Dirk Mohr

Soil degradation in simple oak coppice forests of the Ahr-Eifel

- Implications for forest management derived from soil ecological studies -

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Dirk Mohr

Für Pata

Contents

I Introduction

The present composition and distribution of most central European forests is the result of various impacts by man dating back to the Stone age (HÜTTL et al. 2000). Oak forests were exploited as cattle pastures or as resources for firewood, charcoal burning and tanbark from the fifteenth century on. As a consequence of the short felling cycles (16-20 years), simple oak coppice forests ("Eichen-Niederwald") dominated over other oak forest systems and were widely distributed in the German low mountain ranges during the past centuries (MÜLLER-WILLE, 1980). In the last decades, the economical importance of coppice management has decreased in most of the West-German forest regions so that simple coppice forests have been transformed to high forests, conifer forests or have been left unmanaged (MANZ 1995). As a result, their distribution in the German low mountain ranges tends to decrease and MÜLLER-WILLE (1980) even regards them as a dying forest type. However, the ecological significance of simple oak coppice forests as unique and rare ecosystems is indisputable and has been stressed by many foresters and scientists (HACKER 1983, SCHMIDT 1986, DENZ 1994, POTT 1995).

The importance of gaining knowledge about effects of abiotic and biotic factors on the interrelationships in forest ecosystems is growing (NILSSON et al. 1995). But so far little is known about the abiotic and biotic interactions which determine the stability of simple oak coppice forests in terms of their capacity to return to a norm or "steady-state" following perturbation by man (KHANNA & ULRICH 1991). The stability of forest ecosystems depends, to a high degree, on the functioning of nutrient mobilisation and recycling in the soil (COLE 1995, POWERS et al. 1998).

In a previous study strong indications for forest soil degradation in simple oak coppice forests of the Ahr-Eifel were found (MOHR & TOPP 2001). In extended areas the ground vegetation was totally removed, soil layers mixed and organic soil horizons eroded resulting in reduced contents of several soil nutrients. In view of the observed damages done to the trees by browsing and bark peeling these soil disturbances were mainly attributed to the grazing and trampling activity of red deer which regionally appears in population densities by far surpassing the carrying capacity of the forests.

Preliminary investigations indicated that not only red deer but many other environmental factors may affect soil quality in the investigation area. I hypothesized that the abiotic factors "relief position" and "slope gradient" as well as the biotic factors "wild boar", "stand density" and "stand composition" influence soil degradation in simple oak coppice

forests of the Ahr-Eifel. To test these assumptions four independent field investigations were set up including twelve different forest sites. Soil quality was assessed determining several physical, chemical and biotic soil properties.
The following questions were addressed:

1. Do abiotic factors such as relief position and slope gradient influence soil degradation in the investigation area?
2. Does exclusion of red deer result in an improvement of soil quality?
3. Does soil bioturbation by wild boar grubbing affect soil degradation in simple oak coppice forests?
4. To what extent does a reduced stand density by thinning affect soil properties in oak forests?
5. Which effects on soil characteristics occur when hazel is associated with oak in mixed stands compared to oak-monocultures?

Another main goal of this study was to find out if soil microbial properties are appropriate indicators for soil degradation in the investigation area. Microbial activity, microbial biomass (C_{mic}), metabolic quotient (qCO_2) and the ratio of microbial carbon to soil organic carbon (C_{mic}/C_{org}) have been proposed as indicators for soil quality in many studies and are supposed to constitute an early warning system for soil deterioration (INSAM & DOMSCH 1988, ANDERSON & DOMSCH 1993, BAUHUS et al. 1998, STADDON et al. 1999).
In addition to the field investigations, I conducted microcosm experiments to examine the influence of nutrient availability and substrate quality on microbial characteristics. It was thereby intended to find out if the observed relationships in the field can be reproduced under controlled conditions in the lab.
Three further questions were addressed:

6. Do microbial activity, C_{mic}, qCO_2 and C_{mic}/C_{org} depend on the soil nutrient status and other specific soil properties which determine soil quality in the field?
7. Do microorganisms depend on the nutrient availability under controlled conditions in microcosm-experiments and do the results reflect the relationships found in the field studies?
8. As a conclusion of 6.) and 7.), are microbial properties useful as indicators for soil degradation in sloping oak forests of the Ahr-Eifel?

II Material & methods

II.1 Investigation area

All field studies were conducted in the forestry district Adenau at the Ahr-Eifel (7211), about 60 km south of Cologne (Germany). The Ahr-Eifel is an eastern part of the Eifel-mountains in the Central European low mountain range and is characterized by steep forested hills with elevations up to 700 m above sea level. The dominant wind direction is west to southwest. Mean annual rainfall generally ranges from 600-800 mm and mean annual temperature varies between 6 and 9° C, both depending on elevation and exposure. For climatic conditions in the investigation area during this study see table II.1.

Tab. II.1: Climatic conditions in the investigation area (weather station Nürburg-Barweiler) in the years 2000, 2001 and 2002.

	Mean annual temperature [°C]	Annual rainfall [mm]	Frost days	Dominant wind direction
2000	9.1	762.1	51	W-SW (58 %)
2001	8.6	733	86	W-SW (52%)
2002	9.0	851.2	59	W-SW (49 %)

The parent material is of Devonic origin, mainly slate. Characteristic soil types are acid brown earth and ranker, with a variety of subtypes depending on loess-content, exposure, inclination, vegetation and also degree of degradation.

Oak (*Quercus petraea*) is the dominant tree species in the investigation area. Oak forest are mainly abundant as simple coppice forests which are characterized by clear cutting in regulated areas and the regeneration by stool shoots (BÜRGI 1999). However, coppice management stopped about 70 years ago. Nowadays these forests are not economically relevant. Traditionally, oaks were an important resource of the local industries as firewood, for charcoal burning and tanning. Therefore most of the oaks originate from the stump sprouts and root suckers of harvested trees which is one reason for their stunted growth. At the dry South and South-West exposed hillslopes oak is often associated with pine (*Pinus sylvestris*). Plant-sociologically these forests are categorized as *Hieracio glaucini-*

Quercetum petraea (LOHMEYER 1978). The humid leeward hillslopes are mostly stocked with mixed deciduous forests consisting of oak (*Quercus petraea*), hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*) and often associated with other deciduous tree species like ash (Fraxinus excelsior), maple (*Acer pseudoplatanus*), lime (*Tilia cordata*) and cherry (*Prunus avium*). Also present are large areas stocked with Douglas fir (*Pseudotsuga menziesii*) and spruce (*Picea abies*) which were planted strictly for economical use. In the shrub layer of oak forests hazel (*Corylus avellana*), sloe (*Prunus spinosa*), juniper (*Juniperus communis*) and whitethorn (*Crataegus spec.*) are common species.

Another important characteristic in the investigation area is the, at least locally, very high game density. Red deer (*Cervus elaphus* L.) densities were calculated to be at least 20 individuals per 100 hectare which is much higher than documented for most of the semi-natural and natural forests across Europe (2-12 ind./100 ha) (RATCLIFFE 1984, BERTOUILLE & DE CROMBRUGGHE 1995, MAYLE 1996). This high density is maintained by supplemental feeding and a limited culling policy. As a consequence, population densities of the European wild boar (*Sus scrofa*) are also high but there are no reliable calculations yet. The high game density results in visible damage to vegetation and soil. Red deer grazing and trampling and wild boar grubbing destroy the protective ground vegetation, mix soil layers, modify soil structure and change the surface micro-topography in the investigation area. The degree of soil disturbance seems to be dependant on the slope aspect, the slope gradient and the frequency of game occurrence.
The patterns of deer and wild boar activity are diverse and may vary between habitats. Therefore some of the activity patterns of wild boar and red deer that are relevant in the investigation area are described in the following paragraphs:

Patterns of red deer activity

Red deer are not very selective with their feeding preferences and predominantly feed on grasses, herbs, mosses, buds, lichens and shoots or seedlings of shrubs and trees. In the study area a large part of their diet seems to be taken from the shrub and herb layer so that locally both are completely removed. When the protective ground vegetation is missing large herds of red deer (up to 140 individuals) enhance wind and water erosion by trampling, especially at windward sites with high inclinations (HOLTMEIER 1999). Soil disturbance mainly occurs on slopes, where game leave their fixed routes perpendicular to the slope. Particularly susceptible areas have favourable climatic conditions, e.g. sunny

sites in wintertime and shady sites on hot summer days which draw large groups of red deer to feed or rest. Moreover, undirected downhill movements of game, either because of escape situations or on the way to a water place or glade, affect the soil profile structure resulting in soil disturbance. It has to be stressed that deer trampling does not provoke soil compaction at sloping sites but rather the disruption of soil aggregates and the displacement of rock fragments. MITCHELL & KIRBY (1990) and REID (1996), with additions from REIMOSER et al. (1999), produced lists of generic indicators of grazing and browsing pressures in woodland. According to this list grazing and browsing was very heavy at all sites of this investigation. Some of the characteristics of very heavy browsing and grazing pressure are: No shrub layer; obvious browse line on mature trees; ground vegetation < 3 cm tall with grasses, mosses or bracken predominating; trampling down of ground flora; extensive patches of bare soil; suppression of growth, and killing of seedling and saplings by browsing soon after germination and, therefore, virtually absent; very abundant dung; bark stripped from trees and from branches on the ground; mosses scarce or absent (see fig. II.1).

Patterns of wild boar grubbing

Wild boars are omnivorous but find the majority of their diet on the soil surface or in the soil. To attain their food they often grub in soil to search for seedlings, saplings, roots, mushrooms and soil invertebrates, both in meadows and forests (fig II.2). Generally, the patterns of grubbing differ from location to location depending on the soil type, the vegetation cover, the food resources, the season and the herd size (WELANDER 2000). Rooting may be superficial, affecting only the litter layer, or detrimental, breaking through the surface layer of vegetation and excavate soil to a depth typically ranging between 5 and 15 cm (KOTANEN 1995, GROOT BRUINDERINK & HAZEBROEK 1996). This often includes the mixing of organic topsoil with mineral soil. The displaced vegetation and soil may be left in place or moved aside burying untouched vegetation or forming mounds. The area grubbed sometimes extends for more than a hectare or is just composed of many small (~1 m²), overlapping disturbed patches ("feeding stations" – VALLENTINE 1990). In the investigation area wild boar grubbing is rarely superficial and in the most cases includes the excavation of soil and the mixing of soil horizons. Uprooting and feeding on seedlings constitutes a direct effect on trees. According to the local foresters in some areas wild boars turn over the forest soil about 3 to 4 times a year.

Fig. II.1: Typical phenotype of soils in simple oak coppice forests confronted to very heavy browsing and grazing pressure by red deer.

Fig. II.2: Extensive soil bioturbation by wild boar grubbing in a simple oak coppice forest of the Ahr-Eifel.

II.2 Investigations – design and site description

This study includes four complementary investigations to test for the influence of several abiotic (slope aspect, slope gradient, relief position) and biotic factors (deer, wild boar, stand density, plant species composition) on soil degradation in simple oak coppice forests of the Ahr-Eifel. In these four investigations soil properties of 12 different forest sites were studied. For the investigations II, III and IV the forest sites were split into experimental plots to test the effects of different treatments under the same site conditions.

In a fifth approach microbial properties (microbial activity/biomass, qCO_2 and C_{mic}/C_{org}-ratio) were correlated with selected soil properties from the investigations I-IV to evaluate the significance of microbial properties as indicators for soil degradation in simple oak coppice forests. The selected soil properties were soil pH, maximum water retention capacity (WRC_{max}), ratio of organic carbon to total nitrogen (C/N) and the contents of organic carbon (C_{org}), total nitrogen (N_t) and phosphate-P (PO_4^{3-}-P) Additionally, microcosm experiments were conducted to study the influence of substrate quantity and quality on microbial characteristics under controlled lab-conditions.

II.2.1 Investigation I (relief position)

Eight forest sites were sampled to evaluate the effects of the abiotic factors slope aspect (windward/leeward) and slope position (plateau/ upper slope/lower slope/foot slope) on selected physical and chemical soil properties of simple oak coppice forests.

All sites were similar in soil forming bedrock, plant species composition, elevation and slope gradient but differed in exposure. Four were windward-exposed, the other four were leeward-exposed (fig. II.3). Dominant tree species was oak (*Quercus petraea*) and soil types were acid brown earth, acid brown earth ranker and ranker. For more site characteristics see table II.2.

Soil pH and the contents of potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}) and aluminium (Al^{3+}) were monitored at all sites in July 1999, October 2001, May 2002 and October 2002 with a replicate number of n = 8. Microbial characteristics (activity, C_{mic}) and the contents of organic carbon, total nitrogen and phosphate-P were only measured in July 1999. These data are shown in the Appendix (tab. Appendix-1.3) and were used for correlation and regression analyses (see II.2.5).

In a second part of this investigation, soil texture (proportion of sand, silt and clay) and soil chemistry (C_{org}, N_t, K^+, Ca^{2+}, Mg^{2+}, Al^{3+}, pH) were examined at different relief positions of the windward forest site IV (tab. II.2, fig. II.3). The relief positions taken into account were plateau with inclinations between 0 and 15°, upper hillslope and lower hillslope area with average inclinations of 30° and 32° respectively and foot slope with inclinations ranging from 0-5°. Plateau and upper slope are divided by a convex break of slope, upper slope and lower slope are divided by a concave break of slope. Soil samples (n = 8) were taken once in October of the year 2001.

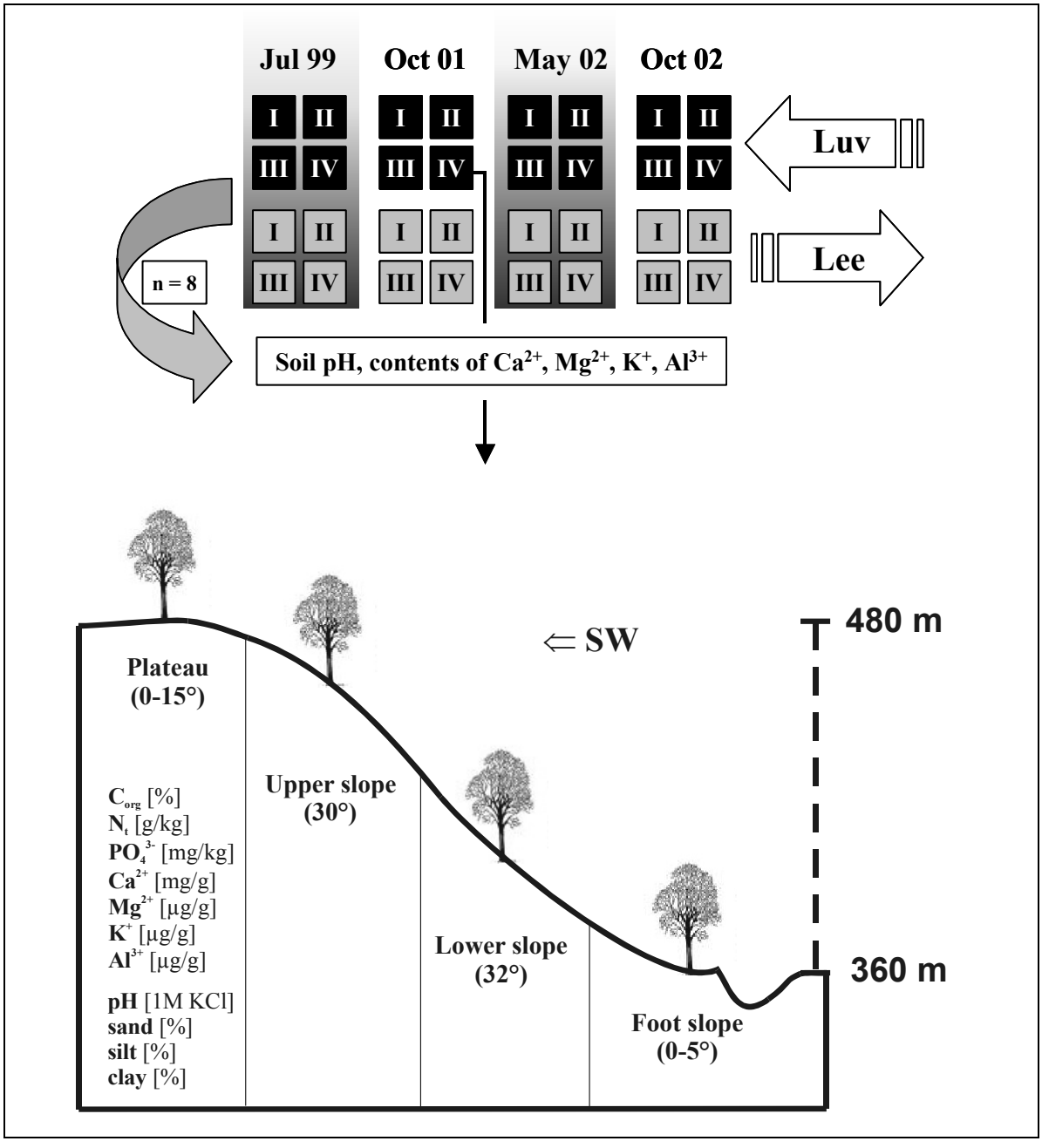


Fig. II.3: Investigation I - Experimental design. The number of replicates (n) relates to the number per plot and per sampling date. Luv = windward, Lee = leeward.

Tab. II.2: Investigation I – Site characteristics of the windward and leeward sites I-IV. For the average bdh and the WRC_{max} median values are shown (n = 8).

Slope aspect	**windward**				**leeward**			
Site	**I**	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**
Inclination [°]	27	25	34	29	30	33	23	27
Elevation [m]	380	420	450	420	340	340	420	460
Tree density [trees/500 m²]	46	84	64	24	31	53	17	21
Average bdh [cm]	13.8	17.7	15.9	19.1	31.9	27.4	36.2	32.8
Soil texture (DIN 4220)	Ls4	Slu	Ts4	Sl3	Ls4	Ls2	Ls3	Ls3
WRC_{max}	60.3	69.0	58.2	48.7	51.1	67.6	73.6	62.0

II.2.2 Investigation II (deer/stand density)

In this investigation the impact of the factors deer activity and stand density on several soil properties of a steep (28°) and windward (SW) hillslope at an elevation of 400 m was studied. Four plots extending 25 m in length and 25 m in width were established, two of them in a fenced exclosure to prevent access of game and two further plots adjacent to the fenced exclosure. The fence was erected in February 2001. Forest thinning conducted in autumn 1999 reduced the stand density in parts of this forest site by about the half (tab. II.3). The thinned areas included one plot inside and one plot outside the fenced exclosure. The sites are labelled as Ud (unfenced, dense), Ut (unfenced, thinned), Fd (fenced, dense) and Ft (fenced, thinned). For graphical illustrations of the experimental design see figure II.4. A photograph of the fenced exclosure is presented as figure II.5.

Soil samples for soil physical and chemical properties (n = 10) and the soil mesofauna (n = 9) were taken from all plots in September 2001, April 2002, October 2002 and May 2003. Litter samples for macrofauna extraction (n = 8) were also taken at these sampling dates but additionally in April 2001. Soil texture was only analysed in May 2003 (n = 8). Oak leaves for foliar nutrient analyses were sampled at all plots in June 2002 but foliar nutrients were only analysed from trees of the plots Ft and Ud. Herb layer coverage was determined in June 2001 and June 2003. For additional vegetation characteristics of the plots see table II.3. Before the erection of the fence soil chemical and microbial characteristics were analysed to ensure that plots of same stand density have the same initial soil conditions.

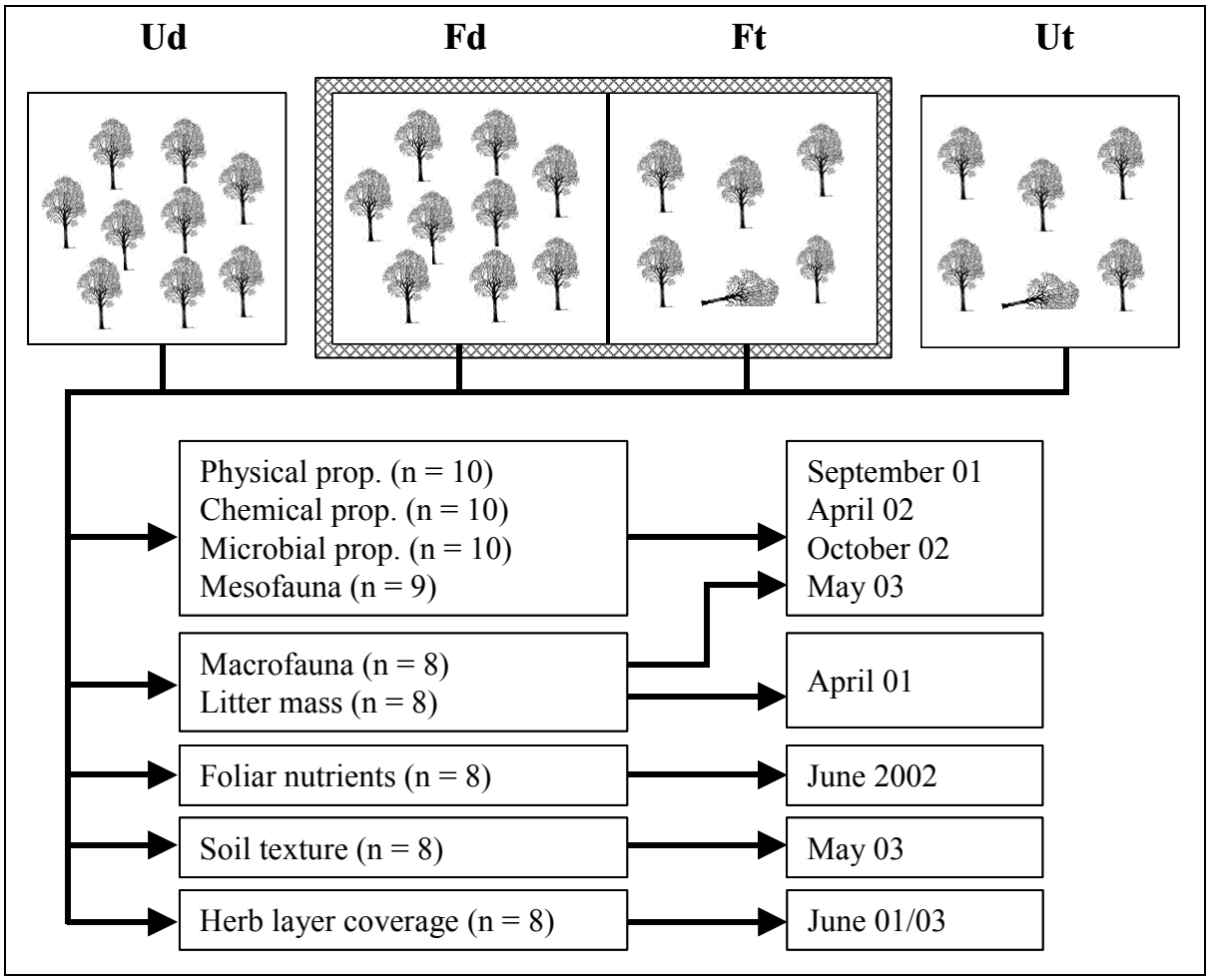


Fig. II.4: Investigation II – experimental design. The number of replicates (n) relates to the number per plot and per sampling date. F = fenced; U = unfenced, d = dense; t = thinned.

Tab. II.3: Investigation II: Several vegetation characteristics of the plots Ud, Ut, Fd and Ft. F = fenced; U = unfenced, d = dense; t = thinned. Diameter at breast height (dbh), rejuvenation and the herb layer coverage are presented as median ± MAD (n = 8).

plots	Ud	Ut	Fd	Ft
Tree density [trees/625 m²]	92	30	65	35
Species	*Q. petraea*	*Q. petraea*	*Q. petraea*	*Q. petraea*
Median dbh [cm]	5.7 ± 0.6	12.0 ± 3.3	8.3 ± 0.9	9.6 ± 1.0
Crown closure [%]	65	45	80	35
Height [m]	10-15	10-15	10-15	10-15
Rejuvenation [saplings/6.28 m²]	0	0	0	3 ± 3
Understory [ind./625 m²]	0	0	0	0
Herb layer coverage [%]				
June 2001	0	20.0 ± 0.0	2.5 ± 2.3	37.5 ± 21.3
June 2003	0	14.4 ± 5.6	8.8 ± 8.8	87.5 ± 0.0

Fig. II.5: Fenced exclosure of investigation II.

Fig. II.6: Unfenced plot with experimental soil bioturbation of the investigation III.

II.2.3 Investigation III (wild boar/deer)

This investigation aimed at evaluating the impacts of wild boar grubbing and deer activity on soil ecological parameters of a leeward exposed (SE) forest site (elevation: 450 m) with an average slope gradient of 25°.

Because it is hard to predict the activity range of wild boars (see above) the grubbing pattern of wild boars was simulated with rakes in a predetermined area. The rakes resemble the morphology of wild boar fangs and allowed to uproot the soil down to a typical depth of about 10 cm, mixing soil horizons, burying the ground vegetation and forming mounds. Thereby a grubbing pattern was created which is typical for the investigation area. Two experimental plots (25 m x 25 m) were grubbed, one in a fenced exclosure (Bf; bioturbation, fenced) and one outside the exclosure (Bu; bioturbation, unfenced) to test for the possible impact of wild boar grubbing on soil properties under deer exclusion and with deer access (fig II.7). Before the grubbing process soil chemical and microbial characteristics were analysed to ensure that grubbed and undisturbed plots have the same initial soil conditions.

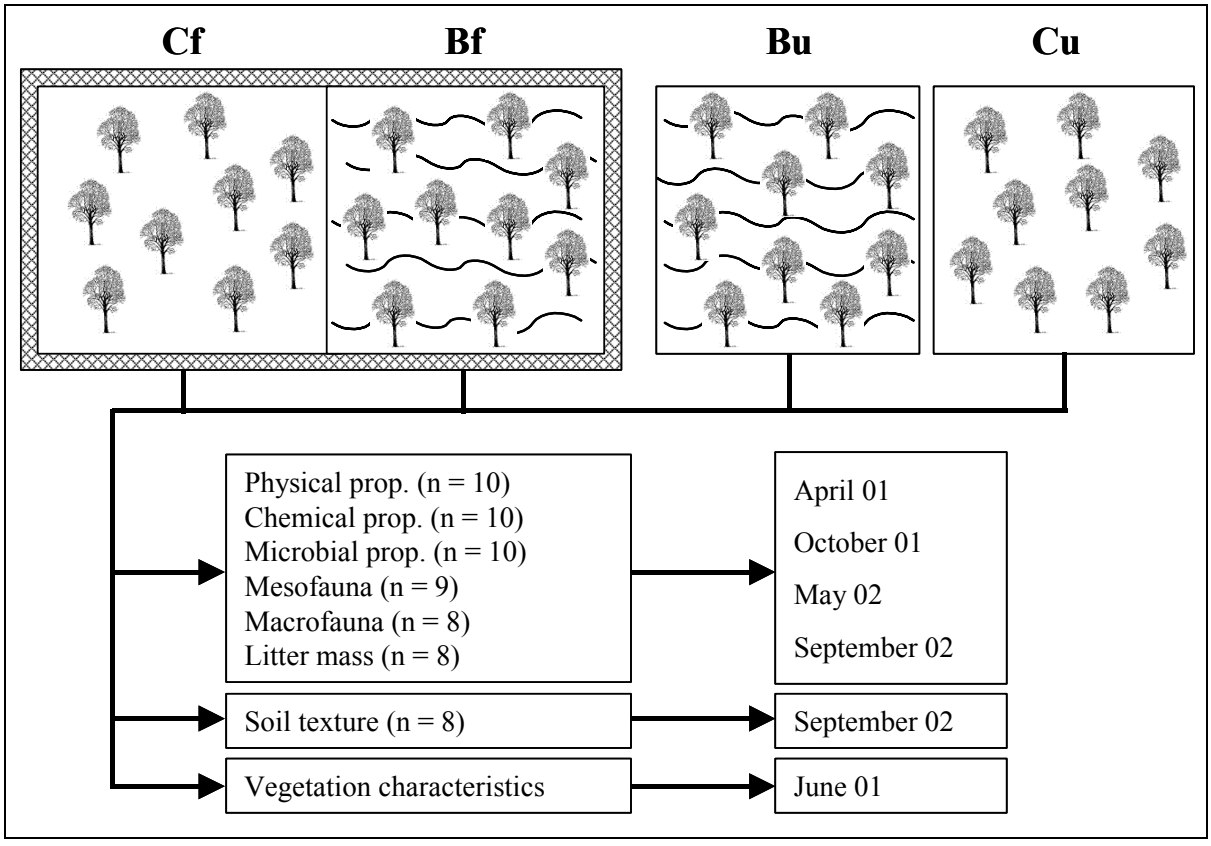


Fig. II.7: Investigation III – Experimental design. The number of replicates (n) relates to the number per plot and per sampling date. C = control; B = bioturbation; f = fenced; u = unfenced.

Adjacent (10 m) to the grubbed plots I established two control plots, fenced (Cf) and unfenced (Cu), without any experimental soil bioturbation. The bioturbation process was performed in November of the years 2000 and 2001. In the late autumn wild boar grubbing activity is generally high (KOTANEN 1995) because of moist soil, freshly fallen litter and seeds (especially acorn) and the high abundances of fungi and ground dwelling arthropods. The forestry office arranged for the construction of the fence in 1998 as a result of the high deer activity and in order to protect the soil and the trees from additional deer damage. Comparing the interior and exterior plots of the exclosure delivered information on the impact of deer activity on soil properties. The exclosure was 50 x 100 m square approximately. The soil type of all plots is an acid brown earth with a shallow Ah-horizon (≤ 5 cm). The dominant tree species is sessile oak. In contrast to the unfenced plots ground vegetation was well established inside the exclosure. It was dominated by bramble (*Rubus fructiosus*). Oak saplings were also numerous. For further vegetation characteristics of the plots see table II.4. Soil samples for the determination of soil physical/chemical properties (n = 10) and the abundance of the soil mesofauna (n = 9) as well as litter samples for macrofauna extraction (n = 8) were taken in the spring following the bioturbation procedure (April 2001, May 2002) and in the fall of the same years (October 2001, September 2002). Soil texture was only analysed in September 2002 (n = 8). Vegetation characteristics were determined in June 2001.

Tab.II.4: Investigation III: Vegetation characteristics of the plots Cf, Bf, Cu and Bu. C = control; B = bioturbation; f = fenced; u = unfenced. Diameter at breast height (dbh), rejuvenation and the herb layer coverage are presented as median ± MAD (n = 8).

plots	**Cu**	**Bu**	**Cf**	**Bf**
Tree density [trees/625 m²]	18	28	19	26
Species	*Q. petraea*	*Q. petraea*	*Q. petraea*	*Q. petraea*
Median dbh [cm]	16.3 ± 2.5	16.2 ± 1.6	15.8 ± 2.9	16.4 ± 1.5
Crown closure [%]	65	65	50	50
Height [m]	10-15	10-15	10-15	10-15
Rejuvenation [saplings/6.28 m²]	8 ± 5	3 ± 3	22 ± 21	10 ± 8
Understory [ind./625 m²]	6	9	1	0
Species	*Corylus avellana, Carpinus betulus*		*Carpinus betulus*	-
Herb layer coverage [%]	0.2 ± 0.1	1.4 ± 1.2	75.0 ± 12.5	20.0 ± 5.6

II.2.4 Investigation IV (stand composition/slope gradient)

In this fourth investigation the impact of stand composition on soil characteristics at different slope gradients was studied. Two study sites were selected for this investigation: at both sites oak-monocultures were growing adjacent to mixed stands in which oak (*Quercus petraea*) was associated with hazel (*Corylus avellana*) growing in the understory of oaks. The two site-replicates were about 300 m apart and notably differed in their slope gradient. One slope is rather gentle with slope gradients ranging from 13° to 14°, the other site is steep with slope gradients between 25° and 27°. The steep sites are indicated as Mono1 (monoculture, 27°) and Mix1 (mixed stand, 25°), the gentle slopes are indicated as Mono2 (14°) and Mix2 (13°). The sites did not differ in elevation (450 m), exposure (W) and bedrock (Devonic slate). An illustration of the experimental design is shown in figure II.8. At all sites soil samples (n = 10) were taken in January, April, July and November of 2002. Litter samples (n = 8) were taken in November 2001 after litter fall and in September 2002 before litter fall. The abundance of Lumbricidae was determined in May 2003.

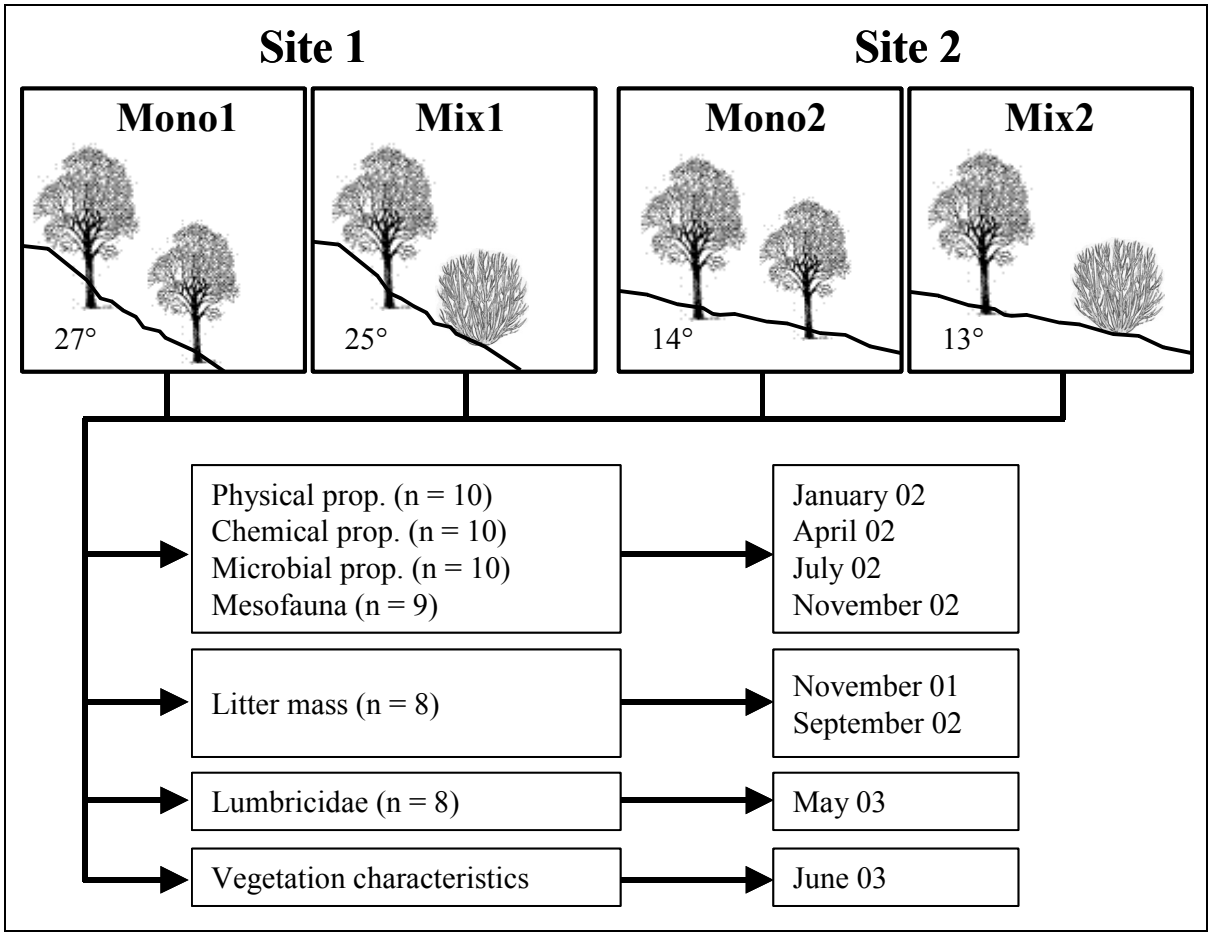


Fig. II.8: Investigation IV – experimental design. The number of replicates (n) relates to the number per plot and per sampling date. Mono = oak-monoculture; Mix = oak-hazel mixed stand; 1 = steep slope (25-27°); 2 = gentle slope (13-14°).

Vegetation characteristics of the sites were monitored in June 2003. Oak was the dominant tree species at all sites. The height of the oak trees ranged from 10-20 m, crown closure of trees varied between 50 and 60 % at the mixed stands and between 70 and 90 % at the monocultures. Crown closure of hazel at the mixed stands ranged from 40 to 60 %. The herb layer covered 1.4 to 8.8 % of the soil area of the investigated forest stands. For further vegetation characteristics see table II.5.

Table II.5.: Vegetation characteristics (tree/shrub/herb layer) of the investigation sites Mono1, Mix1, Mono2 and Mix2 (Mono = oak-monoculture; Mix = oak-hazel; 1 = 25-27°, 2 = 13-14°). Diameter at breast height (dbh) and the herb layer coverage are presented as median ± MAD (n = 8).

sites	**Mono1**	**Mix1**	**Mono2**	**Mix2**
Slope gradient [°]	27	25	14	13
Tree layer (625 m²)				
Number of trees	60	17	24	9
Oak	53	5	23	7
Beech	7	5	0	1
Others	0	7	1	1
Median dbh [cm]	10.4 ± 1.4	13.0 ± 2.8	15.7 ± 3.7	20.3 ± 3.8
Height [m]	10-15	15-20	10-15	15-20
Crown closure [%]	60	90	50	70
Understory (625 m²)				
Number of ind.	0	30	0	20
Hazel	0	28	0	15
Others	0	2	0	5
Height [m]	-	5-10	-	8-10
Crown closure [%]	0	60	0	40
Herb layer (8 plots à 6.28 m²)				
Coverage [%]	8.8 ± 6.3	1.4 ±1.2	2.5 ± 0.0	2.5 ± 1.2

II.2.5 Microbial properties as indicators for soil quality

Soil degradation in terms of soil organic matter and nutrient depletion may be reflected by constraints on the soil biota. Especially microbial properties such as microbial activity, biomass (C_{mic}), specific microbial respiration (qCO_2) and the C_{mic}/C_{org}-ratio have often been suggested as useful indicators for soil quality (BAUHUS & KHANNA 1999; JOERGENSEN & SCHEU 1999). In this fifth approach the relationships between microbial properties and several soil properties which determine soil quality were evaluated using the

field data from the investigation I-IV. Additionally, microcosm experiments were conducted to specify the effects of nutrient addition on soil microbial activity, C_{mic} and qCO_2.

Field data

The field data from the investigations I-IV were used to conduct Spearman-rank-correlations and linear regression analyses. The goal was to test for relationships between microbial properties (microbial activity, C_{mic}, qCO_2, C_{mic}/C_{org}) and several soil properties (C_{org}, N_t, PO_4^{3-}, pH, WRC_{max}, C/N) and to deduce from these results if soil microbial properties reliably reflect soil quality. Correlation and regression analyses contained either the median values of all plots/sites per sampling date (n = 56) or were conducted separately for each investigation resulting in 8-16 replicates per analysis. In investigation I microbial properties were only determined in July 1999 so that from this investigation eight values (eight sites) per variable contributed to the statistics (see tab. Appendix-1.3). From the investigations II, III and IV 16 values each (four sites/plots, four sampling dates) contributed to the analyses. The regressions between microbial characteristics and the contents of organic carbon, total nitrogen and phosphate-P were plotted in graphs.

