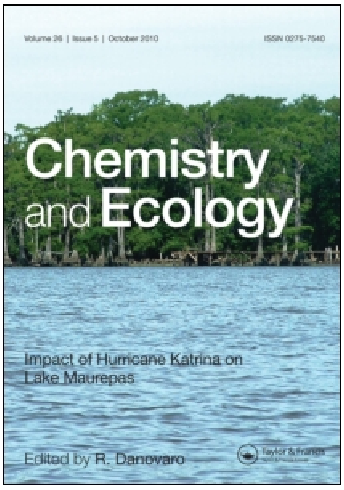

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Dissolved Organic Matter in Forest Soils: Sources, Complexing Properties and Action On Herbaceous Plants

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DISSOLVED ORGANIC MATTER IN FOREST SOILS: SOURCES, COMPLEXING PROPERTIES AND ACTION ON HERBACEOUS PLANTS

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Dissolved organic matter (DOM) is an important component of plant-soil systems. Its essential role in soil solution chemistry, soil-forming processes and its effects on biota, including soil fauna, bacteria, fungi and plants, is extensively documented in literature. In this contribution several forest leaf litter types are compared as sources of DOM and the released organics are subjected to gel permeation chromatography to reveal their molecular-size distribution. Moreover, complexing properties, as an indication for the podzolization potential of the litter leachates, were established. The occurrence and properties of DOM in different soil horizons were monitored beneath a stand of Scots pine. The effects of the different groups of soluble organics including phenolic, fulvic and humic acids, and of water-extractable humic substances on the performance of herbaceous plants of the forest floor are briefly reviewed.

KEY WORDS: Forest soils, dissolved organic matter, soil solution, complexation, humic substances, plant growth, mycorrhizae

INTRODUCTION

Plant-soil systems are characterized by the accumulation with time of an organic matter pool at the interface between vegetation and soil (Duchaufour, 1991). In forests of the temperate and boreal zone, soil organic matter represents an especially important fraction of the total amounts of nutrients cycling in the ecosystem. Part of the soil organic matter is water-soluble and is encountered in the soil solution as dissolved organic matter (DOM). Generally, no correlation is found between DOM and the immobile soil organic matter pool (Zsolnay and Steindl, 1991). DOM has an important role in soil solution chemistry, soil-forming processes, elemental cycling and plant nutrition (Stevenson, 1983; Duchaufour, 1991) and is also important in the transport of N to the mineral soil (Qualls *et al.*, 1991). Additionally, DOM has been shown to affect the stabilization of soil aggregates (Chaney and Swift, 1984).

When rain water interacts with the forest canopy it becomes enriched with dissolved organic carbon (DOC) released from living tissue (Malcolm and McCracken, 1968; Bruckert *et al.*, 1971). However, DOC concentrations show largest increases with passage of rain water through the decaying litter layer of the forest floor (Nykvist, 1963; McClaugherty, 1983; Kuiters and Sarink, 1986). The turnover of fine roots may also contribute substantially to the presence of dissolved organics in the soil solution. Spatial and temporal variations in DOM are determined by many factors including climate, vegetation composition, litter quality, soil chemistry and atmospheric inputs (Qualls *et al.*, 1991; Cronan *et al.*, 1992). DOM is a heterogeneous mixture of components classified into two categories: a) well defined compounds such as polysaccharides, proteins, amino acids, amino sugars, amines, fatty acids, aliphatic and phenolic acids; b) humic substances, highly variable in molecular structure and chemically less well defined.

In this contribution, the role of decaying litter as a source of DOM is considered with emphasis on differences existing between leaf litter types. The metal-complexing properties of DOM are briefly discussed and attention is paid to the effects of different components of DOM, including simple phenolic acids and more humified organic substances, on plant growth and mycorrhizal fungi.

