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ORIGINAL PAPER

Rhizosphere and bulk soil enzyme activities in a *Nothotsuga longibracteata* forest in the Tianbaoyan National Nature Reserve, Fujian Province, China

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Abstract The rhizosphere, distinct from bulk soil, is defined as the volume of soil around living roots and influenced by root activities. We investigated protease, invertase, cellulase, urease, and acid phosphatase activities in rhizosphere and bulk soils of six *Nothotsuga longibracteata* forest communities within Tianbaoyan National Nature Reserve, including *N. longibracteata* + either *Phyllostachys pubescens*, *Schima superba*, *Rhododendron simiarum*, *Cunninghamia lanceolata*, or *Cyclobalanopsis glauca*, and *N. longibracteata* pure forest. Rhizosphere soils possessed higher protease, invertase, cellulase, urease, and acid phosphatase activities than bulk soils. The highest invertase, urease, and acid phosphatase activities were observed in rhizosphere samples of *N. longibracteata* + *S. superba*. Protease was highest in the *N. longibracteata* + *R. simiarum* rhizosphere, while cellulase was highest in the pure *N. longibracteata* forest rhizosphere. All samples exhibited obvious rhizosphere effects on enzyme activities with a significant linear correlation between acid phosphatase and cellulase activities ($p < 0.05$) in rhizosphere soils and between protease and acid phosphatase activities ($p < 0.05$) in bulk soils. A principal component analysis, correlating 13 soil chemical properties indices relevant to enzyme activities, showed that protease, invertase, acid phosphatase, total N, and cellulase were the most important variables impacting rhizosphere soil quality.

Keywords Bulk soil · Enzyme activities · Rhizosphere soil · Tianbaoyan National Nature Reserve · *Nothotsuga longibracteata*

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Introduction

Soil enzymes, acting as biological catalysts, can accelerate chemical reactions involving soil organic matter (Jin et al. 2009). Because soil enzymes are main regulators of the biochemical processes within the soil environment, they play a critical role in the development of soil characteristics. Soil characteristics are determined by the interplay between enzymes and substances produced by a wide range of animals, plants, microorganisms, and their residues (Zhang et al. 2005). Soil enzymes, which are intimately associated with decomposition of organic matter within ecosystems, nutrient cycling, and energy transfer, greatly impact resulting environmental quality (Johansson et al.

2000; Böhme et al. 2005; Jin et al. 2009; Kaiser et al. 2010; Burke et al. 2012). Therefore, soil enzyme activities can be used as an evaluation index of microbial activity and soil fertility (Monreal and Bergstrom 2000; Alvarez and Guerrero 2000). Changes in enzymes are known to alter the availability of nutrients for uptake by plants, and these changes are potentially sensitive indicators of soil quality (Albiach et al. 2000; Aon et al. 2001; Aon and Colaneri 2001; Sinsabaugh et al. 2009). Therefore, there is practical significance to research soil enzyme activities, especially the impact of rhizosphere soil enzymes on the mechanisms that drive ecosystem degradation and restoration (Nausch and Nausch 2000; Fioretto et al. 2001).

The rhizosphere is a special ecological zone that is impacted by interactions between plants, soil, and microorganisms (Orwin et al. 2010; De Graaff et al. 2010; Bell et al. 2014). Currently, a highly active area of biochemical research, the rhizosphere is an important site of material cycling and energy flow within the soil. Because soil properties depend on secretion of various organic substances and absorption of unbalanced nutrients by tree roots, changes in soil properties within the rhizosphere are early indicators of changes in tree roots. Because the physiological activities of tree roots are determined by their own genetic characteristics and because activities vary greatly between the different developmental stages of trees, the properties of rhizosphere soil are affected directly by changes in tree root characteristics as a forest changes with time (Kardol, et al. 2010; Sanaullah et al. 2011).

Nothotsuga longibracteata (W.C. Cheng) Hu ex C.N. Page is a relict tree species endemic to China, having originated in the Tertiary Period, belonging to the genus *Nothotsuga* in the family Pinaceae. It is mainly distributed within subtropical mountain areas in southern China, including Fujian, Jiangxi, Hunan, Guizhou, Guangdong, and Guangxi Provinces. Nanling Mountain and the Daiyun Mountains are the main distribution areas of *N. longibracteata*, and trees mainly exhibit a patchy distribution tendency (Qiu et al. 2013). This species plays a crucial part in the promotion of forest succession, maintenance of balance and stability of ecosystems, and water conservation (You et al. 2013b, c). The distribution area of *N. longibracteata* forest is 186.7 hm^2 in the Tianbaoyan National Nature Reserve. The primary area of pure *N. longibracteata* forest is 20 hm^2, and this forest community is the largest area of *N. longibracteata* pure forest in China (Xiao et al. 2012). The community is composed of large areas of primeval forest and has vital significance for researching ecosystem responses to global climate changes (You et al. 2013a).