Microcosm experiments

From March to June 2002 (series I) and from January to April 2003 (series II) two microcosm experiments were conducted to study the effect of nutrient addition to soil substrates on microbial activity, C_{mic} and qCO_2. The two experiments only differed in the forest soil added to the soil substrate. Both soil substrates consisted of 25 % Pleistocene sand, 25 % loess and 50 % forest soil. The sterile sand and loess substrates were taken from the lignite open-cast mine Hambach in the Rhineland, Germany, in a depth of 30-40 cm. The fertile forest soils were taken from the Ah-horizon of a degraded soil in the Ahr-Eifel (series I) and from the Ah-horizon of a beech high forest in the Westerwald, Germany (series II). The soil from the Ahr-Eifel was nutrient-poor and the abundant microorganisms were supposed to be limited by the availability of organic carbon. The forest soil of series II was rich in organic carbon, total nitrogen and mineral nutrients so that nutrient limitation for microorganisms was unlikely to occur. Fertile forest soils were used instead of inoculating a sterile soil substrate with microorganisms of a forest soil suspension. Thereby external sources of friction should be minimized and a site specific microorganism-community in a natural density could be obtained. All substrates were air dried, passed

through a 2 mm sieve, thoroughly mixed and stored under dry conditions until use. According to FRANZLUEBBERS (1999) dried and coarsely sieved soil compares favourably to field-moist-intact soil cores for estimating soil microbial biomass and potential activity.
There were two reasons why different soil substrates were taken for the experiments. First of all, the obtained results should be reproducible in a second experiment and should not be the result of unique and randomly chosen conditions. Secondly, differences in the microbial community between the soils were expected: The soil from the Ahr-Eifel should favour autochthonous microorganisms which are highly competitive under nutrient-poor conditions and are capable of surviving unfavourable conditions (K-strategists) (GISI et al. 1997). The soil from the Westerwald was taken close to downed deadwood from a nutrient-rich and stable environment. Under these conditions highly specialized zymogene microorganisms may occur in higher densities. Zymogene populations (r-strategists) are more competitive under nutrient-rich conditions but less competitive when nutrients are limited. They react with a higher growth rate to large substrate additions than K-strategists.

Before the start of the experiments the samples of the mixed substrates were analysed for texture, pH, WHC_{max} and contents of C_{org}, N_t, PO_4^{3-}, K^+, Mg^{2+} and Ca^{2+} (see table II.6). On the basis of these results I determined the amounts of water and nutrients to be added to the different approaches to adjust soil moisture and nutrient contents to a predetermined level.

Tab. II.6: Several properties of the soil substrates I and II before the start of the experiment.

Soil properties	**Soil substrate I**	**Soil substrate II**
Texture (German DIN 4220)	Sl4	Ls2
WRC_{max} [%]	32.0 ± 0.3	38.7 ± 0.4
Soil pH (1M KCl)	5.0 ± 0.0	4.8 ± 0.0
Organic carbon [%]	3.2 ± 0.3	8.5 ± 0.7
Total nitrogen [mg/g]	1.7 ± 0.0	4.2 ± 0.1
C/N-ratio	19.8 ± 0.9	20.0 ± 1.6
Phosphate-P [µg/g]	2.3 ± 0.2	13.5 ± 0.5
Potassium [µg/g]	180 ± 4	112 ± 5
Magnesium [µg/g]	114 ± 5	272 ± 16
Calcium [mg/g]	1.6 ± 0.1	1.6 ± 0.1

PVC-dishes (10 mm in diameter; 3 mm height) were used as experimental units (fig. II.8). A gauze with a mesh size of 100 µm was introduced into the lid to minimize water loss from the soil by evapo-transpiration and to allow gas exchange between chamber and atmosphere at the same time. One week before the start of the experiment 100 g of dry soil substrate was filled into the dishes and adjusted to a moisture content of 65 % of its water retention capacity by adding distilled water. Soil moisture content was maintained between 50 and 65 % of the WRC_{max} throughout the experiment by adding distilled water to a pre-determined mass. The microcosms were pre-incubated at 17.5° in a controlled environmental facility without light for one week. GEMESI (1996) found that one week of incubation is sufficient to build up a microbial population.

At the beginning of the experiment defined amounts of nitrogen, phosphate and different carbon sources were added to the soil substrates (tab. II.7). Nitrogen and phosphate (N+P) were added as ammonium-nitrate (Merck) and potassium-phosphate-trihydrate (Merck). The amended carbon sources were D(+) glucose (Glu) (anhydrous, Merck), cellulose (Cell) (Sigma) and lignin (Lig) (organosolv, Aldrich). Control treatments (C) received no nutrients. For each treatment (Control, N+P, Glu+N+P, Cell+N+P, Lig+N+P) eight replicates were prepared. The substrates were added in amounts to raise the initial C_{org}-content of the soil substrate I from 3.2 to 5 % while keeping the nutrient ratios (C/N/P) in a predetermined range (tab. II.7). The amount of nutrients added was identical for both experimental series but their final contents differed due to different initial nutrient contents in the added forest soils. The C_{org} content ranged from 3.2 to 10.2 %, the N_t content ranged from 1.7-5.2 mg/g and the PO_4^{3-} -P content ranged from 2.3-230 µg/g in the different approaches (tab. II.7).

After nutrient addition soil samples were taken from the PVC-dishes in defined intervals. The intervals were 1, 2, 4, 8, 16, 32 and 64 days after nutrient addition. At each sampling date microbial activity and microbial biomass were determined and the metabolic quotient calculated from these data. On day 32 of series II the microbial activity and biomass were not determined due to illness. The methods were identical to those used for the field investigations but due to the experimental design pre-incubations could be omitted.

The experimental design is illustrated in figure II.9.

Tab. II.7: Contents of C_{org}, N_t and PO_4^{3-}-P and ratios of C/N/P in the soils of the different approaches of both series.

Approach		C_{org} [%]	N_t [mg/g]	PO_4^{3-} -P [µg/g]	C/N/P
Control	Series I	3.2	1.7	2.3	20/1/0.001
	Series II	8.5	4.2	13.5	20/1/0.003
N+P	Series I	3.2	3.0	219	11/1/0.07
	Series II	8.5	5.5	230	15/1/0.04
Glu+N+P	Series I	5.0	3.0	219	17/1/0.07
	Series II	10.2	5.5	230	19/1/0.04
Cell+N+P	Series I	5.0	3.0	219	17/1/0.07
	Series II	10.2	5.5	230	19/1/0.04
Lig+N+P	Series I	5.0	3.0	219	17/1/0.07
	Series II	10.2	5.5	230	19/1/0.04

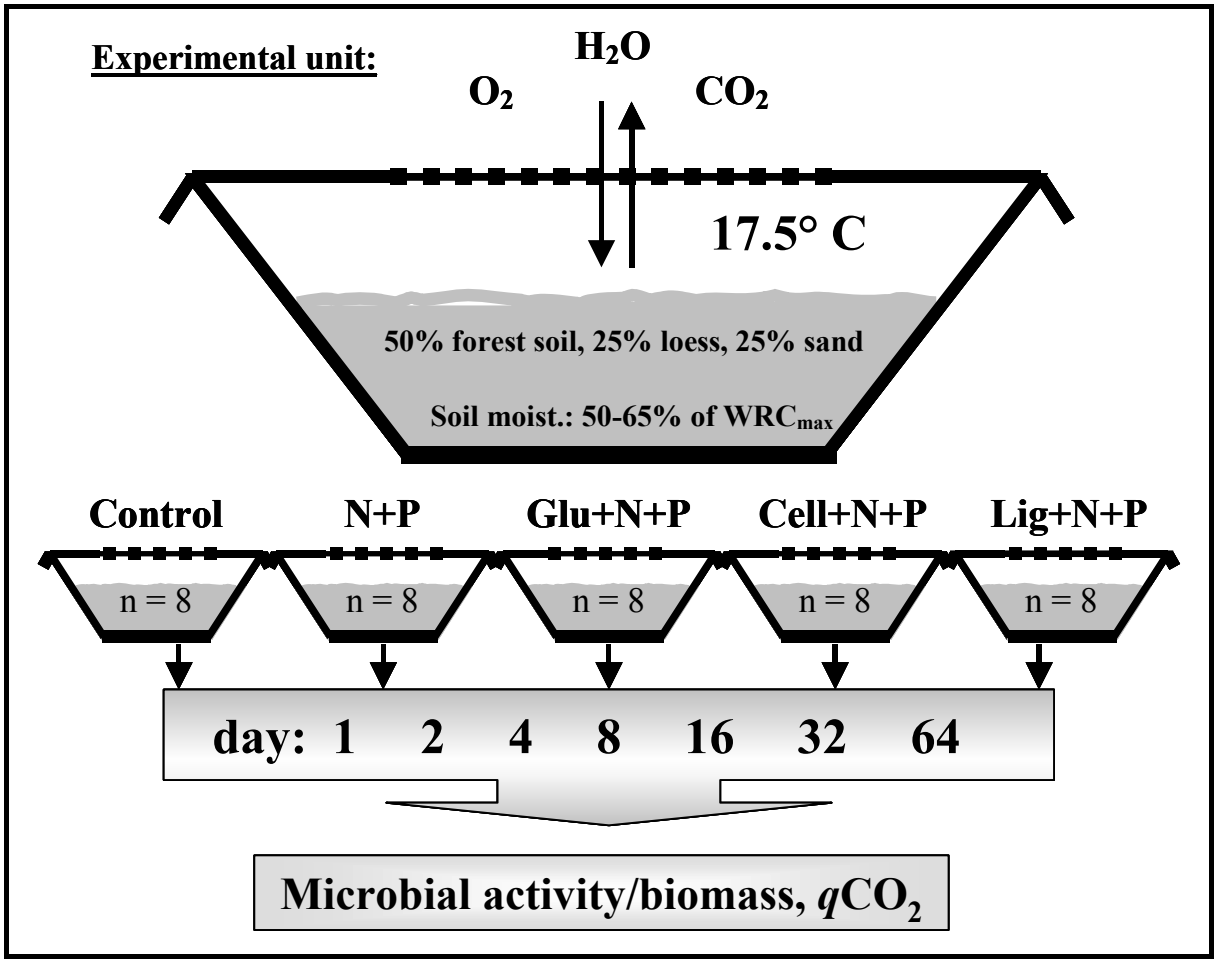


Fig. II.9: Experimental design of the microcosm experiments. N = nitrogen; P = phosphate; Glu = glucose; Cell = cellulose; Lig = lignin. The two different series only differed in the forest soil contributing to the soil substrate. All PVC-dishes were stored at 17.5°C in a controlled environmental facility.

II.3 Methods

II.3.1 Sampling procedure

All samples were taken at random from the topsoil (0-5 cm) but no closer than 2 m to the fences to avoid edge effects. The number of replicates per plot and sampling date was ten (eight for Investigation I) for soil samples, nine for mesofauna sampling and eight for macrofauna and litter sampling. In most cases soil and fauna sampling was repeated four times but the sampling dates differed between the investigations. Thereby data-sets of 32 to 40 replicates were attained for each site/plot depending on the parameter evaluated.
To assess the effect of deer exclosure on nutrients in foliage (investigation II) leaves from the mid-canopy of eight trees (*Quercus petraea*) of one fenced and one unfenced site were collected in July 2002. The leaves, comprising sun- and shadow-leaves, were obtained by climbing. All leaves per tree were dried, thoroughly mixed and treated as separate replicates obtaining eight replicates per site.

II.3.2 Vegetation characteristics

Vegetation parameters were recorded at all sites/plots of this study. The number of trees and shrubs within an area of 625 m² were counted and the species determined. The diameter of a tree at breast height (dbh) was taken from eight oak trees at each site/plot. The height of the trees was determined using a clinometer (Clinomaster; Silva). The crown density and the coverage of the herb layer were estimated independently by two persons. The herb layer coverage and the number of oak saplings were determined within randomly chosen plots of 6.28 m² area (n = 8) after BRAUN BLANQUET (1964).

II.3.3 Soil physical properties

Maximum water retention capacitiy (WRC_{max}) was only analyzed for sieved soils (< 2 mm) because soils were too stony to collect undisturbed soil samples. WRC_{max} and soil humidity were measured gravimetrically (ALEF 1991). The soil texture was determined by wet-sieving and by using the pipette method (GEE & BAUDER, 1982). The mass % of coarse soil particles (> 2 mm) was within a similar range at all sites. Therefore nutrient contents were not related to the proportion of fine soil (< 2 mm) at the sites.

II.3.4 Soil chemical properties

All analyses were carried out with 2 mm sieved and air-dried soils. Soil pH was determined according to SCHLICHTING & BLUME (1966) with an microprocessor pH-Meter (pH 320, WTW) after extraction with 1 M KCl. Al^{3+}-analysis was performed reflectometrically with MERCK-teststrips after extraction with 2M KCl solution (10 g soil with 40 ml KCl). Analysis of organic carbon (C_{org}) was conducted with a Total Organic Carbon Analyzer (TOC, STRÖHLEIN instruments) by burning the soil (100-200 mg) at 550°C (SCHLICHTING & BLUME 1966). Total Nitrogen (N_t) content was analysed using the KJELDAHL-method (2.5 g soil). Plant available contents of calcium (Ca^{2+}), magnesium (Mg^{2+}) and potassium (K^+) were extracted from 10 g soil with 50 ml 1M NH_4NO_3 solution (ZEIEN & BRÜMMER 1989; HORNBURG et al. 1995) by homogenisation (horizontal shaker for 2 hours) and filtration. The ion contents in the suspension were analysed with an Atomic Absorbance Spectrophotometer (AAS, PERKIN-ELMER GmbH). The content of extractable phosphate-ions in soil (2.5 g) was determined colorimetrically at a wavelength of 406 nm (Vanadate-Method), as described in STEUBING & FANGMEYER (1992). To calculate the phosphate content in the soil from the extinction (E) a calibration was conducted with KH_2PO_5 (E [406] = 70.9 ± 0.1 [P_2O_5], R = 0.999, n = 7, $p \leq 0.001$). The phosphate content in the soil is presented as PO_4^{3-} -P [mg/kg] which is 43.64 % of the actual phosphate content.

II.3.5 Soil microbial properties

For microbial analyses the moist soils were, if necessary, adjusted to 40-60 % of the maximum water retention capacity of the sieved soils and incubated at 20°C for two to three days. Potential microbial activity was determined using the method of SKAMBRACKS & ZIMMER (1998), modified for soil samples. For each replicate 10 g dry wt. of moist soil was transferred to CO_2-free glass vessels (volume: 300 cm²) and incubated for 16-18 h at 25°C. The CO_2 from microbial respiration was measured with a TOC Analyser (see II.3.4.) and related to the soil weight and time of incubation as µg CO_2-C/(g*h). Microbial biomass (C_{mic}) was analysed using the fumigation-extraction method according to VANCE et al. (1987). The extraction of the extractable organic carbon and the microbial components was conducted with a 0.5 M K_2SO_4 solution from 12.5 g moist soil (dry wt.). The C-content of the suspensions was measured with the TOC. The content of organic C

without fumigation was subtracted from the values with fumigation and then multiplied with the factor 2.64 (VANCE et al. 1987; ALEF 1991) to receive results in µg C_{mic}-C/g. The specific microbial respiration (qCO_2) as the ratio of microbial activity to C_{mic} in µgCO_2-C/(mgC_{mic}*h) and the C_{mic}/C_{org}-ratio were calculated from the data.

II.3.6 Litter layer and soil fauna

Leaf litter was collected within a 300 cm² metal frame taking eight replicates per plot and sampling date. After transportation in plastic bags the litter was placed in Tullgren funnels and the soil fauna extracted over a one to two week period. After extraction the dry litter was cleaned, weighed and multiplied by 33.3 to receive g/m² values. The soil macrofauna was transferred to alcohol, counted and determined to the group-level. For the presentation of the total macrofauna all individuals, adults as well as juveniles, of the groups Coleoptera, Diptera, Aranaea, Isopoda, Diplopoda, Chilopoda and the rest (Lumbricidae, Formicidae, Gastropoda etc.) were taken into account. The Diptera results are not shown because they are not extracted quantitatively with the chosen sampling method. When presenting the abundances of Coleoptera, Arachnidae, Isopoda, Diplopoda and Chilopoda it was not distinguished between adults and juveniles.

Mesofauna-sampling was conducted with soil cores of different diameter to a depth of four cm (Ah-horizon). For the sampling of Collembola, Acarina, Pauropoda, Symphila, Protura, Diplura and Pseudoscorpionidae soil cores with a diameter of 31.17 cm² were used. Extraction was carried out according to MCFADYEN (1962), modified according to KOEHLER (1993). Enchytraeidae sampling (n = 9) was carried out with 55.42 cm² soil cores. Extraction of Enchytraeidae was conducted according to O`CONNER (1962). For the presentation of the total mesoauna all individuals of the groups Collembola, Acari, Diplura, Protura, Symphila, Pauropoda, Pseudoscorpionidae and Thysanoptera were taken into account.

Earthworm abundance was determined for an area of 1/8 m² by hand selection from the litter and a consecutive formalin-extraction (RAW 1961). Eight 1/8 m² circles per site were chosen at random and sampled in May 2003 (investigation IV). The number of individuals per m² was calculated by summing up the number of earthworms of each single replicate per site.

II.3.7 Nutrients in foliage

Foliage samples were separated from the branch and petiole and oven dried at 70° C. Nitrogen concentration in the leaves (0.5 g dry wt.) was analysed using the KJELDAHL method. For analysis of PO_4^{3-}, Ca^{2+}, Mg^{2+} and K^+ the leaves (100 mg) were digested by dry ashing and then treated as described in STEUBING & FANGMEYER (1992) using the same methods as for the soil nutrient analyses.

II.3.8 Statistical analyses and data presentation

Normal distribution of all data sets was tested with the KOLMOGOROFF-SMIRNOFF-test, modified after LILLEFORS. Because not all data sets showed a normal distribution median values and median absolute deviation (median ± MAD) are presented. The non-parametric KRUSKAL-WALLIS-H-test and the MANN-WHITNEY-U-test were used in succession to test for differences between data sets. The limit of significance was set at $p \leq 0.05$. Significance of differences between separate laboratory series in the microcosm experiments were tested using the FRIEDMANN-test and the WILCOXON-test ($p \leq 0.05$).

In investigation I the data of the four windward and the four leeward sites were pooled for statistical analyses and graphical presentation to attain a replicate number of n = 32 per slope aspect and sampling date. The results of the single sites (n = 8) are shown in the appendix. In the investigations II to IV the data of the four sampling dates were pooled for statistical analyses and graphical presentation to attain a replicate number of 32-40 for most of the investigated soil properties at each site/plot. In the results-section the median ± MAD values of the pooled data are shown whereas the median values of the different sampling dates are shown in the appendix.

Two-way analyses of variance (ANOVA) and two-way analyses of covariance (ANCOVA) were conducted to estimate the extent of the different biotic and abiotic factors on parameters distribution. In investigation II ANCOVA was conducted to test the influence of the factors “deer” (access/exclusion) and “stand density” (dense/thinned) on several soil properties. Including the factor “season” as a covariate to the analyses of covariance allowed to neutralise a priori differences resulting from seasonal variations (spring/fall). In the investigation III the factors “wild boar” (ungrubbed/grubbed), “deer”

(exclusion/access) and the covariate "year" (2001/2002) were included to conduct a two-way ANCOVA. Adding "season" and "year" as ANOVA factors implies that repeated sampling never occurred at the same positions within the plots. The factors for two-way analyses of variance (ANOVA) in the investigation IV were species composition (oak-monoculture/oak-hazel) and slope gradient (steep/gentle). Each factor appeared in a replicate number of n = 2 and therefore the degree of freedom of the single factors was d.f. = 1. All data were log (x+1) transformed to minimize violation of normal distribution. Following SACHS (1992) and BORTZ (1993), normality and also homogenous variances can be neglected as ANOVA conditions if the level of significance is increased. Therefore only those factors with $p \leq 0.001$ were regarded. In the result-tables the F-value, the significance-level and the R^2-value are presented. The experimental design of the investigation II-IV created a common statistic basic totality and prevented pseudo-replicates.

SPEARMAN-rank-correlation and linear regression analyses were performed to test for relationships and dependencies between microbial properties and specific soil properties from the investigations I-IV. For correlations and regression analyses the median values of each site/plot per sampling date were taken into account. The limit of significance was set at $p \leq 0.05$.

Statistical analyses were conducted with the computer programs SPSS 11.0, Prism 4.01 and Excel 2000.

Soil Fauna

The mesofauna and the macrofauna results are presented in two different ways: in the case that several soil fauna groups were combined (e.g. total mesofauna, total macrofauna) resulting in a high number of individuals per replicate, all single data are taken into account (n = 32/36) for graphic presentation (box & whisker-plots). In contrast, presenting the results of single groups of the meso- and macrofauna the number of individuals of randomly chosen replicates of each sampling date were summed up to receive nine replicates for each site. This was done to eliminate the differences between sampling dates and to reduce the high number of 0-values for many groups. The results are presented in tables as median ± MAD [ind./area*sampling dates]. Analyses of variance were exclusively conducted with log (x+1) transformed sum-values.

III Results

III.1 Investigation I (relief position)

III.1.1 Influence of slope aspect on soil chemistry

The contents of the soil nutrients Ca^{2+}, Mg^{2+} and K^{+} were significantly ($p \leq 0.012$) lower at windward sites than at leeward sites for all sampling dates (fig. III.1, tab. Appendix-1.2). Al^{3+}-content was generally higher at windward sites compared to leeward sites. However, the October 2001 values did not differ significantly from each other (tab. Appendix-1.2). The windward and leeward sites did not differ significantly regarding the soil pH (fig. III.1). The contents of Ca^{2+}, Mg^{2+} and K^{+} in soil continuously decreased from July 1999 to values 0.5-5 times lower in October 2002 at both windward and leeward sites (fig. III.1). Differences in the content of base cations between the sampling dates were significant in most cases for both slope aspects and all nutrients were significantly lower ($p \leq 0.012$) in October 2002 compared to July 1999 (tab. Appendix-1.2). The content of Al^{3+} was generally higher in autumn compared to summer/spring values ($p \leq 0.072$) at each slope aspect and reached the highest values in October 2002 (windward: 306 µg/g; leeward: 458 µg/g). Soil pH significantly decreased ($p \leq 0.05$) from July 1999 (windward: 3.7; leeward: 4.0) to May 2001 (windward: 3.5; leeward: 3.5) at both exposures but again increased in October 2002 to reach values comparable to those in 1999 (windward: 3.8; leeward: 3.8).

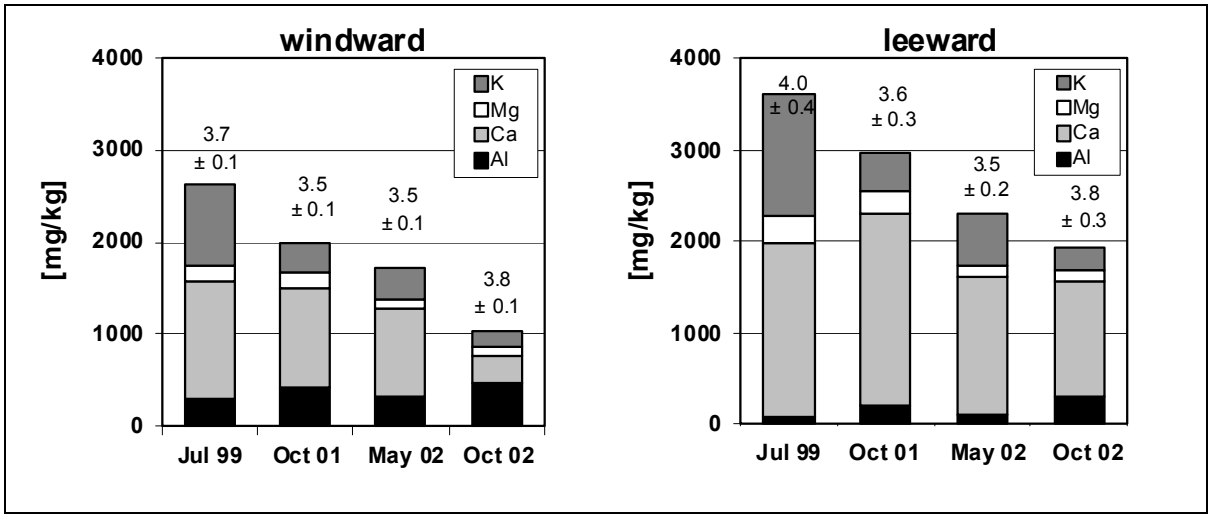


Fig. III.1: Contents of extractable potassium (K^{+}), magnesium (Mg^{2+}), calcium (Ca^{2+}) and aluminium (Al^{3+}) at four sampling dates (July 1999, October 2001, May 2002, October 2002) and varying slope aspect (windward, leeward). The data represent the median values of four different forest sites per slope aspect with eight replicates each (n = 32). The numbers above the bars represent the soil pH as median ± MAD.

III.1.2 Influence of slope position on soil chemistry and soil texture

Soil nutrient contents differed remarkably between the relief positions plateau, upper slope, lower slope and foot slope (fig. III.2).

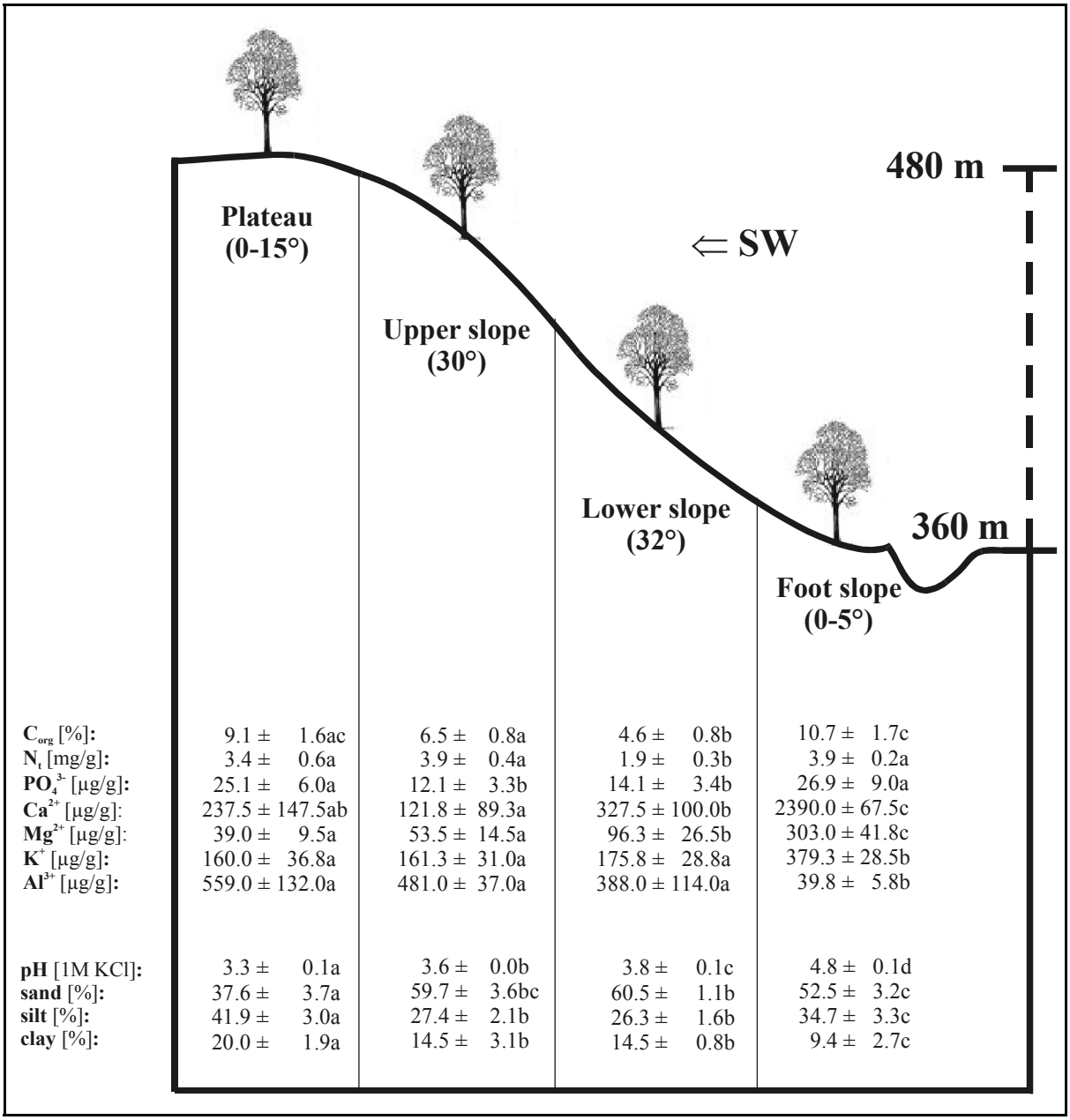
The contents of organic carbon and phosphate-P were significantly higher ($p \leq 0.001$) at the plateau and the foot slope compared to the upper and lower slope position (fig. III.2). These differences were significant ($p \leq 0.05$) except for the differences in C_{org} between plateau and upper slope. The N_t-content was significantly lowest ($p \leq 0.001$) at the lower slope (1.9 mg/kg) compared to the other relief positions (3.4-3.9 g/kg) which did not differ from each other (fig. III.2).

The contents of calcium, magnesium and potassium reached maximum values at the foot slope with significantly higher values ($p \leq 0.001$) than at all the other relief positions (Ca^{2+} = 2.4 mg/g; Mg^{2+} = 303 µg/g; K^{+} = 379 µg/g). Apart from calcium, minimum values for the basic cations were obtained on the plateau (Mg^{2+} = 39 µg/g; K^{+} = 160 µg/g) but values at the upper and the lower slope were only marginally higher.

The soil pH significantly decreased ($p \leq 0.001$) from the foot slope to the plateau from 4.8 to 3.3. In contrast, the content of Al^{3+} increased in the same direction being more than ten-fold higher at the plateau (559 µg/g) than at the foot slope ($p \leq 0.001$).

There were also remarkable differences in soil texture among the relief positions. The plateau was characterized by the significantly highest ($p \leq 0.05$) proportion of fine particles (61,9 % silt and clay) and the significantly lowest proportion of sand (37.6 %) forming a sandy loam (Ls2 after German DIN 4220). The soil textures at the upper and lower slope were almost identical (Sl4) but tended to be coarser than at the foot slope (Sl3). At the foot slope the fine material fraction was slightly but not significantly higher (44.1 %) than at the upper and lower slope (41.9 and 40.8 %). The proportion of soil particles greater than 2 mm (gravel, rock fragments) was much higher in the upper and lower slope compared to the plateau and the foot slope but was not quantified because of the high number of irregular distributed rock fragments.

The foot slope exhibited the highest contents of all observed nutrients except for nitrogen. In most cases the differences to the other slope positions were significant.



	Plateau (0-15°)	Upper slope (30°)	Lower slope (32°)	Foot slope (0-5°)
C_{org} [%]:	9.1 ± 1.6ac	6.5 ± 0.8a	4.6 ± 0.8b	10.7 ± 1.7c
N_t [mg/g]:	3.4 ± 0.6a	3.9 ± 0.4a	1.9 ± 0.3b	3.9 ± 0.2a
PO_4^{3-} [µg/g]:	25.1 ± 6.0a	12.1 ± 3.3b	14.1 ± 3.4b	26.9 ± 9.0a
Ca^{2+} [µg/g]:	237.5 ± 147.5ab	121.8 ± 89.3a	327.5 ± 100.0b	2390.0 ± 67.5c
Mg^{2+} [µg/g]:	39.0 ± 9.5a	53.5 ± 14.5a	96.3 ± 26.5b	303.0 ± 41.8c
K^+ [µg/g]:	160.0 ± 36.8a	161.3 ± 31.0a	175.8 ± 28.8a	379.3 ± 28.5b
Al^{3+} [µg/g]:	559.0 ± 132.0a	481.0 ± 37.0a	388.0 ± 114.0a	39.8 ± 5.8b
pH [1M KCl]**:**	3.3 ± 0.1a	3.6 ± 0.0b	3.8 ± 0.1c	4.8 ± 0.1d
sand [%]**:**	37.6 ± 3.7a	59.7 ± 3.6bc	60.5 ± 1.1b	52.5 ± 3.2c
silt [%]**:**	41.9 ± 3.0a	27.4 ± 2.1b	26.3 ± 1.6b	34.7 ± 3.3c
clay [%]**:**	20.0 ± 1.9a	14.5 ± 3.1b	14.5 ± 0.8b	9.4 ± 2.7c

Fig. III.2: Schematic hillslope profile of a southwest exposed slope of the Ahr-Eifel. Presented are median and MAD (n = 8) of several soil chemical characteristics (pH, C_{org}, N_t, PO_4^{3-}-P, K^+, Al^{3+}) and the soil texture (sand-, silt-, clay-proportion) of the upper soil at different relief positions (plateau, upper hillslope, lower hillslope, foot slope). Slope gradient at the relief positions is given in brackets. Elevation ranges from 360 m (foot slope) to 480 m (plateau). Differences between the slope positions are indicated by different letters behind the median ± MAD values ($p \leq 0.05$; Mann-Whitney-U-test)

III.2 Investigation II (deer/stand density)

III.2.1 Soil physical and chemical properties

The soil pH ranged from 4.1 to 5.0 at the investigation plots and was significantly higher ($p \leq 0.001$) at the dense plots (Ud/Fd) compared to the thinned plots (Ut/Ud) when comparing same treatments (tab. III.1). Additionally, the pH was significantly higher at the fenced plot Ft than at the corresponding unfenced plot Ut but the dense plots Fd and Ud did not differ from each other. The median C/N-value ranged from 14.9-16.2 and did not differ significantly between the sites (tab. III.1). The WRC_{max} and the soil moisture were significantly lowest at the site Ud ($p \leq 0.001$). WRC_{max} and soil moisture at the other plots were in a similar range (WRC_{max}: 56.1-61.9; soil moisture: 30.0-38.8). However, at the plot Ft the significantly highest ($p \leq 0.05$) values were obtained (tab. III.1).

The soil texture was similar at all sites. Only the plot Ud differed slightly from the other plots with higher sand content and significantly higher ($p \leq 0.001$) clay content (Ls3). The soils of the other plots were defined as loamy sandy silts (Uls) according to the German DIN 4220.

Tab. III.1: Several soil properties of the investigation plots Ud (unfenced, dense), Ut (unfenced, thinned), Fd (fenced, dense) and Ft (fenced, thinned). Presented are median ± MAD of all sampling dates (n = 8-40). Differences between the plots are indicated by different letters ($p \leq 0.05$; Mann-Whitney-U-test).

site	n	**Ud**	**Ut**	**Fd**	**Ft**
pH (1M KCl)	40	5.0 ± 0.4^{a}	4.1 ± 0.3^{b}	5.0 ± 0.3^{a}	4.6 ± 0.3^{c}
C/N	40	15.9 ± 2.2^{a}	16.2 ± 3.9^{a}	15.1 ± 2.3^{a}	14.9 ± 3.5^{a}
litter [g/300 cm^2]	32	0.0 ± 0.0^{a}	11.1 ± 8.9^{b}	11.8 ± 10.0^{b}	18.6 ± 10.5^{c}
WRC_{max} [%]	40	44.1 ± 1.7^{a}	58.2 ± 3.3^{b}	56.1 ± 2.9^{b}	61.9 ± 3.2^{c}
soil moisture [%]	40	17.8 ± 4.5^{a}	34.8 ± 4.2^{b}	30.0 ± 4.0^{b}	38.8 ± 3.6^{c}
sand [%]	8	40.6 ± 1.0^{a}	34.1 ± 2.2^{b}	38.9 ± 1.3^{a}	34.7 ± 1.8^{b}
silt [%]	8	37.4 ± 3.0^{a}	53.8 ± 1.7^{b}	50.2 ± 1.9^{b}	51.6 ± 1.7^{b}
clay [%]	8	22.7 ± 3.4^{a}	12.0 ± 0.7^{b}	11.4 ± 1.3^{b}	13.4 ± 2.0^{b}

The contents of C_{org} and N_t were significantly higher ($p \leq 0.05$) at thinned than at dense plots when regarding unfenced and fenced plots separately (fig. III.3). Comparing fenced and unfenced plots of the same stand density I generally found higher C_{org} and N_t values at the fenced plots. These differences were significant ($p \leq 0.05$) except for the organic carbon content at the thinned plots. Significantly lowest C (5.5 %) and N contents (2.9 mg/g) were found at the plot Ud which was neither fenced nor thinned.

Analyses of covariance (ANCOVA) delivered highly significant ($p \leq 0.001$) model explanations for both elements (tab. III.2). The highest influence was found for the factor "stand density" which explained up to 36 % of the model. The factor "deer" explained 11 % of the model for organic carbon and 24 % of the model for total nitrogen. However, interaction occurred in both cases (C_{org}: $R^2 = 0.08$; N_t: $R^2 = 0.10$). An influence of the covariate "season" (spring/fall) could not be derived from analyses of covariance.

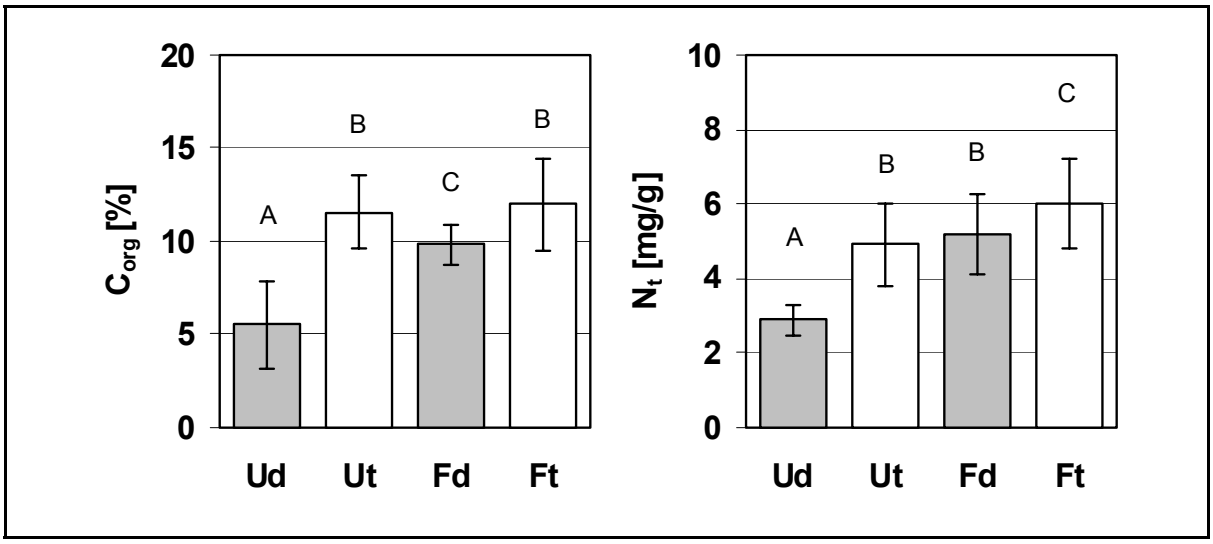


Fig. III.3: Contents of organic carbon (C_{org}) and total nitrogen (N_t) at the investigation plots Ud (unfenced, dense), Ut (unfenced, thinned), Fd (fenced, dense) and Ft (fenced, thinned). Presented are median and MAD of all data (n = 40). Differences between the plots are indicated by different letters above the columns ($p \leq 0.05$; Mann-Whitney-U-test).

The content of phosphate-P differed strongly among the plots (fig. III.4). Phosphate increased significantly ($p \leq 0.001$) in the order Ud (11.6 µg/g) < Fd (28.0 µg/g) < Ut (44.6 µg/g) < Ft (63.1 µg/g). Accordingly, analysis of covariance revealed a highly significant influence of the factors "deer" ($R^2 = 0.21$) and "stand density" ($R^2 = 0.52$) on the phosphate content in the soil (tab. III.2). The highly significant result for the covariate "season" reveals that there were differences in the phosphate content between the spring and the

autumn samples. The phosphate contents tended to be higher in spring at all plots (tab. Appendix-2.1,2.2)

The contents of extractable magnesium, calcium and potassium responded differently to the plot characteristics (fig. III.4). Magnesium contents were generally higher at the exclusion treatments Fd (868 µg/g) and Ft (790 µg/g) than at unfenced plots Ud (608 µg/g) and Ut (603 µg/g) but neither inside nor outside the fenced exclosure I found differences between dense and thinned plots. Hence, only the factor "deer" significantly ($p \leq 0.001$) contributed to the model explanation ($R^2 = 0.25$) (tab. III.2). Additionally, the covariate "season" significantly influenced the magnesium content in the soil. Higher values were obtained in spring (see tab. Appendix-2.1/2.2).

