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Soil Microbial Biomass and Rhizosphere Effects in Natural Forest Stands

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S u m m a r y

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In 12 natural forest stands of 6 different forest types, soil microbial biomass and microbial activity were assessed. In order to identify the readily available substrates for soil microbes, low molecular weight compounds in the soil organic matter were analysed.

Across the forest stands studied, values of microbial biomass varied widely. Differences between microbial biomass measured by fumigation-extraction (FE) and by substrate-induced respiration (SIR) were attributed to the fact that both methods apply to different subsets of the soil microbial biomass. While FE-biomass was mainly related to overall forest nutrient status, SIR-derived biomass was correlated to soil respiration and pH.

In all forest types glucose and trehalose were the sugars found in highest concentrations. Of the amino acids analysed, glutamine, alanine, valine and leucine were prevailing. Each forest stand showed a distinct pattern of individual amino acids, which reoccurred at all sampling dates. Absolute amounts varied depending on season.

Among forest types, different limitations were found acting upon the growth of the microbial biomass. In the more acidic soils, microbial biomass was significantly correlated to soil pH. Positive correlations between microbial biomass and soil moisture and total soil N were found in soils of all forest types except the oak forests. By comparing soils from various forest types, effects of forest vegetation on the quantity and composition of low molecular weight compounds in the soil organic matter were shown.

The forest stands selected for this study were widely unaffected by management practices and therefore were especially suited for ecosystem studies. We suggest that soil microbial biomass-characteristics of natural forests are valuable reference-data for studies in cultivated or stressed ecosystems.

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Introduction

The quantity and the composition of the soil microbial biomass are particularly sensitive to changes in the soil environment. That is why microbial biomass parameters have frequently been used as indicators of ecosystem stress and disturbance (ANDERSON & DOMSCH 1993). Still, information about microbial biomass-characteristics in natural, undisturbed ecosystems is limited when compared with agricultural systems (WARDLE 1992).

In the present study, soil microbial parameters were measured in different types of natural forest which are typical of the eastern region of Austria. The microbial community is the main agent responsible for litter decomposition and nutrient cycling in forest soils. The rhizosphere is continually supplying readily available forms of carbon and nitrogen to the soil system (SMITH & PAUL 1990). Thereby, the growth of the microbial biomass is promoted. In order to specify the readily available substrates for the soil microbes, sugar compounds and amino acids in the soil organic matter of the forest stands were analysed. By comparing soils of different forest types, the influence of forest vegetation on ecophysiological properties was examined.

Materials and Methods

Study sites were located in 12 natural forest stands, including oak-hornbeam forests (oak), woodruff-beech forests (beech), acidophilous beech forests (acid. beech), spruce-fir-beech forests (spruce-fir-beech), flood plain forests (flood plain) and Austrian pine forests (pine). For each forest type two forest stands were chosen.

At each site, 10 soil samples were taken from the mineral layer (0-10 cm) within transects of 50 m. Soils were sampled in spring and autumn 1997 and 1998, each transect being placed at 1 m distance from the previous one to guarantee undisturbed sampling. The soil samples were taken to the laboratory in cooling boxes and then stored at -20 °C. Prior to analysis, the soils were sieved to 2 mm.

Percent soil organic carbon (C_{org}) and total soil nitrogen (N_t) were analysed after dry combustion. Soil pH was measured in H_2O by glass electrode. Nitrogen mineralisation potential was determined by anaerobic incubation of soil samples for 7 days at 40 °C (KANDELER 1996). Microbial biomass-N (N_{mic}) was determined as ninhydrine-reactive N by a fumigation-extraction technique as described by ÖHLINGER 1996 and calculated as ninhydrine–reactive N * 3.1. Soil respiration and substrate induced respiration (SIR) were measured using an infra red gas analysor without and with glucose-amendment. Biomass-C (C_{mic}) was calculated from the maximum initial respiratory response of SIR according to ANDERSON & DOMSCH 1978 where µg biomass-C g^{-1} dw = µl CO_2 g^{-1} dw h^{-1} * 40.04. Low molecular weight organic compounds were determined in extracts of 60 % v/v acetone (BACHMANN & KINZEL 1992). After ion exchange, the cationic fraction was analysed for its content of amino acids by means of HPLC and the neutral fraction was analysed for sugars using GC.