DECAYING LEAF LITTER AS SOURCE OF SOLUBLE ORGANICS

Decaying litter is an important source of soluble organics (Nykvist, 1963). In the first period after leaf shedding, high amounts of organic substances are released by leaching. Dissolved organics in litter leachates are broken down partly by biological mineralization in the upper organic layer even before they are transported through the soil profile. Carbohydrates in the hydrophylic neutral fraction of DOM (McDowell and Likens, 1988; Qualls *et al.*, 1991) are an easily available carbon and energy source and stimulate the activity of decomposing fungi and bacteria. Therefore, the decay rate of forest litter in the first stage of decomposition is often correlated positively with the amount of leachable, easily mineralizable organics (McClaugherty *et al.*, 1985), which stimulate the development of the decomposing subsystem necessary for the breakdown of the structural and more recalcitrant components of plant tissue (Swift *et al.*, 1979).

The amount and chemical nature of the organics and their release rate from decaying leaf litter are thought to be largely dependent on litter type. This was investigated by collecting litter material of several common coniferous (*Pinus sylvestris* L. and *Pseudotsuga menziesii* Mirb., Franco) and deciduous trees (*Betula pendula* Roth., *Fagus sylvatica* L., *Populus nigra* L., *Quercus robur* L.) during autumnal leaf fall. The stands were growing adjacent to each other on a soil substrate of sandy texture. After bringing the material to the laboratory, the unsterilized material with the leaf microflora still intact, but without soil fauna, was incubated during a period of 7 weeks at 12°C. Leaching by rain water was simulated weekly by adding 250 ml distilled water to 10 g litter material. After 20 h the leachates were collected and passed through a 0.45-μm membrane filter prior to chemical analyses. The cumulative amounts of DOC released from the decaying litter material are shown in Figure 1. For deciduous litters, 10–25 mg C g^{-1} dry matter was released during a period of 7 weeks, whereas coniferous needles released a lower amount (<5 mg C g^{-1} dry matter). Freshly fallen needles are less water-permeable compared to leaf litter and the material must first undergo some weathering or fragmentation before its soluble organic substances become available for leaching by rain water. Such contrasting substrate-specific leaching patterns of DOC are often found in coniferous and deciduous species (Cronan and Aiken, 1985; Kuiters and Sarink, 1986). In the presence of soil fauna, the amounts of soluble carbon leached are significantly higher (Huhta *et al.*, 1988).

Litter leachates were further subjected to gel permeation chromatography (GPC), where dissolved organics are fractionated on the basis of molecular size. Sephadex G-25 was used with a fractionation range from 100 to 5000 Dalton as determined

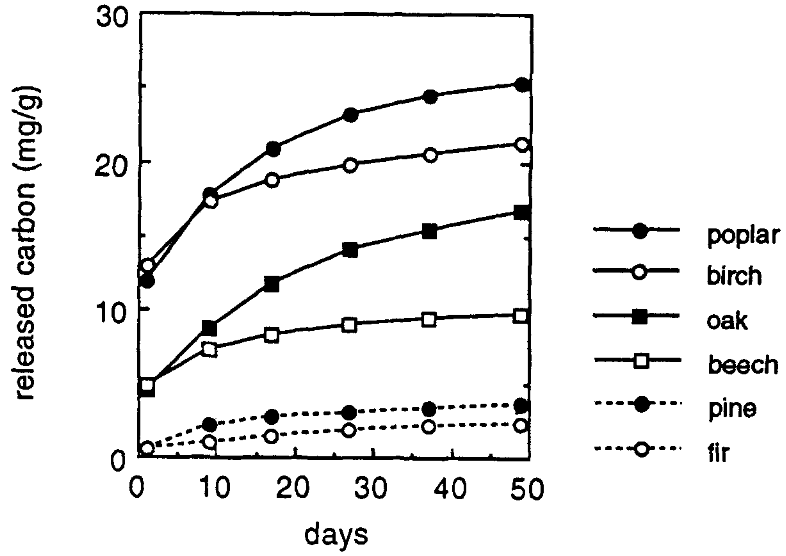

Figure 1 Cumulative amounts of soluble organic carbon leached from decaying forest leaf litter expressed per mass unit of substrate (incubation at 12°C *in the dark in the presence of microbes but without* soil fauna).