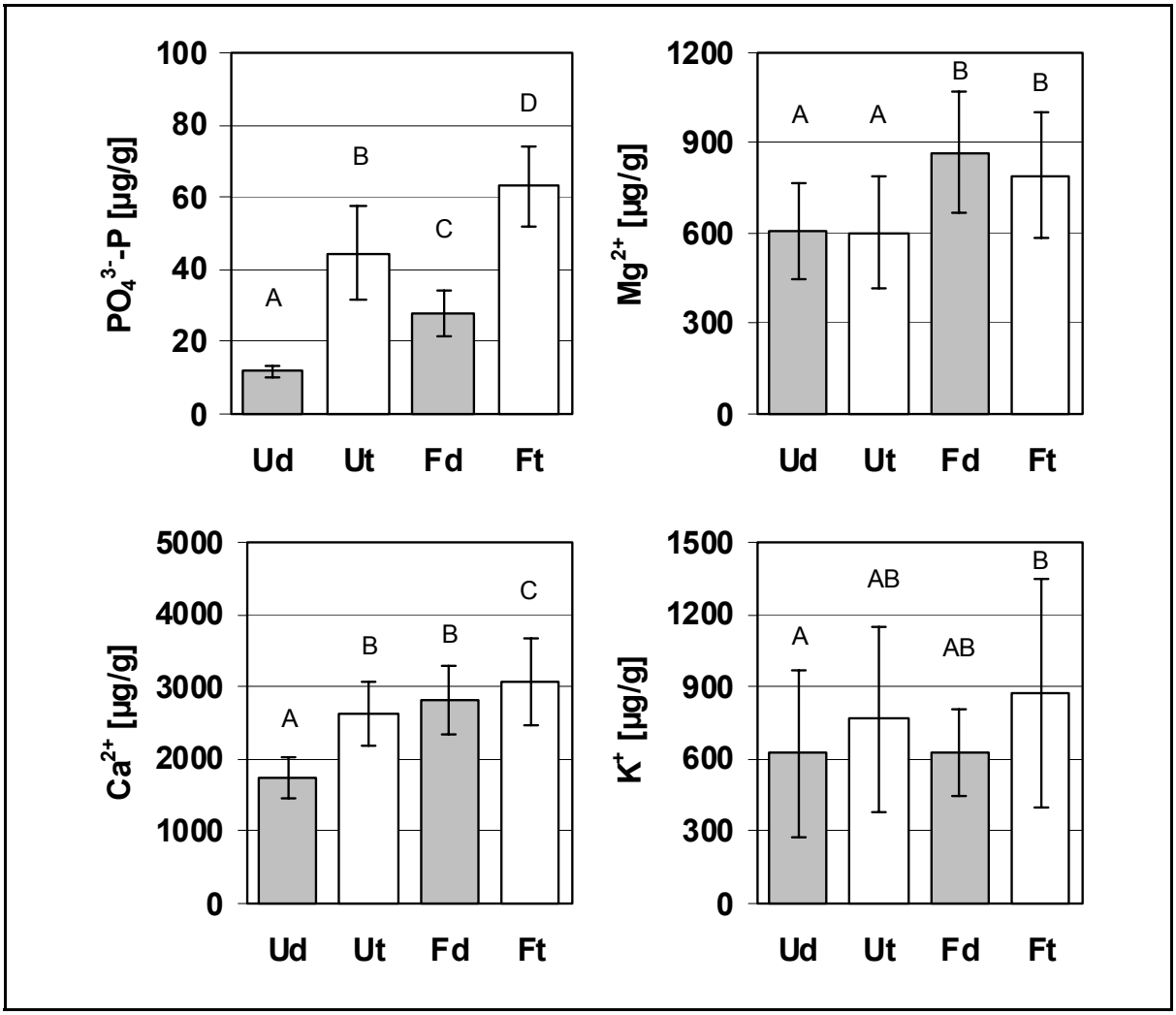


Fig. III.4: Contents of phosphate-P (PO_4^{3-}-P), magnesium (Mg^{2+}), calcium (Ca^{2+}) and potassium (K^+) at the investigation plots Ud (unfenced, dense), Ut (unfenced, thinned), Fd (fenced, dense) and Ft (fenced, thinned). Presented are median and MAD of all data (n = 40). Differences between the plots are indicated by different letters above the columns ($p \leq 0.05$; Mann-Whitney-U-test).

The calcium content significantly increased in the order Ud (1.7 mg/g) < Ut (2.6 mg/g) < Fd (2.8 mg/g) < Ft (3.1 mg/g) (fig. III.4). All plots differed significantly ($p \leq 0.05$) from each other except for the couple Ut/Fd. ANCOVA-results (tab. III.2) indicate a strong influence of the factors "deer" ($R^2 = 0.11$) and "stand density" ($R = 0.25$) on the content of extractable calcium in soil. Also the interaction of both factors significantly ($R^2 = 0.05$) contributed to the model explanation ($R^2 = 0.05$).

The potassium content differed little between the plots (fig. III.4). Only the lowest value at plot Ud (622 µg/g) and the highest value at plot Ft (871 µg/g) differed significantly ($p \leq 0.05$) from each other. Analysis of covariance did not deliver a significant model explanation for potassium.

Tab. III. 2: Two-factorial ANCOVA on the effects of "deer" (exclusion/access) and "stand density" (dense/thinned) on the contents of several soil nutrients (C_{org}, N_t, PO_4^{3-}-P, K^+, Mg^{2+}, Ca^{2+}) at the investigation plots. As covariate the season was taken into account (spring/autumn). ***: $p \leq 0.001$, ns: not significant.

Analysis of covariance (two-factorial)		**C_{org}**			**N_t**			**PO_4^{3-}-P**		
	df	F		R^2	F		R^2	F		R^2
covariate (season)	1	3.1	ns		0.5	ns		27.0	***	
deer	1	33.2	***	0.11	126.1	***	0.24	154.6	***	0.21
stand density	1	81.7	***	0.28	188.6	***	0.36	393.5	***	0.52
interaction	1	22.9	***	0.08	54.4	***	0.10	17.0	ns	
model	4	35.2	***	0.48	92.4	***	0.70	148.9	***	0.80
		Mg^{2+}			**Ca^{2+}**			**K^+**		
	df	F		R^2	F		R^2	F		R^2
covariate (season)	1	14.8	***		1.3	ns		1.7	ns	
deer	1	35.4	***	0.17	74.3	***	0.25	4.6	ns	
stand density	1	2.6	ns		53.2	***	0.18	0.1	ns	
interaction	1	2.6	ns		16.1	***	0.05	0.0	ns	
model	4	15.6	***	0.25	36.3	***	0.49	1.6	ns	

III.2.2 Soil microbial properties

Microbial activity ranged from 2.5-5.7 μgCO_2-C/mg*h and was significantly lower ($p \leq 0.01$) at dense plots compared to the equivalent thinned plots inside or outside the fenced exclosure (fig. III.5). Moreover, microbial activity in the unfenced plot Ud was significantly lower ($p \leq 0.001$) than in all the other plots. However, the unfenced thinned plot Ut did not differ significantly ($p = 0.099$) from the fenced plots.

For microbial biomass the significantly lowest ($p \leq 0.001$) value (1.86 mgC/g) was found at the plot Ud (fig. III.5). The other plots did not differ significantly from each other (2.48-2.68 mgC/g).

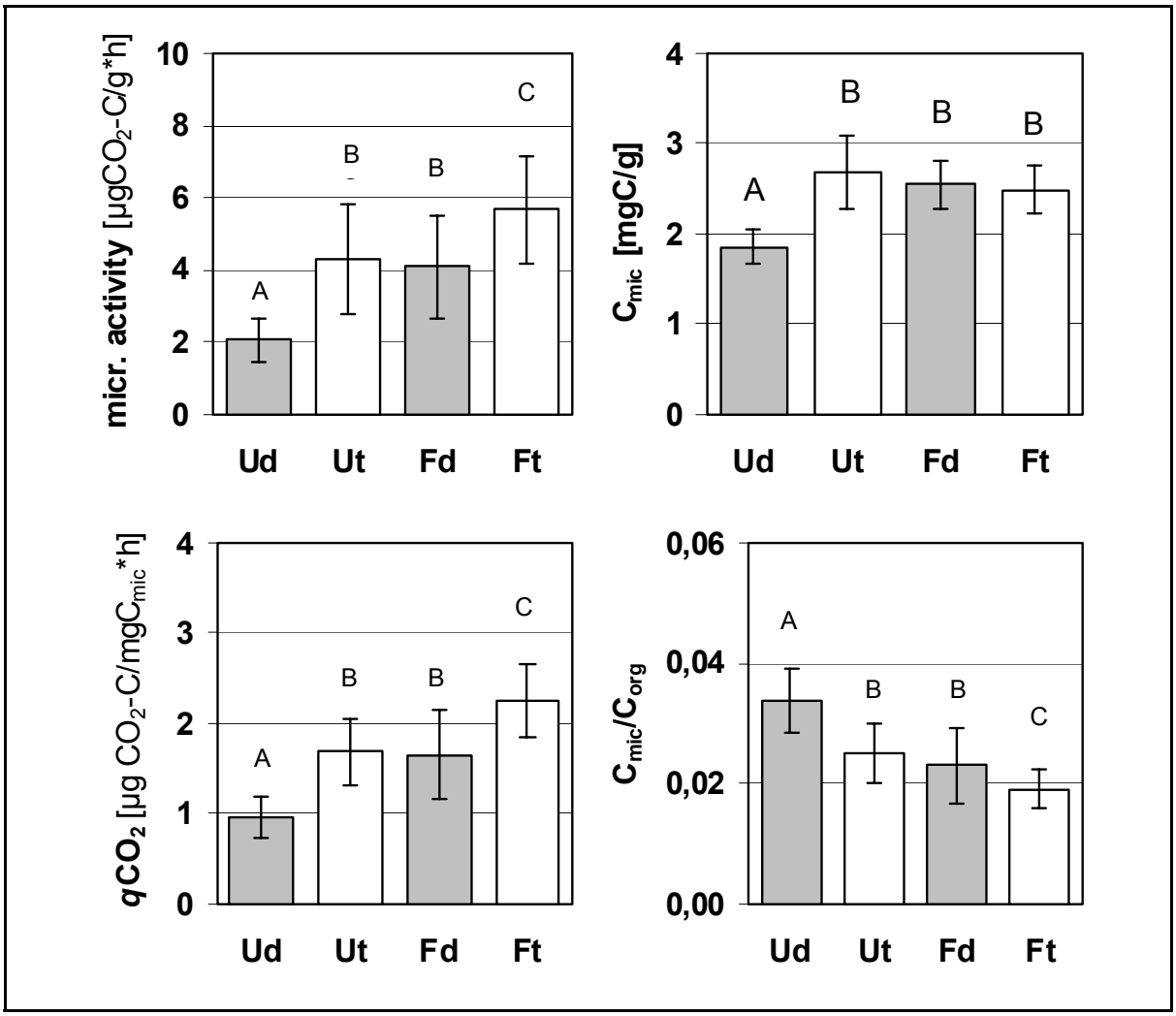


Fig. III.5: Microbial activity, microbial biomass (C_{mic}), metabolic quotient (qCO_2) and C_{mic}/C_{org}-ratio at the investigation plots Ud (unfenced, dense) and Ut (unfenced, thinned), Fd (fenced, dense) and Ft (fenced, thinned). Presented are median and MAD of all data (n = 40). Differences between the plots are indicated by different letters above the columns ($p \leq 0.05$; Mann Whitney-U-test).

The specific microbial respiration (qCO_2) was significantly lowest ($p \leq 0.001$) at the plot Ud (1.0 μgCO_2-C/mgC_{mic}*h) and significantly highest ($p \leq 0.001$) at the plot Ft (2.3 μgCO_2-C/mgC_{mic}*h). The plots Ut and Fd did not differ significantly from each other (fig. III.5). The opposite trend was found for the C_{mic}/C_{org}-ratio with significantly highest ($p \leq 0.001$) values at the plot Ud (0.019) and significantly lowest ($p \leq 0.01$) values (0.034) at the plot Ft (fig. III.5).

According to analyses of covariance "stand density" was the most important factor for microbial properties (tab. III.3). It explained the variances at 24 % for microbial activity, at 12 % for microbial biomass, at 23 % for the qCO_2 and at 15 % for the C_{mic}/C_{org}-ratio. The exclusion of deer by fencing also influenced microbial properties (except for C_{mic}) significantly ($p \leq 0.01$) but was less important than "stand density" with R^2 values ranging from 0.07 to 0.11. For the microbial biomass interaction between the factors was revealed ($R^2 = 0.16$). Seasonal variations were of minor importance for the microorganisms.

Tab. III. 3: Two-factorial ANCOVA on the effects of "deer" (exclusion/access) and "stand density" (dense/thinned) on microbial properties (microbial activity/biomass, qCO_2, C_{mic}/C_{org}) at the investigation plots. As covariate the season was taken into account (spring/autumn). ***: $p \leq 0.001$; ns: not significant.

Analysis of covariance (two-factorial)		**Microbial activity**		**Microbial biomass**	
	df	F	R^2	F	R^2
covariate (season)	1	0.4 ns		0.4 ns	
deer	1	21.3 ***	0.09	6.4 ns	
stand density	1	58.2 ***	0.24	28.0 ***	0.12
interaction	1	8.0 ns		36.2 ***	0.16
model	4	21.9 ***	0.36	17.8 ***	0.31
		qCO_2		**C_{mic}/C_{org}**	
	df	F	R^2	F	R^2
covariate (season)	1	0.4 ns		6.4 **	
deer	1	25.0 ***	0.11	14.6 ***	0.07
stand density	1	53.8 ***	0.23	30.3 ***	0.15
interaction	1	0.4 ns		1.5 ns	
model	4	19.9 ***	0.34	13.2 ***	0.25

III.2.3 Litter layer and soil fauna

Litter layer

The dry mass of leaf litter collected from the plots was significantly highest ($p \leq 0.05$) at the thinned exclusion treatment (Ft: 18.6 g/300cm²) and significantly lowest ($p \leq 0.001$) at the unfenced dense plot (Ud: 0 g/300cm²) (tab. III.1). At the plot Ud hardly any litter was found at any of the sampling dates. There were no statistical differences in the amount of litter between the plots Ut and Fd. The high MAD-values indicate that there were large differences in the thickness of the litter layer between sampling dates (see tab. Appendix-2.1, 2.2).

Mesofauna

The abundance of the soil mesofauna at the plots was highly variable (fig. III.6). Regarding the median values (ind./31.17 cm²; n = 36) the significantly highest ($p \leq 0.05$) abundance of mesoarthropods was found at plot Fd (42 ± 20 ind./31.17 cm²) and the significantly lowest at plot Ud (17 ± 9 ind./31.17 cm²). The thinned plots (Ut/Ft) did not differ from each other. The enchytraeids were more abundant ($p \leq 0.05$) at the thinned plots than at the dense plots when comparing similar treatments (fig. III.6). The plots Ut and Fd did not differ significantly from each other. The significantly ($p \leq 0.001$) lowest abundance was obtained for the plot Ud (1 ± 1 ind./55.42 cm²).

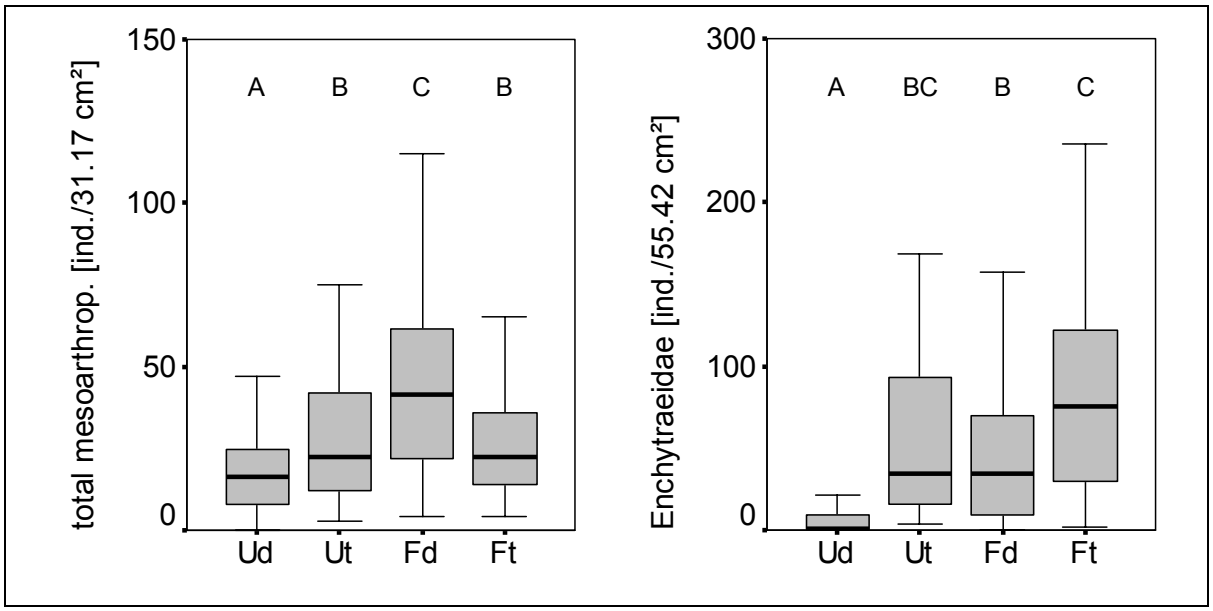


Fig. III.6: Abundances of mesoarthropoda [ind./31.17 cm²] and enchytraeidae [ind./55.42 cm²] at the investigation plots Ud (unfenced, dense), Ut (unfenced, thinned), Fd (fenced, dense) and Ft (fenced, thinned). Presented are box and whisker-plots (n = 32). Mann-Whitney-U-tests were conducted to test for differences between the study plots. Different letters indicate significant differences ($p \leq 0.05$).

Tab. III.4: Abundance of the soil mesofauna at the investigation plots Ud (unfenced, dense), Ut (unfenced, thinned), Fd (fenced, dense) and Ft (fenced, thinned). Presented are median and MAD of the sum-values (n = 9) as individuals per 124.7 cm² (221.7 cm²). Different letters represent significant differences between the plots ($p \leq 0.05$; Mann-Whitney-U-test).

Mesofauna sites	Ud	Ut	Fd	Ft
Total mesoarthr. [ind./124.7 cm²]	75 ± 8^{a}	124 ± 52^{b}	196 ± 34^{c}	109 ± 29^{b}
Enchytraeidae [ind./221.7 cm²]	21 ± 8^{a}	219 ± 136^{bc}	196 ± 43^{b}	342 ± 84^{c}
Collembola [ind./124.7 cm²]	34 ± 8^{a}	46 ± 9^{ab}	88 ± 22^{b}	64 ± 19^{b}
Oribatidae [ind./124.7 cm²]	31 ± 8^{a}	74 ± 32^{ab}	85 ± 25^{b}	31 ± 14^{a}
other Acari [ind./124.7 cm²]	29 ± 6^{a}	33 ± 8^{a}	53 ± 17^{b}	35 ± 14^{a}
Protura [ind./124.7 cm²]	2 ± 2^{ab}	1 ± 1^{ab}	5 ± 3^{a}	0 ± 0^{b}
Diplura [ind./124.7 cm²]	0 ± 0^{a}	0 ± 0^{a}	5 ± 3^{b}	1 ± 0^{a}
Pauropoda [ind./124.7 cm²]	3 ± 2^{a}	0 ± 0^{b}	2 ± 1^{a}	1 ± 0^{ab}
Symphila [ind./124.7 cm²]	0 ± 0^{a}	2 ± 1^{ab}	2 ± 1^{ab}	3 ± 1^{b}
Pseudoscorp. [ind./124.7 cm²]	0 ± 0	0 ± 0	0 ± 0	0 ± 0

The most abundant groups of the mesoarthropods, the Collembola and the Acari, displayed a similar distribution pattern as shown for the sum of all mesoarthropods (fig. III.6, tab. III.4). Highest abundances were generally found at plot Fd and lowest abundances at plot Ud but differences were not always significant. The abundances were higher at the dense plots than at the thinned plots of the exclosure treatment. The opposite was found outside the fenced exclosure.

The abundances of other mesofaunal groups (Protura, Diplura, Pauropoda, Symphila, Pseudoscorpionidae) ranged from 0-5 individuals per 125 cm² (tab. III.4). In most cases no significant differences between the plots were found. Pseudoscorpionida data was based on single individuals.

Macrofauna

The abundance of the macrofauna (ind./300 cm²) at the plots increased in the order Ud (0 ± 0) < Ut (7 ± 4) < Fd (10 ± 6) < Ft (16 ± 7) (fig. III.7). All plots differed significantly ($p \leq 0.05$) from each other except for the plots Ut and Fd. The beetles were the most abundant among all macrofaunal groups with 0 to 21 individuals per 0.15 m² (tab. III.5). Spiders (0-7 ind./0.15 m²), millipedes (0-8 ind./0.15 m²) centipedes (0-6 ind./

0.15 m²) and woodlice (0-4 ind./0.15 m²) were by far less abundant. Other common soil invertebrates like ants, earthworms and bugs were extracted in low number from the litter samples and were only considered for the calculation of the total macrofauna.

Coleoptera, Aranaea, Isopoda, Diplopoda and Chilopoda all showed the same distribution pattern among the plots as described above for the total macrofauna (tab. III.5). The abundances were always significantly lowest ($p \leq 0.05$) at the unfenced dense plot (Ud) and highest at the plot Ft. However the abundances at Ft did not always differ significantly from the plot Fd (Coleoptera, Aranae, Chilopoda). The abundances at the plots Ut and Fd were statistically identical for all groups.

Analysis of covariance delivered highly significant model explanations for all macrofaunal groups with R^2-values ranging from 0.51 to 0.77 (tab. III.6). The factor "deer" explained 32-43 % of the variances. The factor "stand density" explained the variances at 16-25 %. Significant interaction occurred for the abundance of Coleoptera contributing 14 % to the model explanation.

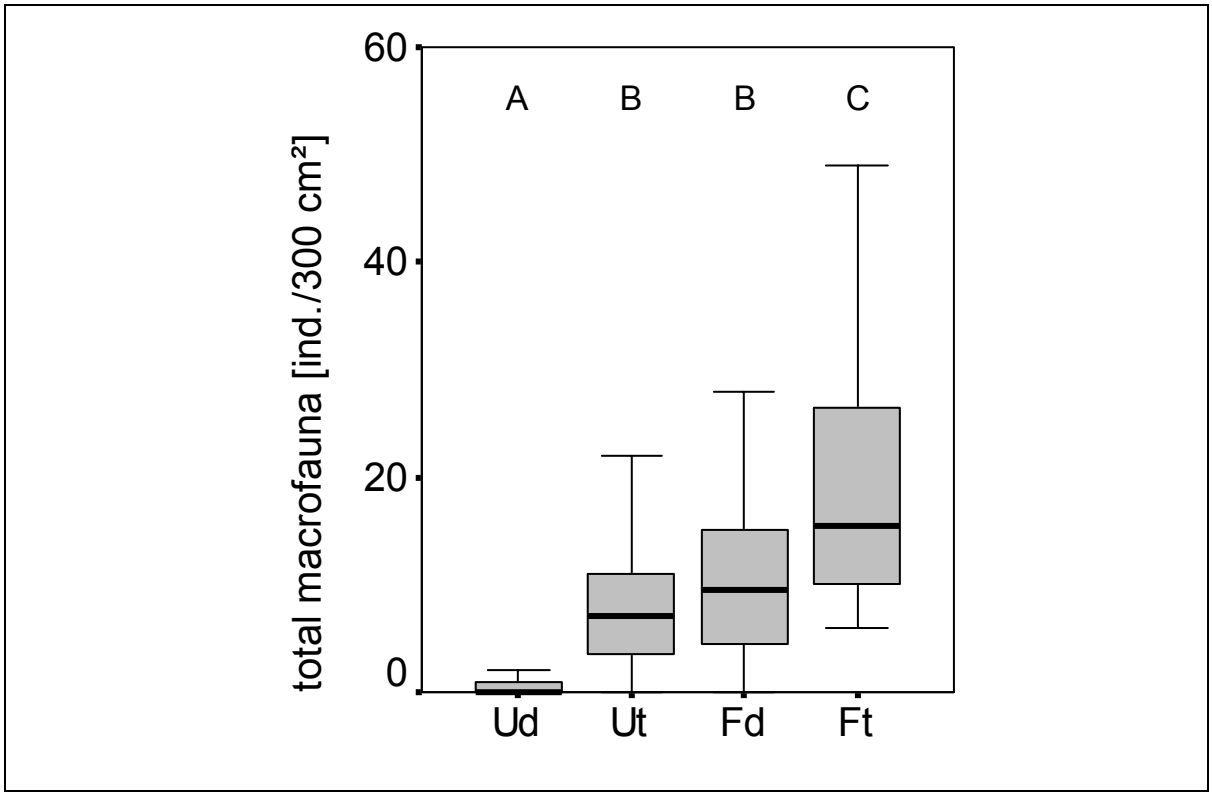


Fig. III.7: Abundance of the macrofauna [ind./300 cm²] at the investigation plots Ud (unfenced, dense), Ut (unfenced, thinned), Fd (fenced, dense) and Ft (fenced, thinned). Presented are box and whisker-plots (n = 45). Mann Whitney-U-tests were conducted to test for differences between the study plots. Different letters indicate significant differences between the plots ($p \leq 0.05$).

Tab. III.5: Abundance of the soil macrofauna at the investigation plots Ud (unfenced, dense), Ut (unfenced, thinned), Fd (fenced, dense) and Ft (fenced, thinned). Presented are median and MAD of the sum-values (n = 9) as individuals per 0.15 m². Different letters represent significant differences between the plots ($p \leq 0.05$; Mann Whitney-U-test).

Macrofauna sites	**Ud**	**Ut**	**Fd**	**Ft**
Total macrof. [ind./0.15 m²]	4 ± 3^{a}	41 ± 6^{b}	60 ± 11^{b}	107 ± 12^{c}
Coleoptera [ind./0.15 m²]	0 ± 0^{a}	12 ± 3^{b}	15 ± 5^{bc}	21 ± 4^{c}
Aranaea [ind./0.15 m²]	0 ± 0^{a}	4 ± 2^{b}	6 ± 3^{bc}	7 ± 1^{c}
Isopoda [ind./ 0.15 m²]	0 ± 0^{a}	1 ± 1^{b}	1 ± 1^{b}	4 ± 1^{c}
Diplopoda [ind./ 0.15 m²]	0 ± 0^{a}	1 ± 0^{b}	3 ± 2^{b}	8 ± 2^{c}
Chilopoda [ind./ 0.15 m²]	0 ± 0^{a}	2 ± 2^{b}	4 ± 2^{bc}	6 ± 1^{c}

Tab. III. 6: Two-factorial ANOVA on the effects of deer (exclusion/access) and stand density (dense/thinned) on the abundance of the macrofauna (total macrofauna, Coleoptera, Aranaea, Chilopoda, Isopoda, Diplopoda) at the investigation plots. ***: $p \leq 0.001$; ns: not significant.

Analysis of variance (two-factorial)	**total macrofauna**			**Coleoptera**			**Aranaea**		
	df	F		R²	F		R²	F		R²
deer activity	1	50.4	***	0.43	48.2	***	0.39	28.0	***	0.35
stand density	1	29.0	***	0.25	29.7	***	0.24	12.6	***	0.16
interaction	1	10.2	ns		17.6	***	0.14	10.9	ns	
model	3	29.9	***	0.76	31.8	***	0.77	17.1	***	0.65

	Chilopoda			**Isopoda**			**Diplopoda**		
	df	F		R²	F		R²	F		R²
deer activity	1	22.6	***	0.40	21.7	***	0.32	49.9	***	0.53
stand density	1	5.8	ns		15.5	***	0.23	14.9	***	0.16
interaction	1	0.5	ns		1.7	ns		0.7	ns	
model	3	9.7	***	0.51	12.9	***	0.58	21.8	***	0.70

III.2.4 Foliar nutrients

None of the sampled trees of the investigation plots suffered nutrient deficiencies or imbalances at least concerning the foliar nutrients analysed (N_t, PO_4^{3-}, Ca^{2+}, Mg^{2+}, K^+). The nutrient concentrations as well as the calculated nutrient ratios were in the class 2 or 3 indicating a normal or adequate and optimal to high range respectively according to STEFAN et al. (1997) (tab. III.7). The N/P ratio at the plot Ft was the only parameter in the range of "nutritional imbalance".

Only some of the nutrients differed significantly ($p \leq 0.05$) between the plots. Concentrations of nitrogen and phosphorus and the N/C ratio were significantly higher in oak leaves of the exclusion treatment Ft. In contrast, the concentration of calcium was significantly higher in leaves of unfenced oak trees (plot Ud).

Tab. III.7: Foliar nutrient concentrations and nutrient ratios of oak trees (*Quercus petraea*) at the sites Ud (unfenced, dense) and Ft (fenced, thinned) of the investigation. Presented are median and MAD (n = 8) and results of the Mann-Whitney-U-test (exact significance). Criteria used for the judgement of the foliar nutrient concentrations and ratios are taken from the FFCC report, STEFAN et al., 1997.

Nutrient concentrations/ nutrient ratios	**Site**		p	**Class/criteria[1)]**		
(n = 8)	Ud	Ft		1	2	3
N [mg/g]	23.06 ± 1.32	31.54 ± 4.21	0.000	< 15	15-25	> 25
P [mg/g]	2.03 ± 0.14	3.24 ± 0.58	0.021	< 1.0	1.0-1.8	> 1.8
Ca [mg/g]	8.25 ± 2.38	4.73 ± 0.68	0.028	< 3.0	3.0-3.8	> 8.0
Mg [mg/g]	2.70 ± 0.80	3.05 ± 0.78	0.234	< 1.0	1.0-2.5	> 2.5
K [mg/g]	10.03 ± 1.53	11.38 ± 1.20	0.161	< 5.0	5.0-10	> 10
N/P	23.57 ± 1.64	31.91 ± 4.45	0.234	< 8.3	8.3-25	> 25
N/Ca	2.81 ± 0.84	6.48 ± 3.46	0.002	< 1.9	1.9-8.3	> 8.3
N/Mg	8.1 ± 3.00	10.44 ± 6.33	0.798	< 6.0	6.0-25	> 25
N/K	2.29 ± 0.6	2.72 ± 1.06	0.161	< 1.5	1.5-5.0	> 5.0

[1)] 1 = low, 2 = normal or adequate, 3 = optimal to high. For nutrient concentrations low values were used as an indication of an insufficient nutrient availability. For nutrient ratios high values were used as an indication of an unbalanced nutrient status.

III.3 Investigation III (wild boar/deer)

III.3.1 Soil physical and chemical properties

The soil pH was significantly lower ($p \leq 0.05$) at the plot Bu than at the plots Cf and Bf but altogether the pH-range among the plots was small (3.3-3.5) (tab. III.8). The C/N-ratio was higher at the unfenced plots (16 ± 2) than at the exclusion treatments (14 ± 3) but differences were not always significant (tab. III.8). Soil pH and C/N-ratio did not differ between grubbed and ungrubbed plots.

The median WRC_{max} ranged from 57.8 to 66.6 % and the median soil moisture from 30.8 to 41.4 % at the plots. Both were generally higher ($p \leq 0.05$) at the unfenced plots compared to the fenced plots (tab. III.8) and tended to be higher at ungrubbed than at grubbed plots when comparing similar treatments. But only in the fenced exclosure and only for the WRC_{max} were significant differences found ($p \leq 0.05$).

Soil texture slightly differed between the plots (tab. III.8). At the plots Cf, Bf and Bu the soil was a sandy loam (Ls2) and at the plot Cu the soil was a loamy sandy silt (Uls) according to the German DIN 4220. The exclosure treatments did not differ from each other. Outside the fenced exclosure there were no differences in the proportion of sand but the proportion of silt was significantly higher ($p \leq 0.05$) at the ungrubbed plot whereas the opposite was found for the clay content.

Tab. III.8 : Several soil properties of the investigation plots Cf (control, fenced), Bf (bioturbation, fenced), Cu (control, unfenced) and Bu (bioturbation, unfenced). Presented are median and MAD of all sampling dates (n = 40). Differences between the plots are indicated by different letters ($p \leq 0.05$).

site	n	**Cu**	**Bu**	**Cf**	**Bf**
pH (1M KCl)	40	3.4 ± 0.1^{ab}	3.3 ± 0.1^{b}	3.5 ± 0.1^{a}	3.5 ± 0.1^{a}
C/N	40	16 ± 2^{b}	16 ± 2^{b}	14 ± 3^{a}	14 ± 3^{ab}
litter [g/300 cm^2]	32	12.7 ± 4.0^{b}	8.3 ± 4.8^{a}	7.5 ± 3.1^{a}	5.4 ± 3.2^{a}
WRC_{max} [%]	40	66.6 ± 2.6^{c}	65.7 ± 1.8^{c}	61.6 ± 3.1^{a}	57.8 ± 1.4^{b}
soil moisture [%]	40	41.1 ± 6.9^{b}	38.9 ± 4.4^{b}	34.0 ± 6.5^{a}	30.8 ± 3.4^{a}
sand [%]	8	33.6 ± 1.5^{c}	34.9 ± 0.6^{c}	37.4 ± 4.1^{ac}	38.9 ± 1.6^{a}
silt [%]	8	52.0 ± 1.5^{b}	42.1 ± 2.0^{a}	42.3 ± 1.2^{a}	43.1 ± 1.1^{a}
clay [%]	8	14.1 ± 1.2^{b}	22.9 ± 2.5^{c}	19.7 ± 1.0^{a}	17.9 ± 0.9^{a}

The contents of organic carbon and total nitrogen were significantly ($p \leq 0.001$) higher at the unfenced plots (11.5/11.0 %) compared to the fenced plots (8.2/7.6 %) (fig. III.8). There were no statistical differences between grubbed and ungrubbed plots neither inside nor outside the fenced exclosure. Analysis of covariance showed that only the factor "deer" influenced the contents of organic carbon and nitrogen (tab. III.9). R^2-values were 0.27 (C_{org}) and 0.32 (N_t) respectively.

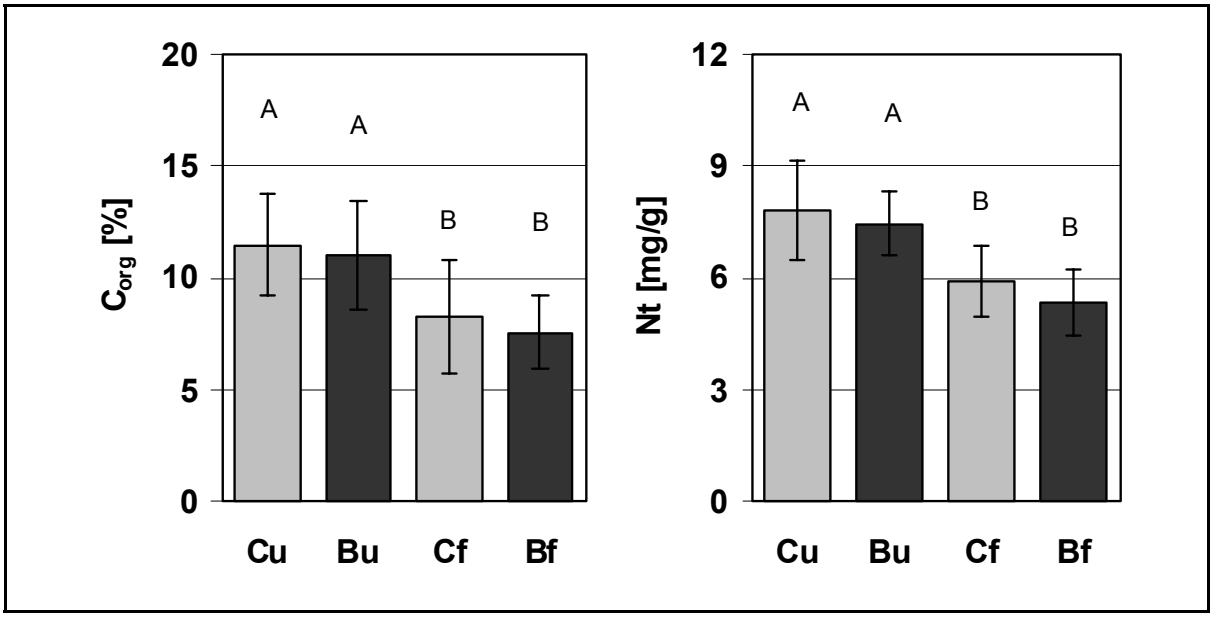


Fig. III.8: Contents of organic carbon (C_{org}) and total nitrogen (N_t) at the investigation plots Cu (control, unfenced), Bu (bioturbation, unfenced), Cf (control, fenced) and Bf (bioturbation, fenced). Presented are median and MAD of all data (n = 40). Differences between the plots are indicated by different letters above the columns ($p \leq 0.05$; Mann-Whitney-U-test).

Contents of phosphate-P (16.9-24.3 µg/g), potassium (250-361 µg/g), magnesium (91-165 µ/g) and calcium (780-1285 µg/g) were generally higher at the control plots than at the bioturbation plots (fig. III.9). For potassium and magnesium the differences between grubbed and ungrubbed plots were significant ($p \leq 0.05$) inside and outside the exclosure, whereas differences for phosphate were only significant ($p \leq 0.05$) comparing exclusion treatments and for calcium only comparing unfenced plots. Moreover contents of PO_4^{3-}, Mg^{2+} and Ca^{2+} tended to be higher at the unfenced than at the fenced plots (fig. III.9).
ANCOVA delivered highly significant model explanations for all mineral nutrients (tab. III.9). The factor "wild boar" was only important for the elements K^+ ($R^2 = 0.24$) and Mg^{2+}

($R^2 = 0.07$) (tab. III.9). The factor "deer" significantly ($p \leq 0.01$) influenced the contents of Mg^{2+} ($R^2 = 0.13$) and Ca^{2+} ($R^2 = 0.12$).

The covariate "year" delivered highly significant results for the nutrients C_{org}, PO_4^{3-}, Mg^{2+} and K^+. This was due to large differences in the contents of these nutrients between the years 2001 and 2002 (see tab. Appendix-3.1/3.2). Contents of organic carbon and phosphate were higher in 2002 than in 2001, for magnesium and potassium the opposite trend was found.

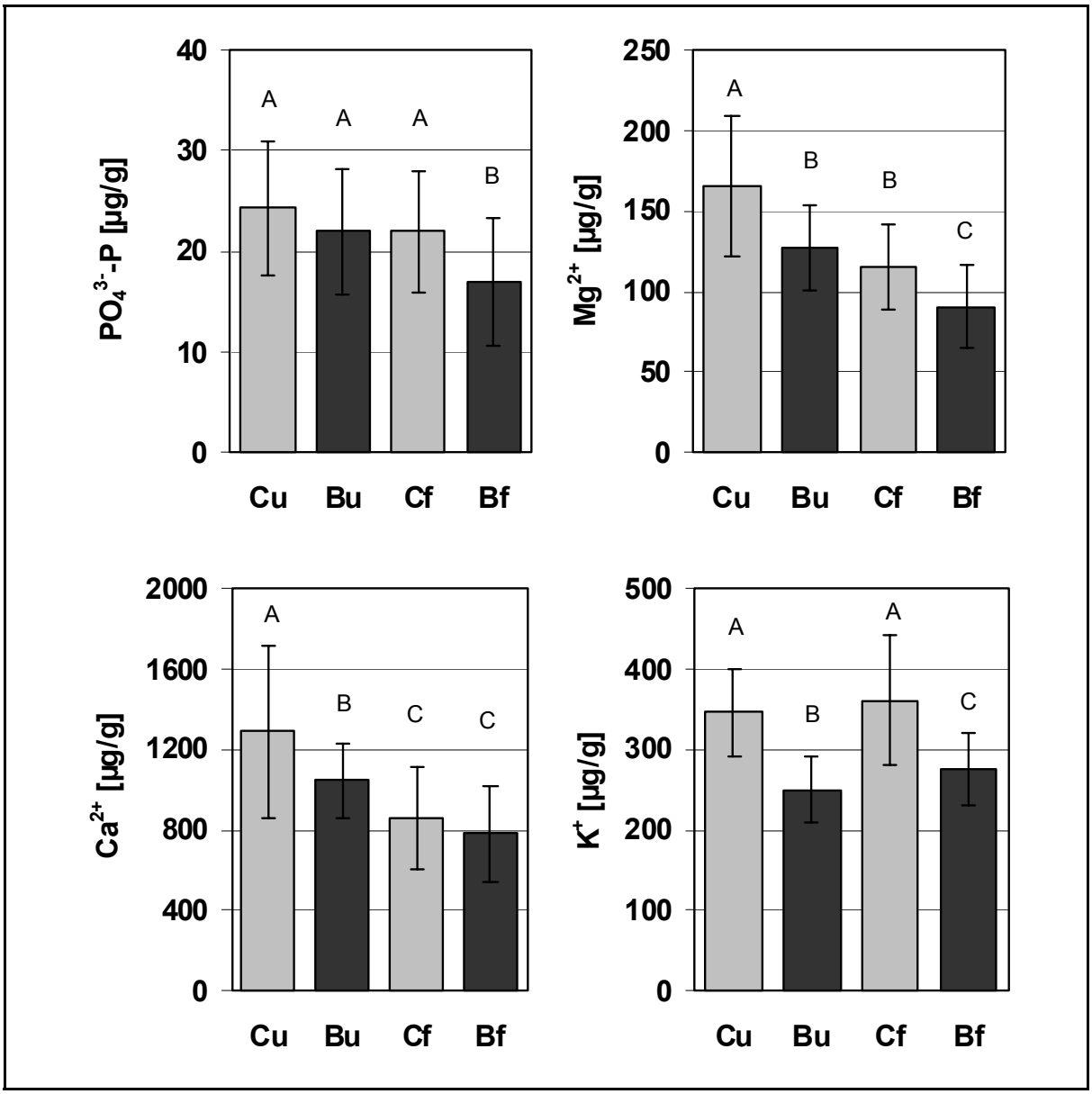


Fig. III.9: Contents of phosphate-P (PO_4^{3-}-P), magnesium (Mg^{2+}), calcium (Ca^{2+}) and potassium (K^+) at the investigation plots Cu (control, unfenced), Bu (bioturbation, unfenced), Cf (control, fenced) and Bf (bioturbation, fenced). Presented are median and MAD of all data (n = 40). Differences between the plots are indicated by different letters above the columns ($p \leq 0.05$; Mann-Whitney-U-test).

