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Adaptation of Microbial Activities to the Environmental Conditions in Alpine Soils*

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Summary. The adaptation of soil microorganisms to different environmental conditions was investigated in the Austrian Central Alps (Hohe Tauern). The floristic composition of the soil fungi at different sites was determined and the CO_2-release from soils taken from different altitudes was measured at different temperatures. The results showed a decreasing diversity of soil fungi with increasing altitude and a change in the dominating species at different altitudes and/or with vegetation patterns. The relative rates of CO_2-release from soils from different altitudes did not differ at different incubation temperatures. It was concluded that, among soil fungi the selection of species is a more effective mechanism for the adaption to changed environmental conditions than metabolic adaptations.

Introduction

The changing climatic conditions at different altitudes are accompanied by differences in the composition of the vegetation. Thus the microflora that subsequently decompose the litter of this vegetation may require a different range of metabolic reactions than those utilized in other environments. At present it is not known how microorganisms adapt to changes in environmental conditions at different altitudes. Recent investigations on soils from different climatic zones (Mishustin 1978) have pointed to the presence of different ecological strains of one species. It was the aim of the work described here to study microbial adaptation in mountain habitats at different elevations with different vegetation patterns. For this purpose the altitudinal range of soils fungal species has been examined and the CO_2 release from soils from different altitudes has been measured in the laboratory at different temperatures.

Materials and Methods

Sites, Vegetation and Soils

The samples were taken in the Austrian Central Alps (Hohe Tauern) from southern slopes in altitudes between 1560 m and 2550 m. Sampling date: August 1978

Site 2,550 m: Alpine zone, open vegetation dominated by *Silene acaulis, Poa alpina, Saxifraga bryoides, Ranunculus alpestris, Salix herbacea.*

Soil[1]: Alpine pseudogley (A_h 1–3 cm, M 3–5 cm, bA 5–7 cm, B_s 7–16 cm, M 16–45 cm, C_v), pH 5.3 ± 0.7

Exponential mean temperature[2] of the soil (20.7–20.9.1979) $_eT$ at 10 cm: 11.0° C

Aspect: SSE

Site 2,300 m: Alpine zone, alpine grassland dominated by *Carex curvula.*

Soil: Alpine pseudogley (A_h 0–4 cm, E_g 4–13 cm, B_{vs} 13–70 cm) pH 4.3 ± 0.1

Soil temperature: (11.8.–30.9.1978): at 5 cm 6,84° C ± 2.24 K, at 10 cm 8.08 ± 2.03 K

Exponential mean temperature of the soil (20.7.–20.9.1979) $_eT$ at 10 cm 11.6° C

Aspect: S.

Site 1,920 m: Subalpine zone, alpine pasture dominated by *Nardus stricta, Poa alpina, Alchemilla vulgaris, Leontodon helveticus, Potentilla aurea, Ranunculus montanus.*

Soil: Pseudogleic brown soil (A_h 1–3 cm, AB 3–12 cm, B_v 12–45 cm, B_c 45–60 cm, C) pH 4.1 ± 0.3

Soil temperature (6.8–30.9.1978): at 5 cm 10.5° C + 2.9 K, at 10 cm 10.59° C + 2.64 K

Exponential mean temperature of the soil (20.7.–20.9.1979) $_eT$ at 10 cm 17.1° C

Aspect: S.

Site 1,650 m: Tall grass meadow dominated by *Dactylis glomerata, Trisetum flavescens, Arrhenatherum elatius, Trifolium repens, Trifolium pratense, Taraxacum officinale, Alchemilla vulgaris, Plantago lanceolata.*

Soil: Pararendsina (A_h 0–110 cm, C_v) pH 6.3–0.4

Soil temperature: (5.8.–30.9.1978): at 5 cm 12.1° C + 2.4 K, at 10 cm 11.98° C + 2.35 K

Aspect: SW.