for dextrans. The method is described in full detail in Kuiters and Mulder (1992). The chromatographic behaviour of the organic solutes is described by the distribution coefficient K_{av}, representing the relative elution volume following the expression:

$$K_{av} = (V_e - V_o)/(V_t - V_o)$$

where V_o, V_e and V_t denote the void, elution and total gel bed volume, respectively. A few chromatograms are presented in Figure 2 and reveal that the litter leachates comprise a mixture of compounds ranging in molecular weight (Figure 2). UV absorbing material was eluted in three fractions. The presence of an excluded fraction (K_{av} is 0) indicates the presence of substances apparently high in molecular weight (MW > 1 k Da). This fraction was dominant in oak litter leachates but was of minor importance in the others. The main part of the dissolved organics was eluted within the inclusion limit and consisted of compounds predominantly low in MW (< 1 k Da). In most leachates, a third fraction was distinguished beyond the inclusion limit of the column (K_{av} is 3.0). Although the separated MW fractions were not subjected to any further chemical identification, from the literature it is obvious that the intermediate fraction will comprise amino acids, amines, sugars and organic acids (Yavitt and Fahey, 1986; McDowell and Likens, 1988; Guggenberger *et al.*, 1989) whereas the high MW fraction comprises polysaccharides, polyphenols, peptides and polyphenol-protein complexes. It is even likely that chemically less well defined humic substances did occur in this fraction. Bruckert *et al.* (1971) demonstrated that polymerization and condensation reactions of soluble organics start before leaf shedding. The third group, eluting after the inclusion limit of the gel, was composed of

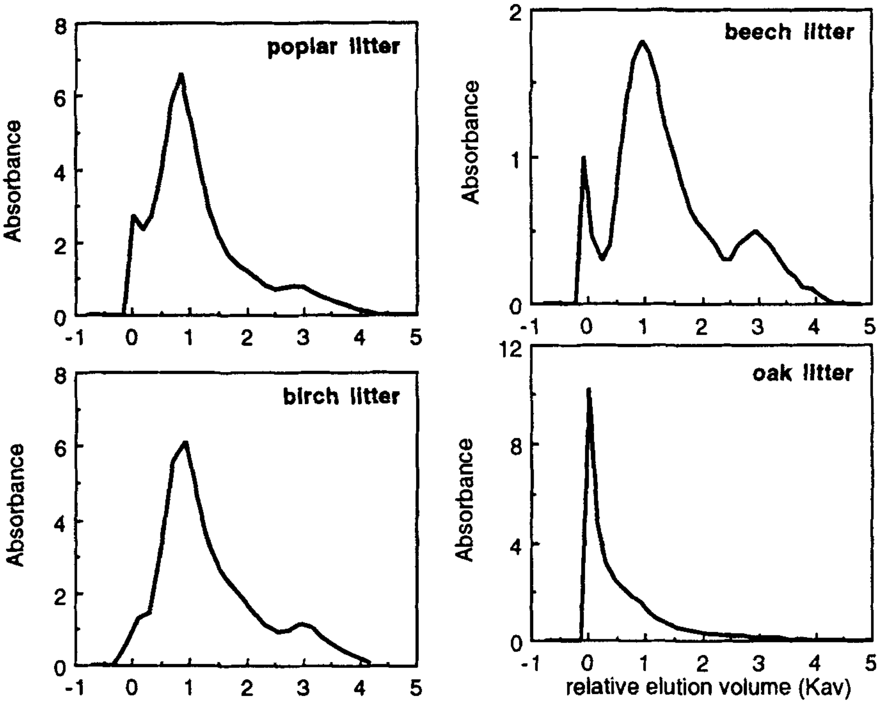

Figure 2 Molecular-size distribution of dissolved organic material released from decaying forest leaf litter (Sephadex G-25, with 0.01 M sodium acetate pH 5.5 as mobile phase). Absorbence is expressed in arbitrary units.

compounds retarded by the gel due to adsorption. Low MW phenolic acids and their derivatives are eluted here (Kuiters and Mulder, in prep.) and are known to occur in considerable amounts in fresh leaf litter leachates (McClaugherty, 1983; Kuiters and Sarink, 1986; Yavitt and Fahey, 1986).

