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ORIGINAL PAPER

Variation of soil enzyme activity and microbial biomass in poplar plantations of different genotypes and stem spacings

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Abstract To improve the productivity of poplar plantations, a field experiment of split-plot design with four tree spacings and three poplar clones was established, and four soil enzyme activities and microbial biomass were monitored in the trial. Soil enzyme activities, in most cases, were significantly higher in topsoil (0–10 cm) than in lower horizons (10–20 cm). Soil cellulase, catalase and protease activities during the growing season were higher than during the non-growing season, while invertase activity followed the opposite trend. Soil invertase, cellulase and catalase activities varied by poplar clone but soil protease activity did not. Cellulase and protease activities in the plantation at 5 × 5 m spacing were significantly higher than in the other spacings. The highest catalase activity was recorded at 6 × 6 m spacing. At the same planting density, invertase activity was greater in square spacings than in rectangular spacings. Soil microbial biomass was also significantly affected by seedling spacing and poplar clone. The mean soil MBC was significantly lower in topsoil than in the lower horizon, while MBN showed the opposite pattern. Significantly positive correlations were observed among soil cellulase, protease and catalase activities ($p < 0.01$), whereas soil invertase activity was negatively and significantly correlated with cellulase, protease and catalase activities ($p < 0.01$). Soil microbial biomass and enzyme activities were not correlated except for a significantly negative correlation between soil MBC and catalase activities. Variations in soil enzyme activity and microbial biomass in different poplar plantations suggest that genotype and planting spacing should be considered when modeling soil nutrient dynamics and managing for long-term site productivity.

Keywords Microbial activity · Nutrient availability · Planting density · Poplar clone · Seasonal variation

Introduction

Soil enzymes are the product of biological activities, and can reflect the circumstances of biological metabolism and substance transformation, and characterize the direction and the grade of biochemical processes. Activities of soil enzymes have been reported to be correlated with some soil properties including soil temperature, moisture contents, nutrient status, organic matter contents, and soil pH (Venkatesan and Senthurpandian 2006; Bobul'ská et al. 2015). To be soil catalysts, soil enzymes participate in many important biochemical processes, accelerating soil metabolism, and promoting the circulation of nutrient elements. Previous studies have shown that soil enzyme activities are correlated with microbial activity, soil carbon (C) availability, mineral nitrogen (N) availability, soil

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microbial biomass C (MBC) and soil respiration (Wallenstein et al. 2009; Wang et al. 2014). Some studies showed strong correlation between soil organic carbon and soil enzymatic activity, revealing soil organic matter participated in influencing the stability of enzymes (Gavrilenko et al. 2011; Raiesi and Riahi 2014). Therefore, soil enzyme activity has been reported to be an index of soil activity and soil productivity (Tang et al. 2007), and an early indicator of natural and anthropogenic disturbances (Hinojosa et al. 2004).

Soil microbial biomass is also an important indicator of soil fertility. As the active component of the soil organic pool, soil microbes can mediate the transformation of biogenic nutrients (N, P and S) between inorganic and organic components (Bolat 2014). Moreover, plants may directly or indirectly impact soil nutrient availability by influencing soil enzyme activities through releasing extracellular enzymes and/or altering microbial communities that are major contributors to enzyme activities in soil (Tabatabai 1994; Yang et al. 2007). Research has focused on agricultural ecosystems and less is known of the relationship between soil microbial biomass and enzyme activities in forest ecosystems.

Plant growth is affected by plant nutrient acquisition, which is closely coupled with microbial activities. Fast-growing, high-production, short-rotation poplar plantations have been widely planted in China in recent years, leading to concerns for long-term maintenance of site productivity. Soil microbial activities are correlated with site quality and poor site conditions limit the growth and ecological function of newly established poplar plantations (Fang et al. 2007, 2008). However, further studies are needed to better understand the vertical and seasonal dynamics of soil enzyme activities and microbial biomass as well as the relationships between soil enzyme activities and microbial biomass. In this study, we explored the vertical and seasonal variations of four soil enzyme activities and microbial biomass among three poplar clones and four planting spacings. Here we discuss correlations between soil enzyme activities and microbial biomass. The aims of this study were to guide selection of appropriate poplar clones and to identify optimum planting spacings at a specific site. We hoped to provide a scientific basis for maintaining the long-term productivity of poplar plantations.

Materials and methods

Site description and plantation establishment

Our research was conducted at Chenwei forest farm (35°15′N, 118°18′E) in Sihong County, northern Jiangsu Province. Soils at this location were formed on fine sediments of Hongzhe Lake and have a clay-loam texture (Table 1, based on the International Union of Soil Science classification system).

Poplar plantations were established in March 2007 with one-year-old seedlings. A split-plot randomized block design was adopted to test four stem spacings and three poplar clones. Stem spacings were 6 × 6 m, 4.5 × 8 m, 5 × 5 m, and 3 × 8 m, which included two rectangles and two squares. Spacings 4.5 × 8 m and 6 × 6 m were of the same density (278 stems ha^{-1}), as were spacings of 3 × 8 m and 5 × 5 m (400 stems ha^{-1}). The three poplar clones were Nanlin-95, Nanlin-895 and Nanlin-797, which are hybrids of clone I-69 (*Populus deltoides* Bartr. cv. 'Lux') × clone I-45 (*P.* × *euramericana* (Dode) Guineir cv. 'I-45/51'). We tested seven treatments (four spacings: 6 × 6 m, 4.5 × 8 m, 5 × 5 m, and 3 × 8 m of clone Nanlin-95 and three clones (Nanlin-95, Nanlin-895, and Nanlin-797 at the spacing of 6 × 6 m). We analyzed vertical and seasonal variation in soil enzyme activities and microbial biomass.