The current study investigated protease, invertase, cellulase, urease, and acid phosphatase activities of rhizosphere and bulk soils from six different *N. longibracteata* forest communities within the Tianbaoyan National Nature Reserve. The forest types included five mixed forest types (*N. longibracteata* + *Phyllostachys pubescens* forest, *N. longibracteata* + *Schima superba* forest, *N. longibracteata* + *Rhododendron simiarum* forest, *N. longibracteata* + *Cunninghamia lanceolata* forest, and *N. longibracteata* + *Cyclobalanopsis glauca* forest) and one pure forest (*N. longibracteata* pure forest).

Materials and methods

Site description for sample collection

The study site is located in the Tianbaoyan National Nature Reserve (25°50′51″–26°01′20″N, 117°28′3″–117°35′28″E), Sanming City, Fujian Province of China (Fig. 1), and covers a total area of 11,015 hm^2. The altitudinal gradient of Tianbaoyan Reserve is from 580 to 1604 m and is within the Daiyun Mountain Range. The Tianbaoyan National Nature Reserve has a mid-subtropical oceanic monsoon climate with a mean annual temperature of 15 °C and a frost-free period of about 290 days. The extreme high temperature is 40 °C and extreme low is −11 °C. Annual average precipitation is 2039 mm, occurring mostly between May and September. Mean annual relative humidity is greater than 80%. The reserve has four distinct seasons with a warm and humid climate, where the light, heat, and water conditions are sufficient for forests growth. Devonian and Jurassic sedimentary rocks and granite are exposed in the reserve. Upland red, zonal soils occur below 800 m asl. Upland yellowish soils occur between 800 and 1350 m asl and upland yellow soils occur above 1350 m asl. There is abundant species diversity in the reserve, retaining a large number of natural *R. simiarum*, *N. longibracteata*, and *Cryptomeria japonica* forests. All the three types of forest communities are of high conservation value.

Procedure for soil sampling

All soil samples were collected from the Tianbaoyan National Nature Reserve in July 2012 from a depth of 0–20 cm within the topsoil layer. Samples for this study were collected from six *N. longibracteata* forests within Tianbaoyan National Nature Reserve (*N. longibracteata* + *P. pubescens*, *N. longibracteata* + *S. superba*, *N. longibracteata* + *R. simiarum*, *N. longibracteata* + *C. lanceolata*, *N. longibracteata* + *C. glauca*, and pure *N. longibracteata* forest). Six similar stands were chosen from the forests as study sites; each stand contained three plots per stand with each plot defined by dimensions 20 × 30 m. Longitude and latitude, altitude, slope, slope aspect, and crown coverage in each plot were recorded. The site

