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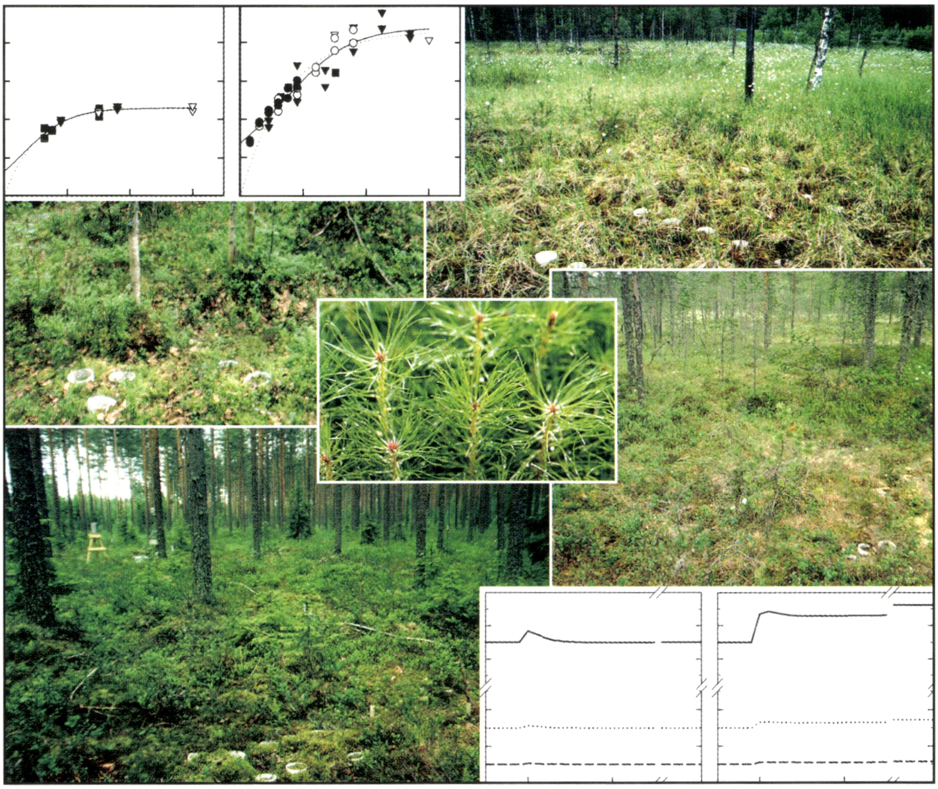

Effects of soil temperature on Scots pine biomass allocation and litter decomposition in peat

Timo Domisch

JOENSUUN TUTKIMUSKESKUS
JOENSUU RESEARCH CENTRE

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Timo Domisch

Academic dissertation

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Abstract

Domisch, T. 2002. Effects of soil temperature on Scots pine biomass allocation and litter decomposition in peat. Finnish Forest Research Institute, Research Papers — Metsäntutkimuslaitoksen tiedonantoja 874. 65 p. + 5 appendices.

This thesis investigates the effects of peat soil temperature on biomass production and allocation in one-year-old seedlings of Scots pine (*Pinus sylvestris* L.) and on the decomposition of Scots pine needle and root material. Two laboratory experiments were conducted to study shoot and root growth and biomass allocation during the first half of the growing season, one extending over 9 weeks, in which constant soil temperatures of 5, 9, 13 and 17°C were used, while the other, lasting up to 18 weeks, tested the effects of cold soil periods (5°C) of different length and a subsequent increase to 13°C. The decomposition of needle and root litter was studied in three experiments with plant material obtained from one and two-year-old Scots pine seedlings, at soil temperatures of 5, 10, 15 and 25°C. In two experiments ^{14}C-labelled material was used in order to trace the carbon released during decomposition. Decomposition and carbon relocation from the litter were monitored for up to 500 days. The experiments were performed in peat soil under controlled laboratory conditions and in the field. Pooled results from all the experiments were used to simulate carbon relocation at elevated soil temperatures.

Bud break and the start of shoot height growth were not affected by the soil temperature treatments, whereas the final height was clearly dependent on soil temperature but not on the length of the cold soil period. Soil temperature did not affect the onset of root elongation, but higher soil temperatures promoted greater root length at 9 weeks. The cold soil periods delayed the start of new root growth, but new roots emerged quickly when the soil temperature was raised to 13°C. Higher soil temperatures clearly increased the biomass production of the seedlings, but the highest total biomass was observed at 13°C and not at 17°C. A longer period of cold soil reduced the biomass of new roots, but when the soil temperature increased, the new root biomass increased to a level similar to that in the treatments with shorter cold soil periods. Biomass allocation was not greatly affected by the soil temperature treatments, although a trend for greater allocation below ground at higher soil temperatures was observed.

Mass losses from the needle litter were always higher than those from the root litter, and the decomposition of needle litter was more dependent on soil temperature. The temperature dependence of the decomposition rate decreased with time, so that the mass losses from both needles and roots showed a non-linear relationship to the accumulated soil temperature sum and converged to an asymptote, i.e. a limit value for mass loss, which was 88% for needles and 46% for roots. The greatest part of the carbon released from the litter during decomposition was emitted into the atmosphere, 80% of that from the needle litter and 70% of that from the root litter. A considerable amount of the carbon released was retained in the peat and moss layers, approx. 15% for the needles and 25% for the roots, while smaller amounts, 5% on average, were leached into the groundwater.

The simulations showed that on an average drained peatland supporting a Scots pine stand, when above and below-ground litter fall each accounts for 100 g C $m^{-2}a^{-1}$, the carbon flux into the atmosphere from decomposing tree litter would be 150 g C $m^{-2}a^{-1}$, relocation into the soil would be around 30 g C $m^{-2}a^{-1}$ and leaching into the groundwater approx. 10 g C $m^{-2}a^{-1}$. The simulations also showed that an increased litter input into the soil at elevated soil temperatures could result in increased carbon emissions to the atmosphere and leaching into the groundwater, although carbon relocation into the soil would also increase. This could mean greater carbon accumulation into the soil of drained peatlands, provided that other environmental conditions will not counteract.

Keywords: Allocation, Biomass, Carbon, Climate change, Decomposition, Growth, Needle, Peatland, *Pinus sylvestris*, Relocation of carbon, Root, Shoot, Simulation, Soil temperature

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Preface

This study was carried out mainly at the Joensuu Research Centre of the Finnish Forest Research Institute during 1997–2002. I am grateful for the excellent working facilities provided by the Joensuu Research Centre, for which I wish to thank its director Jari Parviainen. The study was financially supported by the Academy of Finland, the Graduate School in Forest Sciences, the Faculty of Forestry at the University of Joensuu, the Joensuu Research Centre of the Finnish Forest Research Institute and the Metsämiesten Säätiö Foundation, all of which are appreciatively acknowledged.

I want to thank also the Department of Forest Ecology at the University of Helsinki, where I actually started this study, the Hyytiälä Forestry Field Station and the Isotope Laboratory, both of the Faculty of Agriculture and Forestry at the University of Helsinki, as well as the metal workshop at the University of Joensuu for providing support and working facilities.

I wish to express my sincere thanks to numerous people who have contributed to this work, in one way or another. My warmest thanks go to my supervisors Leena Finér, Tarja Lehto and Jukka Laine, who patiently supported me on my way into science. Sincere thanks also to my other coauthors of the papers, Marjut Karsisto and Raija Laiho, for valuable discussions and encouragement.

I got valuable statistical advice from Jaakko Heinonen and Hannu Rita. Thanks also to Pedro Aphalo, Hannu Mannerkoski, Tapani Repo, Risto Rikala and Aija Ryyppö for scientific advice, Anki Geddala and Pekka Järviluoto for laborious root work in the laboratory, as well as Urho Kettunen for technical help. Thanks to the Suonenjoki Research Station of the Finnish Forest Research Institute, Jussi Nuutinen in particular, for the Scots pine seedlings used in all experiments reported in this thesis. I appreciate the help and expertise of Antti Uusi-Rauva and Kaj-Roger Hurme concerning radioactive nuclides, oxidisers and scintillation counters.

Thank you also to my fellow researchers of the Graduate School in Forest Sciences, as well as of the Joensuu Research Centre and its staff for a pleasant working atmosphere. Jukka Alm and Frank Berninger are acknowledged for reviewing the manuscript and for valuable comments. Malcolm Hicks skilfully revised the language of this thesis and of most of the articles. Leena Karvinen kindly helped with the layout of this thesis. Thank you also to all other people not mentioned here, who have contributed to this work.

Finally, I want to thank my family, my parents Maila and Rainer, as well as my sister Nina and my brothers Mika and Sami, for their support and encouragement. Vielen Dank! Last, but not least at all, my greatest thanks are due to my wife Marjoriitta for her support and love. Kiitos! This thesis is dedicated to our newborn son.

Joensuu, October 2002 Timo Domisch

Nicht Kunst und Wissenschaft allein,
Geduld will bei dem Werke sein.
Ein stiller Geist ist jahrelang geschäftig,
die Zeit nur macht die feine Gärung kräftig.
(Faust I, Johann Wolfgang von Goethe)

CONTENTS

List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals **I–V**.

I Domisch, T., Finér, L. and Lehto, T. 2001. Effects of soil temperature on biomass and carbohydrate allocation in Scots pine (*Pinus sylvestris*) seedlings at the beginning of the growing season. Tree Physiology 21: 465–472.

II Domisch, T., Finér, L. and Lehto, T. 2002. Growth, carbohydrate and nutrient allocation of Scots pine seedlings after exposure to simulated low soil temperature in spring. Plant and Soil. In print.

III Domisch, T., Finér, L. Laiho, R. and Laine J. 2002. Decomposition and N dynamics of Scots pine needle litter in *Carex*-peat soils from two climatically different regions. Manuscript.

IV Domisch, T., Finér, L., Laiho, R., Karsisto, M. and Laine, J. 2000. Decomposition of Scots pine litter and the fate of released carbon in pristine and drained pine mires. Soil Biology & Biochemistry 32: 1571–1580.

V Domisch, T., Finér, L., Karsisto, M., Laiho, R. and Laine J. 1998. Relocation of carbon from decaying litter in drained peat soils. Soil Biology & Biochemistry 30: 1529–1536.

T. Domisch did most of the planning of the experiments and writing the articles, and was responsible for doing the measurements and performing the statistical analyses. The ^{14}C-analyses reported in papers **IV** and **V** were also carried out by him. The carbohydrate and nutrient analyses were performed at the Finnish Forest Research Institute.

1 INTRODUCTION

1.1 Carbon cycling in boreal peatlands

Pristine peatlands (mires) are wetland ecosystems characterised by the accumulation of organic matter, which is produced and deposited at a greater rate than it is decomposed, leading to the formation of peat (Gore 1983), and thus to the accumulation of carbon (C) in the long-term. Carbon is bound from the atmosphere as biomass in photosynthesis by autotrophic plants and deposited as above and below-ground litter (Fig. 1). Due to the high water table in pristine peatlands throughout most of the year, the peat soil is mainly anoxic and thus provides unfavourable conditions for decomposition, leading to accumulation of peat. Peat accumulation can take place only when net primary production (NPP) exceeds decomposition. On average, 2–16% of the NPP is accumulated as peat (see reviews by Päivänen and Vasander 1994 and Paavilainen and Päivänen 1995). The highest long-term peat accumulation rates in the boreal zone of Finland have been measured in raised bogs and the lowest accumulation rates in minerotrophic fens (Tolonen and Turunen 1996).

Peatlands, particularly those in the boreal zone, are huge reservoirs of C and thus a very important factor in the global C balance. The amount of C accumulated in northern peatlands is estimated to be approx. 455 Pg (Gorham 1991), which is about 60% of the C pool of the atmosphere and one third of the total C store found in soils (IPCC 1996). Turunen et al. (2002), however, estimated the total C pool of all boreal and subarctic mires to be lower, at 270–370 Pg. The greatest C stores in Finland can be found in peatlands (Minkkinen 1999), which cover about one third of the land area, i.e. 10.4 million ha (Paavilainen and Päivänen 1995). Almost 15 million ha of peatlands are drained for forestry worldwide, of which approx. 5.7 million ha are located in Finland (Paavilainen and Päivänen 1995). Pine mires are the most common peatland sites drained for forestry in Finland (Keltikangas et al. 1986).

Drainage for forestry sets in motion a vegetation succession in which the plants typical of pristine peatlands are gradually replaced by a forest vegetation (Sarasto 1962, Laine and Vanha-Majamaa 1992, Laine et al. 1995). The initial nutrient status of the peatland and the intensity of drainage are of significance in this context (Laine et al. 1995). The recovery of tree growth after drainage differs between minerotrophic and ombrotrophic peatlands, in that the aerated zone suitable for enhanced root growth and for peat and litter decomposition is still superficial in the latter even after drainage. The *Sphagnum* peat itself does not provide favourable conditions for decomposition, due to its low pH and low nutrient availability (Isotalo 1951, Johnson and Damman 1993, Bergman et al. 1999).

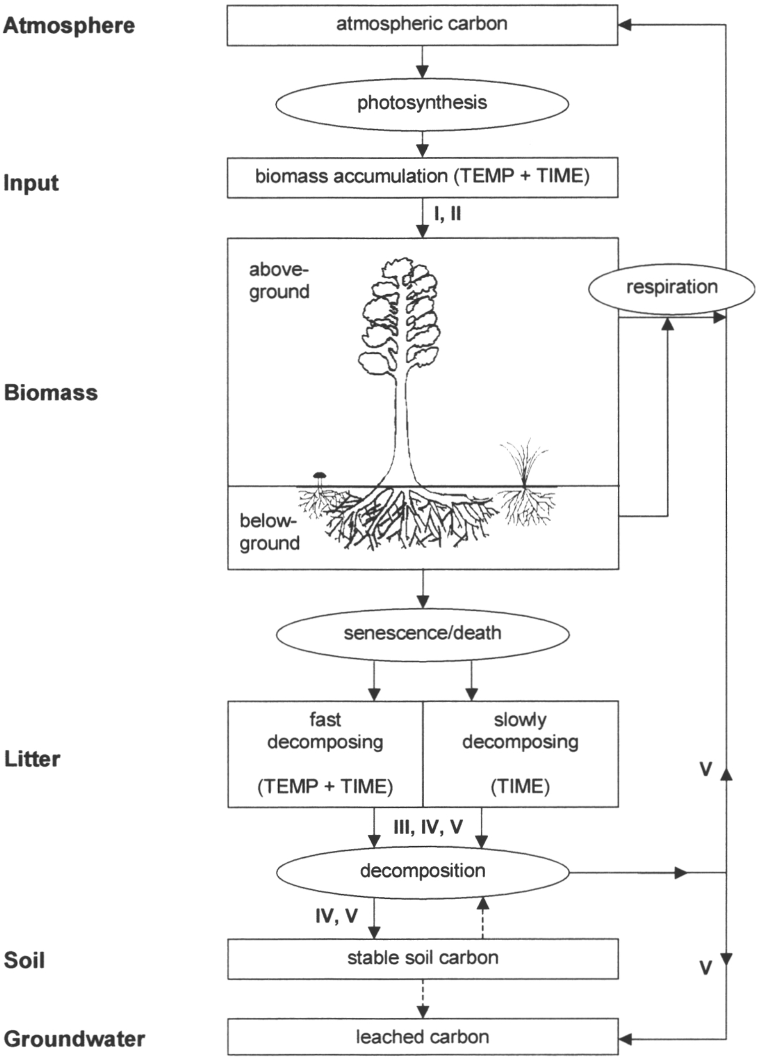


Figure 1. Carbon pools and fluxes in a forested peatland ecosystem. Boxes represent carbon pools or measurable carbon movements, ovals represent processes changing these carbon pools and arrows represent the fluxes. Roman numerals refer to the original papers.

The fine root biomass of developing boreal coniferous forests generally increases until canopy closure occurs (Vogt et al. 1983, Helmisaari et al. 2002), and the root biomass was also observed to increase rapidly after drainage in the study of Laiho and Finér (1996) and to reach its peak after 22 years. Following this rapid increase, the absolute biomass remains relatively stable but the relative biomass (in relation to total biomass) decreases (Vogt et al. 1987b, Laiho and Finér 1996, Monserud et al. 1996, Nikinmaa 1996, Helmisaari et al. 2002), although increases in absolute and relative fine root biomass have also been observed in Scots pine (*Pinus sylvestris*) stands throughout an age sequence of 18 to 212 years (Vanninen et al. 1996). Canopy closure is also a turning-point for the root:foliage ratio (Vanninen and Mäkelä 1999), the proportion of the foliage biomass remaining stable or decreasing after a maximum in early stand development (Gower et al. 1994, 1995, Vanninen et al. 1996, Helmisaari et al. 2002). After canopy closure, the absolute allocation of biomass to the foliage remains relatively stable or may increase slightly with age (Monserud et al. 1996, Vanninen et al. 1996). The total (above and below-ground) litter production of a forest stand may thus be assumed to be relatively stable over time (after canopy closure) if a large enough area is considered (Fig. 2).

Both above and below-ground tree growth is enhanced after drainage, and consequently also the increase of needle and root litter production may be significant (Laiho and Laine 1996, 1997, Finér and Laine 1998). The estimated increases in above-ground litter production are up to five-fold (Laiho and Laine 1996) and that of below ground two-fold (Vasander 1982). It can not be concluded that above-ground litter production increases to higher levels than below-ground production, however, since the initial levels of production may be different. The ratio of the increased litter production of the tree stand and the decomposition of the previously formed peat is of great importance (Vompersky and Smagina 1984, Cannell et al. 1993, Minkkinen and Laine 1998a,b).

Due to water level draw-down, the structure of the initially wet peat collapses and the peat surface sinks rapidly (Lukkala 1949). The surface peat dries, and its thermal conductivity decreases (Päivänen 1982), so that the mean peat temperature drops. This is also accentuated by the shading and snow-collecting effects of the tree stand (Yli-Vakkuri 1960, Heikurainen and Seppälä 1963, Hytönen and Silfverberg 1991, Minkkinen et al. 1999), which reduces the depth of the insulating snow cover (Päivänen 1973). The lower water content and improved aeration of the surface peat increase microbial activity (Chmielewski 1991), enhancing the decomposition of organic matter (Lieffers 1988, Bridgham et al. 1991), but this may be partly counteracted by the lower soil temperatures caused by the lower thermal conductivity of the drier peat. The enhanced microbial activity is limited to the surface layer, although the water table remains relatively low during the growing season (Paarlahti and Vartiovaara 1958, Karsisto 1979).

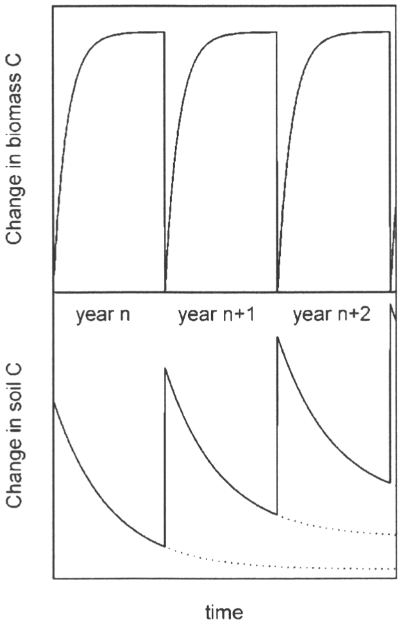


Figure 2. Theoretical changes in needle or root biomass carbon (relatively stable) and soil carbon (increasing) within and between years.

Drainage of peatlands for peat harvesting or agricultural purposes changes them from C sinks into sources of C (Armentano and Menges 1986, Nykänen et al. 1995), whereas drainage for forestry has been found to increase peat C stores in many cases in Finland, at least for the first 60–80 years (Minkkinen and Laine 1998a,b, Minkkinen et al. 1999). The increases in peat C stores on drained sites have been greater in Southern Finland than in the North (Minkkinen and Laine 1998b).

Although peatlands drained for forestry may act as sinks for atmospheric C, the mechanism of C accumulation seems to be different from that in pristine peatlands. The latter accumulate C through height growth, predominantly from plants of the field and bottom layers (*Sphagna* and sedges), whereas the increased tree litter production above and below the ground may be more important on drained peatlands. No research has been carried out earlier, however, into the fate of C released during the decomposition of litter on either pristine or drained peatlands.

1.2 Effects of soil temperature on plant growth

The boreal forest zone is characterised by low air and soil temperatures leading to short growing seasons and favouring the accumulation of organic matter. Thus cold soils (i.e. soils with sub-optimal temperatures concerning biological processes) are characteristic of boreal forests, especially at the beginning of the growing season. This holds true particularly for drained peatlands, since drainage causes a decrease in mean soil temperature (Pessi 1958, Heikurainen and Seppälä 1963, Hytönen and Silfverberg 1991, Minkkinen et al. 1999).

Soil temperature is one of the primary factors affecting plant growth (Cooper 1973, Bowen 1991). Low soil temperature reduces the growth of tree roots (Aaltonen 1942, Ritchie and Dunlap 1980, Tryon and Chapin 1983, Lopushinsky and Max 1990) and also impedes shoot growth and hampers nutrient uptake (Lopushinsky and Max 1990, Marschner 1995). Thus the present restraints on tree growth in boreal forests represent the direct or indirect repercussions of temperature, although its role is somewhat controversial (Briffa et al. 1998, Vaganov et al. 1999, Jarvis and Linder 2000). Increasing temperatures resulting from global climatic changes may have direct effects on the physiology of the tree, in that trees growing in a warmer climate will fix more C, resulting in accelerated growth. There may also be indirect effects, since a warmer environment provides greater nutrient availability, resulting in faster annual growth rates (Strömgren 2001). An increase of +5°C in soil temperature resulted in a very significant increase in stem volume growth in boreal Norway spruce (*Picea abies*) (Strömgren 2001).

The root growth of boreal forest trees starts at a critical, species specific soil temperature in spring and reaches its maximum at around 20°C (Tryon and Chapin 1983, Andersen et al. 1986, Vapaavuori et al. 1992). The soil temperature required for maximal Scots pine root growth has been shown to be 16.5°C (Korotaev 1989), whereas root growth in the lodgepole pine (*Pinus* *contorta*) is highest at 20°C (Lopushinsky and Max 1990). Scots pine root growth has been reported to start at a soil temperature of 3–5°C (Korotaev 1987, 1989), that of the lodgepole pine at 5°C (Lopushinsky and Max 1990) and that of other boreal conifer species between 3 and 6°C (Lyr and Hoffmann 1967, Kaufmann 1977, Tryon and Chapin 1983, Lopushinsky and Max 1990). In contrast, a temperature of 8°C continued to suppress root growth in the Scots pine in hydroponic culture and root growth increased almost exponentially with increasing soil temperatures above 8°C (Vapaavuori et al. 1992). One possible explanation for this higher threshold temperature may be that roots respond differently in media of different textures and compositions. Also mycorrhizas, which are crucial for nutrient uptake, are absent in hydroponic cultures. The optimal soil temperature for shoot growth in Scots pine seedlings is known to be somewhat lower than that for roots. Vapaavuori et al. (1992) and Lyr and Garbe (1995) found soil temperatures of 12°C and 15°C respectively to lead to the most pronounced new shoot growth.

The allocation of plant biomass between the above and below-ground parts is also affected by soil temperature. Within the temperature range prevailing in the boreal forest zone, higher soil temperature usually results in an increased allocation of photosynthates and biomass below ground (Lippu 1998), and nutrient concentrations in plant material also increase with soil temperature (Domisch et al. 2002). Results of allocation studies conducted with small seedlings cannot necessarily be generalised to larger trees growing in forests, however.

Future climate scenarios predicting increases in air temperature may also mean a rise in soil temperature, enhanced root growth and perhaps increased below-ground C allocation. The temperature rise in Europe during the last 150 years has been mainly confined to the winter months, with no warming during the summer months to be observed in the long-term records (Balling et al. 1998). This could mean a warming in the spring and autumn, and thus a prolonged growing season, which could in turn result in higher biomasses of forest stands and an increased allocation of C below ground and higher above and below-ground litter production. Forests may be subject to changes in species distribution under changing climatic conditions, however (Kellomäki and Kolström 1992, Sykes and Prentice 1996), which could also have consequences for litter production, quality and decomposition.

1.3 Effects of soil temperature on decomposition of organic matter

Together with moisture, temperature is one of the most important factors affecting the decomposition of organic matter (e.g. Waksman and Gerretsen 1931), and it is usually a minimum factor restricting decomposition in boreal forest soils even during the growing season. Lower decomposition rates are found at higher latitudes (Mikola 1960, Johansson 1984), and this can mainly be attributed to climatic effects such as lower temperatures or actual evapotranspiration (AET) (Berg et al. 1993, Coûteaux et al. 1995).

The decomposition course generally follows an asymptotic curve (Olson 1963) with relatively high mass loss rates at the beginning (in the first year) and a subsequent slowing down of the process at later stages, resulting in very slow or negligible mass loss rates (Melillo et al. 1989, Berg et al. 1993). Aber et al. (1990) divided the decomposition process into two phases, the first with a constant mass loss rate and the second in which the process slowed down considerably and almost ceased. They also reported that the decomposition of different deciduous and conifer species litter proceeded in a similar manner during the second phase irrespective of the original litter species. Berg and Matzner (1997) divided the decomposition of Scots pine needle litter into three phases, the first regulated by nutrient level and readily available C, the second regulated by the lignin decomposition rate, and the third when the decomposition process practically ceased. Berg and Ekbohm (1991, 1993) suggested a decomposition model for Scots pine needle litter in which the mass losses increase until a limit value is reached (maximal mass loss).

Litter quality is the main factor determining decomposition. Easily leaching compounds disappear first, and sugars and starch are also easily decomposed, while lignin and lignified compounds are more resistant to decomposition (Naucke et al. 1993, Zech and Kögel-Knabner 1994), remaining as residuals forming the soil organic matter (SOM). Since new easily decomposable organic matter is added to the system every year, this may be one reason for the build-up of SOM. Microbes may not necessarily be forced to use lignin or other compounds which are difficult to decompose.

Direct observations on the effects of soil temperature on the decomposition of Scots pine needle litter are relatively scarce. Studies dealing with the effects of climate on the decomposition of Scots pine needles have shown a relatively close relationship between decomposition and climatic variables, decomposition rates being higher in climates with higher actual evapotranspiration, higher mean annual temperatures or higher mean July air temperatures (Berg et al. 1993, Johansson 1994). Summer drought may be a limiting factor for decomposition, however. Studies dealing with the effects of soil temperature on the decomposition of Scots pine root litter are also rare. A soil temperature of 25°C increased mass losses from Loblolly pine (*Pinus taeda*) fine root litter relative to 15°C from 57 to 66% within one year in a laboratory experiment (Ruark 1993). Decomposition of root litter is known to be less sensitive to climatic and environmental factors than to substrate properties (Johansson 1984, McClaugherty et al. 1984, Finér and Laine 1996, King et al. 1997, Silver and Miya 2001), the most important factor explaining root decomposition being the organo-chemical constitution of the litter itself, expressed in terms of Ca or lignin concentrations or the initial C/N ratio, whereas latitude, mean annual temperature or actual evapotranspiration are less important (Berg 1984, Berg et al. 1998, Silver and Miya 2001).

Scots pine needle and root litter differ in initial chemical constitution (Berg and Staaf 1980a,b, Berg 1984, Johansson 1995), and are decomposed at different rates, needle litter usually more quickly than root litter (Berg 1984, Johansson 1994, Bryant et al. 1998). Mass losses from Scots pine needle litter in Northern and Central Europe have been reported to range from 11% to almost 50% during the first year, depending on climatic and environmental factors (Berg et al. 1993, Johansson 1994), while mass losses from Scots pine root litter have been reported to be 10–25%, depending on the diameter of the roots. The differences due to root diameter disappeared after three years, however, when mass losses were approx. 40% (Berg 1984).

The majority of litter decomposition studies have employed the litter bag technique, which has received some criticism in that it underestimates mass losses from the litter, since, depending on the mesh size, larger soil animals are usually excluded. The role of large soil animals in the decomposition process in boreal coniferous forest soils is a relatively minor one, however, since fungi, and particularly soil bacteria, are responsible for most of the primary decomposition and nutrient mineralisation (Persson et al. 1980, Vogt et al. 1986). This should also be the case for pine mires since the abundance of soil animals that are of importance for decomposition (*Enchytraeidae*, *Collembola* and *Acari*) is lower on these peatlands, even drained, than on respective Scots pine mineral soil sites (e.g. Lohm et al. 1977, Standen and Latter 1977, Hotanen 1986). Another point is that air or oven-dried litter is usually used, which, to some extent, leads to an artificial decomposition environment for soil microbes, particularly as far as root litter is concerned, as the soil microbes and the rhizosphere may be washed away during separation of the root material (Vogt et al. 1991). Also, the air-drying of litter material may retard decomposition rates (Taylor 1998).

Soil warming experiments to study the effects of increased soil temperature on the decomposition of tree litter in the field have been performed by McHale et al. (1998), Rustad and Fernandez (1998), Verburg et al. (1999a) and Strömgren (2001), for instance. Increased soil temperatures have generally been found to result in enhanced decomposition rates, when not hampered by increased drought (e.g. Strömgren 2001). Another factor restraining decomposition is the availability of readily decomposable C in the soil, which may be depleted after a relatively short time, as suggested by McHale et al. (1998) and Jarvis and Linder (2000).

1.4 Soil temperature and carbon cycling in drained boreal peatlands

At present the mean soil temperatures in the rooting zone of peatlands in Central Finland during the growing season are 10 to 12°C, with values varying between 5 and 20°C over time. Weekly or monthly average soil temperatures seldom reach 15°C even in the surface layer of drained Finnish peatlands (Hytönen and Silfverberg 1991, Finér and Laine 1998). The decrease in temperature caused by drainage has not been confined only to the soil, especially at the beginning of the growing season, but it also affects local air temperatures during the late summer (Venäläinen et al. 1999).

Future climate scenarios for Finland predict increases in air temperature of 0.3–3.6°C within the next 45 years (Carter et al. 1995), possibly meaning a rise in soil temperature. This may enhance root growth, and thus increase below-ground C allocation, which can be of especial importance for the C sink strength of boreal peatlands (Gitay et al. 2001). Despite elevated mean temperatures and a longer growing season, soil temperatures may also be subject to a decrease in spring, i.e. a longer period of cold soil may occur. Altered temperature and precipitation patterns may affect the time when the insulating snow cover builds up, and whether it takes place before or after the occurrence of frost (Groffman et al. 2001). The depth of the snow cover is also crucial in this context (Verry 1991). A later build-up of the snow cover, or complete absence, together with frost, may cause even deeper soil frost and thus colder soils for a longer time in spring. This may be the case for drained and forested peatlands in particular, as they are already cold sites at the beginning of the growing season.

The effects of forestry drainage may be used to represent possible impacts of climate change, since the effect of drainage on the structure and functioning of an ecosystem is at least to some extent comparable to that predicted after the drying of northern peatlands caused by climate change (Laine et al. 1996). The ratio of tree biomass production and decomposition will probably change under changing environmental conditions, and an increase in soil temperature will result in an increase in plant biomass production, and thus also an increase in the amount of tree litter. Sites with a warmer climate produce many times more litter than boreal Scots pine stands (Berg et al. 1999), a pattern also seen along the temperature gradient within the boreal zone (Albrektson 1988, Berg and Meentemeyer 2001). Decomposition is accelerated at elevated soil temperatures, although the maximal mass loss may not necessarily be altered. A result may be a greater acquisition of C, particularly in boreal peatlands, provided that other environmental factors such as precipitation remain favourable for peat accumulation. This is valid only in an undisturbed system, however, since if any disturbance occurs (e.g. fire), the SOM content will decrease, which seems to be a natural way in the boreal zone to prevent the entrapment of nutrients and C (and thus of energy) in the soil. Also drainage changes the decomposition and accumulation patterns of organic matter and C, since drained peatlands are no longer organic matter accumulating ecosystems, although they may still act as C sinks.