Soil sampling and analysis

Soil samples were collected in the middle of March, June, September and December 2014, respectively. Soil enzyme activity was recorded at each of these four sampling times, while soil microbial biomass was recorded only in September and December 2014. Five sampling points were randomly selected for the measurement at each plot. Soil samples were taken at two layers (0–10, 10–20 cm) after removing the surface litter and plants. After collection, soil samples were sealed in plastic bags and placed in a preservation box cooled by ice during transport to the lab. Each soil sample was air-dried, sieved to pass a 2-mm screen, and stored for the analysis of soil physicochemical properties and soil enzyme activities.

Invertase and cellulase activity in the soil were measured using the 3,5-dinitrosalicylic acid monohydrate colorimetric method (Frankeberger and Johanson 1983; Fang et al. 2010) and were expressed as the amount of glucose released when 1.0 g substrate was cultured under 37 °C for 24 and 72 h (mg glucose g^{-1} d^{-1}).

Protease activity was assayed using the method described by Liu et al. (2012) and the results were expressed as mg NH_3–N g^{-1} d^{-1}. Catalase activity was assayed by back-titrating residual H_2O_2 with $KMnO_4$ (Roberge 1978). The reacted amount of 0.02 mol L^{-1} $KMnO_4$, calculated per gram of dry soil, was used to express the activity of catalase.

Fumigation and microbial biomass was measured following the procedure described by Joergensen and Brookes (1990). Microbial organic C (MOC) in the K_2SO_4 soil extracts was measured by an automated uv-persulphate

Table 1 Soil physical and chemical properties at the study site

Soil layer (cm)	Bulk density (g cm^{-1})	pH	Total N (g kg^{-1})	Total P (g kg^{-1})	Total K (g kg^{-1})	Total Ca (g kg^{-1})	Total Mg (g kg^{-1})
0–10	1.31	7.12	0.77	0.41	9.03	2.06	3.00
10–20	1.37	7.41	0.50	0.31	8.71	1.95	2.97

oxidation method. Microbial biomass C (MBC) was calculated from MBC = 2.22 MOC, where MOC = [(C extracted from fumigated soil)-(C extracted from non-fumigated soil)]. Ninhydrin–N in the K_2SO_4 soil extracts was measured according to the method described by Joergensen and Brookes and was used to calculate microbial biomass N (MBN) (MBN = 5.0 ninhydrin–N).

Statistical analyses

All results are reported here as mean ± standard deviation. A General Linear Model (GLM) One-way ANOVA was used to test vertical and seasonal variations of soil enzyme activities and microbial biomass by poplar clone and stem spacing. Duncan's test was used to differentiate means. All statistical analyses were carried out at $p < 0.05$. Associations among different enzyme activities and soil microbial biomass were tested using Pearson's correlation analysis. All statistical analyses were performed using SPSS 19.0 (SPSS for Windows, Version 19.0, Chicago, IL, USA).

Results

Variation in soil enzyme activities

Poplar clones significantly affected soil enzyme activities in the two soil layers (Fig. 1). The highest annual mean values for invertase, cellulase and catalase activities were observed in Nanlin-895, with 4.21 mg glucose releases g^{-1} d^{-1}, 1.67 mg glucose releases g^{-1} d^{-1} and 3.58 mL 0.02 mol L^{-1} $KMnO_4$ g^{-1} d^{-1} in the topsoil, respectively. The highest protease activity was recorded in Nanlin-797, reaching 5.13 mg NH_3–N g^{-1} d^{-1} in the topsoil. Compared to the values for Nanlin-895 (averaged across two soil layers), the activities of invertase, cellulase and catalase in Nanlin-95 and Nanlin-797 were lower by 3.8–19.5, 1.5–36.0 and 13.5–20.5%, respectively. Protease activity was 6.9% higher for Nanlin-797 and 15.3% lower for Nanlin-95.

Stem spacings significantly affected soil enzyme activities and MBC, but did not affect MBN (Fig. 2). The highest mean values of invertase, cellulase and protease activity were recorded at 5 × 5 m spacing, with 3.45 mg glucose releases g^{-1} d^{-1}, 1.87 mg glucose releases g^{-1} d^{-1} and 5.23 mg NH_3–N g^{-1} d^{-1} in the top soil, respectively. The highest catalase activity was recorded at 6 × 6 m spacing, reaching 2.98 mL 0.02 mol L^{-1} $KMnO_4$ g^{-1} d^{-1} in the topsoil. Cellulase activity in high-density stands (5 × 5 m and 3 × 8 m) was greater than in low-density stands (6 × 6 m and 4.5 × 8 m). Invertase activity in square-spaced stands (6 × 6 m and 5 × 5 m) was higher than in rectangular-spaced stands (4.5 × 8 m and 3 × 8 m) at the same planting density. Compared with the values recorded at 5 × 5 m spacing (averaged across two soil layers), cellulase and protease activity at 4.5 × 8 m, 3 × 8 m and 6 × 6 m spacings was lower by 16.4–19.2 and 5.1–16.2%, respectively. Invertase and catalase activity was higher by 5.2 and 8.9% for 6 × 6 m spacing and lower by 3.9–11.7 and 1.9–11.0% for the other two spacings, respectively.