Tab. III. 9: Two-factorial ANCOVA on the effects of "wild boar" (grubbed/ungrubbed) and "deer" (exclusion/access) on the contents of several soil nutrients (C_{org}, N_t, PO_4^{3-}-P, K^+, Mg^{2+}, Ca^{2+}) at the investigation plots. As covariate the "year" was taken into account (2001/2002). ***: $p \leq 0.001$; ns: not significant.

Analysis of covariance (two-factorial)		**C_{org}**			**N_t**			**PO_4^{3-}-P**		
	df	F		R^2	F		R^2	F		R^2
covariate (year)	1	27.4	***		2.4	ns		71.5	***	
wild boar	1	3.5	ns		5.6	ns		8.9	ns	
deer	1	70.0	***	0.27	77.2	***	0.32	8.8	ns	
interaction	1	3.5	ns		0.2	ns		0.1	ns	
model	4	25.3	***	0.40	21.4	***	0.36	22.3	***	0.37
		Mg^{2+}			**Ca^{2+}**			**K^+**		
	df	F		R^2	F		R^2	F		R^2
covariate (year)	1	22.8	***		3.7	ns		13.67	***	
wild boar	1	16.8	***	0.04	7.4	ns		57.0	***	0.24
deer	1	29.1	***	0.12	22.6	***	0.13	5.8	ns	
interaction	1	1.3	ns		0.2	ns		5.4	ns	
model	4	17.5	***	0.31	8.5	***	0.18	20.5	***	0.35

III.2.2 Soil microbial properties

Microbial activity was significantly lower ($p \leq 0.05$) at the grubbed plots (Bf: 3.8; Bu: 5.5 μgCO_2-C/g*h) compared to the equivalent control plots inside or outside the fenced exclosure (Cf: 5.1; Cu: 6.9 μgCO_2-C/g*h) (fig. III.10). At the same time microbial activity was significantly higher ($p \leq 0.05$) at unfenced plots than at fenced plots when comparing similar treatments. The median microbial biomass values ranged from 2.0 to 3.3 mgC/g and did not differ among the plots except for the plot Bf which had a significantly lower ($p \leq 0.05$) microbial biomass compared to all the other plots (fig. III.10). The metabolic quotient did not differ significantly between the plots with median values ranging from 1.4 (Cf) to 2.4 μgCO_2-C/mgC_{mic}*h (Cu) (fig. III.10).The C_{mic}/C_{org}-ratio was significantly higher ($p \leq 0.05$) at the fenced plots Cf (0.039) and Bf (0.031) compared to the unfenced plots (Cu/Bu: 0.022/0.023) (fig. III.10). Additionally, the value at Cf was significantly higher ($p \leq 0.05$) than at Bf while Cu and Bu did not differ from each other.

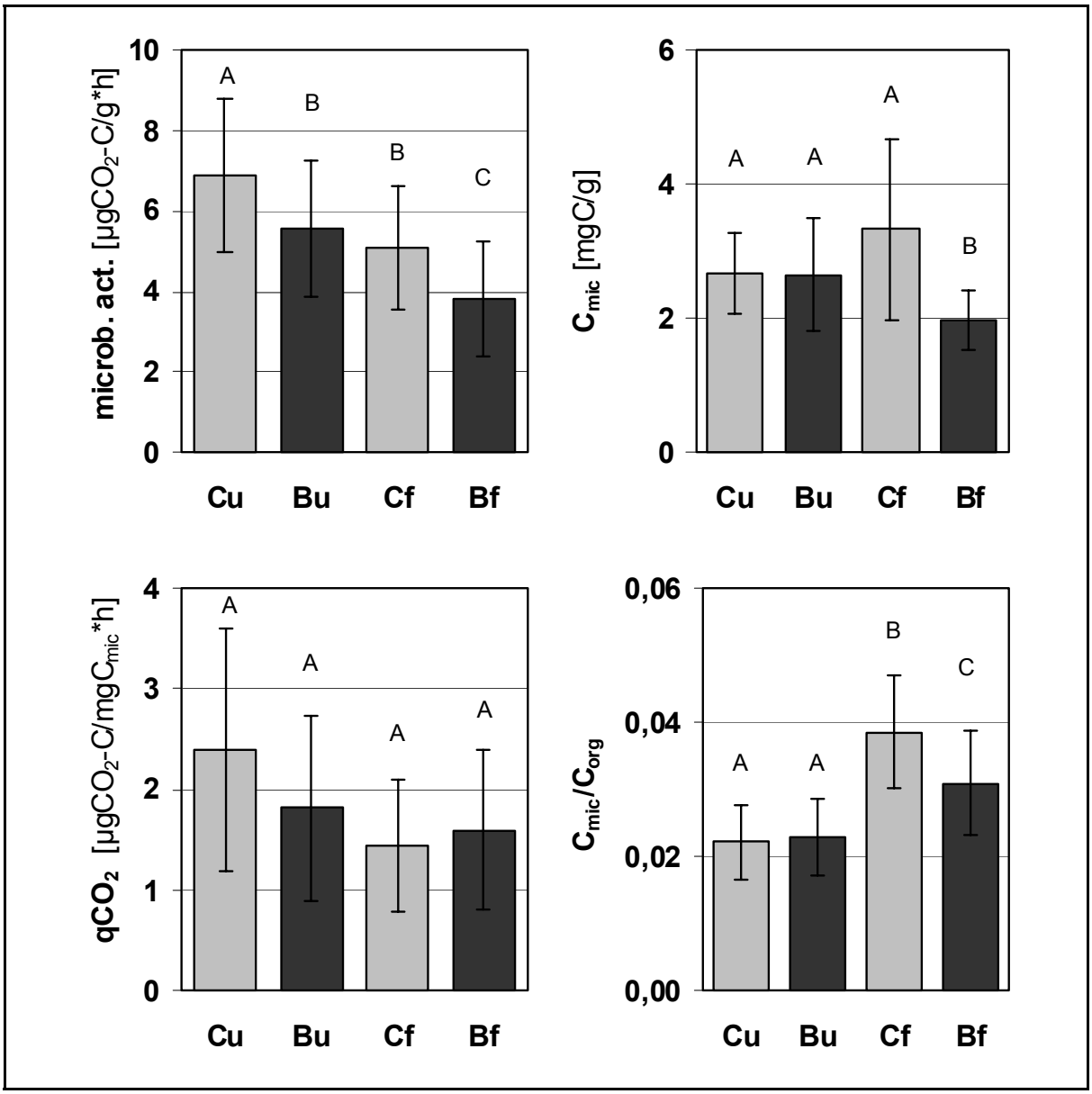


Fig. III.10: Microbial activity, microbial biomass (C_{mic}), metabolic quotient (qCO_2) and C_{mic}/C_{org}-ratio at the investigation plots Cu (control, unfenced), Bu (bioturbation, unfenced), Cf (control, fenced) and Bf (bioturbation, fenced). Presented are median and MAD of all data (n = 40). Differences between the plots are indicated by different letters above the columns ($p \leq 0.05$; Mann Whitney-U-test).

The factor "wild boar" significantly ($p \leq 0.001$) influenced microbial activity ($R^2 = 0.10$) and biomass ($R^2 = 0.04$) (tab. III.10). The factor "deer" explained 7 % of the variance for the microbial activity and 9 % of the variance for the C_{mic}/C_{org}-ratio. The metabolic quotient was not explained by the chosen model. High R^2-values for the model explanations resulted from strong differences between the years 2001 and 2002 for all microbial properties (see tab. Appendix-3.1, 3.2). Microbial activity and metabolic quotient were observed to be higher in 2001 than in 2002 while the opposite was found for the microbial biomass and the C_{mic}/C_{org}-ratio.

Tab. III. 10: Two-factorial ANCOVA on the effects of "wild boar" (grubbed/ungrubbed) and "deer" (exclusion/access) on microbial properties (microbial activity/biomass, qCO_2, C_{mic}/C_{org}) at the investigation plots. As covariate the "year" was taken into account (2001/2002). ***: $p \leq 0.001$, ns: not significant.

Analysis of covariance (two-factorial)		**Microbial activity**			**Microbial biomass**		
	df	F		R^2	F		R^2
covariate (year)	1	73.1	***		125.9	***	
wild boar	1	26.2	***	0.10	12.2	***	0.04
deer	1	19.3	***	0.07	1.7	ns	
interaction	1	1.4	ns		4.7	ns	
model	4	29.7	***	0.44	36.1	***	0.48
		qCO_2			**C_{mic}/C_{org}**		
	df	F		R^2	F		R^2
covariate (year)	1	189.6	***		44.3	***	
wild boar	1	2.0	ns		3.3	ns	
deer	1	4.3	ns		21.2	***	0.09
interaction	1	0.0	ns		3.9	ns	
model	4	49.0	***	0.56	18.2	***	0.32

III.3.3 Litter layer and soil fauna

Litter layer

The median amount of litter collected from the plots ranged from 5.4 (Bf) to 12.7 g/300cm² (Cu) (tab. III.8). The value obtained at plot Cu was significantly higher ($p \leq 0.05$) than at all other plots. The other plots did not differ significantly from each other.

Mesofauna

The median number of mesoarthropods extracted from soil ranged from 31 (Cu) to 52 ind./31.17 cm² (Cf) (fig. III.11). The value obtained at plot Cf was significantly higher ($p \leq 0.05$) than the values at the other plots which did not differ from each other. The enchytraeid-abundance did not differ between the plots with median values ranging from 35-61 ind./55.42 cm² (fig. III.11) or 224-354 ind./221.7 cm² when considering the sum-values (tab. III.11). Among all extracted mesofaunal groups the Enchytraeidae, the Collembola (46-60 ind./124.7 cm²) and the Acari (Oribatidae: 45-102 ind./124.7 cm²; other Acari: 36-61 ind./124.7 cm²) were the most numerous groups at the investigation plots (tab. III.11).

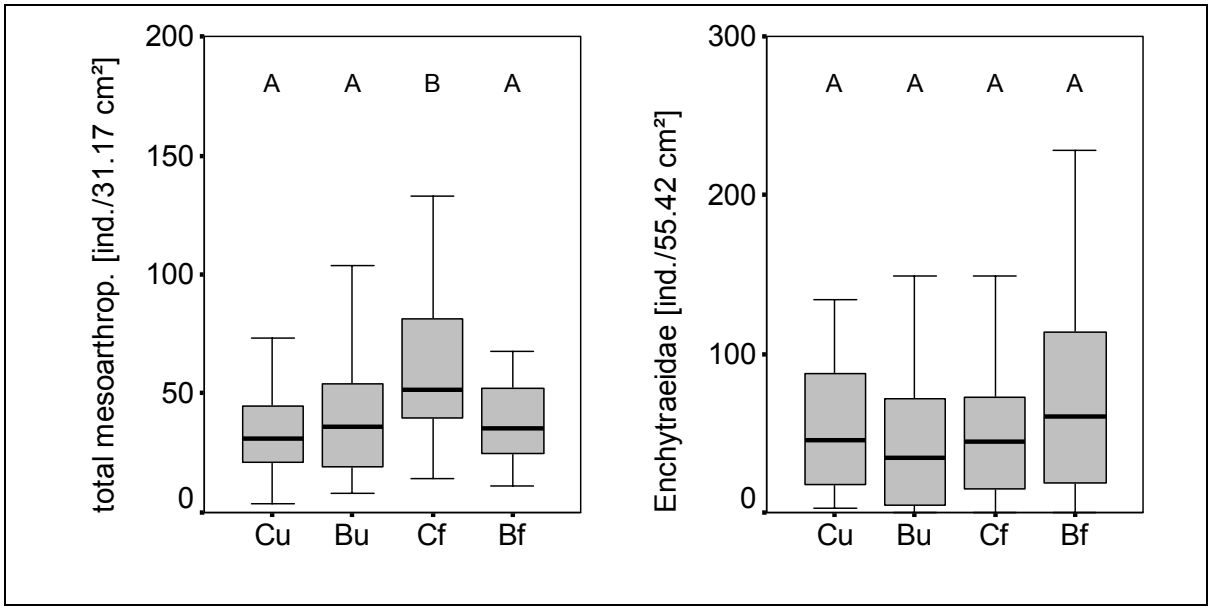


Fig. III.11: Abundances of mesoarthropoda [ind./31.17 cm²] and Enchytraeidae [ind./55.42 cm²] at the investigation plots Cu (control, unfenced), Bu (bioturbation, unfenced), Cf (control, fenced) and Bf (bioturbation, fenced). Presented are box-whisker-plots (n = 32). Mann-Whitney-U-tests were conducted to test for differences between the study plots. Different letters indicate significant differences ($p \leq 0.05$).

Tab. III.11: Abundance of the soil mesofauna at the investigation plots Cu (control, unfenced), Bu (bioturbation, unfenced), Cf (control, fenced) and Bf (bioturbation, fenced). Presented are median and MAD (n = 9) as individuals per 124.7 cm² (221.7 cm²). Different letters represent significant differences between the plots ($p \leq 0.05$; Mann Whitney-U-test).

Mesofauna sites	**Cu**	**Bu**	**Cf**	**Bf**
Total mesoarthr. [ind./124.7 cm²]	129 ± 19^{b}	184 ± 44^{b}	278 ± 38^{a}	173 ± 50^{b}
Enchytraeidae [ind./221.7 cm²]	224 ± 64^{a}	286 ± 136^{a}	254 ± 114^{a}	354 ± 32^{a}
Collembola [ind./124.68 cm²]	46 ± 14^{a}	54 ± 24^{a}	60 ± 13^{a}	47 ± 21^{a}
Oribatidae [ind./124.68 cm²]	45 ± 6^{b}	74 ± 20^{b}	102 ± 27^{a}	59 ± 11^{b}
other Acari [ind./124.68 cm²]	27 ± 5^{b}	37 ± 5^{b}	61 ± 7^{a}	36 ± 10^{b}
Protura [ind./124.68 cm²]	1 ± 1	0 ± 0	3 ± 2	1 ± 1
Diplura [ind./124.68 cm²]	4 ± 2	4 ± 2	7 ± 5	2 ± 2
Pauropoda [ind./124.68 cm²]	0 ± 0	0 ± 0	1 ± 1	0 ± 0
Symphila [ind./124.68 cm²]	2 ± 1	1 ± 1	0 ± 0	0 ± 0
Pseudoscorp. [ind./124.68 cm²]	0 ± 0	0 ± 0	0 ± 0	0 ± 0

Protura, Diplura, Pauropoda, Symphila and Pseudoscorpionidae appeared in very low abundances of 0-7 ind./124.7 cm² (tab. III.11) and were not evaluated statistically. Generally, differences in the abundance of mesofaunal groups were low. However, there was a clear trend towards highest abundances at the fenced control plot Cf as could already be shown for the total mesoarthropods in fig. III.11. The abundances of Collembola, Acari, Protura, Diplura and Pauropoda were all higher at this plot compared to all the other plots and differences were significant for the Oribatidae and the other mites including Gamasidae and Parasitiformes (tab. III.11).

Macrofauna

The abundance of the total macrofauna was significantly higher ($p \leq 0.05$) at the control plots than at the bioturbation plots (tab. III.12). There were no differences between fenced and unfenced plots of similar treatments. Detritivorous species were significantly ($p \leq 0.05$) higher in abundance at the ungrubbed plots compared to the grubbed plots when comparing fenced and unfenced plots separately (fig. III.12). The highest abundance was found in the ungrubbed plot of the exclosure treatment, the lowest in the grubbed plot outside the fenced exclosure (fig. III.12). The differences in the abundance of carnivorous species of the soil macrofauna were less pronounced (fig III.12). The abundances ranged from 35-56 ind./0.12 m² (tab. III.12). The distribution pattern found for beetles (5-28 ind./0.12 m²) and spiders (1-7 ind./0.12 m²) resembled those found for the total macrofauna but for these groups differences between control plots and grubbed plots were not always significant (tab. III.12). The abundance of Coleoptera did not differ significantly between the unfenced treatments. The opposite was found for the spiders. Their abundance differed significantly between grubbed and ungrubbed plots outside the fenced exclosure but there was no significant difference between the exclusion treatments. More than 50 % of the spiders found at the plots belonged to the family Linyphiidae with *Walckenaeria incisa* being the most common species. Lycosidae (8 ind., e.g. *Trochosa terricola*), Theridiidae (6, e.g. *Robertus lividus*) and Agelinidae (4, e.g. *Coelotes inermis*) were less numerous. There were also single findings of Araneidae (not det.), Hahniidae (*Hahnia montana*) and Salticidae (not det.). All the species found are common predators in the litter of deciduous forests. The numbers were too low to compare plots statistically on the species level.

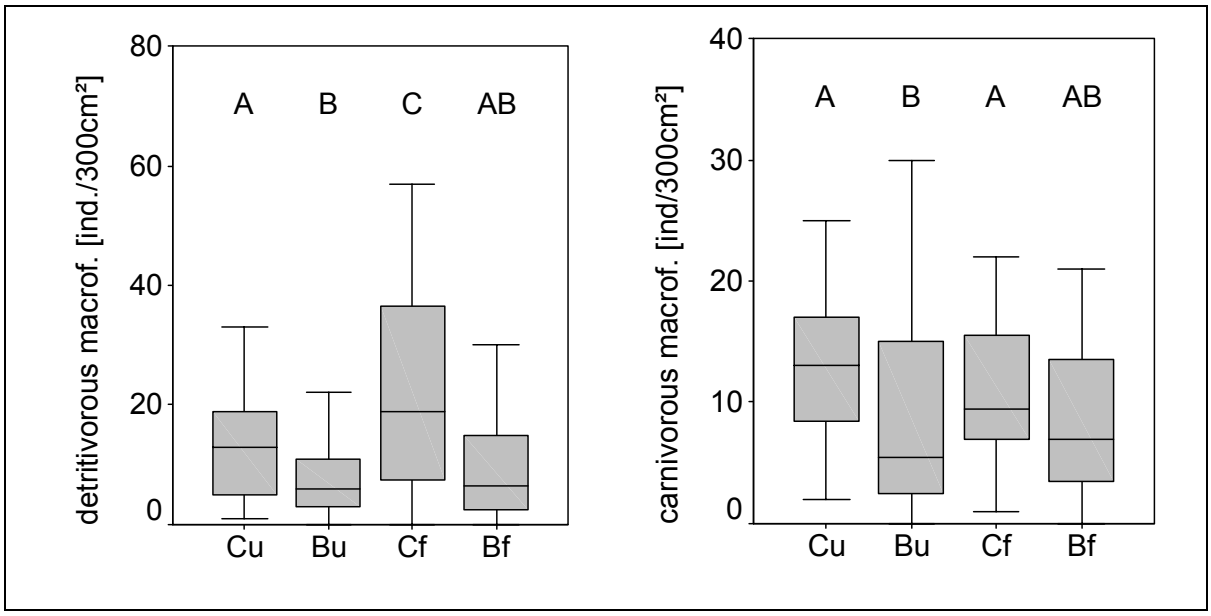


Fig. III.12: Abundance of the detritivorous and the carnivorous macrofauna [ind./300 cm²] at the investigation plots Cu (control, unfenced), Bu (bioturbation, unfenced), Cf (control, fenced) and Bf (bioturbation, fenced). Presented are box and whisker-plots (n = 45). Mann-Whitney-U-tests were conducted to test for differences between the study plots. Different letters indicate significant differences ($p \leq 0.05$).

Tab. III.12: Abundance of the soil macrofauna at the investigation plots Cu (control, unfenced), Bu (bioturbation, unfenced), Cf (control, fenced) and Bf (bioturbation, fenced). Presented are median and MAD of the sum-values (n = 9) as individuals per 0.12 m². Different letters represent significant differences between the plots ($p \leq 0.05$; Mann-Whitney-U-test).

Macrofauna				
sites	**Cu**	**Bu**	**Cf**	**Bf**
Total macrof. [ind./0.12 m²]	121 ± 25^{a}	70 ± 10^{b}	142 ± 34^{a}	77 ± 16^{b}
detritivorous	59 ± 14^{a}	30 ± 7^{b}	93 ± 18^{c}	35 ± 4^{ab}
carnivorous	56 ± 9^{a}	35 ± 4^{b}	41 ± 6^{ab}	38 ± 6^{b}
Coleoptera [ind./0.12 m²]	28 ± 3^{a}	21 ± 5^{a}	23 ± 6^{a}	5 ± 21^{b}
Aranaea [ind./0.12 m²]	7 ± 3^{a}	1 ± 1^{b}	5 ± 3^{a}	3 ± 2^{a}
Isopoda [ind./ 0.12 m²]	1 ± 0^{a}	1 ± 1^{a}	45 ± 21^{b}	4 ± 1^{c}
Diplopoda [ind./ 0.12 m²]	3 ± 1^{a}	2 ± 1^{a}	6 ± 2^{b}	10 ± 5^{b}
Chilopoda [ind./ 0.12 m²]	9 ± 4^{ac}	7 ± 3^{a}	11 ± 3^{a}	14 ± 5^{c}

Analyses of variance revealed highly significant ($p \leq 0.001$, $R^2 = 0.43\text{-}0.81$) model explanations for all macrofaunal groups except for the Chilopoda (tab. III.13). The abundance of Chilopoda hardly differed between the sites (7-14 ind./0.12 m²) (tab. III.12). The factor "wild boar" influenced the abundance of the total macrofauna ($R^2 = 0.50$) and the abundances of Coleoptera ($R^2 = 0.18$) and Aranaea ($R^2 = 0.27$) (tab. III.13). The abundance of beetles was additionally explained by the factor "deer" at 21 %.

Tab. III. 13: Two-factorial ANOVA on the effects of "wild boar" (grubbed/ungrubbed) and "deer" (exclusion/access) on the abundance of the macrofauna (total macrofauna, Coleoptera, Aranaea, Chilopoda, Isopoda, Diplopoda) at the investigation plots. ***: $p \leq 0.001$; ns: not significant.

Analysis of variance (two-factorial)	**total macrofauna**			**Coleoptera**			**Aranaea**		
	df	F		R^2	F		R^2	F		R^2
wild boar	1	31.5	***	0.50	9.0	***	0.18	13.6	***	0.27
deer	1	4.1	ns		10.1	***	0.21	1.2	ns	
interaction	1	0.0	ns		2.0	ns		6.6	ns	
model	3	11.9	***	0.56	7.0	***	0.43	7.1	***	0.43
		Chilopoda			**Isopoda**			**Diplopoda**		
	df	F		R^2	F		R^2	F		R^2
wild boar	1	3.9	ns		81.9	***	0.57	0.6	ns	
deer	1	0.0	ns		17.4	***	0.12	20.7	***	0.40
interaction	1	2.8	ns		16.1	***	0.11	2.1	ns	
model	3	2.2	ns		38.4	***	0.81	7.8	***	0.46

Among the saprophagous individuals obtained quantitatively, Isopods were the most abundant. Altogether, I collected 385 individuals. *Trichoniscus pusillus* was the dominant species at all sites. Additionally, single specimen of *Oniscus asellus* and *Philoscia muscorum* were found.

Isopods and Diplopods were significantly more abundant ($p \leq 0.05$) at the fenced plots compared to plots outside the fenced exclosure. Accordingly, the factor "deer" explained the variances at 57 % for the isopods and 40 % for the millipedes (tab. III.13). Isopod abundance was also significantly ($p \leq 0.001$) influenced by the factor "wild boar" ($R^2 = 0.12$) and the interaction of the factors ($R^2 = 0.11$).

III.4 Investigation IV (stand composition/slope gradient)

III.4.1 Soil physical and chemical properties

There were obvious differences in the soil morphology between the sites (tab. III.14). At the site Mono1 the soil type was a ranker. At the mixed cultures with hazel in the understory and at the oak-monoculture with low inclination acid brown earth was formed. The thickness of the Ah-horizons was higher at the mixed stands (5-10 cm) than at the monocultures (2-5 cm).

Table III.14: Several soil properties of the investigation plots Mono1, Mix1, Mono2 and Mix2 (Mono = oak-monoculture; Mix = oak-hazel; 1 = 25-27°, 2 = 13-14°). Presented are median and median absolute deviation of all sampling dates (n = 8-40). Differences between the plots are indicated by different letters ($p \leq 0.05$; Mann Whitney-U-test).

site	n	**Mono1**	**Mix1**	**Mono2**	**Mix2**
Soil type		ranker	acid brown earth	acid brown earth	acid brown earth
Ah-horizon [cm]		2-5	5-10	3-5	5-10
pH (1M KCl)	40	3.4 ± 0.1^{a}	3.5 ± 0.1^{a}	3.5 ± 0.1^{a}	3.4 ± 0.1^{a}
WRC_{max} [%]	40	63.7 ± 3.1^{a}	65.3 ± 1.4^{a}	65.5 ± 2.7^{a}	73.7 ± 4.0^{b}
soil moisture [%]	40	32.6 ± 6.2^{a}	37.9 ± 4.4^{a}	37.9 ± 4.2^{a}	46.2 ± 7.0^{b}
C/N	40	18.6 ± 1.8^{a}	18.1 ± 2.2^{a}	19.5 ± 2.3^{a}	18.4 ± 2.1^{a}
Litter layer (g/m²)					
Nov 2001	8	393 ± 44^{b}	457 ± 36^{b}	410 ± 19^{b}	507 ± 38^{a}
Sep 2002	8	0 ± 0^{b}	287 ± 36^{a}	92 ± 23^{b}	327 ± 19^{a}
Disappearance [%]		100	37	78	36

The amount of litter after litter fall ranged from 393-507 g/m² and did not statistically differ among the sites except for the site Mix2 which exhibited a significantly higher value (tab. III.14). Ten months later, shortly before the next litter fall, the amounts of litter were substantially lower at all sites. Particularly high amounts of litter (78-100 %) disappeared from the oak-monocultures. At the mixed stands the amount of litter decreased by 36 % (Mix2) and 37 % (Mix1). The litter mass in September 2002 was significantly higher ($p \leq 0.05$) in the mixed stands (Mix1: 287 g/m²; Mix2: 327 g/m²) than in the monocultures (Mono1: 0 g/m²; Mono2: 92 g/m²). The median values of the soil pH (3.4-3.5), the WRC_{max} (63.7-73.7 %), the soil moisture (32.6-46.2 %) and the C/N-ratio (18.1-19.5) were all in a similar range (tab. III.14). However, the WRC_{max} and the soil moisture-values were significantly highest at the site Mix2.

The contents of C_{org} and N_t were generally higher at the sites of low slope gradient than at the steep sites (fig. III.13), but the difference in the content of organic carbon between the monocultures was not significant. Differences between monocultures and mixed stands did not occur except for the gentle slope which had a significantly higher nitrogen content at the mixed stand ($p \leq 0.001$). Accordingly, the factor "stand composition" did not significantly influence C_{org}- and N_t-contents in a two-way ANOVA (tab. III.15). The factor "slope gradient" explained the variances at 9 % (C_{org}) and 23 % (N_t). Interaction did not occur for any of the elements.

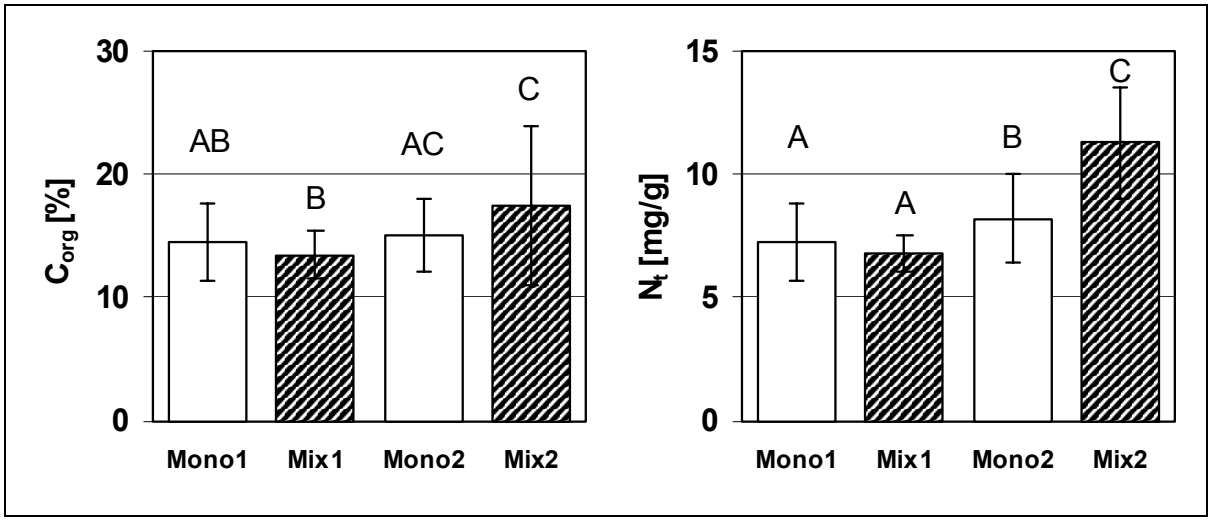


Fig. III.13: Contents of organic carbon (C_{org}) and total nitrogen (N_t) at the investigation plots Mono1, Mix1, Mono2 and Mix2 (Mono = oak-monoculture; Mix = oak-hazel; 1 = 25-27°, 2 = 13-14°). Presented are median and MAD of all data (n = 40). Differences between the plots are indicated by different letters above the columns ($p \leq 0.05$; Mann-Whitney-U-test).

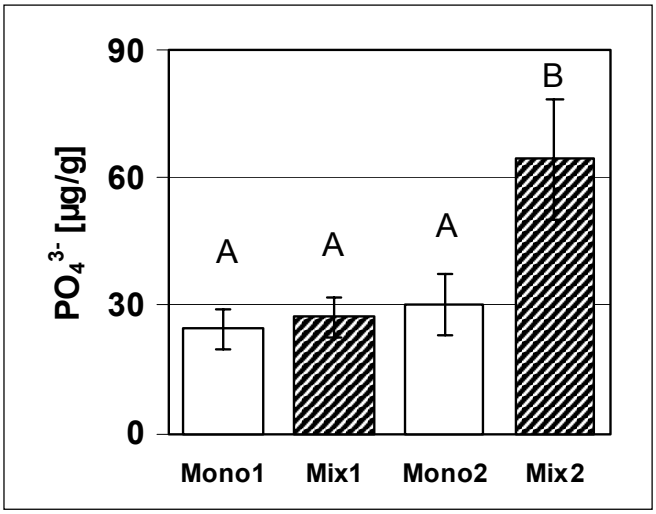


Fig. III.14: Phosphate-contents at the investigation plots Mono1, Mix1, Mono2 and Mix2 (Mono = oak-monoculture; Mix = oak-hazel; 1 = flat, 2 = steep). Presented are median and MAD of all data (n = 40). Differences between the plots are indicated by different letters above the columns ($p \leq 0.05$).

The content of extractable phosphate was more than twice as high ($p < 0.001$) at the site Mix2 (64.2 ± 13.9 mg/kg) than at the sites Mono1 (24.4 µg/g), Mix1 (27.2 µg/g) and Mono2 (30.3 µg/g) which did not differ significantly from each other (fig III.14).

The contents of extractable potassium only differed marginally among the sites (416-469 mg/kg). Only the sites Mono1 and Mix2 differed significantly from each other (fig. III.15).

In respect to the contents of extractable calcium and magnesium there were strong differences between the sites (fig. III.15). They reached the highest values at site Mix2 (Ca^{2+}: 2.6 ± 0.8 mg/g; Mg^{2+}: 390.5 ± 109.5 mg/g) and the lowest values at the site Mono1 (Ca^{2+}: 0.5 ± 0.2 mg/g; Mg^{2+}: 130.3 ± 45.0 µg/g). Differences to the other sites were significant ($p \leq 0.05$) (fig. III.15); only between the sites Mix1 and Mono2 there were no significant differences in the contents of Ca^{2+} and Mg^{2+}.

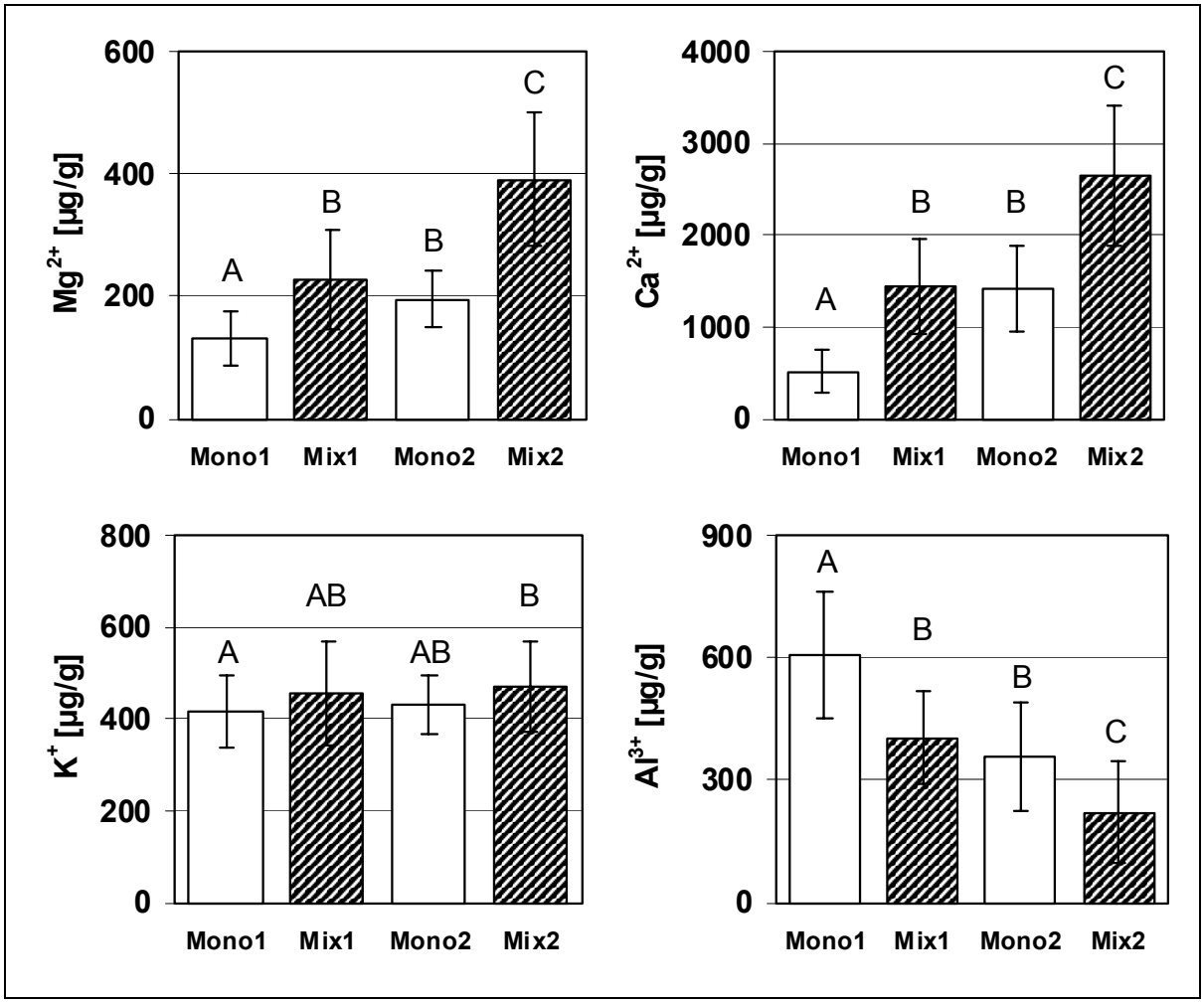


Fig. III.15: Contents of aluminium (Al^{3+}), calcium (Ca^{2+}), magnesium (Mg^{2+}) and potassium (K^{+}) at the investigation plots Mono1, Mix1, Mono2 and Mix2 (Mono = oak-monoculture; Mix = oak-hazel; 1 = 25-27°, 2 = 13-14°). Presented are median and MAD of all data (n = 40).

The content of Al^{3+}-ions exhibited opposite tendencies to those found for the basic cations Ca^{2+}, Mg^{2+} and K^{+} (fig. III.15). The significantly highest value was obtained at the site Mono1 (606.3 ± 156.3 mg/kg), the significantly lowest value at the site Mix2 (221.0 ± 124.8 mg/kg). The Al^{3+} content at the sites Mono2 (356.5 ± 131.8) and Mix1 (401.5 ± 113.8) did not differ significantly from each other.

Two factorial analyses of variance delivered highly significant model explanations for the contents of PO_4^{3-} -P ($R^2 = 0.61$), Ca^{2+} ($R^2 = 0.59$), Mg^{2+} ($R^2 = 0.31$), and Al^{3+} ($R^2 = 0.36$) in the soil (tab. III.15). The factors "stand composition" (oak-monoculture/oak-hazel) and "slope gradient" (flat/steep) both contributed to the model explanation for the contents of PO_4^{3-}-P, Ca^{2+}, Mg^{2+} and Al^{3+} with R^2-values ranging from 0.14 to 0.30 (tab. III.15). Significant interaction ($p \leq 0.001$) only occurred for PO_4^{3-}-P ($R^2 = 0.14$).

Tab. III.15: Two-factorial ANOVA on the effects of stand composition (oak-monoculture/oak-hazel) and slope gradient (steep/gentle) on the contents of soil nutrients (C_{org}, N_t, PO_4^{3-} -P, K^{+}, Mg^{2+}, Ca^{2+}), Al^{3+} and microbial properties at the investigation sites. ***: $p \leq 0.001$; ns: no significance.

