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Full Length Article

Effects of Forest Gaps on Soil Microbial Diversity in a *Cunninghamia lanceolata* Stand after a Severe Ice Storm

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Abstract

This study compared soil microbial community functional diversity of different size gaps in a *Cunninghamia lanceolata* stand to help ecological restoration of stands suffering from ice-snow damage. The functional diversity of soil microbial communities was studied using Biolog-Eco-Plates. We found gap size had a significant effect on average well color development (AWCD) and on the Shannon index of soil microbial diversity. Compared with large gaps, small gaps had higher AWCD. The ten gaps were divided into three groups by cluster analysis and principal component analysis (PCA): group 1 reflected large gaps, while groups 2 and 3 reflected small gaps. Thirty-one sole carbon sources were divided into three groups by PCA. Using an eigenvector greater than 0.5 as a standard for checking carbon (C) sources, nineteen kinds of C sources included in principal components 1 and 2 had a relatively high influence on the soil microbial community, including carbohydrates, amino acids and carboxylic acids. This indicates that the use by soil microorganisms of carboxylic acids, sugars and amino acids was greater than other C sources. These findings suggest that gap size played a key role in the soil microbial diversity after a natural disturbance. © 2018 Friends Science Publishers

Keywords: Biology; Cluster analysis; Forest soil; Ice-snow damage; PCA; Soil microbial activity

Introduction

Soil microorganisms play an important role in forest ecosystems owing to their involvement in important processes, such as litter decomposition, soil structure, and carbon and nutrient cycles (Huang *et al.*, 2008; Velasco *et al.*, 2009), among which, the functional diversity of soil microbial communities is extremely important for the functioning of soil ecosystems. This can be defined as the capacity of the microbial community to use different types of carbon (C) sources as substrates and is very sensitive to environmental changes in perturbed soil ecosystems (Costa *et al.*, 2013). As soil microbial diversity is affected by environmental conditions, such as canopy structure, illumination, soil nutrient conditions, and soil moisture, it can be used as a potential indicator of soil quality (Huang *et al.*, 2008). Although many studies have been conducted in soil microbial diversity since the 1960s, these studies focused on the impacts of land use patterns, vegetation diversity and regeneration, soil moisture, fertility, microbial number and enzymatic activity on soil microbial diversity; relatively few studies on disturbances effect, such as ice storms on soil microbial diversity have been conducted (Velasco *et al.*, 2009).

Biolog system is a common method in studying soil microbial functional diversity, which is used to analyze microbial communities by using a variety of C compounds based on measuring the use of a set of sole C substrates (Marcin and Maria, 2010). Functional diversity of microbial community is related with average well color development (AWCD) in Biolog EcoPlates, which can be estimated with clustering and principal component analysis (PCA) (Klimek *et al.*, 2015).

During January to February in 2008, a severe ice storm hit *Cunninghamia lanceolate* stands in northern area of Guangdong, China, with a damaged area of 79.50 ha, and resulted in many different size gaps, canopy gaps caused by aging tree death or natural and man-made disturbances due to the snapping of tree branches and lodging of trees (He *et al.*, 2010). As a result, illumination reaching the woodland floor increased, altering the soil temperature and moisture (Chen *et al.*, 2015). Moreover, additional ecological niches due to different environmental conditions led to an increase in undergrowth diversity. Environmental factors have important effects on spatial variability of microbial communities and activities (Tian *et al.*, 2015). However, results of gap effect on microbial functional diversity are contradictory and limited due to few studies on soil microbial diversity changes caused by natural gaps.

Studies on ice storm effects on forests have focused on tree damage (Burner and Ares, 2003), forest management after disturbance, forest dynamics (Olthof *et al.*, 2003), understory recovery patterns (Takahashi *et al.*, 2007), vegetation dynamics and regeneration (Yorks

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and Adams, 2003; Holladay *et al.*, 2006; Hou and Xue, 2016), tree species growth (Smolnik *et al.*, 2006) and forest communities (Lloyd, 2000; Yorks and Adams, 2003). However, knowledge of soil, especially soil microbial functional diversity responses to forest gaps is limited (Ou *et al.*, 2009). Hence, it is important to study microorganisms to understand the role of gaps in microbe recovery of soil ecosystem after ice storm damage.

C. lanceolata (Lamb.) Hook. is one of commercial tree species and has been widely planted in southern China with a total forest plantation area of approximately 9.21 million ha (Xu *et al.*, 2016a, 2016b). Stands containing this species were severely damaged by an ice storm in 2008 (Xu *et al.*, 2016b). However, to our knowledge, no research has reported on the soil microbial functional diversity of *C. lanceolata* stands suffering from ice damage. In the present study, we assessed how different sized forest gaps influenced soil microbial functional diversity in a *C. lanceolata* stand after a severe ice storm. This might be useful to understand effects of environmental changes on soil microbial communities and sustainable management of recovery and restoration of *C. lanceolata* stands.

