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Soil CO_2 efflux in boreal pine forests in the current climate and under CO_2 enrichment and air warming

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Academic dissertation

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ABSTRACT

The aims of the study were to identify factors related to temporal and spatial variation in forest soil CO_2 efflux (F_s), compare measurement chambers, and to test effects of a climate change experiment. The study was based on four-year measurements in upland Scots pine forests.

Momentary plot averages of F_s ranged from 0.04 to 1.12 gCO_2m^{-2} h^{-1} and annual estimates for the forested area from1750 to 2050 gCO_2m^{-2}. Soil temperature was a dominant predictor of the temporal variation in F_s (R^2=76–82%). A temperature and degree days model predicted F_s of independent data within 15% on the average but underestimated it during the peak efflux period (July–August), possibly because of seasonal pattern in growth of roots and mycorrhiza. A comparison sub-study indicated that the reliability of the measurement chambers was not related to the principle i.e. non-steady-state through-flow, non-steady-state non-through-flow or steady-state through-flow.

Spatial variability of F_s within 400 m^2 plots in four stands was large; coefficients of variation (CV) ranged from 0.10 to 0.80, with growing season averages of 0.22–0.36. A positive spatial autocorrelation was found at short distances (3–8 m). In data from several stands, thickness of the humus layer explained 28% of the variation in F_s, and with the distance to the closest trees it explained 40%. F_s also correlated with root mass of the humus layer. Between-plot differences in F_s were small.

In the climate change experiment, CO_2 enrichment and air warming consistently, but not always significantly, increased F_s in whole-tree chambers. Their combined effect was additive, with no interaction; i.e. +23–37% (elevated CO_2), +27–43% (elevated temperature), and +35–59% (combined treatment), depending on year. Air warming was a significant factor in the 4-year data according to ANOVA. Temperature sensitivity of F_s under the warming, however, decreased in the second year.

Keywords: soil respiration, climate change, carbon flux, temperature response, spatial variation, elevated temperature

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Vantaa, May 2015

Sini Niinistö

This thesis is dedicated to the memory of my grandparents, Toivo and Irma Alarmo.

LIST OF ORIGINAL PAPERS

This thesis is based on the following papers, which are referred to in the text by the Roman numerals (I–IV). The articles I - III are reprinted with kind permission of the publishers, while the article IV is a manuscript.

I Niinistö S.M., Kellomäki S., Silvola, J. (2011). Seasonality in boreal forest ecosystem affects the use of soil temperature and moisture as predictors of soil CO_2 efflux. Biogeosciences 8: 3169–3186. http://dx.doi.org/10.5194/bg-8-3169-2011

II Pumpanen J., Kolari P., Ilvesniemi H., Minkkinen K., Vesala T., Niinistö S., Lohila A., Larmola T., Morero M., Pihlatie M., Janssens I., Curiel Yuste J., Grünzweig JM., Reth S., Subke J.-A., Savage K., Kutsch W., Østreng G., Ziegler W., Anthoni P., Lindroth A., Hari P. (2004). Comparison of different chamber techniques for measuring soil CO_2 efflux. Agricultural and Forest Meteorology 123: 159–176. http://dx.doi.org/10.1016/j.agrformet.2003.12.001

III Niinistö S.M., Silvola J., Kellomäki S. (2004). Soil CO_2 efflux in a boreal pine forest under atmospheric CO_2 enrichment and air warming. Global Change Biology 10(8): 1363–1376. http://dx.doi.org/10.1111/j.1365-2486.2004.00799.x

IV Niinistö S.M., Kellomäki S., Ylioja T. (2015). Spatial variability of soil CO_2 efflux in boreal pine stands. Manuscript.

Author's contribution:
Papers I and IV:
The field experiment to monitor ecosystem gas exchange in Huhus was initiated and designed by Seppo Kellomäki. Sini Niinistö designed and carried out soil CO_2 efflux measurements as well as measurements of soil moisture and temperature, aboveground litter, root density and physical properties of soil. Sini Niinistö was responsible for collecting and analyzing data and writing of the papers. Spatial autocorrelation analyses were carried out jointly. All authors commented on the papers and contributed ideas for the analysis and writing.

Paper II:
The study was initiated by Pertti Hari, Timo Vesala and Jukka Pumpanen. Jukka Pumpanen and Sini Niinistö carried out a comparative measurement trial prior to this study. Sini Niinistö participated also in a measurement campaign to test the calibration tank and the experimental design at the beginning of the experiment as well as in calculation of preliminary results from this test. Jukka Pumpanen was responsible for analyzing data and writing of the paper, together with Pasi Kolari. All authors commented on the paper.

Paper III:
The climate change experiment at Mekrijärvi was initiated and designed by Seppo Kellomäki. Sini Niinistö participated in the planning of the treatments. She designed and carried out soil CO_2 efflux measurements together with measurements of soil temperature and soil nitrogen content. She was also responsible for collecting and analyzing data and writing of the paper. All authors commented on the paper and contributed ideas for the analysis and writing.

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1. INTRODUCTION

1.1. Soil CO_2 efflux in a global context

Soil CO_2 efflux and global carbon cycle

In the global carbon cycle, carbon circulates between three reservoirs, the atmosphere, the oceans and the terrestrial biosphere that includes carbon storages such as soil organic carbon and plant biomass (Post et al. 1990; Schlesinger 1997). In the carbon exchange between the terrestrial biosphere and the atmosphere, CO_2 is taken up from the atmosphere by plants in photosynthesis and released to the atmosphere from the plant cover and soil in respiration. Net ecosystem carbon exchange (NEE) is determined as a relatively small difference between these two large fluxes, uptake and respiration.

Globally, respiration from soils has been estimated to range from 78 to 98 Pg C yr^{-1} which is approximately 10 times the amount of emissions from fossil fuel combustion and cement production (Raich et al. 2002; Bond-Lamberty and Thomson 2010; Hashimoto 2012). In forest ecosystems, soil respiration constitutes most of the total respiration (e.g. Janssens et al. 2001). It originates from root and mycorrhizal respiration as well as from respiration by soil microbes and fauna associated with decomposition of organic matter. Soil respiration is often measured as a flux of carbon dioxide from the soil surface i.e. as soil CO_2 efflux, which approximately equals soil respiration at annual scale but is influenced by transport conditions over shorter time steps (Raich and Schlesinger 1992).

Soil respiration has been reported to be regulated by two major environmental factors, temperature and moisture, with soil temperature usually having an overriding influence in forest ecosystems (e.g. Witkamp 1966; Schlesinger 1977; Morén and Lindroth 2000, Borken et al. 2002). In addition, substrate availability has been identified as a controlling factor of root- and microbial respiration, variation of which influences temperature response of soil respiration (Högberg et al. 2001; Davidson et al. 2006a; Conant et al. 2011; Kirschbaum 2013).

Climate change and soil CO_2 efflux

Global average temperatures are predicted to rise by 1–3.7°C by the end of the current century, depending on the scenario for the development of greenhouse gas emissions (IPCC 2013). Global warming has been suggested to increase the amount of CO_2 released from soils through enhanced decomposition of soil organic matter. Increased soil CO_2 efflux thus would provide a positive feedback to the atmosphere by further increasing the amount of atmospheric CO_2 (e.g. Jenkinson et al. 1991; Raich and Schlesinger 1992; Kirschbaum 1995; Cox et al. 2000). Experimental warming in various biomes has been found to cause significant increases in CO_2 efflux from soil (Rustad et al. 2001; Wu et al. 2011; Lu et al. 2013). Increase in soil CO_2 efflux has been observed to be more pronounced in forested than in low tundra and grassland ecosystems in some studies (Rustad et al. 2001), yet others have found no difference between ecosystems dominated by herbaceous or woody vegetation (Wu et al. 2011; Lu et al. 2013).

The magnitude of the response of soil CO_2 efflux to warming is predicted to be larger at high northern latitudes, where the storage of organic carbon in the soil and the temperature sensitivity of decomposition are both great (Kirchbaum 1995) and where climate warming is expected to be greater than on the average over the globe (Houghton et al. 2001; IPCC 2013). Results from warming experiments do not necessarily support the assumption of a greater response of soil CO_2 efflux in cooler regions (Rustad et al. 2001; Wu et al. 2011). However, the largest relative increase in soil CO_2 efflux in unmanipulated ecosystems as a response to a rise in ambient air temperature during the past two decades has been found in boreal and arctic ecosystems (Bond-Lamberty and Thomson 2010).

Climate warming significantly stimulates plant biomass and productivity in many ecosystems (Arft et al. 1999; Rustad et al. 2001; Wu et al. 2011; Lu et al. 2013). Growth reductions are, however, possible in drought-prone ecosystems (e.g. Camarero et al. 2015) or because of increased herbivory (e.g. Chung et al. 2013).Warming also increases losses of carbon from the soil to the atmosphere as CO_2 and CH_4 by enhancing the activity of roots and microbes (Rustad et al. 2001; Pendall et al. 2004; Wu et al. 2011). Increased net primary production could, however, provide more carbon inputs to the soil in the long term (Pendall et al. 2004). Warming can also affect terrestrial carbon cycling through its effects on availability of water and nutrients. Warming-induced water stress in upland soils could immobilize nutrients and reduce decomposition (Pendall et al. 2004). On the other hand, nutrient mineralization has been observed to increase under warming which could further stimulate plant productivity (Van Cleve et al. 1990; Peterjohn et al. 1994; Jarvis and Linder 2000; Rustad et al. 2001; D'Orangeville et al. 2014). Altogether, experimental research efforts have not yet resolved the overall response of global soil carbon stocks to global warming or the magnitude of expected feedbacks (Davidson and Janssens 2006; Conant et al. 2011).