Input of C into the soil takes place not only through above and below-ground plant residues, but also in the form of root exudates and allocation of carbohydrates to mycorrhizal symbionts. Carbon input into the soil from roots can be even greater than that from above-ground litter (Vogt et al. 1991). If we assume that not all litter is decomposed immediately (i.e. in the short-term) and not all C is released to the atmosphere but some is preserved in the soil, a positive difference develops between the C uptake for biomass growth and the C release during the decomposition of that same biomass, resulting in a positive C balance (ΔC). The amount of soil organic matter increases if no disturbances occur (Fig. 2, note the similarity to Janssen (1984) for agricultural soil). It may be concluded that this C balance may be even more positive, and thus the amount of SOM even greater, when the amount of litter produced increases due to elevated soil temperatures. This will hold true as long as decomposition will not increase more than litter production, and as long as relocation of C into the soil will not decrease.

Norby and Jackson (2000) stated that “analyses of ecosystem response to warming often focus on the presumed increase in heterotrophic respiration and the loss of C from the system, and it is important that the likelihood of a (partially) counterbalancing increase in C input by roots also be considered”. This, of course, not only concerns roots but the above-ground litter, too, since part of the C from the latter may be retained in the soil as well.

2 AIMS OF THE RESEARCH

The general aims of this work were to determine the effect of soil temperature on biomass production and allocation of Scots pine seedlings, on mass losses from Scots pine needle and root litter, and on the relocation of C released during the decomposition of Scots pine litter. The intention was to use pooled results from these studies to simulate C relocation under conditions of elevated soil temperature.

More specifically, the aims were:

1. to study the effect of different soil temperatures on the dynamics of shoot and root growth and the production and allocation of biomass in one-year-old Scots pine seedlings growing in peat soil under controlled environmental conditions (I),

2. to investigate the effects of the duration of low (5°C) soil temperature during the first half of the growing season on the timing of shoot and root elongation and on biomass production and allocation in one-year-old Scots pine seedlings in peat soil under controlled environmental conditions (II),

3. to assess the effects of soil temperature on the decomposition of Scots pine needle litter in peat soil under both field and laboratory conditions (**III**, **IV** and **V**), on the C dynamics related to the decomposition process (**III**), and on decomposition itself in two peat soils from climatically different regions (**III**), *4.* to study the effects of soil temperature on the fate of C released during decomposition of Scots pine needle and root litter in peat soil under both field and laboratory conditions (**IV** and **V**), and

5. to simulate the effects of elevated soil temperature on the relocation of the C released during decomposition of newly introduced tree litter in peat soil by means of a model describing C pools and fluxes under conditions of increasing soil temperature, based on the results of papers **I** to **V**.

It is obvious, however, that the results of short-term experiments conducted with small seedlings may not be directly generalised to older tree stands, and the effects may be different if the responses are studied over longer periods of time.

3 MATERIAL AND METHODS

3.1 Shoot and root growth and biomass allocation

One-year-old Scots pine seedlings were used in the growth experiments (**I** and **II,** Table 1), which were performed in a walk-in growth room (GR 77, Conviron Ltd., Winnipeg, Canada). The growth medium for paper **I** was derived from a sedge-pine fen (classification after Laine and Vasander 1996) in Central Finland (Lakkasuo mire complex). The mire site had been drained for forestry in 1961 and now supported a Scots pine stand. Intact peat cores were placed directly into plastic tubes of diameter 12 cm and length 30 cm and transported to the growth room. Horticultural peat (Kekkilä Ltd., Tuusula, Finland) was used in paper **II**.

The containerised seedlings were grown for one growing season under similar conditions at the Suonenjoki Research Station of the Finnish Forest Research Institute from seed originating from the same orchard in Central Finland (62°05´N, 26°10´E), which had been established from sources located between 61°07´N and 64°20´N in Finland. The seedlings were planted in plastic pots of volume 5.3 (**I**) or 3.4 dm^3 (**II**) and placed in insulated water tanks with temperature control in order to maintain the desired soil temperature in the pots. The seedlings for paper **I** were subjected to a dormancy period of 8 weeks air and soil temperatures of 3–4°C before the soil temperature treatments, while those for paper **II** had experienced a natural winter in the nursery bed and thus the treatments were started immediately after planting into the pots.

The soil temperature treatments consisted of 9 weeks at 5, 9, 13, or 17°C (**I**), and of 0, 3, 6 or 9 weeks at 5°C and subsequently 9 weeks at 13°C (**II**, Table 1). Samples of 14 seedlings per treatment were taken at three-week-intervals throughout the experiments. The light (approx. 20 µmol m^{-2} s^{-1}) was on for 8 hours per day during the dormancy period, and for 18 hours a day at an intensity of approx. 400 µmol m^{-2} s^{-1} during the soil temperature treatments. Humidity was set at 80% for the duration of the dormancy period and at 60% during the daytime and 80% at night during the soil temperature treatments.

The seedlings were watered once a week with 0.25 dm^3 of deionised water each, and fertilised with 5 mg N, 2 mg P and 11 mg K, together with other nutrients (Superex 5, Kekkilä Ltd., Tuusula, Finland), added to the irrigation water every second week (**I**). A 4-fold amount of fertiliser was added for paper **II**, since the growth medium was nutrient-poor horticultural

Table 1. Descriptions of the experiments reported in papers **I** to **V**.

Paper	Duration days	Plant material	Peat type	Environment	Soil temperature	Treatment soil temperature sum, d.d.	Variables measured
I	63	1-year-old seedlings	*Carex*	Growth chamber	5, 9, 13 and 17°C	315 (min)– 1071 (max)	Production and allocation
II	126	1-year-old seedlings	Horticultural *Sphagnum*	Growth chamber	5 → 13°C	819 (min)– 1134 (max)	Production and allocation
III	360	Needles from 2-year-old seedlings	*Carex*	Growth chamber	5, 10 and 15°C	300 (min)– 5400 (max)	Decomposition
IV	500	Needles and roots from 1-year-old seedlings	*Carex* and *Sphagnum*	Field	Seasonal variation	1280 (min)– 3023 (max)	Decomposition and C relocation
V	240	Needles and roots from 1-year-old seedlings	*Carex* and *Sphagnum*	Growth chamber	15 and 25°C	1800 (min)– 6000 (max)	Decomposition and C relocation

peat. A plastic tube 2 cm in diameter was driven into the peat on one side of the pot for removing any free water that accumulated, since the pots were closed at the bottom (**I** and **II**).

The timing of bud break and the dynamics of main shoot elongation were recorded. At harvesting, the seedlings were cut at the root collar and the needles separated from the stem. The old and new parts (previous and current season) were treated separately. All parts were dried at 60°C to constant mass and weighed and the pots containing the excised root systems were stored at -18°C for later separation, when the frozen pots were thawed at 5°C and the new and old roots separated from the peat soil. The new roots were separated from the original peat plug and all the roots growing out of the plug were considered to be new. All the new roots were examined with a ScanJet 6100 C/T scanner at a resolution of 300 dpi (Hewlett-Packard Co., Palo Alto, CA, USA) and analysed with the WinRHIZO programme (Régent Instrumentals Inc., Québec City, Canada) for total length and root tips.

3.2 Needle and root decomposition and carbon relocation

The needle and root litter was derived from one-year-old (**IV** and **V**) or two-year-old (**III**) Scots pine seedlings (Table 1) grown in the same nursery as those for the growth experiments (**I** and **II**), under similar conditions and from seed originating from the same orchard in Central Finland. Seedlings were labelled with ^{14}C (**IV** and **V**) in order to be able to trace the C released from the litter during decomposition. The labelling was done at the beginning of the growing season and the seedlings were allowed to grow until the autumn, so that the label could be incorporated into their above-ground or below-ground tissues. The current needles were taken from the seedlings and dried at 60°C to constant mass before the experiment (**III**, **IV** and **V**). The fine roots (diameter < 2 mm) were also separated out, washed and dried at 60°C to constant mass (**IV** and **V**). Initial element concentrations in the litter were analysed in all cases (**III**, **IV** and **V**) and the organo-chemical fractions and initial ^{14}C-activity were analysed in subsamples for paper **V**.

The minerotrophic *Carex* and ombrotrophic *Sphagnum* peat soils for paper **V** were taken from two sites on the Lakkasuo mire complex in Orivesi (61°48´N, 24°19´E) that had been drained in 1961. The minerotrophic soil was from the same site as the *Carex* peat used as a growth medium for paper

I. The peat cores were placed directly into plastic tubes of diameter 15 cm and length 60 cm and transported to the growth room (GR 77, Conviron Ltd., Winnipeg, Canada). The southern *Carex* peat for paper **III** was taken in a similar way from the same site on the Lakkasuo mire complex, and the northern *Carex* peat from a peatland in the rural district of Rovaniemi (66°29′N, 25°29′E) that had been drained in 1956. The plastic pots used in the work for paper **III** were of diameter 12 cm and length 30 cm, and were closed at the bottom. The experiment reported in paper **IV** was conducted on peatland sites near the Helsinki University Forestry Station at Juupajoki, Central Finland (61°50′N, 24°17′E), two minerotrophic and two ombrotrophic sites dominated by *Carex* or *Sphagnum* peat, one drained and the other undrained (Table 1).

The decomposition of the litter (**III**, **IV** and **V**) was studied using the litter bag technique with exactly 1 g of each litter type in one bag (mesh size 1 mm). The needle litter bags were placed under the living moss layer (**III**, **IV** and **V**) and the root litter bags 2–3 cm deeper (**IV** and **V**). The desired soil temperature was obtained by placing the peat cores directly into growth chambers (**V**), or by placing the peat core pots in water tanks situated in a growth room (**III**). Soil temperatures of 5, 10 and 15°C (**III**) or 15 and 25°C (**V**) were used. The $^{14}CO_2$ flux from some of the cores (**V**) was determined weekly to estimate the proportion of the litter C that was released into the atmosphere during the decomposition process. The pots were irrigated once a week with water that resembled chemically the rain water at the Lakkasuo mire complex (Sallantaus 1992), in amounts similar to the real precipitation (**III** and **IV**). The water table was maintained at 30 cm from the peat surface for the work in paper **V**, while for paper **III** all free water that had accumulated was removed through a tube driven into the peat on one side of each pot.

The litter bags for paper **V** were sampled at 120 and 240 days, whereas for paper **IV** the bags were lifted at 135, 360 and 500 days (Table 1). In paper **III** samples were taken every 60 days. The remaining litter was removed from the bags and dried at 60°C to constant mass and then weighed to determine the mass loss. The respective peat cores were lifted simultaneously with the litter bags. The cores were divided into the moss layer and 0–1 cm, 1–6 cm, 6–11 cm, 11–31 cm and 31–51 cm layers (**V**). In the field experiment (**IV**) the cores were divided into the moss layer, 0–5 cm, 5–10 cm, 10–20 cm and 20–25 cm layers. All the layers were dried at 105°C to constant mass and weighed, after which they were milled and homogenised. The ^{14}C-activities (**IV** and **V**) were determined by combustion in an oxidiser

(Maricont, Junitek Ltd., Turku, Finland) and subsequent analysis in a liquid scintillation counter (Wallac 1411 Liquid Scintillation Counter, Wallac Ltd., Turku, Finland). The remaining ^{14}C-activity in the litter bag was measured for each litter sample separately. Three subsamples were taken from each peat core layer for measuring ^{14}C-activity and determining the spatial distribution of the C released during the decomposition periods.

3.3 Statistical analyses

The statistical analyses were performed with the SPSS statistical software package (SPSS Inc., Chicago, IL, USA). Repeated measure ANOVA and two and three-way ANOVA were used for testing the effects of the treatments and of time. The treatments blocks in the experiments reported in papers **I**, **II** and **III** were not replicated at the highest possible level, that of the water tank, as this would have been financially and spatially impracticable, but at the pot (i.e. plant or litter bag) level within the temperature treatments. This could mean a confounding effect between temperature treatment and water tank, which was partly avoided by changing the spatial locations of the pots containing the seedlings or litter bags within the temperature treatments every week.

The *p* values from experiments with a confounding factor may be higher in reality than those generated by ANOVA, since the fundamental assumptions of ANOVA are not necessarily valid (see Hurlbert 1984, Milliken and Johnson 1984, Underwood 1997). Thus particular attention was paid to *p* values indicating significant differences between treatments, and these were interpreted with caution when the differences were not clearly visible from the means and standard errors.

3.4 Modelling decomposition and carbon relocation

Trees and understory vegetation accumulate atmospheric C as biomass by photosynthesis (Fig. 1), the magnitude of this accumulation (INPUT), given a certain climate and soil fertility, being mainly governed by temperature (TEMP) and the length of the growing season (TIME). Respiration returns part of the C into the atmosphere, while another part is deposited in the soil as above-ground and below-ground litter. Easily degradable compounds (fast decomposing) in the litter soon disappear, whereas more resistant ones (slowly decomposing) remain in the soil for a longer time, forming part of its organic matter, although these fractions decompose eventually. It is assumed that the decomposition of easily degradable compounds depends on time and temperature (TEMP + TIME), whereas that of the slowly decomposing fraction depends only on time (TIME). The greatest amount of C released through decomposition is emitted into the atmosphere (atmospheric carbon), but considerable amounts are retained by the soil and are protected physically or chemically (stable soil carbon) or incorporated into the microbial biomass. The ultimate long-term fate of this C is not known, however, since small amounts of this stable pool may decompose or leach into the groundwater. A small amount of the C lost from the litter during decomposition is leached into the ground or surface water (leached carbon). The release of C into the atmosphere and leaching into the groundwater means a loss from the system, whereas accumulation in the soil implies an increase in C store of the system.

Scenarios and sensitivity analyses

The following five scenarios were simulated for a Scots pine stand growing on a drained peatland site (Table 2):

1. Base scenario, simulated until steady state (0 to 1000 years). All fluxes are stabilised within this time.
2. Average soil temperature increases by +2°C during the growing season, while biomass and litter production remain unchanged.
3. Average soil temperature increases by +2°C and both above-ground and below-ground biomass and litter production by +15%.
4. Average soil temperature increases by +2°C, above-ground biomass and litter production increases by +20% and below-ground biomass and litter production by +10%.
5. Average soil temperature increases by +2°C, above-ground biomass and litter production increases by +10% and below-ground biomass and litter production by +20%.

For the sensitivity analysis, scenarios 2, 3, 4 and 5 were also simulated with an increase of +4°C in the average soil temperature and with different rates of decomposition of the slowly decomposable litter fraction (0.5% a^{-1} or 2% a^{-1}). Scenarios 2 and 3 were also simulated with a decrease of -2°C in the average soil temperature and a respective decrease in litter production (-15%).

The base scenario (1) was run for a total of 1000 years, until complete stabilisation of the fluxes was achieved. An average soil temperature of 10°C during a growing period of 120 days was assumed, resulting in a soil temperature sum of 1200 d.d. The other scenarios (2 to 5), based on changes in year 1000+1, were simulated for another 1000 years until complete stabilisation of the fluxes was achieved again. The average soil temperature increased from the initial 10°C to 12°C, implying a 20% increase in the soil temperature sum. Extension of the growing season was not simulated here nor was any attempt made to vary the time within which the increase in soil temperature occurred.

Table 2. Short descriptions of the scenarios used in the carbon relocation simulations.

Scenario	Soil temperature sum, d.d.	Increase in above/below-ground production
Base scenario 1	1200	0
2	1440	0
3	1440	15% / 15%
4	1440	20% / 10%
5	1440	10% / 20%

Litter input

In scenarios 1 and 2 the above and below-ground categories of litter accounted for 100 g C $m^{-2}a^{-1}$ each, an average value for drained Scots pine mires which can be concluded from Laiho and Laine (1994, 1996) and Finér and Laine (1998). Each year a new litter input of the same magnitude was added to the soil. In scenario 3, the change in average soil temperature of +2°C, i.e. +20% of the soil temperature sum, was assumed to result in a 15% increase in both above and below-ground production, based on the results of paper **I** (conservatively interpreted), Gowin et al. (1980), Vapaavuori et al. (1992), Gower et al. (1995) and Lyr and Garbe (1995). Scenarios 4 and 5 were simulated with a different effect on above or below-ground production (+10% or +20%). The simulations presuppose that this increase in production is reflected directly in the above and below-ground litter production.

Decomposition

The model of Richards (1959) was chosen for the decomposition of needles and roots, since when mass losses are related to soil temperature sum in a more universal approach, a curve passing through the origin is not rational, as some decomposition may take place even at or very near 0°C (Bleak 1970, Visser and Parkinson 1975). Short-term (i.e. < 10 years) mass losses could then be described with the following equation:

$$m_{loss} = a/((1+e^{b-c*Tsum})^{1/d}) \tag{1}$$

where
m_{loss} is the mass loss at a certain soil temperature sum (T_{sum}),
a is the maximal mass loss (asymptote),
b, c and d are parameters, and
T_{sum} is the accumulated soil temperature sum (threshold 0°C).

Non-linear regression between the accumulated soil temperature sum and mass losses from the needle and root litter (pooled data from papers **III, IV** and **V**) provided the parameters for the models, which are the following:

needles: $m_{loss} = 87.8/((1+e^{2.16-0.0011*Tsum})^{1/1.973})$,
roots: $m_{loss} = 46.0/((1+e^{0.7026-0.0014*Tsum})^{1/0.8685})$.

The limit value for decomposition of the needles would then be 87.8%, similar to the figures observed by Berg et al. (1996). The limit value for roots would be 46.0%.

Relocation of carbon

The model used for simulating the relocation of C released during decomposition was a two-compartment-one consisting of rapidly and slowly decomposing litter compartments (Fig. 3A) similar to those of Berg et al. (1998), Coûteaux et al. (2001) and Thornley and Cannell (2001), for instance. It was assumed that the limit value is the border between the fast decomposing litter fraction, which behaves according to equation (1), and the slowly decomposing fraction, which decomposes in a manner independent of temperature. This decomposition was assumed to be linear, with 1% of the preceding year's mass disappearing each year, so that it takes about 500 years for each litter cohort to decompose totally. The two-compartment-model model used here, with its continuous flow of C, is similar to the Rothhamsted turnover model illustrated by Jenkinson (1990), and can be described as:

$$m_{loss} = deco(fast) + deco(slow) \qquad (2)$$

where
deco(fast) = decomposition described by equation (1), and
deco(slow) = 1% per year of [1-deco(fast)].

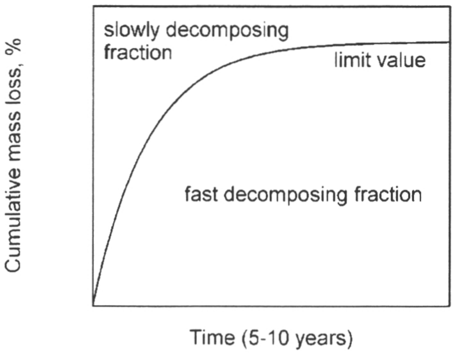
Considering the C relocation model, the limit value is thus valid only in the short-term, since the decomposition pattern of a certain litter cohort over a longer time span follows the curve depicted in Fig. 3B. The limit value for mass loss in this model therefore describes the border between temperature dependent and temperature independent decomposition.

The pathways of the C emitted from the needle litter were assumed to lead mostly (80%) into the atmosphere (Table 3), while retention by the soil and moss layer was assumed to be 15% and the proportion leached into the groundwater 5% (**IV** and **V**). The respective values for root litter were 70, 25 and 5% (**IV** and **V**, Table 3). These pathways were assumed to be the same for the slowly decomposing litter fraction and not to alter with an increase in soil temperature.

Table 3. Relative pathways of carbon released from needle and root litter during decomposition.

	Needles, %	Roots, %
Atmosphere	80	70
Soil and moss layers	15	25
Leaching	5	5

A. short-term



B. long-term

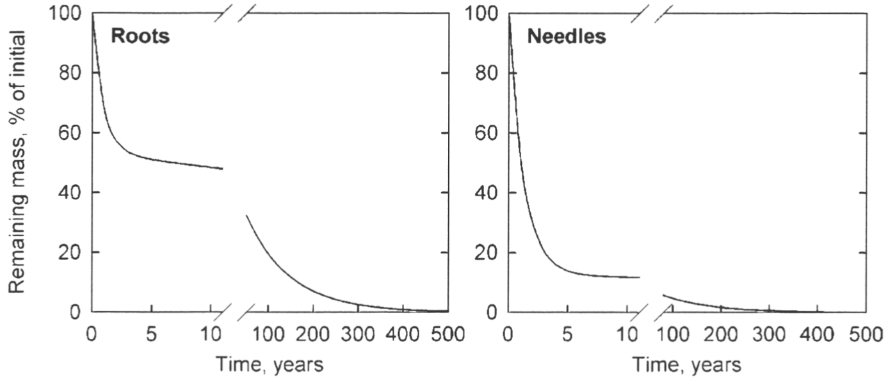


Figure 3. The concept of the limit value, here representing the border between the fast decomposing and slowly decomposing litter fractions (A). In the carbon relocation model, also the slowly decomposing litter fraction disappears in the long-term (B), although an asymptote is reached in the short-term.

4 RESULTS

4.1 Shoot and root elongation

Neither bud break nor the onset or cessation of height growth was affected by soil temperature, whereas the final height of the seedlings nine weeks after the beginning of the growing season was affected, shoot elongation being least at the lowest soil temperature (Fig. 1A in **I**). The length of the low soil temperature treatment at the beginning of the growing season, 3 to 9 weeks at 5°C (**II**), did not affect the timing of bud break or the final height of the seedlings (9 weeks after the rise in soil temperature) (Fig. 1A in **II**), although those growing without any cold soil period developed the tallest shoots (Fig. 1A in **II**). Elongation of the shoots was complete after 4 to 5 weeks in both growth experiments, and by that time the seedlings had grown 45–60 mm in height, depending on the soil temperature treatment (**I** and **II**).

Soil temperature did not affect the onset of root elongation, whereas the length of the new roots at 9 weeks was clearly higher at higher soil temperatures (Fig. 1B in **I**). New root tips started to develop in the first 3 weeks in all the soil temperature treatments. Root elongation was very slow during the cold soil period, but new roots emerged quickly when the soil temperature was increased to 13°C (Fig 1B in **II**). Root elongation at nine weeks did not differ between the 0, 3 or 6 week cold soil period treatments, whereas nine weeks of cold soil resulted in markedly lower root length. The rapid elongation of new roots did not start until shoot elongation had ceased (Fig. 1 in **I** and **II**). The number of new root tips showed a corresponding pattern to that of new root length, and was similar in both experiments.

4.2 Biomass production and allocation

Soil temperature clearly affected the biomass production of the seedlings, and although no effects on the total biomass of the seedlings were observed during the first 3 weeks, the differences became obvious later (**I** and **II**). The total biomass increased with time and temperature after week 3 throughout the experiments (**I** and **II**) with the exception that at the end of the experiment reported in paper **I** the greatest biomass was observed at 13°C and not at 17°C, the highest soil temperature. This was due particularly to the new needle biomass, since the seedlings grown at 13°C had higher new needle biomass than those grown at 17°C (Fig. 2 in **I**). The biomass of new roots did not show this pattern, but was higher at higher soil temperatures, although the difference between 13 and 17°C was not statistically different. New root biomass was very low at 5°C and did not increase any more after 3 weeks (Fig. 2A in **I**).

The longer the duration of the cold soil period the lower was the biomass of new roots (Fig. 3A in **II**), although when growing at 13°C for a similar time, the biomass increased to a level similar to that observed in the treatments with shorter cold soil periods. The reaction of new needle biomass to the cold soil period was not especially apparent, although here again a trend for lower biomass after longer cold soil periods was found (Fig. 3A in **II**). The relative allocation of biomass was not significantly affected by soil temperature (Fig. 2B in **I**), or by the length of the cold soil period at the beginning of the growing season (Fig. 3B in **II**), although trends were observed for increased absolute and relative below-ground allocation of biomass at higher soil temperatures and for an increase in allocation to new roots and new needles (**I**). The length of the cold soil period reduced the relative biomass of new roots slightly, but once the soil temperature had increased to 13°C, the allocation to new roots also increased (**II**). The new needle biomass accounted for ca. 50 % of the total biomass at week 9 and the total below-ground parts for about 20–25 % (**I** and **II**), and these values changed only slightly afterwards (**II**).

4.3 Decomposition of needle and root litter

Mass losses from the needle litter were always higher than from the root litter in the field (**IV**), and also at all the soil temperatures studied in the laboratory (**III** and **V**). The decomposition of the root litter was only slightly affected by soil temperature after the first year, whereas that of the needle litter was clearly dependent on soil temperature later as well (Fig. 4, **III** and **V**). The temperature dependence of the decomposition of the needles nevertheless also decreased with time (Fig. 4). Other environmental factors, such as drainage status or peat type, had a more pronounced effect on the decomposition of needle litter than on that of root litter (**IV** and **V**). Mass losses from the root litter increased with time in the field (**IV**) and at 15°C in the laboratory, but not at 25°C (**V**). Mass losses from the needle litter were slightly higher in the northern *Carex* peat than in the southern variety, although

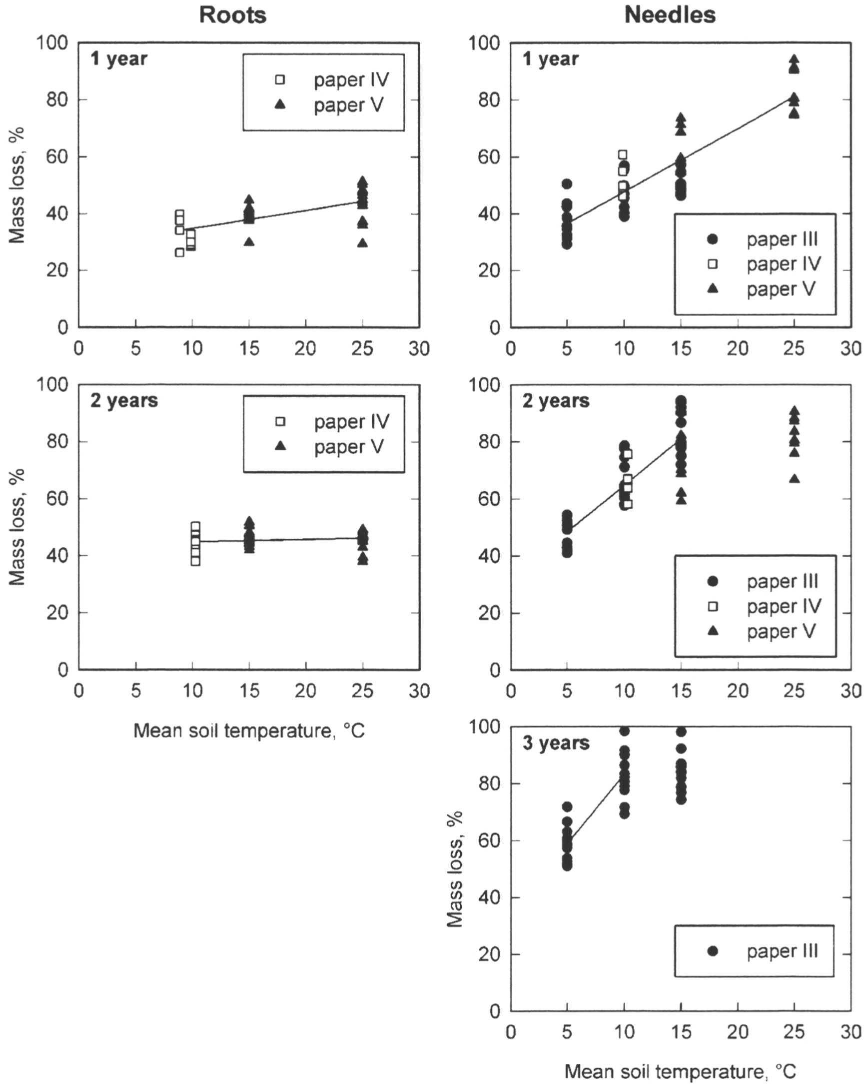


Figure 4. Mass losses from root litter (in *Sphagnum* and *Carex* peat) and needle litter (in *Carex* peat) during the first 2–3 simulated years at different mean soil temperatures. Individual values from papers **III**, **IV** and **V** are indicated.

not significantly so (**III**).

The mass losses from both pooled root litter (all data) and pooled needle litter (only *Carex* peats) showed a non-linear relationship to the accumulated soil temperature sum (Fig. 5, threshold 0°C) and converged to an asymptote, i.e. a limit value for mass loss, which was 87.8% (R^2=0.91) when fitted to the Richards model. The modified model of Berg and Ekbohm

(1991, with time replaced by soil temperature sum) gave a similar value, 86.4% (R^2=0.86). The limit values for the root litter were 46.0% (R^2=0.90) and 46.6% (R^2=0.90), respectively.

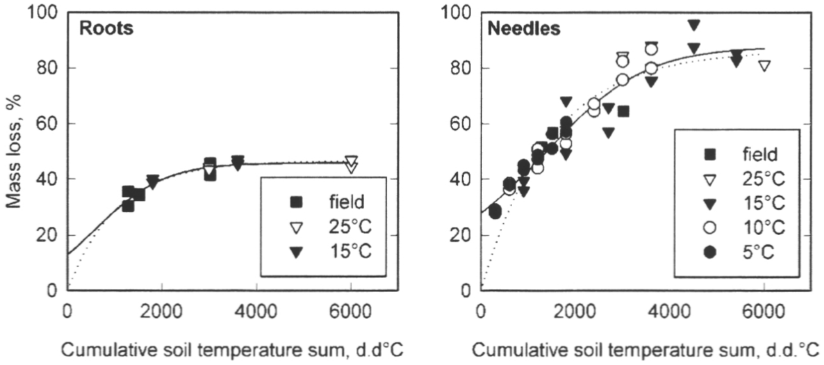


Figure 5. Mass losses from root and needle litter in relation to the cumulative soil temperature sum (threshold 0°C). Different incubation temperatures are indicated. Each point represents the mean of 4–6 observations. Regressions are obtained from the Richards model (solid curve) and the modified equation of Berg and Ekbohm (1993, dotted curve). Data from papers **III**, **IV** and **V**.

4.4 Relocation of carbon from decomposing litter

Soil temperature did not greatly affect the relative pathways of C released from the decomposing litter (**V**). At the end of the relocation experiments (two simulated or factual growing seasons) most of the C released during the decomposition of both needle and root litter was emitted into the atmosphere, an average of 80% of that from the needles and 70% of that from the roots (**IV** and **V**). A considerable amount of labelled C was also found in the peat soil, however, particularly in the peat layers immediately beneath the litter bags (Figs. 3+4 in **IV** and Figs. 3+4 in **V**), which accounted for approx. 10% of the C released from the needle litter and about 20% of that from the root litter. Smaller amounts of the released C, an average of 5%, were trapped by the moss layer growing on top of the peat cores, and similar amounts were leached into the groundwater, leaching being slightly higher from the root litter than from the needle litter. Retention in the peat soil increased between 4 and 8 months in the laboratory experiment (**V**), but no changes were detected after one year in the field (**IV**). No significant effects of drainage status or peat type (*Sphagnum* vs. *Carex* peat) were observed in the field experiment (**IV**).

