each tree on 2 October 2009 and fertilized in pit. Briefly, NH_4NO_3 was fertilized in three pits with size of 15 × 15 × 15 cm which around and about 30 cm away from *eucalyptus* trunks; all the fertilized pits were labeled with flagging to avoid sampling soil on these spots. For the UR and F + UR treatment, the shoots of all understory plants were removed manually with a machete. Trenches were created around each main plot and subplot to prevent roots from growing into or out of these plots and to block the movement of nutrients into and out of the plots. Each month, germinating understory plants were removed manually from the UR subplots; herbicide was not used to avoid potentially impacts on soil organisms.

2.3. Soil sampling and analysis

The soil was sampled on 20 September 2009, 1 October 2009, 6 November 2009, 11 March 2010, 15 June 2010, and 14 October 2010. These dates corresponded to 0, 7, 37, 160, 256, and 376 days after treatment were applied (the day 0 samples were collected just before treatments were applied and are referred to as "background"). Soil cores (2.5 cm diameter, 5 cm high) were taken at 0–5 cm and 5–10 cm depths from eight randomly selected locations in each subplot within each plantation. Eight cores of the same depth from each subplot were combined to form one composite sample; there were three replicate samples for each of the four treatments. The surface litter was carefully removed before the soil sample was taken.

Soil water content (SWC%, g of water per 100 g dry soil) was measured by oven-drying for 48 h at 105 °C. Soil temperature was recorded at every experimental unit within each plantation every 2 h with the DS1922L temperature logger iButtons (Dallas Semiconductor Corp., Dallas, TX) from September 2009 to October 2010. Phospholipid fatty acids (PLFA) were analyzed according to Bossio and Scow (1998). Concentrations of each PLFA were standardized relative to 19:0 internal reference concentrations. Bacteria biomass was considered to be represented by 10 PLFAs (i15:0, a15:0, 15:0, i16:0, 16:1ω7, i17:0, a17:0, 17:0, cy17:0, cy19:0) and fungi biomass was considered to be represented by the PLFAs 18:2ω6,9 (Bossio and Scow, 1998; Bååth, 2003; Frostegård et al., 2011). Other PLFAs such as 16:00, 16:1ω5, 16:1ω9, 18:1ω7, and 18:1ω9 were also used to analyze the soil microbial community.

2.4. Statistical analysis

Repeated-measure ANOVA was employed to determine the time effect and treatment effect through the whole experimental period. Data of soil temperature, soil water content, and soil microorganisms of each sampling event were analyzed using a General Linear Model in a 2^2-factorial design with F and UR as the two main factors and the background data (first sampling data) as covariants (Perkiömäki et al., 2003). Two-way ANOVA was performed to determine the effects of F, UR, and interaction effect of F and UR on soil temperature, soil water content, and on the soil microbial community at each sampling event. Redundancy analysis (RDA) was performed to determine the relationship between microbial community (PLFA profiles) and soil microclimates. The most discriminating soil microclimate variables were selected by 'forward selection' procedure of the program. Microbial community composition was analyzed by transforming the data to their principal components (using Principal Component Analysis (PCA)) and analyzing these using ANOVA (Perkiömäki et al., 2003; Zhao et al., 2012). Data were transformed (natural log, square root, or rank) when required to meet assumptions of normality and homogeneity of variance. Statistical significance was determined at $p < 0.05$. ANOVAs and PCA were performed with SPSS software (SPSS Inc., Chicago, IL). RDA used CANOCO 4.5 software (Ithaca, NY, USA). Forward selection was based on Monte Carlo permutation ($n = 499$)