Materials and Methods

Study Site

This study was conducted at the Lechang Forest Farm (25º09′ N, 113º30′ E), northern Guangdong Province, southern China. The climate of the study area belongs to a classic subtropical monsoon climate. Mean annual temperature mean annual precipitation in the study area were 19.6ºC and 1,522 mm, respectively. The lowest and the highest monthly mean temperatures occurred in January (9.3ºC) and July (28.2ºC), respectively. The extreme low and high temperatures are -4.6ºC in January and 38.4ºC in July, respectively and the relative humidity of the research site ranged from 70 to 84%.

The *C. lanceolata* stands were damaged by ice storms during January to February in 2008. We set up a 2-ha plot in a 17-year-old *C. lanceolata* stand in March 2008, which was located at an altitude of 700 m and had a slope of 30º with a southwest orientation. The understory vegetation was mainly composed of *Elatostema involucratum* and *Woodwardia japonicav*. The branches of *C. lanceolata* trees were broken and some trees were lodged in the study area. The mean diameter at breast height and mean height of trees were 17.99 cm and 12.69 m, respectively. We selected 10 different gaps sizes from the *C. lanceolata* stand. The gap size and canopy degree are given in Table 1.

Microplates and Sampling

Microbial metabolic activity was measured using 96 well Biolog EcoPlates ™ in 2011. As the C source is used, the amount of tetrazolium violet dye is reduced, developing a purple color. The shade of purple reflects the ability of soil microbial communities to use C. The microbial community metabolic functional diversity was determined by measuring the variation in absorbance value.

Ten grams of fresh soil were added to 90 mL of sterilized NaCl solution (0.85%) and shaken at 200 rpm min^{-1} for 30 min at room temperature. A 10^{-3} dilution of soil suspensions was prepared and after removing the residual soil by centrifugation, the supernatant was used for inoculation. Each well of the Biolog Ecoplates was inoculated with 150 µL of the suspension. The rate of use of C sources is indicated by the reduction of tetrazolium dye which changes from colorless to purple. The plates were continuously incubated at 25°C for 120 h, and color development in each well was recorded as optical density (OD) at 590 nm with a plate reader at regular 12-h intervals using an ELISA Microplate Reader (Lagerlöf *et al.*, 2014). Microbial activity in each microplate, expressed as average well color development (AWCD), was determined as described by Garland (Garland, 1996). To overcome the difference of inoculum density, a fixed level of AWCD (0.75) was used to determine the reading times for plate comparisons by taking multiple time point readings (at 12-h intervals). We selected the data at the 72 h incubation time because the AWCD at this time was close to the reference AWCD (Garland, 1997).

Analysis of Microplate Data

The AWCD was determined as follows (Garland and Mills, 1991):

$$AWCD = \Sigma(C_i - R)/31 \quad (1)$$

Where, C_i is the absorbance of each well at 590 nm, and R is the comparable absorbance of the control well (water in control well). Negative (C_i - R) values were set to zero (Garland, 1996).

The 72 h absorbance values were also analyzed to calculate the catabolic diversity (Shannon diversity index, H′) (Rogers and Tate, 2001). The microbial community functional diversity indicated by the Shannon diversity index was calculated as follows:

$$H' = -\Sigma P_i \times \ln P_i, \quad (2)$$

Where, $P_i = (C_i - R)/\Sigma(C_i - R)$, which represents the difference in absorbance values between a medium pore and control.

Richness (s), taken as the number of oxidized C substrates when AWCD **>** 0.25, represents the community richness index (Zak *et al.*, 1994).

Data Analysis

Duncan multiple comparisons were used to determine significant differences in AWCD and the Shannon diversity index. Differences were deemed significant when $P < 0.05$.

Cluster analysis and PCA were performed on the 72 h Ecoplate data. PCA was also used to identify C source utilization characteristics of soil microbials. All statistical analyses were conducted using SPSS 16.0 (SPPS, Inc., Chicago, Illinois) and Microsoft Excel 2003 for Windows.

Results

Average Well Color Development (AWCD) and Shannon Diversity Indices

The AWCD of the gaps ranged from 0.81 to 1.28 at 72 h (Fig. 1). The AWCD of gap D was significantly greater than other gaps, while those of gaps F to J were significantly smaller than other gaps. The Shannon diversity index of soil microorganisms in each gap ranged from 2.80 to 3.25. Significantly higher diversity indexes of soil microbial communities were found in gaps B, D and E.