4.5 Simulation of carbon relocation at elevated soil temperature

Base scenario

The base scenario (scenario 1, Fig. 6A), simulating C pools and fluxes under stable environmental conditions over a period of 1000 years until steady state, implied that, if the above and below-ground litter inputs each accounted for 100 g C $m^{-2}a^{-1}$, the C emissions from litter decomposition to the atmosphere were approx. 150 g C $m^{-2}a^{-1}$. Relocation of C into the soil would account for 30 g C m^{-2} a^{-1} and leaching into the groundwater for 10 g C m^{-2} a^{-1}. The carbon pools in the decomposing litter would be nearly 7000 g C m^{-2} (Fig. 6B). The cumulative amount of C retained in the soil over 1000 years would be approx. 29 kg C m^{-2} if no leaching from already retained C was taken into consideration. The sensitivity analysis showed that the time required for the system to stabilise was dependent on the decomposition rate of the slowly decomposing litter fraction, as a faster decomposition rate would achieve this in less time.

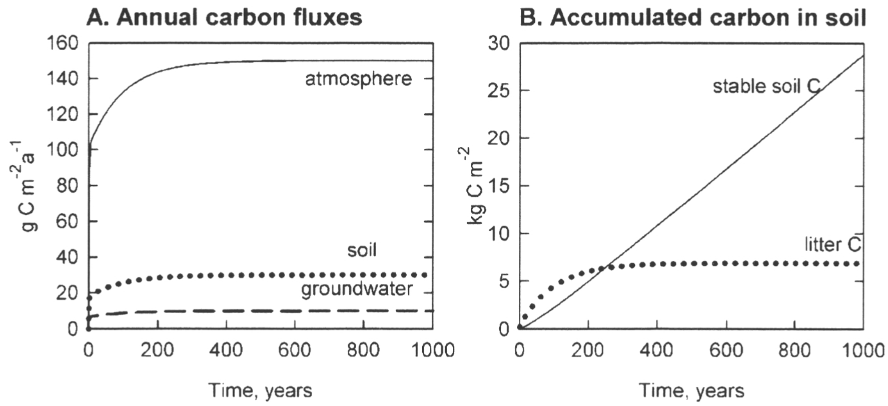


Figure 6. Simulated annual carbon fluxes into the atmosphere (g C $m^{-2}a^{-1}$) over a period of 1000 years until steady state according to the base scenario (A). Annual retention in the soil and leaching into the groundwater are also presented (A), as are the carbon accumulated in the soil (= retention of carbon in the soil over time) and the amount of carbon stored in decomposing litter (B).

Changes due to elevated soil temperature and sensitivity analyses

Scenarios 2 to 5 (relocation scenarios under changed conditions, Fig. 7) were run for 1000 years, within which the emissions from the decomposing litter into the atmosphere and also the retention of C in the soil and its leaching into the groundwater had stabilised.

The main results of the simulations were the following:

1. If litter inputs are not increased at elevated soil temperature, the fluxes are increased for a relatively short time (scenario 2, Fig. 7A), after which stabilisation occurs at the same flux values as before.
2. Increased litter input at an elevated soil temperature results in increased emissions into the atmosphere and leaching into the groundwater (scenario 3, Fig. 7B), but the relocation into the soil also rises, which means a positive C balance for the system. The fluxes show a short peak and then stabilise at a higher level.
3. The sensitivity analysis showed that a higher increase in soil temperature (+4 vs. +2°C) results in a higher peak in the fluxes (Fig. 7C and D). A higher decomposition rate for the slowly decomposing litter fraction will shorten the time within which the fluxes stabilise, but eventually all the scenarios (i.e. different increases in soil temperature or different decomposition rates for the slowly decomposing litter fraction) end up with same values.
4. If needle litter production increases more than that of root litter according to scenario 4, fluxes into the atmosphere and leaching into the groundwater will increase slightly and retention in the soil correspondingly decrease, relative to the values in scenario 3. Conversely, if root litter production increases more than that of needle litter (scenario 5), fluxes into the atmosphere and leaching into the groundwater will decrease slightly and retention in the soil will increase slightly.
5. The sensitivity analysis revealed that a decrease in soil temperature (-2°C) has no effect on the eventual fluxes if the litter input remains unchanged (Fig. 7E). A decreased input at a lower soil temperature results in reduced emissions into the atmosphere and leaching into the groundwater, as well as in a decreased relocation into the soil (Fig. 7F). These reductions are of the same magnitude as the increase of the fluxes due to increased litter input at elevated soil temperature (+2°C).

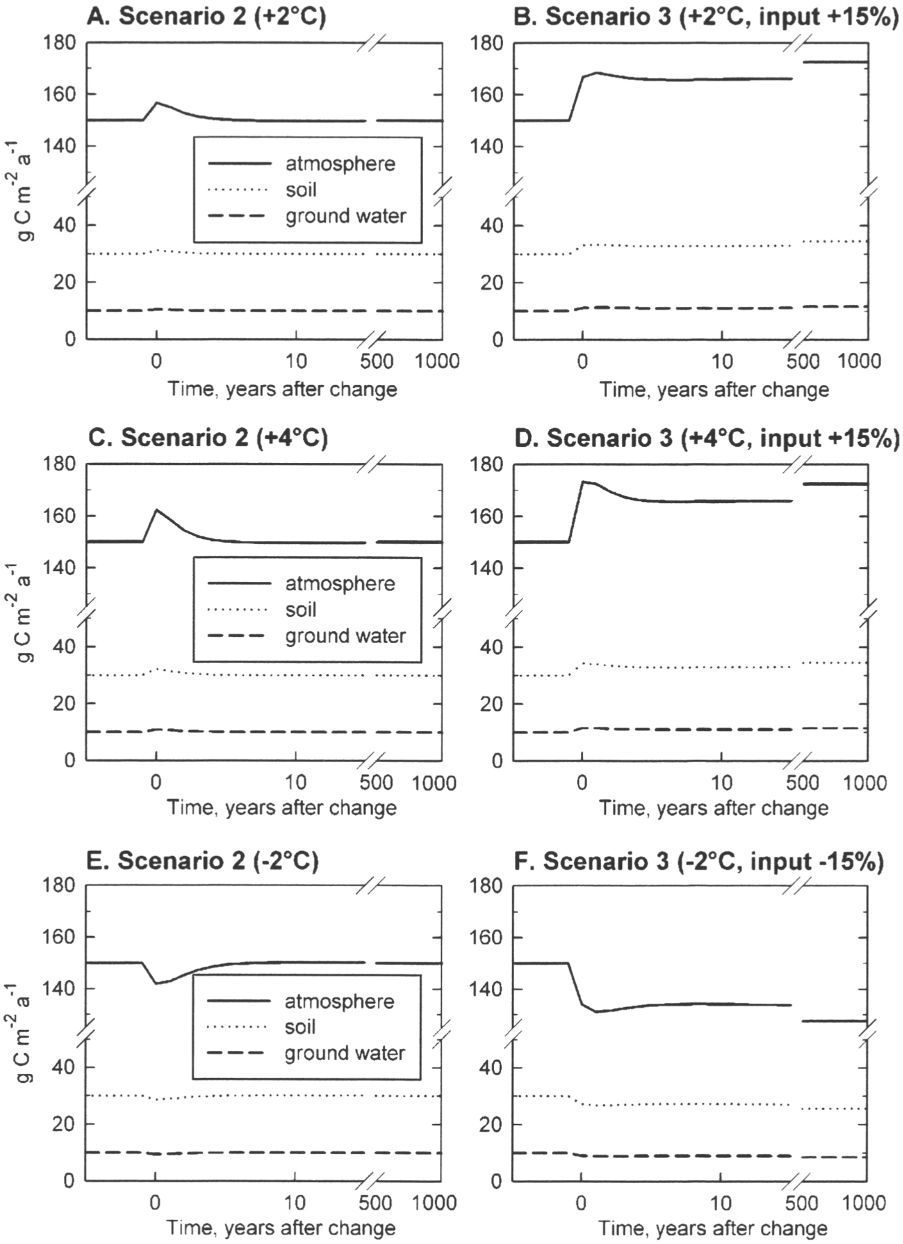


Figure 7. Simulated carbon relocation over a period of 1000 years after a change in soil temperature (A and B: +2°C, see text for details) according to scenarios 2 and 3. Initially, the system is in a steady state. The results of the sensitivity analyses are also shown (C and D: temperature increase of +4°C instead of +2°C; E and F: temperature decrease of -2°C). The curves depict carbon emissions into the atmosphere, retention in the soil and the leaching into the groundwater (g C m^{-2} a^{-1}).

5 DISCUSSION

5.1 Temperature control on shoot and root growth dynamics

The failure of soil temperature variations to influence bud break and the onset of new shoot elongation (**I**) was observed earlier in Scots pine seedlings by Vapaavuori et al. (1992) and Lyr and Garbe (1995), and similarly no effects of artificial soil cooling on the beginning or ending of the height growth of mature Scots pines growing on peatlands were observed by Huikari and Paarlahti (1967). Lopushinsky and Max (1990) found only slight effects of soil temperature on the timing of bud break in two *Abies* species, but noticed a very clear effect on the total length of the new shoot, as also observed in the present papers **I** and **II**, too. Boreal conifers are generally well adapted to variations in climatic conditions between years and during the growing season, e.g. the start and cessation of growth in the Scots pine are governed not only by temperature but also by the photoperiod (Huikari and Paarlahti 1967, Koski and Sievänen 1985). Premature onset of growth (bud break) in boreal conifers, e.g. the Norway spruce, may in any case be prevented in the event of climatic warming, since temperature is not the only determining factor (Partanen et al. 1998).

New root length growth started slowly and did not differ between the soil temperature treatments during the first three weeks except at 5°C (**I**), where it was notably lower than at the higher soil temperatures. Root growth started somewhat more slowly in paper **II**, however, perhaps on account of the fact that the "winter" in paper **I** consisted of a dormancy period of 8 weeks at 3–4°C, milder conditions that might have led to more rapid root growth at the beginning of the growing season, whereas the seedlings referred to in paper **II** had experienced a real winter in the nursery field. The start of new root growth seems to be closely connected with the increase in soil temperature, but high temperature alone is not the only factor, as the time elapsing (i.e. the physiological stage of the seedlings) also seems to be important, since no differences in root growth were observed between the soil temperature treatments during the first 3 weeks (**I**). This may lead to the conclusion that the soil temperature sum is a crucial factor concerning root growth. Pregitzer et al. (2000) found it conceivable that the initiation of root growth could be related to the accumulated soil temperature sum, and this could explain the present observation that root growth did not start at 13 and

17°C, apart from the emergence of new root tips, even the soil temperature should have been favourable for new root growth.

On the other hand, another factor affecting the start of new root growth is shoot growth. During shoot elongation it is the above-ground parts, particularly the new needles, that are stronger sinks for carbohydrates than the roots (Lippu 1998). Since new photosynthates are the main source of new root elongation of conifer seedlings (Gordon and Larson 1970, van den Driessche 1987, Lopushinsky and Max 1990, Horwath et al. 1994, Lippu 1998), new root growth has to occur after shoot growth. When the new needles have grown enough to acting as C sources, photosynthates are also translocated below ground, enabling new root growth to increase. The needles are assumed to be C sinks until they have reached 50% of their final length (Ericsson 1978), which took place three to four weeks from the beginning of the growing season (**I**) and corresponded with the start of fast new root growth. The start of prolific Scots pine root growth only after shoot elongation was also observed by Vapaavuori et al. (1992) and Iivonen et al. (1999) in laboratory experiments, Lyr and Hoffmann (1964) under natural conditions in Central Europe, and Makkonen and Helmisaari (1998) in Scots pine stands in Eastern Finland. Finér and Laine (1998) similarly did not observe a peak in root growth in spring under field conditions on peatlands in Central Finland.

The results of the growth experiments (**I** and **II**) are consistent in that the seedlings with the warmest soil at the beginning of the growing season had the tallest shoots at the end of their respective treatments, and also indicate that the start and cessation of shoot elongation are mainly dependent on air temperature and are largely predetermined in second-year seedlings and older trees (Cannell et al. 1976, Lanner 1976). Soil temperature may nevertheless act as a factor influencing shoot length growth within the limits of the predetermined length. The low soil temperature treatments (**I** and **II**) had similar effects on the start of rapid root growth, suppressing new root growth (see also Lopushinsky and Kaufmann 1984), but as soil temperature increased, root length growth started (**II**). A cold soil period (5°C) at the beginning of the growing season delayed the development of the seedlings (here root growth; for delay in nutrient uptake see Domisch et al. 2002), but when soil temperatures increased from 5 to 13°C, the differences disappeared after a few weeks. Similar results were observed by Lippu and Puttonen (1991) and Lippu (1998) studying photosynthesis or biomass allocation after a period of low soil temperature in spring.

Root elongation showed an exponential response to an increase in soil temperature (**I** and **II**, see also Steele et al. 1997). A slight or moderate increase in soil temperature may, indeed, result in an exponential increase of root growth, and thus increased below-ground C allocation, but respiration costs also increase with soil temperature, so that root growth will not increase endlessly with a rise in soil temperature.

Stem elongation ceased during weeks 4–5 (**I** and **II**), a time when the accumulated air temperature sum was about 500 d.d. Similar observations were also made by Raulo and Leikola (1974) with regard to Scots pine seedlings under field conditions. Needle elongation occurs over a longer period of time than shoot growth since the needles do not reach their final length until the end of July or beginning of August (Parviainen 1974). Root length growth takes place over an even longer period, since the roots continue to grow as long as the soil temperature is favourable (Prokushkin 1982). Root growth in the Scots pine is reported to cease at a soil temperature of 5–7°C in autumn (Korotaev 1989).

Low soil temperatures at the beginning of the growing season are a natural phenomenon in the boreal zone, and the trees have adapted to this situation. Prolonged periods of cold soil due to deeper frost as result of changes in snow cover and soil frost patterns (Groffman et al. 2001) could delay the development of seedlings even more, but may not greatly alter the ultimate development of planted seedlings (**II**). This seems to hold true only as long as the soil is not frozen, however (e.g. Tierney et al. 2001). Also, the fact that drained peatlands are particularly cold sites at the beginning of the growing season does not seem to be too critical. If planted seedlings are in good condition and water and nutrient availability are not limiting factors (e.g. Iivonen et al. 1999), they will survive the time when the soil is cold but unfrozen, but the growth will be reduced substantially during this cold soil period.

5.2 Effects of soil temperature on biomass production and allocation

The reason for the seedlings grown without any cold soil period (**II**) having the lowest biomass at the end of the treatment seems to be the elapsed time, since all the other treatments (with a cold soil period) continued for a longer time. Also, as shoot growth is only to a minor degree dependent on soil temperature, the plants in the treatments with a longer cold but unfrozen soil period had more time to grow their shoots. The root biomass was very low during the cold soil period (and simultaneous shoot growth period, **II**), but increased rapidly after the soil temperature was raised to 13°C. Iivonen et al. (1999) concluded that Scots pine seedlings can compensate for the harmful effects of prolonged low soil temperature at the beginning of the growing season by accelerating their root growth once the soil temperature exceeds 13°C, assuming that nutrient availability is not limited. This situation seemed to exist in the experiments reported in papers **I** and **II**, since additional nutrients had been given to those already in the peat soil.

The metabolic activity of the root system and its sink strength decrease at low soil temperatures resulting in reduced below-ground allocation of photosynthates (Hurewitz and Janes 1983) and correspondingly in above-ground accumulation of biomass, whereas at higher soil temperatures the root system becomes a powerful sink for photosynthates (Lippu 1998). The biomass production of the seedlings, particularly the production of new needles, increased with increasing soil temperature (**I**). The higher above-ground production of boreal conifers in a warmer climate has direct effects on litter production, which is also higher at sites with a higher average temperature (Albrektson 1988, Berg et al. 1999, Berg and Meentemeyer 2001). Root production under natural conditions is likewise highly dependent on mean annual temperature (Gower et al. 1994, 1995), and increasing temperatures result in increasing root productivity. Finér and Laine (1998) observed that fine root production increased with mean monthly soil temperature on peatlands in Central Finland, from which it may be concluded that root litter production also increased.

The allocation of total biomass between the above and below-ground parts of the seedlings was not significantly affected by soil temperature (**I** and **II**). This was also observed by Lippu (1998), although, using ^{14}C as a tracer, he did find a higher percentage of current photosynthates to be allocated to the root system at higher soil temperatures (17°C compared to 5 and 8°C). A slight trend for increased below-ground allocation at higher soil temperatures was observed in papers **I** and **II**, as also by Lippu (1998) in Scots pine seedlings. This could mean not only an increase in root production at elevated soil temperatures, but also an increased allocation to below-ground plant parts, strengthening the role of roots as a C sink within the plant.

The allocation of biomass to the needles reported (**I** and **II**) was much higher than usually found in mature conifers, and the allocation to the stem correspondingly much lower (Vogt et al. 1987b, Gower et al. 1994, Helmisaari 1995, Vanninen et al. 1996, Laiho and Laine 1997, Helmisaari et al. 2002). All in all, the biomass allocation to below-ground parts was 25–30%, which roughly corresponds to the values observed in mature Scots pine stands (Helmisaari 1995, Laiho and Laine 1997) or other boreal conifer stands (Grier et al. 1981, Gower et al. 1994). The allocation patterns of boreal trees may not necessarily change greatly in response to a changing climate (Raich and Nadelhoffer 1989, Nadelhoffer and Raich 1992, Callaway et al. 1994, Gower et al. 1995, Berninger and Nikinmaa 1997, Gower et al. 2001). Fine roots tend to decrease as a proportion of total biomass as the tree grows, but in the Scots pine seedlings considered in papers **I** and **II** all the roots were fine roots, comprising roughly one third of the total biomass. The relative fine root biomass allocation decreases with stand age, as shown by Vanninen et al. (1996) and Helmisaari et al. (2002) with Scots pine stands of different ages (15 to 212 years). Although the absolute fine root biomass of a tree stand may not change greatly after canopy closure, the biomass production, i.e. annual C allocation to the fine roots, may nevertheless increase, so that it usually represents well over 50% of total production in mature conifer stands (Ågren et al. 1980, Grier et al. 1981, Vogt et al. 1987b, Helmisaari et al. 2002).

5.3 Soil temperature and decomposition of litter

Since the temperature dependence of litter decomposition decreased with time (Fig. 4), it may be concluded that the older the organic matter becomes, the less sensitive its decomposition is to soil temperature, as suggested recently by Liski et al. (1999) and Giardina and Ryan (2000). When relating mass losses to temperature, it is a usual convention to use short-term, i.e. first year-mass losses, where a linear relationship can be seen. This easily leads to conclusions entailing a continuous linear effect of temperature on decomposition rates, which is not correct. Easily degradable compounds disappear during the early stages of decomposition and more resistant compounds remain undecomposed, so that the decomposition rate will already have declined by the end of the first year in boreal forests. Elevated soil temperatures or a prolonged growing season will definitely increase mass losses but these are unlikely to continue linearly, since the second-year mass losses will already be much lower than in the first year and the proportion of lignin and lignified decomposition products will increase (Berg et al. 1981, Lähdesmäki and Piispanen 1989). Berg and Ekbohm (1991, 1993) presented the concept of a limit value for mass loss, and this is supported by the results presented in papers **III**, **IV** and **V**, where the mass losses converged towards an asymptote, at least in the short-term (Fig. 5). Latter et al. (1998) similarly found an asymptotic model best for describing the mass losses from *Calluna*, *Eriophorum* and *Rubus* litter during a time span of over 23 years in a peatland in Northern England.

Elevated soil temperatures increase mass losses from organic material, but decomposition proceeds with time at lower soil temperatures, too. Ladd et al. (1985) found that the average decline in residual ^{14}C in decomposing legume material at sites in Southern Australia matched rather well with figures for the decomposition of ryegrass under English and Nigerian conditions, supposing that one year in Nigeria equalled two years in Australia and four years in England. This interaction between time and temperature indicates the significance of the temperature sum, alongside moisture, as a major factor affecting decomposition. The temperature sum has also been used earlier to represent effects of temperature on decomposition or nutrient mineralisation (Andrén and Paustian 1987, Honeycutt et al. 1988, van Cleve et al. 1990, Douglas and Rickman 1992, Sparrow et al. 1992).

As observed earlier, green Scots pine needle material has higher relative mass losses than has brown litter during the early stages of decomposition. This situation is reversed later on, implying that the brown litter reaches asymptotes at a higher level (Berg et al. 1995a, 1996). Although the decomposition experiments (**III**, **IV** and **V**) made use of green needle material, practically the same limit values were observed when calculated with both the modified equation of Berg and Ekbohm (1993) and the Richards model (Fig. 4) as by Berg et al. (1996) for brown needle litter. The accumulated soil temperature sum at the lowest temperature in paper **III**, 5°C, was only 1800 d.d. at the end of the experiment, and an even longer experiment would have been needed to find out whether the decomposition process really proceeded to the same asymptote at that soil temperature as at the higher temperatures (10 and 15°C).

Assuming that decomposition in the field under natural conditions is lower in Northern Finland than in the South (e.g. Mikola 1960), and considering the slightly higher mass losses in the northern peat at 15°C at the end of the laboratory experiment (**III**), an increase in soil temperature could have a proportionally greater effect on decomposition in the North than in the South. However, assuming that an increase in soil temperature will not affect the limit value for the decomposition of pine litter (**III**), it may be concluded that the relatively higher increase in decomposition in the north could accelerate the process, particularly at the beginning, but will not affect the maximal mass loss itself. Observations implying that a temperature rise of the same magnitude will increase mass losses more at high latitudes than at low latitudes have been recorded previously by Bottner et al. (2000) and Coûteaux et al. (2001).

Berg et al. (1993) and Johansson et al. (1995) concluded that the proportion of lignin-like residual material after the same duration of Scots pine needle decomposition was higher when warmer climatic conditions promoted higher initial mass losses. Thus, an increase in soil temperatures due to climatic changes could result in a higher percentage of recalcitrant substances in the litter at later stages of the decomposition process and eventually lead to lower mass losses (Dalias et al. 2001). Verburg et al. (1999b) also came to the conclusion that the amount of refractory organic matter may increase at elevated soil temperatures. The higher soil temperature in paper **III** (15 vs. 10°C) did not result in a lower limit value, however. One important factor affecting decomposition is probably increased nutrient concentrations in the plant material at elevated soil temperatures (Marschner 1995, Domisch et al. 2002) due to increased nutrient mineralisation and uptake rates. This may be reflected in higher nutrient concentrations in the litter (e.g. Berg et al. 1995b), which could result in increased decomposition rates. On the other hand, concentrations of metals, with adverse effects on decomposition, may also increase. Higher initial N concentrations in the litter could also counteract the enhancing effects of increased soil temperature during later stages of decomposition.

The fact that mass losses from the needle litter were higher than those from the roots (**IV** and **V**) could be attributed to the different initial organo-chemical compositions of these types of litter. Also, the initial concentrations of Al and Cu, metals which are known to have adverse effects on the decomposition of conifer roots and needles (Vogt et al. 1987a, Berg et al. 1991), were many times higher in the root litter (**V**). The first-year mass losses (**III**, **IV** and **V**) were higher than those reported for Scots pine litter on boreal mineral soils (Berg 1984, Johansson 1984, Berg and Ekbohm 1991, Berg et al. 1998, Hyvönen et al. 2000), a situation that could be explained by the very much higher temperatures used (**IV** and **V**, 15 and 25°C) and the fact that the litter was derived from nursery-grown seedlings which had experienced regular fertilisation and irrigation, resulting in different initial chemical composition (**V**) and nutrient status (**IV** and **V**). Finér and Laine (1998), using similar litter also observed similar mass losses to those reported here (**III**, **IV** and **V**).

Although root litter decomposition was less dependent on soil temperature than was needle litter decomposition (**V**), it is possible that soil temperature may affect the decomposition of roots for a shorter time than that of needles, and that it was not detected, since the shortest decomposition period was 120 days. Mass losses from Scots pine needle litter, at least during the first year, show a clearer dependence on environmental factors (Mikola 1960, Dyer et al. 1990, Johansson 1994), whereas other factors become more important during the later stages of decomposition, e.g. lignin concentration or the Ca content of the remaining litter (Johansson 1994, Johansson et al. 1995).

The laboratory experiments with regular irrigations (**III** and **V**) seem to have provided favourable conditions for decomposition, even at a soil temperature of 25°C, and featured steady-state moisture conditions in which drought was not a limiting factor. Soil moisture may be a restricting factor at elevated soil temperatures, however, and decomposition on mineral soil may be more susceptible to drought resulting from higher soil temperatures than on peatlands, even if they are drained. When comparing mass losses in the laboratory (**III** and **V**) with the field results (**IV**), it can be seen that the needle mass losses at 10°C during the first 120 and 240 days correspond fairly well to mass losses in the field during the first and second years. The higher soil temperature in paper **III** (15°C) also resulted in slightly higher mass losses, while the mass losses from root litter were to some extent higher at a constant temperature of 15°C in the laboratory (**III**) than in the field (**IV**). It thus seems reasonable to use a laboratory period of 120 days as an analogue for a field period of one year (see also Fig. 4).

5.4 Relocation of carbon during decomposition

Since soil temperature did not greatly affect the relocation of C from decomposing litter to the atmosphere, the soil or the ground water (**V**), the relative pathways of C released during decomposition were assumed to be constant in the simulations. The greatest retention in the soil occurred during the first year (**IV**), with no further increase in the second summer. It cannot be concluded, however, whether relocation in the soil had stopped or whether some of the labelled C moved downward into the groundwater and was replaced by C released from the decomposing litter. It is simply assumed that all C retained in the soil would remain there. Longer experiments would be necessary to investigate the real fate of the C relocated into the soil, since some may be leached into the groundwater or released into the atmosphere during decomposition.

The author is not aware of any earlier studies assessing the fate of the C released during tree litter decomposition on peatlands. Charman et al. (1994) suggested downward transport of younger C in peat soil, a form of leaching that may extend all the way into the mineral soil under the peat layer (Turunen et al. 1999). Witkamp (1966), studying the decomposition of needle litter from two subtropical pine species, suggested a considerable transport of soluble compounds and decomposition products to deeper layers in mineral soil, and Sørensen (1987) observed movements of labelled C down to deeper soil layers during the decomposition of ^{14}C-labelled straw in the field.

Vedrova (1997), studying the decomposition of pine needle litter on mineral soil in Siberia, observed that during the first two years the upper 2 cm of soil retained 15% of the C lost during decomposition and 81% was emitted to the atmosphere. The data in papers **IV** and **V** indicate that the proportion of C retained in drained peat soil is in the range of 10–30%, including the moss layer, which contained approx. 5% of the labelled C released by the end of the experiments. Comparable figures concerning the moss layer are quoted by Strömgren (2001), whereas Coûteaux et al. (2001) observed a much smaller amount of C to be retained in the soil, and in fact did not take the proportion in the soil into account when estimating the initial C content of their litter.

5.5 Simulated carbon relocation at elevated soil temperature

Base scenario

The values for annual emissions into the atmosphere (150 g C m^{-2} a^{-1}), retention in the soil (30 g C m^{-2} a^{-1}) and leaching into the groundwater (10 g C m^{-2} a^{-1}), although calculated from a rather average value for drained peatlands supporting a Scots pine stand, are of reasonable magnitude (Fig. 6A). Silvola et al. (1996a) reported soil respiration values (CO_2-C) of 320–380 g $m^{-2}a^{-1}$ at the site where peat cores for papers **III** (southern peat) and **V** (*Carex* peat) were taken, so that it could be concluded that roughly 40–50% of the soil respiration is derived directly from tree litter decomposition, assuming that no other litter input than that from tree needles and roots is present. Silvola et al. (1996b) concluded the contribution of rhizospheric respiration to the CO_2 flux in drained pine mires to be 35–45%, whereupon the remaining 5–25% must originate from other heterotrophic respiration (e.g. microbes or soil animals not associated with tree roots).

Carbon sequestration values for forested drained peatlands are reported to be 45–60 g C $m^{-2}a^{-1}$ (Minkkinen et al. 1999), while Tolonen and Turunen (1996) reported a mean long-term accumulation rate in Finnish pristine peatlands of 22.5 g C $m^{-2}a^{-1}$. The base simulation (scenario 1) results in a C relocation into the soil of approx. 30 C $m^{-2}a^{-1}$. The simulated values for leaching (10 g C m^{-2} a^{-1}, Fig. 6A) also correspond well to the measured leaching of C from drained peatlands, 10–11 g C $m^{-2}a^{-1}$ (Sallantaus 1994), or from forested catchments with a high percentage of peatlands, on average 6.4 g C m^{-2} a^{-1} (Kortelainen and Saukkonen 1998).

In a state of equilibrium, nearly 7 kg C m^{-2} would be contained in litter at different stages of decomposition and nearly 30 kg C m^{-2} would be relocated into the soil after 1000 years (Fig. 6B). This may well be overestimated, since the simulation does not take account of losses of C due to fire or leaching from already existing stores in the soil. Minkkinen et al. (1999) measured a peat C store of 67 kg C m^{-2} at the drained site of the Lakkasuo mire, where the peat samples for the relocation study (**V**) were taken (mire age 4100 years). No direct comparisons with the results of the simulations can be made, however, since the mire site was drained only 40 years ago and C accumulating in pristine peatlands is derived from other sources than tree litter, mainly *Sphagna* and sedges.

Scenarios at elevated soil temperature and sensitivity analyses

According to scenario 2, the soil temperature increases but litter input does not, and the result would be a sharp increase in C emissions, although stabilisation to the same level as before the temperature increase would occur within 5 to 10 years (Fig. 7A). This can be explained by the fact that the amount of readily decomposable material does not increase. After a few years the majority of this fraction will be exhausted and although new material will be added every year, this will not increase emissions because the time taken for each litter cohort to reach the limit value, i.e. the time after which its decomposition is not dependent on temperature, will be shorter than before. Scenario 2 is based on unlikely assumptions, however, since elevated soil temperatures provide better environmental conditions for growth, assuming no restriction by drought. It is more probable that the biomass will increase, causing an increased input of litter.

Scenario 3, in which both soil temperature and litter input increase, is a more realistic one. There is again a sharp increase in fluxes after the increase in soil temperature, but the fluxes are now higher than in scenario 2, because the litter input increases simultaneously (Fig. 7B). After a short peak, the C emissions into the atmosphere, relocation into the soil and leaching into the groundwater level off slightly but they increase again to higher equilibrium levels when completely stabilised within 1000 years. When soil temperatures are increased by +4°C instead of +2°C, the result is higher peaks immediately after the soil temperature increase, but the flux levels after stabilisation are not affected (Fig. 7C and D). This is due to the fact that the model assumes the apparent limit values for decomposition to remain unchanged and that the decomposition rate of the slowly decomposing litter fraction is not affected by soil temperature. Similarly, a decrease in soil temperature by -2°C results in a temporary reduction of fluxes when the litter input remains unchanged (Fig 7E). The reduced input of litter resulting of a lower soil temperature (Fig. 7F) decreases the fluxes to the atmosphere and the ground water, but also lowers the relocation of C into the soil, indicating a decreasing C sink. In scenarios 4 and 5, where the allocation patterns of above-ground and below-ground production are changed, the flux levels after stabilisation alter, although only to a very minor degree.

In all the scenarios with increasing soil temperature and litter production, the C emissions into the atmosphere and C leaching into the groundwater increase, but so does the relocation of C into the soil. The difference (ΔC) between the C input and output may thus increase, implying a more positive C balance (see also Bonan and van Cleve 1992). Basically, the results of the simulations at elevated soil temperatures are comparable to the results of Thornley and Cannell (2001), whose simulations with elevated soil temperature, but unchanged production, ended up with accelerated soil respiration, although the soil C pool increased in the long-term. Berg et al. (1995a) and Liski et al. (1999) also estimated increases in mineral soil C stores in Scots pine forests due to increasing temperatures. All these simulations, however, presume and require steady-state conditions, a requirement which is seldom met in nature. Carbon accumulation in pristine Finnish peatlands is on average greater in the southern raised bogs than in the northern fens (Tolonen and Turunen 1996), and the observed increases in C stores due to drainage for forestry purposes have also been larger in Southern Finland (Minkkinen and Laine 1998b). A climatic warming may thus result in increased C accumulation in boreal peatlands, due to increased production or changes in vegetation.