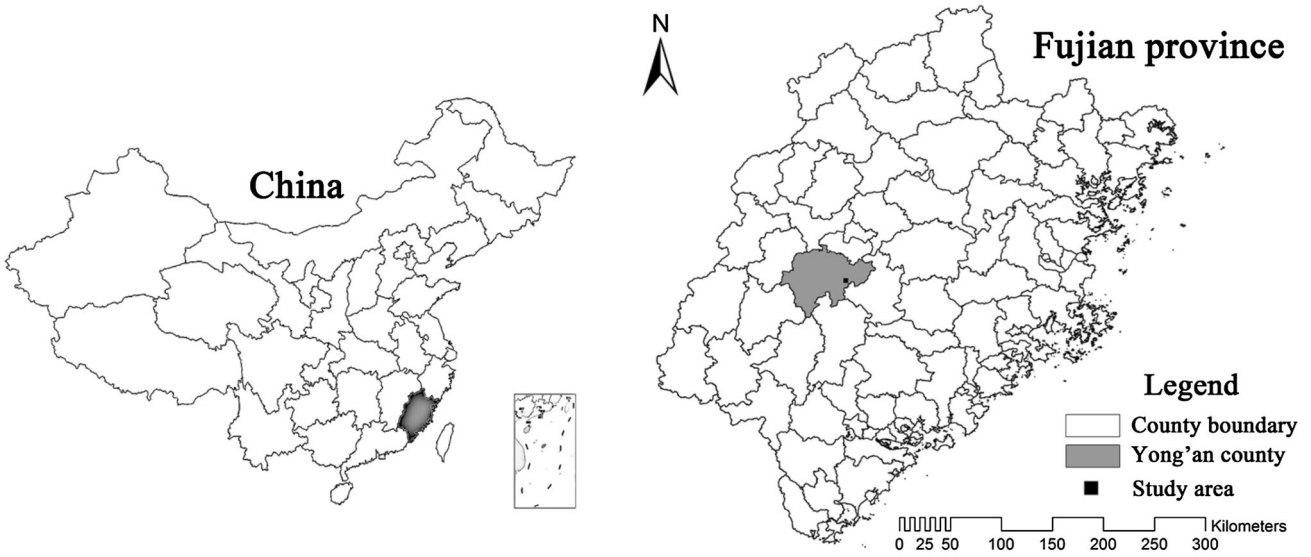

Fig. 1 Geographic location of the Tianbaoyan National Nature Reserve

characteristics of the forest types studied are listed in Table 1. Based on the measurement of all individual trees within the population of each plot, three average trees were chosen as standard trees for rhizosphere soil sampling. Soil adhering to fine roots <2 mm in diameter was defined as rhizosphere soil (Garcia et al. 2005). The remaining soil was defined as bulk soil. All soil samples were collected from a depth of 0–20 cm of the topsoil layer. The rhizosphere soil of *N. longibracteata* was separated from bulk soil by shaking the excavated fine root fragments gently. In each plot, five randomly located soil cores were taken from soil near three average trees. The soil samples were immediately mixed into a single sample for each plot. Root fragments remaining in the rhizosphere and bulk were carefully removed with sterilized forceps. Samples were then air-dried for 10 days at room temperature until they achieved constant mass. Samples were then used for soil enzyme assays.

Enzyme assays

Protease activity was measured according to Zhang et al. (2005). Briefly, 4 g of air-dried soil was incubated for 24 h at 30 °C with 20 mL of 1% (w/v) casein and 1 mL of toluene, then 2 mL of 0.1 mol L^{-1} sulfuric acid and 12 mL of 20% (w/v) sodium sulfate were added and the suspension centrifuged for 15 min (6000 rpm). The amino nitrogen released was reacted with 1 mL 2% (w/v) ninhydrin, and the soil suspension was heated in a boiling-water bath for 10 min, and the absorbance read at 500 nm.

Invertase activity was measured by incubating 5 g of air-dried soil for 24 h at 37 °C with 15 mL of 8% (w/v) sucrose, 5 mL of phosphate buffer at pH 5.5 and 5 drops of toluene. The glucose released was reacted with 3,5-dinitrosalicylic acid, and absorbance measured at 508 nm (Zhang et al. 2005).

Cellulase activity was measured by adding 1 mL of phosphate buffer at pH 5.5 and 0.3 mL of toluene to 5 g of each soil sample. Then 3 mL of 3,5-dinitrosalicylic acid was added, and the soil suspension was heated in a boiling water bath for 5 min. Next, each soil sample was cooled under running water for 3 min. The glucose released was reacted with the 3,5-dinitrosalicylic acid, then measured at 540 nm (Zhang et al. 2011).

Urease activity was assayed by incubating 5 g of air-dried soil with 1 mL of toluene, 10 mL of 10% (w/v) urea solution, and 20 mL of citrate buffer at pH 6.7 for 24 h at

Table 1 Site characteristics of the studied forest communities

Forest types	Latitude and longitude	Slope (°)	Slope aspect	Altitude (m asl)	Canopy coverage (%)
N. longibracteata + *P. pubescens*	25°55′22.2″N, 117°32′22.9″E	15	WN30°	1125	85
N. longibracteata + *S. superba*	25°55′24.3″N, 117°32′22.5″E	20	WS15°	1180	80
N. longibracteata + *R. simiarum*	25°55′30.2″N, 117°32′54.7″E	25	ES30°	1232	90
N. longibracteata + *C. lanceolata*	25°55′29.8″N, 117°32′54.3″E	25	ES	1287	85
N. longibracteata + *C. glauca*	25°55′22.3″N, 117°32′58.4″E	15	EN20°	1370	90
Pure *N. longibracteata* forest	25°55′25.3″N, 117°33′09.5″E	10	WN10°	1520	85

37 °C. Amino nitrogen was measured at 578 nm, and results were expressed as NH_3 released in mg NH_3-N per 1 g of soil at 24 h (Zhang et al. 2011).

Acid phosphatase activity was determined as described by Zhang et al. (2005). Air-dried soil (5 g) was incubated for 24 h at 37 °C with 2.5 mL toluene and 20 mL 0.5% (w/v) disodium benzene phosphate dissolved in acetate buffer at pH 5. The phenol released was measured at 510 nm and results expressed as milligrams phenol per 1 g of soil at 24 h. All absorbances were measured using a UV20600 Unicam UV–Vis spectrometer (Unicam, USA).

Statistical analyses

All reported results were averages of three replicates. Analysis of variance was used to detect whether the rhizosphere soil varied significantly relative to bulk soil. The least significant difference was used to compare means of the different enzyme activities measured ($p < 0.05$ and $p < 0.01$). A principal component analysis (PCA) was used to analyze most of the variance in the data after reducing the number of variables to a few uncorrelated components. PCA was used to identify groups of soil chemical properties and correlate them to enzyme activities in this study. For the PCA, the data was standardized to zero mean and unit variance, and analysis was conducted using the correlation matrix. Statistical procedures were carried out using the SPSS 21.0 software package for Windows (IBM, USA). The rhizosphere effect is usually described using the ratio of values from the rhizosphere and non-rhizosphere zones, namely the rhizosphere effect value (R/S). PCA ordination was implemented using CANOCO software version 5 for Windows (Wageningen UR, Netherlands).