Cluster Analysis of C Source use Patterns

Cluster analysis and PCA of the AWCD generally separated the soil samples according to gap size (Fig. 2 and 3). Cluster analysis and PCA showed that the microbes could be classified into three main groups according to gap size. The first group included gaps F to J, the second group included gaps A, B, C and E, and gap D was in the third group. The eigenvalues of the first and second principal components (PC1 and PC2) were 14.56 and 7.58, which explained 21.89 and 18.09%, respectively.

The PCA of the use patterns of 31 sole C sources is shown in Fig. 4. PC1 and PC2 divided these C sources into three groups: the first group included C sources 12 and 25, the second included C sources 5, 8, 10, 16, 19, 20, 23, 28 and 29, while the remaining C sources belonged to the third group.

Table 2 shows high loadings for PC1 belonged to D-Mannitol (0.874), γ-hydroxybutyric acid (0.826), D-Malic acid (0.757) and putrescine (0.724) and high loadings for PC2 belonged to 2-hydroxybenzoic acid (0.906), D-xylose (0.814), L-threonine (0.858) and alfa-D-lactose (0.715). Table 3 showed the C sources with eigenvector values greater than 0.50. Ten types of sole C sources made a strong contribution to PC1, including two types of carbohydrates (CHs), two types of amino acids (AAs), two types of amines (AMs) and four types of carboxylic acids (CAs). Eight types of sole C sources contributed greatly to PC2 with CHs and AAs each accounting for 37.5%, and CAs and polymers (PMs) each accounting for 12.5%. Therefore, the main C sources suitable for dividing soil microbial communities were CHs and AAs.

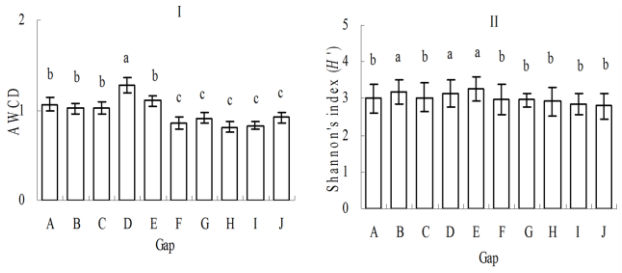

Fig. 1: I: Average well color development (AWCD), II: Shannon's index (*H'*) of the carbon substrate on the Biolog Ecoplate by metabolized by bacterial communities in the soil of the *C. lanceolata* stand. Mean ± standard deviation. Bars with different letters are significantly different ($P < 0.05$) with Duncan's test; n = 3

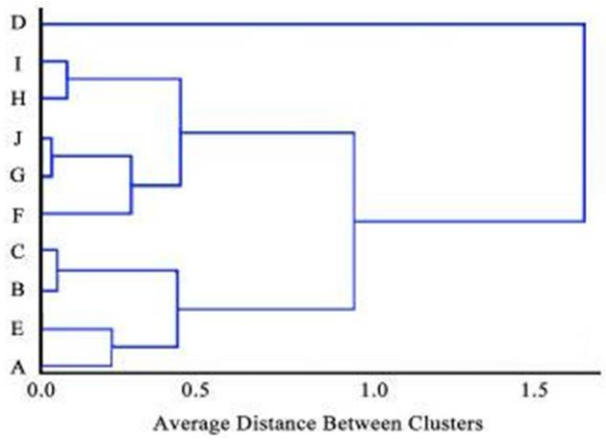

Fig. 2: Analysis of the average well color development (AWCD) from gaps A to J using cluster analysis

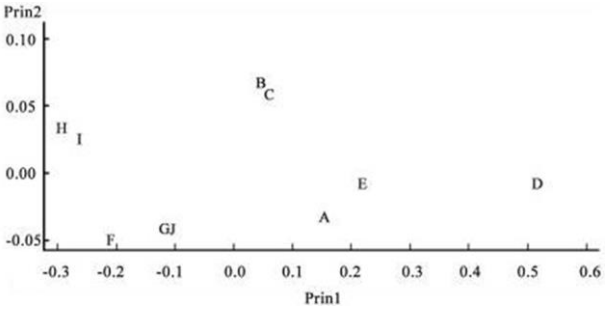

Fig. 3: Principal component analysis of the average well color development (AWCD) for microorganisms at 72-h incubation of the soils from gaps A to J

Discussion

The AWCD reflects the sole C source usage ability of the soil microbial community (Garland and Mills, 1991). The Shannon diversity index is the most widely employed in studies of microbial functional diversity,