Isolation and Identification of Fungi

At each of the study sites in a 10 × 10 m plot, 5 subplots were chosen at random. Soil samples were taken from the top 5 cm of each subplot and put in a sterile test tube. The samples were immediately transported to the laboratory at 6° C ± 2 K. The fungi were isolated the same

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1 Soil descriptions according to Neuwinger (1981 a)

2 Exponential mean temperature ($_eT$) estimated by the sugar inversion method according Pallmann et al. (1940) by Neuwinger (1981 a, b). Soil temperatures: data by Seeber (1981)

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day in order to avoid changes in the microbial populations during storage. 1 g of each soil was suspended in 100 ml of distilled water. From this suspension four replicates were diluted from 10^{-2} to 10^{-6} and 0.1 ml of each dilution was plated on two different nutrient media in petri dishes. After an incubation time of 1–3 weeks at 23° C, the colonies were counted and identified. The identifications were made in accordance with the descriptions: Raper and Thom 1949; Morton and Smith 1963; Zycha 1963; Seth 1970; Ellis 1971; Gams 1971; Raper and Fennell 1973; Arx 1974; Gams et al. 1975.

Culture Media

Medium 1. Mixtures A and B were combined after being autoclaved separately

A sucrose	20 g	B $NaNO_3$	2.0 g
malt extract	10 g	KCl	0.5 g
distilled water	400 ml	$K_2HOPO_4P_4$	0.5 g
		$MgSO_4 \cdot 7H_2O$	0.5 g
		$FeSO_4 \cdot 7H_2O$	0.01 g
		yeast extract	2.0 g
		agar	10.0 g
		distilled water	600 ml

Medium 2. Czapek Dox Agar with the addition of yeast extract (3 g).

Measurement of the CO_2 Release from Soil Samples

The soil samples were from the same subplots as those chosen for fungal identification. A 10 cm diameter soil core was taken from a depth of 40 cm and brought to the laboratory in polyethylene bags at 6° C ± 2 K. The CO_2 release was measured according to the Isermeyer-method (1952) with some modifications. The soils were passed through a 2 mm mesh screen, distilled water was added to attain a moisture content that was 60% of the maximum water saturation. The samples were then put into a sieve coated with nylon gauze, standing 5 cm over 400 ml 0.1 N barium hydroxide solution. The reaction vessels were tightly closed and incubated for 24 hours. Solution errors of the diffusion equalization were minimized by having a long incubation and a large reactive surface (490 cm^2) for the barium hydroxide. After exposure to temperatures of 4° C ± 0,5 K, 18° C ± 0.75 K, 23° C ± 1 K and 30° C ± 1 K, the barium hydroxide solution was titrated with 0.1 N HCl with phenolphthalein as indicator. The CO_2 release of the soils was expressed as g $CO_2 \cdot m^{-2} \cdot d^{-1}$. The values are arithmetic means of five subplot samples at each sites.

Results

Habitat Distribution of Various Species of Fungi

From all samples taken 354 fungal clones were isolated and 44 different strains were found. At 2,550 m altitude the predominating soil fungi (Table 1) were *Chaetomium homopilatum, Cladosporium herbarum* and *Chrysosporium pannorum*. Whereas *Chaetomium* was only isolated at this height, the latter two were also found at 2,300 m. One species from each of the genera *Monascus, Paecilomyces* and *Fusarium* was isolated from the soil of the alpine grass land at 2,300 m. *Trichocladium opacum, Trichoderma inflatum* and *Aspergillus versicolor* were only found in the soils of the alpine pasture at 1,920 m. *Aspergillus fumigatus* and one species from each of the genera *Cylindrocarpon* and *Pseudogymnoascus* was isolated both from the soil of the pasture (1,920 m) and from the tall grass meadow at 1,560 m. Fungi of the genera *Volutella, Monilia, Penicillium* and *Mucor racemosus* predominated only in the tall grass meadow (1,560 m). *Mortierella* was found in all soils investigated, particularly in the alpine soils. The sometimes coprophilic fungus *Mucor racemosus* was found in the manured or pastured soils between 1,560 and 2,300 m. The diversity of fungal species decreased with increasing altitude (Table 1). In addition, it appeared that the dominating fungal species at each altitude were different.