Mean soil enzyme activity averaged across four seasons, varied between by soil depth (Figs. 1, 2). In most cases, soil enzyme activity was significantly higher in topsoil (0–10 cm) than in the lower horizon (10–20 cm). Catalase activity did not vary by stem spacing and protease activity did not vary by poplar clone. Soil enzyme activity in the 10–20 cm deep soil layer was 26.0% lower for invertase, 36.4% lower for cellulase, 14.3% lower for protease and 19.5% lower for catalase.

Variation in soil microbial biomass

Soil microbial biomass in the two soil layers varied significantly by poplar clone (Fig. 3). The highest annual mean value of MBC was recorded for Nanlin-95 at 289.37 mg kg^{-1} in the topsoil. The highest MBN value was recorded for Nanlin-895 at 78.97 mg kg^{-1} in the topsoil. Compared to values recorded for Nanlin-95 and averaged across two soil layers, mean MBC for Nanlin-895 and Nanlin-797 were lower by 14.6 and 27.6%, respectively, while mean MBN was higher by 35.0 and 12.2%, respectively.

The highest mean MBC (289.37 mg kg^{-1}) was recorded in the lower soil layer at 6 × 6 m stem spacing, whereas the highest mean MBN (61.84 mg kg^{-1}) was detected in topsoil of 5 × 5 m spacing (Fig. 4). Compared to the values recorded at 5 × 5 m spacing (averaged across two

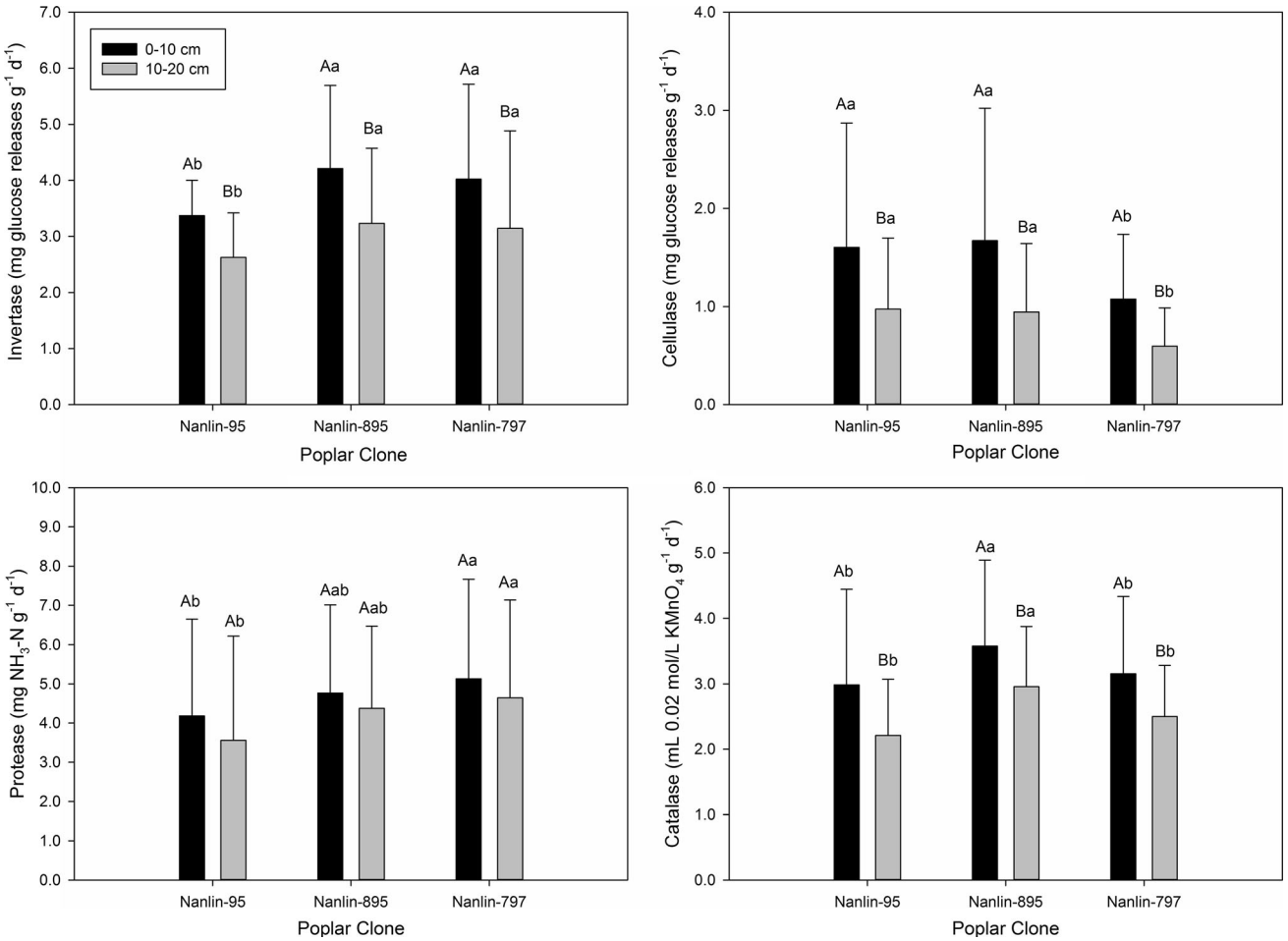

Fig. 1 Annual mean soil enzyme activity (averaged across four sampling times at 6 × 6 m spacing) for three poplar clones. Different capital letters indicate significant differences between two layers at the same time frame ($p < 0.05$), while small letters indicate significant differences among three poplar clones ($p < 0.05$)

