# 中国西部 3 个亚高山森林土壤有机层和矿质层碳储量和生化特性

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**摘要** 为了解土壤和植被界面的有机碳库和生化特性，分别将以云杉 (*Picea purpurea* Masters) (SF)、冷杉 (*Abies faxoniana* Rehder & E. H. Wilson) (FF) 和白桦 (*Betula platyphylla* Sukaczev) (BF) 为优势树种的 3 个亚高山森林地表有机层 (OL) 分成新鲜凋落物层 (LL)、半分解层 (FL) 和分解层 (HL)，并同步测定了有机层和矿质土壤层 (MS) 的有机碳 (OC) 储量、微生物生物量碳 ($C_{mic}$)、微生物生物量氮 ($N_{mic}$) 及转化酶、过氧化氢酶、脱氢酶和多酚氧化酶活性。云杉林、冷杉林和白桦林土壤有机层的有机碳储量分别为 29.38 Mg hm$^{-2}$ ± 1.28 Mg hm$^{-2}$、22.7 Mg hm$^{-2}$ ± 1.12 Mg hm$^{-2}$ 和 8.63 Mg hm$^{-2}$ ± 0.95 Mg hm$^{-2}$，分别为总有机碳储量的 62.2%、53.5% 和 36.6%。云杉林、冷杉林和白桦林土壤有机层和腐殖质层分别储存了 92.8%、99.6% 和 78.7% 的有机碳。所有林型中，HL 具有最高的细菌数量、$C_{mic}$ 和 $N_{mic}$ 及过氧化氢酶活性，FL 具有最高的真菌、放线菌数量及转化酶、脱氢酶和多酚氧化酶活性。微生物数量、微生物生物量和酶活性的垂直分布格局意味着 OL 是土壤和植被之间最活跃的生态界面之一。

**关键词** 亚高山森林；碳库；微生物数量；微生物生物量；酶活性

**文章编号**：1000-0933 (2007) 10-4157-09 **中图分类号**：Q148, Q948, S718 **文献标识码**：A

# Carbon stock and biochemical properties in the organic layer and mineral soil under three subalpine forests in Western China

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***Acta Ecologica Sinica*, 2007, 27 (10): 4157 ~ 4165.**

**Abstract**: The organic layer (OL) on the floor of three subalpine forests, dominated by spruce (*Picea purpurea* Masters) (SF), fir (*Abies faxoniana* Rehder & E. H. Wilson) (FF) and birch (*Betula platyphylla* Sukaczev) (BF) trees, respectively, was divided into a fresh litter layer (LL), semi-decomposed litter layer (FL) and decomposed litter layer (HL), and organic carbon (OC) stock, microbial biomass carbon ($C_{mic}$) and nitrogen ($N_{mic}$) and the activities of invertase, catalase, dehydrogenase and polyphenol oxidase were measured simultaneously in the OL and mineral soil (MS)

**基金项目** 国家自然科学基金资助项目 (30471378, 90202010, 30211130504)；国家“十一五”重大科技支撑计划资助项目 (2006BAC01A11)；四川省重大应用基础研究计划资助项目；四川省青年科技基金资助资助项目 (07JQ0081)；四川农业大学人才引进资助项目

**收稿日期** 2006-08-15；**修订日期** 2007-03-24

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**致谢**：Thanks to the staff in Wanglang National Nature Reserve for their kind help in field investigations. We are also grateful to Malcolm Hicks for his check of the English of this manuscript

**Foundation item**: The project was financially supported by National Natural Science Foundation of China (No. 30471378, 90202010, 30211130504), National Key Technologies R&D Program, China (No. 2006BAC01A11), Key Project of Applied & Basic Research of Sichuan, Program of Sichuan Youth Science and Technology Foundation (No. 07JQ0081), and the Talent-Recruiting Program of Sichuan Agricultural University

