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DIVERSITY OF SOIL ORGANISMS IN ALPINE AND ARCTIC SOILS IN EUROPE. REVIEW AND RESEARCH NEEDS

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SUMMARY.- The diversity of soil organisms and soil ecological processes in different mountain regions of Europe are reviewed. Detailed taxonomic studies on soil organisms have been made in the Alps and in Northern Europe since the end of the last century, however, there is a paucity of data from Southern Europe. Future studies could include the re-sampling of historic study sites to assess if there has been a change in the soil fauna and microorganisms. The role of key abiotic processes such as cryoturbation should be quantified and further research should focus on identifying indicator organisms, keystone species and functional groups. In addition, studies on soil organic matter and particularly on humus forms, the products of soil ecological processes should be encouraged. Ecotones, where the influence of spatial heterogeneity on soil biodiversity is likely to be particularly pronounced, appear to be the most rewarding for such studies.

RÉSUMÉ.-La diversité des organismes du sol et les différents processus écologiques ayant lié dans les diverses régions de montagne en Europe sont détaillés. Des études approfondies sur la taxonomie des organismes du sol ont été developpées dans les Alpes et en Europe du Nord depuis la fin du siècle dernier, mais par contre il y a peu de données sur l'Europe du Sud. Dans l'avenir on pourrait re-étudier les sites bien connus de façon à savoir s'il y a eu de changements dans la faune et les microorganismes du sol. Il faudrait quantifier le rôle des processus abiotiques comme la cryoturbation, identifier les organismes indicateurs, les espèces-clé et les groupes fonctionnels. Il est aussi indispensable de développer les études sur la matière organique et en particulier les types d'humus, en tant que résultat des processus écologiques du sol. Les écotones, dans lesquels l'influence de l'heterogeneité spatiale sur la biodiversité du sol est particulièrement prononcée, semblent les plus pertinents pour de telles études.

RESUMEN.- Presentamos una revisión de los organismos del suelo y de los procesos ecológicos edáficos en las diferentes zonas de montaña de Europa. En los

Alpes y en Europa septentrional se han llevado a cabo estudios taxonómicos detallados sobre los organismos del suelo, pero tenemos pocos datos de Europa meridional. De cara al futuro se tendrían que volver a muestrear los parajes que dieron lugar a estudios clásicos, de modo que se pudiera comprobar si ha habido cambios en la edafofauna y en los microorganismos. Convendría también cuantificar los procesos abióticos como la crioturbación y atender a la identificación de organismos indicadores, especies-clave y grupos funcionales. Hay que apoyar además los estudios sobre la materia orgánica del suelo, particularmente los tipos de humus, como productos que son de los procesos ecológico-edáficos. En todos esos estudios se muestran prometedores los ecotonos, por cuanto la influencia de la heterogeneidad espacial en la biodiversidad edáfica parece primordial.

Keywords: Soil organisms, biodiversity, alpine and arctic Europe.

1. Biodiversity

Conservation of biodiversity has become increasingly topical (e.g. GROOMBRIDGE, 1992; HUSTON, 1994; HEYWOOD & WATSON, 1995; CATIZZONE *et al.*, 1998). From an ecological perspective research on biodiversity is of prime interest in relation to ecosystem functioning (e.g. SCHULZE & MOONEY, 1993; NAEEM *et al.*, 1994; DI CASTRI & YOUNÉS, 1996) and especially to the stability of ecosystems (WALKER, 1989; BERENDSE, 1993; GREENLAND & SZABOLCS, 1994; CHERNOV, 1995). Investigations on biodiversity are nowadays often related to sustainability (e.g. HAWKSWORTH, 1991) or global climate change (BOER & KOSTER, 1992; CHAPIN *et al.*, 1992; HOLTEN *et al.*, 1993; SOLBRIG *et al.*, 1994; WATSON *et al.*, 1996).