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PAPER I

Domisch, T., Finér, L. and Lehto, T. 2001. Effects of soil temperature on biomass and carbohydrate allocation in Scots pine (*Pinus sylvestris*) seedlings at the beginning of the growing season. Tree Physiology 21: 465–472.

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Effects of soil temperature on biomass and carbohydrate allocation in Scots pine (*Pinus sylvestris*) seedlings at the beginning of the growing season

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Summary We studied effects of soil temperature on shoot and root extension growth and biomass and carbohydrate allocation in Scots pine (*Pinus sylvestris* L.) seedlings at the beginning of the growing season. One-year-old Scots pine seedlings were grown for 9 weeks at soil temperatures of 5, 9, 13 and 17 °C and an air temperature of 17 °C. Date of bud burst, and the elongation of shoots and roots were monitored. Biomass of current and previous season roots, stem and needles was determined at 3-week intervals. Starch, sucrose, glucose, fructose, sorbitol and inositol concentrations were determined in all plant parts except new roots. The timing of both bud burst and the onset of root elongation were unaffected by soil temperature. At Week 9, height growth was reduced and root extension growth was much less at a soil temperature of 5 °C than at higher soil temperatures. Total seedling biomass was lowest in the 5 °C soil temperature treatment and highest in the 13 °C treatment, but there was no statistically significant difference in total biomass between seedlings grown at 13 and 17 °C. In response to increasing soil temperature, belowground biomass increased markedly, resulting in a slightly higher allocation of biomass to belowground parts. Among treatments, root length was greatest at a soil temperature of 17 °C. The sugar content of old roots was unaffected by soil temperature, but the sugar content of new needles increased with increasing soil temperature. The starch content of all seedling parts was lowest in seedlings grown at 17 °C. Otherwise, soil temperature had no effect on seedling starch content.

Keywords: growth, root, shoot, soluble sugars, starch.

Introduction

The boreal forest zone is characterized by low air and soil temperatures and a short growing season. Mean soil temperature in the rooting zone during the growing season is 10–12 °C, with values ranging from 5 to 20 °C. Mineral soil temperatures even in the surface (5 cm) layer seldom exceed 15 °C (Bjor and Huse 1987, Kubin and Kemppainen 1991). This is also the case for peatlands (Hytönen and Silfverberg 1991, Finér and Laine 1998, Domisch et al. 2000), although drainage of peatlands causes a decrease in mean soil temperatures, especially at the beginning of the growing season (Pessi 1958, Heikurainen and Seppälä 1963, Hytönen and Silfverberg 1991).

The forests of the northern European countries, which are dominated by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst.), are intensively managed, and nursery-grown seedlings are frequently planted to reforest harvested areas. Seedlings are usually planted in spring, when the soil is cold. Successful establishment of planted seedlings in reforestation areas is dependent on both soil and air temperatures, because they affect carbon accumulation and water and nutrient uptake from the soil.

There is evidence that root growth of boreal forest trees starts at a critical soil temperature in spring and reaches a maximum rate at about 20 °C (Tryon and Chapin 1983, Andersen et al. 1986, Vapaavuori et al. 1992). The soil temperature for maximal root growth of Scots pine is 16.5 °C (Korotaev 1989), and growth starts at 3–5 °C (Korotaev 1987, 1989), whereas root growth of lodgepole pine (*Pinus contorta* Dougl. *ex* Loud.) starts at 5 °C and is most rapid at 20 °C (Lopushinsky and Max 1990). Root growth of other boreal conifer species is reported to start at between 3 and 6 °C (Lyr and Hoffmann 1967, Kaufmann 1977, Tryon and Chapin 1983, Lopushinsky and Max 1990). Despite the large number of studies on temperature and root growth, relatively few studies have examined the effect of low soil temperature on carbohydrate content in Scots pine seedlings.

Allocation of biomass and photosynthates between the above and belowground parts of a plant is affected by soil temperature. Over the range of soil temperatures prevailing in the boreal forest zone, temperatures in the upper range usually result in an increased absolute allocation of photosynthates and biomass below ground, although the relative allocation to the roots may decrease (Lippu 1998, Hawkins et al. 1999).

Future climate scenarios for Finland predict increases in air temperature of 0.3–3.6 °C within the next 50 years (Carter et al. 1995) that may be accompanied by a rise in soil temperature, enhancing root growth and increasing belowground carbon allocation.

Our objectives were to study the effects of soil temperature on (1) shoot and root growth and (2) biomass and carbohydrate allocation in 1-year-old Scots pine seedlings at the beginning of the growing season.

Material and methods

Experimental layout and plant growth

We used 6-month-old container-grown seedlings of Scots pine (*Pinus sylvestris* L.) grown from seed originating from an orchard in central Finland (62°05′ N, 26°10′ E) established with material from sources in Finland between 61°7′ N and 64°20′ N. Pots (5.3 l, diameter 15 cm, height 30 cm) were filled with undisturbed *Carex*-peat cores from a tall sedge–pine fen (classification after Laine and Vasander 1996) in central Finland (Orivesi, 61°48′ N, 24°19′ E, 150 m a.s.l.) that had been drained for forestry in 1961 and supported a Scots pine forest. The concentrations of some mineral elements in the peat used as the growth medium are reported by Domisch et al. (1998).

The experiment was performed in four insulated water tanks placed in a walk-in growth room (Conviron GR 77, Winnipeg, Canada). One seedling was planted in each pot at the end of the first growing season (mean ± SE heights of seedlings in the soil treatments were: 5 °C, 12.2 ± 0.13; 9 °C, 12.3 ± 0.13; 13 °C, 11.6 ± 0.15; and 17 °C, 12.0 ± 0.17 cm). Forty-two pots were placed in each water tank and maintained at air and soil temperatures of 3–4 °C for a dormant period of 8 weeks before initiation of the treatments. An 8-h photoperiod was provided by 60 W incandescent lamps (Airam Ltd., Helsinki, Finland; photon flux density of about 20 μmol m^{-2} s^{-1}). Relative humidity of the air was set to 80%, but fluctuated between 80 and 90%. After the 8-week dormant period, the air temperature was raised to 17 °C and the soil temperature increased to 5, 9, 13 and 17 °C by increasing the water temperature in the four tanks. The target water temperatures were reached within 24 h and were held constant throughout the experiment. Day length during the soil temperature treatment was 18 h and photon flux density ranged from 370 to 440 μmol m^{-2} s^{-1} with a mean of 400 μmol m^{-2} s^{-1} (60 W incandescent lamps, Airam Ltd., Finland, and 215 W Cool White fluorescent tubes, Osram Sylvania, Danvers, MA). Day/night relative humidity was 60/80%.

During the experiment, seedlings were watered once a week with 0.25 l of deionized water. A 2-cm diameter plastic tube was inserted into the peat on one side of the pot to remove excess water as the pots had no drainage hole. When a groundwater table had formed, the water was removed through the plastic tube some days after watering. Additional nutrients were given with the irrigation water every second week (5 mg N, 2 mg P and 11 mg K plus micronutrients, Superex 5, Kekkilä Ltd., Tuusula, Finland) to minimize any differences in nutritional status among the seedlings caused by the effects of temperature on nutrient mineralization. The soil temperature treatments lasted for 9 weeks, and the seedlings were harvested at 3-week intervals. At each harvest, 14 seedlings were taken at random from each temperature treatment except for the last harvest, when seedlings were randomized in advance for the height measurements. To determine primary biomass and initial contents of carbohydrates, an initial harvest at the beginning of the growing season was performed on 14 randomly selected seedlings.

Plant harvest and measurements

Height growth was monitored once or twice a week throughout the experiment on the same 14 seedlings. At harvest, the seedlings were cut at the root collar and the needles separated from the stems, and the old (previous season) and new (current season) parts treated separately. The parts were dried to constant mass at 60 °C and weighed. The pots containing the excised root systems were stored at –18 °C for later separation except for the root systems of two seedlings that were harvested for dry mass and carbohydrate analysis immediately. One root system was used for starch analysis and the other for soluble carbohydrate determination. The frozen pots were thawed at 5 °C and the new and old roots separated from the peat. New roots were separated from the original peat plug and all roots that grew out of the peat plug were regarded as new roots. New roots were scanned with a ScanJet 6100 C/T 300 dpi scanner (Hewlett-Packard Co., Palo Alto, CA) and analyzed for total length (new roots per seedling) with the WinRHIZO program (Régent Instrumentals Inc., Québec City, PQ, Canada). All roots were dried to constant mass at 60 °C and weighed for dry mass in the same way as the aboveground parts.

For soluble carbohydrate determination, the old and new parts of all seedlings were pooled by harvest and soil temperature treatment, then milled and homogenized. Soluble sugars (sucrose, glucose and fructose) and sorbitol and inositol were determined by the methods described by Mason and Slover (1971) and Marc and Carroll (1982) with a GC 5890 system (Hewlett-Packard Co.) and a 5973 Mass Selective Detector (Hewlett-Packard Co.). Starch was determined spectrophotometrically (UV-240, Shimadzu Scientific Instruments, Inc., Columbia, MD) by the method described by Karkalas (1985). New roots were not analyzed for lack of sufficient material.

Data analysis

Treatment blocks (i.e., water tanks) were not replicated. The locations of the seedlings within the temperature treatments were changed every week.

The statistical tests were performed with the ANOVA procedures of the SPSS 8.0 statistical software package (SPSS Inc., Chicago, IL) and included four temperature treatments and three harvesting dates. The individual seedlings within temperature treatments were considered to be replicates. Repeated measure ANOVA was used to test soil temperature effects on seedling height. Soil temperature was used as a grouping factor, and measuring date as a within-factor variable.

Results

Shoot height and root elongation

Timing of bud burst and cessation of height growth were not affected by soil temperature (Figure 1A). There was a significant treatment effect on mean height increment ($F = 4.520$; $P = 0.007$). The significant interaction between measuring date and soil temperature ($F = 2.199$; $P = 0.001$) indicated that shoot elongation proceeded in different ways at different soil temperatures. Among treatments, shoot elongation was least at the lowest soil temperature (5 °C) and height of seedlings in the 5 °C treatment at Week 9 was about 75% that of seedlings grown at 13 and 17 °C. Seedlings grown at 9 °C were taller than seedlings grown at 5 °C but shorter than the seedlings grown at 13 and 17 °C, which were of similar height (Figure 1A). Shoot growth of seedlings in the 17 °C treatment lagged behind that of seedlings in the 9 and 13 °C treatments until Weeks 4 and 8, respectively, which might have contributed to the significant interaction between measuring date and soil temperature.

Soil temperature did not affect the onset of root elongation, but it significantly affected the length of new roots ($F = 36.681$; $P = 0.001$). There was a significant interaction between harvest date and soil temperature ($F = 11.891$; $P = 0.001$), suggesting that root growth rate differed with soil temperature. Root elongation rate was low at 5 °C throughout the experiment, whereas it increased linearly at 9 °C and exponentially at 13 and 17 °C until the end of the experiment (Figure 1B). Seedlings grown at 5 °C had a mean of less than 1 m of new roots at Week 9 versus 14 m for seedlings grown at 17 °C (Figure 1B).

Biomass and its allocation

Total seedling biomass increased with increasing soil temperature (main effect of soil temperature: $F = 18.453$; $P = 0.001$). The significant interaction between soil temperature and harvest date ($F = 11.891$; $P = 0.001$) indicated that the effect of soil temperature on total biomass differed with harvest dates. No differences in total root biomass or aboveground biomass were observed between the soil temperature treatments at Week 3 (Figure 2A), but a trend for higher biomass at higher soil temperatures was observed at Week 6. There were clear differences in seedling biomass between the soil temperature treatments at Week 9.

Seedlings grown at a soil temperature of 13 °C had the highest biomass at the end of the experiment, although there was no significant difference in seedling biomass between the 13 and 17 °C treatments or between the 9 and 17 °C treatments. Seedlings grown at 13 °C had the highest new needle biomass and seedlings grown at 5 °C had the lowest new needle biomass (Figure 2A). At 5 °C, root biomass increased only slightly and scarcely at all after Week 3. Root biomass at the end of the 9-week experiment was similar in the 13 and 17 °C treatments, and markedly higher than in the 9 °C treatment.

Soil temperature did not significantly affect relative biomass allocation between the above- and belowground parts of the seedlings. At the beginning of the experiment, 27.3% of the biomass was in the belowground parts (Figure 2B); however, by Week 9, there was a tendency for greater allocation below ground at higher soil temperatures (5 °C: 18.8%, 9 °C: 20.6%, 13 °C: 21.7 and 17 °C: 24.4%). The proportion of new needle biomass also increased with increasing soil temperature (42% at 5 °C versus 58% at 13 °C).

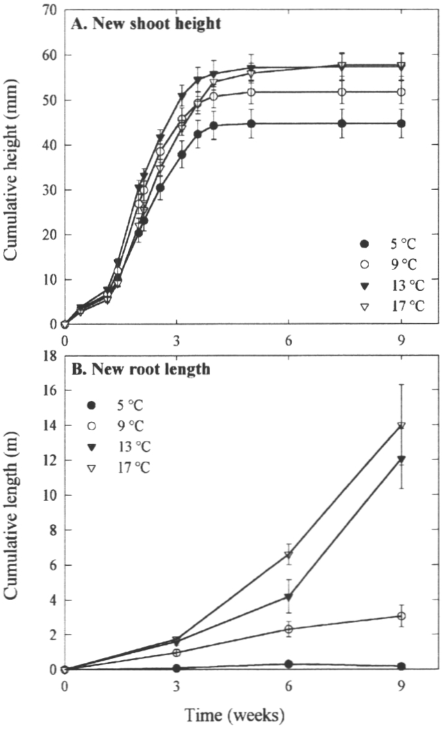

Figure 1. (A) Length of the terminal shoot (mm) of seedlings grown at soil temperatures of 5, 9, 13 and 17 °C for 3, 6 and 9 weeks. Measurements were performed on the same seedlings throughout the experiment. Means of 14 seedlings ± SE. (B) Length of new roots (m) of seedlings grown at soil temperatures of 5, 9, 13 and 17 °C for 3, 6 and 9 weeks. Standard errors are indicated.

Carbohydrates

Soluble carbohydrates in the aboveground parts of the seedlings were mainly in the form of glucose and fructose, whereas those in belowground parts were mainly sucrose. The sugar alcohols sorbitol and inositol usually represented less than 0.1% of the dry mass, except for the new stems where sorbitol made up to 0.9% of the total dry mass at 17 °C, and the old roots, where sorbitol comprised 0.3–1.0% of dry mass. New needles contained more soluble sugars at higher soil temperatures than at lower soil temperatures after Week 3 (Table 1, Figure 3A), but there were no treatment differences in the other aboveground parts or in the old roots. The soluble sugar content of old roots increased during the first three weeks and decreased to low values thereafter (Figure 3A).

Starch was found in all plant parts investigated. Starch con-

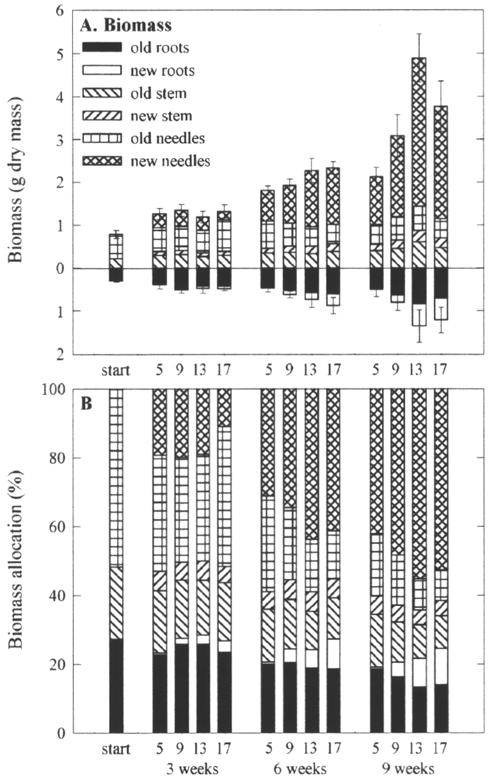

Figure 2. (A) Total biomass (dry mass) of old and new roots, old and new stems and old and new needles of seedlings at the start of the experiment and of seedlings grown at soil temperatures of 5, 9, 13 and 17 °C for 3, 6 and 9 weeks. Standard errors of total above- and belowground biomass are indicated. (B) Relative distribution of biomass among the parts of the seedlings.

tent and concentrations were low at the beginning of the growing season (Figure 3B, Table 2), but increased in all plant parts during the 9-week experiment. The temporal increase in starch in the aboveground parts did not show any clear temperature dependence, although starch content was lowest at the highest soil temperature (17 °C) at Week 3. Old roots contained similar amounts of starch at all soil temperatures, except that old roots of seedlings grown at 17 °C had considerably lower starch contents throughout the experiment than old roots in the other treatments (Figure 3B).

The proportion of carbohydrates in the new aboveground parts that was in the form of sugars increased with increasing soil temperature; however, this pattern was less clear in old needles and old stems. At the end of the 9-week experiment, total soluble carbohydrate content in aboveground parts was lowest in seedlings in the 5 °C treatment (Figure 4A). In response to increasing soil temperature, seedlings allocated relatively more soluble carbohydrates to new parts, especially new needles, and less to their old parts, particularly old roots (Figure 4B).

Discussion

Timing of shoot and root growth

Shoot growth of the Scots pine seedlings started rapidly in all treatments, and new shoot length did not differ between treatments until Week 3, when shoot elongation of seedlings growing at 5 °C slowed relative to that of seedlings growing at the higher soil temperatures. Timing of bud burst and beginning of root growth were not affected by soil temperature. Similar results were obtained by Vapaavuori et al. (1992) and Lyr and Garbe (1995) with Scots pine seedlings. Huikari and Paarlahti (1967) did not observe any effects of artificial soil cooling on the beginning or ending of height growth of mature Scots pine trees growing on peatlands.

Elongation rate of new roots was low in all of the soil temperature treatments during the first three weeks, but it was notably lower in the 5 °C treatment than in the other treatments. New root tips emerged in the 5 °C treatment, as observed in the Scots pine seedlings studied by Vapaavuori et al. (1992). Under the temperature conditions prevailing in boreal forests, Scots pine usually shows seasonal variation in root growth (Laiho and Mikola 1964, Lakhtanova 1971, Prokushkin 1982), one peak occurring before or at the beginning of shoot elongation and one or more peaks occurring when shoot height growth has ceased (Horváth 1958, Laiho and Mikola 1964). We observed that prolific root growth began only after shoot elongation had occurred. Similar findings have been reported by Vapaavuori et al. (1992) and Iivonen et al. (1999) in laboratory experiments, and by Lyr and Hoffmann (1964) under natural conditions in central Europe. Finér and Laine (1998) did not observe any peak in root growth during the spring in Scots pine growing on boreal peatlands.

Current photosynthates are the primary carbon source for new root and shoot growth in conifer seedlings (Gordon and Larson 1970, van den Driessche 1987, Lopushinsky and Max 1990, Lippu 1998). Once the new needles have reached 50% of their final length and can act as carbon sources (Ericsson 1978), photosynthates are translocated below ground to support new root growth. In our experiment, this occurred 3–4 weeks after the beginning of the growing season and coincided with the start of rapid root growth.

Soil temperatures above 13 °C affected shoot and root growth of our Scots pine differently. Root elongation rate increased when the soil temperature was increased from 13 to 17 °C, whereas shoot elongation rate was unaffected by the increase in soil temperature. It is known that, in Scots pine, the stem reaches its maximum length during the first half of the growing season (Raulo and Leikola 1974), whereas the roots continue to grow for as long as soil temperature permits (Prokushkin 1982). Our 9-week experiment extended over about the first half of the growing season, but the air temperature sum (756 d.d., +5 °C threshold) was about 70% of the

Table 1. Concentrations of soluble sugars and sugar alcohols (% of total dry mass) in needles, stem, and roots of seedlings grown at soil temperatures of 5, 9, 13 and 17 °C.

Soil temperature (°C)	Weeks	Needles		Stem		Roots
		Old	New	Old	New	Old
Start	0	20.90	–	10.88	–	8.03
5	3	12.37	7.28	10.08	18.46	10.66
	6	11.52	5.63	9.78	15.13	0.33
	9	11.79	6.74	10.93	14.82	0.25
9	3	14.15	9.82	9.49	34.02	5.05
	6	12.33	8.06	10.33	16.12	0.28
	9	20.61	6.16	10.76	8.49	0.88
13	3	24.32	14.46	11.50	28.75	10.08
	6	17.49	7.84	5.05	10.36	0.43
	9	16.65	7.26	8.86	13.12	0.21
17	3	17.30	10.13	16.58	32.59	11.73
	6	21.83	11.71	7.50	12.30	0.33
	9	15.82	11.96	10.98	12.88	0.57

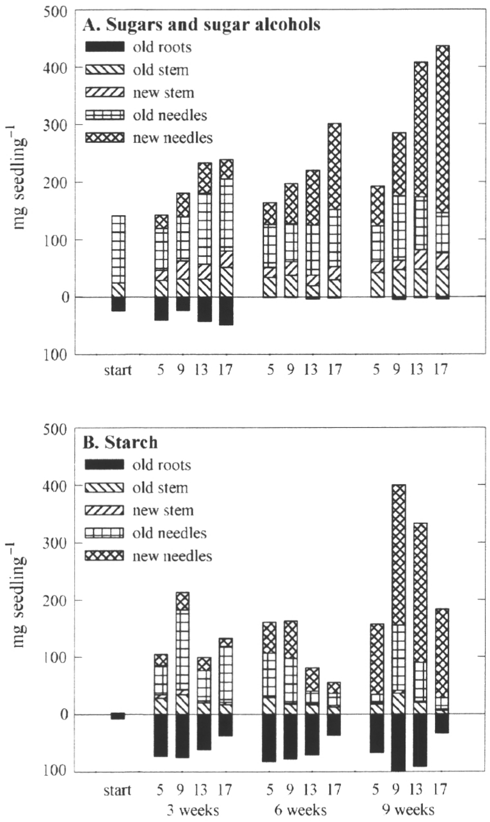

Figure 3. Soluble sugars (A) and starch (B) in the parts of seedlings grown at soil temperatures of 5, 9, 13 and 17 °C for 3, 6 and 9 weeks.

mean for the growing season in southern Finland (Atlas of Finland 1988).

Biomass and carbohydrate allocation

At Week 9, total seedling biomass and new needle biomass were highest in the 13 °C treatment, which is between the optimum soil temperatures of 12 and 15 °C found for Scots pine by Vapaavuori et al. (1992) and Lyr and Garbe (1995). Soil temperatures above 13 °C promoted root growth but did not increase total biomass, aboveground biomass being lower at 17 °C than at 13 °C, indicating that the seedlings were adapted to relatively low soil temperatures.

The distribution of biomass between shoots and roots of the seedlings was not greatly affected by soil temperature (cf. Lippu 1998), although there was a trend for increased absolute and relative allocations of biomass below ground with increasing soil temperature. The metabolic activity of the root system and its sink strength decrease at low soil temperatures, resulting in reduced belowground translocation of photosynthates (Hurewitz and Janes 1983) and a corresponding aboveground accumulation of biomass, whereas at higher soil temperatures the root system becomes a strong sink for photosynthates (Lippu 1998). However, the results from our short-term experiments conducted with small seedlings may not be directly applicable to older trees; furthermore, the effects may be different if the responses are studied over longer periods of time.

The sugar content of new needles increased at all soil temperatures and was greatest at the highest temperature, indicating high metabolic activity. No clear temperature effect was observed for the other aboveground parts. In old roots, the content of soluble sugars showed no temperature dependence, which is in accordance with the results of Andersen et al. (1986) who studied the roots of red pine (*Pinus resinosa* Ait.) at soil temperatures ranging from 8 to 20 °C.

At the end of the 8-week dormant period at a temperature of

Table 2. Concentrations of starch (% of total dry mass) in needles, stem, and roots of seedlings grown at soil temperatures of 5, 9, 13 and 17 °C.

Soil temperature (°C)	Weeks	Needles		Stem		Roots
		Old	New	Old	New	Old
Start	0	0.28	–	0.69	–	0.40
5	3	9.18	6.07	9.73	6.39	8.32
	6	11.70	7.62	8.57	2.66	8.91
	9	3.07	11.17	4.50	1.36	7.44
9	3	24.76	8.20	10.97	9.17	15.89
	6	14.73	7.42	4.85	1.24	8.49
	9	20.29	12.99	8.15	2.74	12.97
13	3	10.20	7.00	7.57	4.48	8.33
	6	4.79	3.07	4.86	1.63	3.57
	9	11.75	7.04	3.36	0.99	6.80
17	3	13.31	7.13	5.71	4.62	10.07
	6	4.68	1.45	3.37	1.56	2.39
	9	4.56	5.90	1.28	1.00	4.87

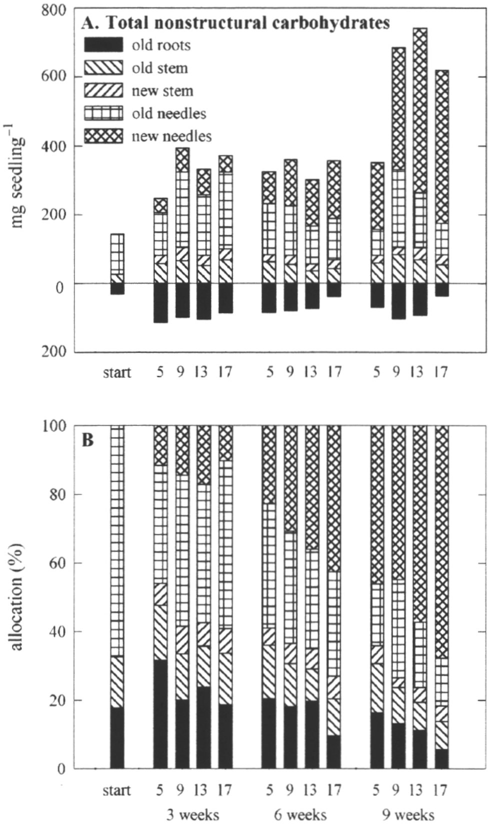

Figure 4. (A) Total nonstructural carbohydrate content (starch and soluble sugars) and (B) relative allocation of total nonstructural carbohydrates among the parts of the seedlings.

3–4 °C, starch reserves were negligible suggesting that they were transformed to soluble sugars during this period (Ericsson et al. 1996). Starch concentrations initially increased in all treatments, but subsequently decreased in all investigated plant parts other than needles at all soil temperatures. Decreasing starch concentrations during the early part of the growing season have also been found in 1- and 2-year-old Scots pine seedlings (Sutinen 1985) and mature Norway spruce trees (Egger et al. 1996). The patterns of starch concentrations that we observed in roots of Scots pine seedlings were similar to those reported in roots of 20-year-old Scots pine trees (Ericsson and Persson 1980). In the trees, root starch concentrations decreased from about 25% at the beginning of June to around 10% nine weeks later in trees growing on irrigated, fertilized field plots (Ericsson and Persson 1980).

Ryyppö et al. (1998) suggested that availability of photosynthate limits root growth at low soil temperatures. However, we found starch to be present in old roots at all soil temperatures, which negates this hypothesis.

Lippu (1998) showed a decrease in translocation of photosynthates to the roots at low soil temperatures and an accumulation of photosynthates in the aboveground parts of Scots pine seedlings. This accumulation of nonstructural carbohydrates is a characteristic response to low temperatures and indicates that growth is more sensitive to low temperatures than photosynthesis (Farrar 1988, Ericsson et al. 1996). We found that the starch content of the aboveground parts was highest at 9 and 13 °C, whereas the content of soluble sugars in the aboveground parts tended to be highest in seedlings in the 13 and 17 °C treatments, especially at Week 9. We conclude that active photosynthesis occurred at all soil temperatures and that current photosynthates were mainly sequestered for growth and maintenance respiration by seedlings in the 13 and 17 °C treatments, but mainly stored by seedlings in the 5 and 9 °C treatments.

Several authors have reported that low soil temperatures in spring may severely affect or delay the establishment of planted conifer seedlings by hampering shoot and root growth (e.g., Lopushinsky and Kaufmann 1984, Vapaavuori et al. 1992). Our results suggest that soil temperature also influences the allocation of photosynthates. We conclude that plantation stress may not be a result solely of slow root growth at low soil temperatures, because root biomass growth did not depend on soil temperature during the first three weeks of our experiment. Furthermore, even at 5 °C the roots contained considerable amounts of starch and sugars that could be used under conditions favorable for growth. Shoot growth started simultaneously at all soil temperatures and was unaffected by soil temperature during the first three weeks. Temperatures in the upper soil layers of open reforestation areas increase markedly within a few weeks in early summer (Kubin and Kemppainen 1991), enabling root growth to start.

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PAPER II

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Growth, carbohydrate and nutrient allocation of Scots pine seedlings after exposure to simulated low soil temperature in spring

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Key words: biomass, carbohydrates, nutrients, *Pinus sylvestris*, root, shoot, soil temperature

Abstract

The effects of sustained low soil temperature on growth and allocation of biomass and carbohydrates in Scots pine (*Pinus sylvestris* L.) were studied by exposing 1-year-old seedlings to soil temperatures of 5 °C for 0, 3, 6 or 9 weeks and subsequently for 9 weeks at 13 °C. Growth at 5 °C soil temperature at the beginning of the growing season reduced the height of new shoots but the length of the cold soil period did not affect its final height. Some new root tips emerged during the 5 °C soil temperature period. Prolific root growth did not start until the soil temperature was increased from 5 to 13 °C, but new root growth was scarce during the first 9 weeks even at 13 °C, a clearly more favourable soil temperature than 5 °C. Seedlings exposed to a temperature exceeding 5 °C over any 3-week period during the first 9 weeks had above- and below-ground biomasses that were equivalent, whereas continual exposure to 5 °C reduced shoot and root growth. The above-ground biomass of the seedlings did not increase any more after Week 12, nor did the below-ground biomass after Week 15. Biomass allocation among the different parts of the seedlings was not greatly affected by the length of the cold soil period. Our results indicate that the accumulation of above-ground biomass is mainly dependent on the air temperature and not soil temperature. Element allocation followed the pattern of biomass allocation, except for N, which increased in the above-ground parts throughout the experiment, and Fe, which had already accumulated during the first 3 weeks. The seedlings grown for a longer time at low soil temperatures contained lower amounts of starch but similar amounts of soluble sugars throughout the experiment.

Introduction

Soil temperature is a major factor affecting plant growth (e.g., Bowen, 1991; Cooper, 1973). Root growth is particularly reduced at low soil temperatures (Aaltonen, 1942; Lopushinsky and Max, 1990; Ritchie and Dunlap, 1980; Tryon and Chapin, 1983), but shoot growth and nutrient uptake may also be impeded (Lopushinsky and Max, 1990; Marschner, 1986).

The boreal forests of the Nordic countries are dominated by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies*) and are intensively managed, so that tree generations are frequently established by planting. Seedlings are usually planted in spring, when the soil is cold, and their successful establishment depends on both soil and air temperatures, as these affect carbon accumulation and water and nutrient uptake from the soil. In the soil temperature range prevailing in the boreal forest zone, a higher soil temperature usually results in an increased allocation of photosynthates and biomass below ground (Domisch et al., 2001; Lippu, 1998a; Hawkins et al., 1999).

