

Coniferous Mediterranean Forest Soil Dynamics

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ABSTRACT

Soil organic matter accumulated in the litter of a forest ecosystem is considered the single most important indicator of soil quality because it contributes to plant growth and development through its effect on the chemical, biological, and physical properties of soils. The decomposition of organic matter is an important process responsible for the release of nutrients in soils, which affect the productivity of forest ecosystems, particularly of coniferous forests and other nutrient-poor types. Nutrient release from fresh plant litter occurs via the enzymatic activities of the microbial communities. The varying predominance of the individual enzymes can be related to the amount of soil microorganisms. Thus, fluctuation in the size and turnover of the soil microbial biomass is very important in controlling the turnover of carbon and associated nutrients. Conifers are under strong exploitation pressure in Mediterranean forests; thus, knowledge of litter decomposition process and soil ecological functions is necessary for their adequate conservation. This review summarizes the progress made in recent years in understanding the mechanisms implicated in the dynamics of litter and nutrients release in coniferous forest soils, putting in evidence that the litter decomposition rate for Conifers appears to be limited by low water availability, affected by the initial chemical composition of the litter types, and strongly influenced by biomass, particularly by the proportion of microfungi in the microbial community, which mediate the decomposition of organic matter, influencing nutrient turnover and soil productivity. There is a close relationship between content of microbial biomass, soil organic matter and enzyme activities.

Keywords: litter dynamics, microbial biomass, nutrients, organic matter, phenols, soil enzymes

Abbreviations: DOC, dissolved organic carbon; DOM, dissolved organic matter; LMW, low molecular weight; MBC, microbial biomass carbon; OM, organic matter; SOM, soil organic matter

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INTRODUCTION

Litter dynamics constitute an important aspect of nutrient cycling and energy transfer in forest ecosystems (Maguire 1994). Litter fall is closely related to the growth rate of forests, and it is a principal pathway for the return of nutrients to the soil. However, the growth and productivity of forest ecosystems mainly depend on the amount, the nature and the rate of decomposition of forest litter, which provide organic and inorganic elements for the nutrient cycling processes (Mudrick *et al.* 1994).

Climate conditions (Hart *et al.* 1992), litter supply (Nakane 1995), litter quality (Lisanework and Michelsen 1994), and microbial activity (Edwards *et al.* 1973) are contributing factors to the decomposition of litter.

Each forest species has different nutrient release patterns, which are related to litter quality and environmental factors (Khiewtan and Ramakrishnan 1993). In the hierarchical model concept of Lavelle *et al.* (1993) it is proposed

that processes which operate at large spatial scales constrain those which operate at smaller scales; climatic factors help to determine abiotic soil characteristics, which in turn help to determine litter quality and, ultimately, the activity and composition of soil microbial and invertebrate communities. It is also important to note that there are numerous "feedback" in this hierarchy, with those factors acting at smaller spatial scales also influencing those which operate at larger scales. Thus, the effects of plant litter quality on the soil biota regulate the extent to which the biota in turn facilitates the decomposition of plant litter.

The Mediterranean area is especially sensitive to any climate change because it represents a transition zone between arid and humid regions of the world. Although Mediterranean forest ecosystems represent a small fraction of the world's cover, they are an interesting model system to study the effects of global change on terrestrial ecosystems. Aspects of global change impacts (including high sensitivity of ecosystem productivity to water availability, elevated

susceptibility of natural ecosystems of the region to nitrogen depletion because of slow nutrient cycling, high incidence of fire damages, changes affecting carbon fluxes and energy balance) (Moreno and Fellous 1997) are factors limiting plant growth and causing the virtual disappearance of the most climax forest types from Mediterranean Region (Quézel 1978).

Conifers in the Mediterranean area have been intensively exploited (Naveh 1982), resulting in the loss of soil fertility; thus, the turnover of organic matter becomes essential to maintain soil ecological functions for forest sustainable production and conservation.

The understanding of the mechanisms implicated in litter decomposition and nutrients release are in progress in recent years and briefly summarized in this work.

LITTER DYNAMICS IN FOREST ECOSYSTEMS

The decomposition of dead plant material is an important process responsible for the release of nutrients from the litter. Their release and reutilisation affect the productivity of forest ecosystems, particularly in nutrient-poor types such as coniferous forests (Fioretto *et al.* 1998).

Litter dynamics constitute an important aspect of nutrient cycling and energy transfer in forest ecosystems (Maguire 1994). Litter fall is closely related to growth rate of forests and it is a principal pathway for the return of nutrients to the soil. However, the growth and productivity of forest ecosystems mainly depend on the amount, nature and the rate of forest litter. Decomposition of leaf litter is influenced by the physical environmental conditions under which decay takes place, by the nature and abundance of the decomposing organisms, and by the litter quality (Sariyildiz and Anderson 2003a, 2003b). In general, climate (especially temperature and moisture) governs decay rates on broad regional scales, whereas initial litter quality variables (carbon:nitrogen ratio, lignin and N) are more important in controlling decay rates at small scales, i.e. within the sites (Heal *et al.* 1997). Different species have in fact different nutrient release patterns which are related to litter quality and seasonality environmental factors (Khiewtam and Ramkrishnan 1993). In deciduous and sclerophyllous forests the humus profile (L, F and H layers) is usually thinner than in coniferous forests (van Wesemael and Veer 1992). Nakane (1995) suggested that the lower rate of decomposition of the leaf litter in a red pine (*Pinus resinosa* Aiton) forest, compared to that of an oak (*Quercus ilex* L.) forest may be due to their chemical properties. Muscolo and Sidari (1998) demonstrated a different trend of organic matter between *Fagus sylvatica* L. and *Pinus laricio* Poiret, evidencing a different sensitivity of the organic matter on mineralization or humification processes between the different species. These findings were supported by the C/N

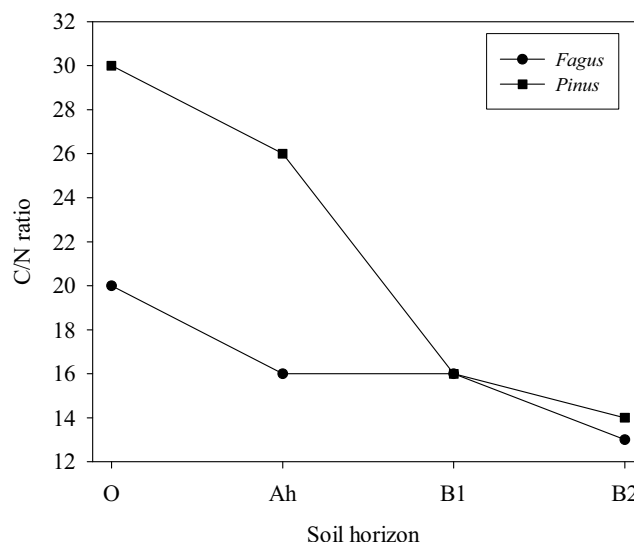


Fig. 1 C/N ratio in soil profiles under *Fagus sylvatica* and *Pinus laricio* trees.

ratio, an index used to monitor the decomposition of litter and to predict weight loss (Taylor *et al.* 1989). In fact, the greatest value of the C/N ratio is observed in the *Pinus laricio* stand (Fig. 1) where there is a higher content of humic carbon with respect to the amount of organic matter (Fig. 2), indicating that the humification process prevailed in this site, whereas the lowest C/N ratios and levels of humic carbon were observed in the soil under *Fagus sylvatica*, suggesting that in this site the mineralization process prevailed (Figs. 1, 2). The different trend of organic matter observed could be related to differences in litter quality. In general, litters with high lignin and low N concentration have a slower decomposition rate and immobilise more N than litters with low lignin and high N content (Hendricks and Boring 1999). In Mediterranean ecosystems the role of litter decomposition in nutrient cycling becomes still more important when considering the degradation of forest vegetation and soils. Studies conducted on natural sites of three coniferous Maritime pine (*Pinus pinaster* Aiton), Black pine (*Pinus nigra* Arnon) and Bulgarian fir (*Abies borisii-regis* Matf.) in northern Greece quantified the litter fall and its nutrient element content and determined at what extent site quality and tree species influenced forest floor mass and chemical properties assessing the turnover rates of Mediterranean forest ecosystems. Results reported by Kavvadias *et al.* (2001) showed that mass and nutrient content of litter fall and forest floor horizons substantially differed among forest vegetation, showing a clear difference in litter decomposition and turnover not only between coniferous and broad-leaved species

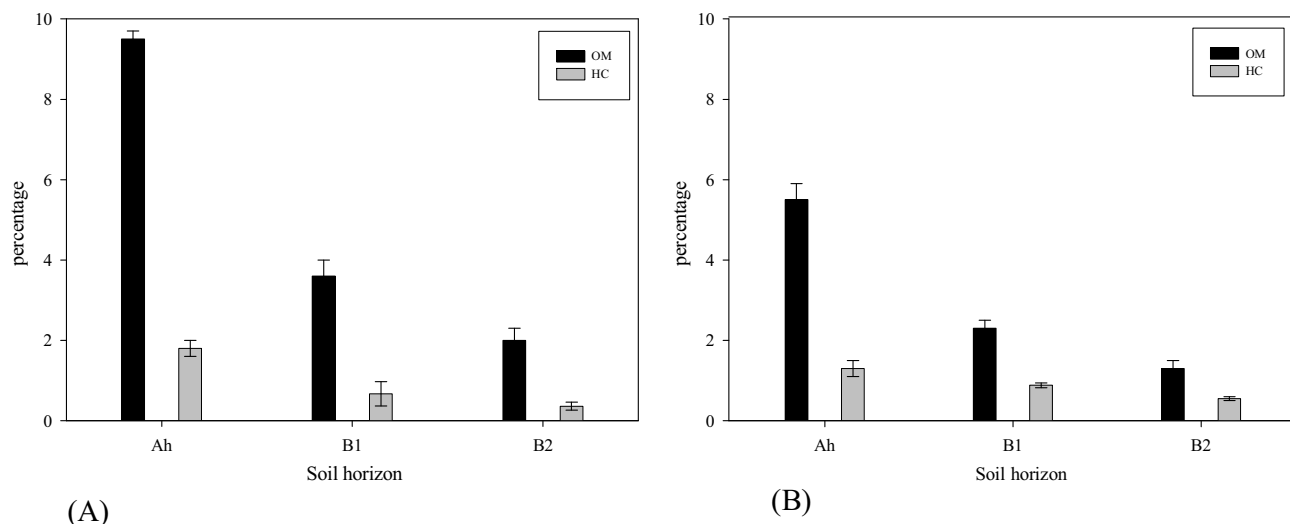


Fig. 2 Organic matter (OM%) and humic carbon (HC%) in soil profiles under (A) *Fagus sylvatica* and (B) *Pinus laricio* trees.

but also within conifers, demonstrating that the residence time for the forest floor litter was higher in coniferous than in deciduous forests. The site quality, generally, did not considerably influence litter fall and litter accumulation, thus differences in litter decomposition rate are associated with the litter fall input and to the chemical composition of litter.

Fioretto *et al.* (1998) showed that the decomposition dynamics of the litters of Corsican pine (*Pinus laricio* Poir.), Stone pine (*P. pinea* L.), and Scots pine (*P. sylvestris* L.) in a Corsican pine forest in the South Italy Apennines were affected by the initial chemical composition of the three litter types. The highest content of the macronutrients Ca, N, S were found in the Stone pine litter while the highest content of P and K was in Corsican pine litter; among the micronutrients, Mn, Zn, and Cu contents were high in Scots pine. The decomposition rates of the three types of litter were very low during the period April-September. The scarcity of precipitation appeared to be the main cause of the low decomposition rates in this site which is characterized by a relatively low Lang aridity index (Virzo de Santo *et al.* 1993). The aridity may have been the cause of the low amount of litter fungal biomass in all three pine species during decomposition. Differences were observed in decomposition rate among the three different conifers: Corsican pine and Scots pine showed the same decay while Stone pine had the lowest decomposition rate. The chemical composition of the litters may have caused the differences in decomposition rate. Even if differences were found for most nutrients, the highest lignin content may be the main cause of the delay in the start of decomposition in Stone pine litter. Of all naturally produced organic chemicals, lignin is probably the most recalcitrant. This recalcitrant material has to be broken down and recycled by microorganisms to maintain the earth's carbon cycle. Lignin biodegradation has diverse effects on soil quality. The microbial degradation of litter results in the formation of humus, and ligninolysis probably facilitates this process by promoting the release of aromatic humus precursors from the litter. Conditions that disfavour the biological breakdown of lignin-cellulose lead to soils with pronounced accumulations of litter. The soils under coniferous forests in the Mediterranean region, as in the northwest of the United States, can accumulate litterfall, because the low pH of the litter and the lack of summer rainfall inhibit microbial activity. Warm temperature, high moisture content, high oxygen availability, and high litter palatability to microorganisms (usually estimated from the frequency and intensity of its burial in the soil), all favour decomposition. The more highly lignified litter is, the less digestible it is, and the more its decomposition depends on the unique organisms that can degrade lignin-cellulose. The organisms principally responsible for lignin-cellulose degradation are aerobic filamentous fungi, in particular *Basidiomycetes* (Kirk and Farrell 1987), which make a large contribution to wood decay, especially in coniferous forests (Dix and Webster 1995).