Metabolic products of the litter decomposers may have contributed to the dissolved organics found in the litter leachates. However, the main part consists of organics from plant cell contents, especially from vacuoles. Gas-chromatographic analysis (Kuiters and Sarink, 1986) revealed that with respect to phenolics, a spectrum of compounds is released which is partly specific for the particular litter type and is related to secondary plant metabolism. Further research is needed here to understand the relation between forest DOC chemistry and the dominant tree species in the canopy. In this respect pyrolysis-field ionization mass spectrometry (Py-FIMS) has been shown to be a useful technique (Hempfling and Schulten, 1990).

SPATIAL AND TEMPORAL VARIATIONS IN DOM

Monitoring soil solutions in forests gives insight into variations in DOM occurring with depth and with season, essential for an understanding of its pedological and ecological significance. This was shown in a field study lasting for 18 months from April 1991 through September 1992 under a forest stand of Scots pine (*Pinus sylvestris* L.) growing on a sandy soil with a mor humus profile (Wekerom, the Netherlands). Percolation water from the litter layer (Ol) was collected by a funnel

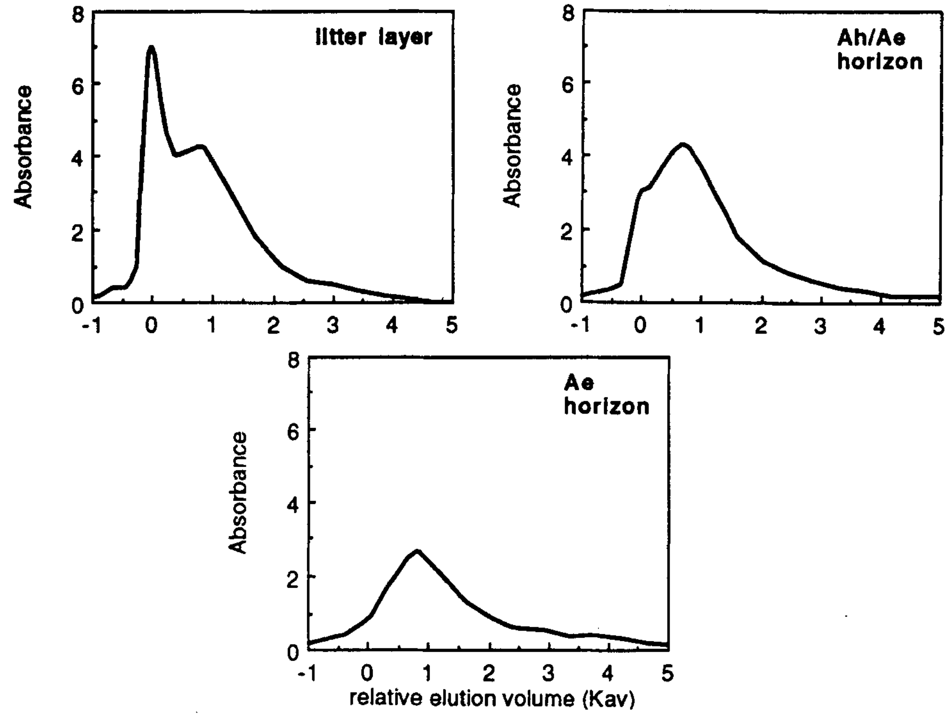

Figure 4 Molecular-size distribution of forest soil DOC, collected at three depths in the humus podzol profile beneath Scots pine. (Sephadex G-25, with 0.01 M sodium acetate pH 5.5 as mobile phase). Absorbence is in arbitrary units.

Qualitatively, considerable differences in DOM are found between soil depths but less between vegetation types (Cronan and Aiken, 1985; Kuiters and Mulder, 1992). With increasing depth, a shift towards relatively more hydrophilic acids (*e.g.* aliphatic carboxylic acids) lower in MW is usually observed. Besides a selective removal of hydrophobic acids, the soluble components undergo significant chemical transformation during their leaching to deeper soil horizons. Processes such as oxidation, polymerisation and condensation modify the organic solutes, whereby hydrophilic acids are produced (Qualls *et al.*, 1991). In contrast to the litter specific spectrum of compounds found in superficial soil layers, the transformation processes ultimately result in a convergence to the humic structures found in deeper soil layers. Molecular-size distributions and chemical properties of humic compounds from A and B horizons show smaller differences between vegetation types (Candler and Van Cleve, 1982; Kuiters and Mulder, 1992).