Table 1. Distribution of the dominating fungi in soils at different altitudes

Altitude	2,550 m	2,300 m	1,920 m	1,560 m
Vegetation	open veg. (cushions)	alpine grass-land	alpine pasture	tall grass meadow
Soil type	alpine pseudo-gley	alpine pseudo-gley	brown soil	para-rend-zina
pH	3.5 ± 0.7	3.4 ± 0.1	4.1 ± 0.3	6.3 ± 0.4
Cheatomium homopilatum	**			
Cladosporium herbarum	**	*		
Chrysosporium pannorum	**	*		
Monascus sp.		*		
Paecilomyces sp.		*		
Fusarium sp.		*		
Trichocladium opacum			*	
Trichoderma inflatum			*	
Aspergillus versicolor			*	
Aspergillus fumigatus			*	*
Cylindrocarpon sp.			*	*
Pseudogymnoascus sp.			**	**
Volutella sp.				*
Monilia sp.				*
Penicillium sp.				**
Mucor racemosus				*
Mucor parvisporus		**	**	*
Mortierella	**	**	*	*

CO_2 Release

At all sites investigated in the rise in temperature from 4° to 18° C brought about an increase in CO_2 release by a factor of 4, whereas from 18° to 30° C, the increase was only by a factor of 1.2 (Fig. 1). In the range from 18° to 30° C the CO_2 release was in step with the optimum growth curve of the soil microorganisms. The absolute values for CO_2 release were higher in samples taken from the lower altitudes than in those from the higher altitudes. If the values measured at 30° C are taken to present 100% (Fig. 2), then the relative values for all soils were almost identical. The Q_{10} values were 1.45 between 5° C and 15° C, 1.40 between 10° and 20° C, 1.27 between 15° C and 25° C and 1.10 between 20° and 30° C for all soils. There appeared to be an almost linear increase in CO_2 release between 5° and 20° C. However, as the Q_{10} values for the very complex conditions in this experiment had very little biological significance, a CO_2 release matrix was constructed (Table 2). This

Tabelle 2. Change in CO_2 release at different temperatures, y → x shows the decrease in the CO_2 release between two temperatures, x → y the increase as a percentage of the initial value

CO_2 release matrix

30° C	95	75	50	30	10	3
25° C	92	72	47	27	7	
20° C	85	65	40	20		
15° C	65	45	20			
10° C	45	25				
5° C	20					
	0° C	5° C	10° C	15° C	20° C	25° C

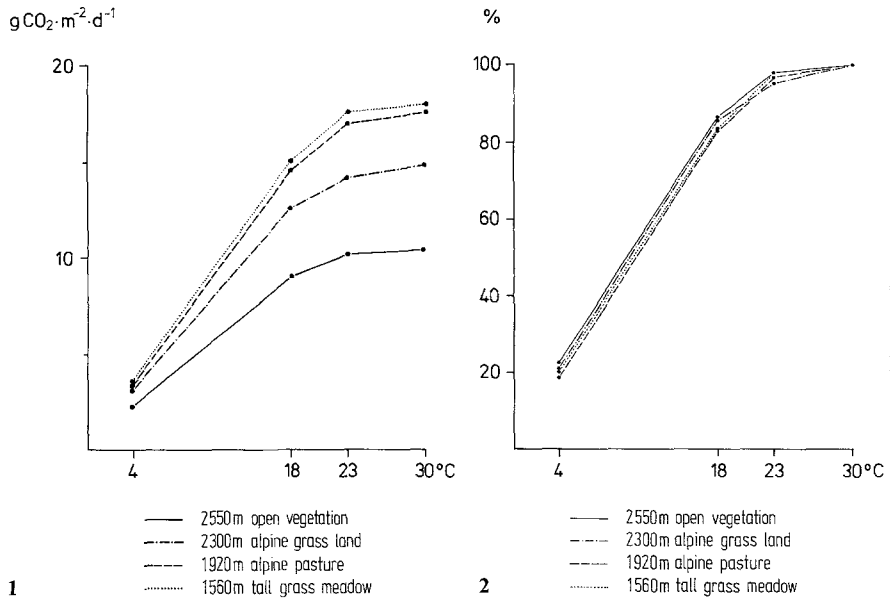

Fig. 1. CO_2 release of soil samples taken from different altitudes at 4° C, 18° C, 23° C and 30° C during an incubation time of 24 h

Fig. 2. Relative CO_2 release of soil samples taken from four different altitudes at 4° C, 18° C, 23° C and 30° C. The CO_2 release of the soils at 30° C was assumed to be 100%

matrix provides information on the change in CO_2 release (to be read as a percentage) with temperature changes in the range between 5° and 30° C. If the diagram is read from y→x there is seen to be a decrease in CO_2 release with decreasing temperatures, while if it is read from x→y then the diagram shows an increase in CO_2 release with an increase in temperature. For example, a temperature drop from 20° to 15° C caused a decrease in CO_2 release of 20%.