soil layers), the mean values of MBC and MBN at the other 3 stem spacings were lower by 13.3–39.2 and 12.2–37.3%, respectively.

Mean soil MBC and MBN, averaged over two seasons, differed by soil depth (Figs. 3, 4). In most cases, a significant difference in MBC and MBN was detected between the topsoil (0–10 cm) and the lower layer (10–20 cm). But MBC did not vary by soil depth in the high-density plantations (5 × 5 m and 3 × 8 m). MBN was similar at the two soil depths in Nanlin-895 plantations. Mean soil MBC, averaged across September and December, was significantly lower in topsoil than in the lower layer, while MBN showed the opposite trend. Considering means for all four stem spacings and all three poplar clones, MBC in the lower soil layer was higher by 24.2% and MBN in the lower layer was lower by 28.1%.

Seasonal variation in microbial activity

Seasonal variation in soil enzyme activity was consistent across all poplar plantations (Fig. 5). In general, soil cellulase, catalase and protease activity during growing season was higher than during non-growing season. The trend for soil invertase activity was the opposite. A polynomial function best described the relationship between soil enzyme activities and sampling season, and all coefficients of determination (R^2) were significant at $p < 0.01$. The polynomial equations explained more than 64, 61, 70 and 36% of seasonal variation in invertase, cellulase, protease and catalase activity, respectively.

Patterns of seasonal variation in activity varied by enzyme (Fig. 5). Mean invertase activity, averaged across two soil layers, declined in the order of March > December > September > June, while mean cellulase activity declined in the order of September > June > March > December. Similar to cellulase activity, mean catalase activity peaked in September and