PODZOLIZATION POTENTIAL OF LITTER LEACHATES

Litter leachates have a certain potential to solubilize aluminium and iron ions, by their complexing properties (Blaser and Sposito, 1987; Pohlman and McColl, 1988; Tam and McColl, 1991). The process of solubilization of aluminium and iron, their transport as organic complexes and their subsequent precipitation at a deeper soil layer, is an indication of podzolization (Duchaufour, 1991). By measuring the complexing capacity of litter leachates, their potential to induce podzolization can be established. This was done for several of the litter leachates. Complexometric measurements were carried out using a modified gel permeation method, with Cu(II) as cation (Kuiters and Mulder, 1992). Copper is mostly used as a model-ion in complexometric studies to determine the complexing capacity of humic substances (Stevenson, 1983).

Figure 5 shows the complexing capacity expressed per mass unit of carbon for the different litter leachates. For each litter type, four to six leachates obtained after repeated leaching were analyzed. For most litter types, the values varied within the range from 0.45 to 0.75 μmol mg^{-1} dissolved carbon. Significantly higher values were found for oak leachates with an average of 1.45 μmol mg^{-1} C. These data confirm those reported by Luster *et al.* (1989) for larch and chestnut litter leachates using an ion exchange technique. The complexing capacity of soil solutions increased with soil depth, with values beyond 3.0 μmol mg^{-1} C in the Ah and Ae horizon (Kuiters and Mulder, 1992). This is partly the result of a decrease in overall molecular size of the dissolved organics with depth (Figure 4), resulting in an increase in the number of charged sites per mg carbon. Further research is needed to investigate more extensively the extent to which the intensity of podzolization, known to be different between tree types (Miles, 1985), is related to differences in the complexing capacity of their litter leachates.

SOLUBLE ORGANIC MATTER AND PLANT GROWTH

Plants of the forest floor spread a large part of their roots in the holorganic layer (Duchaufour, 1991), where nutrients become available by mineralization of soil

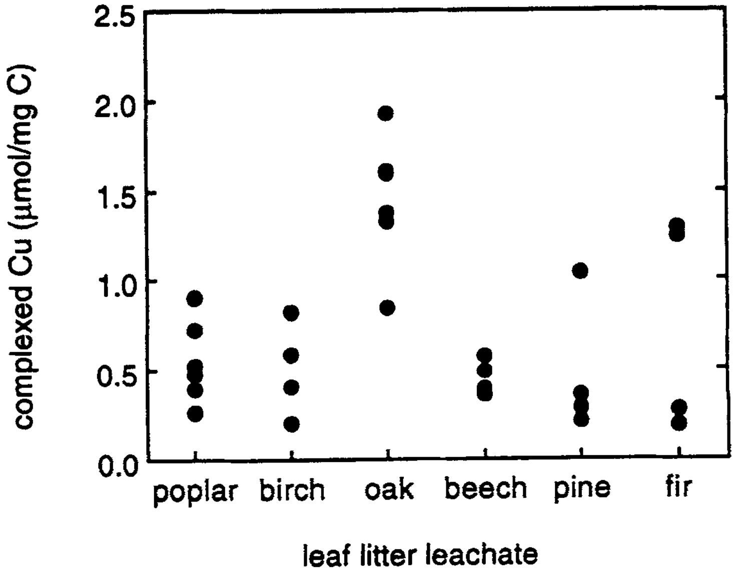

Figure 5 Complexing capacity (μmol mg^{-1} carbon) of leaf litter leachates as determined for Cu(II) at pH 5.5 using a modified gel permeation technique.

organic matter. Obviously, roots are confronted here with dissolved organics which may affect plant growth (Vaughan and Malcolm, 1985; Kuiters, 1990). Numerous plant growth experiments with organic substances have been carried out and both inhibitory and stimulatory effects have been reported. All growth stages have proved to be affected by dissolved organic substances, including seed germination, seedling development, the growth of established individuals (Vaughan and Malcolm, 1985; Kuiters, 1990) and even flowering and fruiting (Ernst *et al.*, 1987). Results largely depend on the nature of the applied organic substances and particularly on experimental conditions, *e.g.* whether experiments are carried out in nutrient solution or in a soil culture where the applied humic species can interact with organic and mineral soil components and effects are often less pronounced.