Results

Enzyme activities

Figure 2a–e shows protease, invertase, cellulase, urease, and acid phosphatase activities of both rhizosphere and bulk soils of the six *N. longibracteata* forest communities. It is clear that the rhizosphere had higher enzyme activities than bulk soils. The highest protease activities were found in both rhizosphere and bulk soils of *N. longibracteata* + *R. simiarum* forest (96.047 μg g^{-1} and 87.230 μg g^{-1}, respectively), and the lowest in bulk soils of *N. longibracteata* + *C. lanceolata* forest (92.613 μg g^{-1}) and rhizosphere of *N. longibracteata* + *P. pubescens* forest (85.523 μg g^{-1}) (Fig. 2a). Rhizosphere invertase activities varied from 16.927 mg g^{-1} in *N. longibracteata* + *S. superba* forest to 15.706 mg g^{-1} in *P. pubescens* forest; bulk soil invertase activities varied from 13.313 mg g^{-1} in *N. longibracteata* + *C. glauca* forest to 12.479 mg g^{-1} for *N. longibracteata* + *S. superba* forest (Fig. 2b). Cellulase activity tended to be the highest in the rhizosphere soil in the pure *N. longibracteata* forest; the lowest activity was observed in *N. longibracteata* + *C. lanceolata* forest. In bulk soil, the highest cellulase activity was observed in *N. longibracteata* + *S. superba* forest (0.861 mg g^{-1}) and the lowest in *N. longibracteata* + *R. simiarum* forest (0.744 mg g^{-1}) (Fig. 2c). Urease levels ranged from 0.794 mg g^{-1} in the rhizosphere soil of *N. longibracteata* + *S. superba* forest, to 0.677 mg g^{-1} in pure *N. longibracteata* forest, while these activities varied from 0.645 mg g^{-1} in bulk soils of *N. longibracteata* + *C. glauca* forest vs. 0.564 mg g^{-1} for *N. longibracteata* + *R. simiarum* forest (Fig. 2d, e shows that the maximum acid phosphatase activity was observed in the rhizosphere soil of *N. longibracteata* + *R. simiarum* forest (0.637 mg g^{-1}) and the minimum was observed in soil of pure *N. longibracteata* forest (0.504 mg g^{-1}), while in bulk soil the maximum was observed for *N. longibracteata* + *S. superba* forest (0.324 mg g^{-1}) and the minimum observed for *N. longibracteata* + *R. simiarum* forest (0.288 mg g^{-1}). There was a significant difference ($p < 0.05$) between the rhizosphere and bulk soils within the same forest. The rhizosphere effect values of all enzyme activities in all six forests were all >1, indicating that rhizosphere effects were obvious.

Relationships among enzyme activities in rhizosphere and bulk soils

The canonical correlation analysis elucidated the relationships among rhizosphere soil enzyme activities of different *N. longibracteata* forests within the Tianbaoyan National Nature Reserve (Table 2). There were significant linear correlations between acid phosphatase and protease activities ($p < 0.01$) and acid phosphatase and cellulase activities ($p < 0.05$). However, no significant relationships were found among other rhizosphere soil enzyme activities.

Table 3 shows the canonical correlation analysis among enzyme activities in bulk soils of the six *N. longibracteata* forests. There were significant linear correlations among bulk soil enzyme activities between protease and acid phosphatase activities ($p < 0.05$) and between invertase and cellulase activities ($p < 0.01$). Significant relationships were not found among other enzyme activities.

Principal component analysis

A partial form of PCA was used to estimate the importance of properties variables in the grouping of the studied fields. The data set of rhizosphere and bulk soil chemical properties and enzyme activities in different *N. longibracteata*