Results and Discussion

In Tables 1a and 1b, site characteristics and soil chemical properties of the forest stands studied are presented. Values of soil microbial biomass (Table 2) ob-

tained both by fumigation-extraction (FE) and substrate-induced respiration (SIR) method varied widely across the 12 forest stands. In spring, highest amounts of SIR-derived biomass-C were measured in soils of the flood plain and pine forests. Highest amounts of FE-biomass-N were found in an indigenous spruce-fir-beech forest (R), where biomass-C also was at a high level. In autumn, high values of biomass-C were obtained in soils of the spruce-fir-beech forests and the flood plain forests. According to the FE-method, differences were less pronounced except for the spruce-fir-beech-forest (R) which had significantly higher amounts of biomass-N. Differences between data achieved by fumigation-extraction and substrate-induced respiration may be expected because both methods apply to different subsets of the microbial biomass (WARDLE & GHANI 1995).

Table 1a. Site characteristics of the forest stands under study.

Forest type (site)	Forest community	Soil type
Oak (JE)	Carpinion	Dystric Planosol
Oak (K)	Carici pilosae-Carpinetum	Calcaric Planosol
Beech (JB)	Eu-Fagenion	Dystric Planosol
Beech (Kl)	Hordelymo-Fagetum	Dystric Cambisol
Acid. Beech (D)	Luzulo-Fagenion	Dystric Cambisol
Acid. Beech (S)	Luzulo-Fagenion	Dystric Cambisol
Spruce-fir-beech (R)	Adenostylo glabrae-Fagetum	Chromic Cambisol
Spruce-fir-beech (N)	Cardamino trifoliae-Fagetum	Stagnic Luvisol
Flood plain (M)	Pruno-Fraxinetum	Calcaric Fluvisol
Flood plain (B)	Fraxino-Populetum	Calcaric Fluvisol
Pine (St)	Euphorbio saxatilis-Pinetum nigrae	Rendzic Leptosol
Pine (Me)	Euphorbio saxatilis-Pinetum nigrae	Rendzic Leptosol

Table 1b. Soil chemical properties (in spring 1997) of the forest stands under study.

Forest type (site)	**Soil moisture (%)**	**pH**	**NH_4-N** ($\mu g\ g^{-1}$ dw)	**NO_3-N** ($\mu g\ g^{-1}$ dw)	**N_t (%)**	**C_{org} (%)**	**C/N**
Oak (JE)	34.2	4.5	17.6	55.6	0.22	5.04	23.4
Oak (K)	29.8	5.4	10.5	53.8	0.20	4.23	21.0
Beech (JB)	35.4	5.1	26.0	58.4	0.19	4.38	22.5
Beech (Kl)	34.3	4.1	15.4	54.5	0.33	4.36	13.1
Acid. Beech (D)	40.9	4.6	68.8	11.1	0.35	9.45	26.9
Acid. Beech (S)	32.0	4.0	296.6	0.3	0.30	7.03	23.5
Spruce-fir-beech (R)	57.9	4.9	127.4	150.9	0.94	16.00	17.1
Spruce-fir-beech (N)	43.3	4.0	56.1	96.0	0.38	6.46	16.9
Flood plain (M)	38.7	7.2	1.5	109.50	0.47	5.46	11.7
Flood plain (B)	29.4	7.4	0.9	89.05	0.23	3.92	17.2
Pine (St)	35.4	7.4	14.4	2.0	0.61	16.99	28.0
Pine (Me)	22.7	7.4	3.4	1.0	0.26	9.64	37.0

Using SIR, the metabolically active, glucose-responsive microbial biomass was quantified. SIR-derived biomass-C was strongly related to the basal respiration rate (r=0,759****). Additionally, highly significant correlations were found between biomass-C and pH in soils of the oak forests, the acidophilous beech forests and the spruce-fir-beech forests, where soil pH was low (Table 3). Measuring mi-

crobial biomass in soils of 40 beech forests, ANDERSON & JOERGENSEN 1997 also found that SIR was more affected by soil pH and basal respiration than FE, and FE was more affected by organic matter.

Table 2. Mean amounts of FE- and SIR-derived microbial biomass (µg biomass-N g^{-1} dw and µg biomass-C g^{-1} dw) and N_{mic}/N_t-ratios in the forest soils in spring and autumn 1997 (n= 10). Different superscripts indicate that the values are significantly different between sites at $p<0.05$.

