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Heterotrophic soil respiration in drained peatlands: Abiotic drivers, and changes after clearfelling and afforestation

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Academic dissertation

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Climate change is likely to affect the large carbon (C) stocks of northern peatlands. These C reservoirs may further be affected by human-induced forestry activities and changes in land use. Possible responses of peatland C storages to these changes have significant uncertainties mainly because of the difficulties in predicting peat decomposition rates in changing conditions.

This study aims at revealing the effects of abiotic drivers, especially soil temperature and water table level (WL), on peat decomposition rate indicated by heterotrophic peat soil respiration (R_{PEAT}) in drained forested peatlands. Furthermore it aims to describe the changes in R_{PEAT} following clearfelling in forestry-drained peatlands and afforestation of former agricultural organic soil croplands. For this, R_{PEAT} was estimated using chambers to measure CO_2 efflux from trenched litter-free plots, at nine afforested organic soil cropland sites and one forestry-drained site with clearfelling treatment.

This study revealed that within the studied sites soil temperature was the main driver of R_{PEAT}. It was also apparent that the old peat storage in these sites was rather resistant to the short-term changes in WL conditions; i.e. fluctuations of WL caused only minor changes in R_{PEAT}. The study also demonstrated that in low water level conditions there were mechanisms that could hinder R_{PEAT}. Excessive WL drawdown (>61cm) was observed to reduce R_{PEAT} and furthermore, in low water level conditions the temperature sensitivity of R_{PEAT} was reduced. These findings suggest that climate change and the associated increase in temperature would have the potential to substantially increase soil C release from drained peatlands. This C release may, however, be constrained, if warming is accompanied by changes in evapotranspiration, precipitation regimes, or the frequency of extreme events (e.g. droughts) that would severely affect WL and surface soil moisture conditions.

Changes in environmental conditions following clearfelling caused only small absolute changes in R_{PEAT}. Following clearfelling, a decrease in evapotranspiration raises water table level which in turn decreases the volume of aerated peat layers. Furthermore the soil surface is exposed to direct solar radiation which causes excessive dryness in surface soil. These factors are capable of compensating and overruling the effect of increased soil temperatures on R_{PEAT} following clearfelling. Below the logging residue piles, however, considerable increase in R_{PEAT} was observed. This indicates that human induced forestry activities could potentially cause significant C release from the oldest and largest C stocks in these ecosystems This C release may, however, be avoided if logging residue is removed from the site. Further investigations on longevity of the effect of logging residues on CO_2 emissions as well as on the sources of CO_2 under logging residues are required to confirm these findings.

The estimated R_{PEAT} from the afforested organic soil croplands varied widely between the sites (from 750 to 2000 g CO_2 m^{-2} a^{-1}). It appeared that afforestation has the potential to reduce the extremely high soil CO_2 effluxes of actively cultivated peat soils. Despite this, agricultural history has obvious effects on peat properties and observed R_{PEAT}, with the result that these soils remain sources of CO_2.

Keywords: peat decomposition, climate change, land use change, temperature sensitivity, water table level, logging residue retention

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Asikkala, January 2012, Päivi Mäkiranta

LIST OF ORIGINAL ARTICLES

The thesis is based on the following articles, which are referred to by their Roman numerals I-V. Articles are reproduced with the kind permission from the publishers.

I Mäkiranta, P., Minkkinen, K., Hytönen, J. & Laine, J. 2008. Factors causing temporal and spatial variation in heterotrophic and rhizospheric components of soil respiration in afforested organic soil croplands in Finland. Soil Biology and Biochemistry 40: 1592–1600. http://dx.doi.org/10.1016/j.soilbio.2008.01.009

II Mäkiranta, P., Laiho, R., Fritze, H., Hytönen, J., Laine, J. & Minkkinen, K. 2009. Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity. Soil Biology and Biochemistry 41: 695–703. http://dx.doi.org/10.1016/j.soilbio.2009.01.004

III Mäkiranta, P., Riutta, T., Penttilä, T. & Minkkinen, K. 2010. Dynamics of net ecosystem CO_2 exchange and heterotrophic soil respiration following clearfelling in a drained peatland forest. Agricultural and Forest Meteorology 150: 1585–1596. http://dx.doi.org/10.1016/j.agrformet.2010.08.010

IV Mäkiranta, P., Laiho, R., Penttilä, T. & Minkkinen, K. 2012. The impact of logging residues on soil GHG fluxes on a drained peatland forest. Soil Biology and Biochemistry 48: 1–9. http://dx.doi.org/10.1016/j.soilbio.2012.01.005

V Mäkiranta, P., Hytönen, J., Aro, L., Maljanen, M., Pihlatie, M., Potila, H., Shurpali, N.J., Laine, J., Lohila, A., Martikainen, P.J. & Minkkinen, K. 2007. Soil greenhouse gas emissions from afforested organic soil croplands and cutaway peatlands. Boreal Environment Research 12: 159–175. http://www.borenv.net/BER/pdfs/ber12/ber12-159.pdf

Author's contribution

I P. Mäkiranta was the main author, participated in planning of the research and was responsible for the measurements and data analysis.

II P. Mäkiranta was the main author, participated in planning of the research and was responsible for the measurements and data analyses, except for the laboratory work related to the determination of microbial community structure (PLFA) and furthermore for the analysis of PLFA data.

III P. Mäkiranta was the main author, participated in planning of the research and was responsible for the measurements and data analysis except for analyzing the NEE and R_{ECO} data.

IV P. Mäkiranta was the main author, participated in planning of the research and was responsible for the measurements and data analyses, except for the N_2O and CH_4 measurements, their data analyses and reporting.

V P. Mäkiranta was the main author, participated in planning of the research and measurements and was responsible for the data analysis, except for simulations of 30 year weather derived variation in R_{PEAT} and for the N_2O and CH_4 measurements, their data analyses and reporting.

DEFINITIONS

Peat is soil material consisting of partially decomposed organic matter. Peat formation occurs in functionally undisturbed mire ecosystems in which high water table level and associated anoxia causes incomplete decomposition processes.

Afforestation is practise in which forest or stand of trees is introduced to an area where there was no forest previously. In this thesis afforestation refers to establishment of a tree stand to former organic soil croplands.

Forestry-drained peatland is a peatland drained for forestry purposes without agricultural history.

Afforested organic soil croplands are peatlands originally drained for agriculture where a tree stand has been introduced after cessation of agricultural activity.

Drained forested peatlands are forests in drained lands on which the soil is formed of peat. Within this thesis this definition includes forestry-drained peatlands and also afforested organic soil croplands.

Clearfelling is a silvicultural practice which involves cutting all trees, removing commercial stem wood and, usually, leaving logging residues (foliage, twigs, branches, stumps, and root systems) on the site.

Water table level (WL) is the measured distance of ground (perched) water table from the soil surface which reflects the 'surface' of peat layers that are saturated. In this thesis WL was measured from the perforated water table tubes and in these measurements peat surface was considered as 0 cm from which positive values indicate decline of WL to deeper peat layers. In discussions high WL refers to conditions where WL is close to the soil surface and low WL to conditions where WL is in deep peat layers.

Soil respiration refers to respiration of soil organisms which can be measured as the emission of carbon dioxide (CO_2) from the soil surface to the atmosphere. Sources of CO_2 from soil include root respiration of plants, the processes occurring in the rhizosphere and heterotrophic respiration of microbes and fauna.

Heterotrophic peat soil respiration (**R_{PEAT}**) refers to the respiration of heterotrophic microbes that consume peat. In this study R_{PEAT} is measured in field conditions from the plots which contained organic matter that was at least 1 year old or older and where new litter inputs were excluded.

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1. INTRODUCTION

1.1. Background

Northern peatlands serve as long term carbon (C) stores. The high water table level and associated anoxia favours accumulation of partially decomposed organic matter (OM) as peat. This accumulated soil C accounts for a considerable share of the global terrestrial C pool with an estimated C reservoir of 250–455 Pg (10^{15} g) (Gorham 1991, Turunen et al. 2002).

Rising concentrations of greenhouse gases (GHG) in the atmosphere are causing the Earth's climate to change (IPCC 2007). This climate change is expected to have the most pronounced effects at high latitudes (IPCC 2007) where the majority of northern peatlands are located (Gorham, 1991). Indeed, longer and drier growing seasons have in fact already been recorded in these areas (Keyser et al. 2000, Goetz et al. 2005). Responses of peatland C pools to climate change have significant uncertainties partly because of the difficulties in predicting the decomposition rate of peat in these forthcoming conditions (Laiho et al. 2006). Detailed information on the dependence of peat decomposition on environmental factors, especially on temperature and water level and their interaction, could help to overcome these difficulties.

With regard to drained forested peatlands, not only the forthcoming changes in climate but also human-induced forestry activities and changes in land use may threaten their large C stocks. The primary effects of drainage for forestry (Glenn et al. 1993, Silvola et al. 1996a, 1996b, Minkkinen and Laine 1998, Minkkinen et al. 2002, Hargreaves et al. 2003, Laiho et al. 2004, von Arnold et al. 2005a, 2005b, Byrne and Farrell 2005, Minkkinen et al. 2007, Lohila et al. 2010, 2011) and for agriculture (Nykänen et al. 1995, Langeveld et al. 1997, Maljanen et al. 2001a, 2004, Lohila et al. 2004) on ecosystem and the soil C balance in peatlands have drawn great interest during the last decades. However, only scattered information on the effects of silvicultural practices (Zerva and Mencuccini 2005) and afforestation of former agricultural areas (Maljanen et al. 2001b, Lohila et al. 2007) on ecosystem and soil C balance in peat soils are available.

In Finland approximately one third of the land area consists of peatlands (8.9 milj. ha) and half of this original area has been altered by land use; Peatlands have been drained, for agriculture, but especially for forestry (Keltikangas et al. 1986, Virtanen et al. 2003, Hökkä et al. 2002). The forestry-drained peatlands are reaching maturity and forest activities are carried out in these areas with increasing rate (Hökkä et al. 2002). Removal of trees changes the environmental conditions and litter input rates (Jandl et al. 2007), which could alter peat decomposition rates and potentially cause a substantial C release to the atmosphere. Better understanding of the effects of management practices on peat decomposition rates could help to protect these C reservoirs and ensure that the most sustainable forestry activities would be selected in the future.

Reclaiming peatlands for agricultural use have caused these areas to lose considerable amounts of C from their peat C storage (Armentano and Menges 1986, Nykänen et al. 1995, Langeveld et al. 1997, Maljanen et al. 2001a, 2004, 2009, Lohila et al. 2003, 2004). Further land use change from agricultural lands into forests through afforestation has been recognised as a useful means to reduce soil degradation and increase sequestration of C to the ecosystem (Watson et al. 2000). The most evident effect of afforestation is the sequestration of atmospheric CO_2-C into the growing tree biomass. The changes in soil C stocks are, however, more difficult to predict, which causes uncertainties when the effectiveness of afforestation is evaluated (Paul et al. 2002, Guo and Giffords 2002). This is especially the case in organic soil croplands, which are rapidly losing soil C; after afforestation the fate of old peat layers may well determine whether these ecosystems act as a sink or a source of C to the atmosphere.