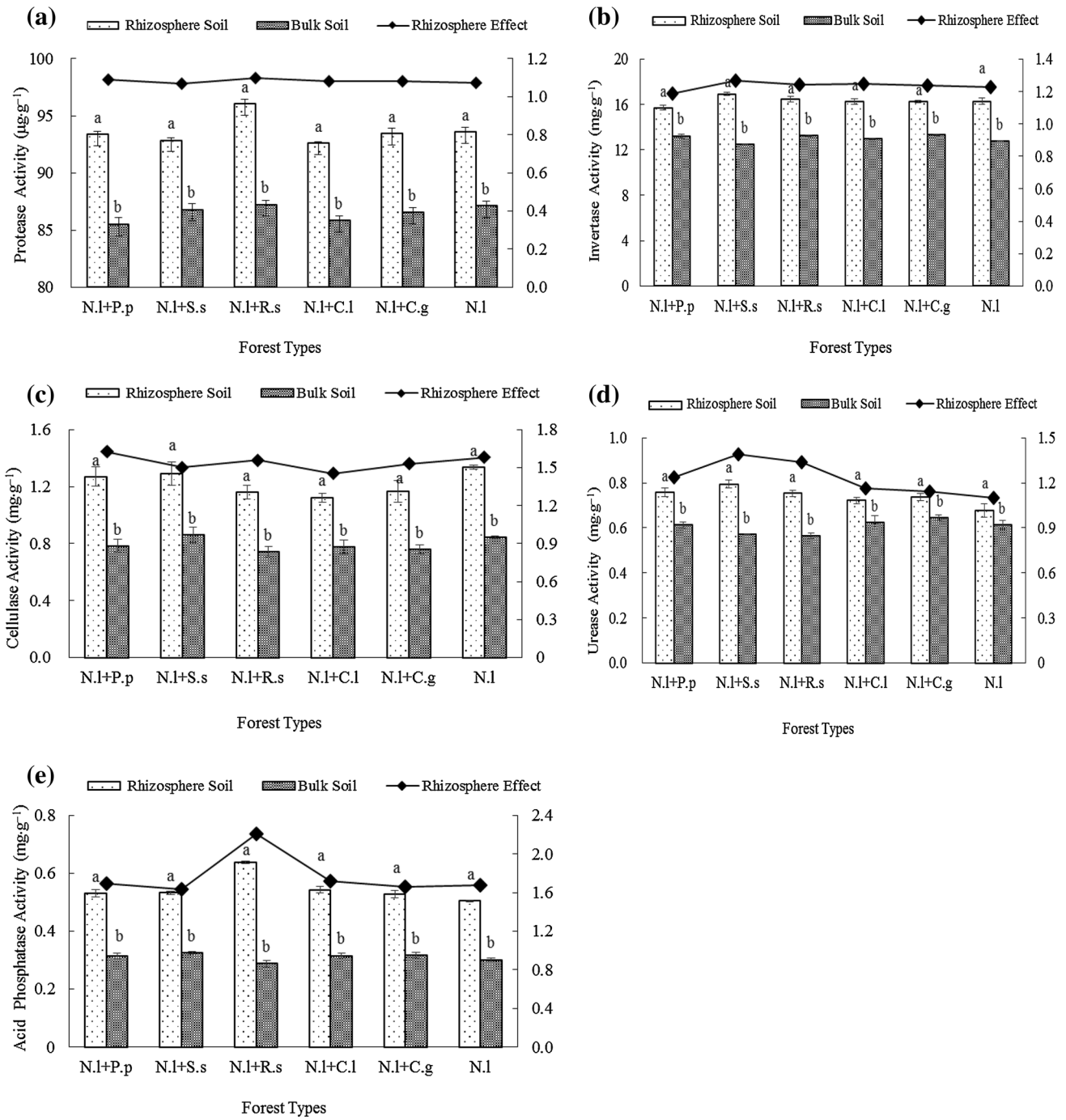

Fig. 2 Comparison of protease (**a**), invertase (**b**), cellulase (**c**), urease (**d**), acid phosphatase (**e**) activities (mean ± SE, $n = 6$) in rhizosphere and bulk soils of different *N. longibracteata* forest types. Notes: N.l + P.p: *N. longibracteata* + *P. pubescens* forest; N.l + S.s: *N. longibracteata* + *S. superba* forest; N.l + R.s: *N. longibracteata* + *R. simiarum* forest; N.l + C.l: *N. longibracteata* + *C. lanceolata* forest; N.l + C.g: *N. longibracteata* + *C. glauca* forest; N.l: pure *N. longibracteata* forest; different letters denote significant differences between rhizosphere and bulk soil in the same forest ($p < 0.05$)

forests was analyzed using the PCA. The rhizosphere and bulk soil chemical properties (pH, organic matter [OM], total N [TN], hydrolysable nitrogen [HN], total P [TP], available P [AP], total K [TK], and available K [AK]) were measured in 2014. Table 4 and Fig. 3 show that the first principal component (PC1) accounted for 61.233% of the total variance, and the properties with higher loading included protease, invertase, acid phosphatase, total N, and cellulase activities. The second principal component (PC2) accounted for 15.422% of the total variance and were

Table 2 Canonical correlation analysis among enzyme activities in rhizosphere soil of *N. longibracteata*

Enzyme	Protease	Invertase	Cellulase	Urease	Acid phosphatase
Protease	1.000				
Invertase	0.021	1.000			
Cellulase	−0.167	0.122	1.000		
Urease	0.011	0.312	−0.0810	1.000	
Acid phosphatase	0.838**	0.164	−0.445*	0.292	1.000

Significance at * $p < 0.05$ and ** $p < 0.01$ level. All other values are not significant at $p > 0.05$ level

Table 3 Canonical correlation analysis among enzyme activities in bulk soil of *N. longibracteata*

Enzyme	Protease	Invertase	Cellulase	Urease	Acid phosphatase
Protease	1.000				
Invertase	−0.217	1.000			
Cellulase	0.280	−0.725**	1.000		
Urease	−0.333	0.330	−0.121	1.000	
Acid phosphatase	−0.433*	−0.258	0.111	0.282	1.000

Significance at * $p < 0.05$ and ** $p < 0.01$ level. All other values are not significant at $p > 0.05$ level

positively related to total K and available K with negative loadings. The highly loaded properties under the third principal component (PC3) included available P. Other soil chemical properties and enzyme activities contributed relatively low loadings to the PCs (e.g. pH, organic matter, hydrolysable N, total P, and urease) indicating that their variability was much more muted and contributed less to the overall soil chemical properties and enzyme activities variability in the study area.