Atmospheric CO_2 concentration is also increasing and that will enhance the net CO_2 assimilation of plants (Kimball et al. 1993, Curtis and Wang 1998, Saxe et al. 1998, Ainsworth and Long 2005, Luo et al. 2006; Wang et al. 2012a), accompanied by an increase in aboveground biomass, root growth, litter production and in consequent carbon inputs to the soil (Hyvönen et al. 2007; Pendall et al. 2004; Dieleman et al. 2010). Growth of trees has been found in some studies to be more responsive to elevated atmospheric CO_2 than that of herbaceous species (Ainsworth and Long 2005; de Graaff et al. 2006), and forests ecosystems have been identified as the most responsive to elevated CO_2 among the ecosystem types studied (Luo et al. 2006). However, no difference in growth response between woody and herbaceous species was detected in some other studies (e.g. Kimball et al. 1993; Wang et al. 2012a). A few studies in boreal or temperate tree stands have even reported little or no aboveground growth response to elevated CO_2 (Sigurdsson et al. 2001; 2013; Hättenschwiler et al. 2002; Bader et al. 2013).

In the combined elevated atmospheric CO_2 and warming experiments, plant biomass production is also enhanced (Dieleman et al. 2012). Reduced transpiration via altered stomatal conductance under elevated atmospheric CO_2 could alleviate possible warming-induced water shortage (e.g. Körner 2006; Huang et al. 2007). Alternatively, enhanced nitrogen mineralization under warming could provide nutrients needed to sustain greater plant productivity under atmospheric CO_2 enrichment. However, nitrogen limitation is likely to restrict increases in plant productivity and carbon sequestration in woody biomass in long-term, especially in boreal forests (Oren et al. 2001; Johnson 2006; Hyvönen et al. 2007; Sigurdsson et al. 2013).

As carbon inputs to the soil have been found to increase under conditions of elevated atmospheric CO_2, soil CO_2 efflux has also been observed to increase in various ecosystems (Luo et al. 1996; King et al. 2004; Jackson et al. 2009; Dieleman et al. 2010; Selsted et al. 2012). Fluxes of carbon dioxide between the ecosystem and atmosphere are thus likely to increase under atmospheric CO_2 enrichment but long-term carbon storage in soil might not be affected as much (Hungate et al. 1997; Schlesinger and Lichter 2001; Norby and Zak 2011). Although more carbon has been estimated to be stored both in plant and soil pools under elevated CO_2, the capacity to store carbon in long-term has been suggested to be greater in litter and soil carbon pools than in plant pools (Luo et al. 2003; Norby and Zak 2011). An increased global plant biomass stock has been reported in recent decades (Myneni et al. 1997), but more recently aboveground carbon stocks in European forests have even been reported to show signs that their carbon sequestration potential is saturating (Nabuurs et al. 2013). The overall effect of elevated atmospheric CO_2 on soil carbon storage has been difficult to assess in manipulation experiments because soil carbon pool is large compared to possible changes in input rates, and temporal and spatial variation in size of soil carbon pools is high (Hungate et al. 1996; Lukac et al. 2009; Luo et al. 2011). Conclusions have mostly varied from the neutral to positive response, with nitrogen additions in combination with CO_2 enrichment enhancing the positive response (Jastrow et al. 2005; de Graaff et al. 2006; Luo et al. 2006; Hungate et al. 2009; Dieleman et al. 2010; Norby and Zak 2011).

The combined impact of atmospheric CO_2 enrichment and climate warming on soil carbon storage has been predicted to be small in some studies (e.g. Kirchsbaum 2000). However, the limited experimental data to date implies that soil carbon cycling, i.e. inputs to the soil and decomposition may increase notably under elevated atmospheric CO_2 and climate warming (e.g. Pendall et al. 2004; Lukac et al. 2009; Dieleman et al. 2012; Dawes et al. 2013; Giardina et al. 2014). Long-term responses will depend on whether substrate availability will be stimulated to the same degree as decomposition and whether substrate quality will change enough to have an impact on sequestration rates (Pendall et al. 2004). Other terrestrial biogeochemical feedbacks under increased CO_2 and warming could also be important in modifying future climate change; such as effects induced by nitrogen availability, tropospheric ozone content and aerosols or effects caused by nitrous oxide (N_2O) and methane (CH_4) emissions especially from northern peatlands (e.g. Davidson and Janssens 2006; Arneth et al. 2010; van Groenigen et al. 2011).

1.2. Soil CO_2 efflux in northern forests and impact of a changing climate

Temporal and spatial variability of soil CO_2 efflux

In addition to temperature and moisture, factors affecting soil respiration and its temporal and spatial variability include vegetation and substrate quality, ecosystem productivity, relative allocation of primary production above- and belowground, dynamics of the above- and belowground flora, fauna and microorganisms and land-use and disturbance regimes including forest management (Rustad et al. 2000).

Seasonal variation in soil CO_2 efflux in northern forests originates from distinct seasons with seasonally fluctuating environmental factors and ecosystem processes. Noticeable peak periods of soil CO_2 efflux are observed in the summer or early autumn whereas soil efflux is lowest during the often-long winters (e.g. Rayment and Jarvis 2000; Högberg et al. 2001; Shibistova et al. 2002a; Pumpanen et al. 2003a; Domisch et al. 2006). In addition to seasonal changes in temperature and moisture, the seasonal pattern of soil CO_2 efflux is influenced by many factors; root production of boreal plants and as well as mycelial production of ectomycorrhizal fungi have been found to vary seasonally in northern ecosystems (Wallander et al. 1997; 2001; Steinaker et al. 2010), which most likely also influence the temporal variation of forest soil CO_2 efflux through root respiration and root-associated heterotrophic respiration. As soil CO_2 efflux has been observed to be strongly influenced also by the flux of recent photosynthates to the roots (Högberg et al. 2001; Keel et al. 2006; Savage et al.

2013), the short and intense period of photosynthesis of boreal forests (Linder and Lohammer 1981; Teskey et al. 1994), for instance, has an impact on seasonal pattern of soil CO_2 efflux. Microbial populations and litter inputs also vary seasonally (Lipson et al. 1999; Schadt et al. 2003).

Seasonality of soil CO_2 efflux has often been studied as a seasonality of the temperature response of the soil CO_2 efflux (e.g. Janssens and Pilegaard 2003; Curiel Yuste et al. 2004). Seasonality affecting soil respiration and soil CO_2 efflux can be seen as a combination of the seasonal variation in environmental variables, in substrate availability and quality, and their interactions. In addition to factors that influence CO_2-producing processes, i.e. soil respiration, some factors such as snow cover, soil moisture and pressure fluctuations can affect transportation of CO_2 from soil to the atmosphere, and thus apparent soil CO_2 efflux.

Spatially, soil CO_2 efflux has been observed to vary greatly within a forest stand, even in relatively homogenous tree stands (Raich et al. 1990; Martin and Bolstad 2009). Spatial variability has been concluded to be one of the greatest disadvantages of chamber measurements of soil CO_2 efflux (Mosier 1990). In some studies, spatial variability has, however, been assessed to be of minor importance on a larger scale, such at the level of watershed (Buchmann 2000). Yet, temporal variation in soil CO_2 efflux in forests has received more attention so far than the spatial variation and possible factors contributing to it.

Impact of changing climate

Boreal forests constitute a substantial terrestrial storage of carbon. Under the climate change, temperature is expected to rise in the boreal zone more than the global average does, with a greater increase in winter than in summer (IPCC 2013). Correspondingly, impact of changing climate on soil CO_2 efflux is anticipated to be great in the northern ecosystems (Kirschbaum 1995; Bond-Lamberty and Thomson 2010). For Finland, annual mean temperature is predicted to rise by 3 to 6 °C by the end of the current century (Jylhä et al. 2009). Precipitation is expected to increase as well, by 10 to 25%, more in winter than in summer (Jylhä et al. 2009).

In managed boreal forests in Scandinavia, higher temperatures, longer growing seasons and rising concentration of atmospheric CO_2 may considerably increase forest growth during the current century (Bergh et al. 2003; Kellomäki et al. 2008). However, periodical shortages of water and occurrence of different pests and diseases may become more frequent which could result in tree growth reductions as well as in shifts in tree species composition (Kellomäki et al. 2005; 2008).

In boreal forest soils, climate warming is predicted to increase the annual temperature, considerably shorten the period of persistent snow cover, shorten the length and depth of soil frost and advance soil warming in spring as well as to cause more freeze–thaw cycles in winter (Mellander et al. 2007; Kellomäki et al. 2010). Snow cover is predicted to develop later and melt earlier as the climate warms, which could conversely lead to colder soils in the wintertime and more frequent freezing events in soil. This has been found to damage fine roots and increase nutrient loss in northern forests although no effect on soil CO_2 emissions has been observed (Groffman et al. 2001; 2006). On the other hand, winter precipitation is likely to increase in most boreal ecosystems in future climate, which could result in local increases in snow depth also in Finland (Kellomäki et al. 2010; IPCC 2013). This could stimulate wintertime decomposition by moderating temperatures under the snowpack (Allison and Treseder 2011).