Discussion

Only small differences in soil temperature were observed between the plots at the different altitudes during the vegetation period (2,300 m in 5 cm 6.8° C, 1,560 m in 5 cm 12.1° C). This variation contrasts strongly with the distinctly different vegetation types at the different altitudes. Thus it might be expected that there should have been differences in the fungal species to reflect the differences in the available substrates rather than differences in climate. This expection was confirmed by the observation that there were quite different fungal species in the soils at the different altitudes. Furthermore, a decrease in the diversity of fungal species at higher altitudes was paralleled by a decrease in the diversity of plant species. Just as the rate of litter decomposition is controlled by differences in the chemical composition of litter (Schinner 1978), so the spectrum of fungal species concerned with litter decomposition is likely to differ in the same way. In addition to the differences in the contents of lignin, cellulose and hemicellulose, considerable differences in the content of compounds that store energy may also occur. *Ericaceae* in particular are known to accumulate considerable amounts of starch and lipids (Larcher et al. 1973). It is quite clear that the pattern of distribution of fungi is affected by many environmental factors. Nutritional conditions (Rehder and Schäfer 1978) and microclimatic factors must have a decisive influence on the distribution of individual species. The widespread distribution of *Mucor parvisporus* in this study was of particular interest, since it often grows on manure (Zycha 1963). This species was found frequently in the alpine sedge meadow (2,300 m), on which sheep and cattle graze, and also in the alpine pasture at 1,920 m, used by cattle. However, the tall grass meadow (1,560 m), which had been top-dressed with stable manure, showed only a few records of this species. It would seem that this fungus prefers substrates with a high content of nitrogen and decomposed carbohydrates. However, the distribution of the genus *Mortierella*, which was isolated at all sites, appeared to be almost independent of substrate or environmental conditions. The domination of the fungus, *Cladosporium herbarum*, at the sites at 2,550 m and 2,300 m, appeared to be a characteristic of these soils. Dowding and Widden (1974) investigated the relationship between fungi and their environment in different tundra regions and observed the ubiquitous presence of the genus *Cladosporium*. The basidiomycetes and ascomycetes mycoflora offers further examples of the species selection and adaptation (limitation) in the transitional zone from subalpine forests to alpine tundra (Moser 1981).

The measurement of CO_2 release gives indirect information on the metabolic activities of the soil micro-organisms. However, it does not differentiate between the metabolic activity arising from a low number of species with high activities, and that arising from a high number of species with low activities. The measurement of CO_2 release reflects the microbial activity that is controlled by substrate concentrations, by variations in the microclimate, and by other environmental factors. Some of the CO_2 that is released is quickly bound by organisms in the soil by anaplerotic reactions and by microbially autotrophic processes. Thus the CO_2 release that is measured represents a net balance of a series of reactions. In the present investigation the activity of soil samples taken from soils at 1,560 m, 1,920 m, 2,300 m and 2,550 m was determined at 4° C, 18° C, 23° C and 30° C. While the absolute values for CO_2 release in the soil samples taken from each altitude differed as a result of variability in litter content and in the activities of individual microbial species (Fig. 1), the relative values were almost identical (Fig. 2). If the soil micro-organisms are able to adapt to differences in soil temperature, then the alpine soil at an elevation of 2,550 m and at a temperature of 4° C ought to show, according to a homoeostatic adaptation, a relatively higher CO_2 release than soil at 1,560 m above sea level. Mishustin (1978) found different ecological strains of one species of micro-organism in soils in different climatic zones. This was not observed in the present investigation. The results of the present investigation indicate that soil micro-organisms adapt to different altitudes (and hence to different vegetation and soil types) by a selection of species

and not by metabolic adaptation or by forming new ecological strains.

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