The amount and quality of aboveground and belowground litter, soil properties, soil temperature, and soil moisture affect the decay rate and thereby the sequestration of soil organic matter. Tree species may greatly influence the sequestration of soil organic matter in many ways. Berg and McClaugherty (2003) described wide variation in nutrient content, substrate composition, and litter structure among tree species. Litter quality may affect biomass and activity of the microbial community, and thus the decomposition process. For example, Bauhus *et al.* (1998) reported larger C and N concentrations in microbial biomass under birch and aspen trees than under coniferous trees. Not only litter quality but also environmental conditions may vary among tree species as a result of variation in crown structure and foliation. Spruce forests receive generally higher element inputs than beech forests because of canopy interactions with the atmosphere during the dormant season (Borken and Matzner 2004). In addition to aboveground effects, tree species have different root-system, root-biomass, and

water-uptake patterns. Overall, tree species are considered to affect chemical and biological processes, soil moisture, and soil temperature in the organic horizon through the root system, crown structure, foliage, leaf structure, and litter quality. Forest soils store a large fraction of soil organic carbon in the O horizons that is not physically protected against microbial decay. Changes in litter quality, soil moisture, soil temperature, and element input caused by forest conversion could alter the C stock as well as the respiration rate of the O horizons and mineral soils. Because the O horizon has a temperature and moisture regime distinct from those of mineral soil, microbial activity in the two compartments may respond differently to micrometeorological changes. Borken and Beese (2005) evaluated the effect of the conversion of pure spruce forests to mixed or deciduous forests, on the decay of soil organic matter and the release of nutrients and pollutants. Soil respiration was measured in adjacent pure and mixed stands of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) at Solling, Germany. Forest type had a significant effect on soil respiration, which was highest in the pure beech stand and lowest in the pure spruce stand. Both throughfall and soil temperature increased with the proportion of beech. Additionally, microbial respiration and biomass in the organic horizons increased sequentially from the pure spruce to the pure beech stand, suggesting that abiotic and biotic factors enhanced the decomposition of litter under beech. Because the spruce litter decomposition rate was low, carbon stocks of the O horizons increased with the proportion of spruce, from 1.6 to 5.1 kg C.m⁻². The removal of the O horizons decreased soil respiration by 31%-45%, indicating a large contribution of the mineral soil and roots to total soil respiration. Turnover times of organic C in the O horizons ranged between 5.5 years in the pure beech stand and 20.6 years in the pure spruce stand. These results suggest that soil C dynamics is affected by tree species and by variation in abiotic and consequently biotic parameters. In most forest ecosystems, an organic forest floor develops over mineral soil as a result of litterfall accumulation. Litterfall inputs into the forest floor increase with age, reach a peak, and then decline at older ages in southern pine plantations (Switzer and Nelson 1972; Gholz *et al.* 1985). Nutrient storage in the forest floor also increases with plantation age and can amount to as much as 350-400 kg N-ha⁻¹ at age 30 and 740 kg N-ha⁻¹ at age 40 (Richter *et al.* 2000). In contrast to this accumulation, soil nutrient supply usually declines as stands age because of plant uptake and immobilization (Miller *et al.* 1979; Allen *et al.* 1990; Richter *et al.* 2000), in some cases resulting in nutrient limitations to forest productivity. The role of the forest floor in supplying nutrients in midrotation stands is uncertain. Switzer and Nelson (1972) and Jorgensen *et al.* (1980) calculated that forest floor releases substantial amounts of macronutrients, but more recently, others (Piatek and Alien 2001; Sanchez 2001) suggested that the forest floor is largely a sink for N and P, while releasing other macronutrients. In addition, decomposition studies have mainly focused on macronutrient release, and there is a lack of information about micronutrient release dynamics for stands of most forest species. Vegetation control can significantly alter plant community composition, which, in turn, may affect the quality of forest floor. In general, hardwood litter decomposes and releases nutrients more rapidly than coniferous litter because of higher nutrient concentrations and lower lignin and phenolics concentrations (Prescott *et al.* 2000; Piatek and Allen 2001). Vegetation control may also alter forest floor temperatures and moisture contents, which, in turn, influence the rates of decomposition, since they have effects on microbial activity and diffusion of substrate. The effects of these environmental factors are usually most important during the initial stages of the decomposition, while litter recalcitrance becomes more important in later stages (Edmonds and Thomas 1995). Nevzat *et al.* (2003) determined the effects of vegetation control on needle decomposition rates and macro- and micronutrient release dynamics in a midrotation loblolly pine

(*Pinus taeda* L.) plantation, suggesting that vegetation control reduced release of N, P, S, and Zn, and increased release of B. The mineral soil may be the main source of plant available N and P in midrotation southern pine stands based on the slow release of these elements from decomposing needle litter. Berg *et al.* (2003), studied, for 3 years, the decomposition dynamics of four types of needle litter and three types of leaf litter at two very contrasting coniferous forest systems, a nutrient-rich silver fir (*Abies alba* Mill.) forest in south Italy (Monte Taburno) and a nutrient-poor Scots pine (*Pinus sylvestris* L.) forest in central Sweden (Jädraås). Decomposition of the same litter type at the two sites did not differ in the early stages but proceeded further at the nutrient-rich forest site than at the nutrient-poor one. Limit values for decomposition were calculated and the differences for the same litter type between the two contrasting coniferous systems were investigated. At both sites six of the seven litter types gave significant (asymptotic) limit values for decomposition, which varied with litter type. For four litter types out of six the limit values differed significantly between the two sites and were always higher at the nutrient-rich site (Monte Taburno). Using all available data for litters incubated at the two sites revealed that at the nutrient-poor site (Jädraås) there was a significant negative relationship between litter N levels and limit values and there was also a significant negative relationship between initial concentrations of heavy metals (e.g. Zn, Cd, Cu) and limit values. In contrast, at the site Monte Taburno, rich in nutrients and in heavy metals, there was no such relationship. The results of this study show that the limit values at the two sites have different levels, i.e. they are higher at the nutrient-rich Monte Taburno site. Moreover, limit values are related to litter chemical composition only at the nutrient-poor site Jädraås. Thus accumulation of organic matter is found not only over a wide spectrum of litter chemical composition (Berg and Ekbohm 1991; Berg 2000; Berg *et al.* 2001) but also, as indicated by the results of this research, over soil types of very varying concentrations of nutrients and heavy metals. That means that although the limit-value may be considered a general phenomenon, the regulating factors are different.

Topographic effects on decomposition

A number of studies have also shown that even at small topographical landforms (especially different aspects and slope position) can create different environmental conditions which can retard or accelerate litter decomposition through negative or positive effects on the activity of organisms (Scowcroft *et al.* 2000). In the northern temperate zone, slope aspect is an important topographic factor influencing local site microclimate, mainly because it determines the amount of solar radiation received. The amount of insulation governs air and soil temperatures and soil water availability, which in turn affect establishment and growth of plants (Barnes *et al.* 1998).

It is common knowledge that topography, in the forest ecosystem, significantly affects soil texture, soil moisture, soil temperature, and soil organic matter (SOM) trend that is acknowledged to be among the most important soil physicochemical properties influencing microbial population activity, dynamic, and ecology of the soil microbiota (Stotzky 1997).

In general, effects of topography on litter quality and decomposition have received little attention. Sariyildiz and Anderson (2003a, 2003b) and Sariyildiz *et al.* (2005) showed that aspect and slope position within an ecosystem affect the soil chemistry, litter quality, and nutrient cycling. Muscolo and co-workers in 2005 (unpublished data) evaluated the influence of south- and north-aspect on soil biochemical properties and organic matter trend within a naturally regenerated 80 years old *Pinus laricio* Poiret population forest of Aspromonte Mountains, in Calabria (Southern Italy), demonstrating that soils developed on the same parent material, with the same vegetal cover and climate, differing

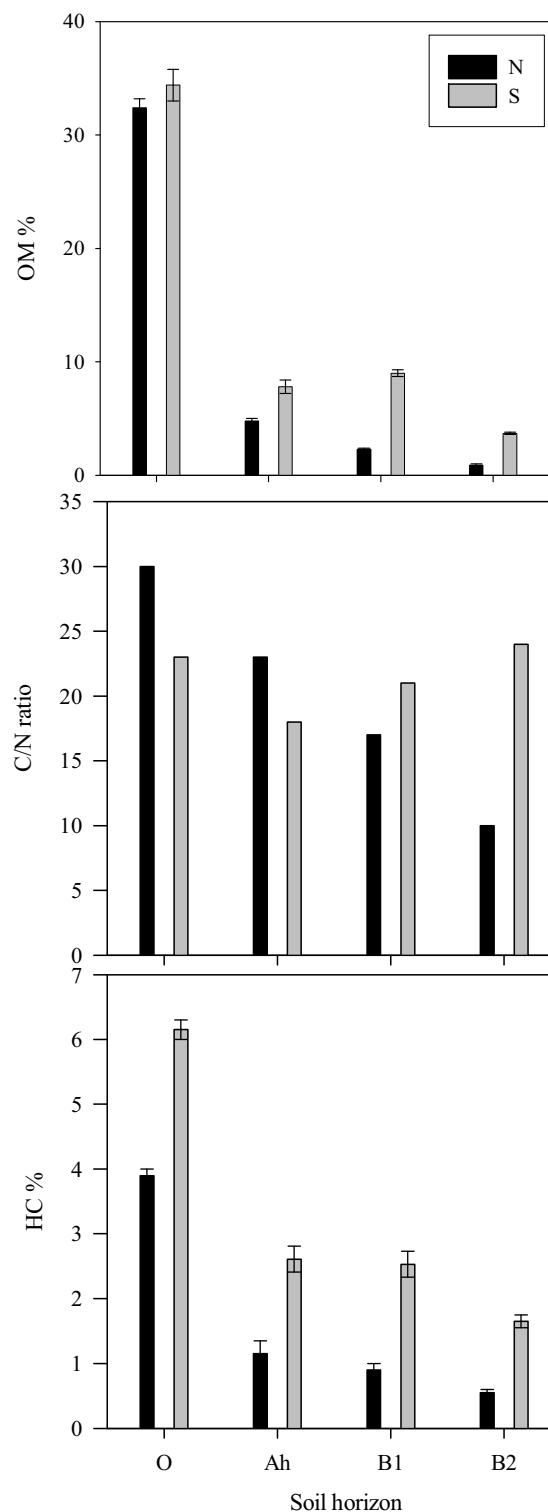


Fig. 3 Organic matter (OM%), humic carbon (HC%) and C/N ratio in soil horizons on the north-facing (N) and south-facing slope (S).

only for the position in the landscape, had diverse microclimatic conditions (soil temperature and moisture), which in turn affected the organic matter. The C/N ratio decreased with increasing soil depth in the soil on the north-facing slope. No significant variation in the C/N ratio between the surface and the illuvial horizons of the site south-facing slope was observed (Fig. 3). The greatest reduction of C/N ratio observed in the soil on the north-facing slope depends on different rates of loss of organic C and N, and, in addition, the lower content of C in humic acid fraction suggested also that, in this site, the mineralization process is more rapid than in the south-facing slope. In the sites on the south-facing slope the higher content of humic carbon with respect to the amount of organic matter and the constant value of C/N ratio along the soil profile indicated that in

these sites the humification process prevailed (Fig. 3).

In conclusion, soil aspect may induce differences in abiotic factors, in particular soil temperature and water content; these soil physical properties affect the biotic soil components which in turn induce differences in litter decomposition and turnover.

Effect of soil fauna on litter decomposition

Most research on decomposition has focused on litter quality and environmental control rather than soil fauna. These three factors are not independent and together determine the most relevant processes that operate during decomposition (Swift *et al.* 1979).