Table 4 Principal component analysis of rhizosphere and bulk soil chemical properties and enzyme activities of different *N. longibracteata* forest types

Variable	PC1	PC2	PC3
pH	−0.584	0.237	0.476
Organic matter	0.497	−0.515	−0.440
Total N	0.942	0.064	−0.061
Hydrolysable N	0.791	0.247	−0.288
Total P	0.818	−0.164	0.461
Available P	0.672	−0.060	0.678
Total K	0.474	0.851	−0.061
Available K	0.468	0.844	−0.084
Protease	0.958	−0.035	0.007
Invertase	0.952	−0.129	−0.139
Cellulase	0.937	0.083	0.019
Urease	0.833	−0.324	0.126
Acid phosphatase	0.948	−0.145	0.023
Eigenvalues	7.960	2.005	1.226
Variance (%)	61.233	15.422	9.434
Cumulative (%)	61.233	76.655	86.089

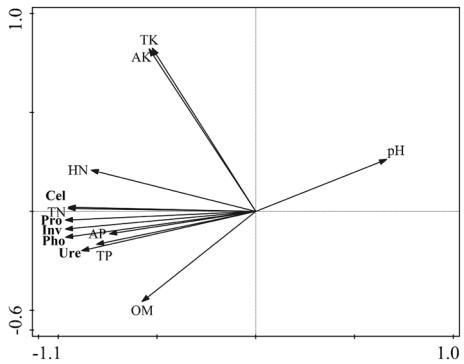

Fig. 3 Correlation of soil chemical properties and enzyme activities with PCA axes

Discussion

Soil enzymes are secreted by the residues of plant roots, soil animals, and their remains and microorganisms. They undoubtedly perform functions critical to the dynamics of nutrient transformation (Zhang et al. 2011). They are considered to be sensitive indicators of soil quality in both natural and agricultural ecosystems due to their rapid response to changes in soil quality (Puglisi et al. 2006). In the past few decades, enzyme activity has been used to evaluate environmental quality indicators such as productivity, fertility, pollution effects, and nutrient cycling potential (Imamura et al. 2006). In general, the soil parameters that were measured in our study (protease, invertase, cellulase, urease, and acid phosphatase) exhibited higher values in the rhizosphere soils than bulk soils, presumably because the rhizosphere induces the synthesis of these enzymes. Levels of soil enzymes have a close

relationship between the organic matter and activity of microbial population (Bastida et al. 2006).

In this study, protease, invertase, cellulase, urease, and acid phosphatase activities all significantly affected the rhizosphere in the six *N. longibracteata* forests. These rhizosphere effects may be due to the physiological activities of the roots under the influence of environmental stressors, which can cause the roots to produce large amounts of enzymes and release them into the rhizosphere soil. Meanwhile, microorganisms near the roots unceasingly secrete various enzymes to the surrounding soil root, resulting in very different enzyme activity profiles between the inner and outer rhizosphere (Yuan et al. 1997). These findings are consistent with these previous studies (Tscherko et al. 2004; Zhang et al. 2011), which suggests that the enzymes in the rhizosphere are more active than those in the bulk soil. However, Zhang et al. (2012) obtained that urease activity in the mineralization of soil N in rhizosphere is lower than that in the bulk soil, which may be due to the composition of the microbial communities. It was reported that soil enzymes are produced by specialized groups of microorganisms (Buée et al. 2009), which have competitive abilities for absorbable plant carbon.

On the other hand, rhizosphere effects may also be due to the physiological metabolic activities of diverse microbial populations that differ between rhizosphere zones (Garcia et al. 2005; Marschner et al. 2005; Wang et al. 2006; Phillips and Fahey 2008; Zhang et al. 2013). For example, higher acid phosphatase and protease activities in the rhizosphere versus bulk soil were observed by Marschner et al. (2005). Wang et al. (2006) found that rhizosphere soil had higher alkaline phosphatase activity than bulk soil. Phillips and Fahey (2008) reported that phosphatase enzyme activity was higher in rhizosphere than in the bulk soil of sugar maples (*Acer saccharum* Marshall) and northern red oak (*Quercus rubra* L.) at the Turkey Hill Plantation, New York (USA). Zhang et al. (2013) found that urease, catalase, invertase, acid phosphatase, and alkaline phosphatase activities in the rhizosphere soil were higher than bulk soil, while neutral phosphatase activity was much lower in the rhizosphere soils. Zhang et al. (2011) found a similar result in that urease and cellulase of rhizosphere soil was higher compared with that of the control soil.

The correlation analysis showed that the relationship among rhizosphere soil enzyme activities varied in the Tianbaoyan National Nature Reserve. There were significant linear correlations between phosphatase and protease activities and between acid phosphatase and cellulase activities in rhizosphere soil. In the study of Zhang et al. (2013), they found significant linear correlations between rhizosphere soil microbial abundances and enzyme activities. However, Ge et al. (2011) found the linear correlations between rhizosphere soil microbial abundances and enzyme activities could be due to the plant species, components of litter and the soil pathway of humus decomposition. Additional effort should be made to identify the microbial abundances to improve our understanding of rhizosphere soil microbial mechanisms.