Most recent studies on arctic and alpine biodiversity have been concerned with plant diversity (e.g. CHAPIN & KÖRNER, 1995) focusing on North America and Russia, where arctic and sub-arctic ecosystem research has had a long tradition (e.g. BEHAN-PELLETIER, 1993; HERSHEY *et al.*, 1995; HOBBIE, 1995; PASTOR, 1995; SCHIMEL, 1995). Relatively little studied have been soil biochemical cycling and interrelationships between soil and plants in alpine (MEYER & THALER, 1995; PASTOR, 1995) or (sub-) arctic areas (BEHAN-PELLETIER & BISSETT, 1992; CALLAGHAN & JONASSON, 1995; CALLAGHAN *et al.*, 1995) in Europe. It would be relatively simple to initiate more research in the specialised field of soils and biodiversity because of the broad background in European mountain research with respect to global change and specified future research needs (BENISTON, 1994; GUISAN *et al.*, 1995; PRICE, 1995)

2. Soil ecology and soil organisms

In this paper soil ecology is defined as the science of interactions among soil biota and between the soil biota and the abiotic environment. Soil ecological research focuses on the interdependence between soil physical and chemical properties and soil organisms, soil organic matter, decomposition, nutrient cycling, and interactions in the rhizosphere. Soil organisms and soil ecological processes respond very sensitively to human disturbances therefore they should be considered in recommendations on environmental change (GISI *et al.*, 1997).

Only those soil organisms which play an important role in ecosystem functioning have been taken into account. Apart from microorganisms, these include the following invertebrate groups: lumbricidae, enchytraeidae, collembola, acari, diplopoda, isopoda, nematoda, protozoa and insect larvae. Some small mammals, especially burrowing rodents, may influence soil properties in alpine areas in many ways (e.g. HOLE, 1981; HUNTLY & INOUYE, 1988; MEADOWS & MEADOWS, 1991; BASSANO *et al.*, 1992; CORTINAS & SEASTEDT, 1996). The interactions between these animals and the vegetation have been investigated (e.g. ANDERSSON & JONASSON, 1986; HANSSON, 1987; MOEN *et al.*, 1993; HERRERO *et al.*, 1994) and an important example is rodent damage to tree seedlings in mountain forests where the regeneration of a whole ecosystem may be affected. Rodents are also important in influencing soil ecological processes in Fennoscandia where many studies have been made on them (e.g. HENTTONEN, 1995). Despite the important role mammals play in soils of arctic and alpine areas they could not be included in this review.

In arctic and alpine regions many soil organisms are adapted to the extreme environmental conditions (viz. MANI, 1968; CALLAGHAN *et al.*, 1992) and both psychrophilic microorganisms (e.g. HERBERT & CODD, 1986) and soil invertebrates have developed special adaptations to survive (e.g. BRINCK, 1974; WALLWORK, 1976b; BLOCK, 1990; SØMME, 1995). For example, glycerol is a very important cryoprotectant for the soil mesofauna (COULSON *et al.*, 1995). Another example is the existence of subnivean food chains (e.g. AITCHISON, 1984). The activity of microorganisms below zero temperatures has long been underestimated (e.g. CLEIN & SCHIMEL, 1995), although some workers in the Alps have reported cold hardiness and tolerance to desiccating conditions by collembola (BLOCK & ZETTEL, 1980) and millipedes (MEYER & EISENBEIS, 1985).

3. Diversity of soil organisms

Although a large body of literature on biodiversity exists, comparatively few investigations have been carried out on biodiversity of soil organisms to date (e.g. LEE, 1991, 1994; BERNARD, 1992 for nematodes; TRÜPER, 1992 for prokaryotes; HAWKSWORTH & COLWELL, 1992; FRECKMAN, 1994; SOMBROEK, 1994). There is a paucity of data at the species level (e.g. GROOMBRIDGE, 1992; HAWKSWORTH & RITCHIE, 1993); only about 11% of estimated bacteria species in the world are described, and the figure for fungi is only 5% (HAWKSWORTH, 1991). In extreme environments such as those in alpine and arctic areas many species are unknown (GROOMBRIDGE, 1992). Many new methods (e.g. molecular biological methods) have been developed for identifying microorganisms that are also available for studying microorganisms in alpine and arctic environments.