This study focuses on determining the decomposition rate of the peat indicated as heterotrophic peat soil respiration (R_{PEAT}) in drained forested peatlands, its driving factors and changes in R_{PEAT} following clearfelling in forestry-drained areas and following afforestation of organic soil croplands. This work started under the Finnish Forest Research Institutes research programme “Greenhouse impact of the use of peat and peatlands in Finland” which aimed among other things to cover the reporting of the Land use, land-use change and forestry sector of organic (peat) soils, for the national GHG inventory to the Secretariat of the United Nations Framework Convention on Climate Change. The results of this study contributed to the present inventory methods and they were utilized in determining the dynamic GHG emission factors for drained forested peatlands (Alm et al. 2007).

1.2. Abiotic drivers of peat decomposition in drained forested peatlands

Pristine peatlands are characterised by high water table level (WL). Within these ecosystems WL is considered the main factor that controls the peat decomposition. Water table level directly regulates the volume of the oxic peat layer (Lähde 1969, Silins and Rothwell 1999), where decomposition can occur in aerobic conditions. In water saturated soil layers the O_2 diffusion rate is much slower (10^4 times slower) compared to that in air (Wild 1981). Within these conditions activity of respiring microbes is reduced as diminished oxygen availability lowers their respiration rate. In the water saturated layers with anoxic conditions decomposition is slow as anaerobic decomposition proceeds much more slowly than aerobic (Bergman et al. 1999, Šantrůčková et al. 2004).

After drainage WL drawdown and the associated increase in the volume of the oxic peat layer has been considered to increase the decomposition rate of the accumulated peat layer (Armentano and Menges 1986, Silvola 1986, Silvola et al. 1996a, Alm et al. 1999, Moore 2002). This increase in decomposition rate of peat related to WL drawdown has been clearly demonstrated in laboratory studies which show that CO_2 emission from peat samples, an indicator of microbial decomposition, rises with increased WL (Moore and Dalva 1993, 1997, Blodau et al. 2004). Observations in field conditions, however, show considerable variability in the relationship between WL and measured soil CO_2 emissions (Silvola et al. 1996a, Lafleur et al. 2005). Studies have further shown that lowering the WL within sites increases CO_2 emissions only to a certain depth (Silvola et al. 1996a, Chimner and Cooper 2003, Flanagan and Syed 2011), and that WL may occasionally sink to a depth at which drying of the peat surface may start to limit decomposition rates (Lieffers 1988, Laiho et al. 2004).

Soil drought reduces the thickness of soil water films, thus inhibiting diffusion of extracellular enzymes and soluble organic C substrates which causes reduction in substrate availability at reaction microsites (Davidson and Janssens 2006). Drought also limits the amount of moisture available to decomposer organisms for use as a medium for tissue growth and impedes the activity of aquatic organisms. Thus soil moisture conditions along with oxygen availability can regulate microbial growth rates (Barros et al. 1995, Alexandre et al. 1999) and rates of organic matter (OM) decomposition (Howard and Howard 1993, Reichstein et al. 2005). Only a few studies have demonstrated that drought would affect OM decomposition rates in peatlands. Within these studies the effect of drought has been limited to the fresh deposition of OM as litter on the soil surface (Lieffers 1988, Laiho et al. 2004). Whether such conditions could occur in well drained sites, where drought would affect decomposition of the accumulated peat layer is unknown.

In conditions where oxygen availability or drought is not limiting decomposition, microbial decomposition of OM is, like all other biochemical reactions, strongly related to temperature. This positive relationship between soil temperature and CO_2 efflux originating from soil is well established in mineral soils (Singht and Gupta 1977, Raich and Schlesinger 1992, Lloyd and Taylor 1994, Knorr et al. 2005, Davidson and Janssens 2006). Also in peatlands the importance of temperature in explaining temporal variation in heterotrophic peat soil respiration (Minkkinen et al. 2007, Ojanen et al. 2010) and soil and ecosystem respiration (Bubier et al. 1998, Silvola et al. 1996a, Updegraff et al. 2001, Lafleur et al. 2005) has been demonstrated by several authors.

The exponential response of OM decomposition to temperature has raised concern that the expected climate change and associated temperature increase could severely affect soil C storages. This would be especially harmful if a warmer climate would not cause an equal increase in net primary production (Kohlmaier et al. 1990), which would result a positive feedback to climate change.

These predictions of the effects of a changing climate on soil C stocks mainly rely on current terrestrial carbon models, such as Roth-C, CENTURY and ECOSSE. These simulation models generally assume that temperature sensitivity of respiration is constant, regardless of the characteristics of the ecosystem or soil in question. However, studies in field and laboratory conditions have demonstrated great variability in the temperature sensitivity of soil respiration between different ecosystems (Boone et al. 1998, Fierer et al. 2006) and soil characteristics (Moore and Dalva 1993, Yavitt et al. 1997, Davidson and Janssens 2006, Hardie et al. 2011). The fixed temperature sensitivity of OM decomposition in the models could thus cause a major source of uncertainty in the predictions of net soil carbon storage in changing climate, particularly since these simulations have been shown to be rather sensitive to even small changes in temperature sensitivity of OM (Jones et al. 2003, Lenton and Huntingford 2003).

Even though the temperature sensitivity of decomposition has been fixed in current simulation models, there are several known factors that can cause variation in temperature sensitivity of decomposition in field conditions. In peatlands these factors may be related to WL conditions (Davidson and Janssens 2006), suggesting that WL would not have only a direct effect on decomposition rates, but that it would also have indirect effects by altering the observed temperature sensitivity of peat decomposition.

This indirect effect of WL on decomposition rates could be caused by WL driven variation in microbial population structure (Jaatinen et al. 2007, 2008). Fluctuations in microbial population structure can affect enzyme concentration in reaction micro sites, which can then affect the temperature sensitivity of decomposition (Davidson and Janssens 2006).

Simultaneous changes in temperature and WL conditions may further cause variation in the observed temperature sensitivity of decomposition. It has been suggested that in peat soils an increase in peat decomposition rates during the summer season is not only caused by an increase in temperature but also by the simultaneous drop in WL (Davidson and Janssens 2006). Thus, the exceptionally high temperature sensitivities of decomposition observed in peat soils would not be solely caused by higher sensitivity of decomposition processes to temperature in these ecosystems, but by the phenomena where simultaneous increase in substrate availability for decomposition process occurs simultaneously with temperature increase (Davidson and Janssens 2006).

The effects of T and WL and their interactions on peat decomposition rates have been studied with laboratory experiments in controlled conditions (Moore and Dalva 1993, Updegraff et al. 2001, Hardie et al. 2011). The applicability of these laboratory results to field conditions is, however, not without debate as sampling may disturb the soil structure and its functions. Furthremore in these measurements usually only the effects of momentary interactions between temperature and WL are created and observed. Thus, transfer of results to the ecosystem level seems dubious (Reichstein et al., 2000). Measurements in field conditions are rare mainly due to the difficulties in separating CO_2 evolved from peat decomposition from total soil CO_2 efflux. These measurements would, however, cause smaller disturbance to the soil structure and functions and are easier to carry out at seasonal and annual scale.

In field conditions soil respiration can be measured using chambers that measure soil CO_2 evolution to the atmosphere. The sources of this CO_2 efflux from the soil surface i.e. total soil respiration (R_{TOT}), include heterotrophic respiration of microbes that consume peat (R_{PEAT}), but also the heterotrophic respiration from the decomposition of newly fallen above ground litter (R_{LITTER}) and root derived respiration including the autotrophic respiration of plant roots and respiration from the processes occurring in the rhizosphere (R_{ROOT}). The relative contribution of these components to R_{TOT} varies between ecosystems (Hanson et al. 2000). These components are also controlled by a range of different biotic and abiotic factors such as temperature, WL, vegetation structure and photosynthetic activity as well as from the input rates of litter and root-derived photosynthetic products (root exudates) to the soil (Howard and Howard 1993, Lloyd and Taylor 1994, Silvola et al. 1996a, Davidson et al. 1998, Buchmann 2000, Kuzyakov et al. 2000, Högberg et al. 2001) to which they may respond differently (Boone et al. 1998). Thus, it is difficult to estimate the decomposition rate of peat and its dependence on environmental factors by using measurements of R_{TOT}.

Several techniques have been used for partitioning these respiration components in field conditions (Subke et al. 2006). One of the most commonly used has been trenching in which root growth and respiration is excluded from the measurement point by inserting a physical barrier into the soil that cuts the roots and prevents their regrowth. The soil respiration measured from such a plot is considered to originate from heterotrophic respiration (Subke et al. 2006). In addition to trenching, other methods include component integration (Sapronow and Kuzyakov 2007), girdling (Högberg et al. 2001), root exclusion (Lalonde and Prescott 2007), clipping (Fu and Cheng 2004) and isotopic methods (Ostle et al. 2000). The measurement of soil processes and their responses to environmental drivers are highly challenging (Subke and Bahn, 2010) and all these techniques have their own caveats which most studies acknowledge (Subke et al. 2006). When interpreted with caution, measurements of bare R_{PEAT} may, however, reveal new insights into soil processes in peat soils and provide information on the responses of peat decomposition to environmental factors in field conditions (Davidson and Janssens 2006).

1.3. Impacts of human-induced land use changes on peat decomposition rate

Drained peatlands have become a large land use category in many northern countries (Paavilainen and Päivänen 1995, Maljanen et al. 2009), where drainage of peat soils has been commonly used to stimulate the productivity of the peatland forests but also to increase the area suitable for agriculture (Maljanen et al. 2009). When pristine peatlands are drained, WL drawdown and the associated increase in the volume of aerated peat layers stimulate the decomposition of those peat layers. In forestry-drained peatlands peat compaction and drop in temperature and pH may reduce the initial increase in peat decomposition rates caused by WL drawdown (Minkkinen et al. 1999, Toberman et al. 2010) and changes in litter input rate and quality may further compensate the increased peat decomposition rates (Toberman et al. 2010, Straková et al. 2011).

In areas drained for agricultural use the drainage is accompanied by continuous cultivation practices such as ploughing and harrowing, fertilization, liming and addition of mineral soil, which change the physical, chemical and biological properties of the old peat (Wall and Hytönen 1996, Hytönen and Wall 1997) and further increase the decomposition rates. As a result, converting natural peatlands to agricultural use turns the peatland from a CO_2 sink into a large source (Nykänen et al. 1995, Maljanen et al. 2001a, 2004, Lohila et al. 2004); whereas the fate of forestry-drained sites is less clear and after drainage for forestry they may become C sources or remain C sinks depending on site type and climate conditions (Minkkinen et al 2002).