3. Results

3.1. Soil temperature and soil water content

Soil temperature in plots with the understory removed was higher than that in plots without the understory removed during the study ($p < 0.001$) (Fig. 1). Soil temperature increased from March to October, 2010 in plots with the understory removed (Fig. 1). There were no apparent effects of fertilization and interaction effects of fertilization and understory removal on soil temperature during the study (Fig. 1). Soil water content in plots with the understory removed was drier than that in plots without the understory removed during the study at 0–5 cm soil depth ($p = 0.026$) (Fig. 2a). Soil water content decreased in plots with the understory removed at 0–5 cm soil depth by 256 days ($p < 0.10$) (Fig. 2a). There were no apparent effects of either fertilization or the interaction between fertilization and understory removal on soil water content during the study at 0–5 cm soil depth (Fig. 2a). Soil water content at 5–10 cm soil depth was similar among treatments (Fig. 2b).

3.2. Soil microbial community

Microbial biomass and bacterial biomass were not significantly affected by understory removal through the whole experimental period or sampling depth (Fig. 3a, b, e and f). Understory removal significantly reduced fungal biomass at 0–5 cm soil depth during the study (Fig. 3c). Additionally, F:B values were smaller at 0–5 cm depth when understory was removed than remained ($p = 0.010$) (Fig. 4a). A similar reduction in F:B values was observed at 5–10 cm but was not significant statistically (Fig. 4b). There was

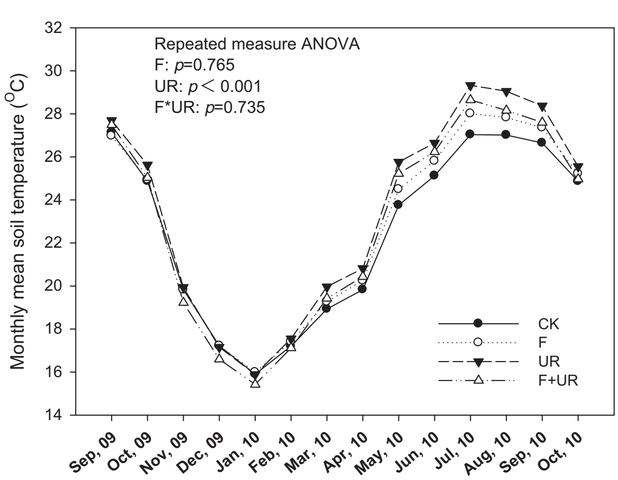

Fig. 1. Soil temperature under 5 cm depth under control (CK), fertilization (F), understory removal (UR), and both fertilization and understory removal (F + UR) from September 2009 to October 2010.

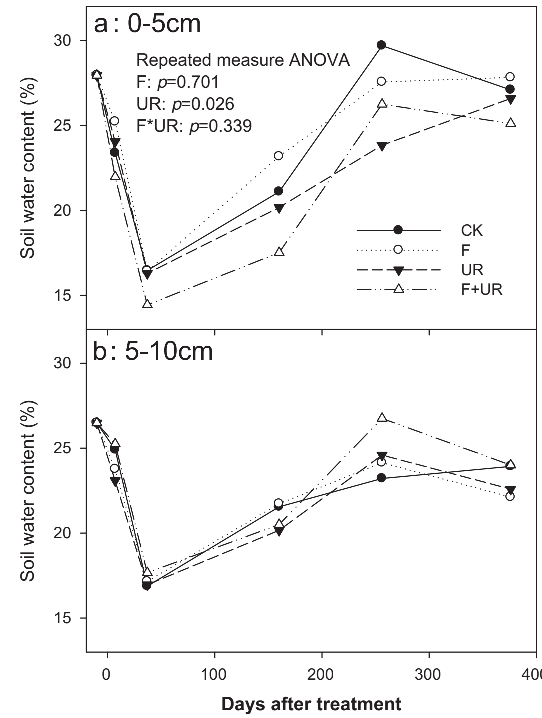

Fig. 2. Soil water content (%) under control (CK), fertilization (F), understory removal (UR), and both fertilization and understory removal (F + UR) of 0–5 cm and 5–10 cm depths in each sample event.

a two-way interaction effect of fertilization and understory removal on fungal biomass at 0–5 cm soil depth (Fig. 3c). Composition of the soil microbial community was altered at 0–5 cm depth in the UR treatment after 256 days ($p < 0.05$) (Fig. 6i and k) and at 5–10 cm depth by 375 days ($p < 0.05$) (Fig. 6l). Composition of soil microbial community was not significantly affected by fertilization treatment nor a two-way interaction between fertilization and understory removal (Fig. 4a and b).