**Received date**: 2006-08-15; **Accepted date**: 2007-03-24

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in order to obtain an understanding of the status of the OC pool and biochemical properties at the interface between the soil and vegetation. The OC stock was 29.38 Mg $hm^{-2}$ ± 1.28 Mg $hm^{-2}$ in the OL in SF, 22.7 Mg $hm^{-2}$ ± 1.12 Mg $hm^{-2}$ in FF and 8.63 Mg $hm^{-2}$ ± 0.95 Mg $hm^{-2}$ in BF, accounting for 62.2, 53.5 and 36.6% of the total OC stock, respectively. 92.8, 99.6 and 78.7% of the total OC in the SF, FF and BF forests were stored in the OL and humus layer, respectively. Regardless of the stand type, HL had the highest bacterial number, $C_{mic}$, $N_{mic}$ and catalase activity, and FL had the highest numbers of fungal and actinomycetes and the highest activities of invertase, dehydrogenase and polyphenol oxidase. The vertical distribution patterns for microbial number, microbial biomass and enzyme activity imply that the OL is one of the most active interfaces between the soil and the vegetation.

**Key Words**: subalpine forests; carbon pool; microbial number; microbial biomass; enzyme activity

## 1 Introduction

Numerous studies undertaken over the past decade have led to the general conclusion that forest soil is a gigantic and steady OC pool and plays an important role in regulating the global carbon cycle [1,2], as a consequence of which soil pool has received more attention than any other ecosystem pool in studies of the contributions of forest ecosystems to the global carbon cycle [3]. Biogeochemical research nevertheless indicates that the OL of the forest floor is a key component in the responses of forests to global change and in the cycles of mass and energy [4]. The OL, as a location of active OC pool in a forest ecosystem, plays an important role in maintaining soil fertility through nutrient inputs from litter decomposition and through its important function in conserving soil and water [4], and affects the carbon pathways [5]. OL also provides energy, nutrients and a living environment for the soil biomes, which is helpful in facilitating litter decomposition and C mineralization through biochemical action and mechanical fragmentation [6], regulated by biotic and abiotic factors [7,8]. The OL, therefore, is one of the most active interfaces between the soil and vegetation for the transfer of nutrient and energy and a dynamic component of carbon cycling in a forest ecosystem. As yet, far less information is available on OC pool in the OL of many forest ecosystems by comparison with whole soil pool, and a detailed understanding of the mechanisms of C processes in the forest floor is still lacking.

Some researchers have indicated that the dynamics of enzyme activities and microbial biomass in litter and soil are important bioindicators of litter decomposition [9-12]. Meanwhile, the OC and nutrient cycles in a soil ecosystem are ultimately regulated by the microorganisms and enzymes present in the OL and MS [6]. This implies that the biochemical properties of these layers constitute an important biological factor controlling the litter stock and carbon pool [3]. Measurements of these biochemical properties combined with the carbon and nutrient pools can therefore be expected to help us to understand forest ecosystem processes. Little is known about the biochemical properties that are related to the OL and MS carbon pool, although a few reports have been published on carbon pool and microorganisms in OL [1,2,14,15].

The subalpine forests of western Sichuan are located in a transitional area between the Qinghai-Tibet plateau and the Sichuan basin on the upper reaches of the Yangtze River, and they play an important role in regulating the regional climate and conserving water and soil [6,17]. Little information has been published on OC pool and biochemical property in the OL and MS of forest ecosystems, although these aspects are central to the structure and function of coniferous forests [6,17]. The objectives of the present work were therefore to quantify the OC pool in the OL and MS under the three forests, and to characterize the biochemical properties of the OL and MS.

## 2 Materials and methods

### 2.1 Site description

This study was conducted in the Wanglang Nature Reserve (32°49′—33°02′ N, 103°55′—104°10′ E, 2300 —

4980 m a. s. l.), having an area of 340 $km^2$, which is located in Pingwu County of western Sichuan, China. The annual mean temperature is 2.9℃, the annual cumulative temperature (≥ 10℃) is 1 056.5℃, and the absolute maximum and minimum temperatures are 26.2℃ and −17.8℃, respectively. Annual precipitation ranges from 801 to 825 mm depending on the elevation, with most falling between May and August. The vegetation consisted mainly of primary dark coniferous, secondary coniferous and deciduous forests. Three 600$m^2$ (20 m × 30 m) permanent plots were established in three typical stands of spruce (*Picea purpurea* Masters) (SF), fir (*Abies faxoniana* Rehder & E. H. Wilson) (FF) and birch (*Betula platyphylla* Sukaczev) (BF) of subalpine forests. Detailed information about the site is presented by Yang *et al.* [6,17].