During the last decades several studies have addressed the effects of forestry drainage on the ecosystem C balance as well as soil C stocks and dynamics of boreal peatlands (Glenn et al. 1993, Silvola et al. 1996a, 1996b, Minkkinen and Laine 1998, Minkkinen et al. 2002, Hargreaves et al. 2003, Laiho et al. 2004, von Arnold et al. 2005a, 2005b, Byrne and Farrell 2005, Minkkinen et al. 2007, Lohila et al. 2010, 2011). These studies have demonstrated that when drained for forestry, a growing tree stand with its CO_2 sequestration and litter input plays an important role in compensating for increased OM decomposition rates following drainage. These studies mainly consider the primary effect of drainage on the peatland C balance, whereas effects of forest management practises on the site C balance have been more or less ignored.

Drained forested peatlands form a regionally significant timber resource in some countries (Paavilainen and Päivänen 1995). For example in Finland, forest management practices are carried out in these areas with growing intensity as drained forested peatlands are reaching maturity (Hökkä et al. 2002). Removal of a tree stand alters the site's microclimate, vegetation structure, litter input rates, the amount of photosynthesising and respiring biomass and consequently the carbon balance of the site (Johnson and Curtis 2001, Kowalski et al. 2004, Jandl et al. 2007). In drained peatland forests removal of trees most probably causes these sites to turn into a source of C to the atmosphere as tree growth no longer compensates for the decomposition of peat. This C source may further be strengthened if peat decomposition rates increase following clearfelling.

After clearfelling soil temperatures may rise and face higher diurnal fluctuations, as the removal of the tree canopy increases the amount of direct solar radiation to the soil surface (Edwards and Ross-Todd 1983, Londo et al. 1999). Increased soil temperature as such should accelerate decomposition of peat if other factors remain unchanged. In drained peatland forests, however, the felling of trees and thus the elimination of canopy evapotranspiration results in rising water table level (Heikurainen and Päivänen 1970, Marcotte et al. 2008). The associated decrease of the volume of the aerated peat layer (Lähde 1969, Silins and Rothwell 1999) should reduce the decomposition of peat. A decrease in soil respiration following clearfelling was shown by Zerva and Mencuccini (2005), but they measured R_{TOT} only. To confirm whether rising water level overcomes the effect of rising soil temperatures on peat decomposition rates following clearfelling, heterotrophic peat soil respiration should be measured alone, without the effect of root respiration.

Furthermore, following clearfelling the addition of fresh OM to the soil in the form of logging residue (LR) may alter soil temperature and moisture conditions (Roberts et al. 2005) and thus microbial respiration rates of the under laying soil layers (Edwards and Ross-Todd 1983). Logging residue may also provide additional nutrients and energy sources to soil microbes, which could increase their ability to decompose peat under the logging residue pile (Fontaine et al. 2004, 2007). Thus, retention of LR could strengthen C release from the old peat layers.

Whereas human-induced forestry activities may endanger the C reservoirs in forestry-drained peatlands, introducing trees to organic soil croplands is generally recognised as a potentially useful means to reduce high CO_2 emissions from these areas (Watson et al. 2000). Afforestation implies that the annual cycle of cultivating and harvesting agricultural crops is replaced by a much longer forest tree rotation with much larger biomass. After afforestation, repeated soil amelioration measures such as tillage, fertilization and liming cease. These gradual changes in the soil structure and biology may cause soil properties to become less favorable for the microbes and thereby lead to a slower decomposition rate of the organic matter.

Studies of soil CO_2 emission following afforestation in organic soil croplands have been scarce (Maljanen et al. 2001b) and they have included R_{TOT} from which R_{PEAT} has contributed an unknown fraction (Subke et al. 2006). Understanding peat decomposition rates following afforestation could, however, reveal new insights into soil carbon stocks and their changes after afforestation.

1.4. Aims of the study

The general aim of the study was to investigate how temperature and WL, and some silvicultural treatments, i.e. clearfelling in forestry-drained areas and afforestation of organic soil croplands, affect the heterotrophic peat soil respiration (R_{PEAT}) in drained forested peatlands.

In more specific terms:

1) To define the most important environmental drivers that affect R_{PEAT} in drained forested peatlands and to discuss the mechanisms behind the dependence of R_{PEAT} on T and WL and their interactions in field conditions (I, II).

2) To define how initial changes following clearfelling affect R_{PEAT} in forestry-drained peatlands (III, IV).

3) To produce estimates of the annual R_{PEAT} from typical afforested organic soil croplands in Finland (V). To reveal the factors causing variation in these annual estimates (I) and to determine the proportion of R_{PEAT} from total soil respiration (I).

2. MATERIALS AND METHODS

The heterotrophic peat soil respiration (R_{PEAT}) in drained forested peatlands was studied by using closed chambers and trenching methods. For the measurements, nine afforested organic soil cropland sites and one forestry-drained peatland, located in central Finland, were selected (Fig. 1). Data from these sites were used to study the dependence of R_{PEAT} on environmental factors such as soil temperature, water table depth, peat characteristics and microbial population structure (I, II,V). The measurements in afforested organic soil cropland sites were further used to evaluate the effects of agricultural history on R_{PEAT} and to obtain annual estimates of R_{PEAT} (V) and to describe the proportion of R_{PEAT} from total soil respiration (I). A part of the forestry-drained site was cleafelled during the measurement period and this site was used to study the effects of clearfelling and logging residue retention on R_{PEAT} (III, IV).

2.1. Study sites

The main afforested organic soil cropland sites (sites 1–6, Table 1) are located within a 30 km radius of each other in Kannus municipality (65º55´N, 23º51´E) in Western Finland (Fig. 1, I, II,V). The mean annual precipitation in the area is 525 mm, of which 330 mm falls during the period from May to October. The annual average temperature is 2.3 ºC and the average cumulative temperature sum (≥+5 °C) 1070 degree days (Long-term average 1961–1990 (Finnish Meteorological Institute 1991)).

Afforested sites were selected to cover different afforestation ages and tree species, so that they represented the variation typical for these areas within the country. All the sites had been efficiently drained to reach the conditions suitable for cultivation. During the agricultural phase, mineral soil was added or mixed from the underlying mineral soil at five of the sites, and all sites were continuously fertilized and limed. Sites were in agricultural use for some decades before afforestation. After cultivation practices ceased, the soil was prepared by single mouldboard plowing. Afforestation on the sites had been done using either seedlings of Scots pine (*Pinus sylvestris*), or downy birch (*Betula pubescens*) 5–35 years before the measurements begun (Table 1). On the younger afforestation sites, the understorey is characterized by closed-cover patches dominated by *Urtica dioica* (L.) and *Epilobium angustifolium* (L.). On the older sites, forest species like *Deschampsia flexuosa* (L.) and *Dryopteris carthusiana* (Will.) dominate.

Measurements from three auxiliary afforested agricultural sites (sites 7–9, Table 1, Fig. 1) were included in the analysis when annual estimates of R_{PEAT} following afforestation were produced (V). This was done to better cover regional variation in afforested organic soil croplands in Finland. All these sites had been in agricultural use for some decades before afforestation. During the agricultural phase mineral soil had been added to some of the sites and fertilization has been used in order to improve the soil properties for cultivation. After the cultivation practices ceased, the soil was prepared and the sites were afforested. Further information on the site characteristics can be found in (V).

The forestry-drained peatland site (II, III, IV) is situated in Padasjoki, Vesijako Research Forest, south-boreal Finland (61º 22´ N, 25º 07´ E) (Fig. 1). The mean annual precipitation in the area is 601 mm out of which 228 mm falls as snow. The annual average temperature is 3.6 ºC and the average cumulative temperature sum (≥+5 °C) 1236 degree days (Long-term average 1961–1990 (Finnish Meteorological Institute 1991)).

The area studied was originally a treed mire with an ombrotrophic centre and a minerotrophic lagg. The area was first drained in 1915 and ditch maintenance operations were carried out in 1933 and 1954. Forest floor vegetation consisted of dwarf shrubs (evergreen *Vaccinium vitis-idaea, Empetrum nigrum*, and *Ledum palustre* and deciduous *Vaccinium myrtillus* and *Vaccinium uliginosum*), and mosses (forest mosses *Pleurozium schreberi, Dicranum polysetum*, and *Hylocomium splendens* and peat mosses *Sphagnum russowii, Sphagnum capillifolium,* and *Sphagnum angustifolium*). On average, the site was considered to represent oligotrophic nutrient status as indicated by the vegetation and fairly low levels of total N in surface peat.

The current tree stand evolved through seed tree cutting in 1945–1950. This second-generation post-drainage Scots pine (*Pinus sylvestris*) stand has been thinned twice before our measurement period started in 2001. In winter 2001–2002 an area of approximately 0.5 ha was clearfelled in the middle of the study area (CF site) (III, IV). Two similar sized (ca. 0.5 ha each) control areas (CTRL site) were left intact on both sides of the CF site (II, III, IV).

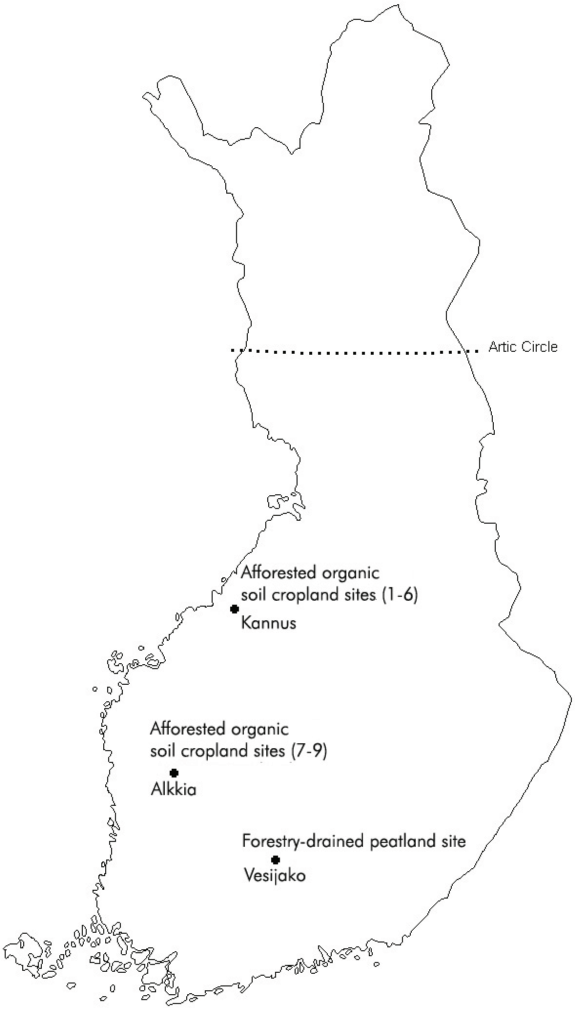

Figure 1. The locations and site numbers of the study sites.

Table 1. Site characteristics of afforested organic soil cropland sites.