In forest ecosystems soil and litter arthropod communities play a major role in the decomposition of fresh organic matter and in the formation of humus profiles (Ponge *et al.* 1986; Bird *et al.* 2000). Microarthropods, particularly Oribatid mites and Collembola are important members of the detrital system (Seastedt and Crossley 1981). They participate in the fragmentation of plant detritus and stimulate the activity of bacterial and fungal colonies. The soil arthropod community is often considered to be a useful bioindicator of forest condition and change (Hole 1981) as soil organic matter dynamics and nutrients mineralization are key processes in ecosystem functioning (Bardgett *et al.* 1998). In Mediterranean forests, soil characteristics may enhance litter decomposition by creating a more favourable microclimate for microbial and faunal activity (Romanyà *et al.* 2000). Feeding activities of soil fauna have a direct effect on decomposition, through their own metabolism, and an indirect effect, by increasing the activity of decomposer microorganisms (Hassall *et al.* 1987; Zimmer and Topp 1999). Faunal population consume a substantial part of soil litter. Garcia-Pausas *et al.* (2004) studied the decomposition of *Pinus halepensis* Mill. litter to determine at what extent faunal activity depends on litter quality or on microsite conditions, suggesting that water availability or soil characteristic seem to limit faunal activity in Mediterranean areas. Faecal pellet production was used as an indication of faunal activity. Under dry conditions faecal pellets were not found during the first stage of decomposition, but they appeared when about a 30% of the initial litter had decomposed. Under wet conditions faecal pellet production was very high and a mass balance suggested that soil fauna activity may result in a net flow of organic matter from the lower organic horizons to the surface Oi horizon. All this suggested that soil microclimate, and in particular water availability, seem to limit faunal activity in Mediterranean areas. According to this fact, litter accumulation in Mediterranean forest soils will likely relate to spatial variability of water rather than to the distribution of soil faunal activity.

Decomposition rate and composition of the soil arthropod community were studied in a severely and less severely burned patch of Mediterranean *Pinus halepensis* Mill. forest burned by a large scale summer wildfire. Aleppo pine forests cover approximately 3×10^6 ha in the Mediterranean basin in a relatively medium rainfall regime. Fire incidents are very common in the Mediterranean. It has long been accepted that fire is an environmental factor shaping the Mediterranean landscapes, consuming a lot of ha of Conifer forest, especially in Greece, Italy, Spain, France and Portugal.

The soil fauna plays an important role in the mineralization of organic matter through its feeding and locomotory activities. Saprophagous invertebrates eat the dead organic matter, assimilate part of it (McBrayer and Reichle 1971) and egest the remainder, which may preferentially be invaded by microflora (Standen 1978). Numerous studies suggested that it is fire regime (frequency and intensity) and season of burning that mostly affects the soil biota, in which a reduction in both the number and the density of taxa in the organic horizon occurs after the fire event.

Radea and Arianoutsou (2000) investigated the decomposing activity of the soil biota estimating the dry mass loss of pure cellulose and describing the composition of the soil

arthropod community in *Pinus halepensis* forest of Greece. The study suggested that the overall decomposition of cellulose follows the same pattern in both burned patches and mesh bag treatments indicating a similar pattern of decomposer biota activity too. The role of soil arthropods in the decomposition process seems to be less critical as decomposition was successfully accomplished despite the obvious reduction in the number and the density of soil arthropod taxa. Although the composition of soil arthropod community was found to be richer in the less-severely burned patch, Radea and Arianoutsou (2000) demonstrated that the seasonality of the Mediterranean climate constituted the principal environmental factor affecting the composition of soil arthropod community.

Eaton *et al.* (2004) studied if Collembolan abundance could be impacted by soil compaction, organic matter removal, and vegetation control on a loblolly pine (*Pinus taeda* L.) plantation.

Results from population analysis suggested that Collembola are sensitive to disturbances in the organic matter layer. These disturbances may be direct, such as the removal of the organic matter layer, or indirect, such as the changes in microclimate and reduction of quality or quantity of litter, that may occur as a result of vegetation control. The most dramatic effects on the Collembola population occurred in the treatments that likely had the greatest impact on humidity and temperature. These treatments can adversely affect Collembolan populations by decreasing or removing the habitat and increasing the variation of litter temperatures, which affects the moisture levels in the litter layer.

Cassagne *et al.* (2004) studied the differences of collembolan communities within the organo-mineral A layer in relation to the litter shift (replacement of beech by spruce) and to relate these changes to physico-chemical soil properties. The substitution of broad leaf forest by conifer plantation clearly favoured the formation of moder humus, showing a decrease in litter quality. This change in humus characteristic after plantation was characterized by slight differences in physico-chemical components by greater differences in the collembolan communities. The main changes in the A horizon were a significant decrease in moisture, cation concentrations (K, Ca, and Mg) and in soil pH. A severe depletion of Collembola under spruce was observed. The loss of mineral elements must indirectly influence distribution of the collembolan species, many authors (Chagnon *et al.* 2000; Cassagne *et al.* 2003) have in fact shown a relationship between Collembola and exchangeable cations. The evergreen growth of spruce enhance the interception of precipitation, leading to lower soil moisture in litter and soil which is linked to arthropod community structure. Thus, Collembola changes are mainly linked to environmental disturbances affecting bioclimatic conditions and the physical characteristic of the soil.

The impact of the admixture of beech in spruce monocultures on structure and function of the decomposer community was studied also by Elmer *et al.* (2004). With respect to ecosystem functioning, the soil invertebrates play a decisive role in decomposition processes (Schröter *et al.* 2003). The structure of the invertebrate decomposer community and its effects on soil processes is determined mainly by habitat parameters.

The functional profile of the nematodes, enchytraeids, lumbricids and dipterans was analyzed on the basis of ecological guilds. Gradual changes with rising coverage of beech culminated in intense differences of entire biomasses and metabolic equivalences between the mature stands indicating a higher decomposition potential of the invertebrate decomposer community by the admixture of beeches in spruce forests, the quality of the beech litter and the microbial community therein seemed to be the most important factors for these changes.

Free-living soil nematode communities represent the most abundant multicellular animal group on earth and are known to be an important component of the soil biota (Bongers and Bongers 1998). Pen-Mouratov *et al.* (2004) studied

the effect of soil water and organic matter content in the rhizosphere of perennial plant in arid environment, demonstrating that during wet periods the increase in soil moisture was followed by an increase in the total number of nematodes. During dry season a change in the total number of nematodes was more dependent on organic matter content than on soil moisture. Altieri (1999), in his paper on biodiversity on agroecosystems, suggested that internal functional regulation depends mainly on the plant and animal biodiversity present in the system. In natural systems, the regulation of inputs is mediated by unpredictable abiotic inputs. Soil nematode adaptation to the fluctuating environment may serve as a valuable mediator of plant-available nutrients, thus aiding in the conservation of nutrient flow in poor natural systems as conifer forests.

THE ROLE AND FUNCTION OF ORGANIC MATTER IN SOIL

Plant litter materials provide the primary resources for organic matter formation in soil. The amount of plant litter, its composition, and its properties are essential controlling factors for the formation of SOM and humification processes in terrestrial ecosystems (Swift *et al.* 1979; Scholes *et al.* 1997; Kögel-Knaber 2002).

Soil organic matter encompasses the soil biota and plant animal tissue at varying stages of decomposition. There is no doubting the importance of SOM in the fertility, productivity, and sustainability of ecosystems. SOM is a critical component of the soil resource base, which affects the biological, chemical, and physical processes of the soil and, through the effect on these processes, fulfils a very wide range of functions (Wild 1995). SOM is the driving force for biological activity as the primary source of energy and nutrients for many soil organisms. A direct effect of this biological activity is seen in the macro structure of soils, through the formation of soil pores as a consequence of faunal activity and root and fungal growth. Larger but less direct effects of biological activity are the resultant changes in the organic compounds of SOM that result from biological breakdown and the concomitant mineralization (transformation of organically bound elements (C, N, S, P) into inorganic compounds (CO_2 , CH_4 , NH_4^+ , NO_3^- , SO_4^{2-} , HPO_4^{2-}) and immobilization of nutrients (microbial sequestration of nutrients) (Zech *et al.* 1997). The microbial biomass is overriding importance for the subsequent delivery of nutrients by SOM turnover particularly in forest. A decrease in microbial biomass, due to seasonal weather change (decrease of temperature and moisture) would be followed by a release of nutrients, while an increase in microbial biomass would result in an immobilization of nutrients.

The relative importance of these different functions varies with soil type, climate, and farming system (Tiessen and Shang 1998).

The most important function of organic matter in soil is as a reserve of the nutrients required by plants. The amount and dynamics of soil C differ with soil type, particularly with mineralogy, climate, and management; decomposition is closely related to humification, mineralization, DOM dynamic, and SOM stabilization. During the first phase of decomposition, rapid mineralization of labile components is the dominant process. In the second phase of decomposition, mineralization still occurs but is slowed down to the accumulation of refractory molecules. Besides temperature and water regime, the amount and chemical composition of the primary and secondary resources control SOM dynamic and, especially, humification (Swift *et al.* 1979).

Dissolved organic matter, consisting of humic substances and other organic compounds dissolved in the soil solution, such as amino acids, carbohydrates, aliphatic acids, aromatic acids, phenolic acids and hydrocarbons (Kalbitz *et al.* 2000a, 2000b), although represents only a small part of soil organic matter, is involved in many soil processes (Chantigny 2003). DOM is an important substrate for mi-

crobial growth in soil, but its production is also partly mediated by microbes (Qualls and Haines 1992). Therefore, DOM may be the key constituent for microbial degradation of organic matter in soils. DOM plays an important role in the cycling of carbon and nutrients, especially N, P, S, because the nutrients in the soil solution are more available, both to soil microbes and plants, than thus occurring in the soil organic matter (Herbert and Bertsch 1995).

Dissolved organic matter in soil

Dissolved organic matter is a major vehicle for the leaching of many elements from the forest floor; for example, in many forest ecosystems half or more than half of the N in soil solution is in organic form (Smolander *et al.* 2001). The primary sources of dissolved carbon are considered to be leaching of substances from fresh litter and the products of plant residue decomposition (Qualls *et al.* 1991). Depending on tree species, there are differences in the leaching of substances from litter; water soluble substances are more easily leached from the leaf litter of deciduous species than from coniferous species. In spite of high variation within tree species, there are species-specific differences in the composition of plant secondary metabolites; e.g. mono-, sesqui- and diterpenes are typical for conifers, while birch contains higher terpenes and other polycyclic compounds. Don and Kalbitz (2005) evaluated the effects of tree species on dissolved organic carbon (DOC) production and the relationship between litter decomposition and the amount and quality of DOC. UV and fluorescence spectra of percolates from pine and spruce litter indicated an increasing degree of aromaticity and complexity with increasing mass loss as often described for decomposing litter. However, for deciduous litter the relationship was less obvious. During litter decomposition the source of produced DOC in coniferous litter tended toward a larger contribution from lignin-derived compounds. Biodegradability of DOC from fresh litter was very high. DOC from degraded litter was less mineralizable than DOC from fresh litter. Leaching of DOC from litter is affected by litter decomposition. The quantity and especially the quality of released DOC depend on the litter species. Taking into account the large DOC production from decomposed needles it possible to suggest the important role of DOC in the accumulation of organic matter in soils during litter decomposition particularly in coniferous forests.

The turnover of dissolved organic matter is considered to be important in cycling of soil carbon and nitrogen (Kalbitz *et al.* 2000). Positive relationships have been reported between CO_2 release and concentration of dissolved organic carbon in soil (Marschner and Kalbitz 2003). The high degradability of DOM has been related to low aromaticity and high proportion of carbohydrates, hydrophilic compounds (Jandl and Sollins 1997) and low molecular weight compounds (Hongve *et al.* 2000). The processes of DOM in soils are affected by the soil physico-chemical environment (Marschner and Kalbitz 2003) and the presence of plants and mycorrhizae (van Hees *et al.* 2003).