Phenolic Acids

Phenolic substances, occurring in high amounts in decaying forest litter and acting as precursors in humification (Kuiters, 1990; Duchaufour, 1991) have been thoroughly investigated for their effects on plant growth. Many reports are available in the literature supporting the hypothesis that phenolic acids (PA) affect ion uptake (Glass, 1973; Al Sadaawi *et al.*, 1986; Kobza and Einhellig 1987; Kuiters and Sarink, 1987; Vaughan and Ord 1991) and water relations (Booker *et al.*, 1992). Effects depend on the phenolic acid, its concentration, the ion being studied and the plant species used. Phenolic acids have also a large effect on the development and morphology of roots (Kuiters, 1989; Vaughan and Ord, 1990).

Figure 6 shows the results of a 5-weeks' experiment with five herbaceous forest floor species growing on a solution culture (0.4 Hoagland) enriched weekly with a mixture of phenolic acids (an equimolar mixture of vanillic, protocatechuic, *p*-hydroxybenzoic, salicylic, *p*-coumaric and caffeic acid). Two types of reactions were observed. Growth of some species (*Deschampsia flexuosa, Milium effusum, Silene dioica*) was stimulated by phenolic acids at concentrations in the range from

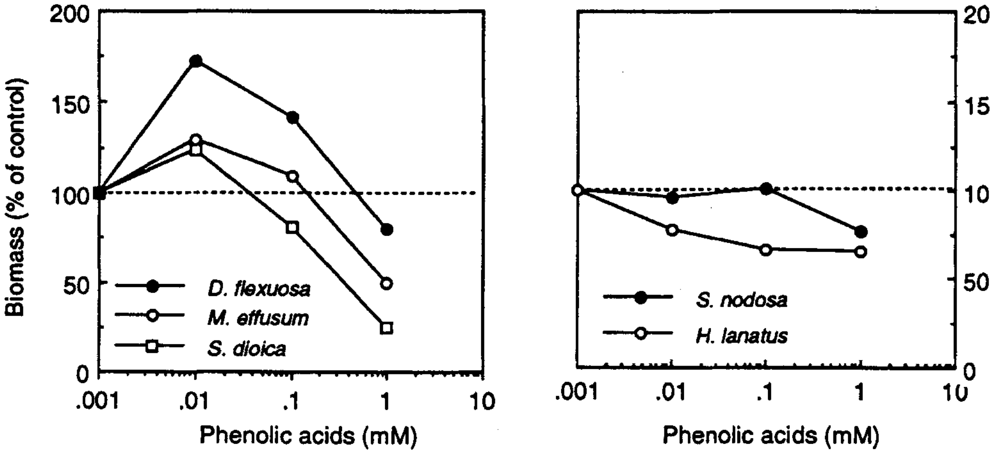

Figure 6 Biomass (as percentage of the control) of several forest floor species after growth for 5 weeks on a solution culture (0.4 Hoagland solution, pH 5.5) enriched with phenolic acids (equimolar solution of *p*-hydroxybenzoic, vanillic, syringic, salicylic, *p*-coumaric, caffeic and ferulic acid).

0.001 to 0.1 mM but inhibited at higher concentrations. Two other species (*Scrophularia nodosa, Holcus lanatus*) were increasingly inhibited with PA concentration. Chemical analysis of the plant material revealed that growth alterations were accompanied by changes in chlorophyll and elemental content. The uptake and translocation of both macro- and micronutrients were affected (Kuiters and Sarink, 1987).

Humic and Fulvic Acids

The effect of fulvic (FA) and humic acids (HA) on plant growth has received considerable attention during the last three decades. Similar to phenolic acids, FA and HA stimulate plant growth at low concentrations, but become inhibitive at higher concentrations (DeKock, 1955; Lee and Bartlett, 1976; Linehan, 1977; Elgala *et al.*, 1978; Vaughan and Malcolm, 1985; Ernst *et al.*, 1987). The range of optimum concentration of humic matter varies with plant species (Vaughan and Malcolm, 1985). A similar phenomenon has been reported with soil microorganisms as test species (Visser, 1985). Humic substances are composed of a heterogeneous mixture of high and low MW components (Piccolo and Mirabella 1987; Kuiters and Mulder, 1992) highly different in biological activity (Piccolo *et al.*, 1992). The low MW fractions are strongly active in the plant-soil systems (Nardi *et al.*, 1989; Albuzio *et al.*, 1989).