ANOVA two-factorial	**Stand composition**		**Slope gradient**		**Interaction**		**Model**	
	F	R^2	F	R^2	F	R^2	F	R^2
df	1		1		1		3	
$C_{org.}$	0.2 ns		**15.3** ***	**0.09**	1.2 ns		**5.6** ***	**0.10**
N_t	3.8 ns		**54.1** ***	**0.23**	10.4 ns		**22.8** ***	**0.31**
PO_4^{3-}-P	**83.3** ***	**0.21**	**101.6** ***	**0.26**	**53.9** ***	**0.14**	**80.0** ***	**0.61**
K^{+}	4.3 ns		1.3 ns		0.5 ns		2.0 ns	
Mg^{2+}	**37.5** ***	**0.17**	**33.3** ***	**0.15**	0.3 ns		**23.7** ***	**0.31**
Ca^{2+}	**113.1** ***	**0.30**	**100.8** ***	**0.26**	11.6 ns		**75.2** ***	**0.59**
Al^{3+}	**34.6** ***	**0.14**	**53.5** ***	**0.22**	0.2 ns		**29.5** ***	**0.36**
micr. act.	**12.8** ***	**0.06**	**33.4** ***	**0.16**	**12.6** ***	**0.06**	**19.6** ***	**0.27**
C_{mic}	**18.5** ***	**0.09**	9.8 ns		**11.9** ***	**0.06**	**13.4** ***	**0.21**
***q*CO_2**	**42.8** ***	**0.21**	5.6 ns		0.2 ns		**16.2** ***	**0.24**
$C_{mic}/_{Corg}$	10.2 ns		6.6 ns		0.3 ns		**5.7** ***	**0.10**

III.4.2 Soil microbial properties

The potential microbial activity was significantly higher at the site Mix2 (7.4 µgCO_2-C/g*h) compared to all the other sites (4.4-4.5 mgCO_2-C/g*h) (fig. III.16) which did not significantly differ from each other. The microbial biomass was almost identical at the sites Mono1, Mono2 and Mix2 (4509-4787 µg C_{mic}-C/g) but significantly lower ($p \leq 0.001$) at site Mix1 (3542 ±1319 µg C_{mic}-C/g) (fig. III.16). The metabolic quotient (qCO_2) was significantly higher ($p \leq 0.05$) at oak-hazel sites than at the oak-monocultures independent of inclination (fig. III.16). There was no significant difference between the oak-monocultures of varying slope gradient but the qCO_2 was significantly higher at the gentle slope Mix2 than at the steep site Mix1.

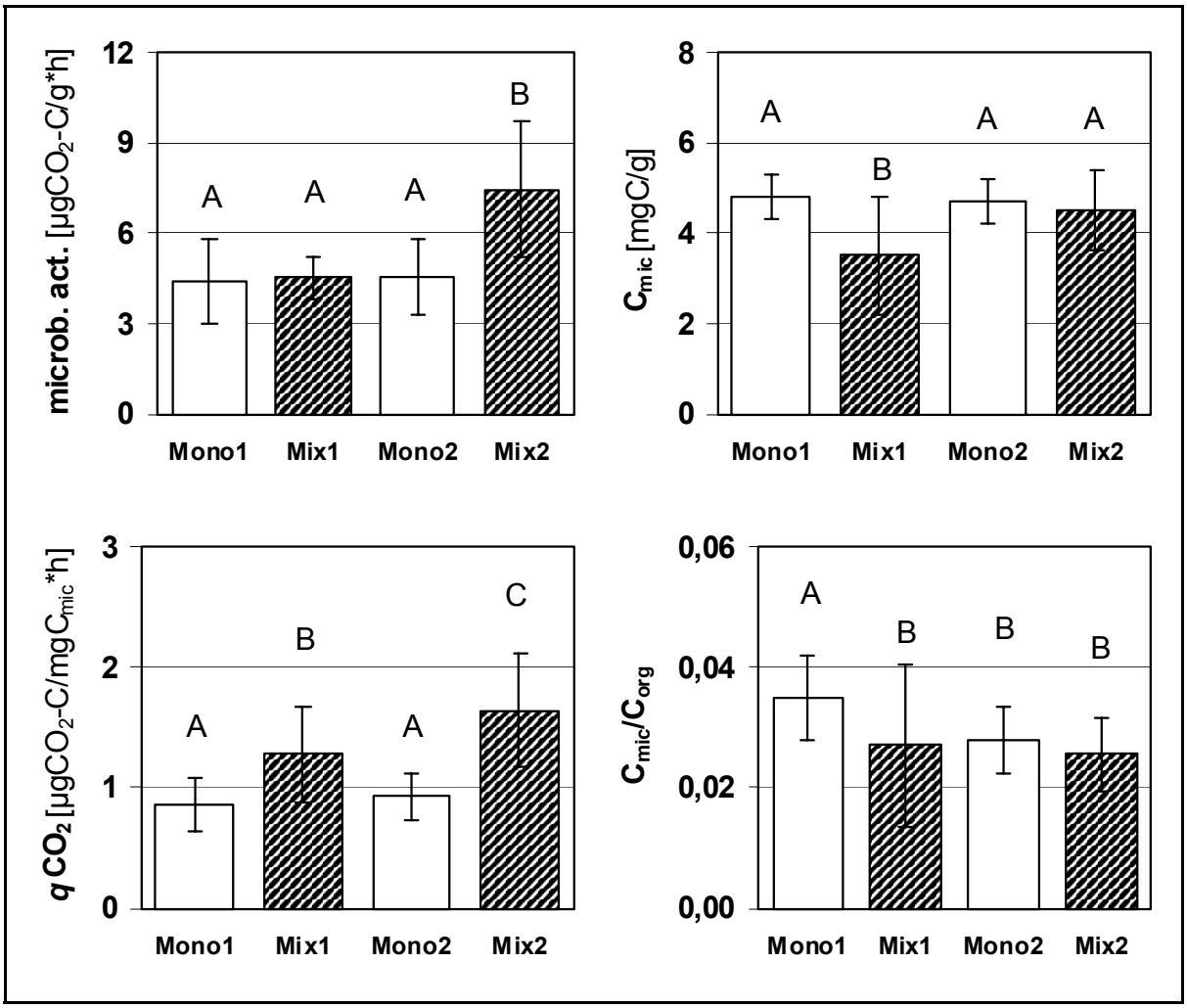


Fig. III.16: Microbial activity, microbial biomass (C_{mic}), metabolic quotient (qCO_2) and C_{mic}/C_{org}-ratio at the investigation plots Mono1, Mix1, Mono2 and Mix2 (Mono = oak-monoculture; Mix = oak-hazel; 1 = 25-27°, 2 = 13-14°). Presented are median and MAD of all data (n = 40). Differences between the plots are indicated by different letters above the columns ($p \leq 0.05$; Mann Whitney-U-test).

The C_{mic}/C_{org}-ratio reached the significantly highest median value at the site Mono1 (0.035). The values at the other sites were within a small range (0.026-0.028) and did not statistically differ from each other (fig. III.16).

All microbial properties were explained significantly by the chosen model ($R^2 = 0.10$-0.27) (tab. III.15). The factor "stand composition" explained the variances of all microbial properties significantly ($p \leq 0.01$). Microbial activity ($R^2 = 0.16$) was additionally influenced by the factor "slope gradient" ($R^2 = 0.16$) and the interaction of the factors ($R^2 = 0.06$). Also for the microbial biomass interaction occurred ($R^2 = 0.06$)

III.4.3 Lumbricid abundance

In total, 54 individuals were extracted from the soils and found in the litter of the investigation sites, 19 of which were adult (tab. III.16). Adults were exclusively found at the gentle slopes, eight at Mix2 and eleven at Mono2. The species were *Dendrodrilus rubidus* and *Lumbricus rubellus.* Juveniles were only determined to the genus but very likely belonged to the same species. The number of individuals per m² was 2 at Mono1, 16 at Mix1, 21 at Mono2 and 15 at Mix2. The abundances were too low to compare sites statistically.

Tab III.16: Abundance of Lumbricidae at the sites Mono1, Mix1, Mono2 and Mix2 (Mono = oak-monoculture, Mix = oak-hazel; 1 = 25-27°, 2 = 13-14°).

sites	**Mono1**	**Mix1**	**Mono2**	**Mix2**
Individuals per ⅛ m² (median values; n = 8)	0 ± 0	1 ± 1	1 ± 1	2 ± 1
Individuals per m²	2 (all juv.)	16 (all juv.)	21 (10 juv./11 ad.)	15 (7 juv./8 ad.)
Dendrodrilus rubidus	0	0	8	8
Lumbricus rubellus	0	0	3	0
Dendrobaena spec.	0	3	3	2
Lumbricus spec.	2	13	7	5

III.5 Microbial properties as indicators for soil quality

III.5.1 Field studies

Spearman rank correlation was conducted to test for relationships between the microbial properties activity, C_{mic}, qCO_2 and C_{mic}/C_{org}-ratio and the soil properties C_{org}, N_t, PO_4^{3-}, pH, WRC_{max} and C/N. Microbial activity was significantly correlated to all of the selected soil properties (tab. III.17). The highest r^2-values were obtained for the WRC_{max} (r^2 = 0.584) and the content of nitrogen (r^2 = 0.646) and phosphate (r^2 = 0.461) in soil. Soil pH (r^2 = -0.383) and C/N-ratio (r^2 = -0.299) were negatively correlated to the microbial activity.

The microbial biomass was significantly ($p \leq 0.05$) correlated to all of the investigated parameters except for the phosphate content. (tab. III.17). Similar to the microbial activity I found strong correlations to the WRC_{max} (r^2 = 0.49) and the contents of organic carbon (r^2 = 0.584) and total nitrogen (r^2 = 0.564). Moreover a negative correlation to the soil pH was detected. In contrast to the microbial activity the C_{mic} was positively correlated to the C/N-ratio. The metabolic quotient was significantly correlated to the phosphate content (r^2 = 0.283) and to the C/N-ratio (r^2 = -0.485) (tab. III.17). The C_{mic}/C_{org}-ratio exhibited significant correlations to the content of C_{org} (r^2 = -0.422) and to the C/N-ratio (r^2 = -0.425) (tab. III.17).

Tab. III.17: Spearman-rank-correlation between soil microbial properties (microbial activity/biomass, qCO_2, C_{mic}/C_{org}) and several soil characteristics (phosphate, pH, WRC_{max}, C/N) of the investigations I-IV. For all analyses the median values per site/plot and sampling date were considered (n = 56). Presented are r^2-values and the significance level. ns = not significant; *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

Spearman-rank-correlation

	Microb. act.	**Microb. biom.**	**qCO_2**	**C_{mic}/C_{org}-ratio**
Org. carbon	0.292*	0.584***	ns	-0.422***
Total nitrogen	0.646***	0.564***	ns	ns
Phosphate	0.461***	ns	0.283*	ns
Soil pH	-0.383***	-0.307*	ns	ns
WRC_{max}	0.584***	0.490***	ns	ns
C/N-ratio	-0.299*	0.287*	-0.485***	-0.425***

Linear regression analyses between microbial properties (activity, C_{mic}) and soil nutrients (C_{org}, N_t, PO_4^{3-}) delivered significant results ($p \leq 0.05$) except for the linear regression between C_{mic} and phosphate (fig. III.17). Regression coefficients varied between 0.11 and 0.35.

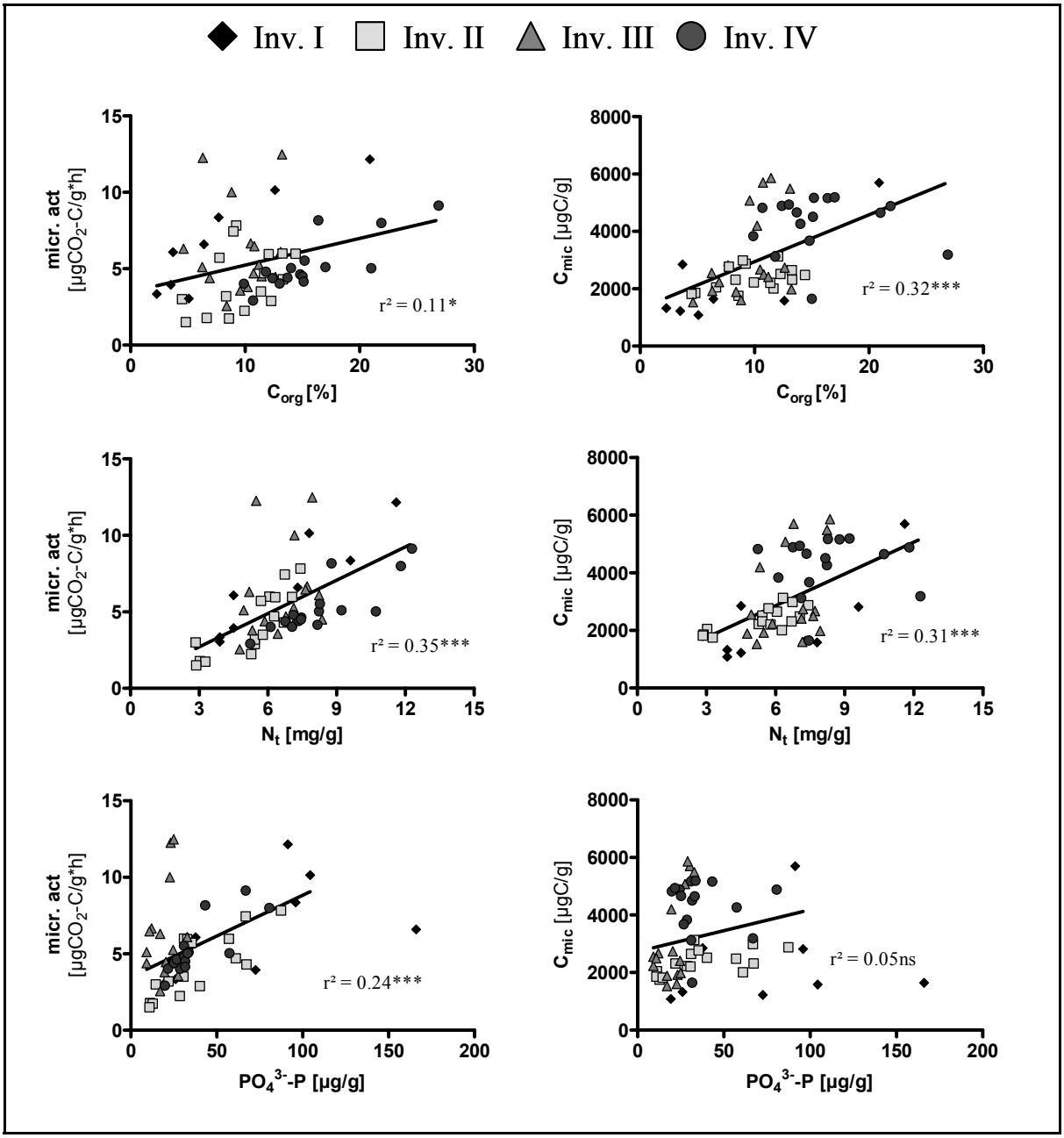


Fig. III.17: Linear regression analyses between soil nutrient contents (C_{org}, N_t, PO_4^{3-}) and microbial properties (microbial activity/biomass). Data pairs are derived from the investigation I-IV and represent the median values of all sites/plots and sampling dates (n = 56). Different symbols indicate to which investigation the data pairs belong. ◆ : Inv. I; □ : Inv. II; △ : Inv. III; ● : Inv. IV. Regression coefficients and significance values are shown in the graphs. ns = not significant; *: $p \leq 0.05$; ***: $p \leq 0.001$.

Microbial activity was closely related to the nitrogen content ($r^2 = 0.35$) but also the relationships between activity and the contents of organic carbon ($r^2 = 0.11$) and phosphate ($r^2 = 0.24$) were significant ($p \leq 0.05$). Microbial biomass strongly depended on the contents of organic carbon ($r^2 = 0.33$) and total nitrogen ($r^2 = 0.31$) ($p \leq 0.001$) but not on the phosphate content (fig. III.17).

Conducting regression analyses separately for each investigation I observed different tendencies between the investigations, at least in some cases (fig. III.17, tab. III.18): Microbial activity was closely related to the Corg content in the investigations I ($r^2 = 0.82$) and IV ($r^2 = 0.65$) but not in the investigations II and III. Regression analyses between the microbial respiration and the contents of nitrogen delivered significant results ($p \leq 0.001$) except for the investigation III. Microbial activity and the phosphate content were significantly correlated ($p \leq 0.001$) in the investigations II and IV but not in investigations I and III.

Microbial biomass was in most cases not significantly correlated to the nutrient contents (tab. III.18). According to regression analyses the organic carbon content was only significantly correlated ($p \leq 0.05$) to the microbial biomass in investigation I. Significant correlations between C_{mic} and the nitrogen content were only found for the investigations I ($r^2 = 0.60$) and II ($r^2 = 0.56$) and the phosphate content only significantly influenced microbial biomass in investigation II ($r^2 = 0.31$) and III ($r^2 = 0.40$) but not in the other investigations.

Tab. III.18: Regression coefficients (linear regression analysis) and significance levels for the relationships between microbial properties (microbial activity/biomass) and soil nutrients (C, N, P) in investigations I-IV. The data pairs for the analyses are derived from the median values of each site/plot and sampling dates resulting in eight replicates for the investigation I and 16 replicates for investigations II-IV. Grey boxes indicate significant differences. ns = not significant; *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

	Microbial activity				**Microbial biomass**			
Investigation	**I**	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**
C_{org}	0.82*	0.18ns	0.00ns	0.65***	0.63*	0.18ns	0.22ns	0.00ns
N_t	0.85***	0.68***	0.06ns	0.68***	0.60*	0.56***	0.14ns	0.00ns
PO_4^{3-}-P	0.29ns	0.61***	0.01ns	0.67***	0.03ns	0.31*	0.40**	0.00ns

III.5.2 Microcosm experiments

Microbial activity

I conducted two microcosm experiments to test for the dependency of microbial activity, microbial biomass and metabolic quotient on substrate availability and quality.

The microbial activity continuously decreased during the course of the experiment from 1.48 to 0.41 μgCO_2-C/mg*h in series I and from 4.12 to 1.02 μgCO_2-C/mg*h in series II (fig. III.18 a) when no substrates were added (control). The control approaches of the two series differed significantly from each other ($p \leq 0.001$). Also the N+P and Lig+N+P approaches continuously decreased over the course of the experiment to values less than a third of the values at day 1 after substrate addition (fig. III.18 a). The N+P approach did not differ from the control in both series but the values obtained for the Lig+N+P-approach were significantly higher ($p \leq 0.05$) than the control and the N+P-approach throughout the experiment.

Addition of glucose together with nitrogen and phosphate evoked an increase of microbial activity compared to the control one day after addition in both series (fig. III.18 a). The increase continued until the fourth day after glucose addition to reach values more than 30 times higher than the control value at both series (series I: 49.3 μgCO_2-C/mg*h; series II: 111.2 μgCO_2-C/mg*h). During the course of the experiment the microbial activity continuously decreased until day 64 to reach values comparable to the control.

Addition of cellulose together with nitrogen and phosphate also caused an increase of microbial activity but the increase was retarded and less pronounced than after glucose addition (fig. III.18 a). Respiration started to increase four days after cellulose addition and reached maximum values at day eight in both series. Microbial activity was at that time about 20 times higher compared to the control approach. The glucose and cellulose approaches differed significantly ($p \leq 0.001$) from all the other approaches of the same series except for the comparison Glu+N+P/Cell+N+P of series I (fig. III.18 a, tab. Appendix-5.2).

Microbial biomass (C_{mic})

Microbial biomass of the control and the N+P-approach remained relatively constant in the course of both experimental series (fig. III.18 b). Microbial biomass was 2.3/1.1 mgC/g (control I/II) and 1.9/1.1 mgC/g (N+P I/II) on day 1. On day 64 after the start of the experiment C_{mic} was 1.7/1.4 (control I/II) and 1.8/1.5 (N+P I/II). The control and the N+P approach differed significantly ($p \leq 0.01$) from each other in series I but not in series II.

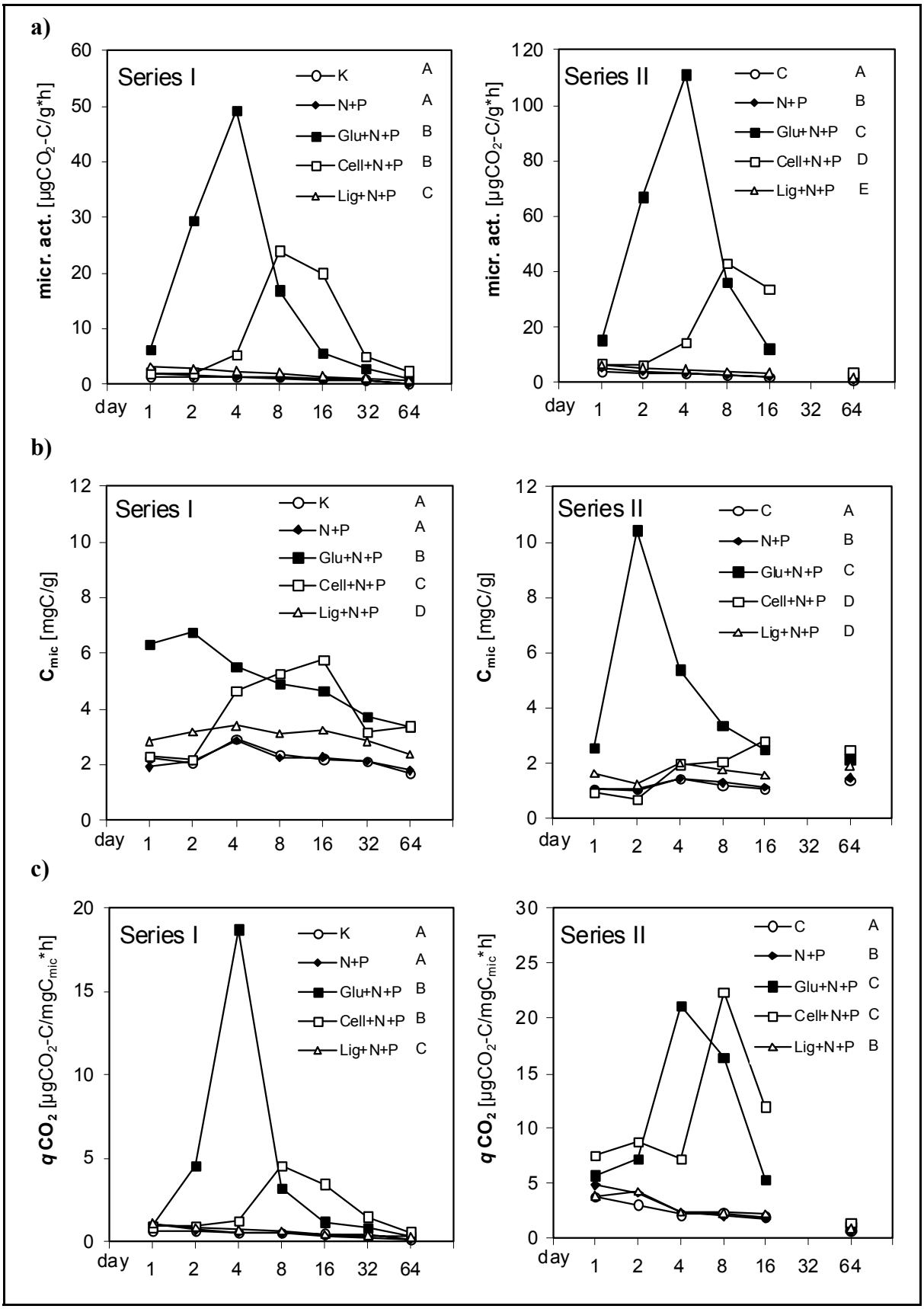


Fig. III.18: a) Microbial activity, b) C_{mic} and c) qCO_2 (median ± MAD, n = 8) over the course of the microcosm experiments series I and series II. Different approaches are C = control; N+P = nitrogen + phosphate addition; Glu+N+P = glucose +N+P, Cell+N+P = cellulose +N+P addition, Lig+N+P = lignin +N+P addition. Differences between the approaches (Wilcoxon-test) are indicated with different letters behind the legends.

The approach Lig+N+P differed significantly ($p \leq 0.001$) from the control and the N+P-approach in both series (tab. Appendix-5.2). Microbial biomass was higher with lignin addition throughout the experiment in both series (fig. III.18 b). The values hardly differed between the sampling days and ranged from 2.4 mgC/g (day 64) to 3.4 mgC/g (day 4) in series I and from 1.2 mgC/g (day 2) to 2.0 mgC/g (day 4) in series II.

In series I, microbial biomass strongly increased one day after Glucose+N+P addition to 6.3 mgC/g compared to 2.3 mgC/g in the control-approach (fig. III.18 b). A maximum value was obtained at day 2 (6.8 mgC/g) whereafter C_{mic} continuously decreased to 3.4 mgC/g. This value was still twice as high as the one found for the control. In series II C_{mic} also increased one day after substrate (Glu+N+P) addition but the strongest increase was found after two days with a value (10.4 mgC/g) ten times higher than the control. On the following sampling days the C_{mic}-content continuously decreased to 2.2 mgC/g at day 64. The glucose approach of series I significantly ($p \leq 0.05$) differed from all other approaches and the glucose approach of series II significantly ($p \leq 0.001$) differed from all other approaches of series II (Tab- Appendix-5.2).

Addition of cellulose together with N and P resulted in a retarded increase of C_{mic} in series I, similar to that found for the microbial activity (fig. III.18 b). The increase started four days after substrate addition to reach a maximum value of 5.8 mgC/g at day 16. The values on day 32 (3.2 mgC/g) and day 64 (3.4 mgC/g) were significantly lower ($p \leq 0.001$) but still more than 1.5 times higher than the control-values. The increase of C_{mic} at series II resembled that in series I. C_{mic} doubled from day 1 (1.0 mgC/g) to day 4 and further increased to 2.8 mgC/g on day 16. Possibly the maximum value was reached on day 32 but microbial analyses was not determined on that day. The C_{mic}-value on day 64 was 2.5 mgC/g and almost twice as high as the Control value. The Cell+N+P-approach of series I differed significantly ($p \leq 0.05$) from all other approaches except for the Glu+N+P-approach of series I (tab. Appendix-5.2). The Cell+N+P-approach series II differed significantly ($p \leq 0.01$) from all other approaches except for the Lig+N+P-approach of series II (tab. Appendix-5.2).

Metabolic quotient (qCO_2)

The metabolic quotient showed similar tendencies as described for the microbial activity. In both series the qCO_2 of the approaches control, N+P and Lig+N+P continuously decreased from the start to the end of the experiment to values less than a third of the initial values (day 1) (fig. III.18 c). The control approach of series I differed significantly from

the Lig+N+P approach ($p \leq 0.001$) but not from the N+P approach (fig. III.18 c). The N+P and the lignin approach differed significantly from each other ($p \leq 0.001$). In the series II the control differed significantly from both the N+P and the Lig+N+P approach ($p \leq 0.05$) but the N+P and the lignin approach did not differ from each other.

Glucose addition evoked an increase of the qCO_2-values on day 2 to reach maximum values on day four in both series (series I: 18.7 μgCO_2-C/mgC_{mic}*h; series II: 21.2 μgCO_2-C/mgC_{mic}*h). Thereafter the values continuously decreased to the control level (series I: 0.3 μgCO_2-C/mgC_{mic}*h; series II: 1.1 μgCO_2-C/mgC_{mic}*h). The Glu+N+P approaches differed significantly ($p \leq 0.001$) from all other approaches of the same series apart from the Cell+N+P-approach (tab. Appendix-5.2).

The addition of cellulose instead of glucose resulted in a retarded increase of qCO_2 compared to the glucose approach (fig. III.18). Maximum values were obtained on day 8 in both series (series I: 4.6 μgCO_2-C/mgC_{mic}*h; series II: 22.4 μgCO_2-C/mgC_{mic}*h). In series II the maximum qCO_2-values after addition of Cellulose even surpassed those determined for the glucose approach. In both series the values decreased in the further course of the experiment to 0.6 μgCO_2-C/mgC_{mic}*h (series I) and 1.5 μgCO_2-C/mgC_{mic}*h respectively (series II). The Cell+N+P approaches differed significantly ($p \leq 0.001$) from all other approaches of the same series with the exception of the Glu+N+P-approach (tab. Appendix-5.2).

IV Discussion

IV.1 Abiotic factors

Abiotic factors play a key role in forest ecology. Especially the climate and the soil forming bedrock determine the vegetation type that is able to compete within a landscape. In the last decades the deposition of anthropogenic air pollutants became increasingly important as an abiotic factor influencing forest ecology. Pollution coupled with climatic variations like summer drought or winter/spring frost are discussed as crucial factors causing forest decline (HÜTTL 1993, THOMAS et al. 2002).

The climatic conditions in the central European low mountain range support the distribution of broad-leaved forest tree species. The European beech (*Fagus sylvatica* L.) and oak species (*Quercus*) are – both economically and ecologically – the most important tree species in Europe. It is known from a large body of literature that sessile oak (*Quercus petraea* Matt.) dominates warm and dry (continental) habitats and is more competitive on nutrient poor soils than pedunculate oak (*Quercus robur* L.) and beech.

At the Ahr-Eifel, the warm and dry climate and nutrient poor soils favour the growth of sessile oak which mostly originates from coppice shoot due to the historical land use. However, the distinct relief with altering relief positions and slope gradients causes small scale climatic variations with possible effects on vegetation and soil. ULRICH (1984) even regards relief positions like leeward, windward and plateau as disposing factors for forest diseases.

In the following sections the effects of slope aspect (windward/leeward), slope position (plateau, upper slope, lower slope, foot slope) and slope gradient on soil ecological characteristics in simple oak coppice forests of the Ahr-Eifel are discussed, relating to the results perceived from the relevant investigations.

IV.1.1 Slope aspect

According to HEINZE & FIEDLER (1992) the sum of precipitation is up to 10 % higher at wind-exposed slopes and about 10 % lower at leeward slopes compared to level sites. Higher loads of acid precipitation at windward sites have been shown to cause a decrease in soil pH (ZEZSCHWITZ, 1987, SCHNEIDER, 1999). Other studies demonstrated that symptoms of forest decline in the German low mountain range are pronounced at

windward exposures (W- and SW-slopes) (ULRICH & MATZNER 1983, WALDMANN 1984, HÜTTL 1985, MÖSSMER 1985). Acid depositions can also result in an impoverishment of base cations in soil and a release of toxic Al^{3+}-ions (SAUVÉ & HANDERSHOT, 1995; THIMONIER et al., 2000).

To evaluate the impact of slope aspect on soil degradation in terms of soil acidification and base cation depletion in the investigation area I monitored eight unfenced forest sites at varying slope aspects (four windward and four leeward) over a time period of three years and analysed soil pH and the contents of extractable Ca^{2+}, Mg^{2+}, K^{+} and Al^{3+} (investigation I). In agreement with previous studies (see above) the contents of extractable cations Ca^{2+}, Mg^{2+} and K^{+} were, in most cases, significantly higher and the Al^{3+}-content significantly lower at the leeward than at the windward sites (fig. III.1). In the aluminium buffer range the content of Al^{3+} rises with increasing H^{+}-load (BERGKVIST 1987). However, the soil pH did not differ between the different exposures. It is known that acid deposition into forest ecosystems can result in a reduction of plant available nutrients such as Ca^{2+}, Mg^{2+} and K^{+} without a change in soil pH (HÜTTL 1992). Small changes in soil pH may be related both to the logarithmic nature of pH and to the fact that acidic soils in the aluminium buffer range often do not acidify further (ULRICH 1980; REUSS AND JOHNSSON 1986).

Also climatic conditions at windward hillslopes could contribute to lower nutrient contents compared to leeward slopes. Despite the higher rainfall, SW-exposed hillslopes of the European low mountain range are classified as dry due to the influence of radiation and wind whereas leeward slopes hardly differ from the regional macro-climate (SCHWANECKE 1970). The conditions at windward slopes may increase nutrient leaching and reduce nutrient mineralisation at the same time and therefore contribute to the observed differences in the cation contents. In a previous study a reduced microbial activity and a lower abundance of Collembola were observed at windward sites compared to leeward sites which reflects climatic constraints on the soil biota (MOHR & TOPP 2001). Also nutrient depletion due to wind erosion has been shown to be pronounced at windward sites (LI ET AL. 2003).

By monitoring soil pH and the cation contents over three years I found the contents of Ca^{2+}, Mg^{2+} and K^{+} continuously decreased from July 1999 to October 2002 at both slope aspects, while the content of Al^{3+} increased over that time (fig. III.1). Comparable nutrient loss and Al^{3+}-increase was found in other studies over a much longer time period of 20-40

years and was attributed to soil acidification, cation leaching and biomass accumulation (FALKENGREN-GRERUP & ERIKSSON 1990, KNOEPP et al. 1994, THIMONIER et al. 2000). Such a strong decrease in the base cation contents as observed for both exposures cannot only be attributed to acid deposition. Other factors most likely contributed to the severe loss of base cations thus exceeding the mineral supply by weathering or mineralisation processes within the study period. Normally, mineral weathering provides a significant supply of most nutrients for plant uptake at a rate typically faster than is lost via leaching (COLE 1995). But ZABOWSKI (1990) states that the supply through weathering can be inadequate in soils which are very young, heavily weathered or derived from parent material low in base elements. Moreover, soils receiving high anion inputs from atmospheric deposition could have high rates of leaching losses, rates potentially exceeding the re-supply from weathering processes (JOHNSON & LINDBERG 1991). Soils in the investigation area are mainly derived from Devonic slate forming nutrient-poor ranker or acid brown earth. Loess layers are extensively eroded and only locally contribute to soil formation. The protective ground vegetation and the litter layer are often completely removed due to deer grazing, trampling and wind drift, resulting in shallow Ah-horizons. The lack of protective ground vegetation enhances wind and water erosion and thus nutrient runoff (FARRISH et al. 1993, GREENE et al. 1994). MITCHELL et al. (1998) showed that erosion by water is the most significant factor affecting the soil organic matter balance in the north central USA with erosion by wind being the second most significant factor. Therefore I consider the combined effects of acid depositions and soil erosion as responsible for the severe nutrient losses which can regionally not be compensated for at several hillslopes of the investigation area. However, due to the limited time period and the restricted number of observed forest sites there remain uncertainties whether the observed trend of severe nutrient losses and accumulation of toxic aluminium is a general and ongoing trend in the investigation area. Long term studies are necessary to gain certainty for this subject.

Nevertheless the results suggest that the permanent soil condition is not only the result of historical land use. Rather, soil quality deterioration is likely to be progressing and obviously an increasing threat to simple oak coppice forest stability. Particularly at windward hillslopes soil degradation in terms of nutrient depletion is enhanced.

IV.1.2 Slope position

Different landforms are likely to have different environmental characteristics, such as soil condition (e.g. texture, moisture, nutrient content) and frequency and intensity of disturbances (NAGAMATSU & MIURA 1997). When investigating soil characteristics of forests on hillslopes it is important to keep in mind that the conditions for soil forming processes may differ along the curvature of a slope as factors like slope gradient, elevation and climate vary. Typical slope positions at the Ahr-Eifel are plateau, upper slope, lower slope and foot slope which are divided by convex and concave breaks of slope. I studied several soil characteristics at these slope positions on a windward exposed hillslope to gather information regarding their influence on selected soil properties (investigation I).
Nitrogen concentrations did not differ remarkably among the relief positions except for the lower slope. At the upper slope loss of organic N by erosion might have been overcome by N-accumulation due to nitrogenous depositions (ZEZSCHWITZ 1987). Continuously decreasing pH and base cation contents and increasing aluminium contents from the foot slope to the plateau also point to higher loads of acid precipitation with increasing elevation. At higher elevations cloud water deposition could increase the total amount of deposition. In the Integrated Forest Study by JOHNSON (1992) covering forest sites in the USA, Canada and Norway it has been shown that atmospheric deposition was highest and percent base saturation lowest in high elevation sites compared to low elevation sites.
At the upper and lower slope the loss of fertile soil was increased reflected in lower contents of organic C and extractable P and a coarser soil texture compared to other slope positions (fig. III.2). Several studies demonstrated that rainfall and the shearing forces of runoff may disintegrate soil aggregates and redistribute fertile topsoil, plant nutrients and organic matter along the slope (ZOBISH et al. 1995, LE BISSONNAIS & ARROUAYS 1997, STALLARD 1998). At the foot slope the accumulation of fertile soil from the upper and lower hillslope may be responsible for high soil pH and increased nutrient contents.

The results of investigation I clearly demonstrate that soil acidity and soil nutrient contents differ among relief positions such as windward, leeward, plateau, upper slope, lower slope and foot slope. Soil degradation is enhanced at windward slopes and high elevations. At high slope gradients increasing soil erosion seems to contribute to soil degradation. The contribution of the factor “slope gradient” to the effects discussed in the previous chapters will be more closely related to in the following paragraph.

IV.1.3 Slope gradient

As shown before (fig. III.2) the upper and lower slope positions were characterized by a coarse texture and the depletion of several soil nutrients. While the exposure and the elevation of the different slope positions most likely affected the amount of acid depositions, effects related to erosion processes are influenced by the slope gradient. It has generally been assumed that diffusive sediment transport on soil-mantled hillslopes is dependant on hillslope gradient (GABET 2000). Previous studies showed that soil erosion is especially detrimental to nutrient-poor sites because it selectively removes the nutrient-rich surface layers and the accumulated organic matter (CLAASSEN & ZASOSKI 1998). In the investigation IV sites with high slope gradients (25-27°) and low slope gradients (14-15°) were compared to find evidence for the effect of slope gradient on several soil characteristics in the investigation area.

Differences in the thickness of the litter layer and the Ah-horizon were low between steep and gentle slopes (tab. III.14) although observations from convex hills indicated that soil thickness decreases with increasing topographic curvature (HEIMSATH et al., 2002). However, the WRC_{max}, soil moisture, the contents of C_{org}, N_t, PO_4^{3-}-P, Ca^{2+} and Mg^{2+} were generally higher at the gentle slopes compared to the steep slopes (fig. III.13, 14, 15). In the most cases these differences were significant ($p \leq 0.05$). Soil erosion generally removes the finest and most fertile soil particles (CARAVACA & ALBALADEJO 1999). Therefore the lower WRC_{max} and the lower contents of soil nutrients at the steep slopes point to the effect of soil erosion and increased run-off of soluble C- and N-compounds at high slope gradients. In a Canadian study, GENG & COOTE (1991) demonstrated that soil loss by erosion caused reductions in soil organic carbon, nitrogen and phosphorus.

These effects may have influenced the microbial activity which tended to be higher at low slope gradients (fig. III.16). In derelict soils subject to a high degree of erosion GARCÍA & HERNÁNDEZ (1997) found low organic matter contents which were positively correlated to basal respiration and biomass C. Also the absence of mature Lumbricids at the steep sites and the virtually absence of individuals at the steep oak-monoculture (tab. III.16) suggest that the conditions at the steep sites might be less favourable for the soil biota.

These results underline that increased soil erosion at high slope gradients contributes to soil degradation in the investigation area.

IV.2 Biotic factors

The large diversity of plants and animals in European deciduous forest ecosystem presupposes the significance of biotic interactions for the functioning of the whole system. Without any internal or external disturbance regimes the multitude of relationships, dependencies and interactions within the biotic world of forests is more or less balanced. As most of the middle European forests have been impacted by mankind for centuries through various disturbances (e.g. clearcutting, afforestation, pollution, extinction of species) today's temperate forests hardly represent a stable and natural ecosystem development state (HÜTTL et al. 2000). Therefore the main goal for foresters and scientists remains to increase the understanding for spatial and temporal ecosystem processes in order to rehabilitate sites to a virtually natural state or to manage existing forests in agreement with the concept of ecological sustainability. However, very often these goals do not go in accordance with socio-economic demands and despite good intentions problems with forest stability arise. In the investigation area the lease of hunting grounds has become an important source of income for the local communities as the economical value of forest management strongly decreased. Keeping game densities at high levels is therefore valuable because it attracts hunters from the close conurbations in Northrhine-Westphalia and neighbouring countries.
In the following paragraphs I relate to the possible consequences of high game densities for forest stability in terms of soil degradation. Moreover, the influence of the biotic factors "stand density" and "stand composition" on several soil characteristics are discussed.