Plants grown at higher temperatures have higher nutrient concentrations and contents, because ion uptake generally occurs faster at higher temperatures (Marschner, 1986). Elevated soil temperatures facilitate the uptake of nutrients by the plant in several ways: by increasing the length of new roots, by physiologically improving nutrient uptake by the roots and by accelerating nutrient mineralisation in the soil.

Cold soils at the beginning of the growing season are characteristic particularly for drained peatlands since drainage causes a decrease in mean soil tem-

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perature, especially in the spring (Heikurainen and Seppälä, 1963; Hytönen and Silfverberg, 1991; Pessi, 1958). Future climate scenarios for Finland predict increases in air temperature of 0.3–3.6 °C within the next 50 years (Carter, 1995) which may also mean a rise in soil temperature. This might enhance root growth and increase carbon allocation below the ground and thus also litter deposition, thereby being of special importance for boreal peatlands which are already significant sinks for atmospheric carbon. Considerable amounts of biomass production of Scots pine trees are allocated below ground (Finér and Laine, 1998; Helmisaari et al., 2002~~, (in print~~). Boreal peatlands alone contain about one-third of all terrestrial carbon stores (Gorham, 1991).

We studied the effect of soil temperature on shoot and root growth and carbohydrate allocation in 1-year-old Scots pine seedlings during the first 9 weeks of the growing season in a previous experiment (Domisch et al., 2001) but this was conducted at constant soil temperatures. According to previous experiments (Domisch et al., 2001; Vapaavuori et al., 1992), a soil temperature of 13 °C seems to be around the optimum for biomass growth in Scots pine seedlings, although not for maximal root growth. It is still unclear, however, how a cold soil period, and its length in particular, might affect the growth of seedlings and the allocation of biomass and carbohydrates during the early growing season. The objectives of this study were thus to investigate the effect of periods of low soil temperature of different duration during the first half of the growing season on (1) the timing of shoot and root elongation, (2) carbohydrate allocation and (3) nutrient uptake and allocation in Scots pine (*Pinus sylvestris* L.) seedlings.

Material and methods

Experimental layout and plant growth

Horticultural peat (low humidified *Sphagnum*-peat, pH 3.5, Kekkilä Ltd., Tuusula, Finland) was compressed into plastic pots of volume 3.4 L to a density resembling that of natural *Sphagnum*-peat (ca. 0.1 g cm^{-3}). The 210 one-year-old Scots pine seedlings used for this experiment were container-grown from seed originating from an orchard in Central Finland (62°05′N, 26°10′W) established with material from sources located between 61°7′N and 64°20′N in Finland, and passed their first winter in the nursery bed. In April, they were transported to the laboratory and thawed for 1 week at 4 °C. One seedling was planted in each pot after filling with horticultural peat and the pots were placed into four insulated water tanks in a growth room (Conviron GR 77, Winnipeg, Canada). One soil temperature treatment started at 13 °C and the others three at 5 °C (Table 1). The temperatures in the water tanks were raised at time intervals of three weeks so that the experiment consisted of growing the seedlings for 0, 3, 6 and 9 weeks at 5 °C after which they were grown for additional 3, 6 or 9 weeks at a soil temperature of 13 °C.

Table 1. Experimental layout. The experiment consisted of four soil temperature treatments: 0, 3, 6, or 9 weeks at 5 °C, followed by 9 weeks at 13 °C. In parentheses the number of harvested seedlings per treatment

Week	Treatment 1 (°C)	Treatment 2 (°C)	Treatment 3 (°C)	Treatment 4 (°C)
3	13 (14)	5 (14)	5	5
6	13 (14)	13 (14)	5 (14)	5
9	13 (14)	13 (14)	13 (14)	5 (14)
12		13 (14)	13 (14)	13 (14)
15			13 (14)	13 (14)
18				13 (14)

The day length was 18 h (corresponding the day length in early summer in Central Finland) and the photon flux density ranged from 370 to 440 μmol $^{-2}$ s^{-2}, with a mean of 400 μmol m^{-2} s^{-1} (60-W incandescent lamps, Airam Ltd., Finland and 215-W Cool White fluorescent tubes, Osram Sylvania, Danvers, MA). Day/night relative humidity was 60/80% and air temperature 17 °C throughout the experiment. A 2-cm diameter plastic tube was inserted on one side of the pot to remove any ground water as the pots were closed at the bottom. The pots were irrigated with 0.25 L of deionised water once a week and fertiliser was given with the irrigation water every second week starting at Week 1 (20 mg N, 7 mg P and 45 mg K among other nutrients, Superex 5, Kekkilä Ltd., Tuusula, Finland).

Harvests and measurements

Height growth was monitored once or twice a week throughout the experiment on the same 14 seedlings of each treatment. Harvests were performed at intervals of 3 weeks. The stems were cut at the root collar and the needles separated from them. Current (new) and previous year (old) parts were separated, as were the new roots from the old roots. The new roots were removed from the original peat plug and additionally all roots growing out of the peat plug were regarded as new roots. The stems, needles and old roots were dried immediately to a constant mass at 60 °C, whereas the new roots were stored at −18 °C for later scanning with a HP ScanJet 6100, resolution 300 dpi, and analysis with the WinRHIZO programme (Regent Instrumentals Inc., Québec, Canada) for total root length and root tips per seedling.

For the analyses of starch and soluble sugars, the respective parts of the seedlings (new roots, old roots, new needles, old needles, new stem, old stem) of each soil temperature treatment and each harvest were pooled together except those seedlings of the final harvest of each soil temperature treatment, which were treated separately. Soluble sugars (sucrose, glucose, fructose, raffinose and pinitol) were determined by the methods described by Mason and Slover (1971) and Marc and Carroll (1982) with a 5890 GC system (Hewlett-Packard) and a 5973 Mass Selective Detector (Hewlett-Packard). Starch was determined spectrophotometrically (UV-240, Shimadzu Scientific Intruments, Inc., Columbia, MD) by the method described by Karkalas (1985).

Data analysis

The water tanks, i.e., treatment blocks, were not replicated. Thus, the experimental design could be regarded as a pseudoreplication (Hurlbert, 1984). However, in order to minimise possible confounding effects between the water tank and soil temperature treatments the locations of the seedlings within the water tanks were changed once a week. In a confounded experiment, any statistically not significant differences will remain not significant, but the P values indicating a significant difference ($P < 0.05$) are in reality not the values generated by ANOVA but greater by an unknown degree since F -values are greater than they should be (Milliken and Johnson, 1984). Attention was paid to P values indicating significant differences between treatments, but these were interpreted with caution where the differences were not obviously perceptible from the means and standard errors.

The statistical calculations were performed with the SPSS statistical package (SPSS 9.0 for Windows). All percentage values were subjected to angular transformation ($x' = \arcsin\sqrt{x}$). ANOVA was used for testing the effect of the length of the low soil temperature treatment (0, 3, 6 and 9) by using this as one factor. Repeated-measure ANOVA was used to test the effects of the treatments on the height of the seedlings. Soil temperature was used as a grouping factor and the measuring date as a within-factor variable.

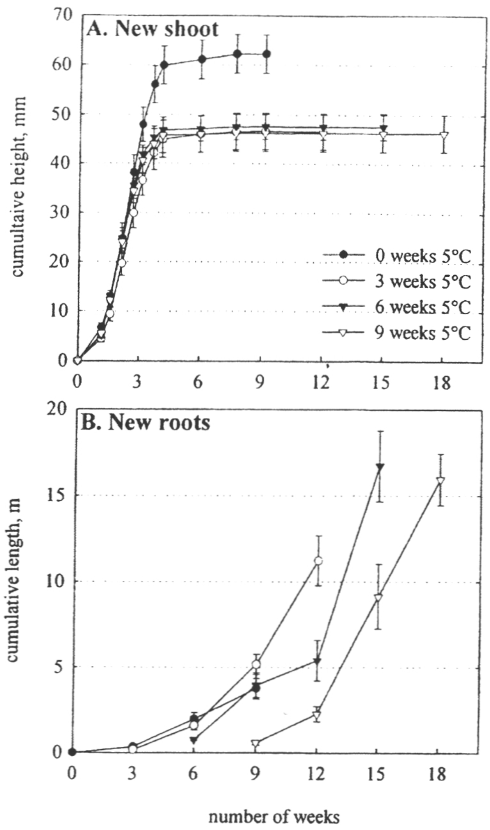

Figure 1. Cumulative height (A) of the new shoot in the different soil temperature treatments during the experiment ($n = 14$). Cumulative length (B) of the new roots. Standard errors are indicated ($n = 14$).

Results

Shoot and root elongation

The seedlings without any cold soil treatment grew the highest new shoots (Figure 1A; main effect of soil temperature $F = 867.6$, $P < 0.001$), being about 25% higher than the shoots of the seedlings with a cold

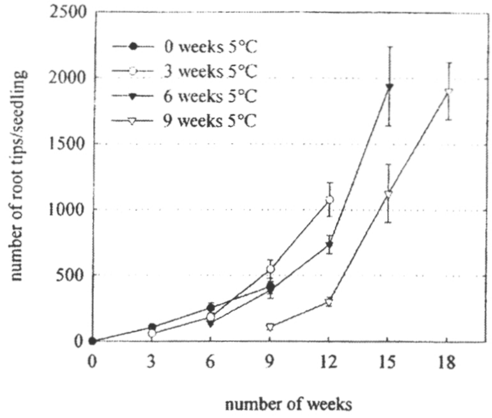

Figure 2. Number of root tips on the seedlings, counted by WinRHIZO after scanning. Standard errors are indicated ($n = 14$).

soil treatment, but the shoot elongation of the cold-treated seedlings was not dependent on the length of the cold soil period.

The start of the rapid elongation of the new roots was delayed relative to the growth of the new shoot (Figure 1B). New root elongation also occurred at the soil temperature of 5 °C, but was very slow. A rapid increase in root tips and prolific new root length growth occurred after soil temperature was raised to 13 °C (Figures 1 and 2). Increasing the soil temperature to 13 °C resulted in a rapid increase in new root length, which was not dependent on the length of the preceding low soil temperature period. The seedlings undergoing the longest cold soil period had a similar final root length to those grown for 6 weeks at 5 °C, and a greater root length than those grown for only 3 weeks at 5 °C.

Biomass

The length of the low soil temperature period did not affect the total above-ground biomass of the seedlings after the cold soil treatment and the subsequent 9 weeks of 13 °C, except for the seedlings grown in the treatment without a cold soil period (Figure 3A), which had a lower biomass, both above and below-ground. At Week 9, all the treatments had a similar above ground biomass, except for the seedlings grown for all 9 weeks at 5 °C, which had lower above- and below-ground biomass.

The seedlings grown for 9 weeks at 5 °C had a lower new needle biomass than the seedlings grown at 5 °C for a period within the 9 weeks ($F = 5.193$; $P = 0.003$); the latter were not significantly different from each other. Also, the below-ground biomass did not differ between seedlings exposed to temperatures exceeding 5 °C. When comparing the biomass after 9 weeks at 13 °C preceded by different periods at 5 °C, those grown only for 9 weeks at 13 °C had smaller biomasses than those grown for longer but at lower soil temperatures, both above ground ($F = 21.52$; $P < 0.001$) and below ground ($F = 24.77$; $P < 0.001$). New needle and new root biomasses in particular were lower, whereas the mass of old needles was equal in all treatments.

The greatest part of the biomass increase within the seedlings was due to the new needles, since about 50% of all biomass was allocated to the new needles, and this pattern no longer changed after Week 9. The allocation between the parts of the plants did not differ between the treatments, although a slight increase in the proportion of new roots was observed over time (Figure 3B).

Element content and allocation

The N, P and Ca content increased only slightly during the first 3 weeks of the experiment (Figure 4), and was mainly above-ground, but the Al and Fe content had already increased at Week 3, mainly below-ground (Figure 5). The total above-ground N content differed significantly between the soil temperature treatments at the end of each treatment ($F = 111.0$; $P < 0.001$). The more time elapsed, the higher the N content of shoots. The below-ground N content also increased with time ($F = 35.56$; $P < 0.001$), except for the treatments with 6 and 9 weeks at 5 °C, where the below-ground N content did not vary (post hoc Tukey test: $P = 0.989$). This was not the case with the other elements studied (P, Ca, Al and Fe), the above and below-ground content of which increased from 9 to 12 weeks but not thereafter.

The above and below-ground element allocations within the seedlings did not greatly differ at the end of each soil temperature treatment (Figures 4 and 5), the greatest part of above-ground content being found in the new needles, while the below-ground content was divided evenly between the old and new roots. About 50% of the total Al and 70% of the total Fe was found in the below-ground parts of the seedlings, whereas the percentages for N, P and Ca were 20–38%.

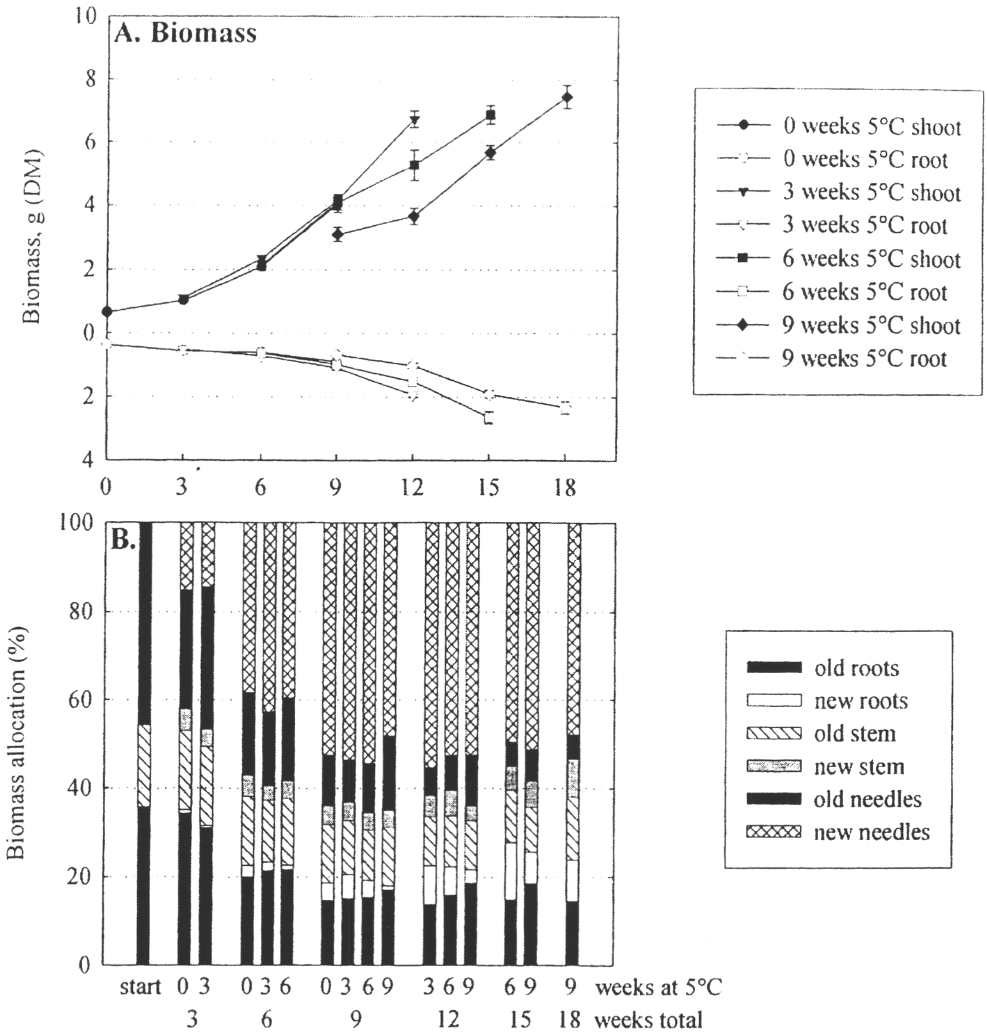

Figure 3. Biomass of the different parts of the seedlings (A) and its allocation within the seedlings (B) during the experiment. Standard errors are indicated ($n = 14$).

Carbohydrates

The starch content increased both at 13 and 5 °C and was highest at 12 weeks in the seedlings that received 3 weeks of the cold soil treatment (Figure 6). The lowest starch content between the treatments was observed in those seedlings which were exposed to cold soil for 9 weeks. The soluble sugar content was relatively low at the beginning of the growing season (Figure 7), but the above-ground sugar content increased rapidly, and from Week 12 onwards there were no differences between the soil temperature treatments. The below-ground changes were small until Week 9, when the highest sugar content was found in those seedlings without cold soil treatment. A shorter cold soil period had a uniformly positive effect on sugar content of the roots (Figure 7).

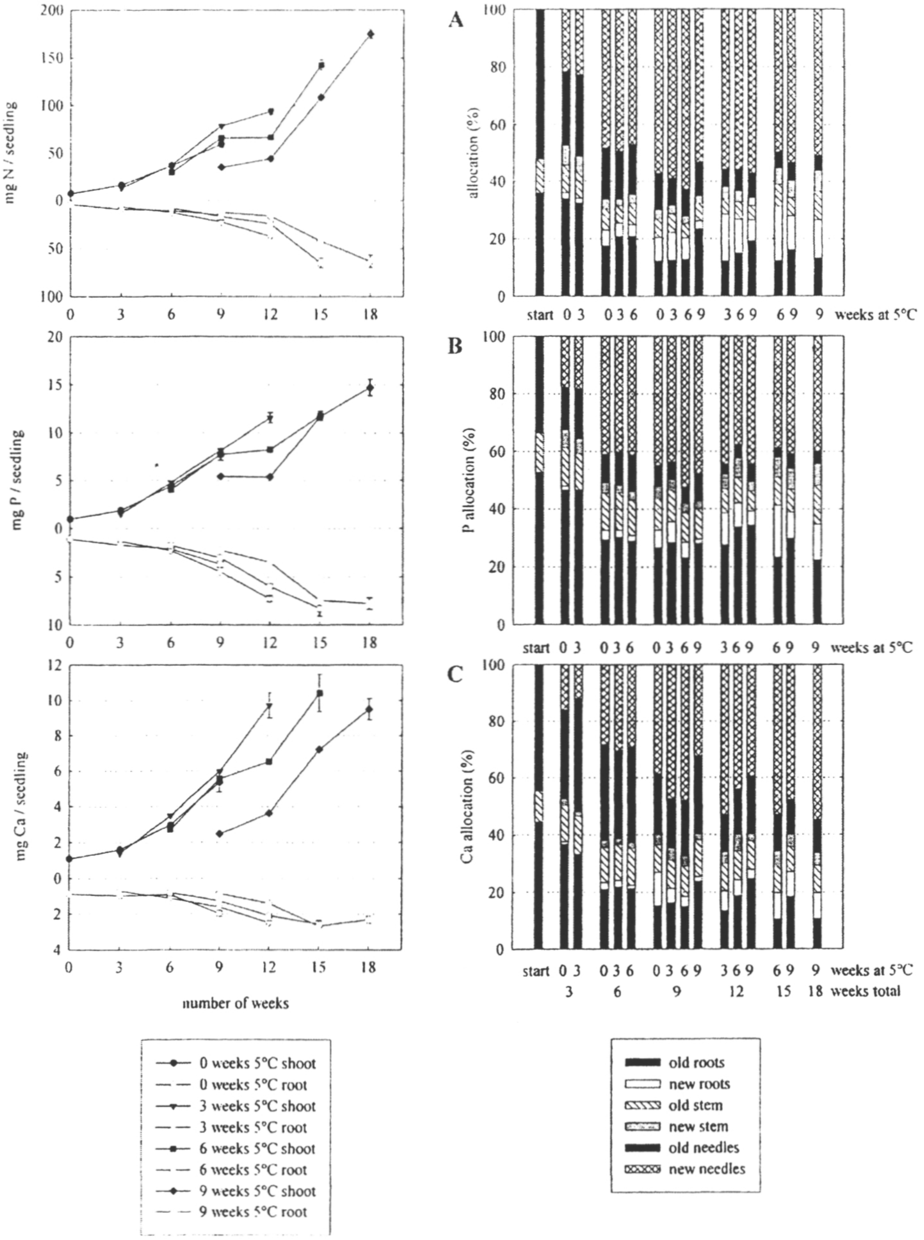

Figure 4. N (A), P (B) and Ca (C) content of the different parts of the seedlings and allocation during the experiment in the different soil temperature treatments ($n = 14$ where standard errors are indicated, otherwise $n = 1$).

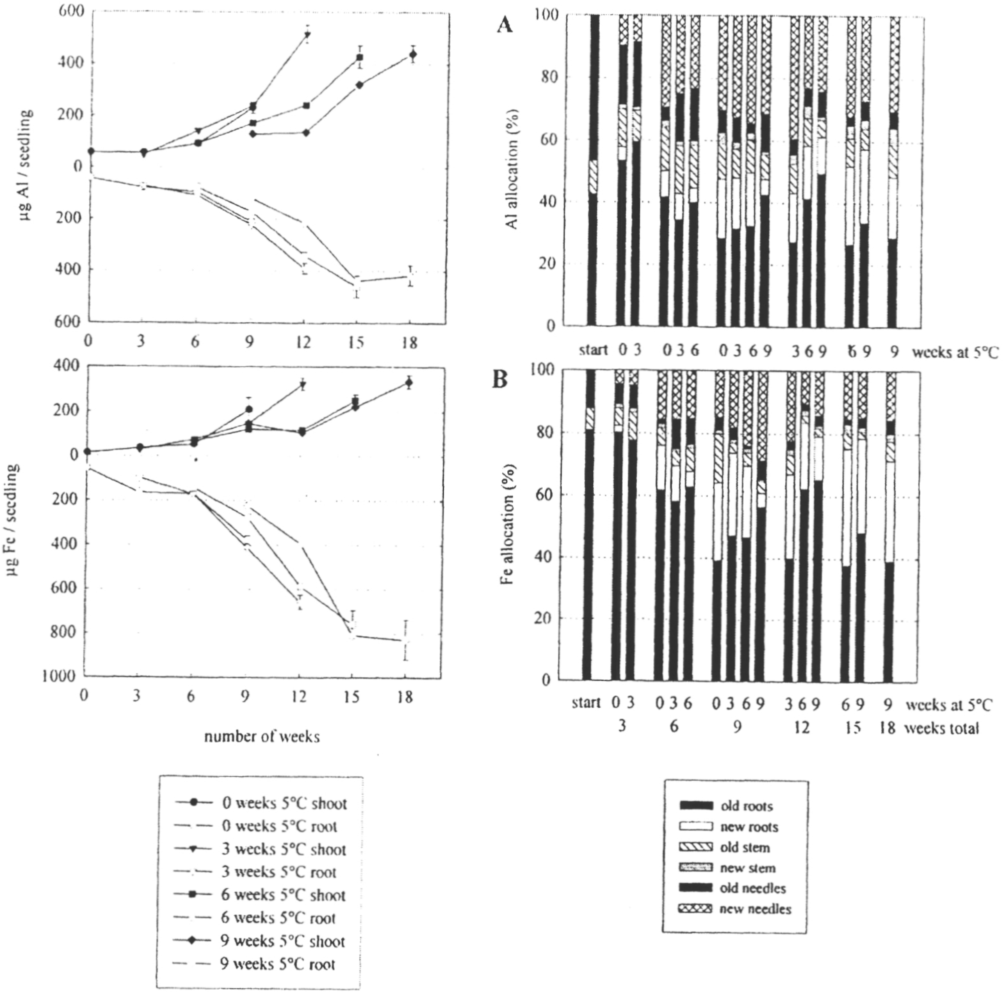

Figure 5. Al (A) and Fe (B) content of the different parts of the seedlings and allocation during the experiment in the different soil temperature treatments ($n = 14$ where standard errors are indicated, otherwise $n = 1$).

Discussion

Shoot and root elongation

Bud burst and the start of new shoot elongation was not dependent on the soil temperature treatment, indicating that these growth processes are mainly dependent on air temperature. Similar observations on Scots pine seedlings have been reported by Vapaavuori et al. (1992), Lyr and Garbe (1995) and Domisch et al. (2001). On the other hand, the length of the cold soil period did not affect the height of the new shoot. Higher soil temperature at the beginning of the growing season increased the height of the new shoot but did not affect the length of the new roots until Week 9.

There was some root growth, both length and biomass, during the cold soil treatment in our experiment. Landhäusser et al. (2001) reported also some new root growth of *Picea glauca* at a soil temperature of 5 °C. The recovery of root length growth was remark-

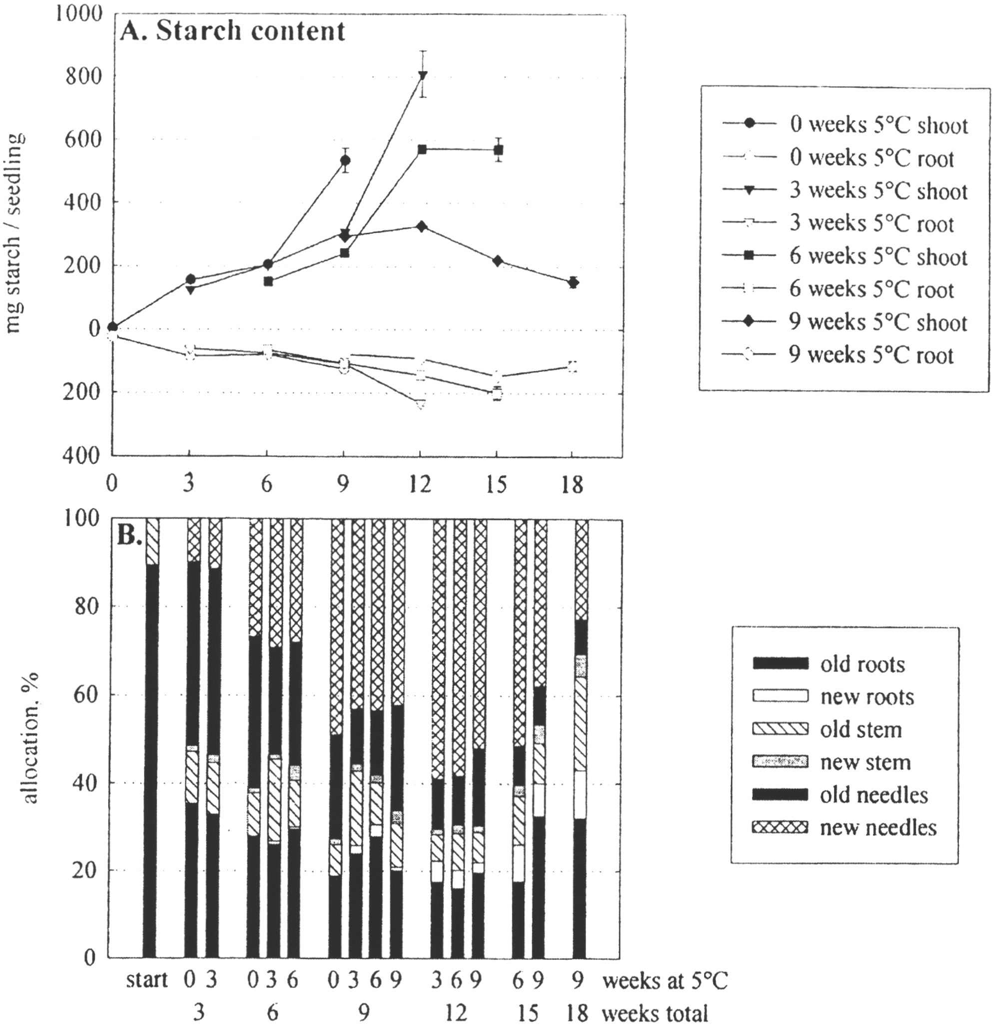

Figure 6. Starch content (A) and its allocation within the seedlings (B) during the experiment (n = 14 where standard errors are indicated, otherwise n = 1).

able, even after 6 or 9 weeks at a soil temperature of 5 °C and a subsequent rise in soil temperature to 13 °C the seedlings had similar root lengths. Scots pine root growth begins at soil temperatures of 3–5 °C, with maximal growth at 16.5 °C (Korotaev, 1987, 1989). Domisch et al. (2001) and Vapaavuori et al. (1992) found maximal root growth at the highest soil temperatures they investigated, i.e., 17 and 20 °C, respectively. Our results indicate that a prolonged period of low soil temperature mainly delays the commencement of new root growth, but does not affect the length of new roots.

New root growth in boreal conifer seedlings is dependent on carbohydrates from current photosynthesis (Lippu, 1998b; van den Driessche, 1987). Rapid root elongation in our experiment was not observed until rapid shoot elongation had finished (Figure 1), although the soil temperature was favourable for root

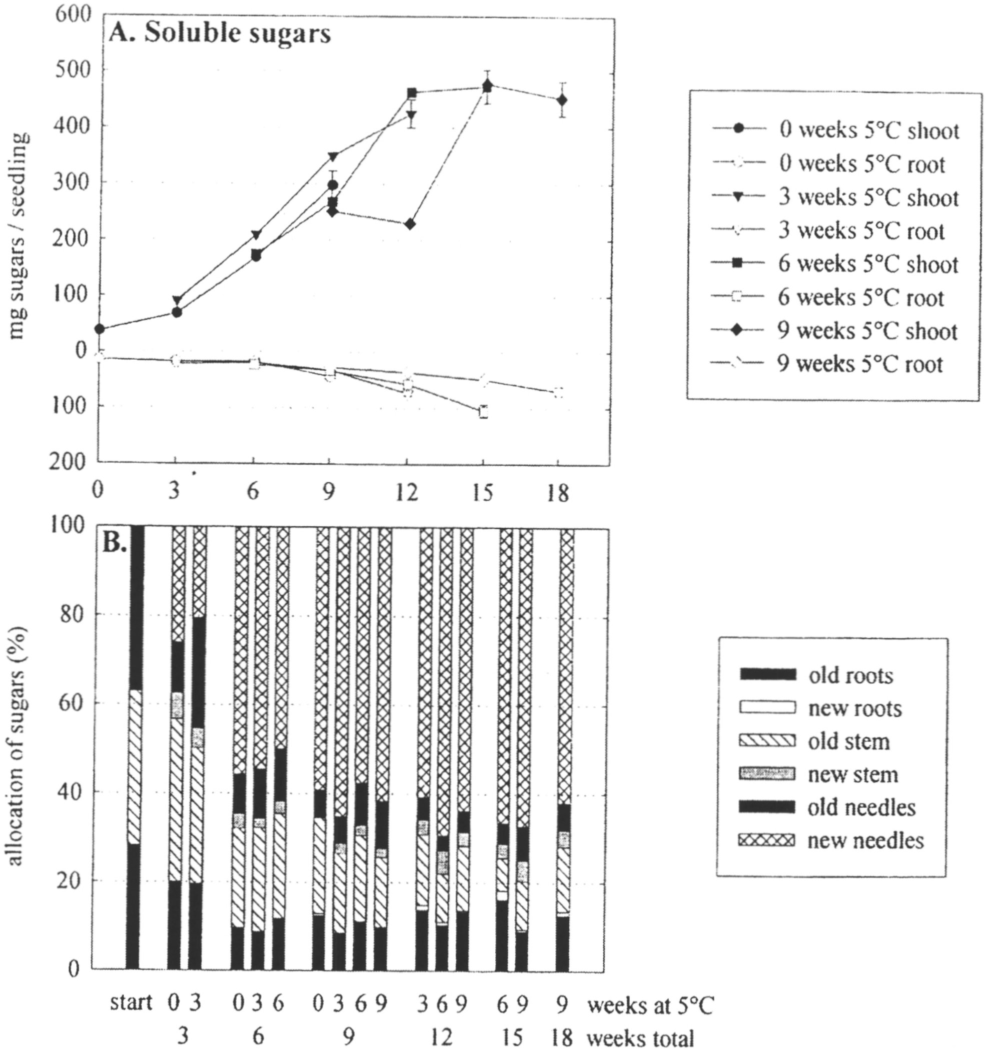

Figure 7. Total soluble sugar content (A) and its allocation within the seedlings (B) during the experiment ($n = 14$ where standard errors are indicated, otherwise $n = 1$).

growth. Translocation of current photosynthates to below-ground parts could not start until shoot elongation had ceased since during shoot elongation the above-ground parts are a greater sink for photosynthates than the below-ground parts (Gordon and Larson, 1968, 1970; Gower et al., 1995). Indeed, Scots pine often shows two peaks in root elongation: one before shoot elongation and one after (e.g., Horváth, 1958; Laiho and Mikola, 1964). On the other hand, other growth rhythms, including no peak in root growth before shoot elongation, have also been found (Domisch et al., 2001; Iivonen et al., 1999; Lyr and Hoffmann, 1964). These experiments began abruptly in spring, however, so that no root growth was possible before shoot elongation. Thus, the delay in root elongation at the beginning of our experiment might be an inherent phenomenon in Scots pine seedlings of northern provenances and not necessarily a consequence of the low soil temperature in spring.