Warming in field experiments in forest stands has been achieved through soil or air warming or actively warming both soil and air, in open-air or using enclosures such as open-top or closed chambers (Table 1). Correspondingly, enrichment of atmospheric CO_2 has been realized in open air as Free-Air CO_2 Enrichment (FACE) or using open- or closed-top chambers. Experiments that combine warming and atmospheric CO_2 enrichment in forest stands have been rare (Table 1). Most of the field experiments have only applied treatments for the snow-free period or growing season. Differences in effects between soil and air warming treatments have not been properly addressed so far, most likely because of the limited number of air warming studies and because of other confounding factors such as possible species- and site quality-specific responses and differences in duration and magnitude of the treatments.

In field experiments, air or soil warming has been observed to enhance tree growth, especially in temperate and boreal forests (Strömgren and Linder 2002; Way and Oren 2010; Melillo et al. 2011; Lu et al. 2013). Carbon inputs to the soil are thus likely to increase in northern forests although carbon allocation pattern can be different under warming: an increase in the total biomass, especially in foliage mass, and thus in aboveground litter, but no similar increase in root mass (Way and Oren 2010). Belowground biomass has, in general, been observed to increase in forests under warming (Lu et al. 2013) although across different biomes no increase has been detected (Dieleman et al. 2012). In boreal forests, fine root mass has been observed to be greater under soil warming compared to ambient control in a Norway spruce forest (Majdi and Öhrvik 2004; Leppälammi-Kujansuu et al. 2013) although no differences were detected in black spruce forest with soil warming (Bronson et al. 2008). In temperate forests, a decline in fine root mass has been observed in a long-term soil warming experiment (Melillo et al. 2011).

Both biomass and net CO_2 assimilation of woody plants increase under conditions of elevated atmospheric CO_2 as well (Curtis and Wang 1998; Saxe et al. 1998; Ainsworth and Long 2005; Kilpeläinen et al. 2005; Norby et al. 2005; Stinziano and Way 2014), accompanied by increases in root biomass and production, litter production and root exudation and in consequent carbon inputs to the soil (Matamala and Schlesinger 2000; Hyvönen et al. 2007; Pendall et al. 2004; Jackson et al. 2009; Lukac et al. 2009; Dieleman et al. 2010; Iversen et al. 2012). Field experiments have usually demonstrated a greater increase in fine root biomass than in aboveground biomass under elevated atmospheric CO_2 (Dieleman et al. 2012). In a long-term alpine study at treeline, no effect in fine roots, however, was detected despite the positive effect of CO_2 enrichment on aboveground biomass of trees (Dawes et al. 2013).

Soil CO_2 efflux has been observed to increase also in warming experiments in temperate and boreal forests (Rustad et al. 2001; Lu et al. 2013; Table 1) as well as in experiments with atmospheric CO_2 enrichment (King et al. 2004; Lukac et al. 2009; Dieleman et al. 2010; Table 1). In some forest experiments, however, no significant treatment effect of soil or air warming or the combination of the two (Strömgren 2001; Comstedt et al. 2006; Bronson et al. 2008) or atmospheric CO_2 enrichment (Bader and Körner 2010) has been discerned. Soil CO_2 efflux in young developing stands appears to be more stimulated by CO_2 enrichment than efflux in more established stands (King et al. 2004) although the small number of field experiments in forest stands of any age makes differentiation difficult (Table 1).

The combination of warming and elevated atmospheric CO_2 has resulted in greater biomass production as well as in greater soil CO_2 efflux (Dieleman et al. 2012; Stinziano and Way 2014; Table 1). Responses of plant productivity to the combined treatment resembled more those observed in the elevated CO_2-only treatment than those observed in the warming treatment (Dieleman et al. 2012); i.e. the combined and elevated CO_2-only produced a larger stimulation of fine root biomass than of aboveground biomass, for instance. In boreal forests, low availability of nutrients could restrict the response of tree productivity to warming or elevated atmospheric CO_2 or to their combination (Sigurdsson et al. 2013).

In general, the magnitude of the response of soil CO_2 efflux to experimental warming of several years diminishes with time but no declining trend was observed for all individual experiments in a meta-analysis (Rustad et al. 2001). The meta-analysis showed no significant warming effect after the first three years (Rustad et al. 2001). Yet in another meta-analysis, there was no significant difference in the response detected most recently between experiments that had lasted less than 5 years and those that had lasted 5 years or more (Lu et al. 2013). In one of the longest experiments, in temperate Harvard Forest, effect of soil warming has either persisted or declined over a period of 7 to 10 years of soil warming (Melillo et al. 2002; 2011).

Effect of atmospheric CO_2 enrichment on soil CO_2 efflux has been observed to persist in experiments in temperate and boreal forests (King et al. 2004; Jackson et al. 2009; Hagedorn et al. 2013; Oishi et al. 2014). However, a decline in the magnitude of the effect has also been reported for long-term experiments (Bernhardt et al. 2006; Hagedorn et al. 2013). In contrast, another measurement campaign in one of these long-term experiments found no sign of a diminishing treatment effect on soil CO_2 efflux or root biomass, after more than a decade of CO_2 enrichment of a temperate pine forest (Jackson et al. 2009). Difficulties in detecting significant treatment effects at the site have been attributed to possibly insufficient spatial resolution of sampling (Daly et al. 2009).

Experimental data have thus far been too scarce for an analysis of long-term combined effects of warming and atmospheric CO_2 enrichment on soil CO_2 efflux. In the short term, the combined effect of these two factors appears to be additive (Dieleman et al. 2012). The small number of warming experiments so far has led to inclusion of both air and soil warming studies as warming experiments in meta-analyses which has made the interpretation of observed effects of warming on above- and belowground components of forest ecosystem challenging. Air warming could have a greater positive influence on tree growth through a greater carbon assimilation due to the possibly longer growing season (Chung et al. 2011) which could signify greater root mass and greater litter inputs to the soil or changes in litter quality (Chung et al. 2011). On the other hand, the greater magnitude of soil warming usually applied in soil warming experiments compared to the air warming experiments could enhance the decomposition and nutrient mineralization to a greater extent than under air warming.

In the long term, soil organic matter pools, roots and associated microorganisms all have distinct responses to elevated CO_2 and temperature but substrate availability will regulate the responses (Pendall et al. 2004) and thus the soil CO_2 efflux in a changing climate. Forest management can have a great influence on substrate availability, thus carbon cycling and storage in forest ecosystems will be moderated by forest management actions in future climate as well (e.g. Hyvönen et al. 2007). In addition, herbivory enhanced by warming could reduce growth of forest trees and thus carbon inputs to forest ecosystems. Warming-induced insect outbreaks could even increase the occurrence of forest fires and thus provide a positive feedback to climate warming (Ayres and Lombardero 2000; Chung et al. 2013).

Table 1. Examples of climate change experiments in temperate and boreal forests and their treatment impacts on soil CO_2 efflux.

Site	Treatment	Method	Ecosystem	Tree age	Duration	Treatment impact on soil CO_2 flux	References
Soil warming experiments in field							
Harvard Forest, MA, USA	soil warming (+5°C)	SC	temperate hardwood	50+	*a*. 1991-2000 *b*. 2003-2009 *c*. 2006-2009	*a*. +40, 14, 20% (years 1-3), +28% (first 6 yrs), +5% (years 7-9), no effect on year 10 *b*. +30% (years 1-2), +10–20% (years 3–7) *c.*+44% (years 2-3)	*a.* Peterjohn et al. 1993, Foster et al. 1997, Melillo et al. 2002, *b.* Melillo et al. 2011, *c.* Contosta et al. 2011
Anna and Archer Huntington Wildlife Forest, NY, USA	soil warming (+2, +5, +7.5°C)	SC	temperate hardwood	mature	2 growing seasons	+22–58% year 1 +2–29% year 2 (depending on T elevation)	McHale et al. 1998
Howland Integrated Forest Study site, USA	warming of Oa horizon (+4–5°C)	SC	temperate coniferous	45-130	3 growing seasons	+25% (static chambers) +40% (soda-lime)	Rustad and Fernandez 1998
Flakaliden, Vindeln, Sweden	soil warming (+5°C) irrigation	SC	boreal coniferous	35	1995-2009	+10–20% (with/without fertilization), +15 % for annual estimates (years 4-6), statist. significant in spring, +2% n.s.(year 15)	Strömgren 2001, Coucheney 2013
Stillberg, Alps, Switzerland	soil warming (+4°C)	surface cables	alpine mixed	32	1st year of warming	+45%	Hagedorn et al. 2009
Northern Limestone Alps, Austria	soil warming (+4°C)	SC	alpine coniferous	120	2 growing seasons	+45% (year 1) +47% (year 2)	Schindlbacher et al. 2009
Thompson, Manitoba, Canada	soil only warming(+5°C), irrigated on heated	SC	boreal coniferous	12	2 years	+24% (year 1) +11% (year 2)	Bronson et al. 2008

Table 1 continued

Site	Treatment	Method	Ecosystem	Tree age at start	Duration	Treatment impact on soil CO$_2$ flux			References
						Elevated T	**Elevated CO$_2$**	**ECO$_2$+ET**	
Field chamber experiments									
Mekrijärvi 1, Finland	air warming: (+2–3°C in summer, Tair >0°C in winter) [CO$_2$] enrichmnt (550 ppm)	OTC	boreal coniferous	20	2 years	no clear effect, +/− 10% in summer 2 depending on T elevation	+40% in summer 2	+40% in summer 2	Pajari 1995
Mekrijärvi 2, Finland	air warming (+5°C) [CO$_2$]enrichmnt (700 ppm) + irrigation	CTC	boreal coniferous	20+	4 years	for snow-free period of years 1–4: +39, +27, +30, +43%	+37, +23, +24, +32%	+59, +42, +53, +35%	This study, Niinistö et al. 2004
Suonenjoki, Finland	[CO$_2$] enrichmnt (650–730 ppm) [O$_3$] enrichment +irrigation	OTC	boreal hardwood	7	3 growing seasons		positive (+8–132%) for clone 1, negative for clone 2(n.s.) (−45–+64%),		Kasurinen et al. 2004
Flakaliden, Vindeln, Sweden	air warming (+2.8–3.5°C) [CO$_2$] enrichmnt (+340 ppm) C-13 labelling	CTC	boreal coniferous	40	2 years	no treatment effect	+48% (year 1) +62% (year 2)		Comstedt et al. 2006
Thompson, Manitoba, Canada	soil (+5°C) + air (5°C) warming (irrigation on heated plots)	OTC	boreal coniferous	12	2 years	−31% (year 1) −23% (year 2)			Bronson et al. 2008