**2.2** Measurements of litter stock and sampling

The litter stock on the forest floor was determined in five randomly distributed positions within each plot in mid-April, late May, mid-July, late August and late October 2002. The samples were obtained by pressing a 1.0 $m^2$ quadrat frame (25 cm deep) into the forest floor and collecting all the organic material lying above the MS. The LL, FL and HL in each of these samples were separated out and carefully placed in plastic bags. The LL was composed of fresh or slightly discoloured material, with little or no breaking up, the FL of medium to strongly fragmented material with many mycelia and thin roots, and the HL of a humified amorphous material [8]. The MS was removed after successive sieving. After determining its fresh weight, each forest floor sample was divided into two parts, one part being oven-dried to constant weight at 70℃ and weighed to estimate the litter stock in each layer of the forest floor per unit area, then ground and passed through a 1-mm stainless steel sieve and stored for analysis of carbon content, and the other, to be used for measurements of microbial number and biomass and analysis of enzyme activity, was chopped into pieces, mixed and passed through a 2-mm stainless steel sieve, placed in sterilized plastic bags and stored in a refrigerator at 4℃.

**2.3** Sampling the mineral soil

Three soil profiles were excavated at each stand site after removing the OL in connection with the litter sampling. 500-g samples from the centre of the humus layer (AL), illuvial layer (BL) and parent material layer (CL) in each profile were taken from bottom to top, respectively, and divided into three parts, which were used for the determination of biochemical properties, nutrient concentrations, and other physical and chemical properties. Meanwhile, five samples of intact soil per soil layer were taken with a cutting ring (diameter 72 mm and height 50 mm) to measure its bulk density. In addition, the thickness of each layer in the profile was measured and the distribution of the root system was recorded.

The intact soil core in each layer was oven-dried at 105℃ to constant weight, in order to measure soil bulk density and soil water content [9]. Soil pH ($H_2O$) was measured with a pH meter [10]. The resulting data are shown in Table 1.

**Table 1　Thickness, bulk density and gravel (≥2 mm) content for MS of forest sites dominated by spruce (SF), fir (FF) and birch (BF)**

| Item | SF | | | FF | | BF | | |
|---|---|---|---|---|---|---|---|---|
| | Humus layer | Illuvial layer | Parent material layer | Humus layer | Parent material layer | Humus layer | Illuvial layer | Parent material layer |
| Soil thickness (cm) | 22.50 ± 6.0 | 15.40 ± 5.1 | 17.00 ± 7.0 | 15.60 ± 4.2 | 15.00 ± 4.7 | 25.20 ± 6.0 | 45.20 ± 8.4 | 50.50 ± 10.7 |
| Bulk density (g $cm^{-3}$) | 0.61 ± 0.12 | 1.65 ± 0.14 | 1.86 ± 0.11 | 1.28 ± 0.13 | 1.58 ± 0.16 | 0.95 ± 0.09 | 1.67 ± 0.11 | 1.83 ± 0.14 |
| Gravel content (%) | 0.0 | 65.00 ± 5.0 | 92.00 ± 6.5 | 9.00 ± 2.1 | 91.20 ± 7.0 | 2.50 ± 2.5 | 34.60 ± 3.9 | 90.00 ± 8.1 |

Values are means per stands (n = 3)

The OC content of the OL and MS was determined by $K_2Cr_2O_7$ oxidation and $FeSO_4$ titration methods [9].

Microbial numbers in the OL and MS samples were measured by the spread plate counting method [10]. Bacteria,

actinomycete and filamentous fungi were incubated onto beef broth-peptone agar, starch-casein agar and Czapek-Dox agar. $C_{mic}$ and $N_{mic}$ in OL and MS were determined by the chloroform fumigation-extraction method [9].