The diversity of soil organisms is of great importance for ecosystem functioning (SCHULZE & MOONEY, 1993; ALLSOPP *et al.*, 1995; COLLINS *et al.*, 1995; LAVELLE *et al.*, 1995; DI CASTRI & YOUNÉS, 1996; HEAL *et al.*, 1996). Most of the reported studies have been made in relation to sustainable agriculture (HAWKSWORTH, 1991; GREENLAND & SZABOLCS, 1994) and natural ecosystems have been of less interest (MOLDENKE *et al.*, 1994). A diverse array of soil organisms is necessary for decomposition and biogeochemical cycles in every ecosystem, natural or managed (LEE, 1991; BEARE *et al.*, 1995). The functioning of nutrient cycles is a good indicator of ecosystem integrity and stability (BERENDSE, 1993; SCHULZE & MOONEY, 1993; COLEMAN *et al.*, 1994). Earlier studies have acknowledged the importance of the diversity of the soil fauna and its role in ecosystem functioning (e.g. WALLWORK, 1976a; DANKS, 1981), but perhaps overlooked the importance of the diversity of microorganisms.

There is an important connection between the diversity of soil organisms and climate change (COLEMAN *et al.*, 1992; DANKS, 1992; SØMME, 1993). An increase in temperature could have a pronounced effect on the carbon and nutrient cycles in alpine and arctic regions (CHAPIN *et al.*, 1992). It is believed that currently these regions act as carbon sinks, but they could become carbon sources through for example increased mineralisation rates (HEAL *et al.*, 1998). The impacts on soil microbial activity could therefore be better predicted if the diversity of soil organisms and soil ecological processes in these extreme environments were better known.

4. Soil ecological processes and the diversity of soil organisms in the different mountain regions of Europe

In the alpine regions of Central Europe there has been a long tradition of research on soil organisms (viz. PERTY, 1849) and there is a large body of literature on the soil fauna in Austria and Switzerland dating back to the turn of the 20[th] century. The collembola and myriapoda (e.g. VERHOEFF, 1896; CARL, 1899; DIEM, 1903; HANDSCHIN, 1919; ATTEMS, 1949; JANETSCHEK, 1949; GISIN, 1957; SCHWEIZER, 1961) and lumbricides (e.g. ROSA, 1887; RIBIAUCOURT, 1896; BRETSCHER, 1900) have especially been well treated. More recently, a large number of ecological studies have investigated the interactions between vegetation and soil mesofauna including changes along altitudinal gradients (e.g. JAHN, 1960; CHRISTANDL-PESKOLLER & JANETSCHEK, 1976; NURMINEN, 1977; THALER *et al.*, 1978; LIENHARD, 1980; MEYER, 1981, 1985; SCHATZ, 1981; TROGER, 1981; REUTIMANN, 1987; JANETSCHEK, 1993; LESER, 1994). Investigations on mesofauna are still being carried out (e.g. THALER *et al.*, 1993) and MEYER & THALER (1995) have recently reported their diversity in alpine regions. Earthworms are important representatives of the soil macrofauna have been studied by SISTANI (1980), KÜBELBÖCK & MEYER (1981), ZICSI (1981) and CUENDET (1987). Austrian workers have been outstanding in their treatment of the soil microfauna (BERGER *et al.*, 1985; FOISSNER, 1985; FOISSNER & PEER, 1985) including nematodes (GERBER, 1985). Reviews on alpine areas along with the results of the Austrian MAB programme «Hohe Tauern» include those by FRANZ (1975, 1980, 1981) and SCHALLER's (1994) general overview on soil zoology in Austria.