Table 1: Gap size and canopy degree

Gap number	A	B	C	D	E	F	G	H	I	J
Gap size (m^2)	10.4	13.2	16.5	16.8	28.9	31.3	31.8	38.6	52	80.4
Canopy degree (%)	12.19	15.15	13.97	11.78	12.46	18.36	15.24	11.67	12.22	12.37

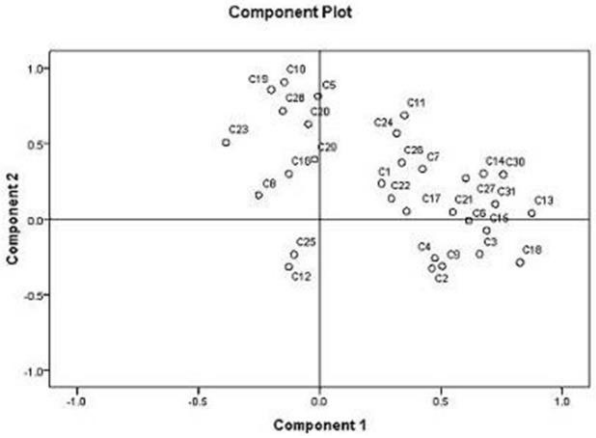

Fig. 4: Distribution of 31 sole carbon sources of soil microbial community by principal component analysis

and can indicate the metabolic diversity patterns and functional diversity of soil microorganisms (Zheng *et al.*, 2005; Pignataro *et al.*, 2012). In the present study, the variation trends in the Shannon diversity index for the soil microbes corresponded to the AWCD variation. Both were higher in small gaps than in large gaps, indicating that the microbial community in soils of the former used C substrates more effectively than the latter. The reason may be that the organic matter, nitrogen (N) and phosphorous (P) contents of the former were significantly greater than the latter in the studied *C. lanceolata* soil (Xu *et al.*, 2016a). Chen *et al*. (2013) reported a lower C metabolic function of the soil microbial community in a *Eucalyptus* stand with low soil fertility. Lagerlöf *et al.* (2014) found that soil nutrients affected microbial diversity due to increasing the effect of nutrients on microbial growth (Zhou *et al.*, 2008). Tian *et al*. (2015) also reported that decreases in soil organic C and nutrients reduced the metabolic diversity of soil microbial communities. Moreover, soil moisture may be important in microbial diversity (Lagerlöf *et al.*, 2014; Tian *et al.*, 2015). Bossio and Scow (1995) found a significant correlation between microbial metabolic diversity and soil water moisture. Low soil water content may decrease the use of C substrates, such as carbohydrates and carboxylic acids. Low soil moisture in the large gaps in the *C. lanceolata* soil may decrease AWCD (Xu *et al.*, 2016a). Additionally, low AWCD in the large gaps may be due to the low activity of catalase, acid phosphatase and urease in the *C. lanceolata* soil (Xu *et al.*, 2016a), since enzyme activity linked with AWCD reflects the physiological state of microbial cells.

Table 2: Varimax rotated component matrix of loadings for carbon sources

Number	Carbon source	PC1	PC2
C1	Beta-methyl-D-glucoside (CHs)	0.255	0.237
C2	D-galactonic acid r-lactone (CHs)	0.463	-0.324
C3	L-arginine (AAs)	0.659	-0.229
C4	pyruvatic acid methyl ester (CAs)	0.474	-0.256
C5	D-xylose (CHs)	-0.007	0.814
C6	D-galacturonic acid (CAs)	0.614	-0.006
C7	L-asparagine (AAs)	0.424	0.333
C8	tween 40 (PMs)	-0.252	0.160
C9	L-erythritol (CHs)	0.505	-0.310
C10	2-hydroxybenzoic acid (PCs)	-0.146	0.906
C11	L-phenylalanine (AAs)	0.349	0.688
C12	tween 80 (PMs)	-0.127	-0.313
C13	D-Mannitol (CHs)	0.874	0.040
C14	4-hydroxybenzoic acid (PCs)	0.675	0.301
C15	L-serine (AAs)	0.689	-0.074
C16	Alfa-cyclodextrin (PMs)	-0.127	0.300
C17	N-acetyl-D-glucosamine (CHs)	0.358	0.053
C18	γ-hydroxybutyric acid (CAs)	0.826	-0.285
C19	L-threonine (AAs)	-0.200	0.858
C20	glycogen (PMs)	-0.047	0.629
C21	D-glucosaminic acid (CAs)	0.549	0.048
C22	itaconic acid (CAs)	0.296	0.138
C23	Glycyl-L-glutamic acid (AAs)	-0.387	0.508
C24	D-cellobiose (CHs)	0.318	0.569
C25	Glucose-1-phosphate (CHs)	-0.106	-0.233
C26	Alfa-ketobutyric acid (CAs)	0.338	0.375
C27	phenyl ethylamine (AMs)	0.603	0.272
C28	Alfa-D-lactose (CHs)	-0.152	0.715
C29	D, L-alfa-glycerolphosphate (CHs)	-0.021	0.395
C30	D-malic acid (CAs)	0.757	0.296
C31	putrescine (AMs)	0.724	0.101