Site	Tree species	Tree age in 2005 yr	Stand volume $m^3\ ha^{-1}$	Tree height m	Bulk density 0–20 cm $kg\ dm^{-3}$	Ash content 0–20 cm %
1	Silver birch	18	16	6.3	0.250	26.2
2	Silver birch	18	27	6.9	0.250	31.5
3	Scots pine	33	137	10.3	0.182	6.8
4	Scots pine	33	75	9.3	0.278	32.4
5	Silver birch	10	2	2.7	0.218	24.2
6	Silver birch	35	193	14.6	0.262	27.7
7	Scots pine	34	157	12.4	0.899	82.1
8	Scots pine	34	177	12.0	0.540	63.0
9	Scots pine	34	121	11.6	0.503	62.2

2.2. Measurement methods

2.2.1. Sample plot preparation for heterotrophic peat soil respiration

In this study the heterotrophic peat soil respiration (R_{PEAT}) was determined in field conditions using a closed chamber method. This required preparation of permanent sample plots where R_{PEAT} could be measured without the contribution of autotrophic components of respiration or heterotrophic respiration from newly deposited litter. The elimination of autotrophic root respiration was done by using the trenching technique; the plots were trenched to a depth of 30 cm using a metal cylinder 40 cm in diameter with the intention of excluding root respiration and the further growth of new roots. Trenching was done 1 year before the actual measurements started. The 30 cm trenching depth was considered to be adequate as most of the roots in peatlands are situated in the topmost peat layers (Saarinen 1996, Laiho and Finér 1996). The aboveground parts of the ground vegetation were removed from the sample plots and plots were kept free of vegetation by regular clippings in order to eliminate their respiration from the measurements. Newly deposited litter was removed, and litter nets served to prevent further accumulation of litter. With these measures, we aimed to exclude the decomposition of new litter from the R_{PEAT} measurements which then contained the decomposition of OM which was at least 1 year old.

These permanent R_{PEAT} plots were established on each study site. In the afforested organic soil cropland sites, five replicate R_{PEAT} plots were established in spring 2002 no more than 20 m apart from each other to cover spatial variation within the sites (I, II, V). In forestry-drained site a systematic grid of R_{PEAT} plots was established in spring 2000 with 19 plots in uncut control sites (II, III, IV) and 15 in clearfelled site (III, IV).

2.2.2. Sample plot preparation for auxiliary CO_2 measurements

To estimate the effect of logging residue (LR) on R_{PEAT} an additional set of measurements were started in spring 2002 in the clearfelled forestry-drained site (IV). These measurements included chamber measurements of soil CO_2 efflux including LR decay on top of the soil surface (R_{TOT+LR}), an incubation study of the LR decomposition, along with the measurements of total soil respiration (R_{TOT}). These measurements served to provide an estimate of the LR decomposition following clearfelling and to describe the effects of LR on R_{PEAT}. For more detailed description of this work see (IV).

For partitioning of different soil respiration components in afforested organic soil cropland sites two additional measurement plots for soil CO_2 were established next to each R_{PEAT} plot. These plots included 1) R_{PEAT} and heterotrophic respiration from above ground litter ($R_{PEAT+LITTER}$) and 2) R_{PEAT} and root-derived respiration ($R_{PEAT+ROOT}$), which in this case is defined to include all processes occurring in the rhizosphere. The aboveground parts of the ground vegetation were removed from all of the sample plots and plots were kept free of vegetation by regular clipping in order to eliminate their respiration from the measurements. The measurements from the additional sample plots lasted from 1st January 2004 until 1st of June 2005. For more detailed description of these arrangements see (I).

2.2.3 Measurements of heterotrophic peat soil respiration using closed chambers

Various chamber techniques are available to measure soil-atmosphere exchange of CO_2. (Luo and Zhou 2006). In this study the CO_2 efflux from R_{PEAT} plots was measured using a closed-chamber system with air circulating in a loop between the chamber and an external infrared gas analyser (EGM-4 CO_2 analyser + modified SRC-1 soil respiration chamber (NSF-11, Pumpanen et al. 2004), PP-Systems Ltd.) equipped with a water vapour equilibrator. A metallic chamber (diameter 31.5 cm, height 16.9 cm) equipped with a fan was manually placed on the sample plot for a measurement period of 81 seconds. The litter net was removed prior to measurement. The CO_2 concentration increase in the chamber was automatically monitored at 1.6-second intervals and averaged for 4.8-second periods. Soil CO_2 efflux was then calculated from the linear increase of CO_2 concentration in the chamber headspace over time. The efflux was corrected for atmospheric pressure and air temperature.

Chamber measurements were carried out weekly during the snow-free season and monthly during the winter. The measurements in afforested agricultural sites lasted from 1st of May 2003 until 1st of June 2005 (I, II, V). In the forestry-drained site the year 2001 served as a calibration season when both sites were measured prior the clearfelling treatment. The measurement period lasted from May 1st 2001 until Sep 30th 2004 (II, III, IV).

2.2.4. Meteorological parameters

Soil temperature and WL depth are considered the main factors to control peat decomposition in peat soils. Thus, soil temperatures at 5 cm below ground (T5) and WL from perforated tubes next to each gas sample plot were measured simultaneously with each CO_2 efflux measurement event (I, II, III, IV, V). These manual T5 and WL measurements were used to formulate the relationship between these environmental variables and measured soil CO_2 efflux.

To obtain information on the prevailing soil temperature conditions continuous temperature measurements at 5cm depth were done at 2 to 4 hour intervals within each site either using temperature sensors (BetaTherm 2K3A1, Beta Therm Sensors, Ireland) wired to a data logger (Campbell CR10X, Campbell Scientific, Inc. USA) (III, IV) or by temperature data loggers (i-button, model 1921G, Dallas Semiconductor Corp.) (I, V). In order to obtain hourly temperature data, the gaps were filled by linear interpolation. Due to failures in data logging, some gaps occurred in temperature data which were filled by using linear regressions between the temperature on the site and temperature measurements of other study sites or by using air temperature data from the nearest weather station (Finnish Meteorological Institute). The site specific continuous WL data were obtained by averaging the manual WL measurements done from all plots at each CO_2 measurement event. Missing values between the measurements were filled by using linear interpolation.

These continuous data sets were used in simulations to reconstruct the daily and seasonal variation in CO_2 effluxes (I, III, IV, V) and for studying the effects of clearfelling on temperature and WL conditions in forestry-drained site; differences in weekly average temperatures and WL between the clearfelled and control site were tested by using a paired sample t-test.

2.2.5. Peat sampling and analyses

In former agricultural areas surface peat ash content and bulk density are closely related to the amount of mineral soil added to the site during the agricultural phase (Wall and Hytönen 1996). The addition of mineral soil has been shown to increase soil temperature (Pessi 1956) as well as nutrient availability (Pessi 1962) both of which can accelerate microbial activity and thus affect R_{PEAT}. To study the effect of soil properties on R_{PEAT} in afforested organic soil croplands, surface soil samples (0–10 cm) were taken and analysed for peat ash content (550 ºC, 8 h), bulk density and pH (water) (I, II,V). The peat samples were taken from inside the R_{PEAT} plots in spring 2005 at the end of soil CO_2 measurements. All plots were sampled so that spatial variation in sites was captured. Linear regression was applied to reveal the correlations between sample plot specific annual R_{PEAT} and soil properties (I,V).

The microbial community structure in surface peat layers was determined by using phospholipid fatty acid (PLFA) analysis (II). In the PLFA analysis the DNA phospholipid fatty acids are extracted from the soil and divided between the PLFAs of predominantly bacterial origin and those of fungal origin. The changes in microbial community structure between the samples can be studied by comparing the proportional contribution of each 48 identified PLFAs from the total identified PLFAs.

Peat samples from the top layer (0–5 cm) were collected for PLFA analysis from inside five sample plots at four afforested agricultural sites (Sites 1–4, II) and from control sites in the forestry-drained site in spring 2005 (II). PLFAs were extracted from 1.5 g of fresh peat (for the exact method, see Pennanen et al. (1999)). Peak areas were quantified by adding methyl nonadecanoate fatty acid (19:0) as an internal standard. To investigate changes in community structure, the 48 PLFAs identified from each sample were expressed as a mole percentage (mol% = area% of a single PLFA from the area sum of all identified PLFAs).

The relationship between spatial variation in the microbial community structure and average WL conditions and therein temperature sensitivity of R_{PEAT} was studied using multidimensional ordination methods, because there were multiple intercorrelated variables in the data (II). Redundancy analysis (RDA) served to investigate which of the measured environmental factors, average water level depth (WL_{AVE}), tree species, bulk density, ash content of the surface peat, and total thickness of the peat deposit, correlated significantly with the patterns in the PLFA composition.

2.3. Data analysis

The nonlinear regression models were used to analyze the R_{PEAT} data. The response of R_{PEAT} on environmental drivers was modelled by using the simultaneous R_{PEAT}, T5 and WL measurements. These models were then used to describe the dependence of R_{PEAT} on temperature and WL and to reconstruct the continuous time series of R_{PEAT}.

2.3.1. Models used to analyze the response of R_{PEAT} to temperature and WL

The response of R_{PEAT} to temperature and WL was first studied at single sample plot level (I, II). This was done to reveal the factors causing temporal variation in R_{PEAT} within one plot and to reveal the basic nature of the temperature and WL relationship of R_{PEAT} in the studied site.

The temperature dependence of R_{PEAT} was described with a function by Lloyd and Taylor (1994) as follows:

$$f(R_{PEAT}) = R_{ref}\exp\left[E_0\left(\frac{1}{T_{ref_1}-T_0} - \frac{1}{T-T_0}\right)\right] \qquad (1)$$

where T is the soil temperature (T5) measured concurrently with the CO_2 efflux measurements. Other parameters were estimated by fitting the model to the dataset using non-linear regression (SYSTAT 10). R_{ref} (g CO_2 m^{-2} h^{-1}) is the soil respiration rate at 10 ºC. E_0 (K) is an exponential parameter depicting the temperature sensitivity of soil respiration. T_{ref1} is the reference temperature set at 283.15 K (i.e. 10 ºC), and parameter T_0 is the minimum temperature at which respiration reaches zero, set at 227.13 K (–45.6 ºC) (Lloyd and Taylor, 1994).

The effect of WL on R_{PEAT} was not tested alone but simultaneously with the soil temperature dependence (I, II) as in these well drained sites T5 explained the major part of R_{PEAT}. To test the effect of WL on R_{PEAT} within single sample plot level, WL was added to the temperature function as a scalar dependent as follows:

$$f(R_{PEAT}) = R_{ref}\exp\left[E_0\left(\frac{1}{T_{ref_1}-T_0}-\frac{1}{T-T_0}\right)\right] + (c \times WL) \tag{2}$$

where WL is the water level depth from the peat surface (m) measured concurrently with R_{PEAT}, and parameter c describes the change in R_{PEAT} related to changes in WL independently of temperature.