INV activity was measured by a colorimetric method using 3, 5-dinitrosalicylic acid. Enzyme activity was expressed in enzyme units ($EU_{INV}$), one unit being the amount of enzyme which produces 1 mg glucose $g^{-1}$ litter/soil $d^{-1}$ at 37℃ [11]. CAT activity was measured by the volumetric titration method. Enzyme activity was expressed in $EU_{CAT}$, one unit being the amount of enzyme which catalyzes 1 mmol $KMnO_4$ $kg^{-1}$ litter/soil $h^{-1}$ [11]. DHA activity was measured by the colorimetric method. Enzyme activity was expressed in $EU_{DHA}$, where one unit represents the amount of enzyme which produces 1 μmol $H^+$ per gram of litter/soil in one day at 30℃ [11]. PPO activity was measured by the volumetric titration method. Enzyme activity was expressed in $EU_{PPO}$, where one unit is the amount of enzyme which produces 1 mmol $I_2$ per gram of litter/soil in 1 min at 30℃ [11].

All the measurements were carried out in triplicate.

### 2.5 Calculations and statistical analyses

The OC stock in OL were estimated according to the OC content of the subsamples and litter stock per unit area, and those in MS according to soil OC content, soil thickness and bulk density.

Analyses of variance (ANOVA) were used to compare the OC stock, microbial numbers, $C_{mic}$, $N_{mic}$ and enzyme activities between OL and MS and between stands.

## 3 Results

### 3.1 OC content and stock of OL and MS

The distributions of OC content and stock in the soil profile were illustrated in Fig. 1. OC content decreased with depth in the soil profile, and the OC content of the OL was higher in SF than in FF and BF, and that of the AL higher in SF and FF than in BF. However, no significant difference was found between SF and BF in the case of both the AL and CL. The highest OC stock was found in FL or AL, but the distribution within the soil profile varied with the stands, the rank order being FL > AL > HL > BL > LL > CL, AL > FL > LL > HL > CL, and AL > BL ≥ FL > LL > HL ≥ CL in the SF, FF and BF, respectively.

The OC stock in the OL and MS was shown in Table 2. The OC stock was significantly higher in OL than in MS in the case of SF, accounting for 62.2 and 37.8% of the total, respectively. The OC stock was higher in OL than in MS in the FF stand, but the differences were not significant. In contrast, the OC stock in BF was significantly higher in MS than in OL. The OC stock in OL showed the rank order SF > FF > BF, while the order in MS was FF > SF > BF, and the rank orders for the total OC stock in OL and MS combined was SF > FF > BF.

**Table 2 Carbon stock in organic layer (OL) and miner soil (MS) of forest sites dominated by spruce (SF), fir (FF) and birch (BF)**

| | Organic carbon stock (Mg $hm^{-2}$) | |
|---|---|---|
| | OL | MS |
| SF | $29.38 \pm 1.28^{aA}$ | $17.84 \pm 1.92^{aB}$ |
| FF | $22.70 \pm 1.12^{bA}$ | $19.74 \pm 1.76^{aA}$ |
| BF | $8.63 \pm 0.95^{cA}$ | $14.92 \pm 1.64^{bB}$ |

Values are means s. d. ($n = 5$ for OL, and $n = 3$ for MS); Different superscripts within a column indicate the significant differences among stands (owercase letter) and between OL and MS (uppercase letter) (ANOVA, $P < 0.01$)

### 3.2 Microbial number

The numbers of bacteria, fungi and actinomycetes in the soil profiles for the three stands are shown in Fig. 2. The numbers of bacteria increased with depth from LL to HL in all the stands, and ranged from 1.98 to $17.03 \times 10^6$ CFU $g^{-1}$ soil/litter in SF, 2.30 to $18.58 \times 10^6$ CFU $g^{-1}$ soil/litter in FF, and 2.68 to $27.36 \times 10^6$ CFU $g^{-1}$ soil/litter in BF, decreasing thereafter with depth from HL to CL. There were no significant differences between FL, HL and AL although the average was higher in HL than in AL and FL. The number of bacteria was significantly higher in

HL than in LL, BL and CL for SF and FF, however, and higher than in LL and CL for BF, i. e., the highest and lowest bacteria numbers were in HL and CL, whereas the differences between FL, HL and AL were not significant.