IV.2.1 Deer

Within Europe and across a large part of the northern hemisphere, populations of red deer (*Cervus elaphus*) and other ungulates have been substantially expanding during recent decades, both in numbers and geographical range (KUITERS et al. 1996). However, due to the increasing anthropogenic land use followed by various disturbance regimes (e.g. traffic, industry and recreation activities) natural habitats for red deer in Germany declined and have become increasingly isolated (PETRAK 2002). As a consequence of the disturbances by man red deer withdrew from their preferred open habitats to woodlands in which they can appear in high densities. In some areas of the Ahr-Eifel the current hunting policy and supplemental feeding in wintertime resulted in a red deer population density of at least 20 individuals per 100 ha which, according to the local foresters, by far surpasses the carrying

capacity of the observed forests. This density is 1.5 to five times higher than reported from other semi-natural and natural forests across central Europe (RATCLIFFE 1984, BERTOUILLE & DE CROMBRUGGHE 1995, MAYLE 1996 DZIĘCIOŁOWSKI et al. 1996). At such high population densities red deer can cause a multitude of damages to forests. Many of these damages affect forests directly. The effects of bark peeling, fraying, browsing and grazing on tree vitality, rejuvenation and plant species composition have been described in detail in many studies and from many countries (AMMER 1996, PUTMAN 1996, MITCHELL et al. 1997, REIMOSER et al. 1999, FULLER & GILL 2001). Whereas much attention has been paid to the effects of ungulates on aboveground vegetation, their impact on edaphic factors has remained a less explored research field. Grazing, trampling and dunging may influence soil ecological processes such as soil formation, erosion and nutrient turnover of the decomposing and mineralising soil biota.

In a previous study (MOHR & TOPP 2001) forest sites which were heavily grazed and browsed were compared with sites which were only moderate to heavy grazed and browsed according to the categories shown in REIMOSER et al. (1999). We found a reduced WRC_{max}, lower contents of organic carbon, total nitrogen and phosphorus and a reduced activity of the soil biota in such heavily disturbed soils. These effects were attributed to deer grazing and trampling. Deer grazing and trampling destroys the protective ground vegetation and disrupts soil layers. Both, grazing and trampling is therefore supposed to increase soil erosion. It has already been stressed by other authors that game may intensify water and wind erosion at high densities (VOSER 1987, MWENDERA & SALEM 1997, HOLTMEIER 1999) and alter the soil micro-climate by removing or reducing the plant cover on the ground (STARK et al. 2000).

According to REIMOSER & SUCHANT (1992) the objective estimation of deer impacts on forest vegetation requires the construction of fenced exclosures. As this may also be valid for the investigation of soil ecological characteristics under the impact of red deer I set up two investigations (II and III) in which I established plots protected from deer by fencing and adjacent control plots accessible to deer. Certainly, other game species such as wild boars and moufflons contribute to soil disturbances outside the fenced exclosures but at the chosen forest sites I considered red deer to have the greatest impact on soil ecological characteristics. Therefore I decided to relate to the effects of red deer, exemplary for the effects of large herbivores in general.

Investigation II

Investigation II examined the effect of deer grazing and trampling by comparing fenced deer exclosure plots with controls at varying stand densities. The establishment of ground vegetation in the fenced exclosure occurred rapidly after the establishment of the fence in 2001, especially in the thinned area (tab. II.3). The herb layer was almost exclusively composed of ruderal and pastural species. The seeds most likely originated and germinated from deer dung. Several studies showed that hoofed game may play a particular role in the dispersal of ruderal and grassland species in forests, either by endo- or by epizoochory (GILL & BEARDALL 2001, HEINKEN & RAUDNITSCHKA 2002). Already two years after fencing the vegetation covered more than 85 % of the ground in the thinned area of the fenced exclosure (tab. II.3). Ground vegetation is crucially important for the stabilization of the soil and as a sink for soil nutrients reducing vernal nutrient leaching (TESSIER & RAYNAL 2003). Outside the fenced exclosure ground vegetation was almost completely removed and restricted to areas close to lying deadwood in the thinned plot. At this position the herbs might have been protected from destruction by trampling and grazing. The increased solar radiation at the thinned plots also supported the colonization of the ground flora. Both factors, deer herbivory and crown closure, have previously been shown to control the establishment of plants on the forest ground (MORECROFT et al. 2001).

Exclusion of deer not only affected the ground vegetation but also several soil characteristics. WRC_{max}, soil moisture, litter mass and the contents of C_{org}, N_t, PO_4^{3-}, Mg^{2+} and Ca^{2+} were all higher at the fenced plots than at the unfenced plots when comparing plots of the same stand density (tab. III.1; fig. III.3,4). Accordingly, ANCOVA delivered a significant ($p \leq 0.001$) influence of the factor "deer" on most of these soil characteristics (tab. III.2). These results support earlier findings (e.g. MOHR & TOPP 2001) and emphasise the view that deer grazing and trampling, possibly in combination with other game species such as moufflon and wild boar, enhance the erosion of the upper soil layers at high slope gradients (MWENDERA & SALEM 1997, GOVERS & POESEN 1998, HOLTMEIER 1999).

Grazing and trampling may not only change the soil nutrient status by enhancing soil erosion but also alter decomposition and mineralisation processes by influencing the soil biota. The composition and the abundance of the decomposer food web can act as a key regulator of mineralisation processes (BENGTSSON et al. 1996), plant nutrient acquisition (SETÄLÄ & HUHTA 1991), and ultimately plant growth (ALPHEI et al. 1996). However, so far little is known about the influence of herbivores on the soil food web and according to

the few existing studies the effects can be diverse depending on the system considered (WARDLE et al. 2001).

In the present study the microbial activity and the abundance of several soil faunal groups (Enchytraeidae, Coleoptera, Aranaea, Isopoda, Diplopoda, Chilopoda) were significantly higher in the fenced exclosure than in the unfenced plots when comparing dense and thinned plots separately (fig. III.5, 6; tab. III.4, III.5). Also ANCOVA indicated that the factor "deer" strongly influences microbial activity and the abundance of several soil arthropods (tab. III.3, 6). Red deer could impact the soil biota either directly or indirectly by altering vital soil characteristics. Soil microorganisms as well as the soil fauna largely depend on the soil pH (DWORSCHAK 1997, ZIMMER & TOPP 1997), a balanced soil micro-climate (KIELHORN et al. 1998, FRANZLUEBBERS 1999), litter amount (JUDAS 1989) and soil organic matter as a food source respectively (ALLEN 1993, SCHEU & SCHÄFER 1998). Soil pH did not remarkably differ between fenced and unfenced plots and was in a range almost optimal for decomposition processes. In contrast, as described above, drier conditions and a reduced nutrient availability outside the fenced exclosure may have reinforced the decline in microbial activity and in the abundance of the soil fauna.

Additionally, not only the amount of substrate but also the substrate quality may have differed between the different treatments influencing the soil biota. The organic matter may be older and less palatable at the grazed area because of the strong reduction of herb litter compared to the conditions in the fenced exclosure. Moose browsing has been reported to influence mineralisation processes and nutrient contents in soil by depressing not only the quantity but also the quality of the litter subject to decomposition (PASTOR et al. 1993). Additionally, the low lignin content of annual plants in the fenced exclosures encourages rapid growth of the microflora (MUN & WHITFORD 1998).

Differences in the soil nutrient status and the abundance and activity of the soil biota were only partly reflected by foliar nutrient concentrations of trees inside (Ft) and outside (Ud) the fenced exclosure. Foliar nitrogen and phosphorus concentration were significantly higher ($p \leq 0.021$, tab. III.7) in trees inside the exclosure but the opposite was found for the calcium concentration. However, analyses of foliar nutrient concentrations did not reveal any nutrient deficiencies or disorders for the standing stock, neither in the fenced exclosure nor in the nutrient-poor control plot. According to the criteria used by STEFAN et al. (1997) and HEINZE & FIEDLER (1992) all nutrients were found to be in a normal or optimal range and similar to values found in other studies (FIEDLER & CZERNY 1970, TOPP et al. 1998). It

has been claimed that oaks compensate for soil nutrient deficiencies in the soil by establishing a root system that is able to absorb water and soluble nutrients from crevices and ravines within the parent rock (MANZ 1995). I also assume that a reduced nutrient supply induces a stunted tree growth resulting in reduced biomass production and the elfinwood-like morphology of the oaks at many degraded forest sites, especially at the dry and wind-exposed forest sites of the investigation area. In a study from Missouri (USA) the stunted tree growth of several oak species was also attributed to very low nutrient levels as well as high levels of aluminium and xeric site characteristics (REICH & HINCKLEY 1980).

Investigation III

This investigation also used exclosures to estimate the influence of red deer on soil properties. Stand density was held constant between the plots but one plot inside and one outside the fenced exclosure were experimentally grubbed to investigate the effects of soil bioturbation by wild boar grubbing on soil ecology, both under deer exclusion and deer access. In this paragraph I will concentrate on the effects of game exclusion and the effects of grubbing will be referred to in the next chapter.

The fence was established in 1999 and by the start of the investigation a dense ground vegetation layer had already developed (cover: 62 %) in the fenced exclosure. The unfenced plots were almost completely grazed (ground cover: 0.2-2.5 %).

Litter layer, WRC_{max}, soil moisture, the contents of organic carbon, total nitrogen and magnesium as well as the microbial activity were significantly higher at the unfenced compared to the fenced plots when comparing same treatments. These results were in contrast to those obtained in investigation II. Many site characteristics such as vegetation, elevation, grazing and browsing pressure, slope gradient and soil type were similar at the sites of both investigations and therefore these different effects of deer exclusion on soil properties were surprising in the first instance. It has already been stated by other authors (STARK et al. 2000, WARDLE et al. 2001) that the impact of deer grazing on soil processes may be the result of complex interactions between different mechanisms.

Differences in the slope aspect between investigations II (windward) and III (leeward) could be one important factor interacting with the detrimental effects of deer trampling and grazing. The slope aspect has already been shown to influence soil nutrient status in the investigation area (Chapter IV.1.1). At windward sites soil acidification and erosion processes are enhanced, thereby reducing nutrient contents in the soil. At leeward sites such effects are less pronounced. In the unfenced control plot of investigation III (Cu) the

litter layer was undisturbed and no indications for litter perturbation and increased soil erosion were found which was in contrast to the equivalent unfenced plot of investigation II (Ud). Hence, deer trampling and grazing may enhance soil erosion only at windward sites in which strong winds and higher rainfall remove the litter and the unprotected and disrupted organic soil layers. However, investigation II demonstrated that windward sites do not necessarily show low pH-values and low contents of basic cations. The presence of loess material covering the slate rock resulted in higher soil pH values and higher contents of Ca^{2+}, Mg^{2+} and K^{+} than at the leeward site of investigation III. Locally loess layers cover the Devonic material in massive layers (LOTHHAMMER & BOR 1982, MANZ 1995) forming soils with a high buffering capacity to compensate for base cation depletion through soil acidification and soil erosion at windward slope aspects.

Higher microbial activity and soil nutrients contents at the unfenced plots of the investigation III cannot be related to the slope aspect but may be associated with game dunging. The excretion of dung and urine by game has been reported to increase microbial activity and nutrient contents in many studies (HAYNES & WILLIAMS 1999, VACCA 2000, WILLOT et al. 2000, STARK et al. 2002). While nutrients derived from excreta supply might not accumulate at windward exposed forest sites due to leaching and erosion they could accumulate at leeward forest sites and largely contribute to nutrient cycling.
Yet, many saprophageous soil arthropods (Oribatidae, Isopda, Diplopoda, Protura, Diplura) did not seem to benefit from the litter and nutrient accumulation at the unfenced plots and appeared at significantly lower abundances outside the fenced exclosure (tab. III.11, 12). Their lower mobility compared to other soil arthropods such as Collembola, Coleoptera and Aranaea which did not exhibit lower abundances at the unfenced plots might subject them to a higher danger of physical damage by trampling.

IV.2.2 Wild boar

Soil bioturbation by vertebrates can have diverse effects on soil properties. Burrowing of the subterranean rodent *Ctenomys talarum* (tuco-tuco) from South America was observed to increase sodium, potassium and magnesium contents in coastal grasslands of South America (MALIZIA et al. 2000). Other studies suggest that the digging activity in gopher or rabbit warrens enhances soil erosion (YAIR 1995, GABET 2000, ELDRIDGE & MYERS, 2001). FORD & GRACE (1998) observed patterns of habitat destruction by nutria and wild

boar which reduced belowground production in coastal marshes. In the steep terrain and shallow soils on Isla Victoria (Argentina) the recently arrived boar is even seen as a grave threat to the native forests (SIMBERLOFF et al. 2002).

Oak woodlands are favoured habitats for wild boars (STERNER 1990, WELANDER 2000), which, due to their high reproductive rate, and secretive nature, still occupy much of their original range in Europe. Wild boars are the ungulates with the highest rate of increase in Central Europe (PETRAK 2001). In many German forests soil bioturbation by wild boar (*Sus scrofa*) predominates over many other mammals` soil disturbances, especially when they appear in high population densities. Severely grubbed areas may extend for a hectare or more causing substantial damage to forests and neighbouring crops. Regeneration of oak (*Quercus robur* and *Q. petraea*) is reported to be negatively correlated with rooting frequency (GROOT BRUINDERINK & HAZEBROEK 1996). However, little is known about the consequences of soil bioturbation for nutrient cycling in European deciduous forests. Aeration of the soil, incorporation of litter into the soil and mixing of soil layers is suspected to affect soil pH, decomposition processes and hence nutrient contents in the soil (BRATTON 1975, LACKI & LANCIA 1983, SINGER et al. 1984), especially in steep terrain.

In the present study soil pH, organic carbon, total nitrogen, the C/N-ratio, soil moisture and soil texture were not affected by soil bioturbation (tab. III.8, III.9, fig. III.8). These results support earlier findings in which an effect of wild boar grubbing on organic matter, nitrogen and soil pH could not be detected (GROOT BRUINDERINK & HAZEBROEK 1996, MOODY & JONES 2000). Indications of accelerated soil erosion due to an increase in bare ground after wild boar rooting as postulated by BRATTON (1975) could not be found either. In contrast, the contents of phosphate, potassium, magnesium and calcium were always lower in grubbed plots compared to the ungrubbed plots, although differences were not always significant (fig. III.9). In a three year experiment at the Smokey mountains SINGER et al. (1984) also observed an accelerated leaching of P, Ca and Mg from soil after wild boar rooting.

As a significant proportion of available soil nutrients is derived from microbial transformations (ANDERSON & DOMSCH 1980) the reduced content of mineral nutrients may also result from a reduction in microbial activity and biomass at the grubbed plots, especially under game exclusion (fig. III.10). However, factors influencing microorganisms such as temperature, soil humidity, soil pH and the contents of organic carbon and nitrogen (WARDLE 1992, MCLAUGHLIN et al., 2000) remained constant and do not explain the variations in microbial activity and biomass among the plots. Direct effects

of the bioturbation process such as physical pressure or alterations in soil structure and soil microclimate may have been destructive for microorganisms. However, this is in contrast to other studies which reported that treatments mixing organic layers into mineral soil can stimulate microbial populations due to better soil aeration and improvement in substrate quality (FOSTER et al. 1980, MALLIK & HU 1997).

As a further explanation for the differences in microbial properties the abundance of the detritivorous soil fauna could be taken into account. Several studies showed that saprophagous soil arthropods may influence the microbial activity and the release of nutrients in the soil (KANDELER et al. 1994, VEDDER et al. 1996, ZIMMER & TOPP 1999, KAUTZ & TOPP 2000). Bioturbation, litter breakdown and the release of microbially colonized faeces are ways in which the saprophagous soil fauna affect microorganisms (HASSEL et al. 1987, TAJKOVSKI et al. 1992).

While there were no remarkable differences in the distribution pattern of the mesofauna among the plots (fig. III.11, tab. III.11) clear differences for the macrofauna were found (fig. III.12, tab. III.12). The total macrofauna as well as the sum of all detritivorous individuals were significantly more abundant ($p \leq 0.05$) at the ungrubbed treatments compared to the bioturbation treatments. These effects were pronounced when game was excluded from the plots. According to analyses of variance wild boar grubbing strongly influenced the abundance of the total macrofauna and of beetles, spiders and isopods (tab. III.13). I mainly attribute the described reduction of macrofaunal abundance to the physical disturbance imposed by the bioturbation process. The additional impact of deer trampling resulted in the lowest abundances of most macrofaunal groups at the grubbed plot outside the fenced exclosure (tab. III.12). Wild boar feeding on the soil fauna may even increase the observed trends. As smaller soil arthropods (soil mesofauna) did not seem to be affected by these disturbance regimes the size of the soil organisms seems to be relevant for their susceptibility to physical disturbance.

From the results it can be concluded that soil bioturbation by wild boar grubbing neither affects the soil organic matter content nor enhances soil erosion. Rather, it reduces the content of several soil nutrients such as P, Mg, Ca and K. This may be the result of increased nutrient leaching or reduced litter decomposition due to lower microbial activity and lower abundances of soil arthropods at grubbed plots. Consequently, wild boar grubbing contributes to soil degradation in the investigation area.

IV.2.3 Stand density

Many European forests are even-aged as a result of historical silvicultural practices (KHANNA & ULRICH 1991). Nowadays, forest management often involves creating gaps and reducing stand density in order to promote forest regeneration and to increase spatial heterogeneity. Gap formation in forest ecosystems is a natural process occurring during secondary succession or as a result of natural disturbances such as wind fall or tree diseases. Gaps change light levels and other characteristics sufficiently to influence forest dynamics over differing spatial and temporal scales (WHITMORE 1989, SPIES & FRANKLIN 1989). While the heterogeneity of plant litter accumulation and its influences on seed germination and seedling growth have been well described (FACELLI & CARSON 1991, FACELLI & PICKETT 1991) there is little information available on nutrient cycling in forest gaps (ZHANG & LIANG 1995). Differences in the floristic composition and the structure of forest stands may have significant impacts on element budgets (BOLTE 1996).

Thinning of forests creates similar conditions as found in forest gaps increasing light intensity and delivering downed deadwood. Under these conditions the growth of the herb layer may be promoted and protected from game access. The accumulation of organic matter may increase nutrient status and biotic activity at thinned forest stands compared to dense forests. The influence of stand density on soil characteristics was examined in investigation II.

Differences in stand density clearly affected soil chemistry and the soil biota. All major groups of the soil macrofauna were higher in abundance at the thinned plots compared to the dense plots (tab. III.5, fig. III.6, III.7). The differences were significant in most cases and analyses of variance revealed a strong influence ($p \leq 0.001$) of stand density on all major groups of the macrofauna except for the centipedes. (tab. III.6).

In a similar study JUNKER & ROTH (2000) found an increase of predatory biomass (Aranaea; Carabidae) comparing thinned and dense plots being exposed to game species. Excluding game species by fencing resulted in a decrease of predatory biomass under open up canopies compared to dense plots, which conflicts with the results of my study. The differences could result from the applied sampling methods. JUNKER & ROTH used pitfall traps which only yield information on activity patterns while I preferred to obtain “real” abundances by extracting the soil fauna from sampled litter. In my opinion, it is not adequate to use the pitfall trap-method when trying to deduce differences in arthropod abundance from small-scale spatial variability in environmental characteristics.

In a further study from a northern hardwood forest of Quebec, Canada (MOORE et al. 2002), millipeds were more abundant in selective cuts than in adjacent undisturbed sites but selective felling had no effects on the abundance of collembolans and carabid beetles. The abundance of spiders was even lower in selective cuts than in dense forests. Selective felling (30 % of the stand volume removed) in boreal spruce forests of Finland had no effects on the decomposers (SIIRA-PIETIKÄINEN et al. 2002).

All these studies suggest that soil arthropods may react unpredictably to forest thinning. This may be due to an interaction of microclimatic changes and the physical disturbances resulting from the forest management practices. In the present study a reduced stand density positively affected the litter dwelling macrofauna and therefore no evidence for a negative effect of the recent (1999) tree felling was found. But, in contrast to other studies, the trees in my study sites were not harvested and remained as downed deadwood on the site. Therefore physical changes like soil compaction and erosion hardly occurred as can be derived from soil texture and WRC_{max} measurements (tab. III.1). I rather suppose that the coarse woody debris in combination with higher ground vegetation cover (tab. II. 3) at the thinned plots strongly influenced the soil macrofauna. Both factors increase the structural heterogeneity and may therefore provide a higher variability of micro-climatic conditions and an increase in food resources for soil arthropods (HARMON et al. 1986, KLINKA et al. 1995). Lying deadwood traps litter which resulted in significantly ($p \leq 0.05$) higher amounts of litter at the thinned plots (tab. III.1). Relationships between resource availability and soil fauna abundance have been proved in several studies (SCHEU & SCHÄFER 1998, PONSARD et al. 2000, MARAUN et al. 2001, MOORE et al. 2002).

Different responses to forest thinning may also be linked to the type of habitat and the soil faunal groups observed (PONGE et al. 1993, MARRA & EDMONDS 1998, BENGTSSON et al. 1998). In my study soil mesofauna response did not parallel the observed changes in the macrofauna. Only the enchytraeids were more abundant in thinned plots compared to the dense plots which is in accordance with the results obtained from gap fellings (SIIRA-PIETIKÄINEN 2001).

Microorganisms are supposed to be “bottom-up” controlled (SCHEU 1990, WARDLE 1992; GALLARDO & SCHLESINGER 1994). In this study the potential microbial activity was significantly ($p \leq 0.01$) higher at the thinned plots than at the dense plots but there was no effect of stand density on the microbial biomass at the fenced plots (fig. III.5). The increased microbial activity could be attributed to the combined effect of a higher macro-arthropod abundance (see above) and the significantly higher supply with organic matter

(ground vegetation, litter, contents of C_{org} and N_t; tab. II.3, III.1; fig. III.3) at the thinned plots. Also soil moisture was significantly higher at the thinned plots despite of higher radiation intensity which reflects the importance of the ground vegetation and the lying deadwood for a balanced soil-microclimate. Higher contents of C_{org} and N_t, PO_4^{3-} at the thinned plots can most likely be attributed to the additional supply of organic material from the well-established ground vegetation and the decaying deadwood. KLINKA et al. (1995) stated that the most distinguishing characteristic of decaying wood seems to be the high concentration of humic acids and the low soil pH relative to pedons without decaying wood. I also observed significantly ($p \leq 0.001$) lower pH values at the thinned plots with deadwood compared to dense plots without coarse woody debris (tab. III.1). However, lower pH-values at the thinned plots may partly be attributed to the increased release of H^+-ions by increased biotic respiration.

The reduction of the soil pH at the thinned plots did not enhance cation depletion. The contents of calcium was even significantly higher ($p \leq 0.05$) at the thinned plots than at the dense plots but there were no differences in extractable magnesium and potassium.

Altogether the results suggest that the reduction of the stand density by forest thinning without removing the fallen logs increases soil nutrient contents and supports soil organisms. Especially in the thinned plot of the fenced exclosure the regenerating ground vegetation and the decomposing wood provide conditions that increase the abundance of several soil arthropods, the microbial activity and several essential soil nutrients in the soil. The results demonstrate that forest thinning as conducted in this study may help to reduce soil degradation and thus to improve soil quality in the investigation area.

IV.2.4 Stand composition

In many simple coppice forests of the European low mountain range oak trees (*Quercus petraea*) are naturally associated with hazel (*Corylus avellana*) (ELLENBERG 1986). Hazel can form a dense shrub layer in the understory below the oak canopy reducing the light intensity on the ground and thus limiting the growth of the ground vegetation. During the last decades many oak coppice forests were converted into monocultures and hazel was cut down to enhance the growth of the target trees or to simplify the accessibility of forests for management practices and the hunt.

In contrast to the economical interests hazel may be of high ecological relevance for forest stability. Therefore, this study (investigation IV) also aimed at evaluating the effect of hazel on soil ecological processes in degraded simple oak coppice forests of the Ahr-Eifel. I hypothesized that a dense hazel community under the oak canopy reduces water erosion and the wind velocity at the ground and traps litter blown away by the wind to keep organic matter at the sites. The forest floor mass after litter fall was similar at all sites, but 10 months later, just before the next litter fall, the litter mass at the oak-monocultures was significantly lower ($p \leq 0.05$) than at the mixed stands (tab III.14). As oak leaves decompose slowly due to the high concentration of phenolic compounds the huge reduction (78-100 %) in forest floor mass between November 2001 and September 2002 in oak-monocultures was mainly evoked by wind drift and downhill transport. On forest paths, in troughs or at foot slopes I generally found thick layers of oak litter accumulating from downhill transport which supports the above assumptions. As a possible consequence of litter mass loss the thickness of the Ah-layer was reduced in the oak-monocultures (tab. III.14). At the mixed stands the litter layer was not perturbed and the reduction of litter mass could be mostly attributed to the decomposition of hazel litter. Thicker Ah-horizons in the mixed stands than in the monocultures reflect the increased decomposition of organic matter. However, differences in above ground organic matter mass and quality between mixed stands and monocultures were not reflected by the contents of organic carbon and total nitrogen or the C/N-ratio in the Ah-horizon (fig. III.13) as would have been expected from previous studies (FINZI et al. 1998, NEIRYNCK et al. 2000). However, the results confirm that a dense shrub layer prevents the loss of aboveground decomposable organic material by reducing the wind velocity and trapping the litter. Thereby the total aboveground (O-horizon) and soil organic matter pool (Ah-horizon) is enriched and protected from continuous depletion.

Decomposers are known to be influenced by microclimatic conditions, nutrient availability and substrate quality (MELILLO et al. 1982, AERTS 1997). Already 40 years ago PEREL & SOKOLOV (1964) noted the relative unpalatability of oak litter compared to that of hazel or lime but conclude that in an oak forest mixed with lime, maple and hazel, where oak-leaf litter constitutes the bulk of the forest floor, *Lumbricus terrestris* worms do not sustain any dietary and play an active role in decomposing forest litter. Subsequent studies confirmed that the chemical composition as well as the species composition of the leaf litter influence its decomposition (SWIFT et al. 1979, VITOUSEK et al. 1994, KAUTZ & TOPP 1998, ZIMMER

2002) and that these factors prevail over other factors controlling litter decomposition under favourable climatic conditions (COÛTEAUX et al. 1995). I therefore hypothesized that Lumbricids and microorganisms are favoured in mixed stand of oak and hazel compared to oak-monocultures.

Abundance and diversity of Lumbricids found in my study was very low, too low to compare sites statistically (tab. III.16). In previous studies (ZAJONC 1971, DAVID et al. 1991) Lumbricid abundances in oak forests were much higher. The low population density in my study may be due to the low soil pH at the sites, which is known to reduce hatching success, enhance weight loss of aging adults and to hamper juvenile growth of Lumbricids (LAVERACK 1961, BENGTSSON et al. 1986, RUNDGREN & NILSSON 1997). Also wild boars may substantially reduce the Lumbricid density as they can uproot soils several times a year in the search for food.

Microbial respiration is supposed to be higher in tree leaf litter mixtures than in single-species litters (MCTIERNAN et al. 1997). Such a relationship was found for the low inclination site but not for the steep site (fig. III.16). The microbial biomass was even lower in soils of mixed stands than in the monocultures which conflicts with relationships found in earlier studies (BAUHUS et al. 1998, KAUTZ & TOPP 1998, PRIHA et al. 2001). The significantly highest ($p \leq 0.001$) microbial activity at the oak-hazel stand of low slope gradient may be the result of a significantly higher ($p \leq 0.05$) WRC_{max}, soil moisture and also higher amounts of litter at this site. Altogether, the influence of stand composition on microorganisms and Lumbricids seemed to be low. Therefore, oak-hazel litter mixtures did not favour microbial activity, C_{mic} and the abundance of Lumbricids under the conditions of the observed sites.

The litter as a fuel for the nutrient cycles in upper soil horizons is particularly important in the nutrition of woodlands on soils of low nutrient status where the trees rely to a great extent upon the recycling of litter nutrients (CARLISLE et al. 1966). Hazel leaves as well as leaves of other trees like lime (*Tilia chordata*) and cherry (*Prunus avium*) are rich in basic cations (Ca^{2+}, Mg^{2+}, K^{+}) (HEINZE & FIEDLER 1992) and easily decomposable because of the low concentrations of polyphenolic substances compared to oak and beech leaves (PEREL & SOKOLOV 1964, SATCHELL & LOWE 1967). Many studies showed that the addition of alkaline plant material to acidic soils can appreciably increase the soil pH and the content of exchangeable soil nutrients (FINZI et al. 1998, NOBLE & RANDALL 1998,

TANG et al. 1999, MARSCHNER & NOBLE 2000). I therefore expected to find a higher soil pH and a higher content of exchangeable nutrients in the soils under oak-hazel mixtures.
The soil pH was not affected when hazel litter contributed to litter decomposition (tab. III.14). Possible reasons for that have already been discussed in chapter IV.1.1. In contrast, the content of Al^{3+} was significantly lower in soils of the mixed stands (fig. III.15). Soil conditions beneath hazel could have favored the complexation of Al^{3+}-ions to organic compounds in the Ah-horizon. The complexation of Al^{3+} to humic substances has already been described in previous studies (THOMAS 1975, HUE et al. 1994, GERKE 1994). Al^{3+}-ions are also known to complex with phosphate-ions in the soil and thus to prevent P-uptake of plant roots (BENGTSSON et al. 1986, ANDERSSON 1988). Consequently, the significantly higher contents of Al^{3+} in the soil of oak-monocultures could have contributed to the lower content of plant available phosphate, especially at low gradients (fig. III.14).
The contents of Ca^{2+} and Mg^{2+} were significantly higher in soils of mixed stands than in oak-monocultures (fig. III.15) which is in accordance with expectations based on previous studies (see above). Ca^{2+}- and Mg^{2+}- contents at the steep oak-hazel stand and the flat oak-monoculture were almost identical but significantly higher ($p \leq 0.001$) compared to the steep oak-monoculture. These results suggest that the negative effects of high slope gradient, e.g. higher erodibility (see chapter IV.1.3), seem to be overcome by the presence of hazel at steep slopes. ANOVA underlined the strong influence of stand composition on the contents of Ca^{2+}, Mg^{2+},Al^{3+} and PO_4^{3-}. Potassium content did not differ between the sites, possibly due to the high mobility of K^{+}-ions (REMEZOV & POGREBNIAK 1969).

From the obtained results I conclude that hazel positively affects nutrient cycling in degraded oak forests in two ways: Firstly, it reduces the wind velocity on the ground and traps litter to allow for accumulation of organic matter. Secondly, the decomposition of hazel or oak/hazel-litter mixtures increases the content of plant available calcium, magnesium and phosphate and supports the complexation of toxic aluminium-ions.
Consequently, sustainable forest management in simple oak coppice forests should include the growth of hazel and further base-rich shrubs and trees and favour mixed stands instead of oak-monocultures in order to reduce soil degradation.

IV.3 Microbial properties as indicators for soil quality

Evaluating soil quality – the inherent capability of soil to support vegetative growth – is difficult because of the diversity of soil properties to be measured (PAGE-DUMROESE et al. 2000). Proposed properties for the assessment of soil quality are, among others, infiltration, available water holding capacity, pH, cation exchange capacity, organic matter and several biological indices (POWLSON et al. 1987, STORK & EGGLESTON 1992, PAPENDICK & PARR 1992, KARLEN & SCOTT 1994). Among the multitude of biological indices several microbial characteristics such as microbial activity, microbial biomass, metabolic quotient and C_{mic}/C_{org}-ratio have gained increasing attention as indicators for soil quality assessment in the last decade because microorganisms react quickly to changes in the soil chemical and physical environment (WOLTERS & JOERGENSEN 1991, BAUHUS et al. 1998) and in turn influence the nutritional status of soils. However, several authors warned that soil microbial properties may have limitations in their use as bio-indicators for forest soil quality (WARDLE & GHANI 1995, RAUHBUCH & BEESE 1999, VANCE & CHAPIN 2001, MOHR et al. 2002).

One goal of this study was to test the usefulness of the microbial properties activity, C_{mic}, qCO_2 and C_{mic}/C_{org} as indicators for soil degradation in terms of soil acidification, soil organic matter loss and nutrient depletion in simple oak coppice forests of the Ahr-Eifel. As good indicators they should be closely related to several soil characteristics which determine soil quality such as the soil pH, the WRC_{max}, the C/N-ratio and the contents of C_{org}, N_t and PO_4^{3-}.

IV.3.1 Field studies

Microbial activity

In several studies the dependency of soil microbial populations on balanced soil moisture, soil pH and nutrient availability was stressed (BÅÅTH et al. 1980, BECK 1989, MURATA et al. 1999, SIMON 2001). In my study correlation analyses indicated a strong influence of the WRC_{max} and the contents of C_{org}, N_t and PO_4^{3-} on microbial respiration (tab. III.17). Microbial activity was negatively correlated to the soil pH (tab. III.17) which is in contrast to several studies in which microbial respiration declined with increasing soil acidity (FRANCIS 1982, HACKL et al. 2000). This result indicates that the microbial community is well adapted to the acidic soils in the investigation area.

According to the correlation coefficients nitrogen is the most important factor influencing microbial activity in this study which has already been claimed by other authors (MELILLO 1982, TAYLOR 1989, TIUNOV & SCHEU 1999). Linear regression analyses confirmed the close relationship between microbial activity and the contents of C_{org}, N_t and PO_4^{3-}. Microbial respiration tends to increase linearly with increasing nutrient availability, at least in the observed range. However, different tendencies within the different investigations avoided closer relationships (fig. III.17; tab. III.18). In investigation III microbial activity was not correlated to any of the soil nutrients. Simulated wild boar grubbing reduced the microbial activity without having an effect on the contents of C_{org}, N_t and PO_4^{3-} (fig. III.8, 9, 10). These results indicate that microbial respiration may react to disturbance regimes long before changes in the soil nutrient status are detected which has been postulated by KENNEDY & PAPENDICK (1995) and STADDON et al. (1999). The observed differences in the dependency of microbial respiration on the content of C_{org}, N_t and PO_4^{3-} among the investigations (fig. III.17, tab. III.18) may also result from site specific variations in soil texture, WRC_{max} and soil pH. VANHALA (2002) demonstrated that the factors soil moisture, temperature, soil pH and organic carbon interact when influencing microbial respiration and that the contribution of each single factor to microbial performance varies depending on the specific site conditions. SPARLING (1997) noted that microbial respiration can show wide natural variation depending on substrate variability, moisture and temperature. This high variability was observed in this study (tab. III.10; tab. Appendix-3.1, -3.2). KNOEPP (2000) argued that this variability makes the microbial activity, taken alone, difficult to interpret in terms of soil quality or health. However, in high replicate numbers microbial activity reliably reflects nutrient availability and WRC_{max} which are important components of soil quality. Moreover, it seems to responds quickly to disturbance regimes in the investigation area and is therefore useful a an indicator of soil degradation in simple oak coppice forests.

Microbial biomass (C_{mic})

A whole bunch of studies reported the dependency of microbial biomass on the soil pH, the soil texture and the amount and quality of available substrates such as C-, N- and P-sources (e.g. FRANCIS 1982, WARDLE 1992, TSCHERKO 1999, BAUHUS & KHANNA 1999). In this study similar results were obtained. Microbial biomass was significantly correlated to the soil pH, the WRC_{max}, the C/N-ratio and the contents of organic carbon and total nitrogen when considering the data of all investigations (tab. III.17). According to correlation and

regression analyses WRC_{max} and the contents of C_{org}, and N_t were the most important factors determining microbial growth. These results point to a general trend towards higher microbial biomass with higher substrate availability and a higher WRC as found in earlier studies (see above). However, regarding the investigations separately, significant correlations between C_{mic} and the contents of C_{org} and N_t were only found in a few cases (tab. III.18). Moreover, the microbial biomass was hardly influenced by any of the chosen environmental factors in this study (fig. III.5., III.10, III.15). The dependency of microbial biomass on the nutrient availability could to a large extent be superimposed by other factors which limit microbial growth. For example, community level control by which growth is inhibited has been documented in several studies (JANZEN & GILL 1995, ENGLAND et al. 1999, STENSTRÖM et al. 2001). Also predator pressure could prevent an increase in microbial biomass. JOERGENSEN & SCHEU (1999) found only small effects of energy and nutrient supply on microbial biomass in field studies and attributed it to faunal regulation mechanisms. Moreover, several studies showed that the feeding activity of saprophagous soil animals may increase the microbial activity without changing the microbial biomass (KANDELER et al. 1994, KAUTZ & TOPP 1998). Also the substrate quality has been shown to limit microbial growth (EILAND et al. 2001, WEBSTER et al. 2001).

Altogether it appears that microbial biomass reacts less sensitive to changes in the soil nutrient availability than the microbial activity does. Factors like density dependant interactions, predator pressure and substrate quality may limit the growth of an active microbial community in a fertile soil and thereby prevent conclusions to be drawn on the quality of a soil. Also CARTER et al. (1999) stated that soil microbial biomass has limitations as an indicator for soil quality assessment but can serve within a minimum data set of other indicators. However, regarding large data sets comprising soils with a broad range of organic carbon content the microbial biomass is closely related to the substrate availability and may deliver an adequate estimate of soil quality as shown in this study (tab. III.17, fig III.16) and several previous studies (WARDLE 1992, BAUHUS & KHANNA 1999, SIMON 2001).

Metabolic quotient (qCO_2)

KENNEDY & PAPENDICK (1995) and STADDON et al. (1999) proposed the qCO_2 as a microbial indicator of soil quality. A lower qCO_2 should indicate a more stable and mature system and therefore reflect microbial community stability, whereas elevated qCO_2 values

should indicate environmental stress (ANDERSON & DOMSCH 1993). Many authors claim that the qCO_2 decreases with increasing substrate quality and that it is higher under unfavourable than under favourable conditions (WOLTERS & JOERGENSEN 1991, WARDLE & GHANI 1995, BAUHUS et al. 1998).

In this study contrasting results were found. Lowest values were obtained at plots confronted with unfavourable conditions and reduced organic matter content (deer trampling/grazing, wind-exposure, high slope gradient, oak-monoculture) and highest values at plots with favourable conditions and a high organic matter content (deer exclusion, lee-exposure, low inclination, association of hazel) (fig. III.5, III.10, III.15). Correlation analyses also indicated that the qCO_2 increases with increasing phosphate content and a decreasing C/N-ratio (tab. III.17). According to the citations mentioned above these results suggest that the microbial biomass utilizes the available C-sources more efficiently under unfavourable than under favourable conditions with organic matter accumulation. This would be plausible if the accumulating organic matter was highly recalcitrant or, in the course of secondary succession, composed of complex organic substances resistant to a further degradation. But in this study an increase in soil organic matter either resulted from hazel litter or from annual plants growing exclusively inside recently erected fenced exclosures. Both should deliver high amounts of easily degradable carbon sources.

It has been shown that the addition of easily degradable C-sources can increase the specific microbial respiration (MARAUN & SCHEU 1996, TIUNOV & SCHEU 1999). This increase was ascribed to a metabolically-active microbial community adapted to continuous additions of nutrients. Also game excretion products may have increased the pool of easily degradable organic substances in the soil which lead to higher metabolic quotients in unfenced than in fenced plots (investigation III). The urine and faeces produced by mammalian herbivores is constituted of labile and N-rich organic substances (MCKENDRICK et al. 1980, RUESS & MCNAUGHTON 1987, FRANK & GROFFMAN 1998).

These results indicate that, at least for the investigation area, the metabolic quotient has restrictions as an indicator of soil degradation. It does neither reflect environmental disturbances to the soil nor changes in the soil organic matter quality. This may to a large extent be due to the weak response of the microbial biomass to changes in environmental conditions relative to the microbial activity. Also WARDLE & GHANI (1995) found that the qCO_2 is not always a reliable or consistent indicator of disturbance and ecosystem development. RAUBUCH & BEESE (1999) came to the same conclusion.

C_{mic}/C_{org}-ratio

It has been proposed that the biomass C is more sensitive to changes in soil quality than the total organic C (SPARLING 1992) and therefore the ratio of C_{mic} to C_{org} may provide an early warning system for changes in organic matter dynamics, e.g. forest soil degradation in terms of soil organic matter loss (POWLSON et al. 1987). The ratio has been found to increase in soils with a high potential for carbon decomposition and to be low in soils which are either more resistant to further rapid C-loss or depress microbial biomass due to contamination, pollution or nutrient limitation (NANNIPIERI et al. 1990, GARCIA 1994, ELLIOT et al. 1996, WEBSTER et al. 2001). According to these earlier findings I expected to find low C_{mic}/C_{org}-ratios in soils subjected to disturbance regimes following nutrient depletion. High C_{mic}/C_{org}-ratios were assumed to be found at plots with accumulation of easily degradable organic compounds. Such conditions were presupposed for soils in fenced exclosures or thinned stands with a dense ground vegetation, in mixed stands in which hazel litter contributes to litter decomposition or for soils with a low erosion potential (leeward, low slope gradient). The results obtained were contradictory to these expectations. In none of the investigations the availability of easily degradable carbon sources was reflected by higher C_{mic}/C_{org}-ratios. Rather, the C_{mic}/C_{org}-ratio significantly decreased with increasing C_{org} content at the plots (tab. III.17).