Table 1 continued

Site	Treatment	Method	Ecosystem	Tree age at start	Duration	Treatment impact on soil CO_2 flux			References
						Elevated T	Elevated CO_2	ECO_2+ET	
Hiroshima University, Japan	air warming, +3°C [CO_2] enrichmnt (550/700 ppm) irrigation	OTC	warm temperate hardwood	3	6 years	annual sums (years 4-6): +4%	+25%(550ppm) +48%(700ppm)	+30% (550 ppm) +65% (700 ppm)	Wang et al. 2012b
Free-Air Carbon Enrichment (FACE)									
FACTS-I Duke Forest, North Carolina, USA	[CO_2] enrichment (+200 ppm) N fertilization	FACE	warm temperate coniferous	13	started in 1994, expanded 1996, up to 12 years	multiple studies with variable sampling : +27% (annual sum for years 2 and 3) +16% (average for years 1-5, midday values for years 1-5: +29, +39, +16, +17, +10) +24% (midday values for years 1–7) +15% (annual sums for years 1–7) +17 or 23% (average for years 1–12) no effect (year 10)			Andrews & Schlesinger 2001, Bernhardt et al. 2006, Daly 2009, Jackson et al2009, Oishi et al.2014
Swiss Canopy Crane, Basel, Switzerland	[CO_2] enrichmnt (550 ppm)	FACE	temperate harwood,	100	7 years	no effect on growing season efflux on year 7			Bader and Körner 2010
Aspen FACE , USDA Forest Service,Rhine-lander, USA	[CO_2] enrichment (+200 ppm) [O_3] enrichmnt	FACE	temperate hardwood	1+	10 growing seasons	+22% on average (years 1-4) (+13, +49, +22, +3 for *Populus*, +43,+60,+22, +29 for *Betula/ Populus*) +8–26% (years 5–7) +29, +31, 25% (years 8-10, significnat))			King et al. 2004, Pregitzer et al. 2006, 2008
ORNL FACE, Oak Ridge Nat. Laboratory, USA	[CO_2] enrichmnt (+200 ppm)	FACE	temperate hardwood	10	4 growing seasons	+12% on average for years 1-4 (+8, +11,+17, +11%)			King et al. 2004

[CO_2] enrichmnt= enrichment of atmospheric carbon, SC=soil cables, OTC= open-top chambers, CTC= closed-top chambers, tree age= tree age at start
ECO_2 +ET =Elevated atmospheric CO_2 and elevated air temperature, n.s.= not statistically significant

1.3. Measuring and modeling of soil CO_2 efflux in forests

Measuring of soil CO_2 efflux

Many different approaches have been used to measure CO_2 emissions from soil to the atmosphere. Traditionally, soil CO_2 efflux has been measured in enclosures in field, i.e. in different types of chambers placed on the surface of soil. Chamber measurements are relatively inexpensive, simple to operate and useful in identifying variation between and within the sites and physical, chemical and biological controls of soil surface fluxes (Livingston and Hutchinson 1995; Matson and Harriss 1995). Automation of chamber measurements has made them more temporally comprehensive but the cost of automation still limits spatial coverage of measurements. Manual chamber measurements usually allow for better spatial coverage whereas continuous observations from automated chambers improve the ability to measure and model effects of rapidly changing environmental variables (Law et al. 1999; Savage and Davidson 2003).

Chamber systems can be classified to steady-state and non-steady state systems depending on whether the concentration gradient between the chamber and the soil is kept as close to prevailing conditions outside the chamber (steady state) or whether the concentration of CO_2 is allowed to grow inside the chamber (non-steady state) which diminishes the gradient (Livingston and Hutchinson 1995). Non-steady state systems can be further divided into flow-through or non-flow-through systems whereas steady-state systems are by definition flow-through systems with an open-path circulation in which a constant flow of external air sweeps through the chamber.

Recently, micrometeorological techniques have also been deployed to quantify CO_2 emissions from the surface of soil. They cover larger, undisturbed surface area, do not affect local turbulence, pressure and CO_2 concentration conditions and provide continuous data (Baldocchi 2003; Lankreijer et al. 2003). In addition to sufficient turbulence below the forest canopy, the micrometeorological techniques such as eddy covariance require absence of other sources and sinks between the soil surface and the sensor, such as understorey vegetation or ground cover, or knowledge or assumption on the insignificance of these sources or sinks (Baldocchi and Meyers 1991; Lankreijer et al. 2003; Wu et al. 2006). Eddy covariance measurements below the canopy have thus often been combined with concurrent chamber measurements (e.g. Law et al. 2001; Shibistova et al. 2002b; Wu et al. 2006). However, large difference in areas sampled by the chamber measurements and eddy covariance measurements complicates the comparison between the two methods (Kelliher et al. 1999; Shibistova et al. 2002b).

Measurements of CO_2 concentration in different depths in soil have also been used to quantify CO_2 produced in soil and released to the atmosphere by applying the diffusion theory (e.g. Billings et al. 1998; Pumpanen et al. 2008). Advantages of this method include that soil horizons in which CO_2 is mostly produced can be identified and the effect of water content on transportation studied (Lankreijer et al. 2003; Pumpanen et al. 2008). On the other hand, estimation of soil and air diffusivity required for efflux calculations can be difficult (Lankreijer et al. 2003; Davidson et al. 2006b).

Processes producing soil CO_2 efflux have also been measured separately under laboratory and field conditions to understand the significance of different CO_2 producing components and their response to environmental changes. In practice, it has been difficult to separate respiration of living roots from the rest of the rhizosphere respiration, which includes respiration of mycorrhizal fungi and associated microorganisms, as well as respiration by decomposing microorganisms operating on root exudates and recent dead root tissue in the rhizosphere (Hanson et al. 2000).

Approaches to separate different components of the soil CO_2 efflux include 1) different root exclusion techniques such as trenching and girdling, 2) physical separation of components such as measurement of respiration from root-free soil cores or excised or *in situ* roots, and 3) isotope techniques such as labelling with ^{13}C or ^{14}C and radiocarbon dating, or a combination of these approaches (Hanson et al. 2000; Hahn et al. 2006; Kuzyakov 2006; Subke et al. 2006; Taylor et al. 2015). Indirect techniques have also been used; such as calculating root activity based on an assumption of a mass-balance between soil CO_2 emissions and rates of carbon input as litter (Raich and Nadelhoffer 1989; Subke et al. 2006). In the climate change experiments, use of sources of CO_2 with a known isotopic signature is an advance with which a better insight into processes behind soil CO_2 efflux in a changing climate can be gained (e.g. Andrews et al. 1999; Comstedt et al. 2006).

Modeling of soil CO_2 efflux

Studies on response of soil CO_2 efflux to environmental variables have been mostly focused on empirical models on the relationship between soil CO_2 efflux and soil temperature and moisture. The body of studies confirms a positive and nonlinear relationship between temperature and soil CO_2 efflux (Reichstein and Beer 2008). The relation between forest soil CO_2 efflux and temperature has been described as exponential early on (Anderson 1973). The most commonly used temperature response functions have been based on the exponential Q_{10} function, its modifications and Arrhenius' activation energy function, adapted from the work of two 19th century chemists, Van't Hoff and Arrhenius (Howard and Howard 1979; Lloyd and Taylor 1994; Davidson et al. 2006a; Reichstein and Beer 2008). Linear, quadratic functions and further-developed forms of the Arrhenius function have also been used (Howard and Howard 1979; Lloyd and Taylor 1994; Wang et al. 2003).

To improve empirical models of soil respiration, soil moisture or precipitation have been used as an additional predictive variables (Schlentner and Van Cleve 1985; Davidson et al. 2006a). The effect of soil moisture can vary. On one hand, soil CO_2 efflux, or its component microbial respiration, has been found to decrease with decreasing soil moisture in the laboratory (Orchard and Cook 1983; Gulledge and Schimel 1998) and in field studies in temperate and boreal forests (Savage and Davidson 2001; Subke et al. 2003; Kolari et al. 2009). On the other hand, insufficient aeration in wet soils has been observed to limit microbial respiration in the laboratory (Miller and Johnson 1964, Linn and Doran 1984) and the soil CO_2 efflux in the field (Kucera and Kirkham 1971). However, no decrease in microbial respiration with increasing soil moisture has been observed in some other laboratory studies (Gulledge and Schimel 1998; Ilstedt et al. 2000; Schønning et al. 2003). Impaired aeration associated with high moisture content can also diminish root respiration (Glinski and Stepniewski 1985). Under field conditions, root respiration or total soil CO_2 efflux has been noted either to decrease during the rain or even to considerably increase during or right after rain events (Rochette et al. 1991; Bouma and Bryla 2000; Savage and Davidson 2003; Lee et al. 2004; Kishimoto-Mo et al. 2015).