3.3. Relationships between soil microclimates and soil microbial community

There was a trend that soil water content correlated with whole soil microbial community ($p = 0.088$) (Fig. 5). Specifically, soil water content was correlated positively to 16:1ω5, 16:1ω9, 18:1ω7, 18:ω9 and correlated negatively to i16:00 a17:00, i17:00 (Fig. 5). Although soil temperature was not associated with whole soil microbial community PLFA ($p = 0.252$) (Fig. 5); Soil temperature was correlated positively to 17:00, 16:1ω7 and correlated negatively to 18:2ω6,9 and 15:00 (Fig. 5).

4. Discussion

4.1. The impacts of understory removal on soil temperature, soil water content and on soil microbial community

Previous studies reported that understory vegetation played important roles on maintaining soil microclimate. Understory removal significantly enhanced soil temperature and reduced soil water content in local-species-mixed plantations, acacia monocultures, and *eucalyptus* monocultures (Li et al., 2010; Wang et al., 2011; Wu et al., 2011b; Liu et al., 2012; Zhao et al., 2012). The same pattern was observed in the present study. Furthermore, Zhao et al. (2012) suggested that the change of soil microclimates was the most likely factor that influenced soil food web (including soil

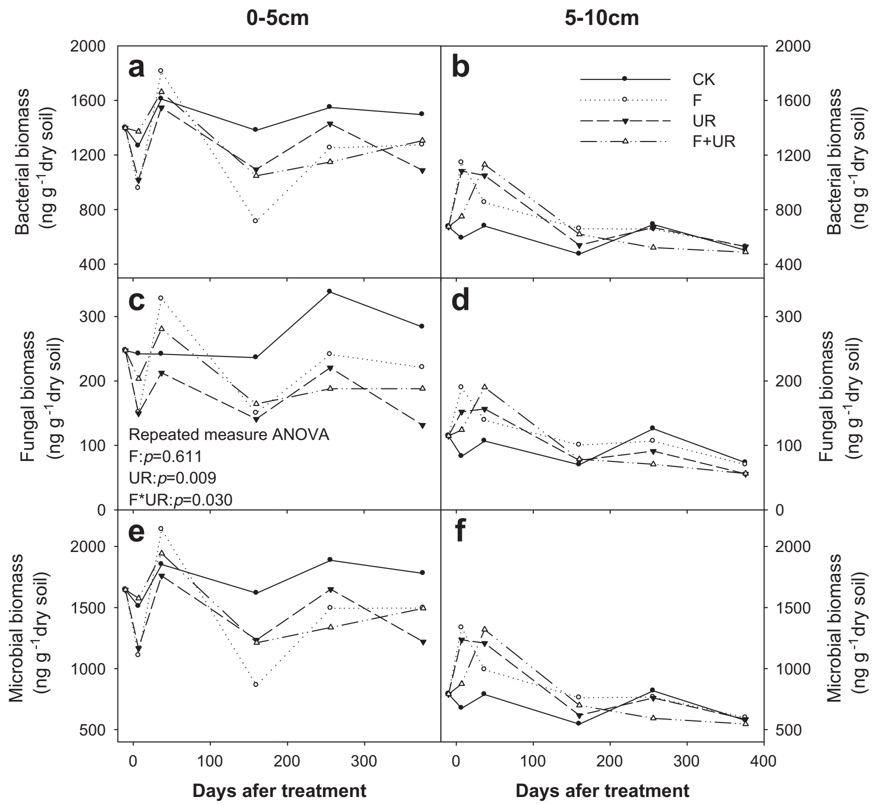

Fig. 3. Bacterial biomass (a and b), fungal biomass (c and d), and total microbial biomass (e and f) under control (CK), fertilization (F), understory removal (UR), and both fertilization and understory removal (F + UR) through time and at 0–5 cm and 5–10 cm soil depths.