Soil under birch showed more microbial activity than did soil under pine or spruce (Smolander *et al.* 2005) and the concentration of DOC has been found to be highest under birch. The composition and degradability of DOM can be different in soils under different tree species. Conifer litter contains more hydrophobic aromatic compounds, whereas deciduous leaf litter contains more easily degradable, hydrophilic, low molecular weight compounds. Kiikkila *et al.* (2005), comparing the degradability of DOC in litter of deciduous and conifer, found that the degradability of DOC was highest in the litter layer under birch. The most degradable fractions were the hydrophilic classes of DOC. The degradability seemed to be related to low C to N ratios and to different role of bacteria and fungi in the mineralization of organic matter. Bacteria and fungi degrade the labile DOM, but fungi degrade mainly the most refractory compounds, suggesting a possible causal relationship between soil microbial activity and characteristics of soil

organic matter.

Phenolic acid in soil

Low molecular weight (LMW) organic acid and phenolic acids, although representing only a small fraction of the DOM, exert a disproportionate influence on soil processes since they are among the most reactive forms of C in the soil (Fox 1995). Phenolic acids in soil represent an important group of compounds with ecological functions, influencing rates of nutrient turnover in soils (Inderjit and Mallik 1997).

Phenolic compounds of low molecular weight occur widely in soils (Flaig 1971); they arise mainly from decomposing plant materials, although some of the compounds may be synthesized by soil micro-organisms (Flaig 1971; Kuiters and Sarink 1986). The presence of plants has been shown to influence litter production quantity (Hobbie 1992) and litter tissue chemical composition (Bonan 1990) such as C:N, lignin:N, and phenolic compound concentrations. Phenolic compounds in soils may play a dominant role controlling many aspects of plant-soil interactions, interfering directly with ion transport, protein synthesis, hormone activity and energy metabolism (Leather and Einhelling 1988; Muscolo and Sidari 1998; Muscolo *et al.* 2001, 2002). Moreover one of the most prominent properties of phenolic compounds is their capacity to form recalcitrant complexes with protein and thus to alter the pool and form of nutrients (Hättenschwiler and Vitousek 2000) influencing supplies of available N.

There is growing evidence that phenolic compounds play a central role in controlling litter degradation rates and nutrient cycling processes in forest systems (Northup *et al.* 1995). Direct toxicity of some of these molecules on tree seed germination (Odén *et al.* 1992; Muscolo and Sidari 2006), tree seedlings (Muscolo *et al.* 2005), and microorganism growth (Blum 1998) is also well documented. The establishment of such interactions has led to the identification of numerous phenolic compounds both in plant material and soil organic layers. The ecological relevance of phenolic compounds, important constituents of coniferous needle material, can be of special interest in N-limited ecosystems such as coniferous Mediterranean ecosystems.

Phenolics have also potential to create a nutrient-poor condition in terms of low availability of certain nutrients, decreasing the amount of organic N, organic matter, and phosphate. This could be due to higher microbial activity at the cost of added phenolic compounds (Harper 1977) explaining why plants on nutrient-poor soils, as coniferous forests, often have high concentrations of phenolics (Chapin 1995). The soil microbial population are able to use phenolic compounds as a carbon source, even when these substances are in high concentrations in the soil, suggesting that phenolics play an important role as regulators of population dynamics of microorganisms in soils. Biologically active concentrations of phenolics in soils can vary throughout the year, depending on various factors such as microbial activity, adsorption on colloids, humidity, etc. (Blum 1998). Soil can be considered the "black box" of the forest ecosystem and the effect of microbial activity on the phenolic pool should not be underestimated.

Souto *et al.* (2000) suggested that plant-produced phenolic compounds inhibited soil microbial activity and were involved in the failure of natural regeneration of Norway spruce (*Abies alba* Mill.) in French forests. Muscolo and Sidari (2006) showed clear seasonal variation of phenolic content in soils, with largest concentrations of water soluble phenolic acids in autumn (598 mg kg⁻¹D.W.) and smallest concentration (187 mg kg⁻¹D.W) in summer (Fig. 4). The observed increase of phenol concentration in autumn resulted from the high leaching rates of phenols from freshly fallen litter during the first stage of the decomposition as already reported by Kuiters and Denneman (1987). The observed decrease in phenol concentration in spring and even more in summer presumably resulted from an increase in

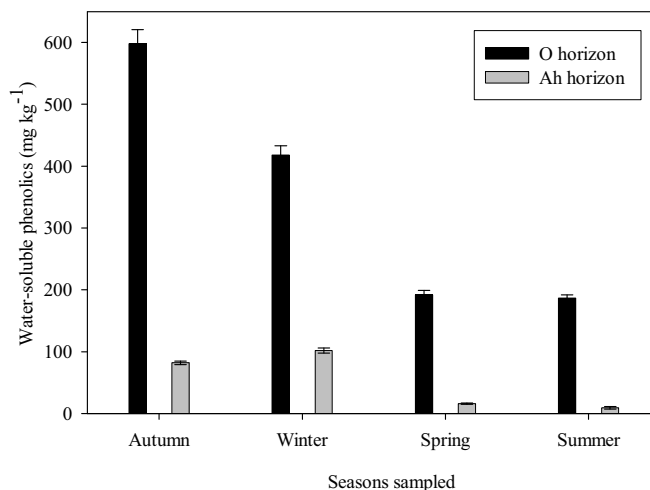


Fig. 4 Seasonal fluctuation in water-soluble phenolics extracted from O and Ah horizons of forest soil supporting *Pinus laricio* trees.

microbial population which used phenolic compounds as carbon source (Blum 1998; Souto *et al.* 2000). Changes in water-soluble phenolic concentration along the soil profile and over the seasons were explained by variation in the composition of microbial species (Souto *et al.* 2000) Qualitative and quantitative differences in water-soluble phenolic compounds were also due to different humication process that occurs among the seasons (Gallet and Pellissier 1997). In short, Muscolo and Sidari (2006) showed that phenolic compounds are always present in forestry soil, their amount and composition is clearly linked to seasonal changes, their effects are species-specific and concentration dependent. These characteristics may influence the density and the composition of individual plant communities inducing, in part, the cycle of natural regeneration of forest tree species.

MICROBIAL BIOMASS

All organic matter deposited on, or in the soil is decomposed and mineralized mainly through the activities of fungi, bacteria and soil animals. Soil microorganisms are therefore of prime importance in maintaining the fertility of terrestrial habitats (Garcia *et al.* 2002), and factors which alter the rates of microbial processes in the soil are consequently of importance for the functioning of forest ecosystems.

The microbial biomass is responsible for the nutrient cycling and the development and functionality of the soil system (Smith and Papendick 1993). Microorganisms play a fundamental role in carrying out biogeochemical cycles in soil and in the formation of soil structure (Roldan *et al.* 1994). Due to the complex dynamics of soil ecosystems, no single property is satisfactory for studying microbial activity. However, there is growing evidence that soil microbiological and biochemical parameters may be used as early and sensitive indicators of soil ecological stress or restoration (Dick 1997), and soil microbial activity in Mediterranean climates (Garcia *et al.* 1997a). Among the many factors which are implicated in the control of soil biogeochemical cycles, microbiological and biochemical parameters have particular importance in Mediterranean coniferous forests, where the degradation of plant cover has a direct bearing on the scarcity of organic matter which is considered as the principal precursor of sustainability. At present, Mediterranean forests are highly constrained by dry conditions and to a lesser extent by nutrient deficiency, N in siliceous soils (Sabaté and Gracia 1994) and P in calcareous soils (Sabaté *et al.* 2002).

Soil humidity is one of the major environmental factors that are decisive for the development of microorganisms; in fact, at prolonged water deficit the development of these organisms is limited. Thus, microbial biomass, representing an important labile pool of nutrients in soil (Henrot and Ro-

bertson 1994), plays an important role in nutrient transformation, so changes in size of the microbial biomass pool may also indicate changes in the soil organic matter pool that are not otherwise easily detectable. Many abiotic factors affect microorganisms in soil. Nicolardot *et al.* (1994) showed that the microbial biomass was highly influenced by temperature: 40-60% of labelled C or N incorporated in the biomass remained in this compartment at 20-28°C, while corresponding values at 4-12°C were only 0-40%. Gestel *et al.* (1993) studied the effect of moisture on turnover of microbial biomass evidencing that high moisture content (70%) is decisive for their development. Kaiser *et al.* (1992) showed that biomass and activity of the soil microflora were significantly related to clay content, suggesting a clay dependent capacity of soils to protect microbial biomass. Carter (1986) found a correlation between pH and microorganisms, low pH values in soil caused the decline of microbial biomass. Topography plays a critical role in modifying microclimate conditions within a landscape; particularly, water availability which can influence or control the type and intensity of soil processes within a landscape (Pennock *et al.* 1992). Microbial response to topographic control on moisture and nutrient redistribution within a forest landscape may alter nutrient cycling processes and, consequently, influence nutrient losses (Chen and Chiu 2000). Thus, it would be logical to suggest that topographic characteristics may affect soil microbiological processes. Muscolo and Sidari (unpublished data) found a strong influence of slope aspect on the microbial population in coniferous mountain soil of Southern Italy. In the soil on the south-facing slope they found that the amount of MBC was three-fold greater (3650 MBC, $\mu\text{g C g}^{-1}$ soil) than in the soil on the north-facing slope (1050 MBC, $\mu\text{g C g}^{-1}$ soil). The highest number of microbial biomass was found on the southern slope as the moisture supply was preserved there. In conclusion, soil aspect may induce differences in abiotic factors, such as soil temperature, water content, and soil physical properties which in turn can modify the biotic soil component. This complex interaction of biotic and abiotic factors related to soil aspects affects microbial biomass and, in turn, forest ecosystem development and productivity.

Microbial biomass varies also with seasonal patterns of soil temperature, moisture, and availability of substrate (Sarithchandra *et al.* 1989). Studies that have examined the seasonal effects on microbial activity and biomass size of the subsurface have been contradictory. Kaiser and Heinemeyer (1993) observed a greater microbial biomass size in the summer as compared to winter and suggested this is a direct consequence of higher temperatures. Sarathchandra *et al.* (1989) showed that soil microbial biomass was greatest in the spring and lowest in the summer and winter. Holmes and Zak (1994) reported no differences in the size of the biomass as related to season. For surface horizon, Buchanan and King (1992) and Palmisano *et al.* (1991) found higher microbial activity in the summer than in the winter.

The range of oscillations of abiotic variables in Mediterranean regions is more pronounced than in temperate regions (Stamou 1998), and climate is seasonal, with a hot, dry summer and a mild, wet winter (Aschman 1973). A prerequisite for a change in microbial activity is if the chemical, physical or microclimatological properties of the soil are altered in some way (Zimmermann and Frey 2002).

Muscolo and Sidari (2006) have shown a seasonal variation in microbial biomass content in the litter and Ah horizon of forest soil supporting *Pinus laricio* trees (Fig. 5). The results indicated largest concentrations of microbial biomass in spring and lowest amount of microorganisms in winter. Soils of the Mediterranean region of Southern Italy are moister in spring, suggesting that fluctuation of microbial biomass can be associated with seasonal change in ground water levels. In coniferous forests, fungi are the major colonizers and contributors to needle litters decomposition (Ormeno *et al.* 2006). The activity of decomposers in litter and soil may vary with season due to changes in temperature or water availability. A relatively high decomposer

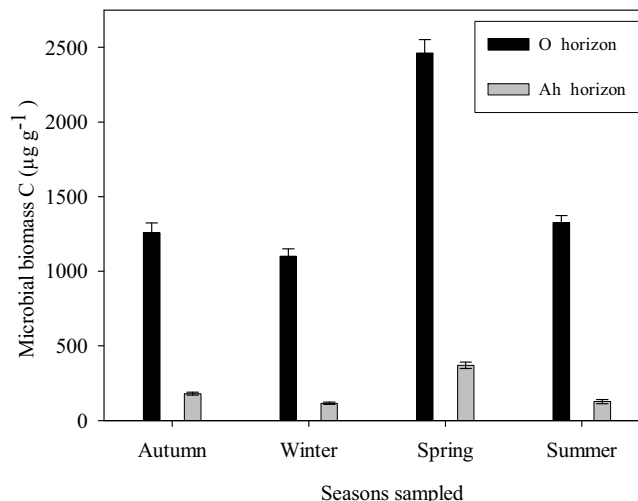


Fig. 5 Seasonal variation in microbial biomass C content in O and Ah horizons of forest soil supporting *Pinus laricio* trees.

number was coupled with high soil moisture (Radea and Arianoutsou 2000), suggesting that in the Mediterranean climate, the seasonality of soil humidity can be more important than temperature for the decomposition processes (De Angelis *et al.* 2000). For litter-decomposing fungi, Berg (1991) demonstrated that a higher soil moisture level had a significant effect on the amount of live fungal biomass in decomposing Scots pine needle litter. Ormeno *et al.* (2006) showed that soil moisture strongly improved leaf litter colonization by fungi in Mediterranean ecosystems. Another important factor improving leaf litter colonization by fungi is litter quality (Albers *et al.* 2004). High content of lignin have a rate-reducing influence on litter decomposition both in early and later stages, in particular, when associated with high N content. Nevertheless, a high nitrogen content generally regulates the early stages by enhancing the growth of microorganisms that degrade labile compounds, and repress the formation of lignolytic enzymes (Keyser *et al.* 1978). In a high N environment, the growth of many microorganisms able to decompose lignin, such as the *Basidio-mycetes*, is reduced, because such slow-growing fungi are unable to compete with fast-growing microbes and are eliminated from decomposer community (Couteaux *et al.* 1995). Lignin, in contrast, regulates the later stages of litter decay and high concentration of Mn, essential for some lignin-degrading enzymes such as Mn peroxidases, which enhance decomposition. Thus, litter decomposition rate is determined by quality of litter in terms of the abundance of its different components as well as soil nutrient availability and climatic factors (Virzo de Santo *et al.* 1993).