Biomass

The duration of the cold soil season did not greatly affect the total biomass of the seedlings at the end of the temperature treatments. At Week 9, all the treatments led to similar above-ground biomasses irrespective of the soil temperature, indicating again that the accumulation of above-ground biomass is mainly dependent on air temperature but not on soil temperature at the beginning of the growing season. Unlike shoot elongation, therefore, the growth of new roots during spring and summer depends particularly on the soil temperature and not on air temperature (e.g., Ericsson et al., 1996).

A shorter period of low soil temperature did not result in higher biomass or increased below-ground allocation. One reason for the fact that the seedlings grown without any cold soil treatment had the lowest biomass at the end of the treatments seems to be time, since they were grown for only 9 weeks, whereas all the other treatments continued for a longer time, and as shoot growth is only dependent on soil temperature to a small degree, the treatments with a cold soil period provided more time for shoot growth. Although shoot elongation ceased during the first 9 weeks, the above-ground accumulation of biomass did not stop and needle elongation still continued (Parviainen, 1974; Raulo and Leikola, 1974). Fertilisation may be another reason for the higher biomass of the seedlings that were grown for a longer time; the longer the seedlings were grown, the more nutrients they received, and the more nutrients could have been released via mineralisation of the peat soil.

The root biomass stayed at a very low level during the cold soil period but it increased rapidly after soil temperature rose to 13 °C. Scots pine seedlings apparently can compensate for the inhibitory effects of prolonged low soil temperature periods at the beginning of the growing season by speeding up their root growth when the soil temperature increases over 13 °C, provided the nutrient availability is not limited (Iivonen et al., 1999). This seems to be applicable to our experiment.

It seems that in boreal forests the above-ground parts naturally grow first at the beginning of the growing season, when low soil temperatures occur, and the below-ground parts start to grow later when the soil temperature has increased. This is confirmed by the observation of the temporal order of growth in the parts of Scots pine: first shoot and later roots.

Element content and allocation

The significant increase in the N content of both the above-ground and below-ground parts of the seedlings after Week 9 seems to be connected with the onset of fast root growth. Another factor may be fertilisation, since the seedlings grown for a longer time also received more N through fertilisation. Although the seedlings also received more of the other elements through fertilisation, nutrient contents did not increase after Week 12, with the exception of Fe in the new roots, where an increase was observed throughout the experiment.

Soil temperature certainly affected the nutrient uptake of the seedlings, in that those grown at 5 °C for the longest time had taken up the least N in relation to that given by fertilisation at Week 9, and this trend was still seen at Weeks 12 and 15. Nutrient uptake at lower soil temperatures could be reduced through the effects of temperature on metabolic processes (Bowen, 1991) or impaired membrane function (Ryyppö et al., 1998), resulting in lower nutrient uptake rates at low soil temperatures. Quick recovery in nutrient uptake after an increase in soil temperature indicated that metabolic effects were dominant.

The allocation of nutrients between the above- and below-ground parts of the seedlings at the end of each soil temperature treatment was not significantly influenced by the length of the cold soil period, and no significant effects of soil temperature on the relative allocation of nutrients were observed in our earlier experiment (Domisch et al., 2002).

Carbohydrate allocation

The low starch content and concentration at the beginning of the experiment seems to be a normal phenomenon since reserves are used during the winter (e.g., Jiang et al., 1994). We also found a negligible amount of starch in Scots pine seedlings at the beginning of the growing season in our previous experiment (Domisch et al., 2001). The highest starch content at Week 12 was observed in those seedlings which were grown for 3 weeks at 5 °C. This treatment may most closely mimic the course of soil temperature prevailing in nature.

A clear trend could be seen for the starch concentrations in the needles and the old roots to be higher the longer the seedlings were exposed to the cold soil (data not shown). The accumulation of non-structural carbohydrates in above-ground plant parts is a characteristic response to low soil temperatures, while the metabolic activity of the root system decreases at low soil temperatures, resulting in reduced below-ground translocation of photosynthates (Hurewitz and Janes, 1983). Another reason is that photosynthesis is not as sensitive to low soil temperature as growth (Ericsson et al., 1996; Farrar, 1988).

CO_2 uptake remains relatively stable over a certain range of air and soil temperatures (5–15 °C; Pelkonen et al., 1977). Thus the accumulation of the main product of photosynthesis, soluble sugars, seemed here to be less influenced by soil temperature. The amount of soluble sugars did not differ between the soil temperature treatments after 12 weeks, but, the total amount of starch in the seedlings was much lower in those seedlings which were exposed to a 5 °C soil temperature for a longer time.

Starch is a carbohydrate reserve and its concentration and amount increases in new needles until August and subsequently decreases drastically (Sutinen, 1985). We obtained similar results, particularly regarding the allocation of starch to the new needles, which decreased after Week 12, corresponding to the middle of August. Allocation to the roots lasted longer, but eventually decreased as well (Figure 6A). One other factor affecting the carbohydrate status of the roots is the photoperiod. The carbohydrate content of, e.g., maize increased with a longer photoperiod (Marschner, 1986). However, light exposure remained unchanged throughout our experiment and did not vary among treatments, either. Thus the decrease in starch content must be due to other factors, mainly the duration of the cold soil period to which seedlings were exposed. In this context, a shorter period of low soil temperature in the spring may be beneficial.

Conclusions

Our results indicate that the prolonged cold soil treatments did mainly shift the development of the seedlings a little later except for new shoot height which is mostly predetermined. Thus, increasing soil temperatures in spring due to global climatic changes may not change greatly ultimate development of planted seedlings but may advance development events.

The results also indicate that Scots pine seedlings establish quickly in spring after a relatively long cold soil period. Thus drained peatlands that are cold sites during spring might not be critical for seedling development as seedlings in good condition will survive the time of cold soil. This study, however, did not assess the effect of a prolonged period of frozen soil, which might be a prospect for future research.

Acknowledgements

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PAPER III

III

Domisch, T., Finér, L., Laiho, R. and Laine, J. 2002. Decomposition and N dynamics of Scots pine needle litter in *Carex*-peat soils from two climatically different regions.

Manuscript.

Decomposition and N dynamics of Scots pine needle litter in *Carex*-peat soils from two climatically different regions

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Abstract

Soil temperature is a major factor affecting organic matter decomposition and possible increases due to global climatic changes may accelerate decomposition although it remains unclear whether the effects will be similar in climatically different regions. The effects of soil temperatures of 5, 10 and 15°C on the decomposition of Scots pine (*Pinus sylvestris* L.) needles were assessed in a one-year growth chamber experiment, the 10°C treatment corresponding to the soil temperature accumulation over three growing seasons under middle boreal conditions in Southern Finland. Intact peat cores from two climatically different peatland sites (in Southern and Northern Finland) were used as the incubation environment. Needle litter from two-year-old Scots pine seedlings was incubated in litter bags beneath the living moss layer, and mass loss and N concentration were determined at 60-day intervals. Soil temperature had a clear effect on the rate of mass loss from the litter, which was significantly lower at 5°C than at the higher temperatures. On the other hand, mass losses were higher at 15°C than at 10°C only between days 180 and 300, when the soil temperature sum had reached 1800 to 3000 d.d. in the 10°C treatment and 2700 to 4500 d.d. in the 15°C treatment. During this period the decomposition rate was higher in the northern than in the southern peat at 15°C. Nitrogen was released from the litter only when the accumulated mass loss was between 50 and 60% and the C/N ratio had decreased from 50 at the beginning of the experiment to 25–25. Accumulated mass loss and N release were clearly related to the accumulated soil temperature sum. The limit value for mass loss was approximately 88%. As a result, it seems that increasing soil temperatures may result in slightly higher rates of needle litter mass loss and consequent N release in northern peat than in southern peat even though the limit value may not change.

Keywords: Climate change; Mass loss; Needle litter; Nitrogen; Peatland; Scots pine; Soil temperature

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Introduction

Boreal peatlands contain about one-third of all terrestrial carbon stores (Gorham 1991) and the greatest part of the carbon stores in Finland can be found in peatlands (Minkkinen 1999). Drainage of peatlands for peat harvesting or agricultural purposes changes them from carbon sinks into carbon sources (Armentano and Menges 1986, Nykänen et al. 1995), whereas in many cases drainage for forestry has been found to increase carbon stores, at least for the first 60–80 years (Minkkinen & Laine 1998ab, Minkkinen et al. 1999). The increases in peat carbon stores at drained sites have proved to be greater in Southern Finland than in Northern Finland (Minkkinen & Laine 1998b).

Although peatlands drained for forestry may act as sinks for atmospheric carbon, the mechanism of carbon accumulation seems to be slightly different from that in pristine peatlands, as the latter accumulate carbon through height growth, predominantly from plants of the field and bottom layers (*Sphagna* and sedges), whereas the increased tree litter above and below the ground seems to be more important on drained peatlands. Drainage also enhances the decomposition processes via improved aeration of the surface peat and the resulting increase in microbial activity (Lieffers 1988, Bridgham et al. 1991, Chmielewski 1991). The relation of the increased decomposition to the input of new litter is very important in this context, and it is this that determines the carbon balance in the drained peatland.

Future climate scenarios for Finland predict increases in air temperature of 0.3–3.6°C within the next 50 years (Carter et al. 1995), which may also mean a rise in soil temperature and a draw-down of the water level, enhancing root growth and increasing below-ground carbon allocation (Finér & Laine 1998). This can be of special importance for the carbon sink strength of boreal peatlands (Gitay et al. 2001).

At present the mean soil temperature in the rooting zone of peatlands in Central Finland during the growing season is 10 to 12°C, with values ranging temporarily from 5 to 20°C (Hytönen & Silfverberg 1991, Finér & Laine 1998, Domisch et al. 2000). Drainage of peatlands has caused not only a decrease in mean soil temperatures, especially at the beginning of the growing season (Heikurainen & Seppälä 1963, Hytönen & Silfverberg 1991) but also a decrease in air temperatures during the late summer (Venäläinen et al. 1999).

It is known that an increase in soil temperature results in higher microbial activity and thus increased rates of mass loss from plant litter. It can be concluded from the results of our earlier experiments (Domisch et al. 1998, 2000) that soil temperature affects the decomposition of Scots pine needle litter more than that of root litter, but these experiments were conducted in the same climatic region and the response of decomposers from climatically different regions to rising soil temperatures has not been studied.

Although the fact that lower decomposition rates found at higher latitudes within the boreal region (Mikola 1960, Johansson 1984) can be mainly attributed to climatic effects such as temperature and moisture (Berg et al. 1993, Coûteaux et al. 1995), the question remains as to whether the decomposition processes would be slower in northern than in southern boreal peats if the environmental factors, such as temperature and moisture, were standardised. Microbial populations in northern climatic environments may be adapted to relatively low soil temperatures, and a possible increase in soil temperature may or may not result in a faster decomposition process (Bottner et al. 2000).

The objectives of the present work were (1) to assess the effect of soil temperature on the decomposition of Scots pine needle litter in peat soil, (2) to investigate the effect of temperature on the decomposition of similar litter in two peat soils from climatically different regions, and (3) to study the C and N dynamics related to the decomposition process.

Material and methods

Litter material and experimental design

The needle litter was derived from 2-year-old nursery grown seedlings of Scots pine (*Pinus sylvestris* L.), the current needles of which were harvested at the end of the second growing season and dried at 60°C to a constant mass. Initial element concentrations in the needle litter material were N 10.16, P 1.42, K 6.75, Ca 2.92, Mg 1.36, Mn 0.32, Fe 0.065, Al 0.080, Cu 0.0042 and Zn 0.036 mg g^{-1} dry mass.

Intact peat cores, including the moss layer, from drained sedge pine fens (classification after Laine & Vasander 1996) in Southern Finland (Orivesi, 61°47'N, 24°18'E, ca. 150 m a.s.l., mean annual temperature 3°C and precipitation 700 mm) and Northern Finland (Rovaniemi rural district, 66°29'N, 25°29'E, ca. 100 m a.s.l., mean annual temperature 0°C and precipitation 535 mm) were placed directly into plastic pots of volume 3.4 litres (diameter 12 cm, height 30 cm, closed at the bottom). Sedge pine fens are the most common peatlands drained for forestry in Finland (Keltikangas et al. 1986). The pots containing the intact peat cores were transported to the laboratory. The element concentrations (mg g^{-1} dry mass) in the surface layer of the peat are shown in Table 1.

Table 1. Concentrations (mg g^{-1} dry mass) of certain elements at the sites from which the peat samples were taken. Concentrations at the southern site were measured in the 0–10 cm and those at the northern site in the 0–5 cm layer.

mg g^{-1}	Southern	Northern
N	16.8	14.3
P	0.67	1.59
Ca	3.41	1.96
K	0.40	0.63
Mg	0.41	0.44
Al	0.68	1.1
Fe	7.2	24.7
Cu	0.004	0.005
Zn	0.033	0.019

A total of 216 litter bags were used for the experiment, 6x6 bags for each treatment. Exactly 1 g of the needle litter was put in each bag, and the bags were placed under the living moss layer, 1–2 cm from the surface, in the plastic pots containing the peat profile. Finally, the pots were placed into water tanks at temperatures of 5, 10 and 15°C.

The pots were supplied once a weak with water that mimicked in its amount and composition the average rain water received by the southern site (Sallantaus 1992). A plastic tube was driven into the peat at one side of the pot for removing any free water, since the pots were closed at the bottom. The water tanks were situated in a walk-in growth room (Conviron GR 77, Winnipeg, Canada) in which the air temperature was maintained at 15°C throughout the experiment. The photon flux was ca. 400 µmol $m^{-2}s^{-1}$ (60 W incandescent lamps, Airam Ltd., Finland, and 215 W Cool White fluorescent tubes, Osram Sylvania, Danvers, MA)and the day/night relative humidity of the air was 60/80%. The water tanks, i.e. treatment blocks, were not replicated, and in order to minimise a possible confounding interaction between the water tank and soil temperature treatment, the locations of the pots within the tanks were changed once a week.

The experiment was carried out for 360 days. The soil temperature sum over 120 days in the 10°C treatment corresponded to the sums observed in the field during one growing season near the southern site in Orivesi (Domisch et al. 2000). The two other soil temperatures, 5 and 15°C had been chosen for comparison. A sample of 6 litter bags was taken from each soil temperature treatment every 60 days, and the residual litter removed and dried at 60°C to a constant mass and subsequently weighed to determine the mass loss. After that, all 6 samples representing each temperature treatment and period were pooled and ground in an A 10 IKA analytical mill for chemical analysis.

Chemical analyses

Total C and N concentrations in the litter samples were determined with a Carlo-Erba elemental analyser (model 1106) and the concentrations of other elements in the litter material at the beginning of the experiment with an atomic absorption spectrometer (Perkin-Elmer 5000) after dry ashing and dissolving in hydrochloric acid, except for P, which was analysed spectrophotometrically (Perkin-Elmer Lambda 11) by the hydrazine-molybdenate method. The mineral element concentrations in the surface peat of the two sites from which the peat cores had been extracted (Table 1) were determined with an ICP-spectrometer (ARL 3580 OES, Fison Instruments, Valencia, CA) after dry ashing and dissolving in hydrochloric acid. Nitrogen concentrations in the peat were analysed with a LECO CHN 600 analyser (Leco Corp. St. Joseph, MI).

Statistical tests and calculations

The initial C and N contents in the litter were obtained from pooled material and were thus common to all the treatments. At the end of each decomposition period the corresponding contents in the residual litter in the retrieved bags were calculated from the mean concentrations and the respective mean masses in each treatment. The losses of mass, C and N from the litter bags were calculated relative to their initial mass or content and all the mass loss percentages were subjected to angular transformation ($x'=\arcsin\sqrt{x}$) before the statistical tests.

Repeated measures ANOVA was used to test the effects of soil temperature, climatic region and length of the decomposition period on the mass losses. Soil temperature (3 levels) and climatic region (2 levels) were used as grouping factors, and the length of the decomposition period (6 levels) as a within-factor. The individual observations regarding each combination of treatments were used as replicates (6). Contrast analyses were performed as post-hoc tests (effects of region at given temperatures and effects of temperature in given regions).

Two alternative models were employed to analyse the relationship between soil temperature sum and accumulated mass losses from the litter: the slightly modified exponential model with an asymptotic level, presented by Berg & Ekbohm (1991):

$$m_{loss}=a*(1-e^{-b*Tsum/a}), \qquad (1)$$

and the sigmoidal growth function of Richards (1959):

$$m_{loss}=a/((1+e^{(b-c*Tsum)})^{(1/d)}), \qquad (2)$$

where

m_{loss} is the accumulated mass loss at a certain temperature sum (T_{sum})

a is the asymptote (limit value for mass loss)

b, c and d are parameters

T_{sum} is the soil temperature sum (0°C threshold).

The model of Berg & Ekbohm (1991) generally fits well but has the weakness from our point of view that it is forced to pass through the origin whereas some decomposition may take place also at or very near 0°C (Bleak 1970, Visser & Parkinson 1975). The Richards growth function has often been used in forestry to model tree growth. Both models were first fitted individually to the southern and northern sets of mass loss data, but since the curves were not statistically different (asymptotic level of each curve within the 95% confidence level of the other), the data were pooled and treated collectively. The statistical analyses were performed with the SPSS statistical package (SPSS for Windows 9.0, 1999).

Results

Mass losses from the needle litter

Mass losses from the litter increased with time (Fig. 1; within-subject effect of decomposition period: $F = 190.7$; $P < 0.001$) The interaction between climatic region and decomposition period was not statistically significant, whereas that between soil temperature and decomposition period was ($F = 13.25$; $P < 0.001$), indicating that the mass losses did not vary between the regions but were greater at higher soil temperatures. The mass losses at 5°C were lowest over the whole experiment in the material from both climatic regions, and the losses recorded on days 180 to 300 were higher at 15°C than at 10°C (Fig. 1). Over this interval the soil temperature sum increased from 1800 to 3000 d.d. in the 10°C treatment and from 2700 to 4500 d.d. in the 15°C treatment.

Contrast analysis revealed that the mass losses were higher in the northern peat only at temperatures of 10 and 15°C. No differences between the peats at temperatures of 10 and 15°C were observed at the end of the experiment, on day 360, however, whereas the mass losses at 5°C were notably lower. The mass losses increased with time in both peats and at all soil temperatures, although at different speeds (Fig. 1). The mass losses did not increase significantly after 300 days.

The mass losses in all the temperature treatments showed a similar non-linear relationship to the accumulated soil temperature sum (Fig. 2). The limit value for mass loss in the pooled data was 88.0% when

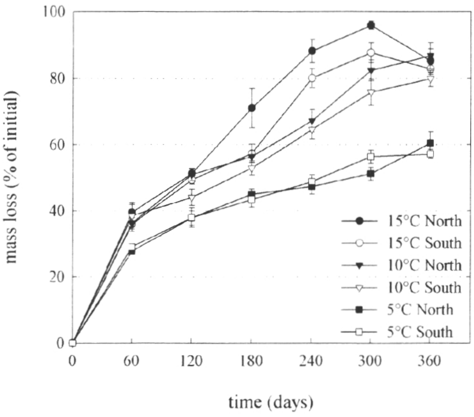

Figure 1. Accumulated mass losses from the needle litter during the experiment at soil temperatures of 5, 10 and 15°C in the southern and northern peat. Standard errors are indicated (n=6).

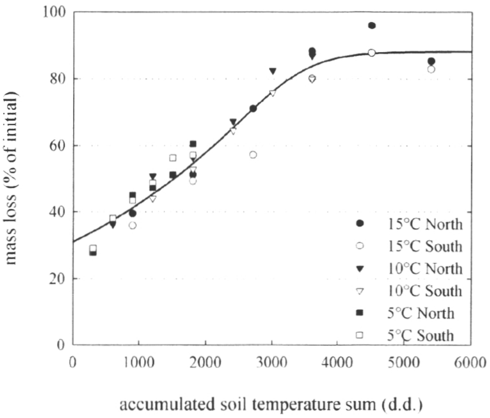

Figure 2. Relationship of accumulated mass losses to accumulated soil temperature sum during the experiment. Values are means of 6 observations. Fitted curve calculated with the Richards model. Asymptote at 88 %, R^2=0.95.

fitted to the Richards model (R^2=0.95), and the equation proposed by Berg and Ekbohm (1991) gave practically the same value, 88.2% (R^2=0.89).

The carbon concentration in the litter increased from about initially 50% to 52–53% on day 180, and decreased thereafter almost to the initial concentration (Fig. 3A). The carbon loss from the litter (Fig. 3B) showed the same pattern as the mass loss.

Changes in N status

The initial mean N concentration in the needle litter was 1.0% of dry mass, increases to 2–3% being recorded by day 180 (Fig. 3C) and decreases thereafter. At 5°C the concentrations increased throughout the experiment.

The N content of the remaining litter was relatively constant during the first 120–180 days (Fig. 3D), but decreased thereafter at 10 and 15°C. No changes were observed at 5°C. The N losses at 10 and 15°C were slightly higher in the northern peat.

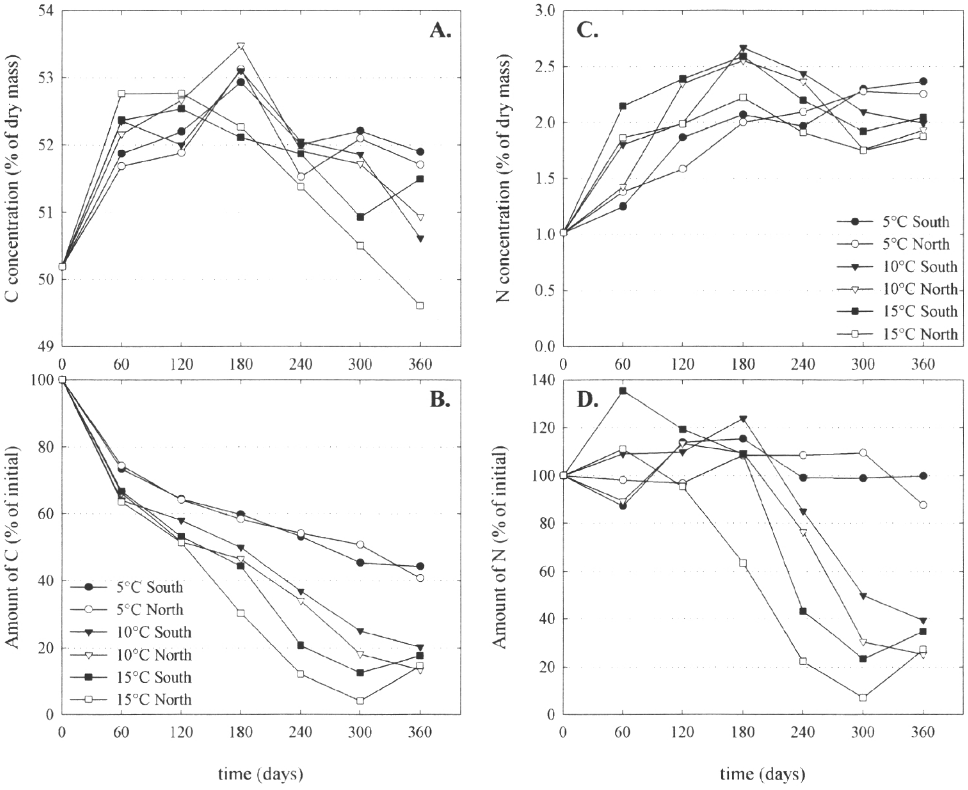

Figure 3. Concentrations of carbon (A) and nitrogen (C) and amount of carbon (B) and nitrogen (D) in the remaining litter during the experiment at soil temperatures of 5, 10 and 15°C in the southern and northern peat. Values for pooled samples (n=1).

The C/N ratio of the needle litter was 50 at the beginning of the experiment (Fig. 4A) and decreased to 20–25 by day 180 at all soil temperatures. During the first 120 days the ratios were higher the lower the soil temperature, but no clear differences between soil temperatures could be observed from day 180 on.

When comparing the changes in N concentrations and contents with the accumulated mass losses, relatively clear patterns were observed (Fig. 5). The N concentration increased until a mass loss of 50–60%, whereupon it decreased (Fig. 5A), while the N content did not change much until a mass loss of 50–60 %, from which point it decreased linearly (Fig. 5B). The C/N ratio of the litter also decreased until a mass loss of 50-60 %, but then increased slightly from somewhat above 20 to nearly 30 (Fig. 4B).

Like the mass losses from the litter, the N concentrations and contents also showed a non-linear relationship to the accumulated soil temperature sum (Fig. 6). The N concentrations in the needle litter increased until a soil temperature sum of approx. 2000 d.d. and thereafter decreased slightly (Fig. 6A), whereas the N content decreased markedly after a soil temperature sum of approx. 2000 d.d. (Fig. 6B), simultaneously with the culmination of the decrease in the C/N ratio (Fig. 6C).

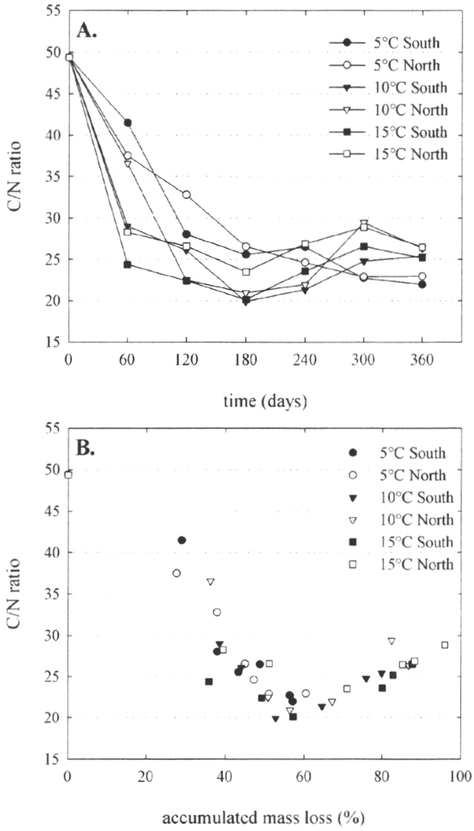

Figure 4. C/N ratio at soil temperatures of 5, 10 and 15°C in the southern and northern peat in relationship to time (A) and accumulated mass loss (B). Values for pooled samples (n=1).

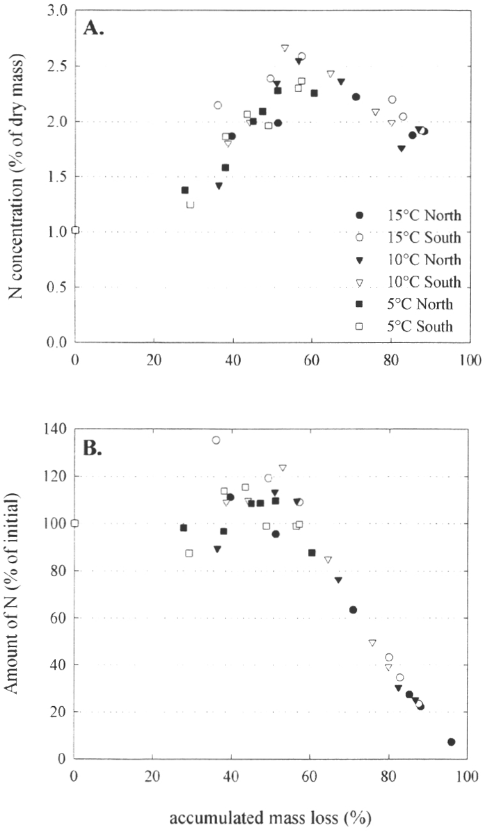

Figure 5. Concentration of nitrogen (A) and amount of N remaining in the litter (B) in relation to accumulated mass losses during the experiment at soil temperatures of 5, 10 and 15°C in the southern and northern peat. Values for pooled samples (n=1).

Discussion

Mass losses

As in many studies with different litter material, we found that after an initial high rate of mass loss, decomposition slowed down asymptotically towards a limit value (maximum mass loss) specific to the litter type (see Aber et al. 1990, Berg & Ekbohm 1991, 1993, Berg & Matzner 1997, Latter et al. 1998, Berg 2000). The limit value for our litter was approx. 88 %, similar to the figures presented by Berg et al. (1996) for brown Scots pine needle litter in mineral soil. The mass loss is regulated by nutrient status, readily available carbon and the lignin content of the litter (Berg & Staaf 1980, Mellilo et al. 1982, Berg & Ekbohm 1991, Berg & Matzner 1997, Berg 1998). Our results indicate that under steady moisture conditions, the accumulated soil temperature sum determines the time required to reach the limit value for a particular litter type (see also Andrén & Paustian 1987, Honeycutt et al. 1988, Van Cleve et al. 1990, Douglas & Rickman 1992, Sparrow et al. 1992, Domisch et al. 2000).

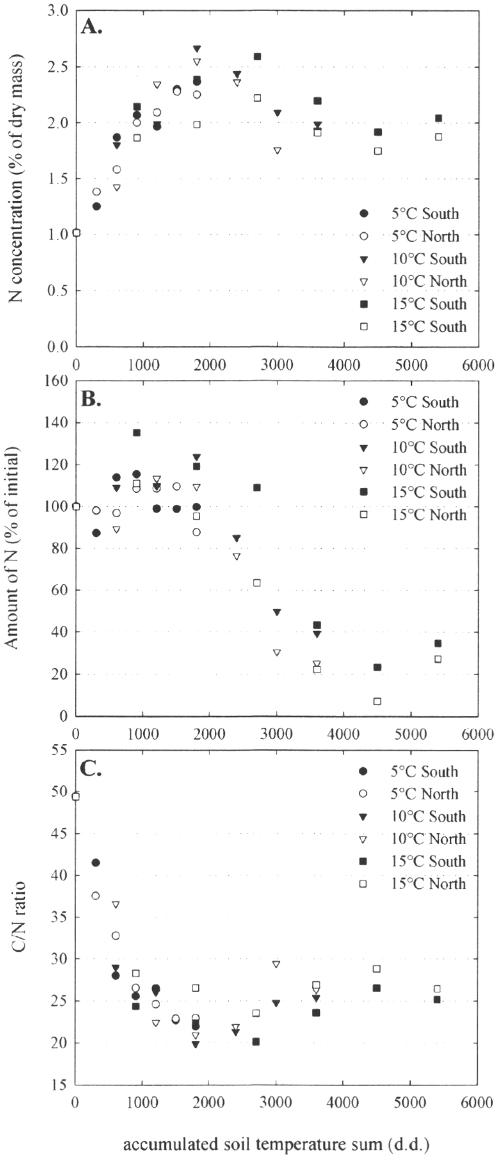

Figure 6. Relationship of N concentration (A), amount of N remaining in the litter (B) and C/N ratio of the remaining litter (C) to the accumulated soil temperature sum during the experiment at soil temperatures of 5, 10 and 15°C in the southern and northern peat. Values for pooled samples (n=1).