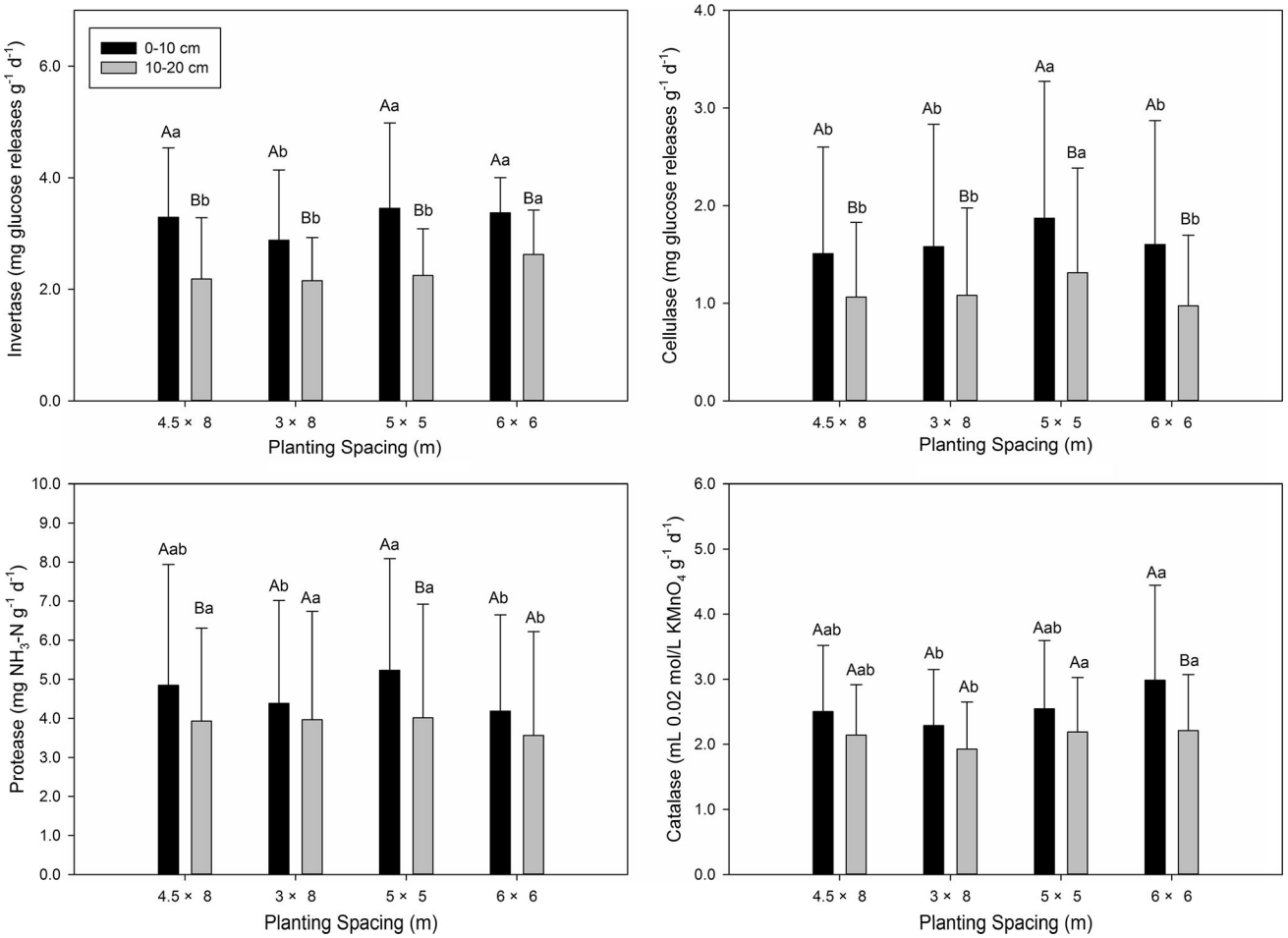

Fig. 2 Annual mean soil enzyme activity (averaged across four sampling times for clone Nanlin-95) by four stem spacings. Different capital letters indicate significant differences between two layers at the same time frame ($p < 0.05$), while small letters indicate significant differences between four stem spacings ($p < 0.05$)

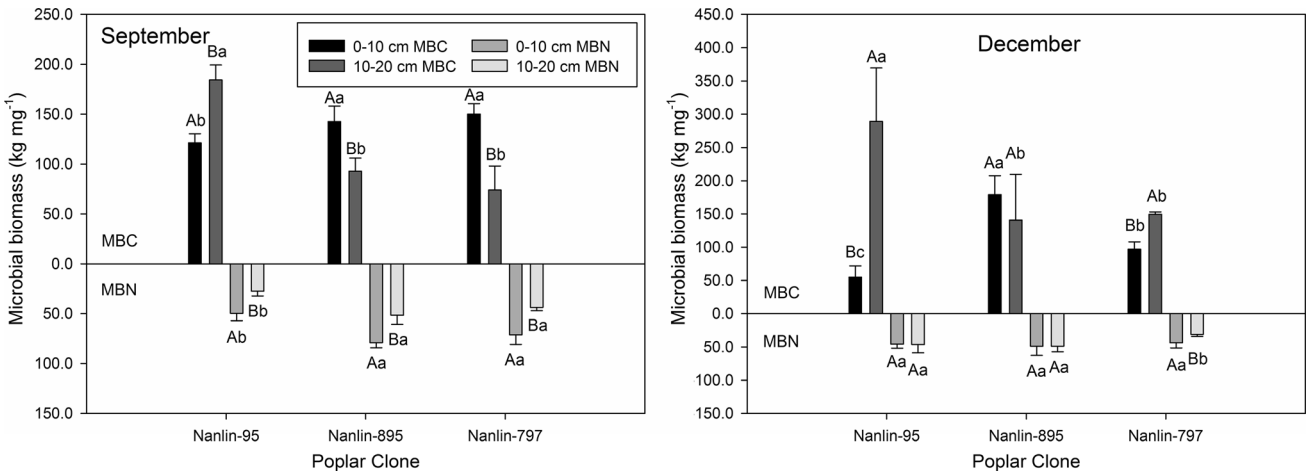

Fig. 3 Mean microbial biomass C and N by poplar clone. Different capital letters indicate significant differences between two layers in the same sampling month ($p < 0.05$), while small letters indicate significant differences among four stem spacings ($p < 0.05$)

was lowest in December. Mean protease activity declined in the order of September > December > June > March.

Mean soil MBC, averaged across two soil layers, declined from non-growing season (December) to growing

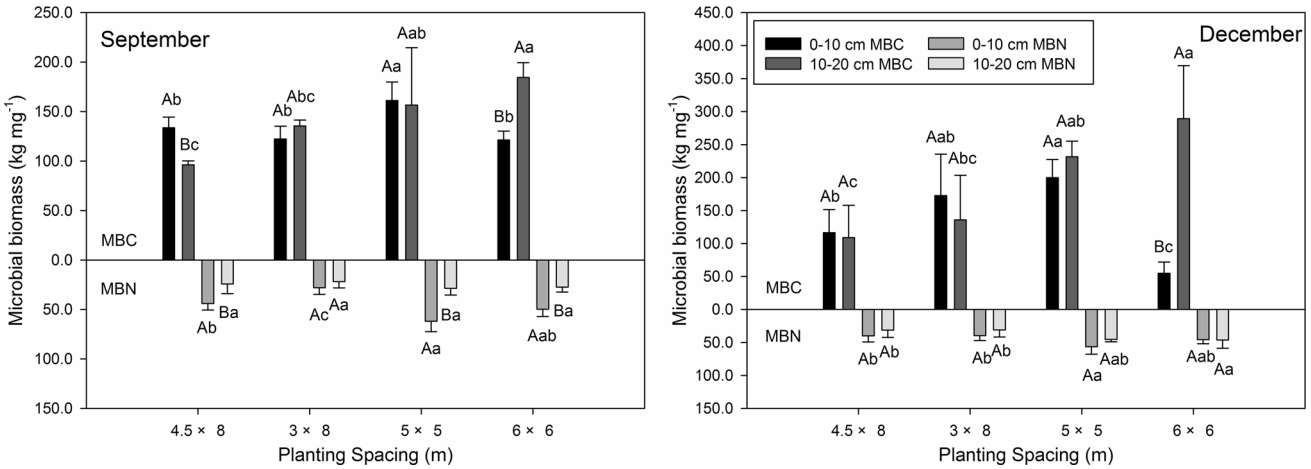

Fig. 4 Mean microbial biomass C and N among by stem spacing. Different capital letters indicate significant differences between two layers in the same sampling month ($p < 0.05$), while small letters indicate significant differences between four stem spacings ($p < 0.05$)