Much uncertainty still exists over the mechanisms that account for the growth-promoting and reducing effects. The possibility that humic substances serve directly as a nitrogen or phosphate source is not very likely as these nutrients do not occur in an easily available form in the humic polymers. In the literature, different explanations have been suggested that are not mutually exclusive. An increase of iron (Linehan and Shepherd, 1979), phosphate (Vaughan and Malcolm, 1985) or nitrate nutrition (Piccolo *et al.*, 1992) has been found. There is increasing evidence that humic substances exert their effect partly by affecting the membrane transport system, *i.e.* the ATPase activity (Nardi *et al.*, 1991).

In other explanations, the hormone-like (auxin-, gibberellin- and cytokynin) activities of humic substances are emphasized (Linehan 1977; Dell'Agnola and Nardi, 1987). It is hypothesized that humic substances are found mainly in a high MW form that is physiologically inactive. Dissociation of these high MW humic substances for instance by root exudates (Albuzio and Ferrari, 1989) will produce low MW fractions with a high biological activity (Nardi *et al.*, 1991). IAA-oxidase activity is inhibited especially by low MW humic fractions (Mato *et al.*, 1972; Albuzio *et al.*, 1989). Results obtained by Piccolo *et al.* (1992) also affirm the hypothesis that with a lower molecular size, the auxin-like activity is higher and positively related to the carboxyl group content of the MW fractions.

Several authors have suggested that the physiological action of humic substances is at least partly the result of their surface activity (Visser, 1985; Samson and Visser, 1989; Nardi *et al.*, 1991). Due to this property, plant root membranes are thought to be one of the prime targets of humic substances and, combined with their ability to cross cell membranes, they are likely to interact with intracellular processes as well. An increased membrane permeability may also have consequences for a greater availability of nutrients or a greater efflux of others as has been found for potassium (Samson and Visser, 1989).

Water-soluble Humic Substances

In contrast to the numerous growth experiments that have been carried out with FA and HA, experiments with natural DOM are scarce. Nevertheless it is very likely that DOM has a slightly different effect on plant growth as it is composed of a mixture of organic compounds, with a dominant low MW fraction (Kuiters and Mulder, in prep.). Therefore, FA and HA are not *per se* representative of the composition of DOM found in different forest soil layers.

In our laboratory, growth experiments have been undertaken using the water-soluble fraction of soil organic matter, or water-soluble humic substances (WSHS). WSHS have been isolated from forest soil material of the Ah horizon by gentle extraction with water. In soil cultures, WSHS were applied weekly to pots filled with sandy material and planted with seedlings of *Agrostis capillaris* L. and *Silene dioica* L. Biomass production and elemental content of root and shoot material was established after a growth period of several weeks. These experiments are described elsewhere in more detail (Kuiters and Mulder, in prep). The main conclusions drawn from these experiments were that plant growth was hardly affected by the WSHS addition to the soil, even at the highest concentration applied, *i.e.* 100 μg C g^{-1} dry soil $week^{-1}$ (see Figure 7). Some minor effects on cation uptake were observed, especially on cadmium and zinc. The uptake of aluminium, iron and copper, forming soluble complexes with WSHS, was not significantly affected. Apparently, metal-organic complexes are not adsorbed by plant roots and cations are taken up predominantly as free ions and not as organic complexes (see also Cabrera *et al.*, 1988). A noticeable increase in manganese uptake was ascribed to the reduction of Mn(IV) to Mn(II) by components present in WSHS, thereby increasing the uptake