For the further analysis of the response of R_{PEAT} to WL, data from the afforested organic soil cropland sites and the control treatments in the forestry-drained sites were pooled (II). This provided a large WL gradient (6–120 cm) which made it possible to apply different response functions to that of the sample plot specific models.

In peat soils WL regulates the volume of the aerobic peat layer. In addition, during low WL the surface peat may dry out and limit decomposition (Lieffers 1988, Laiho et al. 2004). The data with sufficient WL range could reveal an optimum WL for R_{PEAT}. Thus, a Gaussian form was proposed to describe the relationship between WL and R_{PEAT} in a multiplicative model as follows:

$$f(R_{PEAT}) = R_{ref}\exp\left[E_0\left(\frac{1}{T_{ref_1}-T_0}-\frac{1}{T-T_0}\right)\right] \times \left(\exp\left(-0.5\times\left[\frac{(\mathrm{WL}-\mathrm{WL}_{\mathrm{opt}})}{\mathrm{WL}_{\mathrm{tol}}}\right]^2\right)\right) \tag{3}$$

where parameter WL_{opt} (cm) denotes the optimal water level for R_{PEAT}, parameter WL_{tol} (cm) denotes the water level tolerance (i.e. the change in water level that reaches 61% of the optimum level), and WL is the water level depth from the peat surface (cm) measured concurrently with R_{PEAT}. Other parameters are the same as in equation (1).

The sample plot specific models revealed that temperature explained well the temporal variation in R_{PEAT} within one sample plot, but there existed large spatial variation within and between sites in the temperature sensitivity of R_{PEAT} (I, V). To study whether this variation in temperature sensitivity of R_{PEAT} could be related to sample plot average water level conditions (WL_{AVE}) (arithmetic mean of water level depth for the whole study period), the correlation between sample plot-specific parameter values for the temperature sensitivity of R_{PEAT} (E_0, Eq. 2) and WL_{AVE} were studied by using linear regression (II).

To test whether this indirect effect of water level on R_{PEAT} via temperature sensitivity was independent and statistically significant, we further developed our CO_2 model; a linear term ($d*WL_{AVE}$) was added to the temperature sensitivity parameter E_0 as follows:

$$f(R_{PEAT}) = R_{ref} \exp\left[(E_0 + (1 + d \times WL_{AVE})) \left(\frac{1}{T_{ref_1} - T_0} - \frac{1}{T - T_0} \right) \right] \times \left(\exp\left(-0.5 \times \left[\frac{(\mathrm{WL} - \mathrm{WL}_{\mathrm{opt}})}{\mathrm{WL}_{\mathrm{tol}}} \right]^2 \right) \right) \tag{4}$$

where d is a parameter that describes the linear change in the temperature sensitivity of decomposition related to changes in sample plot-specific average water level conditions, $\mathrm{WL}_{\mathrm{AVE}}$ (cm). Other parameters are the same as in equation (3).This model was then fitted to the entire dataset, which provided the parameter value for the optimum water level for $\mathrm{R}_{\mathrm{PEAT}}$ along with the parameter that describes the effect of average water level on the temperature sensitivity of $\mathrm{R}_{\mathrm{PEAT}}$ within the studied sites.

2.3.2. Reconstruction of continuous soil CO_2 effluxes for afforested organic soil cropland sites

In the field conditions changes in soil temperature and water level depth WL can cause rapid temporal variation in $\mathrm{R}_{\mathrm{PEAT}}$. Therefore the weekly and biweekly measurements of $\mathrm{R}_{\mathrm{PEAT}}$ could not be used directly to estimate the seasonal $\mathrm{R}_{\mathrm{PEAT}}$ or to describe the differences between the sample plots and treatments. To solve this problem $\mathrm{R}_{\mathrm{PEAT}}$ was reconstructed by using the relationships of $\mathrm{R}_{\mathrm{PEAT}}$, T5 and WL and continuous time series of these explanatory variables. Simulations were carried out with an hourly time step, and weekly, seasonal and annual estimates were calculated by summing up the simulated hourly values (I, III, IV, V).

In afforested organic soil cropland sites the responses of $\mathrm{R}_{\mathrm{PEAT}}$ to T5 and WL were observed to vary between the sample plots (I, V), indicating that we were not able to explain all spatial variation with temperature and water level. Thus, in order to best capture the variation between the plots the simulation models for afforested organic soil cropland sites were done for each sample plot separately. This had the result that the measured WL gradient remained so small that no WL response occurred (I, V). Thus, simulations where done by using the equations based on temperature only.

In order to find the best possible fit for the relationship between T5 and $\mathrm{R}_{\mathrm{PEAT}}$ several temperature response functions (Linear-function, an exponential function, Q_{10}- function and Arrhenius-type of function by Lloyd and Taylor (1994)) were tested using the $\mathrm{R}_{\mathrm{PEAT}}$ data (I). From these tested functions, an exponential function (Eq. 5, V) and Arrhenius-type of function by Lloyd and Taylor (1994) (Eq. 1, I) were used in the reconstruction of the seasonal $\mathrm{R}_{\mathrm{PEAT}}$. The exponential function is described as follows,

$$R_{PEAT} = R_0 \, \mathrm{e}^{kT5} \tag{5}$$

where R_0 and k are fitted parameters. R_0 is the base respiration rate, and k is related to Q_{10}, the factor by which a reaction increases for an increase of 10 ºC in temperature.

This exponential function fitted well with the warm soil temperatures but with lower soil temperatures the function tended to overestimate the effluxes. Because of this the exponential function was only used to reconstruct the summer season (May–Oct) $\mathrm{R}_{\mathrm{PEAT}}$ (V). The winter season $\mathrm{R}_{\mathrm{PEAT}}$ was calculated by using the average flux rate during the winter (V). The Lloyd and Taylor (1994) function (Eq. 1) fitted well to the data. The residuals from the Lloyd and Taylor (1994) function were evenly spread across the measured temperature range. Thus, it was used for reconstruction of annual $\mathrm{R}_{\mathrm{PEAT}}$ (I).

The annual estimates for additional CO_2 sample plots ($R_{PEAT+LITTER}$, $R_{PEAT+ROOT}$) were obtained with similar modelling procedure to that used for R_{PEAT}. Response functions were fitted separately to each sample plot. For $R_{PEAT+LITTER}$ plots no WL response occurred thus reconstruction was done using the temperature-only function (Eq. 1). On $R_{PEAT+ROOT}$ plots linear WL response was observed and thus reconstruction was done by using the equation 2, where WL is added to the temperature response function. The CO_2 efflux from heterotrophic respiration from litter decomposition (R_{LITTER}) (Eq. 6) and root respiration (R_{ROOT}) (Eq. 7) were calculated using the annual estimates as follows,

$$R_{LITTER} = R_{PEAT+LITTER} - R_{PEAT} \qquad (6)$$

$$R_{ROOT} = R_{PEAT+ROOT} - R_{PEAT} \qquad (7)$$

The total soil respiration (R_{TOT}) was estimated as a sum of R_{PEAT}, R_{LITTER} and R_{ROOT} and this estimate was used when the proportional contribution of R_{PEAT} to R_{TOT} was determined.

2.3.3. Reconstruction of seasonal soil CO_2 effluxes for forestry-drained site

The simulation models in forestry-drained sites were done by pooling the sample plots within the treatments, as this was considered to be the most efficient way to reveal the effects of clearfelling on R_{PEAT} (III, IV). Furthermore some interannual variation in CO_2 effluxes remained unidentified, and in order to estimate unbiased effluxes the model parameterization was done for each season separately. Simulations were done using the equation (2) where WL is added to the temperature function, as R_{PEAT} was found to be dependent on both T5 and WL (III, IV). The effects of clearfelling on R_{PEAT} were studied by using the reconstructed seasonal (May–Oct) estimates of R_{PEAT} for years 2001–2004 from the clearfelled (CF) and control sites (CTRL) (III). Differences in weekly values between the CF and CTRL site in seasons 2001–2004 were tested by using yearly and site specific values and paired sample t-test (SYSTAT 10) (III).

The reconstruction of the seasonal CO_2 effluxes from gas sample plots with logging residue (R_{TOT+LR}) and without LR **(**R_{TOT}) was done similarly to that of the R_{PEAT} data (IV). Model parameterization was done for each season separately and by pooling the sample plots within the treatments. In addition to that, some unidentified spatial variation (between plots) remained in R_{TOT+LR}. When R_{TOT+LR} plots were divided into two groups based on the measured flux levels, models fitted much better and gave unbiased estimates**.**

The CO_2 efflux from logging residue decomposition (R_{LR}) inside the R_{TOT+LR} collars was estimated by using the dry mass of the LR inserted in to the R_{TOT+LR} plots and seasonal (May–Oct) LR mass loss rates calculated using an asymptotic curve (Eq. 8) fitted to the litterbag LR data.

$$Mt = A + BR^t \qquad (8)$$

where, *Mt* (%) is the mass remaining at time *t*, *A* is the asymptote of the curve, *R* is the rate of decomposition, *B* is a regression coefficient and *t* is time in years.

These seasonal LR mass loss estimates were converted to CO_2 efflux by assuming that 50% of the dry mass loss was CO_2-C as follows,

$$R_{LR} = LR\ mass\ loss \times 0.50 \times 3.664 \qquad (9)$$

2.3.4. Simulations used to study the response of R_{PEAT} on clearfelling in forestry-drained site

To illustrate the effects of soil temperature and WL conditions on R_{PEAT} following clearfelling we performed an alternative set of simulations. These simulations were done to separate the two sources of variation in R_{PEAT} following clearfelling; i.e. that caused by difference in *environmental conditions* and that caused by difference in the *response of the system* to the environmental conditions between the clearfelled and control site. In the first simulation we aimed to separate the direct effect of change in soil temperature following clearfelling on $R_{PEAT.}$ For this all R_{PEAT} data was pooled for the model parameterizations (thus, we assumed similar response of R_{PEAT} to T5 in both sites and throughout the years) and calculated the seasonal effluxes using a temperature only function (Eq. 1) with site specific T5 as driving variable. The difference in the obtained seasonal R_{PEAT} estimates between the treatments demonstrates the effects of changes in T5 conditions on R_{PEAT} following clearfelling. In second simulation the effect of WL was taken into the analysis and the parameterization was done otherwise similarly. All data was pooled and seasonal effluxes were calculated by using the equation (2) and site specific T5 and WL as driving variables. Finally, we compared these values to the seasonal estimates obtained from the site- and year-specific models for R_{PEAT}, which then included both the effect of changing conditions but also the difference in responses of the systems to these conditions.

3. RESULTS AND DISCUSSION

3.1. The effects of temperature and WL on R_{PEAT}

In the studied drained forested peatlands soil temperature measured at 5 cm depth (T5) was the main factor controlling temporal variation in R_{PEAT} (I, II, III, IV,V). At the single sample plot level, T5 could almost completely (71–96%) explain the temporal variation in R_{PEAT} (I, II, Fig. 2). It was noticeable that the explanatory power of T5 was almost equally strong between the plots despite the variation in environmental conditions and WL fluctuations between them (I, II).