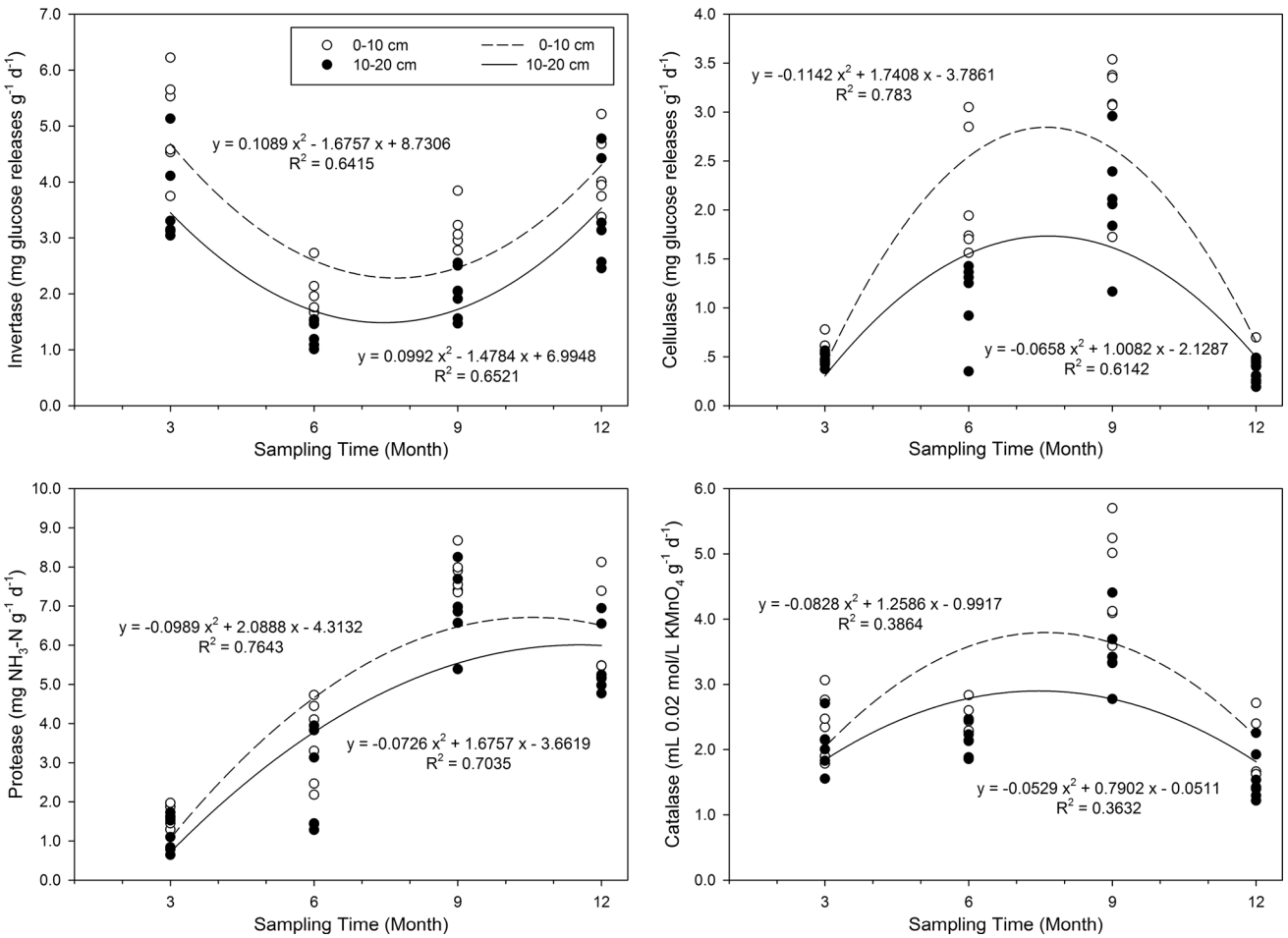

Fig. 5 Seasonal variation in soil enzyme activity by soil depth (n = 28)

season (September). The trend in mean soil MBN was the opposite. Compared with values recorded in September (averaged across two soil layers), mean soil MBC in December was 18.3% higher, while mean soil MBN was 1.4% lower.

Discussion

Soil enzyme activities and nutrient availability

Enzymes in soil ecosystems are produced by microorganisms and plants. Our results showed that the activity of soil invertase, cellulase, protease and catalase was higher in the topsoil (0–10 cm) than at greater depth, consistent with the results of previous studies (Venkatesan and Senthurpandian 2006; Senga et al. 2011; Bobuľská et al. 2015). High activity of enzymes in the top soil layer might be a result of the presence of greater plant root density and the decomposition of forest litter.