Many studies of soil microbiology have been carried out in Austria including an early study by GAMS (1959). One of the most important sources of knowledge in this special field has been the above mentioned MAB projects, where most of the microbiological investigations were made by Schinner and co-workers. Their results on abandoned pastures and along altitudinal gradients were summarised by CERNUSCA (1978, 1989). In addition to taxonomic identification and quantification of soil microorganisms, the following have been characterised: processes of the carbon and the nitrogen cycles (REHDER & SCHÄFER, 1978; HAUNOLD *et al.*, 1980; BRUNNER & BLASER, 1989; HACKL *et al.*, 1995) and decomposition rates (e.g. SCHINNER, 1982; GSTRAUNTHALER & SCHINNER, 1989; SCHINNER & GURSCHLER, 1989; SCHINNER *et al.*, 1989). The investigated alpine soils had a relatively low number of fungi species, high cell counts of bacteria, actinomycetes and yeasts. From soil respiration measurements it has been concluded that soil microorganisms were adapted to low temperatures in the alpine zone. Decomposition has been reported to be most intensive after snow melt in early summer, whilst tends to be followed by a decrease in microbial activity during summer because of low soil moisture. The initial studies on soil respiration at abandoned alpine sites by CERNUSCA *et al.* (1978) have later been extended to include the relationship between soil respiration and secondary succession in the Italian Alps (INTEGRALP project, TAPPEINER & CERNUSCA, 1994). Mycorrhizae have also been studied in the Austrian MAB projects. Ericoid mycorrhiza in the dwarf shrub heath and the vesicular-arbuscular mycorrhiza of the grass and herbaceous species in grass heath communities have been shown to be important for plant nutrition with the ericoid infection intensity decreasing with altitude (HASELWANDTER & READ, 1980; HASELWANDTER, 1989). In alpine areas mycorrhizal infection is of special importance for re-afforestation projects (ALLEN *et al.*, 1987; GÖBL, 1994). Changing abiotic site factors and their influence on soil microorganisms along altitudinal gradients have also been considered (DUTZLER-FRANZ, 1981), however it has been difficult to demonstrate changes along an altitudinal gradient as they may easily be offset by microtopographic heterogeneity (SCHINNER, 1983; McCOY, 1990; RANGGER *et al.*, 1994).

In Germany, there have only been few studies on the soil fauna in alpine soils (e.g. TOPP, 1975; BOLLER, 1986; GEMESI *et al.*, 1995; SKAMBRACKS, 1996). Most of the soil ecological studies in the German Alps have been carried out in the Berchtesgaden National Park as part of a MAB project (HABER *et al.*, 1990). Humification processes, in particular chemical characterisation of humic substances (BOCHTER & ZECH, 1985; KÖGEL, 1987; KÖGEL *et al.*, 1988), have been of primary interest and investigations focused more on the products of soil ecological processes, including humus forms (BOCHTER, 1988), than on the soil organisms themselves.

Studies of soil fauna, lumbricides in particular, and soil ecology have had a long tradition in France (e.g. BOUCHÉ, 1995; LAVELLE *et al.*, 1995). In the Alps, however, the main emphasis has been on microbial activity, especially nitrogen mineralisation (BOUDOT & CHONE, 1985; GOURBIÈRE, 1986; TOSCA, 1986; PORNON & DOCHÉ, 1994).

There is a paucity of data on soil ecological processes in the southern part of the Alps and the Iberian Peninsula. There have been some recent ecological investigations on altitudinal gradients in Italy (e.g. DI CASTRI, 1973; BRANDMAYR *et al.*, 1995) after earlier studies on soil fauna (e.g. VERHOEFF, 1932). SIMON *et al.* (1994) have reported their work on soil organic matter in the Sierra Nevada, Spain.

There is a long list of publications on soil organisms from the eastern part of Europe, however, most of them were published locally. Taxonomic and ecological investigations have been reported for the Carpathians (KURCHEVA, 1972; RUSEK *et al.*, 1975; STRIGANOVA, 1975; POPOVICI, 1984; POP, 1987; NOSEK, 1986; HARSIA, 1995; POP & VASU, 1995), the Caucasus (GHILAROV, 1979; STRIGANOVA & MAZANTSEVA, 1979; SAMEDOV & BABABEKOVA, 1980) and some other regions such as the Pieniny mountains (WASILEWSKA, 1974). Recently, the influence of pollution on mountain forest soils has become of special interest (RUZICKA & ZACHARDA, 1994; BOHAC & FUCHS, 1995; CHALUPSKY, 1995). The number of studies for the southeastern part of Europe e.g. in Greece is few (NAKOS, 1984; LEGAKIS, 1986).