The temperature response of R_{PEAT} was determined from the field measurements using the observed R_{PEAT} that originates from the entire peat column under the measurement chamber and the temperature measured simultaneously with the chamber measurements from the fixed position (T5) in the surface peat layer. The high explanatory power of this single temperature measurement over the measured fluxes from the entire peat column suggest that decomposition processes in the surface layer, experiencing highest temperature fluctuations and having the most labile OM fractions, dominated the observed R_{PEAT}.

Instantaneous changes in water table level (WL) had negligible effect on the plot-wise temporal variation in R_{PEAT} (I, II, V). Adding the linear WL function to the T function did not increase the model r^2, and no relationship between WL and the residuals from the R_{PEAT} versus T model was observed (I, V). The insignificant influence of fluctuations in WL on observed R_{PEAT} is in contrast with the earlier laboratory studies on pristine peat soils by Moore and Knowles (1989) and Blodau and Moore (2003) who showed that the lowering of WL, and associated increase in the volume of the aerated peat layer, linearly increased peat decomposition rates.

Within the studied drained forested peatlands, WL was always 20 cm or more below the peat surface in the majority of plots. This means that the the surface peat layer which has the highest availability of labile carbon, highest temperatures and highest concentration of nutrients

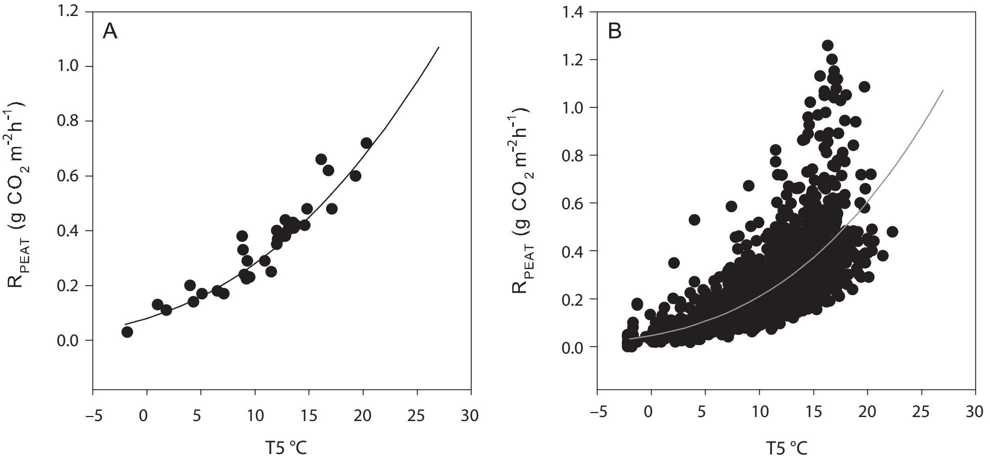

Figure 2. Two examples of the temperature relationships of R_{PEAT}. A) is an example of the temperature response of R_{PEAT} within one individual sample plot (r^2=0.91) B) is the temperature relationship of the entire R_{PEAT} dataset (r^2 = 0.47) (Equation 1, see Section 2.3.).

was continuously aerobic. The significance of these surface layers for peat soil CO_2 release has been demonstrated earlier in laboratory studies by Hogg et al. (1992). The WL fluctuations in deep peat layers that had recalcitrant substrates (Bridgham and Richardson 1992) and low temperatures are likely to have had a minor effect on the observed CO_2 fluxes, which would explain the lack of a relationship between WL and R_{PEAT}. This observation is in agreement with Chimner and Cooper (2003) and Silvola et al. (1996a), who showed that lowering the WL below a certain depth (10–40 cm) within sites, did not lead to further increases in the soil respiration rate.

When entire variation in temporal and spatial WL conditions was taken into the analysis optimum water level for R_{PEAT} was found with WL depth of 61 cm after which a further drop in the water level reduced R_{PEAT} (II, Fig. 3). This was observed even if R_{PEAT} was still quite tolerant of the changing water level and the overall effect of water level fluctuations on R_{PEAT} was relatively weak (II). Within low WL conditions, drought may start limiting the decomposition rates in most surface peat layers as the capillary fringe in the peat soil hardly ever reaches deeper than 60 cm (Verry 1997). The consequent reduction of peat decomposition caused by drying of the surface layers is likely to cause significant changes in observed R_{PEAT} and overrule the effects of WL fluctuation in the deeper inert peat layers. Similar decrease in total ecosystem respiration following WL drop to approximately 55 cm depth was found in pristine treed fen site by Flanagan and Syed (2011).

Even though temperature well explained temporal variation in R_{PEAT} within one sample plot, the shape of the relationship between T and R_{PEAT} strongly varied between the plots (I, II,V). In the original Lloyd and Taylor (1994) model, the temperature sensitivity parameter (E_0) is fixed at 308 K^{-1}. Within the studied sites the temperature sensitivity parameter (E_0) varied from over 800 K^{-1} to 200 K^{-1}. Average WL of the sample plot (WL_{AVE})(arithmetic mean of water level depth for the whole study period) was found to correlate negatively with E_0; temperature sensitivity was lower in sample plots where WL was continuously deeper (WL_{AVE} 50–60cm) compared to that of the plots with higher WL_{AVE} (30–40cm) (Fig 4, II). In mineral soils a decline in the temperature sensitivity of OM decomposition with a commensurate

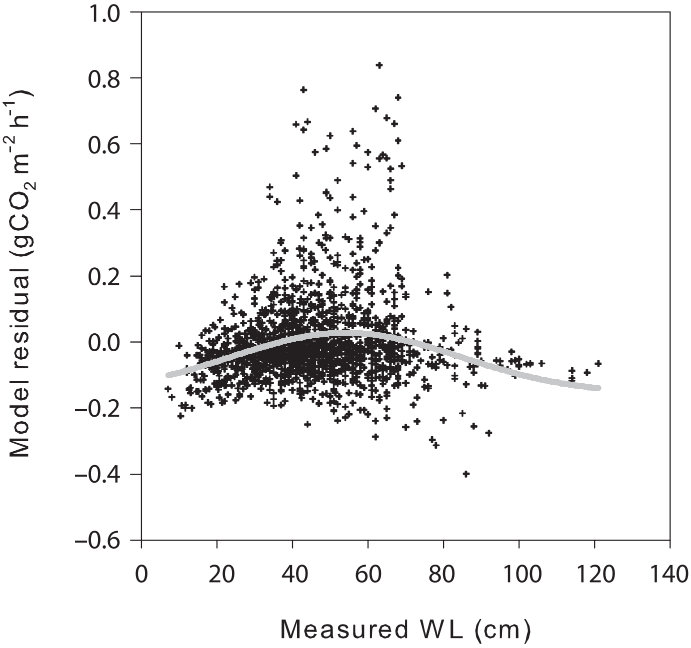

Figure 3. Distribution of residuals (model R_{PEAT} minus observed R_{PEAT}) for the temperature model (Equation 1) shown in Figure 2B as a function of measured water level (WL). The grey line represents the Gaussian form of the relationship between the two variables ($R^2 = 0.053$, $P < 0.005$).

decrease in soil moisture content has been observed both in laboratory and in field conditions (Howard and Howard 1993, Reichstein et al. 2005, Rey et al. 2005).

The observed variation in temperature sensitivity of decomposition could be related to WL_{AVE} which was the strongest factor of the measured variables to explain the changes in microbial community structure in surface peat layer; WL_{AVE} was the strongest determinant of surface soil PLFA composition (II) and WL_{AVE} correlated significantly with microbial biomass in the surface peat layer ($r^2 = 0.35$, $P < 0.005$) (II).

In laboratory studies differences in the PLFA pattern have reflected no differences in the temperature sensitivity of C mineralisation when determined from soil samples collected once and incubated at different temperatures for short periods of time (Vanhala et al. 2008). In this study, the temperature sensitivity of R_{PEAT} was defined using R_{PEAT} data from an entire growing season. The observed temperature sensitivity of R_{PEAT} thus includes the effects of all variables that correlate with temperature during the growing season. These involve the summarised effects of temperature on microbial community, biomass and growth rate as well as the effects of temperature on the actual rate of reactions related to decomposition processes. Thus, we suggest that change in temperature sensitivity, along with the change in microbial community structure, results only partly from changes in the enzyme substrate affinities related to differences in PLFA composition, but more so from the various abilities of different groups of microbes to grow and increase biomass within the observed temperature regimes under varying moisture conditions. In other words microbial community in plots where WL is continuously high was capable of growing and respiring faster than that of the drier plots resulting in higher observed T sensitivity on wet sites.

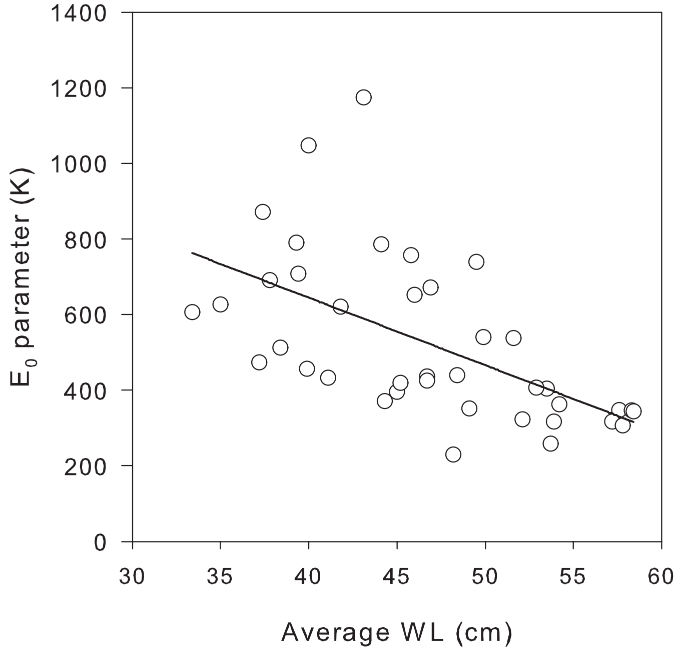

Figure 4. The relationship between the sample plot-specific average water level (WL) and the temperature sensitivity of peat decomposition expressed as a model parameter (E_0) ($r^2 = 0.33$, $P < 0.005$). Parameters derived from equation 2 are fit separately to each sample plot.

There was only weak correlation between soil temperature and WL conditions within the measurement period in the studied sites. This indicates that simultaneous changes in T5 and WL during the measurement period had only a minor effect if any effect at all on temperature sensitivity of R_{PEAT} in the studied sites (II) and that the high temperature sensitivity of peat decomposition in low WL conditions was not caused by correlation between T5 and the amount of decomposable material available in the active decomposition process as suggested by Davidson and Janssens (2006).