Soil enzyme activity is influenced by tree species and trends in the soil physicochemical environment and resource availability (Augusto et al. 2002; Chodak and Niklińska 2010). Wang et al. (2013a) reported that soil invertase activity in a *Cunninghamia lanceolata* plantation was higher than in a *Pinus massoniana* plantation, while soil cellulase and catalase activities were significantly higher in a *P. massoniana* plantation than in a *Michelia macclurei* plantation. Our results indicated that the activities of invertase, cellulase, protease and catalase differed by poplar clone. This suggests that variation in soil enzyme activity depends on not only specific tree species but also on genotypes of tree species. Our results also showed that in most cases soil enzyme activities in high-density stands (5 × 5 m and 3 × 8 m) were higher than in low-density stands (6 × 6 m and 4.5 × 8 m) (Fig. 2), in agreement with Tian et al. (2013). The main reason could be that stem spacing influenced environment factors, understory diversity and litter quality.

Activity of soil cellulase, protease and catalase during the growing season were greater than during the non-growing season (Fig. 4), similar to the pattern reported by Li et al. (2008) for activities of invertase and catalase in *Pinus tabulaeformis* stands, and by Wang et al. (2013b) for cellulase and catalase activities in subtropical forests of China. Our results did not, however, support the hypothesis that enzyme activity peaks in months of high temperature (Burger and Kelting 1999; Criquet et al. 2000). This might be explained by the large amount of rainfall in summer at this research site.

Soil enzyme activity and nutrient availability are key parameters contributing to soil fertility and quality, and consequently impacting plant growth and forest productivity. Soil enzyme activities are believed to be associated with the availability of C and N. Soil nutrient enrichment might enhance enzyme activity for microbial C acquisition (Sinsabaugh et al. 2005; Koyama et al. 2013. But enzyme activities for nutrient acquisition often decline under conditions of high nutrient availability because the microbial need for nutrient acquisition via the decomposition of organic N- and P-containing compounds is reduced (Allison and Vitousek 2005; Sinsabaugh 2010). Our study showed that soil enzyme activity was generally lower in low-density plantations than in high-density stands. This was probably caused by the microbial need for nutrient acquisition. This explanation is supported by Yan et al. (2015) who indicated that mean N nitrification rate and mineralization rates in low-density poplar plantations were higher than those in high-density stands at the same experimental site, confirming that soil enzyme activity is lower in low-density stands with high N availability. We recorded soil enzyme activity that was significantly higher during growing season, consistent with nutrient availability (Yan et al. 2015) where the inorganic N content in the growing season is higher than in the non-growing season due to higher microbial activity and nutrient turnover during the growing season (Schmidt et al. 1999).

Soil microbial biomass and microbial C/N ratio

The variation of microbial biomass with soil depth and season is an important component of its turnover, and thus was likely to have important consequences for nutrient dynamics, plant growth and ecosystem productivity (Wardle 1998; Smith and Paul 1990). Our results indicated that microbial biomass was significantly affected by poplar clones and stem spacings (Fig. 3). Microbial biomass was slightly higher in high-density stands (5 × 5 m and 3 × 8 m) than in low-density stands (6 × 6 m and 4.5 × 8 m). The reason is the extent of canopy closure affects the microclimatic properties of soils (Bolat 2014), which, in turn, affects microbial biomass. We documented higher microbial biomass during the non-growing season than in the growing season, similar to the results of Freppaz et al. (2014) for mid-alpine forest soils, Puissant et al. (2015) for mountain grassland soils and Tripathi et al. (2007) for Indian costal soils. However, our results were not consistent with those of Cochran et al. (1989) for Alaskan forest soils, where soil microbial biomass was higher during the growing season than in the non-growing season.

The soil microbial C/N ratio often defines the structure of the microbial community (Bolat 2014). Previous studies have shown that if the microbial C/N ratio is high (10–12), then the proportion of fungi in the microbial community will be greater. In contrast, a low microbial C/N ratio (3–5) reflects the predominant proportion of bacteria in the microbial biomass (Jenkinson and Ladd 1981; Joergensen et al. 1995; Devi and Yadava 2006). Our study indicated that the microbial C/N ratio ranged from 1.86 to 4.37 and 4.10 to 6.55 at soil depths of 0–10 and 10–20 cm,