AMs: amines; AAs: amino acids; CHs: carbohydrates; CAs: carboxylic acids; PCs: phenolic compounds; PMs: polymers. Factor loadings above 0.7 are highlighted with gray background

Table 3: Carbon sources with eigenvector values greater than 0.50

Carbon source	PC1	PC2
carbohydrates	2	3
amino acids	2	3
carboxylic acids	4	1
polymers	0	1
amines	2	0
phenolic compounds	0	0
total	11	8

The effect of understory cover on litter inputs into the soils and microclimates affects soil nutrients, and thus changes the soil microbial composition and function (Wang *et al.*, 2011; Chen *et al.*, 2013). The understory diversity index was low in large gaps due to strong illumination and high in small gaps due to large spatial heterogeneity (Hou and Xue, 2016), plus the coverage of understory vegetation was low in large gaps in the studied *C. lanceolata* stand (Xu *et al.*, 2016a, b), which may be reflected in low AWCD values.

Microbial functional diversity can be used to estimate forest ecosystem disturbance (Chen *et al.*, 2015).

In this study, the Shannon diversity index indicated that soil microbial functional diversity in the small gaps was higher than in the large gaps. Soil nutrient availability (Wang *et al.*, 2011; Fang *et al.*, 2014) can affect the microbial metabolic activity. Gap size can have an important impact on microclimates in gaps (Gray *et al.*, 2002). Canopy openness affected by gap size is closely associated with light conditions and determines the distribution and intensity of light, thereby affecting temperature and moisture, which can directly influence the soil microbial community (Hughes *et al.*, 2003; Caldwell *et al.*, 2007). The low N and P contents in the present study (Xu *et al.*, 2016a) may decrease the Shannon diversity index in the large gaps. Williamson and Wardle (2007) reported that the soils with high fertility usually lead to higher microbial functional diversity. The large gaps may also provide unfavorable conditions for microorganisms, because strong solar radiation may result in the rise and fluctuation of air and soil temperatures. This may decrease soil moisture because of greater soil water evaporation (Xu *et al.*, 2016a), making it less suitable for microbial growth and thereby decreasing microbial functional diversity in the large gaps. Moreover, the greater spatial heterogeneity and understory vegetation diversity in the small gaps in the *C. lanceolata* stand (Xu *et al.*, 2016b) is favorable to soil microbial functional diversity (Chen *et al.*, 2015). Richer understory vegetation causes diversified litter and root exudates, resulting in higher microbial diversity (Klimek *et al.*, 2015).

Cluster analysis of the AWCD of the soil microbial community generally separated the soil samples according to gap size. Ten gaps were divided into three categories by cluster analysis (Fig. 2), which was consistent with the result of the PCA (Fig. 3). The first group (Gaps F–J) included the large gaps, whereas gap size in the second and third groups (Gaps A–C, E and D) was small. These results were consistent with the results of AWCD and the microbial functional diversity (Fig. 1), indicating that gap size apparently affected the microbial community due to the environmental heterogeneity caused by the change of illumination, temperature, soil moisture, soil available nutrients and understory vegetation.

The ability of soil microbes to use different C sources was strongly correlated with their community structure composition (Tian *et al.*, 2016). In the present study, the soil microbial communities used some of the carbohydrates (CHs), amino acids (AAs), amines (AMs) and carboxylic acids (CAs) to a greater extent than other C sources. Thus, the variance loaded on PC1 seemed to be dependent on the carbohydrates (CHs), amino acids (AAs), amines (AMs) and carboxylic acids (CAs). For PC2, the most correlated substrates belonged mainly to CHs and AAs.

Conclusion

In this study, the effect of gap size on soil microbial community functional diversity was observed. The results showed that three years after ice storm damage, the AWCD and the Shannon index of soil microbial diversity differed significantly between gaps with different sizes in the *C. lanceolata* stand. Small gaps had higher AWCD and Shannon index of soil microbial diversity. Furthermore, thirty-one sole C sources on Biolog EcoPlates were divided into three groups by PCA, indicating that carboxylic acids, sugars and amino acids were main C sources used by soil microorganisms.

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