According to the applications mentioned above these results would imply that microbial biomass was depressed at plots with accumulation of easily degradable soil organic matter but enhanced or at least unaffected at plots subject to soil organic matter loss. Such an explanation is not plausible and must be dismissed. I rather suppose that an increase in highly degradable C-compounds is not necessarily accompanied by an increase in microbial biomass. As shown above, microbial growth may be limited due to grazing pressure or as a consequence of ecophysiological adaptation strategies to the site conditions. On the other hand, even erosive plots may have offered sufficient substrate to allow microbial growth to a certain extent.

As a conclusion the C_{mic}/C_{org}-ratio fails to predict the danger of soil organic matter loss or nutrient limitation as proposed by SPARLING (1992) and POWLSON et al. (1987), at least for this investigation area. It is therefore not applicable as an indicator for soil degradation in simple oak coppice forests of the Ahr-Eifel.

IV.3.2 Microcosm experiments

As already stressed soil microorganisms are believed to be controlled by energy and nutrient availability (HUNT et al. 1987, JOERGENSEN & SCHEU 1999). Two microcosm experiments were conducted to elucidate the effects of substrate availability on basal microbial activity, microbial biomass and the qCO_2 under controlled conditions. One goal of this investigation was to find out if the relationships between nutrient contents and microbial properties as detected in the field studies can be reproduced under stable conditions without external disturbances factors such as climatic variations and arthropod grazing.

Microbial activity

In the control-approach of both series the microbial activity continuously decreased from day 1 to day 64 (fig. III.18, tab. Appendix-5.1). This effect could be attributed to the decline in easily degradable substrates during incubation. Higher microbial activity in the soil substrate of series II than that of series I reflects the higher initial nutrient concentrations in the soil from the Westerwald. The addition of nitrogen and phosphorus slightly increased the microbial activity in both series on day 1, 2 and 4 but there were no significant differences ($p > 0.05$) between the two approaches (tab. Appendix-5.2). Hence, nitrogen and phosphorus were not limiting microbial activity in this experiment. Possibly, soil microorganisms only respond positively to N and P additions when the soluble C-limitation is alleviated (PRESCOTT & MCDONALD 1994, MC LAUGHLIN et al. 2000, VANCE & CHAPIN 2001). On the other hand, in many studies microbial respiration most strongly responded to large C additions when N was abundant (MOORE 1981, VANCE & CHAPIN 2001) which is consistent with hypotheses based on the concept of microbial C vs. N limitations. But this was not tested in this study.

In the course of both experiments lignin degradation was not observed. Slightly higher microbial activity compared to the control-approach resulted from a small proportion of soluble carbon sources in the lignin powder applied to the soils. Assumptions that lignin-degradation could be faster in a soil sampled close to decaying wood (series II) must be omitted.

The development of microbial activity after addition of glucose and cellulose in the course of the experiment was almost identical when comparing the two series. Glucose addition resulted in the highest activity at day 4 and cellulose addition evoked a retarded maximum

at day 8 in both series. An increase in microbial activity after carbon-addition was found in multiple studies (e.g. LIN & BROOKES 2000, DILLY & NANNIPIERI 2001).

The retarded substrate decomposition for the cellulose approach reflected the lower degradability of cellulose compared to glucose. Cellulose breakdown requires a cellulase enzyme complex whereas glucose can be absorbed following attack by a single enzyme (SCHLEGEL 1986, PAUL & CLARK 1989). VANCE & CHAPIN (2001) found that microbial respiration responded more strongly to disaccharide (sucrose and cellobiose) than to cellulose additions. It is well known that the chemical composition of carbon sources determines their degradation velocity (WHALEN et al. 2000, EILAND et al. 2001).

Glucose addition seemed to evoke a stronger increase in microbial respiration than cellulose but as measurements were not conducted daily it was not possible to determine if there were differences between the maximum activity of the glucose and the cellulose approach. However, cellulose and the cellulase enzyme system are relatively immobile in soils (SWIFT et al. 1979, BURNS 1983) so that the synthesis of cellulase may be less sensitive to substrate availability (MANNING & WOOD 1983) than would enzymes specific to more labile C-compounds.

The two soil substrates remarkably differed in their initial nutrient content and therefore differences in the physiological status of the microbial community were expected between the soils. The soil from the Ahr-Eifel should favour autochthonous microorganisms which are highly competitive under nutrient-poor conditions and are capable of surviving unfavourable conditions (K-strategists) (GISI et al. 1997). The soil from the Westerwald was taken close to lying deadwood in a nutrient-rich environment. Under these conditions zymogene microorganisms are supposed to constitute a large part of the microbial community. Zymogene populations (r-strategists) are more competitive under nutrient-rich conditions but less competitive when nutrients are limited. Under nutrient-rich conditions they are supposed to grow faster than K-strategists.

In this study microbial activity was generally higher ($p \leq 0.05$) in series II than in series I after addition of glucose and cellulose at each day of the investigation (fig. III. 18, tab. Appendix-5.1). But relative to the respective control approaches the microbial activity reacted in a almost identical way to glucose and cellulose additions. Therefore it cannot be deduced that there are any differences in the composition or the ecophysiological adaptation of the microbial communities between the two soil substrates.

The results from the microcosm experiments confirmed the findings in the field studies. In both, the field studies and the microcosm experiments, microbial activity was largely influenced by substrate availability. Although there were no indications for microbial nitrogen and phosphorous limitation in the microcosm experiments my results from investigations I-IV and many other studies (SCHEU 1990, JOERGENSEN & SCHEU 1999, EILAND et al. 2001) indicate that not only carbon but also nitrogen and phosphorous availability may be limiting for microorganisms under certain conditions.

Microbial biomass

In many studies the microbial biomass has been shown to be closely related to the availability of substrates (WARDLE 1992, BAUHUS & KHANNA 1999). However, the results from my field investigations indicated that microbial biomass may fail to reflect changes in the nutrient status of the soil. The microcosm experiments supported these findings, at least in some aspects. First of all, microbial biomass was lower in the control of series II than in the control of series I irrespective of the far higher nutrient availability in the soil of series II (fig. III.18, tab. Appendix-5.1). Additionally, there were hardly any changes in the microbial biomass of the control approach from day 1 to day 64 in both series although substrate availability decreased. These results were in contrast to those obtained for the microbial activity and indicate that soil microbial biomass may react unpredictable to the nutrient availability in the soil.

In accordance to the results for the microbial activity the addition of N, P and lignin did not increase the microbial biomass. This may be attributed to the lack of easily degradable carbon sources as described above. Microbial biomass strongly increased after glucose and cellulose addition and continuously decreased after reaching maximum values. Also SHOBHA (2000) found an initial increase of C_{mic} after organic amendments to soil in a laboratory experiment and a corresponding decrease during the course of incubation to the level prior to substrate amendment.

Growth characteristics hardly differed between the two series (fig. III.18). In both series the microbial biomass increased about 2.5-fold only 1 day after glucose addition (tab. Appendix-5.1). However, the increase in microbial C at day 2 was higher in series II than in series I, which may point to a larger proportion of r-strategists in the soil from the Westerwald. Cellulose addition resulted in a retarded two-fold increase in C_{mic} at day 4 compared to day 1 in both series. The retarded microbial growth after cellulose addition compared to glucose addition may again be attributed to the faster degradability of glucose

as already mentioned for the microbial activity. C quality has often reported to impose an overriding constraint on decomposition processes (HOBBIE 2000).

Metabolic quotient (qCO_2)

In both series the qCO_2 reacted in a similar way to nutrient addition as the microbial activity did (fig. III.18). The qCO_2 was generally low in approaches with low C availability (control, N+P) and low C-quality (Lig+N+P) and continuously decreased over the course of the experiments with decreasing substrate availability. The qCO_2 strongly increased following substrate addition and maximum values were obtained the same days as found for the microbial activity. Moreover, the qCO_2-values of the series II were significantly higher ($p \leq 0.05$) than those in series I for all approaches and days. The observed qCO_2 values effects were the result of an over-proportionally higher microbial activity compared to the microbial biomass as a response to higher nutrient availability. Thereby the results of the microcosm experiments reflect the relationships found in the field studies in which an increase of microbial activity due to higher substrate availability was rarely accompanied by an appropriate increase in microbial biomass. These findings are in contrast to the general view that the qCO_2 decreases with increasing substrate quality and that the qCO_2 is higher under unfavourable than under favourable conditions (WOLTERS & JOERGENSEN 1991, BAUHUS et al. 1998). An influence of substrate quality on the metabolic quotient was not evident in my experiments. Glucose and cellulose addition may evoke similar qCO_2-values as shown in the series II but this remains unclear because of the measurement gaps. Moreover it must be kept in mind that the amounts of nutrients added were far higher than occurring under natural conditions.

IV.4 Conclusions

Field studies

According to DORAN & PARKER (1994) soil functions as a medium for plant growth, regulates and partitions water flow and serves as an environmental buffer. Therefore, changes to the soil quality, measured as changes in soil structure, nutrient status and biological activity (KNOEPP et al. 2000), affect the whole ecosystem. SNAKIN et al. (1996) mentioned three main soil quality or conversely degradation indicators: firstly, the physical degradation which is often characterized by the loss of the humus-rich organogenic layer (A-horizon) due to wind and water erosion. Secondly, the chemical degradation which is reflected by nutrient depletion and soil acidification and thirdly the biological degradation of soil which often results in a reduction of the abundance and the activity of the soil biota.
Soil physical, chemical and biotic properties were examined to assess soil degradation in simple oak coppice forests of the Ahr-Eifel under the impact of several abiotic and biotic factors. Many of these factors enhanced soil degradation in terms of soil organic matter loss, nutrient depletion and reduction of biotic activity. Others improved the soil quality. The results of this study imply that the disturbances imposed to the soil have to be divided into "predisposing factors" and "contributing factors" for soil degradation:

❶ Abiotic factors such as slope aspect, slope position and slope gradient predispose oak forests to further disturbances. The results from investigation I indicate that the relief positions "plateau" and "windward" are confronted to higher loads of acid precipitation than leeward sites or foot slopes. Moreover, at relief positions with high slope gradients the potential for soil erosion is enhanced. Hence, at such site conditions the depletion of soil nutrients is stronger than at leeward sites or at low slope gradients.

❷ Contributing factors are those which produce noticeable symptoms in the predisposed soils. The impacts of red deer grazing and trampling and wild boar rooting are regarded as such factors in this study:
At a windward forest site the impact of game trampling and grazing on the soil was noticeable as removed ground vegetation, reduced WRC_{max}, lower content of several soil nutrients, reduced microbial activity and lower abundances of several soil invertebrates when comparing unfenced plots with plots protected from deer access by fencing. Exclusion of deer prevents tree damage and soil disturbance and allows for a fast

regeneration of the protective ground flora. At leeward forest sites game does not produce any noticeable symptoms pointing to enhanced soil degradation. Game can even improve nutrient mineralisation due to the deposition of urine and dung. Nevertheless, lower abundances of several soil arthropods at unfenced plots of any slope aspect support the view that red deer trampling generally imposes a disturbance regime to the soil.

Wild boar grubbing enhances soil degradation by reducing microbial activity, the abundance of several soil arthropods and the contents of several soil nutrients. As the simulation of wild boar grubbing did not include the elimination of soil organisms by feeding, the actual effect of wild boars on the soil biota is supposed to be far higher than observed in this study. I also assume that the effects of wild boar grubbing are pronounced at predisposed windward sites as found for the effects of deer grazing and trampling.

❸ The factors “stand density” and “stand composition” improved soil quality and reduced the risk of soil degradation at windward sites. They represent “opposing factors” to soil degradation in this study:
Reducing the stand density by forest thinning improves soil quality in windward oak stands of the Ahr-Eifel. The combination of downed deadwood and higher insolation on the ground provides conditions with a balanced soil climate, higher food availability and a multitude of protected microhabitats for the decomposing soil biota. At such conditions the growth of the herb layer is promoted and decomposition processes accelerated which results in an enrichment in soil nutrients.

Also the association of hazel with oak in mixed stands improves soil quality. In such mixed stands the forest floor mass, the thickness of the Ah-horizon and the contents of several soil nutrients were increased compared to oak-monocultures. I attribute these effects to the following aspects: Firstly, the presence of hazel below the oak canopy reduces wind and water erosion and therefore prevents the removal of litter and fertile soil from the ground by wind drift and downhill transport. Secondly, hazel litter contains high concentrations of basic cations and is highly palatable for decomposers.

A synthesis on the influence of the different abiotic and biotic factors on soil degradation is illustrated in figure IV.1 on the following page.

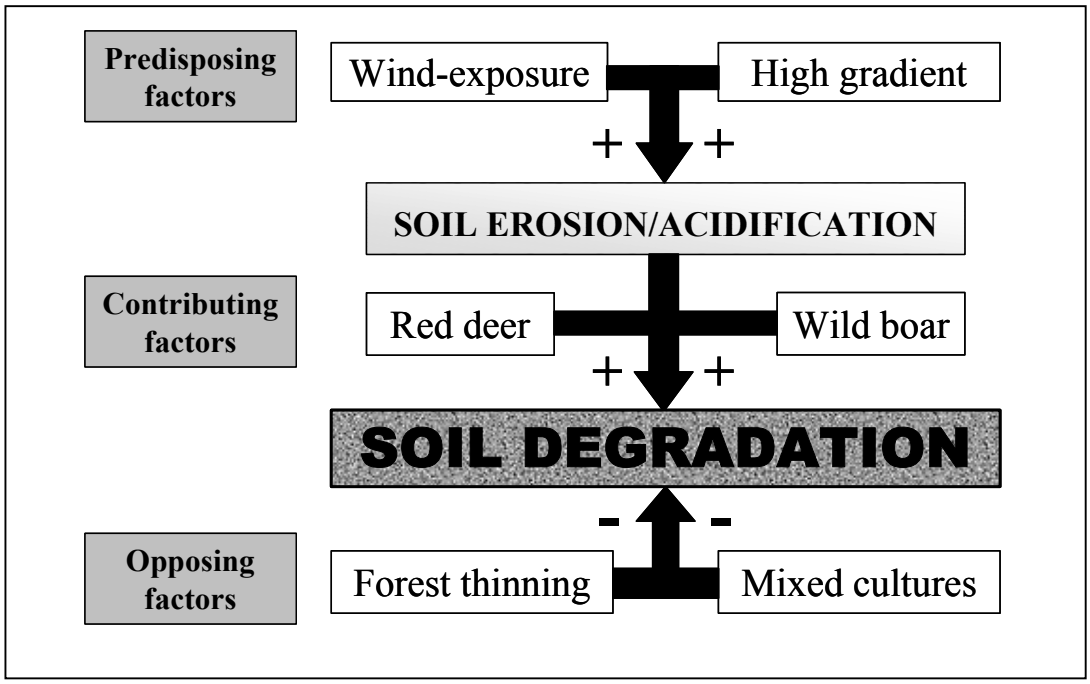


Fig. IV.1: A synthesis on the influence of several factors on soil degradation in simple oak coppice forests of the Ahr-Eifel. Higher rainfall and wind at windward sites, high slope gradient, red deer grazing and trampling and wild boar grubbing enhance (+) soil degradation. Higher solar radiation and lying deadwood at thinned plots and hazel bushes in the understory of oak stands provide conditions that reduce (-) soil degradation.

Microbial properties as indicators for soil quality

From the field studies and the microcosm experiments I derive the conclusion that microbial biomass, the qCO_2 and the ratio of C_{mic} to C_{org} have restrictions as indicators for soil quality or conversely soil degradation in the investigation area.

Microbial biomass reflects nutrient availability on a larger scale (e.g. regional or landscape scale) but is insensitive to various disturbance regimes at the plot scale and therefore fails to constitute an early warning system for soil quality deterioration. Factors like density dependant interactions, predator-pressure and the substrate quality may override the dependency of microbial biomass on nutrient availability. The results from the microcosm experiments underline that even under controlled conditions the C_{mic} does not necessarily reflect nutrient availability.

Also the qCO_2 fails to echo environmental disturbances to the soil and to indicate decreasing substrate quality in the investigation area. Rather, the field studies and the microcosm experiments showed that high qCO_2-values may result from the availability of easily degradable substrates. This can be attributed to the low amplitude of the microbial biomass, relative to the microbial activity following increased substrate availability. The findings of this investigation support the conclusions of WARDLE & GHANI (1995) and

RAUBUCH & BEESE (1999) who found that the qCO_2 is not always a reliable or consistent indicator of disturbance and ecosystem development.
The ratio of C_{mic} to C_{org} clearly fails to predict the danger of soil organic matter loss or nutrient limitation as claimed by SPARLING (1992) and POWLSON et al. (1987). It is therefore not applicable as an indicator of soil degradation in the investigation area either.
From the microbial properties investigated only the microbial activity reflects the soil nutrient status reliably and responds to soil disturbances before changes in the soil nutrient status are detected. However, also microbial activity is very variable in space and time and therefore a high number of replicates at several sampling dates are inevitably to deliver a reliable estimation of forest soil quality.

The results of my study imply that the determination of single soil indices for the assessment of soil quality is not appropriate. Rather, the evaluation of forest soil condition still requires an integrative analyses of various soil properties at different temporal and spatial scales. The soil properties monitored should include soil structure, soil nutrient status, microbial properties and the abundance and diversity of the soil and litter dwelling fauna. Due to the huge variety of forest ecosystems and the multitude of specific interactions that determine ecosystem functioning soil quality indicators may only be applicable for the respective ecosystem examined. The significance of certain indicators for soil quality assessments can not be generalized and must be validated for the respective ecosystem under examination.

IV.5 Implications for forest management

The results of this soil ecological study culminate in a multitude of implications for forest management in order to reduce the risk of soil degradation and oak decline in the investigation area.

First of all, a culling policy that aims to reduce the population density of red deer, but also the densities of moufflons and wild boars, seems to be inevitably to protect the soil from further degradation and to prevent oak decline in the region. This includes stopping supplemental feeding in wintertime.

My studies confirmed that fencing is an appropriate mean to protect trees and the soil from the influence of game. In fenced exclosures the re-settlement of the ground flora is enhanced and retreats and hotspots for the soil biota are provided. Therefore, such fenced exclosures may act as starting points for the successful re-settlement and re-establishment of a diverse flora and fauna in the whole area after game densities have been reduced. However, fenced exclosures are only necessary at locations of high soil degradation potential, which are according to my results steep and windward slopes at upper slope positions. Moreover, it is important to exclude both, grazing herbivores and wild boars because grubbing deteriorates the soil quality in sloping forest sites.

A moderate reduction of stand density by forest thinning was demonstrated to enhance the growth of the ground vegetation and to support decomposition processes in the soil. To achieve the observed effects it is crucially important to leave the fallen trunks at the site. Coarse woody debris improve the soil climate, increase the habitat diversity for the soil biota and improve the nutrient status of the soils. It may be favourable to position the trunks perpendicular to the slope to trap litter, reduce soil organic matter erosion and to allow for organic matter accumulation. To a certain degree fallen deadwood also protects herbs from grazing and trampling. It has been claimed that red deer when moving uphill avoid jumping even over small barriers (WÖLFEL & MEIßNER 2002).

Finally, the association of hazel with oak improved soil quality in the observed oak forests. Therefore mixed stands should be favoured over oak-monocultures. In particular, the growth of shrubs and trees exhibiting highly palatable and base-rich litter should be supported to ensure a sustainable nutrient supply of simple oak coppice forests at the investigation area.

Implikationen für die Waldbewirtschaftung

Aus der vorliegenden bodenökologischen Studie lassen sich verschiedene waldbauliche Maßnahmen ableiten, mit denen der Gefahr einer fortschreitenden Bodendegradation und damit einer nachhaltigen Schädigung der aufstockenden Eichen-Bestände entgegengetreten werden kann.

Eine der wichtigsten Vorraussetzungen scheint mir eine Jagdpolitik zu sein, die darauf abzielt, die Bestände von Rot-, Schwarz- und Muffelwild auf Populationsdichten zurückzuführen, die der Tragfähigkeit des Lebensraumes entsprechen. Hierzu müssen auch Zufütterungen, vor allem in den Wintermonaten, unterbleiben.

Die Gatterung von Waldflächen stellt ein geeignetes Mittel dar, um Baum und Boden vor dem Einfluss des Wildes zu schützen. In eingezäunten Flächen erfolgt ein rasches Wachstum der Boden-Vegetation, wodurch Nischen geschaffen werden, in denen die Bodenfauna verbesserte Umweltbedingungen vorfindet. Eingezäunte Waldflächen könnten demnach für zahlreiche Pflanzen- und Tierarten Rückzugsgebiete darstellen, von denen aus, nach einer Reduzierung der Wilddichte, eine Wiederbesiedlung des gesamten Untersuchungsgebietes erfolgen kann. Wild-Gatter sind aber nur dort notwendig, wo das Potential für Bodendegradation sehr hoch ist. Den vorliegenden Ergebnissen zufolge sind dies steile und wind-exponierte Standorte im oberen Hangbereich. Es ist überdies wichtig, bei der Gatterung auch Schwarzwild auszuschließen, da deren Wühlaktivität in Hanglagen eine Verschlechterung der Bodenqualität zur Folge hat.

Eine moderate Auflichtung von Eichen-Beständen beschleunigt das Wachstum der Bodenvegetation und fördert Dekompositionsprozesse im Boden. Das Belassen von Totholz in den aufgelichteten Beständen stellt hierbei eine wichtige Komponente für die Verbesserung der Bodenqualität dar. Liegendes Totholz verbessert das Bodenklima, erhöht die Strukturvielfalt für Bodenlebewesen, fördert die Nährstoffanreicherung im Boden und schützt überdies vor zu starker Begehung durch Rot- und Schwarzwild (WÖLFEL & MEIßNER 2002). Quer zur Hangrichtung positionierte Baumstämme könnten zudem Bodenerosion vermindern und die Akkumulation organischen Materials fördern.

Schließlich wirkt sich auch eine Vergesellschaftung von Eiche mit Hasel positiv auf die Bodenqualität in Eichen-Wäldern aus. Aus diesem Grund empfiehlt sich die Förderung von Eichen-Mischbeständen gegenüber Eichen-Monokulturen. Vor allem Baum- und Straucharten mit einer leicht zersetzbaren und nährstoffreichen Streu sollten hierbei Berücksichtigung finden, um in dem Untersuchungsgebiet eine nachhaltige Sicherung der Nährelementversorgung aufstockender Eichen-Niederwälder zu gewährleisten.

V Summary

Simple oak coppice forests of the Ahr-Eifel are confronted with extensive soil degradation. Four complementary investigations were conducted to study the impact of the environmental factors “relief position”, “slope gradient”, “red deer”, “wild boar”, “stand density” and “stand composition” on soil degradation in the investigation area. Soil quality was assessed determining several physical, chemical and biotic soil properties in the upper soil (Ah-horizon) of twelve different oak forest sites.

Relief position and slope gradient influenced soil degradation in the investigation area. The content of basic cations (K^+, Ca^{2+}, Mg^{2+}) was significantly lower, the content of Al^{3+} significantly higher at leeward slopes than at windward slopes. Soil nutrient contents were lower and the Al^{3+} content higher at the slope position “plateau” and at sites with high slope gradients than at the foot slope and sites with low inclinations.

Red deer grazing and trampling enhanced soil degradation at a windward forest site. Soil moisture, water retention capacity (WRC_{max}), nutrient availability and microbial activity were lower under the impact of red deer than in fenced exclosures. Opposite tendencies were found at a leeward forest site. The content of several soil nutrients and microbial characteristics were higher outside the fenced exclosure. The abundance of several soil invertebrates was clearly reduced at the unfenced plots of both slope aspects.

Simulated wild boar grubbing affected soil organisms and the soil nutrient status in a leeward forest site. Microbial activity and the abundance of several soil arthropods were noticeably lower at grubbed plots compared to ungrubbed control plots. Consequently, the content of basic cations and exchangeable phosphate were reduced at such grubbed plots. No effects of wild boar grubbing were found on soil texture or on the content of C_{org} and N_t.

Reducing the stand density by forest thinning resulted in an increased accumulation of organic matter compared to that of dense plots. As a result, thinned plots exhibited higher contents of most of the observed soil nutrients, higher WRC_{max}, higher microbial activity and higher abundances of many soil invertebrates than dense plots did.

A comparison of oak-monocultures with mixed oak-hazel stands revealed a positive influence of hazel on soil quality. The Ca^{2+}, Mg^{2+} and PO_4^{3-} contents were higher and the Al^{3+} content was lower in soils of mixed stands than in corresponding oak-monocultures. The forest floor mass and the thickness of the A-horizon were greater in mixed cultures but

the contents of C_{org} and N_t and the C/N-ratio did not differ among the sites. The soil biota was hardly influenced by stand composition.

In a second approach I evaluated the possibility that microbial properties are indicative for soil quality deterioration in simple oak coppice forests of the Ahr-Eifel. Microbial activity, microbial biomass-C (C_{mic}), metabolic quotient (qCO_2) and the ratio of microbial C to soil organic carbon (C_{mic}/C_{org}) have all been proposed to be indicators for soil quality in many studies and are supposed to constitute an early warning system for soil deterioration. In addition to the field, studies two consecutive microcosm experiments were conducted to investigate the effects of nutrient availability on soil microbial properties.
In both the field studies and the microcosm experiments, the microbial activity was closely related to the soil nutrient status and reacted sensitive to soil disturbance regimes. In contrast, microbial biomass did not consistently reflect nutrient availability. None of the environmental factors tested in the field studies exerted a non-ambiguous influence on soil microbial biomass. Hence, C_{mic} was in most cases not correlated to the contents of C_{org}, N_t and PO_4^{3-} when regarding the investigations separately. Moreover, C_{mic} was lower in nutrient-rich than in nutrient-poor soil substrate in the microcosm experiment controls. However, addition of glucose and cellulose to the soil substrates generally increased C_{mic}. The qCO_2 tended to be higher under favourable than under unfavourable soil conditions in the field studies. In addition, the qCO_2 increased with higher nutrient availability in the microcosm experiments. The C_{mic}/C_{org}-ratio was negatively correlated to the C_{org} content and therefore high in soils subjected to disturbance regimes following nutrient depletion and low at plots with accumulation of easily degradable organic compounds.
These results suggest that only microbial activity reflects the soil nutrient status reliably. Microbial biomass, qCO_2 and the C_{mic}/C_{org}-ratio can fail to echo environmental disturbances and to predict the danger of soil organic matter loss or nutrient limitation, a result which conflicts with findings from previous studies.

Zusammenfassung

Eichen-Niederwälder der Ahr-Eifel sind großflächig von Boden-Degradation betroffen. Ich führte vier komplementäre Freiland-Untersuchungen durch, um den Einfluss der Umweltfaktoren „Reliefposition“, „Hangneigung“, „Rotwild“, „Schwarzwild“, „Bestandesdichte“ und „Bestandeszusammensetzung“ auf Boden-Degradation im

Untersuchungsgebiet aufzuklären. Insgesamt wurde in 12 verschiedenen Waldflächen die Bodenqualität durch die Erfassung zahlreicher physikalischer, chemischer und mikrobiologischer Bodeneigenschaften (Ah-Horizont) bestimmt. Zusätzlich wurde die Abundanz der Bodenmesofauna, der Streu bewohnenden Makrofauna und die Mächtigkeit der Streuauflage erfasst.

Reliefposition und Hangneigung beeinflussten Boden-Degradation im Untersuchungsgebiet. Die Gehalte basischer Kationen (K^+, Ca^{2+}, Mg^{2+}) waren im Oberboden von Lee-Flächen signifikant höher, der Al^{3+}-Gehalt signifikant niedriger als in Luv-Flächen. In Plateaulage und in steilen Hangbereichen waren zahlreiche Nährstoff-Gehalte niedriger und der Al^{3+}-Gehalt höher als am Hangfuß oder in gering geneigten Waldflächen.

Rotwild-Äsung und –Vertritt verstärkten Boden-Degradation in einer Luv-Fläche. Bodenfeuchte, maximale Wasserhaltekapazität (WHK_{max}), Nährstoff-Verfügbarkeit und mikrobielle Aktivität waren unter dem Einfluss von Rotwild niedriger als in gegatterten Parzellen. In einer Lee-Fläche ergaben sich gegensätzliche Ergebnisse. Die Gehalte einiger Nährstoffe und mikrobielle Kenngrößen waren außerhalb des Gatters erhöht. Die Abundanz zahlreicher Bodeninvertebraten war unabhängig von der Exposition stets außerhalb des Gatters niedriger.

Boden-Bioturbation durch die simulierte Wühlaktivität von Schwarzwild beeinträchtigte Bodenorganismen und Nährstoff-Gehalte in einer SO-exponierten Waldfläche. Mikrobielle Aktivität und die Abundanz zahlreicher Bodenarthropoden waren in durchwühlten Parzellen deutlich niedriger als in Kontroll-Parzellen. Entsprechend zeigten sich auch der Phosphat-Gehalt (PO_4^{3-}) und der Gehalt basischer Nährionen im Oberboden umgegrabener Parzellen deutlich erniedrigt. Auf die Bodentextur und die Gehalte organischen Kohlenstoffs (C_{org}) und Gesamt-Stickstoffs (N_t) wirkte sich die Bioturbation des Bodens allerdings nicht aus.

Eine Erniedrigung der Bestandesdichte durch forstliche Auflichtungsmaßnahmen verringerte den erosiven Abtrag organischer Bodenschichten. Folglich waren WHK_{max}, mikrobielle Aktivität, die Abundanz zahlreicher Bodenarthropoden und die Gehalte fast aller untersuchten Nährstoffe in den aufgelichteten Beständen deutlich höher als in den dichten Beständen.

Ein Vergleich von Eichen-Monokulturen und Eiche-Hasel-Mischbeständen deutete auf einen positiven Einfluss von Hasel auf die Bodenqualität hin. Die Gehalte an Ca^{2+}, Mg^{2+} und PO_4^{3-} waren in Mischbeständen höher, der Al^{3+}-Gehalt hingegen niedriger als in vergleichbaren Monokulturen. Auch die Streumenge und die Mächtigkeit des

Ah-Horizontes waren in den Mischkulturen deutlich erhöht, ohne sich jedoch auf die Gehalte an C_{org} und N_t auszuwirken. Die Bodenorganismen zeigten sich von der Bestandeszusammensetzung weitestgehend unbeeinflusst.

In einem zweiten Schwerpunkt dieser Studie wurde überprüft, ob mikrobielle Parameter geeignete Indikatoren für Bodenzustandserhebungen in Eichen-Niederwäldern darstellen. Mikrobielle Aktivität, mikrobielle Biomasse (C_{mic}), metabolischer Quotient (qCO_2) und das Verhältnis von C_{mic} zu C_{org} (C_{mic}/C_{org}) wurden in zahlreichen Untersuchungen als Indikatoren für Bodenqualität vorgeschlagen und sollen ein geeignetes Frühwarnsystem für Nährstoff-Verluste im Boden darstellen. In Ergänzung zu den Freiland-Untersuchungen führte ich zwei aufeinanderfolgende Mikrokosmos-Experimente durch, um den Einfluss der Nährstoff-Verfügbarkeit auf mikrobielle Kenngrößen zu ermitteln.
Die mikrobielle Aktivität zeigte sich sowohl in den Freiland-Untersuchungen als auch in den Labor-Experimenten deutlich vom Nährstoff-Angebot beeinflusst. Im Gegensatz dazu spiegelte die mikrobielle Biomasse die Nährstoff-Situation im Boden nicht zuverlässig wieder. Keiner der untersuchten Umweltfaktoren übte einen eindeutigen Einfluss auf den mikrobiellen C-Gehalt aus. Entsprechend konnte in den jeweiligen Freiland-Untersuchungen meist keine signifikante Korrelation zu den Gehalten an C_{org}, N_t und PO_4^{3-} ermittelt werden. Auch in den Mikrokosmos-Experimenten wurden in nährstoffreichen Bodensubstraten meist niedrigere C_{mic}-Werte ermittelt als in nährstoffarmen Bodensubstraten. Allerdings führte die Zugabe von Glucose und Cellulose generell zu einem starken Anstieg von C_{mic}. Der qCO_2 war in den Freiland-Untersuchungen unter günstigen Bodenbedingungen meist höher als in degradierten Böden. Auch in den Mikrokosmos-Versuchen bewirkte eine höhere Nährstoff-Verfügbarkeit einen Anstieg der qCO_2-Werte. Das C_{mic}/C_{org} Verhältnis war negativ mit dem C_{org}-Gehalt korreliert. Demnach wurden in gestörten Böden mit Nährstoff-Verlusten höhere Werte nachgewiesen als in Flächen, die durch Nährstoff-Akkumulation gekennzeichnet waren.
Diese Ergebnisse deuten an, dass nur die mikrobielle Aktivität die Nährstoff-Situation in Böden verlässlich wiedergibt. Mikrobielle Biomasse, qCO_2 und das C_{mic}/C_{org}-Verhältnis waren in der vorliegenden Untersuchung ungeeignet als Bodenzustands-Indikatoren. Im Gegensatz zu früheren Untersuchungen reagierten sie weder auf Bodenstörung, noch reflektierten sie den Rückgang organischer und mineralischer Nährstoffe im Boden.

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VII Appendix

Abbreviations used

µg	µ-gram
2/3/4	Low level/medium level/high level (categories according to the German DIN 4220)
Al^{3+}	Aluminium-ion
ANOVA/ANCOVA	Analysis of variance/covariance
B	Bioturbation
bdh	Diameter at breast height
C	Control series
C	Carbon
C/N	Carbon to nitrogen ratio
Ca^{2+}	Calcium-ion
Cell	Cellulose
cm	Centimeter
C_{mic}	Microbial carbon
C_{org}	Organic carbon
d	Dense
E	Extinction
F/f	Fenced
Fig.	Figure
g	gram
Glu	Glucose
h	hour
ha	hectare
Ind.	Individual
Jul	July
K^{+}	Potassium-ion
kg	kilogram
L/l	Loam/loamy (categories according to the German DIN 4220)
Lee	Leeward
Lig	Lignin
Luv	Windward
m	Meter
MAD	Median absolute deviation
Mg^{2+}	Magnesium-ion
Mix	Mixed stand
mm	Millimeter
Mono	Monoculture
N	Nitrogen
n	Number of replicates
ns	Not significant
Nt	Total nitogen
Oct	October
p	Level of significance
PO_4^{3-}	Phosphate
Prop.	properties
Q.	Quercus
qCO_2	Metabolic quotient/specific microbial activity
r	Correlation coefficient
R^2	Measure of certainty
S/s	Sand/sandy (categories according to the German DIN 4220)
t	Thinned
T/t	Clay/clayey (categories according to the German DIN 4220)
Tab.	Table
U/u	Unfenced
U/u	Silt/silty (categories according to the German DIN 4220)
WRC_{max}	Maximum water retention capacity

VII.1 Investigation I

Tab. Appendix-1.1: Soil chemical characteristics of four different windward and leeward sites at the sampling dates July 1999, October 2001, May 2002 and October 2002.

		windward				leeward			
	month/site	**I**	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**
pH (1 M KCl)	Jul 99	3.7 ± 0.0	3.6 ± 0.1	3.6 ± 0.0	3.7 ± 0.0	4.8 ± 0.1	3.6 ± 0.1	3.7 ± 0.1	4.3 ± 0.2
	Oct 01	3.5 ± 0.0	3.3 ± 0.1	3.5 ± 0.1	3.6 ± 0.0	4.8 ± 0.2	3.3 ± 0.1	3.3 ± 0.1	3.9 ± 0.2
	May 02	3.5 ± 0.1	3.4 ± 0.1	3.5 ± 0.0	3.6 ± 0.0	4.8 ± 0.2	3.4 ± 0.1	3.4 ± 0.1	3.6 ± 0.1
	Oct 02	3.6 ± 0.1	3.5 ± 0.1	3.8 ± 0.1	3.9 ± 0.0	5.4 ± 0.1	3.5 ± 0.1	3.6 ± 0.0	4.0 ± 0.2
Al [mg/kg]	Jul 99	127 ± 23	122 ± 20	514 ± 104	369 ± 38	17 ± 2	218 ± 95	201 ± 68	37 ± 10
	Oct 01	426 ± 83	309 ± 54	511 ± 54	474 ± 55	65 ± 10	570 ± 144	478 ± 165	121 ± 48
	May 02	264 ± 48	66 ± 10	412 ± 20	351 ± 58	32 ± 9	162 ± 80	278 ± 53	95 ± 26
	Oct 02	473 ± 49	189 ± 43	474 ± 52	481 ± 37	28 ± 2	332 ± 53	433 ± 76	181 ± 121
Ca^{2+} [mg/g]	Jul 99	1.7 ± 0.4	1.7 ± 0.2	1.4 ± 0.2	0.5 ± 0.2	2.7 ± 0.3	1.8 ± 0.3	2.0 ± 0.2	1.3 ± 0.2
	Oct 01	1.4 ± 0.3	1.6 ± 0.2	0.9 ± 0.2	0.4 ± 0.1	3.1 ± 0.6	1.6 ± 0.4	1.8 ± 0.4	2.2 ± 0.5
	May 02	1.2 ± 0.2	1.7 ± 0.3	0.6 ± 0.1	0.6 ± 0.3	2.9 ± 0.7	1.6 ± 0.3	1.0 ± 0.3	1.5 ± 0.2
	Oct 02	0.5 ± 0.3	1.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	2.2 ± 0.1	1.3 ± 0.2	1.0 ± 0.3	1.1 ± 0.3
Mg^{2+} [µg/g]	Jul 99	344 ± 52	245 ± 37	219 ± 34	112 ± 42	422 ± 31	271 ± 35	358 ± 34	209 ± 43
	Oct 01	214 ± 72	230 ± 20	112 ± 48	103 ± 20	395 ± 70	176 ± 44	235 ± 37	210 ± 58
	May 02	142 ± 23	167 ± 18	51 ± 20	51 ± 7	292 ± 86	137 ± 26	127 ± 43	102 ± 8
	Oct 02	132 ± 29	138 ± 19	51 ± 21	54 ± 50	284 ± 29	128 ± 11	126 ± 7	99 ± 27
K^{+} [µg/g]	Jul 99	1100 ± 156	778 ± 155	818 ± 58	950 ± 72	1896 ± 273	1651 ± 476	930 ± 128	1238 ± 103
	Oct 01	427 ± 38	315 ± 18	286 ± 50	280 ± 46	727 ± 100	384 ± 50	394 ± 66	429 ± 49
	May 02	607 ± 145	371 ± 59	202 ± 46	311 ± 49	820 ± 165	453 ± 28	271 ± 54	597 ± 100
	Oct 02	201 ± 14	171 ± 30	175 ± 32	161 ± 31	544 ± 27	246 ± 20	204 ± 32	235 ± 18

Tab. Appendix-1.2: Results of Mann-Whitney-U-tests. Presented are the p-values of various test-combinations. It was tested for differences between windward (Luv) and leeward (lee) sites at all sampling dates and for differences between the sampling dates at each slope aspect.

Investigation I		**pH**	**Al^{3+}**	**Ca^{2+}**	**Mg^{2+}**	**K^{+}**
tests				p-values		
Luv/Lee	Jul 99	0.001	0.000	0.000	0.000	0.000
Luv/Lee	Oct 01	0.081	0.155	0.000	0.012	0.001
Luv/Lee	May 02	0.113	0.000	0.000	0.003	0.005
Luv/Lee	Oct 02	0.164	0.000	0.000	0.000	0.000
Jul 99/Oct 01	Luv	0.000	0.002	0.324	0.778	0.000
	Lee	0.016	0.000	0.456	0.052	0.000
Jul 99/May 02	Luv	0.000	0.697	0.725	0.007	0.000
	Lee	0.001	0.212	0.100	0.000	0.000
Jul 99/Oct 02	Luv	0.280	0.005	0.012	0.001	0.000
	Lee	0.466	0.005	0.001	0.000	0.000
Oct 01/May 02	Luv	0.930	0.000	0.091	0.000	0.752
	Lee	0.957	0.001	0.044	0.000	0.196
Oct 01/Oct 02	Luv	0.000	0.925	0.000	0.000	0.000
	Lee	0.037	0.053	0.000	0.000	0.000
May 02/Oct 02	Luv	0.000	0.000	0.000	0.502	0.000
	Lee	0.010	0.072	0.058	0.888	0.000

Tab. Appendix-1.3: Microbial properties (activity, biomass, qCO_2, C_{mic}/C_{org}) and the contents of organic carbon (Corg), total nitrogen (Nt) and phosphate-P (PO_4^{3-}P) at the different windward and leeward sites of the investigation I. Presented are median and MAD (n = 8) of the sampling date July 1999.