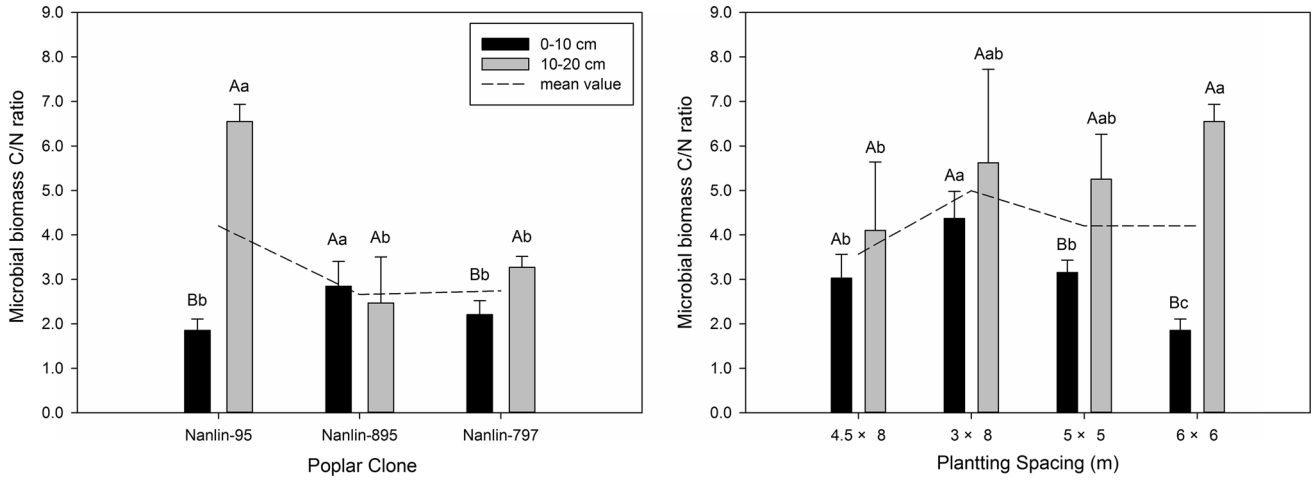

Fig. 6 Mean ratios of microbial biomass C to N among three poplar clones and four planting spacings. Different capital letters indicate significant differences between two soil depths at the same sampling month ($p < 0.05$), while small letters indicate significant differences between four stem spacings ($p < 0.05$)

respectively (Fig. 6). This suggests that bacteria dominate the microbial biomass at our research site.

Correlation between soil enzyme activities and microbial biomass

Several indices based on soil enzyme and microbial activities have been developed to assess soil fertility, soil functionality and the sustainability of agricultural practices (Caldwell 2005; Fang et al. 2010). Many studies showed that soil enzyme activities were correlated with labile organic matter, dissolved organic carbon, microbial biomass carbon, total N, P, K, soil pH and other indexes (Venkatesan and Senthurpandian 2006; Li et al. 2008; Fang et al. 2010; Bobul'ská et al. 2015). In the present study, we did not analyze the relationships between enzyme activity and soil physical and chemical properties but the relationships between soil enzyme activity and microbial biomass were analyzed (Table 2).

We documented significant, positive correlation among soil cellulase, protease and catalase activity ($p < 0.01$, Table 2), whereas soil invertase activity was negatively and significantly correlated with cellulase, protease and catalase activity ($p < 0.01$). These results are consistent with the results of most researches (Wang et al. 2013a). The significant correlation among cellulase, protease and catalase activity suggests that these enzymes have similar origin and C source in soil (Wang et al. 2013b).

The correlations between microbial biomass and enzyme activity are influenced by many factors, and results reported are also inconsistent with different researchers (Böhme et al. 2005; Fang et al. 2013; Lü et al. 2013; Liu et al. 2014). In most cases, soil microbial biomass and enzyme activities were not correlated in this study ($p < 0.05$, Table 2). We did document significantly negative correlation between soil MBC and catalase activity, contrary to the results of Zhang et al. (2011) and Yan et al. (2012). This was probably related to the population dynamics of soil microorganisms. Low values of the soil microbial C/N ratio suggest a relatively small proportion of fungi in the microbial biomass at our research site.

Table 2 Correlation coefficients between microbial biomass and enzyme activity at 0–20 cm soil depth in poplar stands (n = 36)

Variables	MBN	MBC/N	Invertase	Cellulase	Protease	Catalase
MBC	0.161	**0.439****	0.107	− 0.198	− 0.134	− **0.422****
MBN		− **0.706****	0.278	− 0.124	0.032	0.272
MBC/N			− 0.253	0.174	0.004	− 0.282
Invertase				− **0.691****	− **0.669****	− **0.398***
Cellulase					**0.535****	**0.768****
Protease						**0.527****

* Indicate significance at $p < 0.05$ (2-tailed); ** indicate significance at $p < 0.01$ (2-tailed)

Conclusions

Soil enzyme activity and microbial biomass varied by stem spacing and poplar genotype. Higher activities of invertase, cellulase, protease, catalase and soil MBC were observed in the topsoil, whereas MBN was greater in deeper soil. Seasonal variations of cellulase, catalase and protease showed a trend of higher activity during the growing season and lower activity in the non-growing season, whereas invertase activity was the reverse of this trend. Poplar clones significantly influenced soil invertase, cellulase, catalase activities and soil microbial biomass, but did not increase protease activity. The highest soil activities of cellulase and protease and MBN were recorded in the stand planted to 5 × 5 m spacing. The highest catalase activity and MBC were recorded at 6 × 6 m spacing. Significantly positive correlations were documented among soil cellulase, protease and catalase activities ($p < 0.01$), whereas soil invertase activity was negatively and significantly correlated with cellulase, protease and catalase activity ($p < 0.01$). Overall, soil microbial biomass was not correlated with enzyme activity ($p < 0.05$), except that a significantly negative correlation was observed between soil MBC and catalase activity. To obtain high stem biomass production, our results suggest that Nanlin-95 and Nanlin-895 clones with stem spacing of 5 × 5 m could be considered when modeling soil nutrient dynamics and managing for long-term site productivity at the similar sites.

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