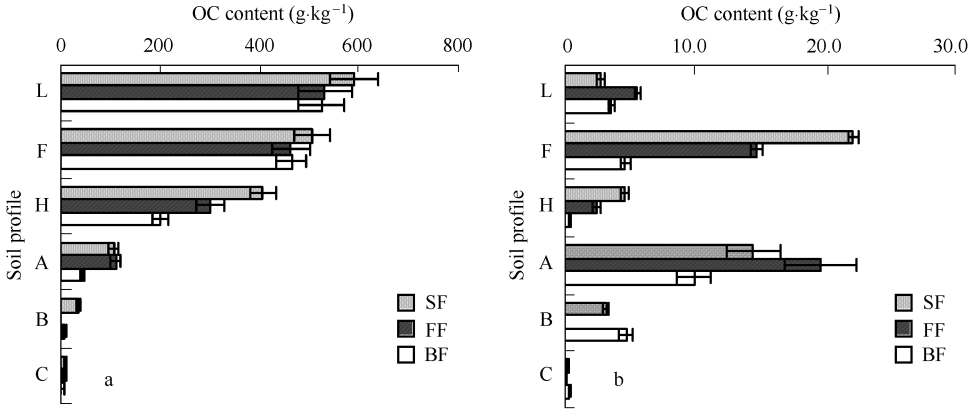


Fig. 1　The organic carbon (OC) content (a) and stock (b) in the soil profiles of forest sites dominated by spruce (SF), fir (FF) and birch (BF) Bars indicate s. d. (a, $n=5$ for L, F and H, $n=3$ for A, B and C)

Similarly, the numbers of fungi and actinomycete increased with depth from LL to FL and then decreased with depth from FL to CL in all the stands. The numbers of fungi ranged from 0.4 to $22.5\times10^5$ CFU $g^{-1}$ soil/litter for SF, 0.5 to $25.2\times10^5$ CFU $g^{-1}$ soil/litter for FF and 0.8 to $27.3\times10^5$ CFU $g^{-1}$ soil/litter for BF, and the figures for actinomycetes from 0.4 to $14.6\times10^5$ CFU $g^{-1}$ soil/litter for SF, 0.7 to $23.6\times10^5$ CFU $g^{-1}$ soil/litter for FF and 1.1 to $28.8\times10^5$ CFU $g^{-1}$ soil/litter for BF. In total, the highest and lowest values for fungi and actinomycetes were in FL and CL in all three stands.

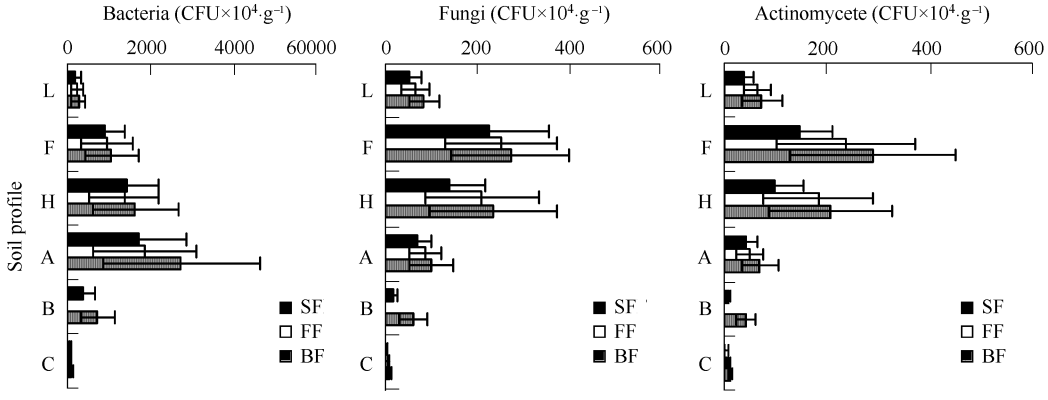


Fig. 2　Microbial numbers in the organic layer (OL) and mineral soil (MS) of forest sites dominated by spruce (SF), fir (FF) and birch (BF) Values are means over one year; Bars indicate s. d.