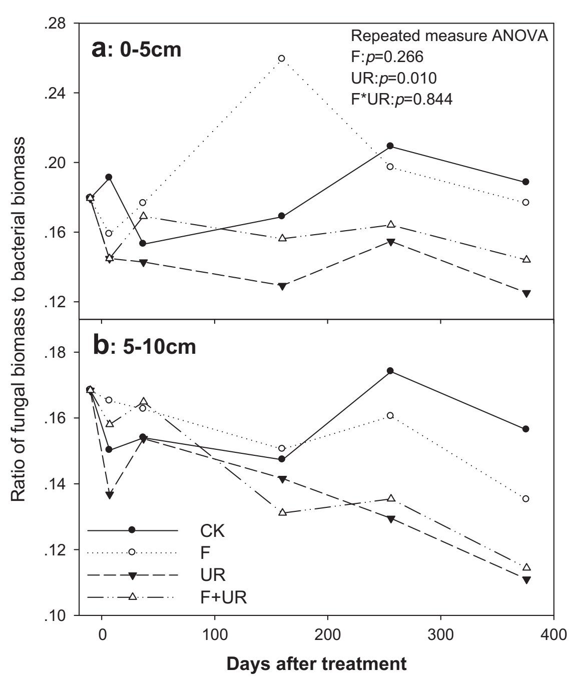

Fig. 4. Ratio of fungal biomass to bacterial biomass under control (CK), fertilization (F), understory removal (UR), and both fertilization and understory removal (F + UR) through time and at 0–5 cm (a) and 5–10 cm (b) soil depths.

microorganisms) and litter decomposition. Consistent with our findings, Wu et al., (2011) and Zhao et al. (2012) reported that understory removal significantly reduced fungal biomass and the F:B ratio in three *eucalyptus* plantations (2-year-old, 4-year-old and 24-year-old). Zhao et al. (2011) reported a trend that understory removal reduced the F:B ratio in local-species-mixed plantations in the studied area. Furthermore, the change of soil temperature after treatment resulted in the fungal biomass change, which because of fungal PLFA biomarker 18:2ω6,9 was correlated negatively with soil temperature (Fig. 5). Other studies reported understory removal reduced soil CO_2 flux, from which we can infer that understory removal might reduce soil microbial biomass (Li et al., 2011; Wang et al., 2011; Wu et al., 2011a). However, another study was failure to detect the change of soil microbial biomass after understory removal in a 20-year-old acacia plantation in southern China; although litter decomposition decreased after understory removal (Xiong et al., 2008).

Generally, soil microorganisms are controlled by bottom-up forces (Fu et al., 2000; Coleman et al., 2002). Although understory vegetation accounts less for biomass than overstory vegetation; it is also an important resource for decomposers and primary consumers in forest ecosystems. Nilsson and Wardle (2005) reviewed the studies of understory vegetation in Swedish boreal forests, and reported the ecological functions of understory vegetation largely depend on species of plants. For instance, poor-quality understory species, black crowberry (*Empetrum hermaphroditum*), contributes to reduce soil microbial activity, reduces soil available N, and increases soil C sequestration; however, high-quality understory species, bilberry (*Vaccinim myrtillus*) and lingonberry (*Vaccinium vitisidaea*), show strong positive effects on soil microbial activity and depletion of soil mineral N. In the present study, the forest understory is dominated by *D. dichotoma* which is a poor-quality fern species (Zhao et al., 2012). Therefore, understory dominated by *D. dichotoma* understory may have minor bottom-up control on soil decomposers. Furthermore, Wu et al. (2011a,b) suggest that dissolved organic carbon (DOC) was unaffected by removal of