Conclusion

Our study explored enzyme activities of rhizosphere and bulk soils of six *N. longibracteata* forests. We found that protease, invertase, cellulase, urease, and acid phosphatase activities in rhizosphere soil were significantly higher than those in bulk soils. Acid phosphatase activity showed significant rhizosphere effects in all six forests. Canonical correlation analysis of rhizosphere soil showed that acid phosphatase activity correlated significantly with protease activity ($p < 0.01$) and cellulase activity ($p < 0.05$). In bulk soil samples, there were significant linear correlations between protease and acid phosphatase activities ($p < 0.05$) and between invertase and cellulase activities ($p < 0.01$). Future studies would explore the relationship between microbial profiles and enzyme activities in rhizosphere soils. The first three PCs of the 13 chemical properties and enzyme activities accounted for 61.233, 15.422, and 9.434% of the total variances, respectively. Protease, invertase, acid phosphatase, total N, and cellulase had higher loadings on PC1, while total K and available K had higher loadings on PC2. PC3 was dominated by available P.

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References

Albiach R, Canet R, Pomares F, Ingelmo F (2000) Microbial biomass content and enzymatic activities after the application of organic amendments to a horticultural soil. Bioresour Technol 75(1):43–48

Alvarez S, Guerrero MC (2000) Enzymatic activities associated with decomposition of particulate organic matter in two shallow ponds. Soil Biol Biochem 32(13):1941–1951

Aon MA, Colaneri AC (2001) Temporal and spatial evolution of enzymatic activities and physico-chemical properties in an agricultural soil. Appl Soil Ecol 18(3):255–270

Aon MA, Cabello MN, Sarena DE, Colaneria AC, Francoa MG, Burgosa JL, Cortassa S (2001) I. Spatio-temporal patterns of soil microbial and enzymatic activities in an agricultural soil. Appl Soil Ecol 18(3):239–254

Bastida F, Moreno JL, Hernández T, García C (2006) Microbiological degradation index of soils in a semiarid climate. Soil Biol Biochem 38(12):3463–3473

Bell C, Carrillo Y, Boot CM, Rocca JD, Pendall E, Wallenstein MD (2014) Rhizosphere stoichiometry: are C:N:P ratios of plants, soils, and enzymes conserved at the plant species-level? New Phytol 201(2):505–517

Böhme L, Langer U, Böhme F (2005) Microbial biomass, enzyme activities and microbial community structure in two European long-term field experiments. Agr Ecosyst Environ 109(1–2): 141–152

Buée M, Boer WD, Martin F, van Overbeek L, Jurkevitch E (2009) The rhizosphere zoo: an overview of plant-associated communities of microorganisms, including phages, bacteria, archaea, and fungi, and of some of their structuring factors. Plant Soil 321(1–2):189–212

Burke DJ, Smemo KA, López-Gutiérrez JC, Hewins CR (2012) Soil enzyme activity in an old-growth northern hardwood forest: interactions between soil environment, ectomycorrhizal fungi and plant distribution. Pedobiologia 55(6):357–364

De Graaff M, Classen AT, Castro HF, Schadt CW (2010) Labile soil carbon inputs mediate the soil microbial community composition and plant residue decomposition rates. New Phytol 188(4):1055–1064

Fioretto A, Papa S, Sorrentino G, Fuggi A (2001) Decomposition of Cistus incanus leaf litter in a Mediterranean maquis ecosystem: mass loss, microbial enzyme activities and nutrient changes. Soil Biol Biochem 33(3):311–321

Garcia C, Roldan A, Hernandez T (2005) Ability of different plant species to promote microbiological processes in semiarid soil. Geoderma 124(1–2):193–202

Ge Y, Zhang CB, Jiang YP, Yue CL, Jiang QS, Min H, Fan HT, Zeng Q, Chang J (2011) Soil microbial abundances and enzyme activities in different rhizospheres in an integrated vertical flow constructed Wetland. CLEAN Soil Air Water 39(3):206–211

Imamura A, Yumoto T, Yanai J (2006) Urease activity in soil as a factor affecting the succession of ammonia fungi. J For Res 11(2):131–135

Jin K, Sleutel S, Buchan D, De Neve S, Cai DX, Gabriels D, Jin JY (2009) Changes of soil enzyme activities under different tillage practices in the Chinese loess plateau. Soil Till Res 104(1): 115–120

Johansson E, Krantz-Rülcker C, Zhang BX, Öberg G (2000) Chlorination and biodegradation of lignin. Soil Biol Biochem 32(7):1029–1032

Kaiser C, Koranda M, Kitzler B, FuchsluegerL Schnecker J, Schweiger P, Rasche F, Zechmeister-Boltenstern S, Sessitsch A, Richter A (2010) Belowground carbon allocation by trees drives seasonal patterns of extracellular enzyme activities by altering microbial community composition in a beech forest soil. New Phytol 187(3):843–858