There were also some other factors that could have contributed to the observed T sensitivity in the studied sites. In field conditions soil temperature in deep peat layers is stable, which means that CO_2 production in these layers should also be more or less stable. Higher fluctuations in temperatures in surface peat layers on the other hand should cause rapid temperature related changes in CO_2 emissions from those layers. Variation in average WL conditions could have caused the change in observed temperature sensitivity of R_{PEAT} by causing a change in the relative contribution of decomposition from different peat layers to observed R_{PEAT}. In other words low temperature sensitivity in plots with low WL_{AVE} could be caused by bigger relative contribution of decomposition from low peat layers with stabile CO_2 fluxes to observed R_{PEAT} in those plots compared to that with plots of high WL_{AVE}.

Another cause for the low temperature sensitivity of R_{PEAT} in the plots with low WL_{AVE} could be the low thermal conductivity of the dry surface peat in those plots. The thermal conductivity of peat soil depends heavily on the water content of the soil; increasing the water content improves the thermal conductivity of the soil (Eggelsmann et al. 1993). A moist surface peat layer could contribute to the more rapid transport of heat to the deeper peat layers, thus causing the temperature in the entire peat profile to rise, whereas with a dry surface peat layer, the effect of temperature would remain more superficial. The overall temperature in the peat profile could thus be higher when the water level is continuously closer to the peat surface. Because we only used the soil temperature at 5 cm depth to define temperature sensitivity, temperature differences in the lower peat profiles between plots with different WL_{AVE} may have partly resulted in the observed variation in the temperature sensitivity of R_{PEAT}.

To confirm and distinguish between these mechanisms future research should focus on determining how interactions in temperature and water level conditions affect surface peat moisture conditions, the peat temperature profile and consequently how this is reflected in observed $R_{PEAT.}$ Furthermore in laboratory experiments where the relative significance of different peat layers for observed R_{PEAT} could be determined, temperature dependences of these peat layers could be studied independently and the possible changes in microbial population structure could be detected in more detail.

Finally, a statistical model was developed to reveal and test the observed relationships of T5 and WL to R_{PEAT} and their significance (II, Eq. 4). This model was able to describe, with a single set of parameters, both spatial (between- and within-site) and temporal variability in R_{PEAT}. The following implications are apparent from the model parameterisation: (1) Water level both directly and indirectly affects R_{PEAT}; both ways are statistically significant and can affect R_{PEAT} independently. (2) The apparent temperature sensitivity of R_{PEAT} depends on plot-specific average water level depth (3) The direct effect of water level on R_{PEAT} followed a Gaussian form.

Previous attempts to describe the factors that cause variation in the soil respiration rate in field conditions have included often only the effects of momentary water level on soil respiration (Chimner and Cooper 2003, Tuittila et al. 2004, Riutta et al. 2007). This procedure has been successful on wet pristine sites, but the effects of water level on the respiration rate on well-drained sites have remained either small or insignificant (Lafleur et al. 2005, Minkkinen et al. 2007). Our present findings show that the effect of instantaneous WL on peat decomposition was actually smaller than the effect of long-term average water level conditions that affected the observed temperature-related processes of peat decomposition.

3.2. The effect of clearfelling on R_{PEAT}

Our results showed that in a forestry-drained peatland site clearfelling of the tree stand did not accelerate the heterotrophic peat soil respiration (R_{PEAT}), on the contrary R_{PEAT} decreased after tree removal (III, Table 2). A decrease in R_{PEAT} was observed even though removal of the forest canopy clearly raised soil temperatures in the clearfelled site compared to that on the control site with a full canopy (III, Table 3). The increasing soil temperatures should have accelerated biotic activity and thus the decomposition rates and CO_2 emissions from the soil (III, Fig. 5). However, this possible increase in R_{PEAT} could have been compensated by the simultaneous rise in WL (III, Table 3, Fig. 5). This result is in accordance with results from temperate forest stands with shallow surface peat layers (Zerva and Mencuccini 2005).

The further investigation on the R_{PEAT} following clearfelling showed that rising WL could not however, solely explain the decrease of R_{PEAT} following clearfelling (III, Fig. 5). The temperature response (parameter E_0, in Eq.2) of R_{PEAT} was clearly weaker on the clearfelled site compared to that under the mature tree stand. Thus the effect of rising soil temperatures following clearfelling on R_{PEAT} was not compensated only be increase in WL but also by lower temperature sensitivity of R_{PEAT} in the clearfelled site compared to that of the control site (III, Fig. 5).

The decrease in the temperature response of R_{PEAT} after clearfelling is most likely caused by the drying of the surface soil and consequent decrease in decomposition rates in the surface peat layers with fresh organic matter. Following clearfelling the surface soil is exposed to direct solar radiation and thereby to more extreme temperatures. This, in turn, may have caused enhanced evaporation rates and drying of the soil surface where decomposition mainly occurs (Hogg et al. 1992). This may have been the case even though the water level was closer to the peat surface on the clearfell site compared to that on the control site: findings on mineral soils show that reduction in soil moisture in the top 3cm and an increase in deeper layers (>15cm) can occur simultaneously following clearfelling (Edwards and Ross-Todd 1983). This drying of the surface soil is proposed to be the reason for the lower litter decomposition rates on clearfelled mineral soil sites compared to those under uncut stands (Yin et al. 1989, Prescott et al. 2000).

It appeared that changes in environmental factors following clearfelling caused rather small changes in R_{PEAT} and that there was no increase in old peat decomposition rates (III). However, when the effect of aboveground logging residue remaining on the site after clearfelling was taken into consideration the picture changed.

Table 2. Simulated seasonal (May–Oct) sums (g CO_2 m^{-2} $season^{-1}$) of heterotrophic peat soil respiration (R_{PEAT}) in control (CTRL) and clearfelled (CF) treatment on forestry-drained site. The difference between the sites were analyzed by paired sample T-test (** $p < 0.001$). Included are also seasonal estimates from sample plots with logging residue (R_{TOT+LR}), without logging residue (R_{TOT}), bare logging residue decay (R_{LR}) in the R_{TOT+LR} sample plot and calculated seasonal logging residue induced soil CO_2 effluxes.

Season	CTRL site	CF site				
	R_{PEAT}	R_{PEAT}	R_{TOT+LR}	R_{TOT}	R_{LR}	LR-induced soil CO_2 efflux
2001^	1550	1570	-	-	-	-
2002	1350	1330	3510	1720	820	970
2003	1070**	910**	3250	1260	460	1530
2004	970**	860**	2450	1355	315	780

^before clearfelling

Table 3. Environmental conditions in forestry-drained site during the measurement periods (May–Oct) from 2001 to 2004. T_5 is the mean soil temperature (°C) 5 cm below ground, WL is mean water level form soil surface (cm) and T_{AIR} is mean air temperature (°C) 2 m above ground. (CTRL= control site, CF= clearfelled site).

Year	T_5 (°C)		T_{AIR} (°C)	WL (cm)	
	CTRL	CF	CF	CTRL	CF
2001^	9.6	9.4	-	48	47
2002	10.0	10.9	11.3	55	45
2003	9.6	10.9	11.6	50	38
2004	10.2	10.7	12.1	35	30

^before clearfelling

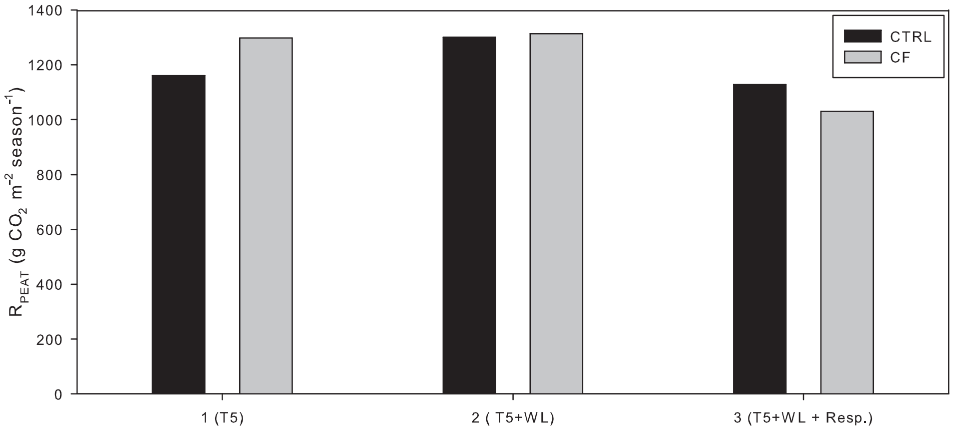

Figure 5. Analysis of the simulated impacts of clearfelling on seasonal R_{PEAT} using 3 different simulation approaches: 1) Temperature (T5) response only (Eq.1), with constant parameters over the years and sites, and site specific T5 data as driving variable. The difference between the sites describes the effect of changing T5 conditions on R_{PEAT} following clearfelling. 2) Temperature and water level response (Eq. 2) with constant parameters over the years and sites and site specific T5 and WL data as driving variables. The difference between the sites describes the effect of changing TS and WL conditions on R_{PEAT} after clearfelling. 3) Same as 2) but different parameters for each year and site. The difference between the sites describes the effect of changing T5 and WL as well as the change in the response of R_{PEAT} to these factors after clearfelling.

Retention of LR increased soil CO_2 evolution remarkably (IV). The measured instantaneous CO_2 effluxes on plots with LR (R_{TOT+LR}) were more than double that of the plots without LR (R_{TOT}) (IV, Table 2). However, less than 40% of this difference was accounted for by the decomposition of logging residue (R_{LR}) indicating that LR promoted R_{PEAT} under the logging residue piles (IV, Table 2).

Logging residues alter the soil environmental conditions by conserving soil moisture (Smethurst and Nambiar 1990, Roberts et al. 2005) and by lowering soil temperature (Roberts et al. 2005). Under LR, soil moisture content is more stable and can thus provide a favorable environment for decomposition (Smethurst and Nambiar 1990). If not covered with LR, the surface soil is exposed to direct solar radiation and extreme temperatures following clearfelling (Londo et al. 1999). This results in drying of the soil surface which may restrict peat decomposition. In mineral soil similar increase in soil respiration on plots with logging residue has been demonstrated by Edwards and Todd-Ross (1983).

The observed high CO_2 efflux from plots with LR could have also been caused by a priming effect whereby decomposition of peat underlying LR is enhanced by the input of fresh organic matter in the form of LR. Laboratory studies have recently demonstrated the existence and importance of priming in soil organic matter decomposition (Fontaine et al. 2004, 2007). This priming effect seems to be especially relevant if old soil organic matter, which itself consists of recalcitrant compounds with low energy content, is exposed to excessive amounts of fresh organic matter (Fontaine et al. 2004). This is because in the natural state, energy from old recalcitrant compounds cannot sustain microbial activity. Delivery of fresh organic matter can provide microbes a source of energy that enables them to decompose these recalcitrant compounds with their enzymes.