In contrast, there is a large body of literature in Northern Europe. One of the oldest study areas for soil zoologists has been the Svalbard (e.g. RÖMER & SCHAUDINN, 1900; NURMINEN, 1965a; RÜPPELL, 1968; BENGSTON *et al.*, 1974; COULSON *et al.*, 1995; HODKINSON *et al.*, 1996; 1998). Recent years have seen some publications on interactions between soil fauna, microorganisms and abiotic site conditions (e.g. SVEUM, 1986; VÄRE *et al.*, 1992; WÜTHRICH, 1994; WÜTHRICH *et al.*, 1994; DÖBELI, 1995; HODKINSON *et al.*, 1996) including global change aspects (HODKINSON *et al.*, 1998). In addition to Svalbard, the mountains of Lapland and the Scandinavian mountains have been the main areas for studies on soil organisms in Scandinavia (TRÄGARDH, 1910; BRINCK & WINGSTRAD, 1949; DALENIUS, 1960; NURMINEN, 1965b; CADWALLADR, 1969; SENICZAK & PLICHTA, 1978; HAGVAR, 1982; KOPONEN, 1984), especially at the IBP sites (FJELLBERG, 1975; HAGVAR & OSTBYE, 1975; SOLHØY, 1975). Many soil zoologists working in Finnish Lapland have focused on soil mesofauna (e.g. KOPONEN & OJALA, 1975; SOLHØY & KOPONEN, 1981). Numerous studies have dealt with microorganisms and decomposition (BERG *et al.*, 1975; CLARHOLM *et al.*, 1975; ROSSWALL *et al.*, 1975; MOSIMANN, 1985; MÜLLER *et al.*, 1994) and some investigated the impact of acid rain (KYTÄVIITA *et al.*, 1990; NEUVONEN & SUOMELA, 1990). Co-operative projects between Finnish and Russian ecologists have researched heavy metal pollution on the Kola Peninsula (GILYASOVA, 1993; KONEVA, 1993; EVDOKIMOVA, 1995). In Greenland and Iceland taxonomic studies have been made for long (e.g. JÖRGENSEN, 1934; SELLNICK, 1940), but little experimental research on soil organisms has been reported (e.g. RICHARD & HARMSTON, 1972).

5. Research needs

Many research recommendations have been made about biodiversity in a changing climate (e.g.: SOLBRIG *et al.*, 1994) and about soils and climate change (ARNOLD *et al.*, 1990; BOUWMAN, 1990; COLEMAN *et al.*, 1992; ROUNSEVELL & LOVELAND, 1994). Some of these concern priorities for further research on biodiversity in mountain areas (e.g. CHEMINI, 1994) and there are many more on mountain research in general (e.g. OZENDA & BOREL, 1991; IVES, 1992; UNCED, 1992). Some of them, however, are reiterations of topics discussed for the past 20 years (*viz.* MÜLLER-HOHENSTEIN, 1974; UNEP, 1980), especially in relation to the stability of alpine ecosystems (GIGON, 1983; IVES & MESSERLI, 1984).

The published recommendations for priority research on biodiversity apply particularly to soil ecology. Comparisons between the results of detailed taxonomic studies on soil organisms made in the late 19th and early 20th century and those of current research have shown a loss of species in several mountain regions (ALPNET, unpublished). However, this kind of comparison (regarding α-diversity) is fraught with uncertainties because of the large number of organisms involved and because there are still many undescribed species. Research has begun to focus on finding indicator soil organisms (HAWKSWORTH, 1992; FOISSNER, 1994) and keystone species (SCHULZE & MOONEY, 1993), but rarely in mountain areas. Important types of keystone species are earth movers which affect soil ecological processes by bioturbation. Decomposers and mycorrhizae are also important types of keystone species for nutrient cycling. Abiotic agents which cause physical disturbances such as cryoturbation, contribute to key proceses which have a bearing on the diversity of soil organisms. In the lowlands and in low mountain areas lumbricides are the most important indicator organisms (e.g. GLASSTETTER, 1991) and they also play an important role in high mountain ranges (e.g. POP, 1987; POP & VASU, 1995; SKAMBRACKS, 1996), with the exception of northern Europe with low temperature.