### 3.3　$C_{mic}$ and $N_{mic}$

$C_{mic}$ and $N_{mic}$ increased with depth from LL to HL in all the stands, but decreased from HL to CL (Fig. 3). $C_{mic}$ and $N_{mic}$ varied from (86 ± 81) μg $g^{-1}$ and (5 ± 7) μg $g^{-1}$ litter in LL to (3 ± 3) μg $g^{-1}$ and (1 ± 1) μg $g^{-1}$ soil in CL in the case of SF, while in the FF stand $C_{mic}$ and $N_{mic}$ varied from (80 ± 103) μg $g^{-1}$ and (3 ± 9) μg $g^{-1}$ litter in LL to (8 ± 11) μg $g^{-1}$ and (1 ± 1) μg $g^{-1}$ soil in CL, and in the BF stand $C_{mic}$ and $N_{mic}$ from (90 ± 99) μg $g^{-1}$ and (6 ± 8) μg $g^{-1}$ litter in LL to (4 ± 12) μg $g^{-1}$ and (1 ± 1) μg $g^{-1}$ soil in CL, respectively. Regardless of the stands, the highest and lowest values for $C_{mic}$ and $N_{mic}$ were in HL and CL, respectively.

### 3.4　Enzyme activity

The activities of INV, CAT, DHA and PPO in the soil profiles of the three stands are illustrated in Fig. 4. The

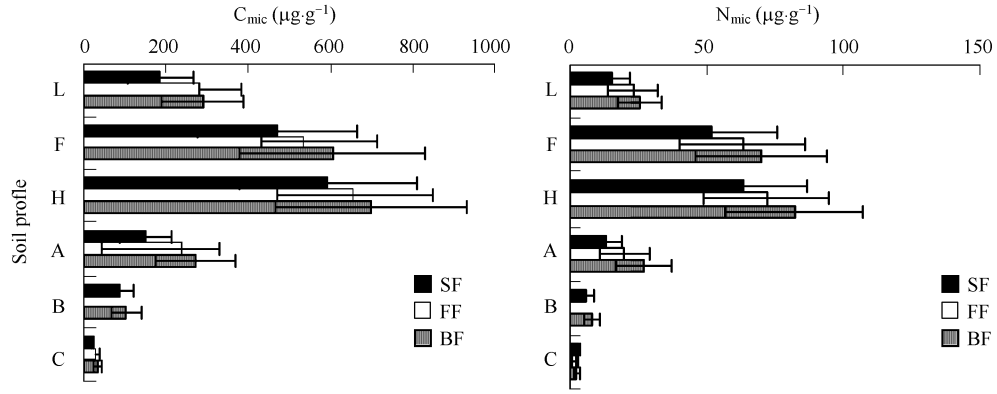


Fig. 3 Microbial biomass carbon ($C_{mic}$) and nitrogen ($N_{mic}$) in the organic layer (OL) and mineral soil (MS) of forest sites dominated by spruce (SF), fir (FF) and birch (BF)

Values are means over one year; Bars indicate s. d.