The effect of soil moisture on soil CO_2 efflux has been described as a linear, logarithmic, quadratic, exponential and parabolic function (Schlesinger 1977; Davidson et al. 2000; Reichstein and Beer 2008; Moyano et al. 2013). In many cases the influence of soil moisture on soil CO_2 efflux in forest ecosystems has been small or not discernible, with little impact on annual efflux (e.g. Lessard et al. 1994; Russell and Voroney 1998; Borken et al. 2002). Yet, it has been difficult to separate the effects of often covarying soil temperature and moisture in field conditions (Schlesinger 1977; Davidson et al. 1998).

Temperature and moisture have also an effect on the substrate supply for the respiratory processes in soil and on the growth of respiring tissues. A decreasing effect of drought on soil CO_2 efflux observed under dry conditions in forest ecosystems may therefore largely result from a substrate limitation caused by a limited diffusion of solutes in soil and not from the direct effect of water shortage on microbial activity (Davidson et al. 2006a).

Multiple seasonally varying ecosystem processes, i.e. phenological changes in processes supplying substrate for the soil respiration or for the growth of respiring tissues, complicate the separation of direct and indirect effects of environmental factors on soil CO_2 efflux. The seasonal variation in carbon allocation below ground can have an effect on specific respiration (i.e. per unit of tissue) and on total respiration of roots, mycorrhizae and rhizosphere microorganisms (Davidson et al. 2006a). For instance, root growth may vary in accordance with seasonal changes in temperature, and consequent changes in total root respiration thus reflect not only the response of root respiration to changes in temperature but also the changes in respiring root biomass (Boone et al. 1998; Davidson et al. 2006a). Thus, the apparent temperature response of root respiration may change although the response of specific root respiration may remain unaltered. The seasonally fluctuating environmental factors and ecosystem processes have indeed been found to result in seasonality of soil CO_2 efflux in forest ecosystems, which has been studied as a seasonality of the apparent temperature response of the soil CO_2 efflux (e.g. Janssens and Pilegaard 2003; Curiel Yuste et al. 2004).

Empirical, statistical models or response functions of soil CO_2 efflux to different environmental variables, based on experimental or monitoring data, have been further utilized in biogeochemical models of carbon cycling in forest ecosystems. However, thus derived soil respiration models do not separate the direct effects of temperature, moisture and substrate availability from the indirect effects of temperature and moisture on substrate diffusion and availability (Davidson et al. 2006a).

More mechanistic models for soil CO_2 efflux have been developed, usually separately for root and heterotrophic respiration: Root respiration models are based on submodels for growth and maintenance respiration whereas heterotrophic respiration is usually modeled as decomposition of 2–8 pools of soil organic matter with different turnover times (Reichstein and Beer 2008; Herbst et al. 2008). Models for soil CO_2 efflux could be further developed to include belowground processes such as priming and growth and turnover of microbes, mycorrhizal fungi and direct links to assimilation by the aboveground vegetation (exudates), as well as transport and storage of CO_2 in the soil (Reichstein and Beer 2008; Herbst et al. 2008; Maier et al. 2011).

2. AIMS OF THE STUDY

The aim of the study was to quantify temporal and spatial variability of soil CO_2 efflux in boreal Scots pine forests growing on mineral soil in the current climate and to test the effect of a changing climate on forest soil CO_2 efflux.

The specific objectives were:

- to compare different chamber techniques to measure soil CO_2 efflux (Paper II)
- to characterize soil CO_2 efflux in the boreal pine forests and to identify factors related to its temporal and spatial variation (Papers I and IV)
- to investigate the response of soil CO_2 efflux to environmental factors such as temperature and soil moisture and to use these response functions to predict soil CO_2 efflux in pine forests (Paper I)
- to study the impact of atmospheric CO_2 enrichment and air warming to soil CO_2 efflux (Paper III).

The study was based on four-year monitoring measurements and climate change experiment in the field conditions. Findings can be further utilized for assessment of carbon exchange of boreal forests at local, regional, national and global level. The study also contributes to the testing of the hypotheses on impacts of global warming and elevated atmospheric CO_2 on carbon flux from soils to the atmosphere.

3. MATERIAL AND METHODS

3.1. Structure of the study

The study consisted of four sub-studies on soil CO_2 efflux in a boreal pine forest. The analysis of the impact of environmental variables on soil CO_2 efflux in the present climate and in a climate change experiment, formed the core of the study (Fig. 1, Papers I and III). The study also yielded an estimate of the level of soil CO_2 efflux in a boreal pine forest during the snow-free period, i.e. spring, summer and autumn, as well as a rough estimate for the winter emissions (Paper I). A sub-study complemented the estimate with an analysis of the spatial variability of soil CO_2 efflux and of possible factors explaining spatial variation (Paper IV). Methodologies to measure soil CO_2 efflux were tested and compared in one of the sub-studies (Paper II), including the chamber that was used in the field measurements of this study.

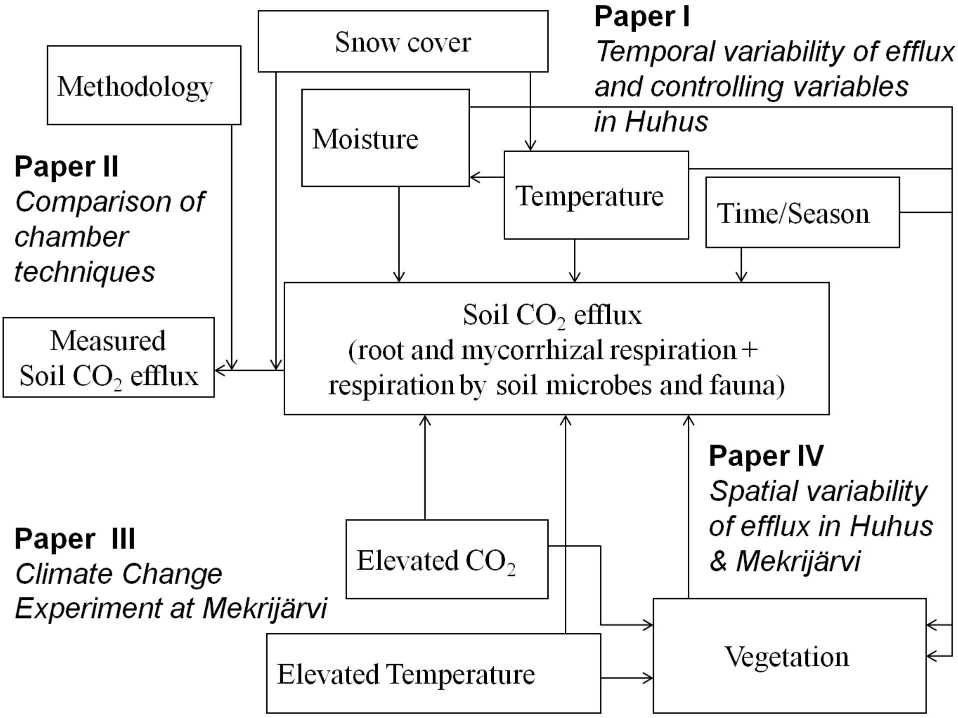

Fig. 1. Structure of the study.

3.2 Experimental set-up

Site and plot descriptions

The study concentrated on two sites within 30 km in Ilomantsi, Eastern Finland. The mean annual temperature at the nearby meteorological station in the area was 2.1°C, with monthly means of 16.0°C for July and −10.6°C for January. Mean annual precipitation was 667 mm, of which an average of 400 mm fell between May and October (Drebs et al. 2002).

The first study site was located in Huhus (62°52’N, 30°49’E) and consisted of two Scots pine (*Pinus sylvestris* L.) stands in a continuous pine forest (Table 2). The second site was located in Mekrijärvi, near the Mekrijärvi Research Station of University of Eastern Finland (62°47’N, 30°58’E). The main site in Mekrijärvi consisted of a young Scots pine stand in which a climate change experiment was also conducted. The auxiliary stand in Mekrijärvi was in an old, mature Scots pine forest. In total, three different stages of forest development were represented by the five plots in Huhus and Mekrijärvi (Table 2). The ground was covered with mosses, such as a feather moss *Pleurozium schreberi* (Brid.) Mitt., dwarf shrubs such as bilberry (*Vaccinium myrtillus* L.) and lingonberry (*Vaccinium vitis-idaea* L.), and lichens. Soils were podsolized with a 3 to 8 cm deep top organic layer consisting of litter and humus layers (Table 2).

Each measurement plot for soil CO_2 efflux was 20 x 20 m (400 m^2) and had 10 randomly chosen permanent measurement collars placed on a 2 x 2 m grid within the plots. In addition, a small plot of 0.7 x 0.7 m (0.49 m^2) was established in Huhus to study the spatial variability on a small scale. The sites and measurement plots for soil CO_2 efflux are described in detail in Papers I, III and IV.

Climate change experiment

The climate change experiment in Mekrijärvi consisted of 16 closed-top chambers built around individual trees in the young pine stand in a factorial design (Fig. 2). Experimental set-up has been previously described in more detail in Kellomäki et al. (2000) and in Paper III. There were three treatments: (1) elevated atmospheric CO_2 concentration, with a target concentration of 700 μmol mol^{-1}, (treatment hereafter referred to as ‘elevated CO_2’); (2) elevated air temperature with a 3–6 °C increase depending on the season (elevated T); and (3) a combination of elevated CO_2 and elevated air temperature (elevated CO_2 and T). There were four chambers in each treatment as well as four control chambers with ambient temperature and CO_2 concentration (Ctrl). Technical details and the performance of the chambers have been presented by Kellomäki et al. (2000). Each chamber covered a ground area of 5.9 m^2. The 20 x 20 m measurement plot in the same stand acted as an outdoor control for this climate change experiment (see the stand description for Plot M1 in Table 2).