	Spring			Autumn		
Forest type (site)	N_{mic} (FE)	C_{mic} (SIR)	N_{mic}/N_t (%)	N_{mic} (FE)	C_{mic} (SIR)	N_{mic}/N_t (%)
Oak (JE)	48.5^{cd}	470.3^{ef}	2.21^{cd}	71.1^{bcd}	587.6^{de}	2.02^{ef}
Oak (K)	60.1^{bcd}	944.9^{cd}	2.97^{bc}	79.9^{bcd}	772.1^{d}	2.91^{de}
Beech (JB)	104.6^{bc}	279.6^{f}	5.44^{a}	97.2^{bcd}	688.3^{de}	3.53^{cd}
Beech (KI)	114.4^{b}	318.6^{f}	3.48^{bc}	123.0^{bc}	582.5^{de}	5.09^{a}
Acid. Beech (D)	99.1^{bcd}	720.7^{de}	2.85^{bcd}	108.6^{bcd}	635.7^{de}	2.42^{e}
Acid. Beech (S)	77.3^{bcd}	526.7^{ef}	2.55^{cd}	44.7^{d}	496.1^{de}	1.38^{f}
Spruce-fir-beech (R)	207.6^{a}	1115.0^{bc}	2.21^{cd}	387.5^{a}	2678.0^{a}	4.54^{ab}
Spruce-fir-beech (N)	89.4^{bcd}	450.4^{ef}	2.47^{cd}	115.3^{bcd}	1154.4^{c}	2.81^{de}
Flood plain (M)	185.0^{a}	1401.0^{ab}	3.97^{b}	133.7^{b}	1784.9^{b}	3.97^{bc}
Flood plain (B)	93.8^{bcd}	1075.6^{c}	4.12^{b}	75.4^{bcd}	1257.4^{c}	2.44^{e}
Pine (St)	84.8^{bcd}	1606.3^{a}	1.48^{d}	110.9^{bcd}	562.4^{de}	2.42^{e}
Pine (Me)	41.2^{d}	972.3^{c}	1.57^{d}	56.8^{cd}	332.3^{e}	2.64^{de}

Table 3. Spearman´s rank correlation coefficients between microbial biomass C and N and soil chemical parameters.

	pH	Soil moisture	N_t	C/N	Glucose	Total sugars	Total amino acids
C_{mic}							
Oak	0.79****	-0.59**	0.33	-0.61**	0.57	0.62	0.60
Beech	0.26	0.37	0.17	0.18	0.42	0.40	0.38
Acid. Beech	0.69***	0.73***	0.76***	0.47*	0.76*	0.71*	0.86**
Spruce-fir-beech	0.68***	0.74***	0.74***	-0.19	0.81**	0.55	0.90**
Flood plain	-0.48*	0.48*	0.57**	-0.44*	0.62	0.57	0.29
Pine	-0.13	0.83****	0.84****	-0.84****	0.62	0.90**	0.76*
N_{mic}							
Oak	0.45*	-0.15	0.47*	-0.16	0.43	0.50	0.17
Beech	0.30	0.58**	0.59**	-0.40*	0.43	0.43	0.71*
Acid. Beech	0.41*	0.56**	0.62**	0.29	0.02	-0.02	0.19
Spruce-fir-beech	0.40*	0.65***	0.58**	-0.12	0.67*	0.60	0.48
Flood plain	-0.83****	0.72***	0.81****	-0.66***	0.83**	0.79*	0.64*
Pine	-0.24	0.67***	0.77****	-0.79****	0.52	0.86**	0.83**

*P < 0.05; ** P < 0.01; *** P < 0.001; **** P < 0.0001.

Table 4. Composition and quantity of sugars extracted from the forest soils in spring 1997; n=4. Different superscripts indicate that the values are significantly different between sites at $p<0.05$.

	Oak		Beech		Acid. Beech		Spruce-fir-beech		Flood plain		Pine	
Sugar	JE	K	JB	Kl	D	S	R	N	M	B	St	Me
						$\mu g\ g^{-1}$ dw						
Glycerole	5.3^{cd}	4.8^{cd}	6.2^{bcd}	2.7^{d}	8.8^{bc}	2.7^{d}	16.4^{a}	3.2^{d}	6.6^{bcd}	4.8^{cd}	9.9^{b}	6.19^{bcd}
Fructose	1.4^{b}	ND[1)]	ND	ND	ND	ND	ND	ND	ND	ND	8.8^{a}	10.30^{a}
Glucose	83.2^{bcd}	72.0^{bcd}	41.5^{bcd}	35.1^{bcd}	98.3^{b}	45.5^{bcd}	168.9^{a}	28.9^{cd}	48.8^{bcd}	26.8^{d}	93.6^{bc}	59.20^{bcd}
Mannitole	1.8^{bc}	ND	ND	ND	0.6^{c}	0.7^{c}	0.1^{c}	ND	ND	ND	8.5^{a}	4.67^{b}
Myo-Inositole	2.7^{bc}	2.4^{bc}	1.3^{c}	1.0^{c}	3.5^{abc}	2.3^{bc}	5.8^{a}	1.0^{c}	4.1^{ab}	1.9^{bc}	5.6^{a}	4.22^{ab}
Sucrose	ND	ND	ND	ND	ND	ND	ND	ND	ND	0.7^{a}	0.2^{a}	0.46^{a}
Trehalose	16.5^{d}	38.9^{bcd}	23.4^{cd}	27.7^{cd}	57.1^{ab}	79.5^{a}	64.3^{ab}	60.4^{ab}	49.8^{bc}	23.3^{cd}	58.6^{ab}	66.28^{ab}
Raffinose	0.8^{bc}	0.3^{c}	0.5^{bc}	ND	ND	ND	ND	ND	1.4^{ab}	ND	0.3^{c}	2.36^{a}
Total sugars	106.3^{bcd}	113.5^{bcd}	66.6^{cd}	63.8^{d}	159.5^{abc}	130.6^{bcd}	239.1^{a}	90.3^{bcd}	104.1^{bcd}	52.7^{d}	182.2^{ab}	147.5^{bcd}