The results of this study indicate that in forestry-drained peatlands logging residues left at a clearfelled site have potential to increase R_{PEAT} considerably compared to the amount CO_2 that is released when logging residues are harvested and burned for energy. This would make the harvesting of LR for biofuel from clearfelled peatland forests more beneficial, in the form of avoided emissions. Further investigations of the longevity of the effect of LR on CO_2 emissions as well as on the sources of CO_2 under LR are needed to confirm these findings.

3.3. Heterotrophic peat soil respiration in afforested organic soil croplands

The estimated annual heterotrophic peat soil respiration (R_{PEAT}) from the afforested organic soil croplands varied between 760 and 1980 g CO_2 m^{-2} a^{-1} (V), which was of the same magnitude as measured on an agricultural peat field in eastern Finland by Nykänen et al. (1995) (1440–1470 g CO_2 m^{-2} a^{-1}) but much lower than that on peat fields in eastern and western Finland (3230–4110 g CO_2 m^{-2} a^{-1}, Maljanen et al. 2001a) and (2530–2900 g CO_2 m^{-2} a^{-1} , Maljanen et al. 2004). Measurements on agricultural fields were done in different weather conditions as well as different geographical locations. Comparisons of the measurement periods reveal that the temperature sums were lower during the measurement periods on the agricultural fields than in this study. When this is taken into consideration it appears that afforestation has the potential to considerably reduce high soil CO_2 effluxes from agricultural soils.

The lower R_{PEAT} following afforestation may result from reduced aeration caused by the cessation of cultivation, the absence of fertilization or liming activities, and because of lower soil temperatures on the afforested sites caused by the shading effect of the growing tree stand (Londo et al. 1999). All these factors may have led to reduced microbial activity and reduced decomposition rates of peat in the afforested sites compared to the cultivated agricultural peat soils.

Even though afforestation may reduce R_{PEAT}, the agricultural history had clearly transformed the peat properties on the studied sites (I, V, Table 1). Peat bulk density and ash content was considerably higher than in peatlands drained for forestry (V, Kaunisto and Paavilainen 1988, Minkkinen et al. 1999). These effects of cultivation practices on peat properties, and also on peat decomposition rates, were still evident even decades after afforestation with the annual R_{PEAT} being positively correlated with peat ash content (I, Fig. 6).

On afforested organic soil croplands, surface peat ash content is closely related to the amount of mineral soil added to the site during the agricultural phase (Wall and Hytönen 1996). Mineral soil addition has been shown to increase soil temperature (Pessi 1956) as well as nutrient availability (Pessi 1962) both of which can accelerate microbial activity and thus explain the high R_{PEAT} related to high ash contents.

The contribution of R_{PEAT} to total soil respiration varied between the sites from 36 to 52% with an average of 42% (I). Our estimates of the relative contribution of roots to annual total soil respiration (33–52% (I)) were higher than those measured on drained ombrotrophic peatlands in Finland (10–40%) by Silvola et al. (1996b) but within the wide range of the reported values on mineral soils (Hanson et al. 2000, Subke et al. 2006). The greater root activity on our sites compared to ombrotrophic peatlands is most probably attributable to higher nutrient availability and therefore better tree stand growth, but also to different vegetation community structures (Wall and Heiskanen 1998).

The partitioning approach provided an estimate of heterotrophic respiration that could be divided between the decomposition of fresh above ground OM (R_{LITTER}) and R_{PEAT}. A major part of the heterotrophic respiration originated from the decomposition of old peat; R_{LITTER} contributed 7 to 25% of the total soil respiration (I). It appeared that even though afforestation

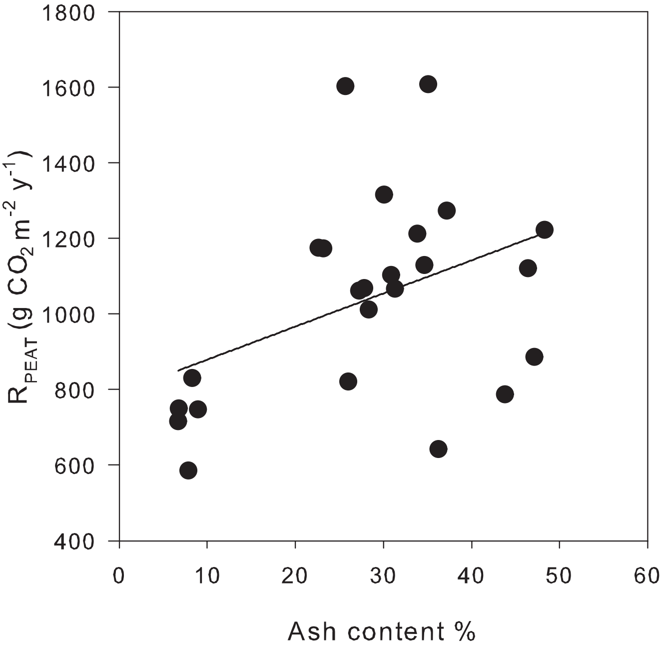

Figure 6. Annual heterotrophic peat soil respiration (R_{PEAT}) in afforested organic soil croplands versus peat ash content (r^2=0.133).

had reduced peat decomposition rates compared to that of the sites in active agricultural use, the entire heterotrophic respiration (R_{PEAT} +R_{LITTER}) in the studied sites was still substantial, due to high R_{PEAT}, and that litter production (Starr et al. 2005) most probably could not compensate for the increase in OM decomposition during the first few decades after afforestation, i.e. despite afforestation these soils were still losing carbon to the atmosphere. This would be in accordance with the measurements of Lohila et al. (2007) who showed that 30- year-old Scots pine plantation established on organic soil cropland acted still as a source of C to the atmosphere (50g CO_2 m^{-2} a^{-1}).

3.4. Errors related to the trenching and partitioning of R_{PEAT} from total soil respiration.

The trenching and partitioning approaches have some known factors that can cause bias in the measured fluxes (Subke et al. 2006). The assumption related to the trenching method is that root activity in the trenched area is completely suppressed because the connections of the roots to the living tree are terminated. However, roots, even without the energy supply from the aboveground parts, can survive and maintain respiration for several months after excision (Tate et al. 1993, Uchida et al. 1998) and some of them may grow deeper than the trenching depth. Furthermore, disturbance to the soil as well as excessive amount of decomposing fine roots and fungal hyphae can cause a significant increase in respiration rates immediately after trenching (Ewel et al. 1987, Wang and Yang 2007). The decomposition of this root material contributes to the measured respiration rate leading to an overestimation of heterotrophic respiration (Subke et al. 2006). Nevertheless, the initial effects of trenching have been shown to last only a few months (Ewel et al. 1987, Bowden et al. 1993, Komulainen et al. 1999).

In this study, we reported R_{PEAT} from the trenched plot one to two years after the trenching procedure took place. Therefore, we assumed that the influence from fine root residues to R_{PEAT} was negligible. The CO_2 efflux from the decomposition of coarse root residues as well as the possible CO_2 emissions from living roots under the trenching depth was ignored even though it may have resulted in a slight overestimation of the measured R_{PEAT}. In future, the proportion of root decomposition from R_{PEAT} in trenched plots could be estimated if the amount of roots present in the plots would be recorded either before or after the trenching experiment and their decay rate would be measured independently by using litter bags in the same environment.

Trenching can have impact on the abiotic soil environment as by trenching and killing the roots, transpiration through vegetation is terminated. This has been shown to affect the soil moisture conditions (Subke et al. 2006) in trenched plots. Similarly, the removal of above-ground vegetation and litter may affect the moisture conditions in the sample plots. Examination of the water content in the 0–10 cm soil profile inside and outside the treatment plots showed that in our study on the R_{PEAT} plots, soil moisture was, indeed, higher inside the treatment plot than outside of the plot (I). This effect could have been even greater in the drier periods during the growing season 2003 when the measurements of soil moisture content were not yet started. Thus the effects of soil moisture on R_{PEAT} may have been underestimated and thus the annual effluxes and proportion of R_{PEAT} from other respiration components overestimated.

Finally, trenched plots lacked substrate input from live roots and plant litter which in natural conditions could have served as addition of labile energy sources, and thus fuelled the decomposition of recalcitrant old peat material leading to higher effluxes trough priming. This would mean that observed R_{PEAT} was underestimated, to what extent, however, is unknown (Subke et al. 2011). At the moment, the priming effect is still an unresolved question; its relevance and magnitude in field conditions has not been firmly established but needs to be addressed in future research.

CONCLUSIONS

In this study we demonstrated that in drained forested peatlands R_{PEAT} was mainly regulated by soil temperature conditions, which would suggest that climate change and the associated increase in temperature would have the potential to substantially increase soil C release in these ecosystems. It was also apparent that the old peat storage in these areas is rather resistant to the short-term changes in WL conditions; fluctuations of WL in deep inert peat layers caused only minor change in R_{PEAT} whereas the majority of R_{PEAT} originated from the continuously aerated surface peat layers. We were, however, able to demonstrate that in low water level conditions there were mechanisms that could hinder R_{PEAT}. R_{PEAT} may be reduced if WL drawdown is excessive (> 61 cm) and drought starts to limit decomposition in surface peat layers. In addition to this, low prevailing water level conditions reduced the effect of temperature on R_{PEAT} i.e. the observed temperature sensitivity of R_{PEAT}. These changes in temperature sensitivity of decomposition were related to changes in microbial population structure in surface peat layers, but also decrease in surface peat heat conductivity as well as increase in proportion of decomposition from deep inert peat layers on observed R_{PEAT} could have contributed to the lower temperature sensitivity of R_{PEAT} in low WL conditions. The appearance of these mechanisms suggest that the warming induced C release from drained peat soils, may be constrained, if warming is accompanied by changes in evapotranspiration, precipitation regimes, and frequency of extreme events (e.g. droughts) that would severely affect WL and surface soil moisture conditions.

In this study we further demonstrated that changes in environmental factors following clearfelling caused rather small absolute changes in R_{PEAT}. This is because following clearfelling apparently two mechanisms hinder decomposition rates from increasing. A decrease in evapotranspiration raises the water table level which decreases the volume of aerated peat layers. Furthermore the soil surface is exposed to direct solar radiation which causes excessive dryness in the surface peat layers. These mechanisms are capable of compensating for the effect of increased soil temperatures on R_{PEAT} following clearfelling. Retention of logging residues, however, considerably increased R_{PEAT}. This indicates that human induced forestry activities could potentially cause significant C release from the oldest and largest C storage of these ecosystems. This C release may, however, be avoided if logging residue is removed from the site. Investigations on longevity of the effect of logging residue on soil CO_2 emissions as well as on the sources of CO_2 under the logging residues are needed to confirm this finding.

It appears that afforestation has potential to reduce the extremely high soil CO_2 effluxes of actively cultivated peat soils. The reduction of R_{PEAT} is due to the cessation of cultivation practices and possibly also by altered environmental conditions after afforestation. The major share (42%) of the total soil respiration after afforestation still originated from R_{PEAT}. The effects of agricultural history were obvious on peat properties and observed $R_{PEAT,}$ which result that these soils were still losing C to the atmosphere, despite afforestation.

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