In the whole-tree chambers, air was warmed by means of a ‘thermal glass’ with a built-in heating system, which covered half of the wall area. The air temperature inside each chamber followed changes in the outside temperature, either *per se* or according to the temperature elevation regime (Fig. 1 in Paper III). The annual mean air temperature in the heated chambers was 5 °C higher than in the non-heated chambers. The temperature elevation was greater in winter than in summer, as predicted for high latitudes (IPCC 2013). The soil temperatures at a 2cm depth in the organic layer were 2–4 °C higher in the heated than in the non-heated chambers at the time of soil CO_2 efflux measurements, during the snow-free period from May to October. The elevated CO_2 concentrations were within the range of 600–725 μmol mol^{-1} for 90% of the exposure time (Kellomäki et al. 2000).

Table 2. Plot characteristics in Huhus and in Mekrijärvi.

Plot	**Huhus H1**	**H2**	**H3**	**H0.1**	**Mekrijärvi M1**	**M2**
Experimental design						
Plot size, m	20 x 20			0.7x 0.7	20 x 20	
Number of CO_2 efflux collars	10	10 (15)	10 (15)	25	10	10
Stand and tree characteristics						
Development class	advanced thinning stand	advanced thinning stand	young thinning stand	see H2*	young thinning stand	mature stand
Past management	thinned	thinned	not thinned		not thinned	thinned
Stand structure	even	even	uneven, dense		clustered, dense	even
Tree age	65	65	40	no trees	25	85
Stocking, pines ha^{-}	600	675	2075		4625	300
Diameter at 1.3m,cm	18.8	21.5	11.2		5.1	30.6
Basal area, m^2 ha^{-1}	18	27	24		9	22
Ground cover						
dwarf shrubs	*Vaccinium myrtillus,V. vitis-idaea*			----	*Calluna vulgaris,* *V. vitis-idaea*	*V. myrtillus,* *V. vitis-idaea*
mosses	*Pleurozium schreberi*, *Dicranum* spp.			*P.schreberi*	*P.schreberi*, *Dicranum* spp.	*P.schreberi*, *Dicranum* spp.
lichens	*Cladonia* spp., *Cetraria islandica*			----	*Cladonia* spp., *C. islandica*	---
Mineral soil	podsolized sandy till (H1-H3, H0.1)				podsolized sandy loam	podsolized fine sand
Organic layer (Oi+Oe+Oa), cm	8	8	8	8	3	5

The year-round treatments of elevated CO_2 and temperature started in September 1996, and the soil CO_2 efflux measurements started in June the following year. Chambers were irrigated during the snow-free period with similar amounts regardless of the treatment. In wintertime, snow was added inside to protect the soil from freezing and to simulate the snow conditions outside. The factorial design of the experiment, with specific control chambers, enabled the effects of the treatments on soil CO_2 efflux to be assessed, even if conditions were somewhat altered by the closed-top chambers. For example, they reduced solar radiation (Kellomäki et al. 2000), which could possibly contribute to a significant chamber effect on soil CO_2 efflux (Nakayama and Kimball 1988; Luo et al. 1996). The isolation of a single tree into each closed chamber possibly further increased the chamber effect, because the high number of trees per hectare in the stand surrounding the chambers and encompassing the outdoor control plot for measurements of soil CO_2 efflux (Table 2).

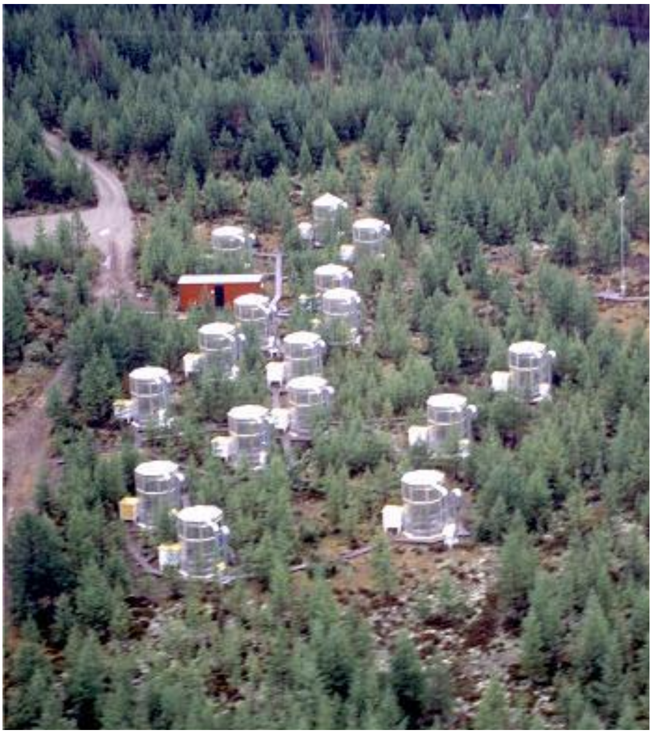

Fig. 2a. Aerial photograph of the climate change experiment in Mekrijärvi (Photograph: Topi Ylä-Mononen). **2b.** Close-up of one of the closed-top chambers built around a Scots pine in the year-round climate change experiment (Photograph: Sini Niinistö).

3.3. Soil CO_2 efflux measurements

Soil CO_2 efflux was measured with an infrared gas analyzer and a portable closed system with an opaque chamber that had a volume of 1.17 dm^3 (EGM-1 with SRC-1, PP Systems, Hitchin, UK). On each 20 x 20 m plot, ten permanently placed steel collars with a diameter of 10 cm were inserted 2–4 cm deep into the surface soil so that their tops were level with the of the mosses or lichens. The small plot of 0.49 m^2 used to study small-scale variability had 25 permanent collars next to each other. Values for soil CO_2 efflux included dark respiration of mosses and lichens which was estimated to have added some 10% to the soil CO_2 efflux in average conditions, as measured in the third year of the study, 1999.

Soil CO_2 efflux measured with the closed chamber used in this study was compared with a known CO_2 efflux, ranging from 0.32 to 10.01 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ (i.e. 0.05–1.59 $gCO_2\ m^{-2}\ h^{-1}$ at 0°C), in a study testing different chamber techniques and chamber designs (Paper II). The known CO_2 efflux was generated by a specially developed calibration tank. Fluxes were measured on coarse sand, fine sand and wetted fine sand with air-filled porosities of 47, 53, 33 vol.%, respectively. As a result, the measurement system used in this study (the infrared gas analyzer EGM with a chamber SRC-1 and closely fitting collars, NSF-2 in Table 1 in Paper II) overestimated soil CO_2 efflux by 5–27 % in conditions of air-filled porosities of 33–53%. However, overestimations or underestimations smaller than 10% were not considered statistically significant.

In field, air-filled porosities in mineral soil ranged from 21 to 29% in 1998 and from 21 to 40% in 1999 (Paper I) which indicated that soil CO_2 efflux was overestimated on the average by 5% in 1999 and less than 5% in 1998, assuming linear dependence between air-porosity and overestimation with the standard chamber. For the topmost layer of organic humus and uppermost mineral soil, the range of air-filled porosities of 27–46 (total porosity of 64%), suggested that the overestimation by the chamber type could have been 10% on the average for the dry year of 1999. For the wetter year of 1998, overestimation can be assumed to be smaller because of smaller air-filled porosities, but it was not quantified because of the lack of water-content measurements for the layer in question that year.

Soil CO_2 efflux measurements were made from the beginning of June 1997 to the end of October 2000. In the regular field plots (Plots H1–H3 and M1, see Table 2), measurements were made twice per measuring day, one or two days a week throughout the snow-free period i.e. May–October, with a three-week gap in September–October 1997 and in August 1998 due to equipment failure. Additional plots to complement the study of spatial variability were measured less frequently: Plot M2 in Mekrijärvi was measured twice a day, on two days a week but only from July to September 1999. Plot for small-scale variability, Plot H0.1 in Huhus was measured once or twice a month from May to October 1999.

In the climate change experiment, three permanent collars within the 16 whole-tree chambers were measured on each measurement day, on 1 or 2 days a week from June to October in 1997 and from May to October in 1998–2000. The outdoor control plot, Plot M1, was measured twice on the same measurement days as the collars in the whole-tree chambers.

Winter measurements were made once a month at 4–6 locations in Huhus in February–April 1999 and March–April 2000. They were carried out to estimate the annual soil CO_2 efflux but were not used in modelling. Larger chambers with a larger surface area (60 cm x 60 cm), and long measurement times were used to capture low winter fluxes. Air in the headspace was sampled every 15 min during each 60 min measurement. The CO_2 concentration of samples was analyzed on the same day with an infrared gas analyzer (Uras 3E, Hartman & Braun AG, Frankfurt/Maine, Germany) (Paper I). More details on soil CO_2 efflux measurements are presented in Papers I, III and IV.

3.4. Measurement of soil temperature, moisture and other environmental variables

Measurements of soil temperature, moisture and root mass are described in Table 3 and in papers I, III and IV.

Table 3. Measurements of soil temperature, soil moisture and root mass.