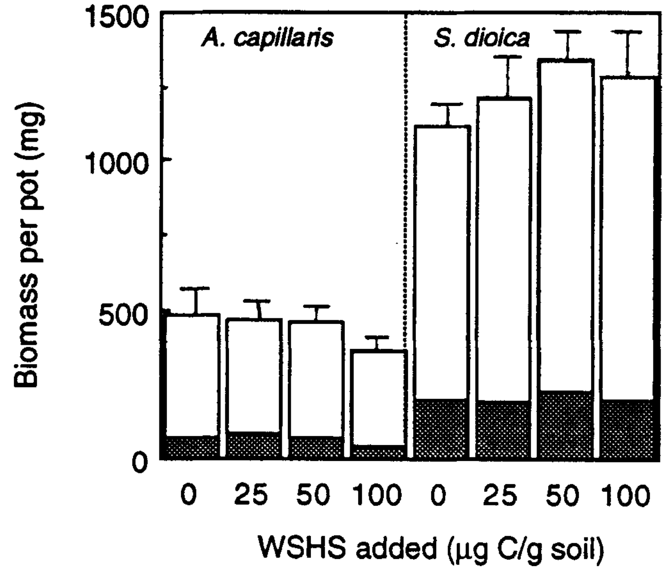

Figure 7 Biomass of *A. capillaris* and *S. dioica* after growth for 30 days on a sandy soil weekly receiving an amount of water-soluble humic substances (WSHS). Root (shaded area) and shoot biomass (white area) with standard deviations of total plant biomass.

of manganese by the plants. The effects of humic substances on the uptake of micronutrients is thus not only mediated by the formation of chelates, but also by redox reactions.

Humic Substances and Mycorrhizal Fungi

There is increasing evidence that non-humic and humic substances may exert their effects on plant growth also by affecting mycorrhizal fungi. Tan and Nopamornbodi (1979) found growth of *Pisolithus tinctorius*, an ectomycorrhizal fungus, to be affected by FA. Concentrations up to 1600 mg l^{-1} were stimulative whereas at higher concentrations the effects were predominantly inhibitive. They suggested that the polysaccharide content of fulvic acid was an easily accessible source of energy for the fungus.

Vesicular-arbuscular mycorrhiza (VAM) has been found to be affected by phenolic substances. Wacker *et al.* (1990) reported negative effects of ferulic acid on the colonization of asparagus roots with *Glomus fasciculatum*. Plant growth was also reduced and there was a significant increase of plant growth with VAM colonization. Pedersen *et al.* (1991) found that certain cinnamic acid derivatives exuded by the roots of *Asparagus officinalis* had a negative effect on VAM root colonization, resulting in reduced plant performance. However, ferulic acid showed inhibitory effects on the growth of non-mycorrhizal plants but not on mycorrhizal plants. Apparently, VAM fungi are also able to alleviate the phytotoxic effects of certain phenolic acids by acting as detoxifiers. This has also been found for ericoid mycorrhiza in Ericaceae (Leake *et al.*, 1989). More research is needed here to establish the precise effects of mono- and polymeric organic substances on mycorrhizal fungi.

CONCLUSIONS AND PERSPECTIVES FOR FUTURE RESEARCH

Despite the importance of DOM for soil solution chemistry and soil-forming processes and its effects on biota, there are still major gaps in our understanding of the production, transformation, vegetation-specific chemistry and turnover of these organic substances in plant-soil systems. There is a need for a comprehensive understanding of DOM with respect to its role in forest succession. On the level of single organisms, the physiological action of non-humic and humic substances, particularly of low MW fractions, on membrane functioning of higher plants and of microorganisms, is a challenging research area. Furthermore, the vegetation-specific properties of dissolved organic substances occurring in the litter layer deserves more attention and several questions have to be answered. For instance, to what extent are mycorrhizal fungi (ecto-, endo- and VAM) evolutionally adapted to a tree species-specific spectrum of organics released from decaying leaf and root litter? Is the succession of higher plants and of associated mycorrhizal species in forest vegetations partly under the influence of dissolved organics in the litter layer? These questions can be answered only if there is a better understanding of the vegetation-specific chemistry of DOM and of the physiological effects they have on both microbial and plant species. Here lies a scientific challenge for organic geochemists, analytical chemists, soil biologists and plant ecophysiologists, whose close cooperation can make scientific progress in this very intriguing field of research.

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