High N litter content has been shown to enhance leaf litter colonization by fungi and leaf litter decomposition (Gartner and Cardon 2004). Virzo de Santo *et al.* (2002) found that under a Mediterranean climate in different *Pinus* forests there was not only a significant correlation with the amount of fungi and substrate quality, but also with seasonality, showing that environmental factors most important in regulating the turnover rate of litter should be those that regulate the activity of fungi or bacteria that constitute the community of microbial decomposers.

ENZYME ACTIVITIES AND NUTRIENT CYCLE

One essential microbial function in soils is the processing and recovery of key nutrients from detrital inputs and accumulated organic matter. This requires the activity of extracellular enzymes to process complex organic compounds into assimilable subunits (sugars, amino-acids, NH_4^+ , PO_4^{3-}).

The trend in soil microbial biomass and enzyme activity varies with plant species, and it is dependent on the combination of soil moisture, temperature, root activity, and organic matter return to soils via litter fall (Kramer and Green

2000). Each change in soil chemistry and litter quality can result in different enzyme activities into the decomposing litter, which in turn can result in an increased rate of litter decomposition (Carreiro *et al.* 2000).

Soil organic matter decomposition by soil microorganisms is regulated by the synthesis of extra-cellular enzymes (Couteaux *et al.* 1995). Soil enzymes are biological catalysts of specific biochemical reactions, fundamental to maintain soil fertility, which can be modified by a variety of factors (Sinsabaugh 1994).

Soil enzymes are "sensors" of soil status since they integrate information about soil microbial biomass and soil physico-chemical conditions. The microbially secreted enzymes constitute an important part of the soil matrix as extracellular enzymes, also called abiotic enzymes (Sinsabaugh 1994). Factors influencing soil microbial activity exert control over soil enzyme production and control nutrient availability and soil fertility (Sinsabaugh *et al.* 2003). Soil enzyme data have been the foundation for the development of conceptual models that provide a more comprehensive understanding of those key processes linking microbial populations and nutrient dynamics. Schimel and Weintraub (2003) developed a simple theoretical model to explore the dynamics of the decomposition-microbial growth system when the fundamental kinetic assumption is changed from simple first order kinetics to decomposition that is catalyzed by an exoenzyme system. SOM decomposition is catalyzed by extracellular enzymes that are produced by microorganisms. An analysis of the enzyme kinetics showed that there must be some mechanism to produce a non-linear response of decomposition rates to enzyme concentration – the most likely is competition for enzyme binding on solid substrates as predicted by Langmuir adsorption isotherm theory. This non-linearity also induces C limitation, regardless of the potential supply of C. The linked C and N version of the model showed that actual polymer breakdown and microbial use of the released monomers can be disconnected, and that it requires relatively little N to maintain the maximal rate of decomposition, regardless of the ability of microbial biomass to use the break-down products. In this model, adding a pulse of C to an N limited system increases respiration, while adding N actually decreases respiration (as C is redirected from waste respiration to microbial growth). For many years, researchers have argued that the lack of a respiratory response by soil microbes to added N indicates that they are not N limited. This model suggests that conclusion may be wrong. While total C flow may be limited by the functioning of the exoenzyme system, actual microbial growth may be N limited.

These model constructs add mechanism to the standard first order decomposition models, and through this, add insight into the nature of soil enzyme and microbial dynamics.

In Mediterranean ecosystems, the most serious effects of climate change may well be those which are related to increased drought, since water stress is already the principal constraint in Mediterranean areas (Mooney 1989). In these water-limited ecosystems, increased temperatures will further decrease soil water-availability, and act as an obstacle to microbial activity.

Soil enzyme activity showed a considerable sensitivity to slight decreases in water availability; Sardans and Peñuelas (2005) indicated a decrease in enzyme activity with drought increase, putting in evidence the critical role of water for microbial enzyme activity in Mediterranean soils. The decrease in the activity of soil enzymes involved in the recycling of phosphorus, nitrogen and carbon will affect, in the long-terms, soil nutrient availability, reducing the nutrient supply by plants.

Numerous studies on enzymes exist and comparisons have been made in various soils subjected to different climatic conditions and management practices. Garcia *et al.* (1997b) found that dehydrogenase activity is a good index of the status of soil microbial activity in the Mediterranean areas. Enzymes involved in the dehydrogenase assay are

mainly intracellular, so that a correlation between dehydrogenase and oxygen uptake or CO₂ release by bacterial population is expected. In fact, dehydrogenase has been widely used to measure the catabolic activities in soil, which are correlated with microbial activity (Skujins 1976) and to compare soils under different crops, as well as natural and cultivated soils (Masciandaro *et al.* 1998). Garcia *et al.* (2002) found a significant correlation among the content of organic matter, microbial biomass and dehydrogenase activity in soil of Central Spain, suggesting that a lower quantity of plant residues contributed to a lesser degree of enzyme synthesis. It is clear that plant cover markedly influence soil microbial parameters. The high concentration of various soil enzymes such as dehydrogenase, urease or phosphatase was found in forest sites with higher organic carbon levels and microbial population numbers.

The effects relative to landscape factors, such as soil aspect and microclimate, on the microbial biomass, enzyme activities, and organic matter have been less investigated.

Topography in forest ecosystems significantly affects the trend of soil organic matter, which is acknowledged to be among the most important soil physicochemical properties influencing population dynamics, activity, and ecology of the soil microbiota (Stotzky 1997). It is generally accepted that the microbial population is positively related to organic matter content (Sparling *et al.* 1994). Muscolo and co-workers (unpublished data) studied the enzyme activities and nutrient cycles in a *Pinus laricio* forest of southern Italy. The stands were characterized by a diverse position in the landscape, which caused a different microclimatic condition (soil temperature and moisture). They found that in soil on the south-facing slope the level of acid phosphatase, alkaline phosphatase, dehydrogenase, protease and urease activities was three-fold greater than in the soil on the north-facing slope, evidencing that the soil enzymes investigated in their study exhibited activities that were related to the MBC amount, according to Dick (1984), who observed a close relationship between content of microbial biomass, soil organic matter and enzyme activities.

Soil aspect may induce differences in abiotic factors, such as soil temperature, and water content, which in turn can modify the biotic soil component. Changes in plant growth and species composition are influenced strongly by dynamic of soil microorganisms which, mediating the decomposition of organic matter, participate in N, P, C, and others chemical cycles influencing nutrient turnover and soil productivity (Donnison *et al.* 2000).

Soil enzyme activity showed a considerable sensitivity to slight decreases in water availability (Papatheodorou *et al.* 2004; Sardans and Peñuelas 2005). The reductions of enzyme activities put in evidence the critical role of water for microbial enzyme activity in the coniferous Mediterranean soil, suggesting that soil enzyme function can be interpreted and discussed on the basis of the amount of soil microorganisms. Muscolo and Sidari found that urease, a hydrolase involved in the N cycle was mainly present in forest soils of southern Italy, under *Abies alba*, where a greater amount of microbial population was found, suggesting not only that this enzyme is greatly dependent on microbial activity, but also that the reduction of soil microbial metabolism affected the biological transformation of N. Similar to urease, the values of phosphatases enzymes involved in the transformation of organic and inorganic P compounds in soil (Amador *et al.* 1997) were higher (1.220 $\mu\text{mol } p\text{-nitrophenol released/g/h}$, with activity ranging from 0.152 to 2.544) in soil with a higher amount of microorganism (fungal population and heterotrophic bacteria), confirming the existence of a positive correlation between enzymatic activity and microbial biomass. These data are in agreement with those of Jha *et al.* (1992) and Garcia and Hernandez (1996) in that low hydrolase values corresponded to low amount of microbial biomass. Enzyme activities can vary also depending on the seasonal climate, in fact, in Mediterranean area the highest activities occur in spring together with the most microbial activity (Garcia *et al.* 2002; Muscolo and Sidari

2006). These findings point to an indirect effect of drought on community productive capacity in coniferous Mediterranean forests through a decreased soil enzyme activity that reduce the potential transformation rate of organic matter. This effect can be a key factor in the possible degradation process that drought can have on Mediterranean plant communities. In Mediterranean areas of Southern Italy, coniferous forest decline can be well correlated with soil enzyme activity decline.

Effect of forest management on soil dynamics

In contrast to other part of the world the Mediterranean basin has a long history of human disturbance that has affected structures and functions of most of the forests and in general plant communities of the region. Sustainability of forest plantations, in terms of long term production and maintenance of site quality, is one of the main objectives of silviculture production. However, concerns have been raised about the sustainability of intensively managed forests, such as plantations, following identification of a range of possible impacts of clearcutting and intensive site preparation techniques on soil properties that determine productivity (Nambiar 1996). Forest management and soil disturbance during site preparation alter soil functions associated with forest sustainability, such as structure, aeration, water retention capacity, and can also disrupt certain biological processes involved in nutrient availability (Ross *et al.* 1995).

Thus, it is necessary to identify and experiment appropriate management procedures for an adequate conservation of ecological functions. Management procedures to be adopted require a better understanding of the soil properties in forest ecosystem, and how it responds to different silvicultural operations.

Fragile and unstable ecosystems, like the Mediterranean ones, are often unable to produce large quantity of woody biomass per unit area; consequently, intensive management is often incompatible with the other roles of forests such as soil conservation. Pressure on these ecosystems can be partially reduced if the more fertile and stable Mediterranean ecosystems are managed in a more intensive, although durable, way.

Many management practices have a detrimental effect on the quantity and quality of soil organic matter which affects soil physical, chemical and biochemical properties and especially soil fertility.

Because SOM influences so many biogeochemical processes any disturbance that alters the organic matter cycle may have far-reaching consequences. Forest harvesting alters the organic matter cycle through the removal of above-ground tree-biomass for wood products and the alteration of the rates of a variety of other ecosystem processes. The removal of forest canopy decreases interception of atmospheric moisture and increases solar radiation inputs at the soil surface. These conditions likely stimulate microbial activity, thereby altering rates of organic matter decomposition (Moore 1989). Any changes in decomposition rates and patterns after clear-cutting are also likely to influence the amount or chemical structure as pH, exchangeable acidity, and CEC. Effects of clear-cutting on the properties of SOM have generally been inferred from changes in critical ratio such as C:N, C:OM, N:OM, and CEC:OM (Johnson 1997). Dai *et al.* (2001) showed that clear-cutting provokes complex hydrological, biogeochemical and ecological changes, suggesting a restructuring of organic matter pools, organic matter compounds, DOC and DOC fractions in soil solution and stream waters. Soluble organic matter pool in the soil became more aromatic after clear-cutting. The differences in soil solution organic matter chemistry are also likely to have implications for metal transport, nutrient availability and acid-base chemistry.

Despite changes in soil solution DOM and the soluble pool of SOM, clear-cutting had little impact on the structural chemistry of SOM.

To achieve ecosystem and economic sustainability a forest practice must achieve three different goals: (I) to be economically profitable and to perpetuate forest cover, (II) to preserve ecosystem structure (e.g. for biodiversity values) and (III) to preserve ecosystem function (e.g. nutrient cycle) (Sverdrup and Svesson 2002). Because of the large quantity of nutrients removed whole-tree harvesting can lead to decreased soil available reserves of limiting nutrients (Olsson *et al.* 2000). In addition to the nutrient export with biomass, nutrient losses by leaching can increase significantly after clear-cutting. Blanco *et al.* (2005) developed a simple biologically based model of nutrient cycling specifically suited for Mediterranean forests to evaluate the sustainability of current forest management practices. The result suggested that under Mediterranean conditions in *Pinus sylvestris* stands, N and P were particularly sensitive to overexploitation and in no case could whole tree removal be recommended as it may have a strong negative effect on nutrient reserves.