Variable, site, method	Make, manufacturer or method	Unit	Frequency	Time period	Soil layer
Soil temperature measurements					
HUHUS and MEKRIJÄRVI	Soil Temperature Probe, PP Systems, UK	°C	with each soil CO_2 efflux measuremnt	snow-free seasons 1997- 2000	humus layer/ topmost mineral soil
HUHUS	Vaisala Weather Station	°C	every 10 min	May 97–Oct 2000	several depths, from humus to 20 cm in mineral soil
MEKRIJÄRVI	Pt-100, Muurlan Elektroniikka Ky, Helsinki, Finland	°C	every 10 min	May 97–Oct 2000	at 5 and 10 cm in mineral soil in CTC's and outside
Soil moisture measurements					
HUHUS					
Soil water potential					
Tensiometers	Soil Moisture Inc., USA	kPa	Once/twice a day	May– Sept 98 May–Oct 99	several depths at 5–30 cm in mineral soil
Soil water content					
Reflectometers	CS615 sensors, CR10X datalogger, Campbell Scientific, LE, UK	vol,%	Every 15 min	Apr 99–Oct 2000	Surface (organic+mineral) and 2–28 cm in mineral soil
Gravimetric	Dry mass (oven 105°C, 24h)	%	Once a day	May–Oct 98	Litter (Oi) Humus (Oe+Oa) 0-10 cm in mineral soil
				Jun–Oct 99	Moss (living) Litter (Oi) Humus (Oe+Oa) 0-10 cm in mineral soil
MEKRIJÄRVI	Theta Probe ML1, Delta-T Devices, Cambridge, UK	vol.%	every 10 min	May 97–Oct 2000	at 5 and 15 cm in mineral soil
Root mass measurements					
HUHUS					
Roots were sieved, washed, identified under a microscope and divided into 1) fine roots of all species (diameter<0.5 mm) and 2) coarse roots (diameter>0.5 mm). Coarse roots were further sorted into pine and dwarf shrub roots. Roots were dried at 70°C (48 h) and weighed.				end of Oct 99	humus layer, topmost 5 cm of mineral soil

4. RESULTS

4.1. Comparison of different chamber techniques for measuring soil CO_2 efflux

Soil CO_2 efflux measured with different types of chambers was compared with a known CO_2 efflux ranging from 0.32 to 10.01 μmol CO_2 m^{-2} s^{-1} (i.e. 0.05–1.59 gCO_2 m^{-2} h^{-1} at 0°C) which was generated by a specially developed calibration tank (Paper II). Different chamber techniques tested were non-steady-state through-flow chambers (NSF), non-steady-state non-through-flow chambers (NSNF) and steady-state through-flow chambers (SSFL).

Results varied greatly among the twenty measurement systems tested: In some cases, the same chambers showed variable results depending on measurement system design or even without apparent differences in design (Table 1 in Paper II). Non-steady-state through-flow chambers (NSF) either underestimated or overestimated the fluxes; underestimation between the fluxes measured with chambers and actual fluxes ranged from 4 to 21% and overestimation from 1 to 33% depending on the type of chamber, collars and the method of mixing air within the chamber's headspace. Average fluxes of all tested systems were, however, within 4% of reference fluxes.

The non-steady-state through-flow chamber (NSF) used in our field measurements (a chamber SRC-1 connected to the infrared gas analyzer EGM-1, PP-Systems) was tested with different designs. The PP Systems' measurement system with chamber-matching collars (NSF-2 in Table 1 in Paper II) yielded an overestimation of 5% in conditions of wet fine sand that most closely resembled the average conditions in mineral soil in the field during the dry year (Paper I).

For our field measurements, the overestimation could similarly be estimated to be on average 5% for mineral soil in 1999, for which the average air-filled porosity was close to the air-filled porosity of the wet fine sand used in the calibration study. For mineral soil in 1998, overestimation can be estimated to be on the average less than 5%, assuming a linear correlation between air-filled porosity and overestimation found in the comparison study (Paper II). For the topmost layer of organic humus and uppermost mineral soil, the soil water content measurements were available only for the dry year of 1999, for which the overestimation by the chamber type could have been 10% on the average. For the wetter year of 1998, the overestimation for this layer can be assumed to be smaller because of lower air-filled porosities.

Non-steady-state non-through-flow chambers (NSNF) mostly underestimated fluxes. On the average, the underestimation was about 13–14% on fine sand and 4% on coarse sand (Table 1 in Article II). Steady-state through-flow chambers (SSFL) worked almost equally well in all sand types used in this study. They overestimated the fluxes on the average by 2–4% (Table 1 in Paper II). Overall, the reliability of the chambers was not related to the measurement principle *per se*.

4.2. Temporal variability and annual estimates of soil CO_2 efflux

The snow-free period started in late April or early May and ended at the end of October. Soil CO_2 efflux peaked in general in July–August, following changes in soil temperature (Fig. 1a, b in Paper I). Plot averages of soil CO_2 efflux ranged from 0.04 to 0.90 gCO_2 m^{-2} h^{-1} for the snow-free period in 1997, 1998 and 1999 in Huhus and from 0.05 to 1.12 $gCO_2\ m^{-2}\ h^{-1}$ in Mekrijärvi (Papers I, III). Effect of drought was evident in the dry year of 1999 as soil CO_2 efflux was some 30% lower in September than in the previous wet year, although mean soil temperature during the measurements was the same and the range of temperatures was similar (Fig. 1c, d in Paper I). In winter, plot means were on the average 0.06 $gCO_2\ m^{-2}\ h^{-1}$ for 1999 and 0.12 $gCO_2\ m^{-2}\ h^{-1}$ for 2000 (Paper I).

Annual estimates of soil CO_2 efflux were 1750 and 2050 $gCO_2\ m^{-2}$ for 1998 and 1999, respectively. For snow-free periods, the estimates were based on response functions with soil temperature, soil moisture and degree days as variables. For winter months, the cumulative efflux was calculated based on the mean of the winter observations. The peak period of soil CO_2 efflux, from June to August, represented some 50% of the annual estimate. The six winter months, from November to April, represented, on the average, 14–25 % of the annual soil CO_2 efflux (Paper I).

4.3. Response of soil CO_2 efflux to soil temperature and moisture

Soil temperature was found to be a good predictor of soil CO_2 efflux during the snow-free period. A regression model with soil temperature and its square as predictors explained 76–82% of the variation in the natural logarithm of efflux (Paper I: Fig. 4 and Table 2). Soil CO_2 efflux was higher at a given temperature of the organic layer later in the snow-free period (in August and September) than in spring and early summer (in May and June) (Fig. 3). According to month-specific temperature response models, the month of May had the lowest predicted CO_2 efflux at 10 °C and August the highest. Regression coefficients for temperature, approximations of a Q_{10} value, of month-specific models decreased with increasing average soil temperatures (Fig. 3). Efflux observations in July showed no clear response to soil temperature or moisture (Paper I).

Relationship between soil CO_2 efflux and soil moisture was two-sided. During the first three months of the snow-free period, May–July, a decrease in soil moisture was correlated with an increase in soil CO_2 efflux. There was also a strong negative correlation between soil water content and time in May–July. A similar strong, but positive correlation was found between soil CO_2 efflux and time. There was no clear correlation between soil CO_2 efflux and soil moisture during the latter part of the snow-free period, August–October, in the two years, 1998 and 1999, for which soil moisture data were available (Paper I). In contrast, soil CO_2 efflux linearly increased with increasing soil moisture when observations for which the soil matric potential was smaller than −10 kPa were considered. The negative effect of dry conditions was notable in 1999: Soil CO_2 efflux at 10°C was one third smaller in September of the dry year 1999 than in September of the wetter year 1998 despite the same average soil temperature and similar range of temperatures (Paper I). Accordingly, variation in water content of mineral soil alone explained 64% of the variation in ln-transformed efflux in the driest conditions of August and September 1999. The month-specific temperature models based on 3-year data equally overestimated the efflux in these conditions (Paper I).

To simultaneously analyze the response of soil CO_2 efflux to soil temperature and moisture, multiple regression analyses were carried out. As a result, soil temperature was found to be the dominant predictor of ln-transformed soil CO_2 efflux. Addition of the square of soil temperature markedly improved the regression model. Degree days or its alternatives, day of year and degree days divided or multiplied by day of year, were better auxiliary predictors than soil moisture was (Table 2 in Paper I). A multiple regression model with soil temperature, degree days as an index of seasonality and their squares as predictors was found to have a good fit for the entire snow-free period (Paper I).