[1)] Not detected or beneath the detection limit.

Table 5. Composition and quantity of amino acids extracted from the forest soils in spring 1997; n=4. Different superscripts indicate that the values are significantly different between sites at $p<0.05$.

	Oak		Beech		Acid. Beech		Spruce-fir-beech		Flood plain		Pine	
Amino acid	JE	K	JB	Kl	D	S	R	N	M	B	St	Me
						$\mu g\ g^{-1}$ dw						
Asparagine	0.13^{e}	0.24^{e}	0.25^{e}	0.26^{e}	0.89^{e}	0.42^{e}	0.62^{e}	0.24^{e}	0.68^{e}	0.30^{e}	3.06^{a}	1.87^{b}
Threonine	0.47^{e}	0.58^{de}	0.58^{de}	0.51^{e}	1.87^{bc}	0.60^{de}	1.91^{bc}	0.49^{e}	1.66^{bcd}	0.93^{cde}	3.86^{a}	2.57^{b}
Serine	0.56^{e}	0.65^{de}	0.66^{de}	1.07^{cde}	1.51^{bcd}	0.92^{cde}	1.57^{bc}	0.95^{cde}	1.58^{bc}	0.69^{de}	2.94^{a}	2.20^{ab}
Glutamine	0.82^{cd}	1.77^{cd}	0.86^{cd}	0.31^{d}	3.29^{cd}	3.71^{c}	2.06^{cd}	0.62^{cd}	3.63^{c}	1.51^{cd}	17.54^{a}	11.10^{b}
Proline	ND[1)]	ND	ND	ND	ND	0.09^{a}	ND	ND	ND	ND	0.06^{a}	0.09^{a}
Glycine	0.28^{e}	0.39^{de}	0.43^{de}	0.52^{de}	1.01^{cd}	0.49^{de}	1.17^{bc}	0.18^{e}	1.32^{bc}	0.53^{de}	2.48^{a}	1.69^{b}
Alanine	0.68^{d}	1.02^{cd}	1.01^{cd}	0.72^{d}	3.04^{bcd}	1.21^{cd}	4.60^{ab}	0.78^{d}	3.81^{abc}	2.28^{bcd}	6.21^{a}	4.57^{ab}
Citruline	0.60^{bcd}	0.62^{bcd}	0.60^{bcd}	0.19^{cd}	0.79^{bc}	1.75^{a}	0.78^{bc}	0.29^{cd}	0.51^{bcd}	0.05^{d}	1.06^{b}	1.11^{b}
Valine	0.77^{c}	1.36^{c}	1.02^{c}	0.63^{c}	3.03^{bc}	0.93^{c}	5.39^{ab}	0.79^{c}	5.19^{ab}	2.65^{bc}	7.24^{a}	5.12^{ab}
Methionine	ND	0.04^{b}	0.05^{b}	ND	ND	ND	0.12^{b}	ND	0.48^{a}	0.07^{b}	0.54^{a}	0.42^{a}
Isoleucine	0.40^{cd}	0.83^{cd}	0.45^{cd}	0.31^{d}	1.46^{bcd}	0.32^{d}	3.20^{ab}	0.26^{d}	3.47^{ab}	1.66^{bcd}	4.25^{a}	2.76^{abc}
Leucine	0.93^{d}	1.44^{cd}	1.23^{d}	1.05^{d}	1.99^{bcd}	1.08^{d}	4.20^{ab}	0.89^{d}	5.55^{a}	2.86^{bcd}	4.13^{abc}	2.59^{bcd}
Tyrosine	ND	ND	ND	ND	ND	ND	ND	ND	0.59^{b}	0.08^{e}	1.28^{a}	0.24^{e}
Phenylalanine	0.18^{cde}	0.30^{cde}	0.17^{cde}	0.23^{cde}	0.56^{bcde}	ND	1.18^{abcd}	0.12^{de}	1.57^{ab}	0.54^{bcde}	2.01^{a}	1.25^{abc}
Total Amino acids	5.80^{d}	9.23^{cd}	7.31^{d}	5.79^{d}	19.43^{bcd}	11.51^{bcd}	26.80^{bc}	5.59^{d}	30.04^{b}	14.17^{bcd}	56.67^{a}	37.57^{b}

[1)] Not detected or beneath the detection limit.