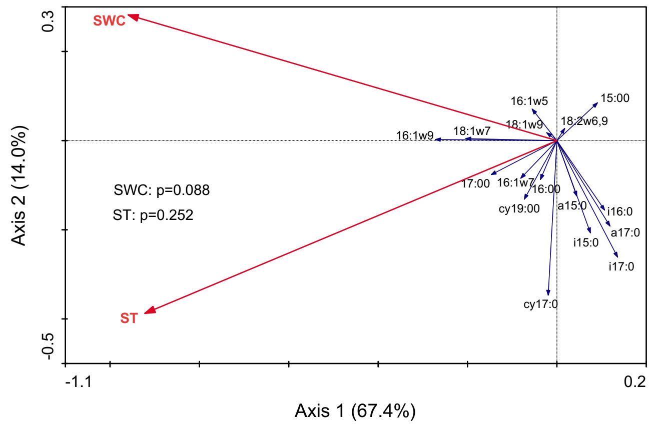

Fig. 5. Bi-plots of redundancy analysis (RDA) of soil microbial PLFA biomarkers. Ordination diagrams presenting species scores and environmental factor scores (vectors). ST, soil temperature; SWC, soil water content.

understory in both 2-yr and 24-yr *eucalyptus* plantations, which infers that bottom-up control induced by understory vegetation was minor.

However, *Dicranopteris* (*D. dichotoma* or *D. linearis*) dominated understory contribute up to 74% of above-ground NEP in a site in Hawaii (Russell et al., 1998) and account 55% of annual production in a mixed forest in southern China (Brown et al., 1995), respectively. Therefore, the contribution of *Dicranopteris* dominated understory as food resources for decomposers and/or primary consumers in forest ecosystems may require further study.

4.2. The impacts of nitrogen fertilization on soil temperature, soil water content and on microbial community

The increase of aboveground biomass and/or root growth that favored by nitrogen fertilization will increased soil microbial biomass which was controlled by bottom-up forces (Hart and Stark, 1997; Zhang and Zak, 1998). In this study, nitrogen fertilization did not affect soil microbial community. One likely reason was that nitrogen fertilization did not influence the growth of *eucalyptus*. Many studies have reported that fertilization improves *eucalyptus* growth (Herbert, 1990; Madeira and Pereira, 1990; Fox and Morrow, 1992; Pampolina et al., 2002; Xu et al., 2002; Graciano et al., 2006; Miranda et al., 2006; Laclau et al., 2009). However, these studies were conducted in young growth *eucalyptus* plantations where trees are about 2–4 years old. Miranda et al. (2006) reported that *eucalyptus* growth was increased by fertilizers (N, P, K, Ca, and Mg) up to age 6 years in Portugal. Addationally, some other studies reported that fertilizers (N, P, or K) modified leaf characteristics but did not affect *eucalyptus* growth (Fox and Morrow, 1992; Pampolina et al., 2002). Therefore, it is possible that nitrogen fertilizer did not increase the *eucalyptus* growth at age 4–5 years and did not influence soil microbial community in the present study.

Decreases in soil pH that caused by nitrogen fertilization affects soil microbial community (Compton et al., 2004; Wallenstein et al., 2006). Chronic nitrogen amendment decreased the pH of the N-treated surface soils by approximately 0.2–1.5 units at the Harvard Forest, Massachusetts, USA (Bowden et al., 2004; Compton et al., 2004; Magill et al., 2004). However, we did not detect any apparent decrease in soil pH (another study) after 1-year of nitrogen treatment. Additionally, nitrogen fertilization may alter soil microbial communities via direct nitrogen effects. Increased inorganic N might result in direct immobilization by microbes either by decreasing their C:N ratio, or increasing their overall biomass (Wallenstein et al., 2006). Nitrogen fertilization may have 'toxicity