In our experiment the mass losses probably reached the limit value at the soil temperature of 15°C, whereas the limit was just about to be reached at 10°C. The mass losses at 5°C definitely did not reach the limit value during the 360 days. The accumulated soil temperature sum at 5°C was only 1800 d.d. at the end of the experiment, and an even longer experiment would have been necessary to find out whether the decomposition at that soil temperature will really proceed to the same limit value as at the higher temperatures.

Decomposition proceeded somewhat faster in the northern peat than in the southern peat for part of the incubation time (Fig. 1). Similarly, Bottner et al. (2000) observed higher mass losses of up to 10% from labelled litter material after 3 years when northern boreal soil was translocated southwards to an extent corresponding to a mean annual air temperature increase of 2.5°C. Coûteaux et al. (2001) and Giardina & Ryan (2000) concluded that the stabilised fraction of the litter may be insensitive to climate variations, but carbon mineralisation will occur earlier at warmer southern sites than at colder northern ones. Our results support these conclusions, since our northern data indicated a higher limit value, although this difference was not significant. An increasing limit value would be in contrast with the conclusions of Berg et al. (1993) and Johansson et al. (1995) that the proportion of lignin-like residual material in Scots pine needle litter at similar stages of decomposition may increase when climatic conditions promote higher initial mass losses, which seems to be applicable to elevated soil temperatures. Indeed, Verburg et al. (1999) and Dalias et al. (2001) observed that the amount of refractory organic matter may increase at elevated soil temperatures. A higher limit value would indicate that the decomposer community in northern peat would be more efficient in utilising the recalcitrant lignin and lignin-like end products in the decomposition process under more favourable temperature conditions.

N status

The concentration of N in the remaining litter increased with time, as is commonly observed (Berg & Staaf 1980, 1981, 1987, Berg et al. 1987, Titus & Malcolm 1999, Hyvönen et al. 2000), but in contrast to this, the N content of the residual needle litter remained relatively unchanged at first and decreased only during the later stages of the decomposition process (Figs 3 C, D). Increasing N concentrations and steadily decreasing N contents during a time span of 4–7 years were observed by Berg et al. (1987) when studying the decomposition of nitrogen-fertilised Scots pine needle litter and by Titus & Malcolm (1999) studying Sitka spruce needle litter (initial N concentration 7-8 mg N g^{-1} and 12 mg N g^{-1}). Berg et al. (1987) observed an unchanged N content during a 4-year experiment to study the decomposition of nutrient-poor Scots pine needle litter (initial N concentration ca. 4 mg N g^{-1}), while Berg & Staaf (1981) observed first an increase in N content after a short leaching period and the a steady release phase after two years, pointing out that one important factor determining whether accumulation will take place or not is the initial N concentration in the litter. We studied green needles with a relatively high initial N concentration, which could explain the somewhat unchanged N content during the early stages of decomposition.

Our observation may be explained by the fact that more easily degradable compounds, such as water-soluble compounds and cellulose having low N concentrations, disappear first (Naucke 1993), and lignin, which contains a considerable amount of the N in Scots pine needle litter (32–43 % of total N, Berg & Staaf 1980) decomposes much more slowly. A further reason may be the binding of N to the lignin fraction and humification products during decomposition (Berg & Staaf 1981, Berg & Theander 1984). No N release from the litter took place before an accumulated mass loss of about 50–60 %, a C/N ratio of 20–30 or a soil temperature sum of ca

2000 d.d., which were in many ways turning-points in the N dynamics of the decomposition process (Figs. 5 and 6).

Conclusions

Our results showed that litter decomposition rates in the higher soil temperature treatments were slightly higher in the northern peat, as also was the limit value, although not significantly higher than in the southern peat. Both mass loss and N release from decomposing litter had a clear non-linear relationship to the accumulated soil temperature sum. We are inclined to link the observed dynamics of N release to the mass loss dynamics related to the sequential decomposition of organic compounds.

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PAPER IV

Domisch, T., Finér, L., Laiho, R., Karsisto, M. and Laine, J. 2000. Decomposition of Scots pine litter and the fate of released carbon in pristine and drained pine mires. Soil Biology & Biochemistry 32: 1571–1580.

IV

PERGAMON

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Decomposition of Scots pine litter and the fate of released carbon in pristine and drained pine mires

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Abstract

A field experiment was carried out to validate the results of a previous laboratory experiment showing that part of the carbon released from decaying Scots pine (*Pinus sylvestris* L.) needle and fine root litter was retained in the peat soil. ^{14}C-labelled litter was incubated for up to 1.5 years in pristine and drained peat soils. During this period, 40–60% of the initial ^{14}C-activity was lost from the litter and 10–30% of the lost activity was retained in the soil. Needle litter decomposed faster than fine root litter. On average, drainage increased the mass and ^{14}C losses from the needle litter in *Carex*-peat but not in *Sphagnum*-peat. Losses from the fine root litter were not clearly affected by drainage. Drainage did not significantly affect the relative proportion of ^{14}C-activity found in the peat. The results support the earlier hypothesis that a flow of organic C from decaying tree litter contributes to C storage in drained peatlands. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Carbon relocation; Decomposition; Drainage; Needle and fine root litter; Peatland; *Pinus sylvestris*

1. Introduction

Pristine peatlands serve as sinks for atmospheric carbon. Most of the litter in these peatlands is produced by plants of the field and bottom layer (*Sphagna* and sedges). Pine mires are the most common peatlands drained for forestry in Finland (Keltikangas et al., 1986). Drainage of pine mires promotes a shift in biomass production from the field and bottom layer to the tree layer (e.g., Reinikainen et al., 1984; Sakovets and Germanova, 1992) so that Scots pine litter is the most abundant litter type on these mires. Along with the increased tree stand productivity following drainage, the above ground detrital input from trees increases, and probably also the below ground input (Laiho and Finér, 1996; Laiho and Laine, 1996).

Drainage of peatlands for peat harvesting or agriculture evidently turns them into net sources of carbon (Armentano and Menges, 1986; Nykänen et al., 1995), but the consequences of forest drainage are not that obvious (Vompersky et al., 1992; Martikainen et al., 1995). Studies comparing the bulk densities and carbon stores of natural and drained peatlands in Finland (Minkkinen and Laine, 1998a, 1998b; Minkkinen et al., 1999) have shown that even 60 years after drainage for forestry most peatlands have not developed into carbon sources. This might be due to the increased litter production by the tree layer, since the ratio between litter input through increased tree layer production and decomposition of previously formed peat is crucial in this respect (Vompersky and Smagina, 1984; Cannell et al., 1993; Minkkinen and Laine, 1998b).

Results of our previous laboratory experiment indicated that part of the carbon released from decaying litter is retained in the peat soil (Domisch et al., 1998)

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and may thus contribute to the increased peat carbon stores observed after drainage for forestry.

The general aim here was to create a field control for the results of the previous laboratory experiment (Domisch et al., 1998). More specifically, the objectives were (1) to determine the differences between Scots pine needle and fine root litter decomposition, (2) to investigate differences in the decomposition of the litter between *Sphagnum*- and *Carex*-peats, both drained and pristine, (3) to assess the fate of the carbon lost from the litter, and (4) to study the vertical distribution of the carbon retained in the peat soil.

2. Materials and methods

2.1. Litter material

The ^{14}C-labelled Scots pine needle and fine root litter material for the litter bags used in the decomposition experiment was produced in the same way as described by Domisch et al. (1998), since this experiment was intended as a field validation of the previous laboratory experiment. Scots pine seedlings were labelled with ^{14}C and were grown for one growing season. After that, current needles and fine roots were harvested and used for the decomposition experiment. Samples of 1 g dry mass were placed in 10 × 10 cm^2 polyester litter bags (mesh size 1 mm). The element and initial ^{14}C-activity analyses and fractionation of the litter material were performed as described by Domisch et al. (1998).

2.2. Experimental design

The experiment was planned to assess the effects of three factors, litter type, drainage status and peat type, at two levels, and that of one factor, decomposition period, at three levels. The experiment was conducted near the University of Helsinki Forestry Station at Juupajoki, Central Finland (61°50′ N, 24°17′ E, 150 m a.s.l.). Four plots were chosen to represent both drained and pristine sites of the same pre-drainage nutrient regime (Table 1). One pair of sites had minerotrophic *Carex*-peat and the other ombrotrophic *Sphagnum*-peat. Three blocks with two needle and fine root litter bags for each block and decomposition period were established on each plot.

Plastic tubes of length 30 cm and diameter 15 cm were driven into the peat and a litter bag was placed in each tube at the beginning of June 1996. The needle litter bags were placed horizontally directly below the living moss layer and the fine root litter bags 2–3 cm deeper. The first decomposition period (period I) lasted 4.5 months, until the end of October 1996, the second (period II) lasted 12 months, until the beginning of June 1997, and the third (period III) lasted 16.5 months, until the end of October 1997.

The element concentrations of the peat layers on the plots (Table 2) were determined with an atomic absorption spectrophotometer (Perkin-Elmer 5000) after dry ashing and dissolving in hydrochloric acid except for P which was analysed spectrophotometrically (Perkin-Elmer Lambda 11) by the hydrazine-molybdenate method. N was determined by the Kjeldahl method.

Climatic variables were monitored continuously with a data logger (Campbell CR-10) on Plot 4 (Fig. 1). Data regarding the depth of the snow cover (Fig. 1) and the temperature sums (952°C in 1996 and 1151°C in 1997, threshold +5°C) were obtained from the Hyytiälä Forestry Station 1.5 km from the furthest Plot 4. On the other plots, water level and soil temperature were measured manually two to three times a week during the summer of 1996. Regression models were then developed for calculating the monthly soil temperatures and water levels for Plots 1, 2 and 3 in 1996 and 1997 using continuous monitoring data from Plot 4 as a basis (Table 3).

2.3. Measurement of mass loss and remaining ^{14}C-activity

At the end of each decomposition period, the litter bags in the corresponding blocks were taken from the soil, their contents dried to constant mass at 60°C and weighed to determine mass loss. The litter in each litter bag was combusted in an oxidiser (Maricont, Junitek, Turku, Finland) and analysed in a liquid scintillation counter (Wallac 1411 Liquid Scintillation Counter, Wallac, Turku, Finland) for remaining ^{14}C-activity. The peat cores from inside the tubes were lifted from

Table 1
Characterisation of the plots used in the experiment. The site type classification refers to Laine and Vasander (1996)

Plot	Drainage status	Nutrient status	Peat type	Site type
1	Pristine	Minerotrophic	*Carex*	Tall sedge pine fen
2		Ombrotrophic	*Sphagnum*	Dwarf-shrub pine bog
3	Drained	Minerotrophic	*Carex*	Tall sedge pine fen
4		Ombrotrophic	*Sphagnum*	Dwarf-shrub pine bog

Table 2
Element concentrations (mg g^{-1} dry mass), pH ($CaCl_2$) and bulk density (D_b, kg m^{-3}) in the surface peat on the plots. The values are means of three observations

Plot	Depth (cm)	N	P	K	Ca	Mg	Fe	Al	Cu	pH	D_b
1	0–10	7.24	0.48	1.30	1.82	0.46	4.60	0.43	0.0061	2.85	24.23
	10–20	12.16	0.63	0.40	2.21	0.41	5.80	0.67	0.0081	2.91	31.16
	20–30	18.63	0.60	0.17	2.82	0.25	9.96	0.70	0.0050	3.02	46.11
2	0–10	14.35	0.44	0.77	2.08	0.47	0.94	0.61	0.0050	2.60	48.12
	10–20	10.39	0.47	0.29	1.36	0.41	0.77	0.59	0.0027	2.47	61.42
	20–30	8.28	0.29	0.06	1.10	0.32	0.58	0.26	0.0021	2.47	50.70
3	0–10	15.53	0.85	0.83	2.48	0.50	6.93	1.19	0.0090	2.80	60.44
	10–20	19.03	1.00	0.33	1.18	0.15	10.15	2.78	0.0089	2.83	107.16
	20–30	18.59	0.77	0.10	1.95	0.12	12.24	3.81	0.0111	3.07	124.53
4	0–10	12.18	0.59	0.63	2.50	0.45	0.79	0.78	0.0065	2.67	65.25
	10–20	14.72	0.64	0.21	1.45	0.34	0.86	1.42	0.0039	2.50	71.41
	20–30	14.45	0.50	0.11	1.28	0.22	0.48	1.98	0.0052	2.58	98.73

the soil and cut into layers starting from the surface (moss layer, 0–5 cm, 5–10 cm, 10–20 cm and 20–25 cm). The layers were dried to constant mass at 105°C and subsequently milled and homogenised. Three subsamples from each layer of every core were then combusted and analysed in the same manner as the litter samples.

2.4. Calculations and statistical tests

The losses of ^{14}C-activity from the litter were calculated relative to the initial activity levels determined in the subsamples at the beginning of the experiment. The ^{14}C-activity lost from the system was estimated in terms of the difference between the initial activity and that found in the remaining litter and in the moss and peat layers.

The statistical tests were performed with the SPSS statistical package (SPSS for Windows 8.0, 1998). Repeated measures ANOVA was used to test the effects of drainage status, peat type and litter type and decomposition period. Drainage status, peat type and litter type were used as grouping factors, and decomposition period as a within-factor. For each treatment the average of the two litter bags of each block was calculated and the blocks (three for each treatment) were then used as replicates.

Fully factorial ANOVA was used to test the vertical distribution of ^{14}C-activity between the different layers in the peat for each decomposition period separately. Drainage status, peat type and litter type were used as factors. All percentage values were subjected to angu-

Table 3
Mean soil temperatures at given depths, and water levels on the plots from the beginning of June to the end of October, 1996 and 1997 (±SD)

Plot	Depth (cm)	1996	1997
Soil temperature			
1	5	10.3 ± 2.4	13.2 ± 3.7
	15	10.9 ± 1.7	12.0 ± 2.8
	30	10.4 ± 2.0	11.2 ± 1.9
2	5	11.0 ± 2.1	12.0 ± 3.2
	15	9.6 ± 1.8	10.7 ± 2.9
	30	8.9 ± 1.4	9.7 ± 2.2
3	5	9.9 ± 2.3	10.3 ± 3.5
	15	8.6 ± 1.7	9.7 ± 2.7
	30	6.7 ± 1.1	7.5 ± 1.8
4	5	8.9 ± 2.7	10.3 ± 4.1
	15	8.0 ± 2.0	9.2 ± 3.3
	30	7.1 ± 1.7	8.2 ± 2.6
Depth to water table (cm)			
1		9.8 ± 8.7	4.1 ± 1.7
2		26.0 ± 14.2	16.4 ± 2.7
3		35.3 ± 19.6	22.7 ± 3.8
4		45.5 ± 19.8	29.8 ± 3.8

lar transformation ($x' = \arcsin\sqrt{x}$) before the statistical calculations.

3. Results

3.1. Mass and ^{14}C-activity losses

Mass losses were significantly higher from needle litter than from fine root litter ($F = 40.920$; $P < 0.001$). On average, the fine root litter lost mass at the same rate in both *Sphagnum*- and *Carex*-peats. No significant effects of drainage status on mass losses from fine root litter could be observed. On average, drainage increased mass losses from needle litter in *Carex*-peat but not in *Sphagnum*-peat.

Decomposition time was statistically significant for mass losses from both litter types ($F = 259.984$; $P < 0.001$). The significant interactions between decomposition time and litter type ($F = 10.732$; $P = 0.005$) and between decomposition time, litter type and peat type ($F = 6.698$; $P = 0.020$) indicated that mass losses from needle litter with time increased more than those from root litter and that this was more pronounced in *Carex*-peat (Fig. 2).

The activity losses from needle litter were higher than those from fine root litter ($F = 53.057$; $P < 0.001$). Drainage increased the activity losses from needle litter but not from root litter ($F = 19.310$; $P < 0.001$). On average, drainage increased activity losses from the needle litter in *Carex*-peat but not in *Sphagnum*-peat. The losses of ^{14}C-activity from both fine root litter and needle litter increased significantly with decomposition time ($F = 95.540$; $P < 0.001$, Fig. 2).

Mass losses during the first summer were 32–52% of the initial mass. Mass losses during the winter were equivalent to 5–10% of the initial mass for both litter types, while the losses occurring during the second summer were notably lower than those during the first summer, around 5–15% of the initial mass.

3.2. Relocation of ^{14}C-activity

Most of the initial ^{14}C-activity was still found in the remaining litter after decomposition period I (June 1996–October 1996). The peat and moss layers in the fine root litter cores retained on average slightly more of the lost ^{14}C-activity than those in the needle litter cores, especially in the case of drained peats, although this was not statistically significant due to high variability (Fig. 3). After periods II and III the peat and moss layers retained the same amounts of lost ^{14}C-activity from the root and needle litter.

The moss and peat layers retained 12–24% of the ^{14}C-activity lost from the fine root litter after decomposition period I, 19–32% after period II and 21–26% after period III (Fig. 3). More of the ^{14}C-activity lost from the root litter was found in the moss and peat layers on the drained peats than on the pristine ones after period I, but no effect of drainage status could be observed after periods II and III. The corresponding percentages for the needle litter were 9–13%, 15–32% and 14–28%. On average, the amount of ^{14}C-activity found in the *Sphagnum*-peat and originating from needle litter increased from period I to period II more than it did in *Carex*-peats (Fig. 3). No increases

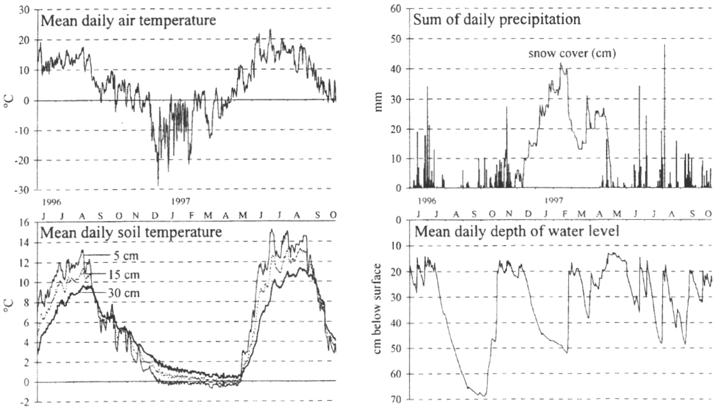

Fig. 1. Air temperature (at height 2 m), soil temperature (at depths 5, 15 and 30 cm), daily precipitation and depth of water level on Plot 4 through 1996–1997. Snow depth measured at the Hyytiälä weather station 1.5 km from the plot.

of ^{14}C-activity were observed from period II to period III. No significant effects of drainage status were observed on the relocation of activity from the needle litter.

3.3. *Vertical distribution of ^{14}C-activity*

The uppermost layers, i.e., the living moss layer and the 5-cm peat layer below it, retained most of the ^{14}C-activity lost from the litter that was detectable in the soil profile (Fig. 4). The 5–10 cm layer also retained noticeable amounts particularly in the fine root litter cores. No significant differences between the drained and pristine moss and peat layer samples were observed in these uppermost layers. On average, the deeper layer of the drained peat (10–20 cm) contained more ^{14}C-activity lost from the litter than did the respective layer of the pristine peat (Fig. 4). The fine root cores contained more activity in the deepest layer (20–25 cm) than the needle litter cores although all these differences were not statistically significant due to high variability. The drained *Sphagnum*-peat in the deepest layer examined (20–25 cm) also retained more ^{14}C-activity on average than the drained *Carex*-peat, but no statistically significant differences could be observed due to the low ^{14}C-activities and high variability.

4. Discussion

4.1. *Mass and ^{14}C-losses*

The losses in mass were greater than those observed for needle and fine root litter of Scots pine on boreal mineral soil sites by Berg (1984, 1986) and Berg et al. (1995). One possible explanation may be that the litter used here was derived from nursery-grown seedlings that had been irrigated and fertilised regularly and had higher concentrations of nutrients, e.g. N, than litter from old trees (Berg and Staaf, 1980a, 1980b; Paavilainen, 1980; Helmisaari, 1990, 1991). Finér and Laine (1996), who used litter similar to that used here, observed mass losses similar to that observed by us.

The percentage of water-soluble compounds in our needle litter, 38%, was considerably higher than the 5–20% reported by Johansson (1995), which may be another reason for the relatively high mass losses from our needle litter. The distribution of ^{14}C-activity between the soluble, cellulose and hemicellulose fractions in the fine root litter material was fairly similar to that of the initial inorganic-chemical composition found in Scots pine root litter by Berg (1984), and this may explain that the ^{14}C-losses from our root litter were similar to the mass losses reported by Berg (1984).

Since the nitrogen concentrations in the fine root

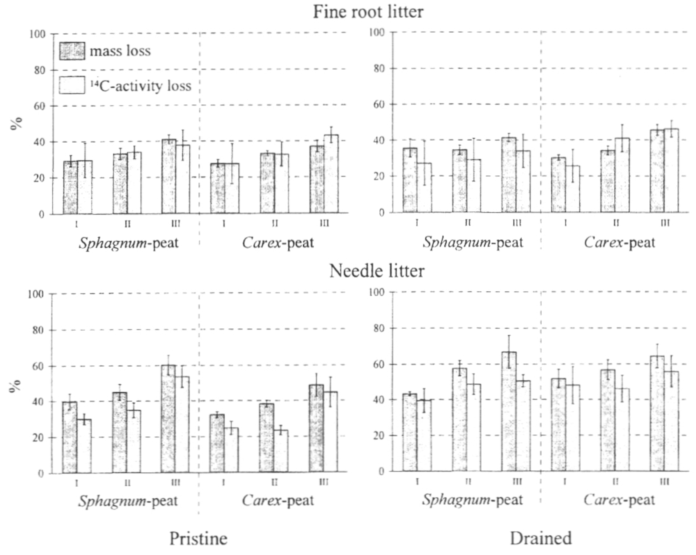

Fig. 2. Mass and ^{14}C activity losses from fine root and needle litter in the *Sphagnum*- and *Carex*-peats at the end of the three decomposition periods. Standard errors are indicated ($n = 3$).

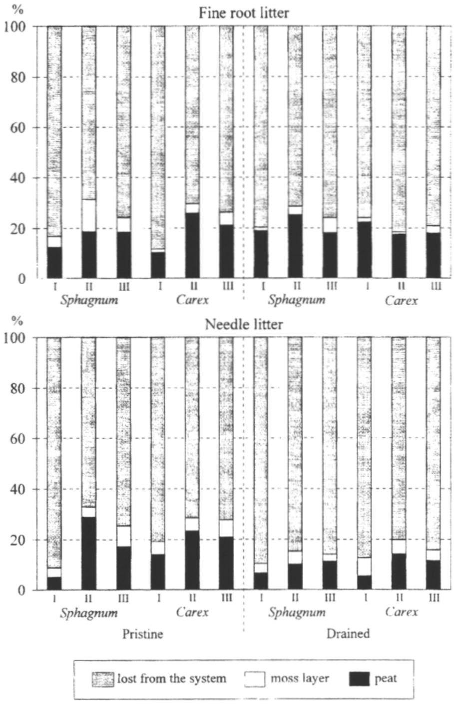

Fig. 3. The relative distributions of ^{14}C activity lost from the needle and fine root litter bags between the loss from the system, moss layer and peat at the end of the three decomposition periods on plots representing undrained and drained *Sphagnum*- and *Carex*-peats ($n = 3$).

and needle litter material were similar, it would appear that the differences in decomposition rates were caused by other factors, e.g. the considerably higher concentrations of Al, Cu and Zn in the fine root litter (Domisch et al., 1998). High Al concentrations and low Ca and Mg concentrations are assumed to slow down the rate of decomposition of fine root litter (Vogt et al., 1987). Elevated concentrations of heavy metals such as Cu and Zn have been found to reduce the microbial biomass in soil and slow down the decomposition of its organic matter (Witter, 1996; Kupermann and Carreiro, 1997).

The observation that the decomposition of fine root litter was less affected by peat type and drainage status than that of needle litter confirms to earlier reports that the early stages of root litter decomposition are influenced less by environmental factors than by substrate properties (Johansson, 1984; McClaugherty et al., 1984; Finér and Laine, 1996; King et al., 1997). Climate and site properties seem to be more important factors explaining decomposition rates on a wider geographical scale than in a climatically more or less homogenous area, even at early stages in decomposition (e.g., Dyer et al., 1990; Johansson, 1994).

It is important to bear in mind that the relative distribution of ^{14}C-activity in the organic fractions of our litter material did not correspond precisely to their mass distributions. This is probably the main reason why the corresponding mass and ^{14}C-activity losses measured from the data may differ. The losses in ^{14}C-activity from the needle litter used here were almost always lower than the corresponding mass losses, although not always significantly so. Relatively more mass than ^{14}C-activity was in soluble substances, which are known to decompose first. Both the mass and ^{14}C-activity losses from the fine roots during the first summer correlated fairly well with the proportions of water and alcohol-soluble organic fractions in the litter material (Domisch et al., 1998), and thus the first year mass losses from the fine root litter may also be mainly due to losses of soluble compounds, as was also found for root litter by McClaugherty et al.

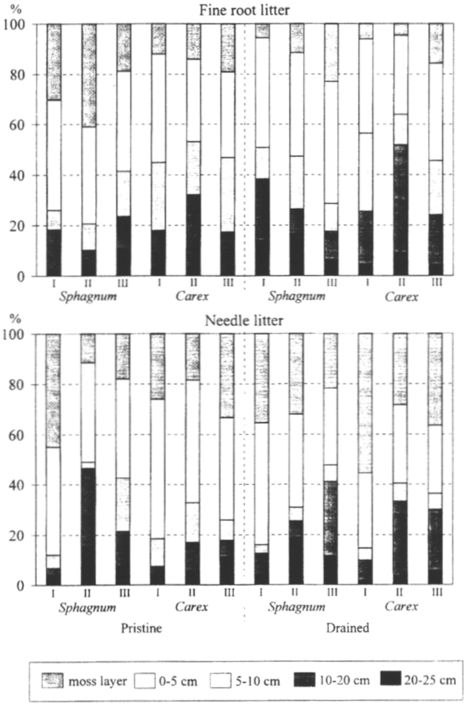

Fig. 4. Vertical distribution of ^{14}C activity lost from the litter bags and retained in the peat and moss layers, expressed in percentages of total activity detected in these layers at the end of the three decomposition periods ($n = 3$).

(1984) and needle litter by Mikola (1954) and Mälkönen (1974). As more of the ^{14}C-activity is found in the cellulose than in the more soluble fractions, ^{14}C-losses probably increase relatively more later on than do the mass losses.

4.2. Relocation of ^{14}C-activity

Based on the results of the previous laboratory experiment (Domisch et al., 1998) it can be concluded that also in this field experiment the biggest proportion of the ^{14}C-activity lost from the system was emitted to the atmosphere and that only a minor part was leached in deeper layers than examined in this study or leached into the ground water. At the end of the experiment, the peat layers examined retained 3–10% of the initial ^{14}C-activity which corresponds to 9–31% of that lost from the litter during decomposition. The amount of ^{14}C-activity found in the peat increased during the winter (period II) in particular. Decomposition during the winter has been observed to take place even at low soil temperatures (Heal et al., 1978; Brække and Finér, 1990; Finér and Laine, 1996). The percolation water in autumn and spring (meltwater from snow) may be responsible for the movement of ^{14}C-activity down the peat profile. The ^{14}C-activities retained in the soil no longer increased during the second summer. It cannot be deduced from the present results whether the relocation of ^{14}C-activity in the peat had ceased, or whether some had passed into the groundwater and had been replaced by ^{14}C-activity from the litter decomposing during the second summer (period III).

The fact that the root litter released more ^{14}C-activity into the deeper layers (5–10 cm and deeper) than did the needle litter may be connected with the location of the decomposing litter: The needle litter was placed directly under the living moss layer but the root litter a few cm deeper in the peat.

The retention of the ^{14}C-activity in the peat profile may be in connection with formation of colloidal metal–organic complexes (e.g., De Vries and Breeuwsma, 1987). This may be an important process for precipitation of organic anions in decomposition processes. Peat soil matrix is typically characterised by a high proportion of small pores (e.g., Päivänen, 1973) and a very heterogeneous pore structure (Loxham, 1980) resulting from plant residues in various stages of decomposition. Thus the peat soil matrix may facilitate the retention of formed colloidal complexes.

Vedrova (1997) studied the decomposition of Scots pine needles and the redistribution of carbon between the two main pathways of decomposition, the soil and the atmosphere, under different conditions (non-forested mineral soil in Siberia), but the results were rather similar. The upper 2 cm of soil fixed 15% of the carbon lost from decomposition during a period of about 2 years and 81% of the lost carbon was emitted into the atmosphere. In our experiments 10–30% of the ^{14}C-activity lost from the litter was found in the moss and peat layers.

The present results indicate that both pristine and drained peatlands may be sinks for carbon released from decaying tree litter, but as peatlands drained for forestry obviously produce more tree litter than pristine peatlands, the absolute retention of carbon from its decomposition will be many times greater. CO_2-flux from the surface peat may increase by about 100% immediately after drainage (Silvola et al., 1996). Assuming that the peak in CO_2 production is relatively short, levelling off later on, the newly introduced tree litter and the carbon released from the decaying litter and retained in the peat soil may play a significant role in compensating for the loss of carbon into the atmosphere from the mineralised surface peat layer.

Recent studies (Minkkinen and Laine 1998a, 1998b; Minkkinen et al., 1999) have shown, that even after a time span of 60 years, the carbon balance of drained peatlands may still be positive. This balance depends on the C budget of 'old' and 'new' litter. The change in the decomposition rate of the 'old', pre-drainage, peat caused by drainage has not actually been quantified.

4.3. Comparisons with the laboratory experiment

This field experiment was not a closed system as the amount of ^{14}C-activity that percolated into the groundwater was not measured. The results were nevertheless fairly similar compared to the previous laboratory experiment (Domisch et al., 1998), although the laboratory experiment entailed constant environmental conditions and the soil temperature in the field experiment was low during the first summer and the water table relatively high during the second (Fig. 1, Table 3). Mass losses from the fine roots both in *Sphagnum*- and *Carex*-peats were 39–46% in the laboratory experiment at 15°C simulating two growing seasons, compared with 37–46% in the field experiment after two real growing seasons and one winter. The respective percentages for the needle litter were 58–74% in the laboratory and 49–67% under field conditions. If we compare these mass losses in the laboratory experiment to those in the drained peat in the field experiment, it may be speculated that temperature and decomposition time may only be factors of secondary importance. If only a certain temperature sum is reached, mass losses seem to be similar (Fig. 5). The asymptotic regression curves of the form $y = a(1 - b^x)$ are also shown. For all cases the coefficients of determination (R^2) of the curves were over 0.95.