A right step would be to identify species ecotypes and functional groups (SINNIGE *et al.*, 1992; ZVYAGINTSEV *et al.*, 1992; SCHULZE & MOONEY, 1993) and to study below-ground food webs in mountain soils. It would also be desirable to understand the ability of species to invade after perturbation and how this affects the habitat. Redundancy aspects should also be taken into account (SCHULZE & MOONEY, 1993; EUROPEAN COMMUNITY, 1994). Until now, such studies in soil ecology have more or less been restricted to agro-ecosystems (e.g. ANDRÉN *et al.*, 1995). There is a considerable scope for experimentation there.

With regard to mineralisation and humification, research should focus on meso- and microhabitats of microorganisms in soil organic matter. Also, this would help to provide recommendations on how to protect humus on mountain slopes, particularly where there is intensive erosion. Another issue is the rhizosphere, where the role of mycorrhizae in alpine and arctic areas should be more intensively investigated.

Soil type, including humus form, is an important tool to characterise habitats. The influence of abiotic site factors such as texture and pH, on soil organisms and their activity has been widely studied. However, the role of soil organisms in pedogenesis is often neglected today, but had previously been studied by KUBIENA (1943) and KÜHNELT (1944). They have shown the impact of lumbricides on the genesis of mull rendzina soils (see MARTINUCCI & SALA, 1979). Some related studies have also been conducted in alpine areas by FREI (1944), ZÖTTL (1965), GILOT & DOMMERGUES (1967), GRACANIN (1970) and SZABÓ (1974). The description of the humus form to characterise habitats for soil organisms is very useful because the humus form is the result of the activity of organisms. Such work has to date been made in forest soils, the results of which only apply to a limited extent to subalpine and alpine situations (F. EDNORZ *et al.*, unpublished). In mountain regions, natural and managed grasslands cover large areas (CERNUSCA, 1991) and an improved classification of grassland humus forms would help classify habitats for soil organisms (BROLL & BRAUCKMANN, 1994).

In addition to elevational gradients (e.g. McCOY, 1990), the spatial heterogeneity in mountain areas —especially at the ecotone level— is of importance for soil ecological processes (JENNY, 1980; NEUWINGER, 1987; HOLTMEIER & BROLL, 1992; BROLL, 1994; BROLL & HOLTMEIER, 1994; HOLTMEIER, 1994; KEPLIN, 1994; ADAM, 1995; BEDNORZ *et al.*, 1999). A further step in understanding ecological dynamics at the ecosystem and landscape scales (GRABHERR, 1994; HUSTON, 1994; DUELLI, 1995) has already been taken in the Arctic interdisciplinary research conducted in North America (e.g. BLISS *et al.*, 1981; SVOBODA & FREEDMAN, 1992; REYNOLDS & TENHUNEN, 1996). This should be sought in Europe. New initiatives on soil ecological research in Europe could build on the knowledge available from MAB and IBP programmes and use their sites (e.g. ROSSWALL & HEAL, 1975; WIELGOLASKI, 1975a; 1975b; FRANZ, 1981; CERNUSCA, 1989). In this respect the Natural Environmental Research Council (U.K.) research programme on «Soils and Biodiversity» is particularly welcome.

In line with general recommendations for biodiversity research, the monitoring of permanent plots could be combined with using existing long-term sites such as those of ITEX. Applied studies on the impact of recreation and tourism in mountain areas (e.g. MOSER *et al.*, 1987; JANETSCHEK *et al.*, 1987; MEYER, 1993; TROCKNER & KOPESZKI, 1994) should have a soil ecological component in the future. Current soil ecological research uses many new methods, e.g. mesocosm studies and molecular biological methods for determination of microorganisms, which could be applied in alpine and arctic areas, also (ROBINSON & WOOKEY, 1997). New classification approaches in soil ecology should be developed to achieve wider ecological applications (e.g. FABER, 1991; SINNIGE *et al.*, 1992; BEARE *et al.*, 1995).

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