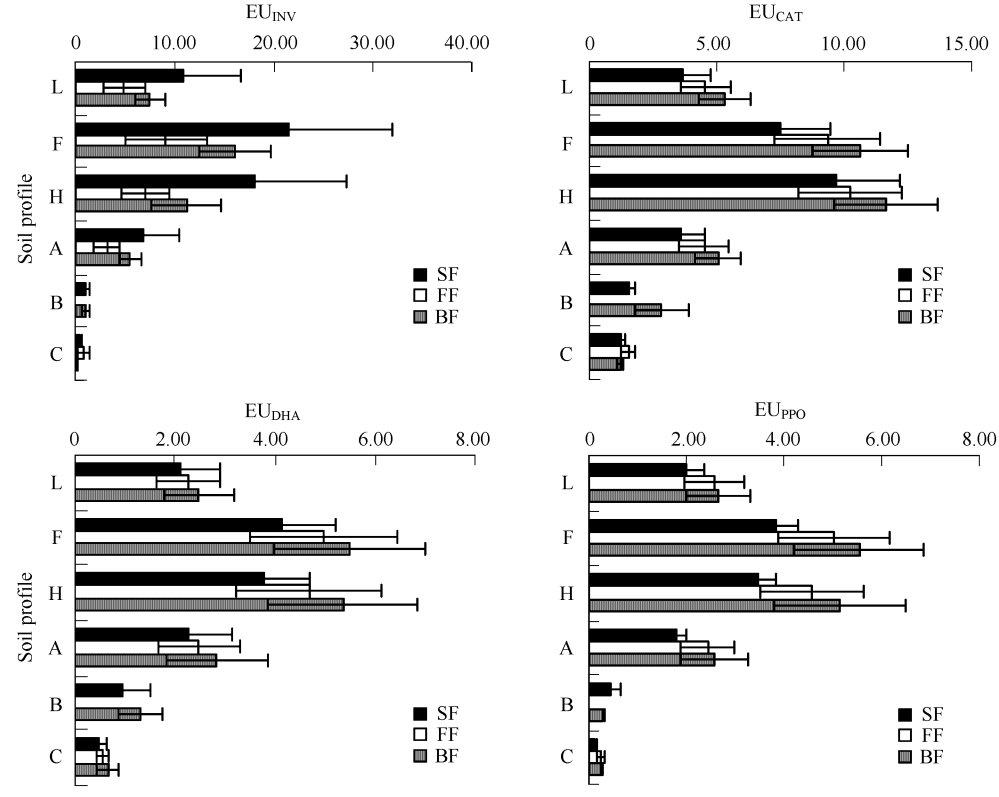


Fig. 4 Invertase (NV), catalase (CAT), dehydrogenase (DHA) and polyphenol oxidase (PPO) activities in the organic layer (OL) and mineral soil (MS) of forest sites dominated by spruce (SF), fir (FF) and birch (BF)

Values are means over one year; Bars indicate s. d.

activities of INV, DHA and PPO increased with depth from LL to FL in all three stands and then decreased with depth from FL to CL. Similarly, the activity of CAT increased with depth from LL to HL, and then decreased with depth from HL to CL. Moreover, the activities of CAT, DHA and PPO were significantly higher in FL and HL than in the other layers, with no marked differences between FL and HL, while the activity of INV was significantly higher in FL than in LL, AL, BL and CL in the case of BF, higher than in AL and CL in FF, and higher than in BL and CL in SF, although the difference between FL and HL was not significant. Regardless of the stands, the highest and

lowest activities of INV, DHA and PPO occurred in HL and CL, respectively, however, and those of CAT in FL and CL, respectively.

## 4 Discussion

### 4.1 OC pool

OC content decreased with depth in the soil profile regardless of the stands. The OC stock was significantly higher in OL than in MS in the SF stand, while in the FF it was higher in OL than in MS but the difference was not significant, and in the BF it was significantly higher in MS than in OL. Moreover, most of the OC was stored in the OL and AL (>2.8% for SF, 99.6% for FF and 78.7% for BF). The results showed that the OL constituted a major OC pool in primary spruce and fir forests, and that OL and AL together accumulated most of the OC in the soil profile in all three stand types, implying that the disturbances on OL and AL lead directly to variations in the OC pool in a subalpine forest ecosystem.

The SF had the highest total OC stock, followed by FF, while BF had the least. The OC pool in OL showed the same trend as the total OC stock. The OC mainly originates from litterfall, which is related to stand age, litter production and litter decomposition [6,17], therefore, the larger OC stocks in the SF and FF stands may be attributed to their higher age (>50 years for SF and 200 years for FF), which has led to long-term accumulation of OC in OL and AL.

### 4.2 Vertical distribution of microbial number

The microbial number varied with the physical and chemical status in the soil profile. Here the bacterial number was higher in HL than in other layers due to the higher humus content and oxygen concentration, implying that HL was a locus of high bacterial activity. Fungal and actinomycete numbers increased with depth from LL to FL, and then decreased with depth from FL to CL, i. e., FL had the highest number of fungi and actinomycetes in the soil profile, owing to its higher organic matter content, higher oxygen concentration and lower pH, which are favourable for fungal and actinomycete propagation [4]. By contrast, the lower fungal and actinomycete numbers in CL may be attributed to its lower organic matter content and lower oxygen concentration, which limit the growth of fungi and actinomycetes. The results are in agreement with those of Yang *et al.*, who showed that 63.6% of bacterial populations, 45.5%—90.9% of fungi and 90.9% of actinomycete populations live in the topsoil [4], and also with those of Priha *et al.*, who indicated that the humus layer of a fertile forest site of the *Vaccinium vitis-idaea* type in Finland had higher numbers of culturable bacteria, pseudomonadas, fungi and yeasts than did the mineral soil [2], of Berg *et al.*, who showed that bacterial populations and mycelial content decreased with increasing depth in a Scots pine forest soil [5], and of Fierer *et al.*, who found that the composition of the soil microbial community decreased with increasing soil depth due to the decline in carbon availability with soil depth [3]. Fungi and actinomycetes are known to possess a diverse set of enzymes that degrade complex compounds for energy and biomass production, therefore the vertical pattern of bacteria, fungi and actinomycetes in the soil profile implies that the FL and HL constitute the most active interface for nutrient cycling and energy transfer between the litter and mineral soil in a forest ecosystem.