Properties	**windward**				**leeward**			
site	**I**	**II**	**III**	**IV**	**I**	**II**	**III**	**IV**
Microb. act. [mg CO_2-C/(g*h)]	8.4 ± 1.4	10.1 ± 2.3	3.0 ± 1.0	3.4 ± 1.9	3.9 ± 0.4	6.6 ± 1.9	12.2 ± 2.4	6.1 ± 1.8
C_{mic} [mg C_{mic}/g]	2.8 ± 0.5	1.6 ± 0.2	1.1 ± 0.3	1.3 ± 0.3	1.2 ± 0.1	1.6 ± 0.2	5.7 ± 1.2	2.9 ± 0.4
qCO_2 [mg CO2-C(g Cmic*h)]	3.3 ± 0.4	7.1 ± 1.7	2.7 ± 0.5	2.5 ± 0.6	3.4 ± 0.1	4.2 ± 0.5	2.1 ± 0.3	2.2 ± 0.2
C_{mic}/C_{org} [%]	3.7 ± 0.7	8.0 ± 1.5	4.9 ± 1.5	2.3 ± 0.5	3.0 ± 0.7	3.8 ± 2.0	3.4 ± 0.7	1.7 ± 1.0
C_{org} [%]	7.7 ± 3.4	12.6 ± 4.0	5.1 ± 2.1	2.3 ± 0.7	3.5 ± 1.1	6.4 ± 1.7	20.9 ± 2.5	3.7 ± 2.9
N_t [mg/g]	9.6 ± 2.1	7.8 ± 1.3	3.9 ± 0.6	3.9 ± 0.9	4.5 ± 0.6	7.3 ± 0.7	11.6 ± 0.4	4.5 ± 0.8
PO_4^{3-}-P [µg/g]	95.9 ± 12.4	104.4 ± 9.1	19.3 ± 2.0	26.0 ± 4.6	72.6 ± 4.8	166.0 ± 32.2	91.4 ± 9.6	37.7 ± 11.8

VII.2 Investigation II

Tab. Appendix-2.1: Soil characteristics of the investigation plots Ud, Ut, Fd and Ft of investigation II at the spring sampling dates April 2002 and May 2003. Presented are median and MAD (n = 10).

spring	**April 02**				**May 03**			
plots:	**Ud**	**Ut**	**Fd**	**Ft**	**Ud**	**Ut**	**Fd**	**Ft**
Soil pH (1M KCl)	5.4 ± 0.3	4.1 ± 0.2	5.0 ± 0.3	4.5 ± 0.3	4.9 ± 0.3	4.2 ± 0.2	5.3 ± 0.2	4.7 ± 0.3
Soil moisture [% w/w]	16.5 ± 5.2	31.7 ± 3.3	26.1 ± 4.3	39.2 ± 5.1	11.3 ± 3.1	40.3 ± 5.1	34.0 ± 2.8	39.0 ± 2.8
WRC_{max} [% w/w]	45.0 ± 2.3	58.4 ± 0.8	55.1 ± 0.8	62.2 ± 5.4	41.7 ± 0.8	51.9 ± 2.8	53.2 ± 4.0	57.4 ± 1.5
Litter [g/300 cm²]	0.0 ± 0.0	8.7 ± 6.8	2.2 ± 1.8	20.3 ± 11.3	0.0 ± 0.0	13.3 ± 4.8	23.2 ± 3.6	24.6 ± 4.2
C/N-ratio	25.0 ± 2.5	25.4 ± 4.4	19.6 ± 2.2	20.7 ± 2.8	15.8 ± 0.7	14.0 ± 1.1	14.1 ± 1.6	12.9 ± 0.6
C_{org} [%]	8.6 ± 0.8	12.3 ± 1.2	10.0 ± 1.1	13.3 ± 2.1	4.5 ± 0.4	9.0 ± 0.5	7.8 ± 1.5	9.2 ± 1.6
N_t [mg/g]	3.3 ± 0.4	5.4 ± 0.4	5.3 ± 0.5	6.7 ± 0.3	2.9 ± 0.4	6.7 ± 3.3	5.7 ± 1.6	7.4 ± 0.7
PO_4^{3-}-P [µg/g]	12.7 ± 1.9	40.2 ± 8.4	28.5 ± 4.6	67.3 ± 12.4	14.5 ± 2.9	66.8 ± 17.3	35.4 ± 9.6	87.4 ± 5.0
K^+ [µg/g]	965 ± 245	1053 ± 115	800 ± 73	1218 ± 125	294 ± 21	364 ± 36	504 ± 40	334 ± 46
Mg^{2+} [µg/g]	915 ± 103	788 ± 68	1078 ± 105	943 ± 190	490 ± 38	460 ± 75	813 ± 98	725 ± 160
Ca^{2+} [mg/g]	2.1 ± 0.4	2.4 ± 0.3	2.8 ± 0.5	3.0 ± 0.5	1.6 ± 0.2	2.3 ± 0.2	3.2 ± 0.5	3.8 ± 0.7
Micr. act. [mg CO_2-C/(g*h)]	1.7 ± 0.9	2.9 ± 0.7	2.2 ± 1.0	4.3 ± 1.5	3.0 ± 0.5	7.4 ± 1.4	5.7 ± 1.3	7.8 ± 1.2
Micr. biomass [mg C_{mic}/g]	1.8 ± 0.6	2.5 ± 0.2	2.2 ± 0.3	2.3 ± 0.3	1.8 ± 0.8	3.0 ± 0.3	2.8 ± 0.3	2.9 ± 0.2
qCO_2 [mg CO_2-C(g C_{mic}*h)]	0.9 ± 0.3	1.2 ± 0.3	0.9 ± 0.3	1.8 ± 0.4	1.6 ± 0.1	2.4 ± 0.2	2.1 ± 0.4	2.7 ± 0.6
C_{mic}/C_{org}-ratio [%]	2.3 ± 0.5	1.8 ± 0.2	2.0 ± 0.3	2.6 ± 0.7	4.0 ± 0.1	3.3 ± 0.6	3.6 ± 0.2	3.3 ± 0.3

Tab. Appendix-2.2: Soil characteristics of the investigation plots Ud, Ut, Fd and Ft (investigation II) at the spring sampling dates April 2002 and May 2003. Presented are median and MAD (n = 10).

autumn	**September 01**				**October 02**			
plots:	**Ud**	**Ut**	**Fd**	**Ft**	**Ud**	**Ut**	**Fd**	**Ft**
Soil pH (1M KCl)	4.7 ± 0.2	4.5 ± 0.3	4.8 ± 0.3	4.4 ± 0.2	5.4 ± 0.3	4.1 ± 0.2	5.0 ± 0.3	4.5 ± 0.3
Soil moisture [% w/w]	17.9 ± 1.2	29.9 ± 3.2	29.4 ± 2.2	33.3 ± 5.6	22.4 ± 2.3	35.9 ± 1.8	32.6 ± 3.0	41.4 ± 3.2
WHC_{max} [% w/w]	44.2 ± 0.7	62.2 ± 3.1	60.4 ± 0.2	61.5 ± 2.5	44.1 ± 0.3	58.0 ± 0.9	57.0 ± 2.6	64.6 ± 0.8
Litter [g/300 cm²]	3.6 ± 2.1	12.9 ± 9.9	0.8 ± 0.5	1.3 ± 0.7	0.8 ± 0.6	15.1 ± 3.0	14.8 ± 5.8	14.7 ± 4.8
C/N-ratio	13.3 ± 1.1	11.8 ± 1.2	11.9 ± 1.4	11.8 ± 0.7	17.6 ± 1.7	18.3 ± 1.2	17.0 ± 2.5	18.6 ± 1.1
C_{org} [%]	6.6 ± 0.8	12.1 ± 2.2	13.3 ± 1.1	14.4 ± 1.8	4.8 ± 0.6	11.4 ± 2.9	8.3 ± 1.9	11.7 ± 0.6
N_t [mg/g]	3.0 ± 0.1	6.3 ± 1.2	6.1 ± 0.3	7.1 ± 0.7	2.9 ± 0.3	5.8 ± 1.3	5.4 ± 1.0	6.3 ± 0.7
PO_4^{3-}-P [µg/g]	11.1 ± 0.8	32.8 ± 9.4	30.9 ± 10.4	57.1 ± 5.7	10.8 ± 1.2	30.6 ± 8.0	22.0 ± 5.9	61.1 ± 8.8
K^+ [µg/g]	1390 ± 428	1058 ± 168	1360 ± 355	1708 ± 413	297 ± 27	288 ± 58	448 ± 18	474 ± 78
Mg^{2+} [µg/g]	645 ± 38	755 ± 98	973 ± 128	965 ± 98	438 ± 23	313 ± 85	550 ± 56	540 ± 60
Ca^{2+} [mg/g]	2.0 ± 0.2	3.1 ± 0.1	2.9 ± 0.4	3.0 ± 0.5	1.6 ± 0.2	2.6 ± 0.4	2.3 ± 0.3	3.0 ± 0.4
Micr. act. [mg CO_2-C/(g*h)]	1.8 ± 0.3	6.0 ± 1.4	6.0 ± 0.6	6.0 ± 0.8	1.5 ± 0.1	3.5 ± 0.6	3.2 ± 0.5	4.7 ± 0.9
Micr. biomass [mg C_{mic}/g]	2.1 ± 0.1	3.1 ± 0.5	2.6 ± 0.2	2.5 ± 0.2	1.9 ± 0.1	2.2 ± 0.3	2.3 ± 0.3	2.0 ± 0.2
qCO_2 [mg CO_2-C/(g C_{mic}*h)]	0.9 ± 0.2	1.9 ± 0.3	2.2 ± 0.2	2.4 ± 0.4	0.8 ± 0.1	1.7 ± 0.4	1.3 ± 0.2	2.2 ± 0.3
C_{mic}/C_{org}-ratio [%]	3.2 ± 0.2	2.6 ± 0.1	1.9 ± 0.2	2.6 ± 0.9	3.8 ± 0.2	2.2 ± 0.4	2.9 ± 0.7	2.6 ± 0.7

Tab. Appendix-2.3: Abundances of the soil invertebrates at the investigation plots Ud, Ut, Fd and Ft of investigation II. Presented are the median ± MAD values of individuals/sample size with the calculated median values of individuals/m² in brackets (n = 36).

Soil fauna	**Ud**	**Ut**	**Fd**	**Ft**
Med ± MAD; ind./31.2 cm² (m²)				
Collembola, total	8 ± 6 (2567)	13 ± 8 (4010)	14 ± 11 (5294)	11 ± 8 (3529)
Entomobryidae	0 ± 0	1 ± 1 (321)	1 ± 1 (321)	2 ± 2 (642)
Isotomidae	1 ± 1 (321)	1 ± 1 (321)	4 ± 3 (1283)	2 ± 2 (481)
Hypogastruridae	1 ± 1 (321)	0 ± 0	1 ± 1 (321)	0 ± 0
Onychiuridae	3 ± 3 (962)	3 ± 3 (802)	6 ± 6 (1765)	2 ± 2 (642)
Sminthuridae	0 ± 0	1 ± 1 (321)	0 ± 0	1 ± 1 (321)
Coll. biomass µg (mg)	76 ± 57 (24.4)	211 ± 182 (67.8)	227 ± 196 (72.7)	170 ± 21 (54.4)
Acari				
Oribatidae	5 ± 3 (1604)	8 ± 5 (2406)	13 ± 12 (4010)	6 ± 3 (1765)
Gamasidae/Parasitif.	6 ± 4 (1765)	6 ± 3 (1925)	8 ± 6 (2564)	7 ± 4 (2085)
Mesoarthropoda, total	17 ± 9 (5294)	23 ± 14 (7218)	42 ± 20 (13314)	23 ± 10 (7218)
Med ± MAD; ind./55.4 cm² (m²)				
Enchytraeidae	1 ± 1 (180)	35 ± 24 (6225)	35 ± 28 (6225)	75 ± 45 (13533)
Med ± MAD; ind./300 cm² (m²)				
Coleoptera, total	0 ± 0	1 ± 1 (33)	1 ± 1 (33)	3 ± 2 (100)
Coleoptera larvae	0 ± 0	0 ± 0	1 ± 1 (33)	2 ± 2 (67)
Coleoptera adults	0 ± 0	0 ± 0	0 ± 0	1 ± 1 (33)
Arachnidae	0 ± 0	0 ± 0	0 ± 0	1 ± 1 (33)
Chilopoda	0 ± 0	0 ± 0	0 ± 0	1 ± 1 (33)
Isopoda	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Diplopoda	0 ± 0	0 ± 0	0 ± 0	1 ± 1 (33)
Macrofauna, total	0 ± 0	7 ± 4 (233)	1 ± 1 (33)	16 ± 7 (515)

VII.3 Investigation III

Tab. Appendix-3.1: Soil characteristics of the investigation plots Cf, Bf, Cu and Bu (investigation III) at the sampling dates April and October of the year 2001. Presented are median and MAD (n = 10).

2001	**April**				**October**			
plots:	**Cu**	**Bu**	**Cf**	**Bf**	**Cu**	**Bu**	**Cf**	**Bf**
Soil pH (1M KCl)	3.3 ± 0.1	3.2 ± 0.0	3.4 ± 0.1	3.3 ± 0.0	3.4 ± 0.1	3.3 ± 0.0	3.6 ± 0.1	3.6 ± 0.1
Soil moisture [% w/w]	48.3 ± 2.8	43.1 ± 2.8	41.2 ± 3.0	34.3 ± 2.7	30.3 ± 1.5	32.5 ± 4.2	21.7 ± 3.1	25.3 ± 4.7
WRC_{max} [% w/w]	64.4 ± 1.7	65.6 ± 0.8	62.4 ± 2.2	59.8 ± 2.2	63.8 ± 3.3	64.2 ± 2.4	55.6 ± 3.8	57.6 ± 1.3
Litter [g/300 cm²]	15.2 ± 7.8	12.9 ± 2.6	13.6 ± 3.2	9.4 ± 5.3	9.2 ± 3.4	3.5 ± 1.0	4.3 ± 0.8	1.8 ± 0.5
C/N-ratio	16.1 ± 2.1	14.9 ± 3.2	12.1 ± 1.4	9,6 ± 1.8	14.6 ± 2.3	15.4 ± 2.2	12.2 ± 1.6	12.9 ± 1.4
C_{org} [%]	13.2 ± 3.0	8.8 ± 0.7	6.3 ± 1.0	4.6 ± 1.0	10.5 ± 1.8	10.8 ± 1.4	6.3 ± 1.2	6.9 ± 1.2
N_t [mg/g]	7.9 ± 1.3	7.2 ± 0.4	5.5 ± 0.4	5.2 ± 1.0	7.7 ± 1.3	7.6 ± 1.0	5.0 ± 0.6	5.9 ± 0.6
PO_4^{3-}-P [µg/g]	24.9 ± 2.2	22.7 ± 1.2	23.2 ± 1.9	17.0 ± 2.8	12.1 ± 2.3	10.8 ± 0.9	9.1 ± 1.6	9.1 ± 1.2
K^+ [µg/g]	381 ± 54	282 ± 27	372 ± 80	256 ± 50	313 ± 44	271 ± 24	382 ± 105	325 ± 42
Mg^{2+} [µg/g]	170 ± 20	133 ± 8	145 ± 18	105 ± 33	187 ± 55	143 ± 20	141 ± 33	118 ± 34
Ca^{2+} [mg/g]	1.2 ± 0.1	0.9 ± 0.2	0.8 ± 0.3	0.5 ± 0.2	1.4 ± 0.5	1.1 ± 0.1	1.0 ± 0.3	0.8 ± 0.2
Micr. act. [mg CO_2-C/(g*h)]	12.5 ± 2.3	10.0 ± 2.0	12.3 ± 3.7	6.3 ± 2.9	6.7 ± 1.5	6.5 ± 1.6	5.1 ± 1.0	4.4 ± 2.1
Micr. biomass [mg C_{mic}/g]	2.0 ± 0.3	1.6 ± 0.1	1.9 ± 0.1	1.5 ± 0.3	2.7 ± 0.3	2.5 ± 0.3	2.5 ± 0.5	2.2 ± 0.4
qCO_2 [mg CO_2-C/(g C_{mic}*h)]	6.3 ± 0.9	6.2 ± 1.0	7.5 ± 1.6	4.1 ± 0.8	2.5 ± 0.3	2.2 ± 0.4	2.2 ± 0.3	2.2 ± 0.5
C_{mic}/C_{org}-ratio [%]	1.7 ± 0.3	1.7 ± 0.3	2.8 ± 0.7	2.6 ± 0.5	2.7 ± 0.5	2.3 ± 0.3	3.5 ± 0.3	2.6 ± 0.3

Tab. Appendix-3.2: Soil characteristics of the investigation plots Cf, Bf, Cu and Bu (investigation III) at the sampling dates May and September of the year 2002. Presented are median and MAD (n = 10).

2002	**May**				**September**			
plots	**Cu**	**Bu**	**Cf**	**Bf**	**Cu**	**Bu**	**Cf**	**Bf**
Soil pH (1M KCl)	3.4 ± 0.0	3.4 ± 0.0	3.5 ± 0.1	3.5 ± 0.0	3.4 ± 0.1	3.5 ± 0.1	3.5 ± 0.1	3.5 ± 0.1
Soil moisture [% w/w]	43.5 ± 3.5	44.5 ± 4.1	37.1 ± 2.1	34.1 ± 1.4	41.9 ± 5.5	37.4 ± 2.4	28.6 ± 3.1	29.6 ± 3.0
WHC_{max} [% w/w]	65.9 ± 1.3	65.2 ± 2.9	59.7 ± 1.6	57.8 ± 0.9	71.8 ± 3.2	67.2 ± 1.3	63.6 ± 3.2	59.0 ± 1.9
Litter [g/300 cm²]	16.3 ± 4.3	11.8 ± 5.3	10.1 ± 3.3	8.3 ± 4.6	12.4 ± 2.2	8.3 ± 2.4	6.2 ± 1.8	6.3 ± 0.9
C/N-ratio	16.8 ± 1.1	17.7 ± 1.3	17.6 ± 2.0	18.0 ± 2.9	15.5 ± 2.0	14.4 ± 2.0	15.0 ± 1.8	15.9 ± 2.0
C_{org} [%]	11.2 ± 1.9	12.7 ± 2.4	10.2 ± 1.7	8.4 ± 2.2	13.1 ± 2.2	11.4 ± 3.1	10.7 ± 1.8	9.6 ± 2.0
N_t [mg/g]	7.1 ± 1.1	7.2 ± 0.9	5.3 ± 1.3	4.8 ± 0.5	8.2 ± 1.1	8.4 ± 1.5	6.8 ± 1.2	6.4 ± 0.8
PO_4^{3-}-P [µg/g]	24.6 ± 3.9	20.4 ± 3.7	19.7 ± 2.6	17.0 ± 2.0	32.8 ± 5.0	29.1 ± 4.3	30.3 ± 4.6	27.5 ± 1.6
K^+ [µg/g]	364 ± 37	244 ± 23	279 ± 60	252 ± 31	343 ± 43	142 ± 38	379 ± 52	274 ± 16
Mg^{2+} [µg/g]	110 ± 21	94 ± 21	77 ± 18	76 ± 10	206 ± 23	128 ± 26	113 ± 12	100 ± 17
Ca^{2+} [mg/g]	0.9 ± 0.2	0.9 ± 0.1	0.8 ± 0.2	0.7 ± 0.1	1.8 ± 0.4	1.4 ± 0.3	0.9 ± 0.2	1.2 ± 0.2
Micr. act. [mg CO_2-C/(g*h)]	5.3 ± 1.2	4.5 ± 1.1	3.8 ± 0.8	2.6 ± 0.6	6.1 ± 1.2	4.5 ± 1.2	4.7 ± 0.7	3.6 ± 0.9
Micr. biomass [mg C_{mic}/g]	2.4 ± 0.4	2.7 ± 0.3	4.2 ± 0.3	1.9 ± 0.1	5.5 ± 0.5	5.9 ± 0.7	5.7 ± 0.8	5.1 ± 0.4
qCO_2 [mg CO_2-C(g C_{mic}*h)]	2.0 ± 0.3	1.7 ± 0.1	0.9 ± 0.2	1.4 ± 0.3	1.0 ± 0.1	0.8 ± 0.1	0.9 ± 0.1	0.7 ± 0.1
C_{mic}/C_{org}-ratio [%]	2.2 ± 0.1	2.3 ± 0.2	4.5 ± 0.3	2.4 ± 0.5	4.8 ± 0.7	4.9 ± 0.8	5.8 ± 1.2	5.2 ± 1.2

Tab. Appendix-3.3: Abundances of the soil invertebrates at the investigation plots Cf, Bf, Cu and Bu of investigation III. Presented are the median ± MAD values of individuals/sample size with the calculated median values of individuals/m² in brackets (n = 36).

Soil fauna	**Cu**	**Bu**	**Cf**	**Bf**
Med ± MAD; ind./31.2 cm² (m²)				
Collembola, total	11 ± 5 (3529)	10 ± 6 (3048)	18 ± 8 (5775)	9 ± 7 (2887)
Entomobryidae	2 ± 1 (642)	2 ± 2 (642)	5 ± 4 (1444)	3 ± 2 (962)
Isotomidae	5 ± 3 (1604)	2 ± 2 (642)	6 ± 4 (1765)	4 ± 3 (1283)
Hypogastruridae	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Onychiuridae	0 ± 0	1 ± (160)	1 ± (160)	0 ± 0
Sminthuridae	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Coll. biomass µg (mg)	197 ± 95 (63.0)	219 ± 190 (70.3)	358 ± 222 (114.8)	207 ± 141 (66.2)
Acari				
Oribatidae	13 ± 7 (4010)	11 ± 9 (3529)	20 ± 12 (6256)	12 ± 7 (3689)
Gamasidae/Parasitif.	5 ± 3 (1604)	8 ± 4 (2567)	11 ± 6 (3529)	7 ± 4 (2246)
Mesoarthropoda, total	31 ± 12 (9945)	36 ± 17 (11550)	52 ± 20 (16522)	36 ± 14 (11389)
Med ± MAD; ind./55.4 cm² (m²)				
Enchytraeidae	224 ± 64 (8210)	286 ± 136 (6225)	254 ± 114 (8120)	354 ± 32 (11007)
Med ± MAD; ind./300 cm² (m²)				
Coleoptera, total	6 ± 3 (200)	3 ± 3 (100)	5 ± 2 (167)	3 ± 2 (100)
Coleoptera larvae	5 ± 2 (167)	2 ± 2 (67)	3 ± 1 (100)	2 ± 2 (67)
Coleoptera adults	1 ± 1 (33)	1 ± 1 (33)	2 ± 1 (67)	0 ± 0
Arachnidae	1 ± 1 (33)	0 ± 0	1 ± 1 (33)	0 ± 0
Chilopoda	2 ± 2 (67)	1 ± 1 (33)	2 ± 2 (50)	2 ± 2 (67)
Isopoda	0 ± 0	0 ± 0	2 ± 2 (67)	1 ± 1 (17)
Diplopoda	0 ± 0	0 ± 0	1 ± 1 (33)	0 ± 0
Macrofauna, total	27 ± 9 (883)	12 ± 8 (400)	36 ± 17 (1183)	16 ± 8 (533)

VII.3 Investigation IV

Tab. Appendix-4.1: Soil characteristics at the forest sites Mono1, Mix1, Mono2 and Mix2 (investigation IV) at the sampling dates January 2002 and April 2002.

	January 02				April 02			
sites:	**Mono1**	**Mix1**	**Mono2**	**Mix2**	**Mono1**	**Mix1**	**Mono2**	**Mix2**
Soil pH (1M KCl)	3.5 ± 0.0	3.5 ± 0.0	3.5 ± 0.0	3.6 ± 0.2	3.4 ± 0.1	3.5 ± 0.1	3.5 ± 0.1	3.4 ± 0.0
Soil moisture [% w/w]	34.6 ± 3.1	41.6 ± 2.3	38.3 ± 3.0	50.5 ± 3.6	38.3 ± 2.0	50.5 ± 3.6	34.6 ± 3.1	41.6 ± 2.3
WRC_{max} [% w/w]	60.9 ± 1.2	65.7 ± 0.3	64.2 ± 0.4	71.4 ± 1.0	65.3 ± 1.9	65.0 ± 0.3	66.0 ± 2.2	65.7 ± 6.4
C/N-ratio	19.7 ± 1.5	18.5 ± 1.7	18.3 ± 2.8	18.9 ± 1.2	19.6 ± 1.8	15.7 ± 1.8	20.2 ± 0.9	16.8 ± 1.6
C_{org} [%]	10.7 ± 1.0	12.4 ± 2.0	13.0 ± 1.9	16.4 ± 3.1	13.7 ± 1.5	9.9 ± 1.2	14.8 ± 3.0	14.0 ± 2.3
N_t [mg/g]	5.2 ± 1.2	6.8 ± 0.5	7.1 ± 0.6	8.8 ± 0.9	7.4 ± 1.7	6.1 ± 0.6	7.5 ± 2.2	8.2 ± 1.0
PO_4^{3-}-P [µg/g]	19.8 ± 0.6	24.4 ± 1.9	21.7 ± 1.4	43.3 ± 4.0	25.2 ± 2.2	28.6 ± 3.9	26.8 ± 8.4	57.4 ± 8.4
K^+ [µg/g]	366 ± 34	401 ± 53	405 ± 22	421 ± 46	514 ± 88	653 ± 173	489 ± 103	588 ± 199
Mg^{2+} [µg/g]	98 ± 15	179 ± 37	165 ± 23	390 ± 143	353 ± 23	475 ± 118	440 ± 75	518 ± 140
Ca^{2+} [mg/g]	0.4 ± 0.1	1.3 ± 0.3	1.4 ± 0.3	3.0 ± 0.6	0.8 ± 0.1	1.8 ± 0.4	1.5 ± 0.6	1.6 ± 0.6
Micr. act. [mg CO_2-C/(g*h)]	2.9 ± 0.8	4.4 ± 0.9	4.0 ± 0.7	8.2 ± 1.7	4.4 ± 1.0	4.0 ± 0.7	4.6 ± 2.1	5.0 ± 1.2
Micr. biomass [mg C_{mic}/g]	4.8 ± 0.3	4.9 ± 0.5	4.9 ± 0.2	5.2 ± 0.5	4.7 ± 0.7	3.8 ± 0.5	3.7 ± 0.5	4.3 ± 0.7
qCO_2 [mg CO_2-C(g C_{mic}*h)]	0.6 ± 0.1	0.9 ± 0.2	0.8 ± 0.1	1.6 ± 0.3	0.9 ± 0.2	1.0 ± 0.2	1.1 ± 0.3	1.1 ± 0.2
C_{mic}/C_{org}-ratio [%]	4.6 ± 0.6	3.7 ± 0.3	2.6 ± 0.3	2.8 ± 0.5	2.6 ± 0.3	4.3 ± 0.3	2.6 ± 0.4	3.1 ± 0.5

Tab. Appendix-4.2: Soil characteristics at the forest sites Mono1, Mix1, Mono2 and Mix2 (investigation IV) at the sampling dates July 2002 and November 2002.

	July 02				November 02			
sites:	**Mono1**	**Mix1**	**Mono2**	**Mix2**	**Mono1**	**Mix1**	**Mono2**	**Mix2**
Soil pH (1M KCl)	3.3 ± 0.1	3.5 ± 0.1	3.4 ± 0.1	3.4 ± 0.1	3.4 ± 0.1	3.5 ± 0.1	3.5 ± 0.1	3.4 ± 0.1
Soil moisture [% w/w]	23.0 ± 1.4	33.9 ± 3.2	24.1 ± 4.4	43.8 ± 9.4	48.5 ± 4.7	46.3 ± 2.6	49.6 ± 5.1	61.4 ± 3.1
WRC_{max} [% w/w]	66.3 ± 2.6	66.4 ± 1.5	65.5 ± 1.8	78.3 ± 3.4	57.5 ± 5.6	65.2 ± 5.2	68.2 ± 3.6	75.2 ± 2.0
C/N-ratio	19.6 ± 1.8	15.7 ± 1.8	20.2 ± 0.9	16.8 ± 1.6	16.3 ± 1.8	20.3 ± 4.7	20.5 ± 5.0	20.2 ± 4.6
C_{org} [%]	15.2 ± 3.1	11.8 ± 1.1	17.0 ± 3.5	21.9 ± 5.4	15.1 ± 2.3	15.0 ± 1.0	21.0 ± 4.6	26.9 ± 5.2
N_t [mg/g]	8.3 ± 1.4	7.1 ± 1.1	9.2 ± 1.7	11.8 ± 1.3	8.2 ± 2.4	7.5 ± 0.7	10.7 ± 3.9	12.3 ± 1.0
PO_4^{3-}-P [µg/g]	30.9 ± 2.8	31.1 ± 4.2	33.8 ± 3.1	80.6 ± 12.7	31.6 ± 10.1	31.6 ± 6.2	33.1 ± 2.8	66.8 ± 3.7
K^+ [µg/g]	482 ± 96	440 ± 88	456 ± 68	490 ± 97	424 ± 82	503 ± 163	412 ± 92	586 ± 141
Mg^{2+} [µg/g]	130 ± 12	151 ± 46	167 ± 20	295 ± 50	105 ± 18	228 ± 55	190 ± 35	405 ± 90
Ca^{2+} [mg/g]	0.6 ± 0.2	1.4 ± 0.4	1.5 ± 0.4	3.0 ± 0.8	0.3 ± 0.1	1.6 ± 0.5	1.1 ± 0.3	2.6 ± 0.7
Micr. act. [mg CO_2-C/(g*h)]	5.5 ± 0.6	4.8 ± 0.4	5.1 ± 1.1	8.0 ± 2.8	4.2 ± 1.5	4.5 ± 0.7	5.0 ± 1.6	9.1 ± 1.2
Micr. biomass [mg C_{mic}/g]	5.2 ± 0.7	3.1 ± 0.7	5.2 ± 0.5	4.9 ± 1.4	4.5 ± 0.9	1.6 ± 0.3	4.6 ± 0.8	3.2 ± 0.5
qCO_2 [mg CO_2-C(g C_{mic}*h)]	1.0 ± 0.2	1.5 ± 0.2	0.9 ± 0.1	1.7 ± 0.2	1.0 ± 0.2	2.6 ± 1.0	1.2 ± 0.4	2.8 ± 0.7
C_{mic}/C_{org}-ratio [%]	2.6 ± 0.3	2.5 ± 0.2	2.8 ± 0.3	2.5 ± 0.2	2.5 ± 0.3	1.1 ± 0.1	2.1 ± 0.2	1.1 ± 0.4

VII.3 Investigation V

Tab. Appendix-5.1: Median ± MAD values of the microbial activity, the microbial biomass and the metabolic quotient (qCO_2) of the different experimental approaches of the microcosm series I and II at all sampling dates.

Microbial activity day		**Control**	**N+P**	**Glu+N+P**	**Cell+N+P**	**Lig+N+P**
1	Series I	1.5 ± 0.1	2.0 ± 0.1	6.1 ± 0.6	2.0 ± 0.2	3.2 ± 0.1
	Series II	4.1 ± 0.1	5.3 ± 0.2	15.4 ± 4.1	6.7 ± 0.5	6.4 ± 0.2
2	Series I	1.3 ± 0.1	1.6 ± 0.1	29.5 ± 1.4	2.0 ± 0.1	2.7 ± 0.1
	Series II	3.3 ± 0.2	4.0 ± 0.2	67.1 ± 0.2	6.5 ± 0.3	5.5 ± 0.2
4	Series I	1.3 ± 0.1	1.5 ± 0.1	49.3 ± 1.5	5.2 ± 0.4	2.4 ± 0.1
	Series II	3.1 ± 0.1	3.5 ± 0.1	111.2 ± 16.6	14.4 ± 1.8	4.8 ± 0.1
8	Series I	1.2 ± 0.1	1.1 ± 0.1	16.9 ± 1.7	24.0 ± 1.2	2.0 ± 0.1
	Series II	2.7 ± 0.1	2.7 ± 0.1	36.1 ± 4.5	43.0 ± 3.9	4.1 ± 0.1
16	Series I	1.1 ± 0.0	0.8 ± 0.0	5.8 ± 0.6	19.9 ± 1.2	1.4 ± 0.4
	Series II	2.1 ± 0.1	2.0 ± 0.1	12.2 ± 1.4	33.6 ± 0.7	3.6 ± 0.2
32	Series I	0.8 ± 0.0	0.6 ± 0.0	2.9 ± 0.3	5.0 ± 0.3	1.1 ± 0.0
	Series II	n. d.	n. d.	n. d.	n. d.	n. d.
64	Series I	0.2 ± 0.0	0.2 ± 0.0	1.1 ± 0.2	2.3 ± 0.3	0.7 ± 0.0
	Series II	1.0 ± 0.0	0.9 ± 0.0	2.4 ± 0.1	3.5 ± 0.5	1.2 ± 0.1
Microbial biomass day		**Control**	**N+P**	**Glu+N+P**	**Cell+N+P**	**Lig+N+P**
1	Series I	2.3 ± 0.0	1.9 ± 0.0	6.3 ± 2.1	2.3 ± 0.1	2.8 ± 0.1
	Series II	1.1 ± 0.0	1.1 ± 0.0	2.6 ± 0.2	1.0 ± 0.1	1.6 ± 0.0
2	Series I	2.0 ± 0.1	2.1 ± 0.1	6.8 ± 1.5	2.2 ± 0.1	3.2 ± 0.2
	Series II	1.0 ± 0.0	1.0 ± 0.0	10.4 ± 1.4	0.7 ± 0.0	1.2 ± 0.0
4	Series I	2.9 ± 0.4	2.9 ± 0.0	5.5 ± 0.1	4.6 ± 0.4	3.4 ± 0.2
	Series II	1.4 ± 0.0	1.4 ± 0.0	5.4 ± 1.6	2.0 ± 0.1	2.0 ± 0.1
8	Series I	2.4 ± 0.1	2.2 ± 0.1	4.9 ± 0.1	5.3 ± 0.2	3.1 ± 0.1
	Series II	1.2 ± 0.0	1.3 ± 0.0	3.4 ± 0.3	2.1 ± 0.3	1.8 ± 0.0
16	Series I	2.2 ± 0.0	2.3 ± 0.1	4.6 ± 0.3	5.8 ± 0.3	3.2 ± 0.2
	Series II	1.1 ± 0.0	1.1 ± 0.0	2.5 ± 0.3	2.8 ± 0.1	1.6 ± 0.0
32	Series I	2.1 ± 0.1	2.1 ± 0.1	3.7 ± 0.2	3.2 ± 0.6	2.9 ± 0.2
	Series II	n. d.	n. d.	n. d.	n. d.	n. d.
64	Series I	1.7 ± 0.1	1.8 ± 0.1	3.4 ± 0.2	3.4 ± 0.1	2.4 ± 0.1
	Series II	1.4 ± 0.0	1.5 ± 0.0	2.2 ± 0.2	2.5 ± 0.2	1.9 ± 0.0
qCO_2 day		**Control**	**N+P**	**Glu+N+P**	**Cell+N+P**	**Lig+N+P**
1	Series I	0.7 ± 0.0	1.0 ± 0.0	0.9 ± 0.4	0.9 ± 0.1	1.1 ± 0.0
	Series II	3.8 ± 0.1	4.9 ± 0.3	5.7 ± 1.5	7.5 ± 1.5	3.9 ± 0.2
2	Series I	0.7 ± 0.1	0.7 ± 0.0	4.6 ± 1.1	1.1 ± 0.0	0.8 ± 0.0
	Series II	3.1 ± 0.2	4.1 ± 0.3	7.2 ± 1.7	8.9 ± 1.2	4.3 ± 0.4
4	Series I	0.5 ± 0.1	0.5 ± 0.0	18.7 ± 0.9	1.3 ± 0.1	0.7 ± 0.0
	Series II	2.2 ± 0.0	2.4 ± 0.0	21.2 ± 4.0	7.3 ± 0.7	2.4 ± 0.2
8	Series I	0.5 ± 0.0	0.5 ± 0.0	3.2 ± 0.6	4.6 ± 0.2	0.6 ± 0.0
	Series II	2.3 ± 0.1	2.0 ± 0.2	16.4 ± 1.7	22.4 ± 5.8	2.4 ± 0.1
16	Series I	0.5 ± 0.0	0.3 ± 0.0	1.2 ± 0.1	3.5 ± 0.2	0.4 ± 0.0
	Series II	2.0 ± 0.1	1.8 ± 0.1	5.4 ± 0.2	12.0 ± 0.6	2.3 ± 0.1
32	Series I	0.4 ± 0.0	0.3 ± 0.0	0.8 ± 0.1	1.5 ± 0.3	0.4 ± 0.0
	Series II	n. d.	n. d.	n. d.	n. d.	n. d.
64	Series I	0.1 ± 0.0	0.1 ± 0.0	0.3 ± 0.1	0.6 ± 0.1	0.3 ± 0.0
	Series II	0.7 ± 0.0	0.6 ± 0.0	1.1 ± 0.0	1.5 ± 0.3	0.9 ± 0.1

Tab.: Appendix-5.2: Wilcoxon-tests for the different experimental approaches of the microcosm series I and II showing the p-values and the significance levels. *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$, ns: not significant.

Microbial activity

	approach	1	2	3	4	5	6	7	8	9	10
Control series 1	**1**		0.615	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
N+P series I	**2**	ns		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Glu+N+P series I	**3**	***	***		0.230	0.000	0.000	0.000	0.000	0.712	0.000
Cell+N+P series I	**4**	***	***	***		0.000	0.001	0.02	0.000	0.000	0.179
Lig+N+P series I	**5**	***	***	***	***		0.000	0.000	0.000	0.000	0.000
Control series II	**6**	***	***	***	***	***		0.004	0.000	0.000	0.000
N+P series II	**7**	***	***	***	*	***	**		0.000	0.000	0.000
Glu+N+P series II	**8**	***	***	***	***	***	***	***		0.043	0.000
Cell+N+P series II	**9**	***	***	ns	***	***	***	***	***		0.000
Lig+N+P series II	**10**	***	***	***	ns	***	***	***	***	***	

Microbial biomass

	approach	1	2	3	4	5	6	7	8	9	10
Control series 1	**1**		0.642	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000
N+P series I	**2**	ns		0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000
Glu+N+P series I	**3**	***	***		0.031	0.000	0.000	0.000	0.004	0.000	0.000
Cell+N+P series I	**4**	***	***	*		0.001	0.000	0.000	0.433	0.000	0.000
Lig+N+P series I	**5**	***	***	***	***		0.000	0.000	0.382	0.000	0.000
Control series II	**6**	***	***	***	***	***		0.009	0.000	0.000	0.000
N+P series II	**7**	***	***	***	***	***	**		0.000	0.000	0.000
Glu+N+P series II	**8**	***	***	**	ns	ns	***	***		0.000	0.000
Cell+N+P series II	**9**	**	**	***	***	***	***	***	***		0.372
Lig+N+P series II	**10**	***	***	***	***	***	***	***	***	ns	

qCO_2

	approach	1	2	3	4	5	6	7	8	9	10
Control series 1	**1**		0.985	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
N+P series I	**2**	ns		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Glu+N+P series I	**3**	***	***		0.737	0.000	0.761	0.907	0.000	0.000	0.518
Cell+N+P series I	**4**	***	***	ns		0.000	0.122	0.078	0.000	0.000	0.020
Lig+N+P series I	**5**	***	***	***	***		0.000	0.000	0.000	0.000	0.000
Control series II	**6**	***	***	ns	ns	***		0.036	0.000	0.000	0.000
N+P series II	**7**	***	***	ns	ns	***	*		0.000	0.000	0.323
Glu+N+P series II	**8**	***	***	***	***	***	***	***		0.184	0.000
Cell+N+P series II	**9**	***	***	***	***	***	***	***	ns		0.000
Lig+N+P series II	**10**	***	***	ns	*	***	***	ns	***	***	