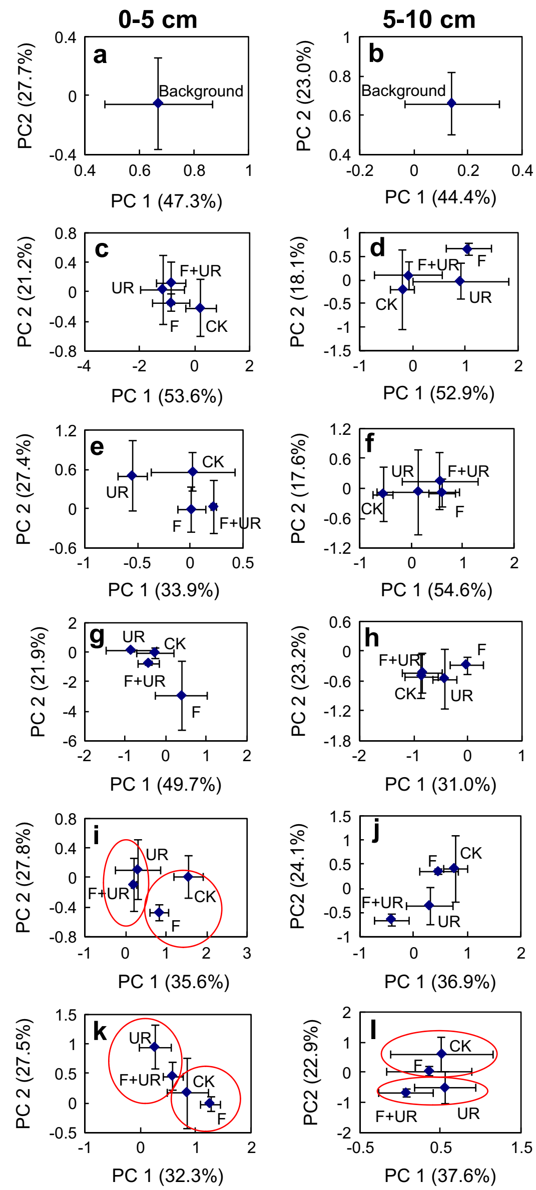

Fig. 6. Principal component analysis (PCA) of microbial PLFA biomarkers of the first (a and b), second (c and d), third (e and f), fourth (g and h). fifth (i and j) and sixth (k and l) sampling events at 0–5 cm and 5–10 cm depths under control (CK), fertilization (F), understory removal (UR), and both fertilization and understory removal (F + UR).

effects or salt effects' on soil biota (Lohm et al., 1977; Huhta et al., 1983; Thirukkumaran and Parkinson, 2000). However, this 'toxicity effects or salt effects' might be insignificant in the present study, because of our fertilized-in-pit method. Our soil samples were kept away from the fertilized pits. Therefore, 'toxicity effects or salt effects' of nitrogen fertilizer might be ineffective in this study.

5. Conclusions

Understory vegetation is an important component of forest ecosystems because it affects seedling regeneration, litter decomposition, nutrient cycling, succession, and the incidence and intensity of wildfire, (Nilsson and Wardle, 2005). In the present study, understory removal suppressed the fungal biomass and altered the soil microbial communities. The present of understory is favorable for sustaining soil microclimates and acts as an important driver of soil microbial communities in *eucalyptus* plantations. The contribution of understory vegetation as food resource for soil biota is still poorly understood and requires further studies. To date, results of previous studies of the effects of nitrogen fertilization on soil microbial communities are equivocal, especially in *eucalyptus* plantations. In the current one-year study, nitrogen fertilization did not affect the soil microbial communities. The long-term effects of nitrogen fertilization on soil microbial communities, plant growth, and soil pH need further study in *eucalyptus* plantations.

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