### 4.3 Vertical distribution of $C_{mic}$ and $N_{mic}$

Soil microbial biomass is an essential component of terrestrial ecosystems, since it is directly or indirectly responsible for nutrient cycling and serves as a source and sink of nutrients [4]. Both $C_{mic}$ and $N_{mic}$ were observed here to increase with depth from LL to HL, but to decrease from HL to CL. The range of $C_{mic}$ in MS and OL is consistent with the results reported by Yang *et al.*, who found that each gram of dry soil contained $C_{mic}$ 308—870 μg and each gram of dry OL contained $C_{mic}$ 216—653 μg in a spruce soil on Tatachia Mountain in Taiwan [4], but is

lower than the values reported by Qi *et al.* [17], and far lower than the annual average for $C_{mic}$ quoted by Chen *et al.*, who indicated that the mean $C_{mic}$ in MS in the forest in New Zealand was 808 μg C $g^{-1}$ dry soil, that in FL 7 331 μg C $g^{-1}$ dry organic material, and that in LL 3 292 μg C $g^{-1}$ dry organic material [25,26], due to the low soil temperature in the present study. The value for $N_{mic}$ in OL was in the range reported by Yang *et al.*, from 10.3 to 33.8 μg N $g^{-1}$ dry OL, and that in MS in the range 16 to 257 μg N $g^{-1}$ dry soil reported by Chen *et al.* at an early stage in the establishment of a hoop pine plantation [25,26], but lower than the value of 107 − 653 μg N $g^{-1}$ dry soil obtained by Yang *et al.* for a spruce soil on Tatachia Mountain in Taiwan [4] and that reported by Qi *et al.* [17], as a result of the lower soil temperature in the present subalpine forest ecosystem. Moreover, the vertical distributions of $C_{mic}$ and $N_{mic}$ in the present soil profiles are consistent with the results of Chen *et al.*, who reached the conclusion that the decrease in microbial biomass with soil depth was due to the decline in organic matter in that direction [25,26]. The vertical distributions of $C_{mic}$ and $N_{mic}$ confirm the observation that the transition between FL and HL is one of the most active interfaces in the carbon and nutrient cycle and in the transfer of energy between the soil and litter.

### 4.4 Vertical distribution of enzyme activity

Enzymes in MS and OL are the catalysts of important processes such as litter decomposition and the C, N, P and S cycles, and can be indicative of the microbial response to environmental changes, so that data on these can be used for modelling biogeochemical cycling [6, 28–30]. The patterns of the vertical distribution of enzyme activities in a soil profile reflect the combined effects of temperature, moisture, substrate availability and other environmental factors [2]. The present results showed that the activities of INV, DHA and PPO increased with depth from LL to FL and then decreased with depth from FL to CL in all the stands, which was consistent with the vertical patterns of fungal and actinomycete numbers described above. CAT activity also increased with depth from LL to HL and decreased with depth from HL to CL, which was consistent with the distribution of bacterial numbers in the soil profile. The vertical distribution of enzyme activity in the soil profile also confirms that FL and HL are very active interfaces for mass cycling and energy transfer between the soil and vegetation, since INV is an enzyme that hydrolyses sucrose, DHA is an oxidoreductase enzyme existing only in viable microbial cells and dehydrogenating the macromolecule in the litter [19], CAT is an intracellular oxidoreductase enzyme catalyzing the decomposition of hydrogen peroxide to water and oxygen and dehydrogenating the macromolecules in litter, and PPO is an oxidoreductase enzyme reducing the macromolecular compounds in litter [1,8]. The vertical distribution of enzyme activity also supports the hypothesis that OL is one of the most active interfaces for mass cycling and energy transfer between the soil and vegetation in a forest ecosystem.

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