By means of the fumigation-extraction technique, the chloroform-susceptible microbes were quantified. The microbial biomass itself represents a labile pool of plant-nutrients (MARTENS 1995). In all soils under study, FE-derived microbial biomass-N was highly correlated (r=0,719****) to the amount of N mineralised under anaerobic conditions (data not shown). Thus, FE gave a measure for the nitrogen stored in the microbial biomass which constitutes a substantial part of the potentially mineralisable N-pool.

Incorporation of N into microbial biomass is expressed by N_{mic}/N_t-ratios, which were highest in the woodruff-beech forests and the flood plain forests. In soils of the spruce-fir-beech forest at site R, high amounts of microbial biomass in autumn were accompanied by a high N_{mic}/N_t-ratio (Table 2). In soils under forest stands of the same forest type, similar N_{mic}/N_t ratios were observed, indicating similarities in microbial N-immobilisation. Except for the oak and the woodruff-beech forests, N_{mic} and C_{mic} were both significantly correlated to total soil N (Table 3).

Soil microbial biomass parameters were positively correlated with amounts of sugars and amino acids in the soil organic matter, with significant correlations found in soils of all forest types except the oak forests (Table 3). Nevertheless, relationships were less pronounced than those of microbial biomass and other chemical and physical parameters analysed. It seemed that microbial population size was strongly influenced by soil pH, water content and humus and that microbial growth was not primarily restricted by the availability of organic compounds.

To specify the C and N-substrates available for soil microbes, soil extracts were screened for their contents of individual sugars and amino acids. Glucose and trehalose were the sugars found in highest concentrations (Table 4). In addition, glycerole and myo-inositole were detectable in all forest soils. Trehalose is known as a metabolite of mycorrhyzal fungi (MARTIN & al. 1988, NIEDERER & al. 1989) and therefore may be of special importance in forest soils. Glucose was also detected in tropical savannah and agricultural soils in the greatest amount, but there the next most abundant sugar was mannose (LARRE-LARROUY & FELLER 1997).

Of the amino acids analysed, glutamine, alanine, valine and leucine were prevailing. Amounts of individual amino acids varied considerably among forest stands. Absolute amounts of amino acids varied depending on the season. However, each forest stand showed a distinct pattern of individual amino acids which reoccurred at all sampling dates. Forest stands with a similar forest vegetation showed similar patterns of amino acids (Table 5). Amino acid profiles appeared to be highly influenced by vegetation composition, probably due to specific leaf litter chemistry and specific patterns of rhizodeposition from trees and herbaceous vegetation. Comparing arctic tundra ecosystems, KIELLAND 1995 found a unique distribution of individual amino acids in soils under each of the plant communities. There, glycine, serine, aspartic acid and arginine were prevailing. In agricultural soils, asparagine and aspartic acid as well as glutamine and glutamic acid were found in highest amounts (SENWO & TATABAI 1998).

Low molecular weight compounds enter the soil through plant litter decomposition, rhizodeposition and microbial metabolism as well as from decaying soil organisms. Once in soil, these substances may be used up very rapidly, with

typical half lives for amino acids being in the region of 1 to 12 hours (JONES 1999). Therefore, the concentrations of sugars and amino acids measured did not only depend on the amount, quality and decomposition rate of litter and on rhizodeposition, but were also determined by the turnover times of these substances. High concentrations of sugars and amino acids may indicate high substrate abundance as well as low turnover rates.

By correlating chemical parameters to microbial biomass within one forest type, we attempted to identify the predominant limitations to microbial growth in the investigated ecosystems. For example, in the more acidic soils microbial growth apparently was limited by low soil pH. By comparing soils of forest types, we investigated the relationships between ecophysiological parameters of microbial communities and vegetation. The forest stands selected for this study are widely unaffected by management practices and are mainly determined by natural environmental factors. Thus, they are especially suited for ecosystem studies. We suggest that soil microbial biomass-characteristics of natural forests are valuable reference-data for studies in cultivated or stressed ecosystems.

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