The total amounts of activity retained in the differ-

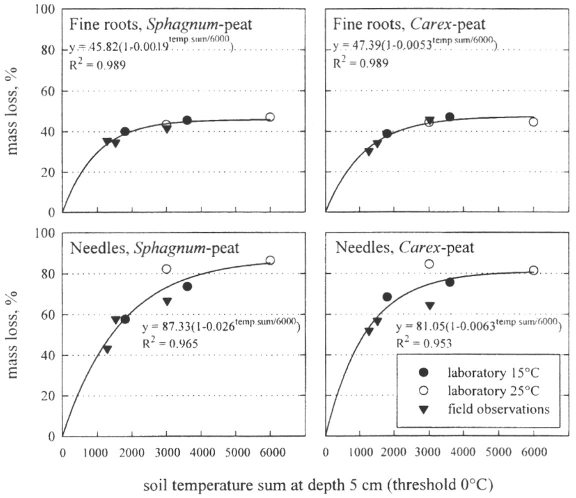

Fig. 5. The relationship between the temperature sum of the soil at depth 5 cm (threshold 0°C) and respective mass losses from needle and fine root litter in *Sphagnum*- and *Carex*-peats observed in the laboratory at constant 15°C and 25°C soil temperatures (Domisch et al., 1998) and in the field. Concerning the field data, mass losses are shown only for the drained peats.

ent peat layers were comparable to the amounts found in the laboratory experiment. Only the moss layer yielded less ^{14}C-activity in the field experiment, possibly for technical reasons. The laboratory experiment was carried out in growth chambers, so that the $^{14}CO_2$ emissions may have lingered for a while before leaving the chamber, thus allowing the moss layer to retain more ^{14}C-activity than under field conditions, where the $^{14}CO_2$ might have been able to escape more easily.

5. Conclusion

The results indicate that in peat soil, environmental factors such as nutrient or drainage status of the peat influence the decomposition of fine root litter less than that of needle litter. They also show that the possible increase in carbon storage in pine mires after forest drainage may be caused at least to some extent by the decomposition of newly deposited tree litter and the retention of carbon lost from the decaying litter by the peat soil.

Possibly, boreal peatlands drained for forestry act as sinks of atmospheric carbon as do pristine peatlands, at least for the first rotation period (Minkkinen and Laine, 1998b). However, the origin of carbon and the mechanism involved seem to be different between pristine and drained peatlands. Carbon accumulation in drained peatlands may thus continue analogously to 'root peat' formation in sedge-dominated vegetation communities.

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RELOCATION OF CARBON FROM DECAYING LITTER IN DRAINED PEAT SOILS

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Summary—Recent findings have indicated that the carbon density and store in peat soil may increase after drainage for forestry, even if soil respiration has clearly increased. This is caused by the increased organic C flow from tree stands into soil and consequent retention in the peat matrix. Relocation of ^{14}C-activity released from the labelled needle and fine root litter during 4- and 8-month incubation experiments showed that, on average, only 60–80% of the activity lost from litter was emitted to the atmosphere. The proportion retained in the moss layer was from 7 to 14%, in the peat soil from 7 to 18% and in the water percolated through the peat from < 1 to 8%. The results thus support the hypothesis that organic C flow may contribute to C storage in drained peat soils. © 1998 Elsevier Science Ltd. All rights reserved

INTRODUCTION

Most of the organic matter accumulated as peat in pristine boreal mires derives from plant material deposited below the mire surface, i.e. *Carex* roots and the lower parts of *Sphagnum* mosses. The decay of organic matter takes place mainly in the surface peat layers (e.g. Clymo, 1965). Besides an insufficient supply of oxygen, the slow decay rate in deeper layers may be partly attributable to the effects of temperature, pH, and mineral nutrients (Dickinson, 1983).

After drainage for forestry and the consequent water level drawdown the thickness of the aerated surface peat layer increases. The wetter the site originally, the more significant is the change in growth conditions caused by drainage. Mire plants adapted to wet conditions decline rapidly, and secondary vegetation succession towards more forest-like communities begins (e.g. Laine *et al.*, 1995). Biomass production is thus largely directed to the tree stand (Reinikainen *et al.*, 1984; Sakovets and Germanova, 1992). This results in increased tree stand biomasses (Laiho and Finér, 1996; Laiho and Laine, 1997) and increased above-ground (Laiho and Laine, 1996) and probably also below-ground litter production (Finér and Laine, 1996b).

Improved aeration increases the populations of aerobic decomposers (e.g. Chmielewski, 1991) and thus enhances the decay of organic matter (e.g. Lieffers, 1988; Bridgham *et al.*, 1991). However, the enhanced activity is located in the superficial layer (0–10 cm) even when water tables remain below 50 cm during most of the growing season (Paarlahti and Vartiovaara, 1958; Karsisto, 1979). Results from cellulose decomposition in field experiments show, however, a positive correlation between mass loss at greater depths and water table level (Karsisto, 1979).

Drainage for agriculture or peat harvesting has been found to change a mire from a sink to a source of C to the atmosphere (e.g. Armentano and Menges, 1986; Nykänen *et al.*, 1995). The consequences of forest drainage are not as obvious (e.g. Vompersky *et al.*, 1992; Martikainen *et al.*, 1995). It can be concluded from Vompersky and Smagina (1984); Cannell *et al.* (1993); Martikainen *et al.* (1995) and Minkkinen and Laine (1996) that the change in the C balance of both the soil and the whole ecosystem largely depends on the relation between the rates of C input via the tree stand and decomposition of previously accumulated peat C.

Recent results indicating increased C accumulation into soil after drainage (Minkkinen and Laine, 1996) are contradictory to previous findings (e.g. Armentano and Menges, 1986; Silvola, 1986). The increased accumulation may be explained by a combination of increased litter accumulation on the mire surface (Laiho and Laine, 1996) and increased organic C flow into soil and retention in the peat matrix, as discussed by Minkkinen *et al.* (1996). However, the potential of the peat matrix to retain

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Table 1. Total initial ^{14}C-activity (n = 80) and its distribution in the organic fractions (n = 6) of the litter material. Mass distribution of the organic fractions is also shown. The values are means ± standard deviations

	Root litter		Needle litter	
Fraction	activity	mass	activity	mass
Total activity (MBq g^{-1})	14.16 ± 5.22		53.04 ± 11.16	
Water soluble (%)	10 ± 0.7	26 ± 2.3	18 ± 0.8	38 ± 1.3
Alcohol soluble (%)	9 ± 1.2	5 ± 0.3	8 ± 0.6	6 ± 0.3
Acid soluble (%)	54 ± 2.0	57 ± 2.6	55 ± 0.9	46 ± 1.5
Acid insoluble (%)	27 ± 1.3	12 ± 0.3	19 ± 0.7	10 ± 0.4

Table 2. Initial element concentrations of the litter material (mg g^{-1} dry mass)

Element	Root litter	Needle litter
C	532.7 ± 4.6	536.3 ± 8.5
H	58.0 ± 0.4	61.8 ± 0.2
N	11.0 ± 0.2	11.8 ± 0.1
P	3.9 ± 0.3	2.8 ± 0.2
K	7.4 ± 0.5	11.5 ± 0.4
Ca	5.1 ± 0.3	2.9 ± 0.03
Mg	1.6 ± 0.1	1.7 ± 0.01
Mn	0.064 ± 0.021	0.26 ± 0.04
B	0.0076 ± 0.0003	0.018 ± 0.001
Fe	0.79 ± 0.08	0.11 ± 0.001
Al	0.22 ± 0.02	0.067 ± 0.01
Cu	0.21 ± 0.01	0.0064 ± 0.001
Zn	0.12 ± 0.01	0.093 ± 0.01

organic C from decomposing litter has not been evaluated and quantified.

^{14}C-litter material has been used in decomposition studies to estimate the C loss by trapping the evolving $^{14}CO_2$ (e.g. Nyhan, 1975; Jones and Darrah, 1994; Nelson *et al.*, 1996). In our study labelled needle and fine root litter was utilized to assess the relocation of carbon, released in the decomposition processes, in the atmosphere–soil–water-system.

Our objectives were (1) to determine the decay rates of needle and fine root litter in a peat environment under controlled conditions, (2) to show the temporal pattern of the $^{14}CO_2$ emission, (3) to assess the fate of the carbon lost from the litter and (4) to study the vertical distribution of the carbon retained in the peat soil. The study was part of the research project Carbon Balance of Peatlands and Climate Change within the Finnish Research Programme on Climate Change.

MATERIAL AND METHODS

The litter material

The litter material used derived from 600 nursery grown Scots pine (*Pinus sylvestris* L.) seedlings labelled with $^{14}CO_2$ in a plexiglass chamber. The ^{14}C was given as a ^{14}C-bicarbonate, which was released to the chamber atmosphere by reaction with hydrochloric acid. The seedlings were kept for 2 h in the chamber placed in full sunlight. An activity of 6.66 MBq was used per 100 seedlings. After labelling, the seedlings were grown for one growing season using a standard irrigation and fertilization regime.

Litter material, i.e. current year needles and fine roots, was harvested and dried at 60°C to constant mass. Fine roots were defined as roots less than 2 mm dia; in this case all lateral roots of the seedlings. Samples with a dry mass of exactly 1 g were placed in $10 \times 10\ cm^2$ polyester litterbags with a mesh size of 1 mm.

The initial ^{14}C-activity of both litter types (Table 1) was measured from 80 random subsamples. The organic composition of both litter types (Table 1) was determined from six samples which were divided into two subsamples. The fractionation of the litter into water, alcohol and acid soluble components and the acid-insoluble component (Klason-lignin) was done by sonicating the milled samples first in water, then in alcohol and last in 72% H_2SO_4, according to Berg and Lundmark (1985) and Johansson (1994).

The mineral nutrient concentrations in the litter (Table 2) and in the peat used as incubation cores (Table 3) were analyzed with an ICP-spectrometer (ARL 3580 OES, Fison Instruments, Valencia, CA) after dry ashing and dissolving in hydrochloric acid. C, H and N concentrations were analyzed with a Leco CHN 600 analyzer (Leco Corp., St. Joseph, MI). All determinations were done with duplicate samples.

The incubation experiment

The study was carried out as a fully factorial experiment containing four factors (litter type, temperature, peat type, incubation time) at two levels. The incubation period started on 25 January, 1995. Half of the cores were incubated for 4 months and the rest for 8 months. The incubation temperatures used were 15°C and 25°C.

Table 3. Concentrations of some mineral elements (mg g^{-1} dry mass), pH($CaCl_2$) and bulk density (D_b, kg m^{-3}) of the peat types used in the experiment

Peat type	Depth	N	P	K	Ca	Mg	Fe	Al	pH	D_b
Sphagnum	0–20	8.1	0.572	0.580	2.64	0.455	0.990	0.592	2.6	69.9
	20–40	8.9	0.338	0.140	1.47	0.343	0.780	0.267	2.7	56.1
	50–75	7.3	0.269	0.109	2.16	0.339	1.169	0.203	2.9	57.9
Carex	0–20	23.8	0.783	0.250	2.42	0.170	3.407	0.726	2.9	96.1
	20–40	24.3	0.536	0.100	2.31	0.257	3.622	0.868	3.2	75.5
	50–75	23.4	0.483	0.051	2.69	0.240	2.099	1.283	3.5	72.5

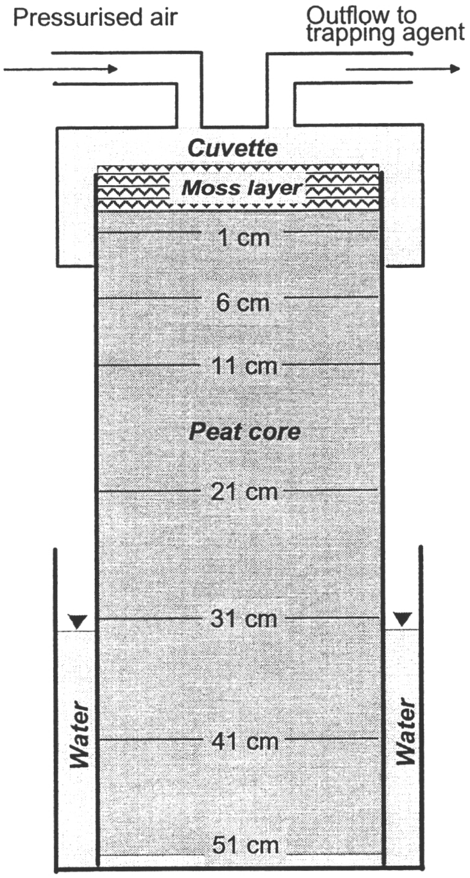

Fig. 1. Schematic presentation of a peat core used in the experiment. The needle litterbags were placed directly under the living moss layer and the fine root litterbags 2–3 cm deeper. The layers for measuring the vertical distribution of ^{14}C at the end of the experiment are also shown

The two peat types used in the experiment were dominated by either *Sphagnum* or *Carex* residues, the first representing ombrotrophic nutrient status and the second minerotrophic level. The peat cores with undisturbed structure, containing also the moss layer (i.e. living mosses and litter), were taken from the Lakkasuo mire complex in Orivesi, central Finland (61°48′N, 24°19′E, 150 m above sea level). The peat cores were directly taken into plastic tubes of 12 cm dia and 60 cm in length and transported to the laboratory.

Four weeks before the start of the experiment the peat cores were placed into the growth chambers (CONVIRON PGW36, PGR15) to adapt to their new environment. The water table was maintained at 40 cm depth in all peat cores. The initial water table was obtained by filling the buckets containing the peat cores up to the desired height with distilled water (Fig. 1). The cores were watered once a week with water which mimicked the amount and chemical composition of the local rain water at the Lakkasuo mire. The water table was kept at a constant level by removing any excess amount in the bucket after percolation and the water was stored for analyses.

At the beginning of the incubation one litterbag was placed horizontally in each peat core. The needles were placed under the 1–2 cm thick living moss layer and the roots were placed 2–3 cm deeper.

The relative humidity of air in growth chambers was kept at 80% during the day (8.00–18.00) and at 90% during the night (18.00–8.00). The lights were switched on from 8.00 to 16.00. The light intensity was kept constant at 650–720 μmol m^{-2} s^{-1} throughout the experiment.

Measurement of the ^{14}C-activity

The measurement of the ^{14}C-activity was done by combustion in a Junitek-oxidiser (Junitek Oy) in which the samples are totally combusted into water and carbon dioxide. The $^{14}CO_2$ was trapped in a Wallac Lumasorb II trapping agent and a Wallac Carboluma liquid scintillation cocktail was added automatically after which the sample was measured for ^{14}C-activity in a Wallac 1411 liquid scintillation counter.

After the experiment, the litterbags were taken from the peat. The remaining litter was carefully removed and dried at 60°C to a constant mass. The mosses were harvested and dried at 60°C to a constant mass. The peat cores were cut into layers 0–1 cm, 1–6 cm, 6–11 cm, 11–21 cm, 21–31 cm, 31–41 cm and 41–51 cm (Fig. 1) and dried at 105°C to a constant mass. Three subsamples (100–400 mg, depending on peat type and layer) were taken from each layer. The ^{14}C-activity of the samples was measured as described above.

After both incubation periods the water in the bucket and the stored "excess" water were combined. The ^{14}C-activity in the water was measured from a subsample (4 ml), into which the scintillation cocktail (Wallac Optiphase "Hisafe") was added. By knowing the total amount of percolated water and the ^{14}C-activity of the subsample, the ^{14}C-activity leached from the peat could be estimated.

The ^{14}C-activity loss to the atmosphere was estimated as the difference between the average initial activity and the total activity found in each peat core after the incubation, i.e. the activity in the litterbag, the moss and peat layers, and the percolation water.

The $^{14}CO_2$-flux from 32 cores (four of each treatment) for the 8 month incubation period was analysed weekly to study the dynamics of the CO_2 emission. A cuvette with a transparent top was placed over the peat cores, and pressurised air was directed through the cuvettes and CO_2 was trapped with Wallac Lumasorb II (Fig. 1).

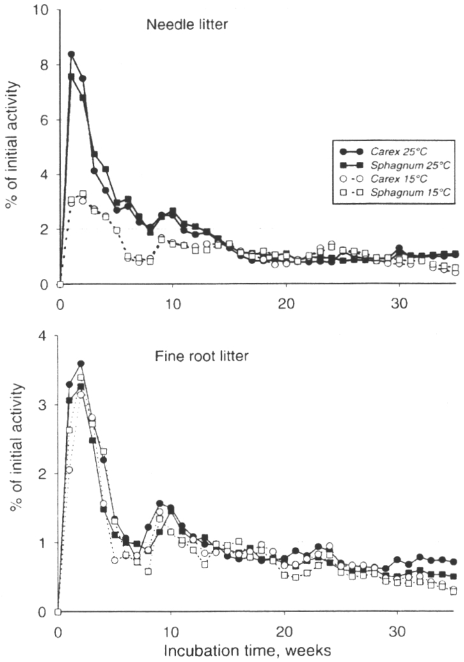

Fig. 2. $^{14}CO_2$-flux from needle and fine root litterbags during 8 months at 15°C and 25°C incubation temperatures. The weekly ^{14}C-fluxes are expressed as percentage of the initial ^{14}C-activity. Note the different scales in the *y*-axes

Calculations and statistical tests

All statistical tests were performed with the SYSTAT statistical package (SYSTAT for Windows, 1992). For all percentage values, an angular transformation was made before statistical testing ($x' = \arcsin \sqrt{x}$). Fully factorial ANOVA was used in testing the factor effects. In the tests of the emissions into the atmosphere sampling time was used as a repeated measure.

RESULTS

$^{14}CO_2$-emission into the atmosphere

The $^{14}CO_2$-flux from the labelled litter into the atmosphere showed a sharp increase during the first few weeks of the incubation but levelled off after 3 to 4 weeks (Fig. 2). The initial increase was highest at the 25°C incubation temperature in the needle litter material (significant interaction between sampling time, litter type and temperature, $F = 2.59$, $P < 0.001$), where about 8% of the initial ^{14}C-activity was trapped during the first week. After this, the emissions were rather similar from all treatments. Table 4 shows the average proportions of the initial activity emitted to the atmosphere and trapped during the 4 and 8 month incubation periods.

Mass and ^{14}C-activity losses from litterbags

The mass losses were significantly higher ($F = 542.4$, $P < 0.001$) from the needles than from the fine roots at both incubation temperatures (Table 5). The needles decomposed faster at 25°C than at the lower temperature ($F = 21.49$, $P < 0.001$). No temperature or peat type effects could be seen for fine root litter. The mass losses of both litter types were significantly higher ($F = 8.40$, $P = 0.005$) after 8 months than after 4 months only at 15°C.

The same significant effects were observed for the activity losses, except that the activity loss continued after 4 months also at the higher temperature ($F = 11.22$, $P = 0.001$). An almost significant effect was found for the peat type ($F = 3.61$, $P = 0.060$).

From 60 to 70% of the initial activity was still found in the fine root litter bags after 8 months' incubation, and from 15 to 60% in the needle litter bags.

Relocation of ^{14}C-activity released from the litter

Most of the ^{14}C-activity lost from the litterbags was released to the atmosphere: approximately 80% from the cores incubated for 4 months, and 55–75% from the cores incubated for 8 months, estimated as the difference between the average initial activity and the activities found from the other components (Fig. 3). The relative proportion was significantly smaller after 8 months' incubation ($F = 6.23$, $P = 0.014$).

The moss layer contained, on average, 7–14% of the ^{14}C-activity lost from the litter and no signifi-

Table 4. ^{14}C-activities emitted to the atmosphere during 4 and 8 months in the different treatments. Activities are percentages of the initial activity in the litter. The values are means ± s.d. of four trapped incubation cores

Litter type	Temperature (°C)	Peat type	^{14}C-activities 4 months	8 months
Fine roots	15	*Carex*	21.0 ± 6.5	31.3 ± 5.9
		Sphagnum	24.7 ± 11.0	34.3 ± 12.2
	25	*Carex*	31.7 ± 13.0	47.9 ± 19.3
		Sphagnum	28.4 ± 14.4	41.5 ± 20.6
Needles	15	*Carex*	28.2 ± 3.6	43.5 ± 3.5
		Sphagnum	24.7 ± 1.2	39.9 ± 1.4
	25	*Carex*	54.7 ± 4.9	73.3 ± 6.1
		Sphagnum	53.4 ± 7.6	71.8 ± 9.2

Table 5. Mass and ^{14}C-activity losses during the incubation periods. Losses are percentages of the initial mass and the average initial ^{14}C-activity, respectively

Litter type	Temperature (°C)	Peat type	Incubation time (months)	Mass loss (%)	Activity loss (%)
Fine roots	15	*Carex*	4	38.7 ± 3.8	30.4 ± 15.4
			8	47.0 ± 3.6	44.0 ± 16.3
		Sphagnum	4	40.0 ± 2.4	33.4 ± 14.7
			8	45.5 ± 1.3	38.2 ± 15.9
	25	*Carex*	4	44.3 ± 7.2	38.6 ± 12.7
			8	44.5 ± 4.0	40.8 ± 9.9
		Sphagnum	4	43.4 ± 4.9	33.4 ± 12.6
			8	47.0 ± 1.3	38.6 ± 19.1
Needles	15	*Carex*	4	68.4 ± 13.1	59.8 ± 17.2
			8	75.5 ± 12.2	72.6 ± 20.6
		Sphagnum	4	57.6 ± 6.5	40.2 ± 11.5
			8	73.6 ± 7.4	63.0 ± 9.4
	25	*Carex*	4	84.4 ± 7.9	76.5 ± 12.7
			8	81.4 ± 7.8	81.1 ± 11.4
		Sphagnum	4	82.2 ± 14.0	72.9 ± 18.8
			8	86.3 ± 11.0	84.9 ± 12.7

cant factor ($P > 0.05$) effects were found (Fig. 3). The peat retained 7–12% of the ^{14}C-activity lost after 4 months and 8–18% after 8 months ($F = 6.23$, $P = 0.014$ for the incubation time effect) but no other significant factor effects were found.

The water percolated through the fine root incubation cores contained, on average, 1–2% of the lost ^{14}C-activity after 4 months and 5–8% after 8 months. From the needle litter cores the respective values were < 1% and ca. 1%. The incubation time effect was statistically significant ($F = 54.90$, $P < 0.001$). Significantly highest amounts were found in the water from *Sphagnum*-peat cores ($F = 7.95$, $P = 0.006$ for the peat type effect) containing fine root litter ($F = 44.80$, $P < 0.001$ for the litter type effect). The significant interactions between litter type and incubation time ($F = 20.62$, $P < 0.001$) as well as peat type, litter type and incubation time ($F = 3.95$, $P = 0.049$) indicate that the relative proportion of ^{14}C-activity found in the water was highest after the longer incubation period from fine root litter in *Sphagnum*-peat.

Vertical distribution of ^{14}C-activity found from the peat

Much of the ^{14}C-activity released into the peat soil from the fine root litter bags was found in the deeper layers, whereas in the needle litter cores most of the activity remained even after 8 months in the uppermost 1 cm peat layer, i.e. immediately below the litter bag (Fig. 4). There was some tendency towards increasing proportions in the deepest layer during the longer incubation period, especially in the *Sphagnum*-peat cores (Fig. 4).

DISCUSSION

Reliability of the results

The fact that it was not possible to measure the initial ^{14}C-activity from each litterbag used in the experiment, gives the results some uncertainty and a high variability. However, the reliability of the results could be ascertained from the submaterial (32 incubation cores) from which the ^{14}C-flux into the atmosphere was trapped and measured, and thus the actual initial activity in the litterbag could be calculated. The comparison of the measured ac-

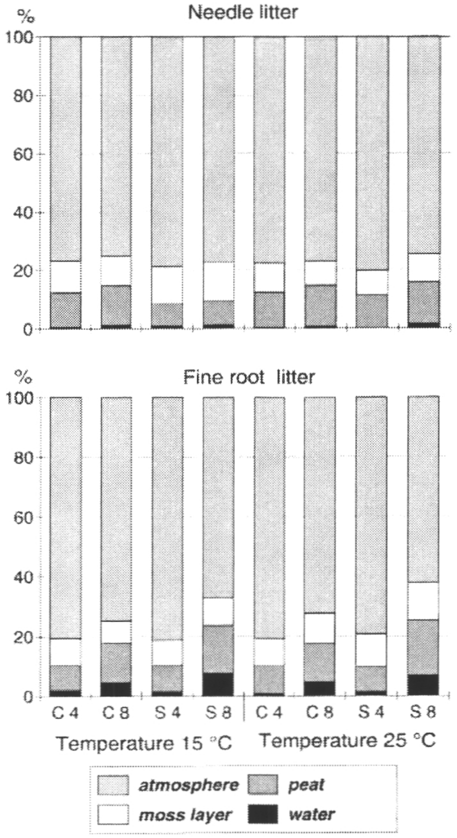

Fig. 3. The relative distribution of ^{14}C-activity lost from needle and fine root litterbags after 4 and 8 months at 15°C and 25°C incubation temperatures

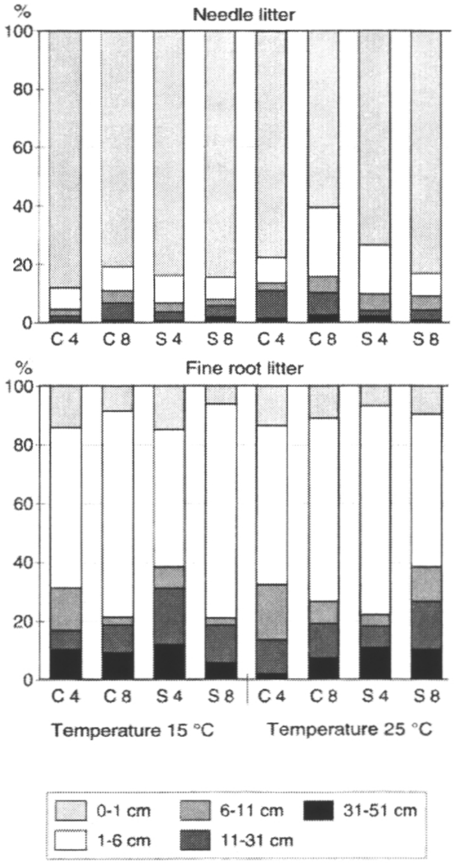

Fig. 4. Vertical distribution of ^{14}C-activity lost from needle and fine root litterbags, found in the peat soil, expressed as a percentage of the lost activity

tivity losses based on the actual initial ^{14}C-activities showed a significant correlation (r = 0.936) with the activity loss calculated from the average initial activity.

The litter material used in this study differed from natural litter since it originated from 1-y-old seedlings and the needles and fine roots were harvested alive. On average, the water-soluble mass fraction in our needle litter material was relatively higher and the acid-insoluble (lignin) fraction smaller than in Scots pine needle litter reported by Berg and Staaf (1980a,b) and Johansson (1995). However, the ^{14}C-activity distribution in the organic fractions (Table 1) was nearer to their mass distribution.

In our fine root litter material the distribution of mass in the organic fractions was similar to that presented by Berg (1984) and Berg and Lundmark (1985), but there was relatively less ^{14}C-activity, than mass, in the water-soluble fraction and more activity than mass in the alcohol-soluble fraction. The N, P and K concentrations in both our needle and fine root litter materials were clearly larger than the values reported by Berg and Staaf (1980a,b); Berg (1984) and Johansson (1995).

As the rate of decomposition at a given site is largely dependent on the substrate quality (e.g. Berg and Staaf, 1980b), it is obvious that the decomposition rate in our material may be faster than it would have been with natural litter. The needle litter results by Berg and Lundmark (1985) confirm this assumption but similar fine root litter has decomposed in field conditions at about the same rate (Finér and Laine, 1996a) which indicates that the experimental conditions were relevant.

$^{14}CO_2$-flux from the litterbags

The pattern of $^{14}CO_2$-emissions into the atmosphere found in our study probably correlated with the oxidation of different organic compounds in the litter. The peak of the CO_2-flux at the beginning of the incubation may have resulted from the oxidation of water and alcohol soluble compounds (Berg, 1984). Later on, the C-emissions are mainly due to the oxidation of cellulose and hemicellulose (i.e. H_2SO_4-solubles) (Berg, 1984). The higher initial emissions from needle litter in our data (Fig. 2) may be attributed to a larger water soluble fraction in this litter type (Table 1).

Mass and activity losses after 4 and 8 months

The mass and activity losses from the needle litter bags correlated very well with each other, whereas for the root litter no significant correlation was found which may be caused by the higher variability in the distribution of the ^{14}C-activity in the fine root litter and the very narrow range of mass loss variation in this litter type (35–50%). This may influence the interpretation of the ^{14}C-activity loss results of the fine root litter.

As there was no significant difference in the mass loss between the 4 and 8 month incubations (Table 4), the results indicate a fast decomposition process at the beginning and a slowing down in the later stages found also in earlier studies (e.g. Berg, 1984, Ruark, 1993; Berg *et al.*, 1995).

The litter type, needle vs fine root, was the most important factor determining the rate of decomposition. The higher mass losses from the needle litter may be due to the differences in the organic and inorganic composition of these litter materials. The root litter material contained less water-soluble and more acid-insoluble compounds, and had higher concentrations of heavy metals and Al than the needle material (Tables 1 and 2). High Al concentrations have been suggested to slow down the decomposition of fine roots (Vogt *et al.*, 1987).

Relocation of ^{14}C-activity after the experiment

Part of the activity retained in the moss layer, may be attributed to photosynthesis of liverworts and algae, especially in cores in the higher temperature treatment where mosses had clearly suffered during the incubation. However, Tolonen *et al.* (1992) have estimated a similar fraction (ca. 20%) of soil CO_2 taken up by *Sphagnum*, when using high resolution ^{14}C dating in locating the ^{14}C peak from nuclear bomb tests in the surface peat profile.

The observed higher retention of ^{14}C-activity in the uppermost layers of the *Carex* peat profiles may be connected to the higher Fe and Al concentrations in this peat type (Table 2). Correspondingly, in the *Sphagnum* peat profiles clearly more activity was found in the deepest peat layers with the highest Fe concentrations. Formation of colloidal metal-organic complexes (e.g. De Vries and Breeuwsma, 1987) may be an important mechanism for precipitation of organic anions released in decomposition processes.

Peat soil matrix may facilitate the retention of formed colloidal complexes as it is characterized by a high proportion of small pores (e.g. Päivänen, 1973) and a very heterogeneous pore structure derived from plant residues in various stages of decomposition. According to Loxham (1980), six different pore categories can be identified: large, multiple and simply connected open pores, dead-end pores, completely isolated pores and pores in cell structures. The structure of the peat matrix thus elicits a retention environment very different to that of the granular porous structure of mineral soils.

Concluding remarks

Despite the high variability in the material, our results support the conclusions in Minkkinen and Laine (1996) and Minkkinen *et al.* (1996), who found increased peat bulk densities and carbon stores on peatlands drained 50–60 y earlier, in comparison to pristine peatlands. In an average drained peatland forest stand (nutrient content as in our minerotrophic peat, Scots pine stand, stem volume ca. $100\ m^3\ ha^{-1}$) in southern Finland the above-ground litter production has been reported as ca. $150\ g\ C\ m^{-2}\ a^{-1}$ (Laiho and Laine, 1996) and below-ground litter production approximately $100\ g\ C\ m^{-2}\ a^{-1}$ (Finér and Laine, 1996b). If fine root litter mass losses on these sites were 32% (Finér and Laine, 1996a), and the respective mass losses from needle litter 45% (unpublished data from the Lakkasuo mire) during the first year of decomposition, nearly $200\ g\ C\ m^{-2}\ a^{-1}$ would remain in the litter and the amounts retained deeper in the soil, in conditions less favourable for further oxidation, would be 10 to $15\ g\ C\ m^{-2}\ a^{-1}$ according to the distribution of the activity loss from litter in this study.

Earlier decomposition studies presupposed, that the loss from the litterbags is also entirely a loss of carbon to the atmosphere. Our findings of this study show, however, that those results should reevaluated. Not all the carbon lost from the litterbags was lost to the atmosphere, but a small but significant amount was found in the peat cores after 4 and 8 months incubation; the relative proportion retained in the soil being even higher after the longer incubation.

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