Thinning may cause temporal increase in soil fertility as a consequence of decomposition of logging residues (the aspart flux phenomenon, *sensu* Kimmins 2004). However decrease in litterfall and, therefore, in nutrients input to soil (Chertov *et al.* 1999, Blanco *et al.* 2006) following thinning, combined with nutrient removal in harvested biomass, may result in reduction of soil fertility if such practices are repeated in the long term (Blanco *et al.* 2005).

Muscolo *et al.* (2006) studied change in soil chemistry in small (185 m²) and medium (410 m²) gaps, created in mature silver fir (*Abies alba* Mill) stands (mean height 30 m) in the Calabrian Apennines (Southern Italy).

Within small gaps a greater amount of organic matter, compared to under canopy cover sites and medium gaps, was observed. On the contrary, in medium gaps a lower amount of organic matter content was detected. Moreover a different trend of the organic matter between small and medium gaps was observed. In fact, the decrease of organic matter content, associated to a lower amount of humic acid, compared to under canopy cover sites and small gaps, suggested that the organic substrate undergoes a mineralization rather than a humification process. An opposite trend is instead observed in small gaps. In fact, the increase of organic matter content, associated to an increase of humic acid amount, evidenced a better humification process compared to medium gaps and to forest sites, suggesting small gaps as the best silvicultural practices.

Muscolo *et al.* (2007), examined the impacts of small (380 m²), medium (855 m²) and large (1520 m²) gaps on microclimate, soil properties and microbial biomass, a 'sink' and 'source' of plants nutrients, in *Pinus nigra* (*Pinus laricio* Poiret) stands in Calabrian Apennine, Southern Italy. PAR transmittance significantly increased with increasing size of the gaps, consequently an effect of gaps size was found on microclimate: soil moisture and temperature were different among the gaps of different size showing the highest values of temperature in the large gaps and the highest values of moisture in the small gaps. Within small gaps the greatest amount of organic matter, humic matter and microbial biomass, and the highest C/N value were observed. The highest values of phosphatases, urease and FDA activities were detected in small gaps. An impact of gap size on C, N and P cycles was significant in small gaps in terms of higher availability of these nutrients and greater amount of humic matter, suggesting that small gaps may be important from an ecosystem perspective representing the appropriate management procedures for an adequate conservation of ecological functions, capable to preserve soil properties and favour *Pinus laricio* natural regeneration.

Lopez-Serrano *et al.* (2005) studied the effects of different silvicultural practices (thinning, scrubbing, pruning, and particular combination of them) on seedlings nutrient status in *P. halepensis* forest stands in South-eastern Spain, because nutrient content in plants could be used as a status indicator, closely related to the soil nutrient content. Silvicultural treatments affected foliar nutrient concentration, so

that the concentration of N, P and K were higher when treatments included thinning than those that did not. The effect of the treatments was markedly high along the first year after they were applied but the differences were attenuate 2 years later. For all cases analyzed in conifer forests of Mediterranean regions whole tree-removed should not be used as it may compromise long-term sustainability. Long term effects on current silvicultural practices must be evaluated for management effects on regeneration, harvesting age or size as well as forest to compile with current economic demands and ecological sustainability of forest resource management.

CONCLUSION

Over the last century, in Mediterranean ecosystems water stress is the principal constraint because temperatures have shown an overall trend towards warming (Peñuelas *et al.* 2002). Precipitation has either exhibited a long-term downwards trend, principally in the dry season (Esteban-Parra *et al.* 1998) or no significant change at all, even though in all cases a rise in the evapotranspiration potential has led to increased aridity (Piñol *et al.* 1998). Mediterranean coniferous forest soils often suffer from nutrient deficiencies and this precarious status can be enhanced by climate change. Drought has been found to affect microbial biomass and consequently soil enzyme activities and nutrient cycles. Higher temperatures can encourage microbial metabolism, increasing the nutrient turnover and availability, but, on the other hand, higher temperatures decrease soil water availability, which will very likely result not only in a decrease in nutrient uptake by roots but also in an obstacle to microbial activity. A decrease in soil microorganism and in enzyme activities in Mediterranean coniferous forest ecosystem, under drier conditions, might be critical because of the decrease in nutrient supply which affects coniferous growth.

Thus, these findings suggest that litter decomposition rate in coniferous forest soils of Mediterranean area varies according to plant species; soil organic matter decomposition and nutrient turnover depending on microbial biomass and enzyme activities, which are strongly affected by water content.

REFERENCES

- Albers D, Migge S, Schaefer M, Scheu S (2004) Decomposition of beech leaves (*Fagus sylvatica*) and spruce needles (*Picea abies*) in pure and mixed stands of beech and spruce. *Soil Biology and Biochemistry* **36**, 155-164
- Allen HL, Dougherty PM, Campbell RG (1990) Manipulation of water and nutrients- practice and opportunity in southern U.S. pine forests. *Forest Ecology and Management* **30**, 437-453
- Altieri MA (1999) The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems and Environment* **74**, 19-31
- Amador JA, Glucksman AM, Lyons JB, Gorres JH (1997) Spatial distribution of soil phosphatase activity within a riparian forest. *Soil Science* **162**, 808-825
- Aschman H (1973) Distribution and peculiarity of Mediterranean ecosystem. In: Di Castri F, Mooney HA (Eds) *Mediterranean Type Ecosystem*, Springer-Verlag, Berlin, Germany, pp 11-19
- Bardgett RD, Keiller S, Cook R, Gilburn AS (1998) Dynamic interactions between soil animals and microorganisms in upland grassland soils amended with sheep dung: a microcosm experiment. *Soil Biology and Biochemistry* **30**, 531-539
- Barnes BV, Zak DR, Denton SR, Spurr SH (1998) *Forest Ecology* (4th Edn), Wiley, NY, 774 pp
- Bauhus J, Paré D, Coté L (1998) The effect of tree species, stand age and soil type on soil microbial biomass and its activity in a southern boreal forest. *Soil Biology and Biochemistry* **30**, 1077-1089
- Berg B (1991) FDA-active fungal mycelium and lignin concentrations in some needle litter types. *Scandinavian Journal of Forest Research* **6**, 451-462
- Berg B (2000) Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology and Management* **133**, 13-22
- Berg B, Ekbohm G (1991) Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest VII. *Canadian Journal of Botany* **69**, 1449-1456
- Berg B, McLaugherty C (2003) *Plant Litter, Decomposition, Humus Formation, Carbon Sequestration*. Springer Verlag, Berlin, 286 pp
- Berg B, McLaugherty C, Virzo de Santo A, Johnson D (2001) Humus buildup in boreal forests- effects of litter fall and its N concentration. *Canadian Journal of Forest Research* **31**, 988-998
- Berg B, Virzo de Santo A, Rutigliano FA, Fierro A, Ekbohm G (2003) Limit values for plant litter decomposing in two contrasting soils- influence of litter elemental composition. *Acta Oecologica* **24**, 295-302
- Bird S, Coulson RN, Crossley DA Jr. (2000) Impacts of silvicultural practices on soil and litter arthropod diversity in a Texas pine plantation. *Forest Ecology and Management* **131**, 65-80
- Blanco JA, Imbert JB, Castillo FJ (2006) Effects of thinning on nutrient content pools in two *Pinus sylvestris* forests in the western Pyrenees. *Scandinavian Journal of Forest Research* **21**, 143-150
- Blanco JA, Zavala MA, Imbert JB, Castillo FJ (2005) Sustainability of forest management practices: Evaluation through a simulation model of nutrient cycling. *Forest Ecology and Management* **213**, 209-228
- Blum U (1998) Effects of microbial utilization of phenolic acids and their utilization of phenolic acid breakdown products on allelopathic interaction. *Journal of Chemical Ecology* **24**, 685-708
- Bonan GB (1990) Carbon and nitrogen cycling in North American boreal forests. 1. Litter quality and soil thermal effects in interior Alaska. *Biogeochemistry* **10**, 1-28
- Bongers T, Bongers M (1998) Functional diversity of nematodes. *Applied Soil Ecology* **10**, 239-251
- Borken W, Beese F (2005) Soil respiration in pure and mixed stands of European beech and Norway spruce following removal of organic horizons. *Canadian Journal of Forest Research* **35**, 2756-2764
- Borken W, Matzner E (2004) Nitrate leaching in German forest soils: an analysis of long-term monitoring sites. *Journal of Plant Nutrition and Soil Science* **167**, 277-283
- Buchanan M, King LD (1992) Seasonal fluctuations in soil microbial biomass carbon, phosphorus, and activity in no-till and reduced-chemical-input maize agroecosystems. *Biology and Fertility of Soils* **13**, 211-217
- Carreiro MM, Sinsabaugh RL, Repert DA, Pankhurst DF (2000) Microbial enzyme shifts explain litter decay responses to simulated nitrogen decomposition. *Ecology* **81**, 2359-2365
- Carter MR (1986) Microbial biomass and mineralizable nitrogen in Solonchic soils: influence of gypsum and lime amendments. *Soil Biology and Biochemistry* **18**, 531-537
- Cassagne N, Bal-Serín MC, Gers C, Gauquelin T (2004) Changes in humus properties and collembolan communities following the replanting of beech forests with spruce. *Pedobiologia* **48**, 267-276
- Cassagne N, Gers C, Gauquelin T (2003) Relationships between Collembola, soil chemistry and humus types in forest stands (France). *Biology and Fertility of Soils* **37**, 355-361
- Chagnon M, Paré D, Hebert C (2000) Relationships between soil chemistry, microbial biomass and the collembolan fauna of southern Quebec sugar maple stands. *Ecoscience* **7**, 307-316
- Chantigny MH (2003) Dissolved and water extractable organic matter in soils: a review on the influence of land use and management practices. *Geoderma* **113**, 357-380
- Chapin III FS (1995) New cog in the nitrogen cycle. *Nature* **377**, 199-200
- Chen J-S, Chiu C-Y (2000) Effect of topography on the composition of soil organic substances in a perhumid sub-tropical montane forest ecosystem in Taiwan. *Geoderma* **96**, 19-30
- Chertov OG, Komarov AS, Tsiplianovsky AM (1999) A combined simulation model of Scots pine, Norway spruce and silver birch ecosystems in the European boreal zone. *Forest Ecology and Management* **116**, 189-206
- Couteaux M, Bottner P, Berg B (1995) Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution* **10**, 63-66
- Dai KH, Johnson CE, Driscoll CT (2001) Organic matter chemistry and dynamics in clear-cut and unmanaged hardwood forest ecosystems. *Biogeochemistry* **54**, 51-83
- David JF, Devernay S, Loucougaray G, Le Floch E (1999) Below-ground biodiversity in a Mediterranean landscape: relationships between saprophagous macroarthropod communities and vegetation structure. *Biodiversity and Conservation* **8**, 753-767
- De Angelis P, Chigwerewe KS, Scarascia Mugnozza GE (2000) Litter quality and decomposition in a CO₂-enriched Mediterranean forest ecosystem. *Plant and Soil* **224**, 31-41
- Dick WA (1984) Influence of long-term tillage and crop rotation combinations on soil enzyme activities. *Soil Science Society of America Journal* **48**, 569-574
- Dick RP (1997) Soil enzyme activities as integrative indicators of soil health. In: Pankhurst CE, Doube BM, Gupta VVSR (Eds) *Biological Indicators of Soil Health*, CAB International, NY, pp 121-150
- Dix NJ, Webster J (1995) *Fungal Ecology*, Chapman and Hall, London, 549 pp
- Don A, Kalbitz K (2005) Amounts and degradability of dissolved organic carbon from foliar litter at different decomposition stages. *Soil Biology and Biochemistry* **37**, 2171-2179
- Donnison LM, Griffith GS, Bardgett RD (2000) Determinants of fungal growth and activity in botanically diverse haymeadows: effects of litter type and fertilizer additions. *Soil Biology and Biochemistry* **32**, 289-294
- Eaton RJ, Barbercheck M, Buford M, Smith W (2004) Effects of organic matter removal, soil compaction, and vegetation control on Collembolan pop-