Kardol P, Campany CE, Souza L, Norby RJ, Weltzin JF, Classen AT (2010) Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. Glob Change Biol 16(10):2676–2687

Marschner P, Grierson PF, Rengel Z (2005) Microbial community composition and functioning in the rhizosphere of three *Banksia* species in native woodland in Western Australia. Appl Soil Ecol 28(3):191–201

Monreal CM, Bergstrom DW (2000) Soil enzymatic factors expressing the influence of land use, tillage system and texture on soil biochemical quality. Can J Soil Sci 80(3):419–428

Nausch M, Nausch G (2000) Stimulation of peptidase activity in nutrient gradients in the Baltic Sea. Soil Biol Biochem 32(13): 1973–1983

Orwin KH, Buckland SM, Johnson D, Turner BL, Smart S, Oakley S, Bardgett RD (2010) Linkages of plant traits to soil properties and the functioning of temperate grassland. J Ecol 98(5):1074–1083

Phillips RP, Fahey TJ (2008) The influence of soil fertility on rhizosphere effects in northern hardwood forest soils. Soil Sci Soc Am J 72(2):453–461

Puglisi E, Del Re AAM, Rao MA, Gianfreda L (2006) Development and validation of numerical indexes integrating enzyme activities of soils. Soil Biol Biochem 38(7):1673–1681

Qiu YJ, Liu YF, Kang M, Yi GM, Huang HW (2013) Spatial and temporal population genetic variation and structure of *Nothotsuga longibracteata* (Pinaceae), a relic conifer species endemic to subtropical China. Genet Mol Biol 36(4):598–607

Sanaullah M, Blagodatskaya E, Chabbi A, Rumpel C, Kuzyakov Y (2011) Drought effects on microbial biomass and enzyme activities in the rhizosphere of grasses depend on plant community composition. Appl Soil Ecol 48(1):38–44

Sinsabaugh RL, Hill BH, Follstad Shah JJ (2009) Ecoenzymatic stoichiometry of microbial organic nutrient acquisition in soil and sediment. Nature 462(10):795–798

Tscherko D, Hammesfahr U, Marx MC, Kandeler E (2004) Shifts in rhizosphere microbial communities and enzyme activity of *Poa alpina* across an alpine chronosequence. Soil Biol Biochem 36(10):1685–1698

Wang AS, Angle JS, Chaney RL, Delorme TA, Mcintosh M (2006) Changes in soil biological activities under reduced soil pH during *Thlaspi caerulescens* phytoextraction. Soil Biol Biochem 38(6):1451–1461

Xiao SH, He DJ, You HM, Liu JS, Cai CT (2012) Storage of coarse woody debris in three typical forests in Tianbaoyan National Nature Reserve, Fujian Province of eastern China. J Beijing For Univ 34(5):64–68 **(in Chinese)**

You HM, He DJ, Cai CT, Liu JS, Hong W, You WB, Wang L, Xiao SH, Hu J, Zheng XY (2013a) Assessment on effect of fallen woods on soil fertility in *Tsuga longibracteata* forest in Tianbaoyan National Nature Reserve. Chin J Appl Environ Biol 19(1):168–174 **(in Chinese)**

You HM, He DJ, Liu JS, Cai CT, You WB, Xiao SH (2013b) Effect of covering with fallen logs on soil physicochemical property of *Tsuga longibracteata* forest in Tianbaoyan National Nature Reserve. J Plant Resour Environ 22(3):18–24 **(in Chinese)**

You HM, He DJ, You WB, Liu JS, Cai CT (2013c) Effect of environmental gradients on the quantity and quality of fallen logs in *Tsuga longibracteata* forest in Tianbaoyan National Nature Reserve, Fujian province, China. J Mount Sci 10(6): 1118–1124

Yuan L, Huang JG, Yu SQ (1997) Responses of nitrogen and related enzyme activities to fertilization in rhizosphere of wheat. Pedosphere 7(2):141–148

Zhang YM, Wu N, Zhou GY, Bao WK (2005) Changes in enzyme activities of spruce (*Picea balfouriana*) forest soil as related to burning in the eastern Qinghai-Tibetan Plateau. Appl Soil Ecol 30(3):215–225

Zhang C, Liu GB, Xue S, Song ZL (2011) Rhizosphere soil microbial activity under different vegetation types on the Loess Plateau, China. Geoderma 161(3–4):115–125

Zhang C, Liu GB, Xue S, Zhang CS (2012) Rhizosphere soil microbial properties on abandoned croplands in the Loess Plateau, China during vegetation succession. Eur J Soil Biol 50:127–136

Zhang L, Song L, Shao H, Shao H, Shao C, Li M, Liu M, Brestic M, Xu G (2013) Spatio-temporal variation of rhizosphere soil microbial abundance and enzyme activities under different vegetation types in the coastal zone, Shandong, china. Plant Biosyst 148(3):403–409