- pulations. *Pedobiologia* **48**, 121-128
- Edmonds RL, Thomas TB** (1995) Decomposition and nutrient release from green needles of western hemlock and Pacific silver fir in an old-growth temperate rain forest, Olympic National Park, Washington. *Canadian Journal of Forest Research* **25**, 1049-1057
- Edwards CA, Reichle DE, Crossley DR** (1973) The role of soil invertebrates in turnover of organic matter and nutrients. In: Reichle DE (Ed) *Analysis of Temperate Forest Ecosystem*, Springer, Berlin, Germany, pp 147-172
- Elmer M, La France M, Förster G, Roth M** (2004) Changes in the decomposer community when converting spruce monoculture to mixed spruce/beech stands. *Plant and Soil* **264**, 97-109
- Esteban-Parra MJ, Rodrigo FS, Castro-Diez Y** (1998) Spatial and temporal patterns of precipitation in Spain for the period 1880-1992. *International Journal of Climatology* **18**, 1557-1574
- Fioretto A, Musacchio A, Andolfi G, Virzo de Santo A** (1998) Decomposition dynamics of litters of various pine species in a Corsican pine forest. *Soil Biology and Biochemistry* **30**, 721-727
- Flaig W** (1971) Organic compounds in soil. *Soil Science* **111**, 19-33
- Fox TR** (1995) The influence of low-molecular weight organic acids on properties and processes in forest soils. In: McFee WW, Kelly JM (Eds) *Carbon Forms and Functions in Forest Soils*. Soil Science Society of America, Madison, WI, USA, pp 43-62
- Gallet C, Pellissier F** (1997) Phenolic compounds in natural solution of coniferous forest. *Journal of Chemical Ecology* **23**, 2401-2411
- García C, Hernández T** (1996) Influence of salinity on the biological and biochemical activity of a calciorithid soil. *Plant and Soil* **178**, 225-263
- García C, Hernández T, Roldán A, Albaladejo J** (1997b) Biological and biochemical quality of a semiarid soil after induced revegetation. *Journal of Environmental Quality* **26**, 1116-1122
- García C, Hernández T, Roldán A, Martín A** (2002) Effect of plant cover decline on chemical and microbiological parameters under Mediterranean climate. *Soil Biology and Biochemistry* **34**, 635-642
- García C, Roldán A, Hernández T** (1997a) Changes in microbial activity after abandonment of cultivation in a semiarid Mediterranean environment. *Journal of Environmental Quality* **26**, 285-291
- García-Pausas J, Casals P, Romanyà J** (2004) Litter decomposition and faunal activity in Mediterranean forest soils: effects of N content and the moss layer. *Soil Biology and Biochemistry* **36**, 989-997
- Gartner TB, Cardon ZG** (2004) Decomposition dynamics in mixed-species leaf litter. *Oikos* **104**, 230-246
- Gestel MV, Merckx R, Vlassak K** (1993) Microbial biomass and activity in soils with fluctuating water contents. *Geoderma* **56**, 617-626
- Gholz HL, Perry CS, Cropper WP Jr., Hendry LC** (1985) Litterfall, decomposition, and nitrogen and phosphorus dynamics in a chronosequence of slash pine (*Pinus elliotii*) plantations. *Forest Science* **31**, 463-478
- Harper JL** (1977) *Population Biology of Plants*, Academic Press, NY, 892 pp
- Hart SC, Firestone MK, Paul EA** (1992) Decomposition and nutrient dynamics of ponderosa pine needles in a Mediterranean-type climate. *Canadian Journal of Forest Research* **22**, 306-314
- Hassall M, Turner JG, Rands MRW** (1987) Effects of terrestrial isopods on the decomposition of woodland leaf litter. *Oecologia* **72**, 597-604
- Hättenschwiler S, Vitousek PM** (2000) The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends in Ecology and Evolution* **15**, 238-243
- Heal OW, Anderson JM, Swift MJ** (1997) Plant litter quality and decomposition: a historical overview. In: Cadish G, Giller KE (Eds) *Driven by Nature: Plant Litter Quality and Decomposition*, CAB International, London, pp 3-30
- Hendricks JJ, Boring LR** (1999) N₂-fixation by native herbaceous legumes in burned pine ecosystems of the southeastern United States. *Forest Ecology and Management* **113**, 167-177
- Henrot J, Robertson GP** (1994) Vegetation removal in two soils of the humid tropics: effect on microbial biomass. *Soil Biology and Biochemistry* **26**, 111-116
- Herbert BE, Bertsch PM** (1995) Characterization of dissolved and colloidal organic matter in soil solutions: A review. In: Kelly JM, McFee WW (Eds) *Carbon Forms and Function in Forest Soils*. Soil Science Society of America, Madison, WI, USA, pp 63-88
- Hobbie SE** (1992) Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* **7**, 336-339
- Hole FD** (1981) Effects of animals on soil. *Geoderma* **25**, 75-112
- Holmes WE, Zak DR** (1994) Soil microbial biomass dynamics and net nitrogen mineralization in Northern hardwood ecosystems. *Soil Science Society of America Journal* **58**, 238-243
- Hongve D, van Hees PAV, Lundström US** (2000) Dissolved components in precipitation water percolated through forest litter. *European Journal of Soil Science* **51**, 667-677
- Inderjit, Mallik AU** (1997) Effects of *Ledum groenlandicum* amendments on soil characteristics and black spruce seedling growth. *Plant Ecology* **133**, 29-36
- Jandl R, Sollins P** (1997) Water-extractable soil carbon in relation to the below-ground carbon cycle. *Biology and Fertility of Soils* **25**, 196-201
- Jha DK, Shanna GD, Mishra RR** (1992) Soil microbial population number and enzyme activities in relation to altitude and forest degradation. *Soil Biology and Biochemistry* **24**, 761-767
- Johnson CE, Romanowicz RB, Siccama TG** (1997) Conservation of exchangeable cations after clear-cutting of a northern hardwood forest. *Canadian Journal of Forest Research* **27**, 859-868
- Jorgensen JR, Wells GG, Metz LJ** (1980) Nutrient changes in decomposing loblolly pine forest floor. *Soil Science Society of American Journal* **44**, 1307-1314
- Kaiser EA, Heinemeyer O** (1993) Seasonal variations of soil microbial biomass carbon within the plough layer. *Soil Biology and Biochemistry* **25**, 1649-1656
- Kaiser EA, Müller T, Roergensen RG, Insam H, Heinemeyer O** (1992) Evaluation of methods to estimate the soil microbial biomass and the relationship with soil texture and organic matter. *Soil Biology and Biochemistry* **24**, 675-683
- Kalbitz K, Geyer S, Geyer W** (2000a) A comparative characterization of dissolved organic matter by means of aqueous samples and isolated humic substances. *Chemosphere* **40**, 1305-1312
- Kalbitz K, Solinger S, Park JH, Michalzik B, Matzner E** (2000b) Controls on the dynamics of dissolved organic matter in soils: a review. *Soil Science* **165**, 277-304
- Kavvadias VA, Alifragis D, Tsiontsis A, Brofas G, Stamatelos G** (2001) Litterfall, litter accumulation and litter decomposition rates in four forest ecosystems in northern Greece. *Forest Ecology and Management* **144**, 113-127
- Keyser P, Kirk TK, Zeikus IG** (1978) Ligninolytic enzyme of *Phanerochaete chrysosporium*: synthesized in the absence of lignin in response to nitrogen starvation. *Journal of Bacteriology* **135**, 790-797
- Khiewtam RS, Ramakrishnan PS** (1993) Litter and fine root dynamics of a relic sacred grove forest at Cherrapunji in north-eastern India. *Forest Ecology and Management* **60**, 327-344
- Kiikkilä O, Kitunen V, Smolander A** (2006) Dissolved organic matter from surface organic horizons under birch and conifers: degradation in relation to chemical characteristics. *Soil Biology and Biochemistry* **38**, 737-746
- Kimmins JP** (2004) *Forest Ecology. A Foundation for Sustainable Management and Environmental Ethics in Forestry*. Prentice Hall, New Jersey, 611 pp
- Kirk TK, Farrell RL** (1987) Enzymatic combustion. The microbial degradation of lignin. *Annual Review of Microbiology* **41**, 465-505
- Kögel-Knaber I** (2002) The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. *Soil Biology and Biochemistry* **34**, 139-162
- Kramer S, Green DM** (2000) Acid and alkaline phosphatase dynamics and their relation to soil microclimate in a semiarid woodland. *Soil Biology and Biochemistry* **32**, 179-188
- Kuiters AT, Sarink HM** (1986) Leaching of phenolic compounds from leaf and needle litter of several deciduous and coniferous trees. *Soil Biology and Biochemistry* **18**, 475-480
- Kuiters AT, Denneman CAJ** (1987) Water-soluble phenolic substances in soils under several coniferous and deciduous tree species. *Soil Biology and Biochemistry* **19**, 765-769
- Lavelle P, Blanchart E, Martin A, Spain A** (1993) A hierarchical model for decomposition in terrestrial ecosystems: Application to soils of the humid tropics. *Biotropica* **25**, 130-150
- Leather GR, Einhelling FA** (1988) Bioassay of naturally occurring allelochemicals for toxicity. *Journal of Chemical Ecology* **14**, 1821-1828
- Lisanework N, Michelsen A** (1994) Litter fall and nutrient release by decomposition in three plantations compared with a natural forest in the Ethiopian highland. *Forest Ecology and Management* **65**, 149-164
- López-Serrano FR, de las Heras J, González-Ochoa AI, García-Morote FA** (2005) Effects of silvicultural treatments and seasonal patterns on foliar nutrients in young post-fire *Pinus halepensis* forest stands. *Forest Ecology and Management* **210**, 321-336
- Maguire DA** (1994) Branch mortality and potential litter fall from Douglas-fir trees in stands of varying density. *Forest Ecology and Management* **70**, 41-53
- Marschner B, Kalbitz K** (2003) Controls of bioavailability and biodegradability of dissolved organic matter in soils. *Geoderma* **113**, 211-235
- Masciandaro G, Ceccanti B, Gallardo-Lancho JF** (1998) Organic matter properties in cultivated versus setaside arable soils. *Agriculture and Ecosystem Environment* **67**, 267-274
- McBrayer J, Reichle E** (1971) Trophic structure and feeding rates of forest soil invertebrate populations. *Oikos* **22**, 381-388
- Miller HG, Cooper JM, Miller JD, Pauline OJL** (1979) Nutrient cycles in pine and their adaptation to poor soils. *Canadian Journal of Forest Research* **9**, 19-26
- Mooney H** (1989) Chaparral physiological ecology-paradigms re-examined. In: Keely SC (Ed) *Science Series No 34*, Natural History Museum of Los Angeles County, Los Angeles, USA, pp 85-90
- Moore TR** (1989) Dynamics of dissolved organic carbon in forested and disturbed catchments, Westland, New Zealand. 1. Miami. *Water Resource Research* **25**, 1321-1330
- Moreno JM, Fellous JL** (1997) Global change and the Mediterranean region. Report of the ENRICH/START International Workshop held in Toledo, Spain, Comité IGBP, Madrid España, 78 pp
- Mudrick DA, Hoosein M, Hicks RR, Townsend EC** (1994) Decomposition of

- leaf litter in an Appalachian forest: effects of leaf species, aspect, slope position and time. *Forest Ecology and Management* **68**, 231-250
- Muscolo A, Panuccio MR, Sidari M** (2001) Respiratory enzyme activities during germination of *Pinus laricio* seeds treated with phenols extracted from different forest soils. *Plant Growth Regulation* **35**, 31-35
- Muscolo A, Panuccio MR, Sidari M** (2002) Glyoxilate cycle in germination of *Pinus laricio* seeds. Effects of phenolic compounds extracted from different forest soils. *Plant Growth Regulation* **37**, 1-5
- Muscolo A, Sidari M** (1998) Evolution of phenolic compounds and humic substances in different forest soils of Aspromonte (Southern Italy) under different tree species. *Fresenius Environmental Bulletin* **7**, 197-202
- Muscolo A, Sidari M** (2006) Seasonal fluctuation in soil phenolics of a coniferous forest: effects on seed germination of different coniferous species. *Plant and Soil* **284**, 305-318
- Muscolo A, Sidari M, Mercurio R** (2007) Influence of gap size on organic matter decomposition, microbial biomass and nutrient cycle in calabrian pine (*Pinus laricio*, Poiret) stands. *Forest Ecology and Management* **242**, 412-418
- Muscolo A, Sidari M, Panuccio MR, De Santis C, Finocchiaro A** (2005) Early effects of phenolic compounds, extracted from two forest litters, on ammonium uptake and assimilation in *Pinus laricio* and *Pinus pinaster*. *Plant and Soil* **269**, 309-320
- Nakane K** (1995) Soil carbon cycling in a Japanese cedar (*Cryptomeria japonica*) plantation. *Forest Ecology and Management* **72**, 185-197
- Nambiar EKS** (1996) Sustained productivity of forests is a continuing challenge to soil science. *Soil Science Society of American Journal* **60**, 1629-1642
- Nevzat Gurlevik D, Keltling L, Allen HL** (2003) The effects of vegetation control and fertilization on net nutrient release from decomposing loblolly pine needles. *Canadian Journal of Forest Research* **33**, 2491-2502
- Naveh Z, Lieberman AS** (1993) *Landscapes Ecology, Theory and Application*, Springer, New York, USA, 360 pp
- Nicolardot B, Fauvet G, Cheneby D** (1994) Carbon and nitrogen cycling through soil microbial biomass at various temperatures. *Soil Biology and Biochemistry* **26**, 253-261
- Northup RR, Yu Z, Dahlgren RA, Vogt K** (1995) Polyphenol control of nitrogen release from pine litter. *Nature* **377**, 227-229
- Odén PR, Brandberg P, Andersson R, Gref R, Zackrisson O, Nilsson MC** (1992) Isolation and characterization of a germination inhibition from leaves of *Empetrum hermophroditum* Hagerup. *Scandinavian Journal of Forest Research* **7**, 497-502
- Olsson BA, Lundkvist H, Staaf H** (2000) Nutrient status in needles of Norway spruce and Scots pine following harvesting of logging residues. *Plant and Soil* **23**, 161-173
- Ormeño E, Baldy V, Ballini C, Larchevêque M, Périssol C, Fernandez C** (2006) Effects of environmental factors and leaf chemistry on leaf litter colonization by fungi in a Mediterranean shrubland. *Pedobiologia* **50**, 1-10
- Palmisano AC, Schwab BS, Marusick DA, Ventullo RN** (1991) Seasonal changes in mineralization of xenobiotics by stream microbial communities. *Canadian Journal of Microbiology* **37**, 939-948
- Papathodorou EM, Stamou GP, Giannotaki A** (2004) Response of soil chemical and biological variables to small and large scale changes in climatic factors. *Pedobiologia* **48**, 329-338
- Pen-Mouratov S, Rakhimbaev M, Barness G, Steinberger Y** (2004) Spatial and temporal dynamics of nematode populations under *Zygophyllum dumosum* in arid environments. *European Journal of Soil Biology* **40**, 31-46
- Pennock DJ, van Kessel C, Farrell RE, Sutherland RA** (1992) Landscape-scale variations in denitrification. *Soil Science Society of American Journal* **56**, 770-776
- Peñuelas J, Filella I, Comas P** (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology* **8**, 531-544
- Piatek KB, Allen HL** (2001) Are forest floors in midrotation stands of loblolly pine (*Pinus taeda* L.) a sink for nitrogen and phosphorus? *Canadian Journal of Forest Research* **31**, 1164-1174
- Piñol J, Terradas J, Lloret F** (1998) Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. *Climatic Change* **38**, 347-357
- Ponge JF, Vannier G, Arpin P, David JF** (1986) Caractérisation des humus et des litières par la faune du sol intérêt sylvicole. *Revue Forestière Française* **38**, 509-516
- Prescott CE, Zabek LM, Staley CL, Kabzems R** (2000) Decomposition of broadleaf and needle litter in forest of British Columbia: influence of litter type, forest tipe, and litter mixture. *Canadian Journal of Forest Research* **30**, 1742-1750
- Qualls RG, Haines BL** (1992) Biodegradability of dissolved organic matter in forest throughfall, soil solution and stream water. *Soil Science Society of America Journal* **56**, 578-586
- Qualls RG, Haines BL, Swank WT** (1991) Fluxes of dissolved organic nutrients and humic substances in a deciduous forest. *Ecology* **72**, 254-266
- Quézel P** (1978) Analysis of the flora of Mediterranean and Sahara Africa. *Annals of the Missouri Botanical Garden* **65**, 479-534
- Radea C, Arianoutsou M** (2000) Cellulose decomposition rates and soil arthropod community in a *Pinus halepensis* Mill. Forest of Greece after a wildfire. *European Journal of Soil Biology* **36**, 57-64
- Richter DD, Markewitz D, Heine PR, Jin V, Raikes J, Tian K, Welles GG** (2000) Legacies of agriculture and forest regrowth in the nitrogen of old-field soils. *Forest Ecology and Management* **138**, 233-248
- Roldan A, Garcia-Orenes F, Lax A** (1994) An incubation experiment to determine factors involving aggregation changes in an arid soil receiving urban refuse. *Soil Biology and Biochemistry* **26**, 1699-1707
- Romanyà J, Casals P, Cortina J, Bottner P, Coûteaux MM, Vallejo VR** (2000) CO₂ efflux from a Mediterranean semi-arid forest soil. II. Effects of soil fauna and surface stoniness. *Biogeochemistry* **48**, 283-306
- Ross DJ, Sparling GP, Burke CM, Smith CT** (1995) Microbial biomass C and N, and mineralizable-N, in litter and mineral soil under *Pinus radiata* on a coastal sand: influence of stand age and harvest management. *Plant and Soil* **175**, 167-177
- Sabaté S, Gracia CA** (1994) Canopy nutrient content of a *Quercus ilex* L. forest: fertilization and irrigation effects. *Forest Ecology and Management* **68**, 31-37
- Sabaté S, Gracia CA, Sánchez A** (2002) Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region. *Forest Ecology and Management* **162**, 23-37
- Sanchez FG** (2001) Loblolly pine needle decomposition and nutrient dynamics as affected by irrigation, fertilization, and substrate quality. *Forest Ecology and Management* **152**, 85-96
- Sarathchandra SU, Perrot KW, Littler RA** (1989) Soil microbial biomass: influence of simulated temperature changes on size, activity and nutrient content. *Soil Biology and Biochemistry* **21**, 987-993
- Sardans J, Peñuelas J** (2005) Drought decreases soil enzyme activity in a Mediterranean *Quercus ilex* L. forest. *Soil Biology and Biochemistry* **37**, 455-461
- Sariyildiz T, Anderson JM** (2003a) Decomposition of sun and shade leaves from three deciduous tree species, as affected by their chemical composition. *Biology and Fertility of Soils* **37**, 137-146
- Sariyildiz T, Anderson JM** (2003b) Interactions between litter quality, decomposition and soil fertility: a laboratory study. *Soil Biology and Biochemistry* **35**, 391-399
- Sariyildiz T, Anderson JM, Kukuc M** (2005) Effects of tree species and topography on soil chemistry, litter quality, and decomposition in Northeast Turkey. *Soil Biology and Biochemistry* **37**, 1695-1706
- Scowcroft PG, Turner DR, Vitousek PM** (2000) Decomposition of *Metrosideros polymorpha* leaf litter along elevational gradients in Hawaii. *Global Change Biology* **6**, 73-85
- Schimel JP, Weintraub MN** (2003) The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. *Soil Biology and Biochemistry* **35**, 549-563
- Scholes MC, Powlson D, Tian G** (1997) Input control of organic matter dynamics. *Geoderma* **79**, 25-47
- Schröter D, Wolters V, de Ruiter PC** (2003) C and N mineralisation in the decomposer food webs of a European forest transect. *Oikos* **102**, 294-308
- Seastedt TR, Crossley DA Jr.** (1981) Microarthropod response following cable jogging and clear-cutting in the southern appalachians. *Ecology* **62**, 126-135
- Sinsabaugh RL** (1994) Enzymic analysis of microbial pattern and process. *Biology and Fertility of Soils* **17**, 69-74
- Sinsabaugh RL, Antibus RK, Linkins AE, McLaugherty CA** (2003) Wood decomposition: nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. *Ecology* **74**, 1586-1593
- Skujins J** (1976) Extracellular enzymes in soil. *Critical Review of Microbiology* **4**, 383-421
- Smith LJ, Papendick RI** (1993) Soil organic matter dynamics and crop residue management. In: Metting B (Ed) *Soil Microbial Ecology*, Marcel Dekker, NY, pp 65-94
- Smolander A, Kitunen V, Mälkönen E** (2001) Dissolved soil organic nitrogen and carbon in a Norway spruce stand and an adjacent clear cut. *Biology and Fertility of Soils* **33**, 190-196
- Smolander A, Loponen J, Suominen K, Kitunen V** (2005) Organic matter characteristics and C and N transformations in the humus layer under two tree species, *Betula pendula* and *Picea alba*. *Soil Biology and Biochemistry* **37**, 1309-1318
- Souto XC, Chiapusio G, Pellissier F** (2000) relationships between phenolics and soil microorganism in spruce forests. Significance for natural regeneration. *Journal of Chemical Ecology* **26**, 2025-2034
- Sparling GP, Hart PBS, August JA, Lesli DM** (1994) A comparison of soil and microbial carbon, nitrogen, and phosphorus contents, and macro-aggregate stability of a soil under native forest and after clearance for pastures and plantation forest. *Plant and Soil* **17**, 91-100
- Stamou GP** (1998) *Arthropods of Mediterranean-Type Ecosystem*, Springer, Berlin, 135 pp
- Standen V** (1978) The influence of soil fauna on decomposition by microorganisms in blanket bog litter. *Journal of Animal Ecology* **47**, 25-38
- Stotzky G** (1997) Soils as an environment for microbial life. In: Van Elsas JD, Trevors JT, Wellington EMH (Eds) *Modern Soil Microbiology*. Marcell Dekker, New York, USA, pp 1-20
- Sverdrup H, Svensson MGE** (2002) Defining sustainability. In: Sverdrup H, Stjernquist I (Eds) *Developing Principles and Models for Sustainable Forestry in Sweden*, Kluwer Academic Publishers, Dordrecht, pp 21-32

- Swift MJ, Heal OW, Anderson JM** (1979) *Decomposition in Terrestrial Ecosystems*, Blackwell Scientific Publication, Oxford, UK, 372 pp
- Switzer GL, Nelson LE** (1972) Nutrient accumulation and cycling in loblolly pine (*Pinus taeda* L.) plantation ecosystems: the first twenty years. *Soil Science Society of America Proceedings* **36**, 143-147
- Taylor BR, Parkinson D, Parson WFJ** (1989) Nitrogen and lignin content as predictors of lignin decay rates. A microcosm test. *Ecology* **70**, 97-104
- Tiessen H, Shang C** (1998) Organic matter turnover in tropical land use systems. In: Bergstrom L, Kirchmann H (Eds) *Carbon and Nutrient Dynamics in Natural and Agricultural Tropical Ecosystems*, Cab International, Wallingford, UK, pp 1-14
- van Hees PAV, Godbold DL, Jentschke G, Jones DL** (2003) Impact of ectomycorrhizas on the concentration and biodegradation of simple organic acids in a forest soil. *European Journal of Soil Science* **54**, 697-706
- van Wesemael B, Veer MAC** (1992) Soil organic matter accumulation, litter decomposition and humus forms in Mediterranean forests of southern Tuscany, Italy. *Journal of Soil Science* **43**, 133-144
- Virzo de Santo A, Berg B, Rutigliano FA, Alfani A, Fioretto A** (1993) Factors regulating early-stage decomposition of needle litters in five different coniferous forests. *Soil Biology and Biochemistry* **25**, 1423-1433
- Virzo de Santo A, Rutigliano FA, Berg B, Fioretto A, Puppi G, Alfani A** (2002) Fungal mycelium and decomposition of needle litter in three contrasting coniferous forests. *Acta Oecologica* **23**, 247-259
- Zech W, Senesi N, Guggenberger G, Kaiser L, Lehmann J, Miano T** (1997) Factors controlling humification and mineralization of soil organic matter in the tropics. *Geoderma* **79**, 117-161
- Zimmer M, Topp W** (1999) Relationships between woodlice (Isopoda: Oniscidea) and microbial density and activity in the field. *Biology and Fertility of Soils* **30**, 117-123
- Zimmermann S, Frey B** (2002) Soil respiration and microbial properties in an acid forest soil: effects of wood ash. *Soil Biology and Biochemistry* **34**, 1727-1737
- Wild A** (1995) *Soils and the Environment: An Introduction*, Cambridge University Press, Cambridge, 307 pp