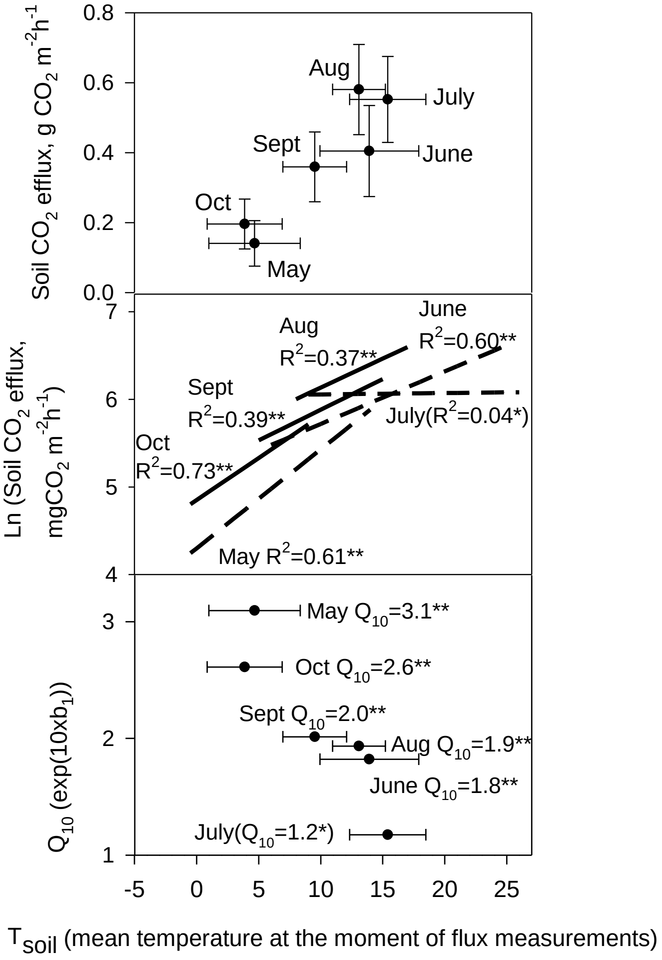

Fig. 3. a. Means for soil CO_2 efflux and soil temperature for monthly subsets of three-year data (1997–1999). Error bars represent standard deviation. Number of observations varied from 50 (May) to 126 (July).

b. Month-specific temperature-response models based on three-year data (1997–1999). Models formulated as LnFlux= $b_0 + b_1 \times T_{soil}$.

c. Q_{10} calculated as $Q10 = e^{10\times b1}$, b_1 from the temperature-response model formulated as LnFlux= $b_0 + b_1 \times T_{soil}$. Constants, b_0's were 4.302 (May), 5.121 (Jun), (6.042 (Jul)), 5.475 (Aug), 5.182 (Sep), and 4.851 (Oct). Regression coefficients, b_1's, did not differ statistically significantly between May and October, but the constants did ($p < 0.001$). The same was true for comparisons between June, August and September. (Figure originally published in Paper I, i.e. Niinistö et al. 2011)

The performance of the different regression models, i.e. the response functions parameterized with the 1998 and 1999 data, was consequently compared to independent sets of soil CO_2 efflux data collected on two sites, Huhus and Mekrijärvi, in the year 2000. In general, the models overestimated the efflux at low temperatures, i.e. in May and October at both sites, but underestimated the efflux somewhat during the time of peak efflux (July–August) in summer (Fig. 4, Paper I). On the whole, the quadratic temperature and degree days model performed best, with a high correlation between measured and predicted flux at both sites. Inclusion of degree days in the temperature model resulted in a notable improvement, i.e. in a decrease in average difference between measured and predicted flux for both sites (Fig. 7 in Paper I). It especially improved predictions at low temperatures in May but also, in general, in June to September, although not in October (Fig. 4). The difference between measured and predicted fluxes in 2000 was on the average 14% for Huhus and 12% for Mekrijärvi.

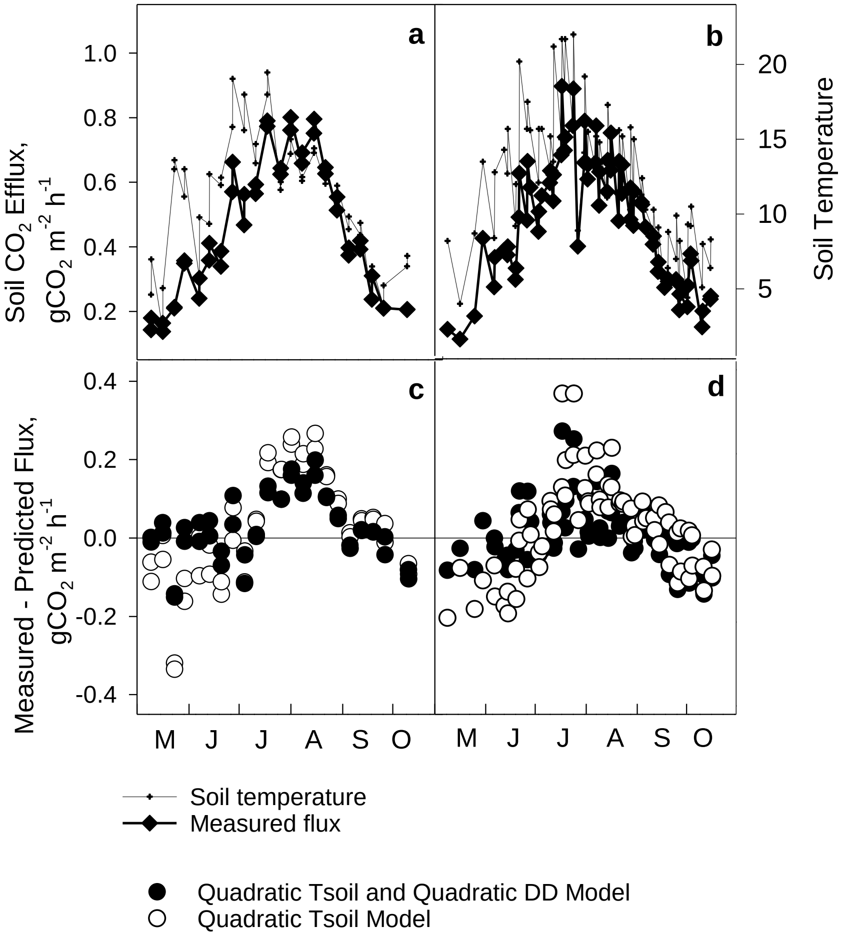

Fig. 4. Model evaluation: Soil CO_2 efflux and soil temperature at the time of measurements in 2000 (**A.** in Huhus and **B.** in Mekrijärvi) and the difference between measured and predicted efflux (**C.** in Huhus and **D.** in Mekrijärvi). Models formulated as LnEfflux= $b_0 + b_1 \times T_{soil} + b_2 \times T_{soil}^2$ and LnEfflux= $b_0 + b_1 \times T_{soil} + b_2 \times T_{soil}^2 + b_3 \times$degree_days+ $b_4 \times$degree_days^2. *N.B.* Degree days= Sum of effective temperature (>5°C), i.e. heat sum. See Table 2 in Paper I for values of regression coefficients. (Figure originally published in Paper I, i.e. Niinistö et al. 2011)

4.4. Response to atmospheric CO_2 enrichment and air warming

In the whole-tree chamber experiment, elevated atmospheric CO_2 and elevated air temperature consistently increased, although not constantly statistically significantly, soil CO_2 efflux over the 4-year period. The combined treatment of elevated CO_2 and elevated temperature generally yielded the highest monthly mean of soil CO_2 efflux during the first three exposure years (Fig. 5). The relative differences between the controls and the combined treatment were clear and usually significant both early and late in the snow-free period, that is, in May and in September–October (Fig. 5, Table 1 in Paper III). The positive effect of the elevated temperature treatment appeared to be more pronounced early and late in the snow-free period, whereas that of the elevated CO_2 alone was especially notable late in the snow-free period (Fig. 5, Table 1 in Paper III). In the fourth exposure year, unlike during the first three years, the elevated temperature treatment generally yielded the highest monthly efflux (Paper III).

The mean soil CO_2 efflux for the snow-free periods for the four years of the experiment was 35–59% higher in the combined treatment of elevated CO_2 and elevated temperature than the control value. The difference was the greatest and statistically significant in the first year (Fig. 5, Table 1 in III). The corresponding increase for the elevated CO_2 treatment alone was 23–37% (Fig. 5, no significant differences). The increase found in the elevated temperature treatment alone, 27–43% depending on the year, did not differ significantly from the control value.

Temperature elevation, with or without CO_2 enrichment, emerged as a significant factor in the analysis of variance on the combined four-year data of soil CO_2 efflux (Table 5). However, both CO_2 enrichment and elevated temperature significantly affected the mean soil CO_2 efflux in the first year. Inclusion of the needle area from the pre-treatment year of 1996, an indicator of initial tree size, as a covariate, emphasized the effects of CO_2 enrichment and elevated temperature in the models, especially for the first year but also for the second year. No significant effects were found in the third or fourth year, although there was an indication that both elevated CO_2 and temperature might explain some of the variance found in data for the third year (Table 2 in Paper III). None of the analyses suggested any significant interaction between the two main factors, elevated CO_2 and elevated temperature.

The temperature response functions were used to examine the effects of the treatments independently of the temperature regime. The elevated CO_2 treatment appeared to maintain the highest soil CO_2 efflux at a given soil temperature over the 4-year period (Fig. 6). All three treatments manifested a greater CO_2 efflux at a specific soil temperature than the controls in the first year (Fig. 6). By contrast, in the second year the temperature sensitivity of soil CO_2 efflux appeared to be lower in both the elevated temperature treatments, with or without CO_2 enrichment, than in the controls, and their slopes were smaller than those of the controls although not significantly so (Fig. 6, Table 3 in III). In the third and fourth years, the differences between the treatments and between each treatment and the control chambers were marginal. On the other hand, the elevated temperature treatment and elevated CO_2 treatment appeared to yield a slightly higher CO_2 efflux at a given soil temperature than the controls in the fourth year; the intercepts i.e. baselines of soil CO_2 efflux were significantly greater (Table 3 in III, Fig. 6).

Estimates of the needle area of single trees were used in a linear regression analysis to study the variation in soil CO_2 efflux among the chambers, and thus, to shed light on the nature of the relationship between soil CO_2 emissions and tree size, and indirectly also on the whole-tree physiology of the treatment trees. Needle area was found to be a significant predictor of soil CO_2 efflux, together with or without soil temperature as a predictor, in August of the first year and in July–September of the second year. Variation in needle area alone explained 24–39% of the variation in soil CO_2 efflux data, with greater needle area signifying greater efflux (Paper III). Soil CO_2 efflux in the whole-tree chambers appeared, however, to be most influenced by soil temperature alone during the early and late parts of the snow-free period.

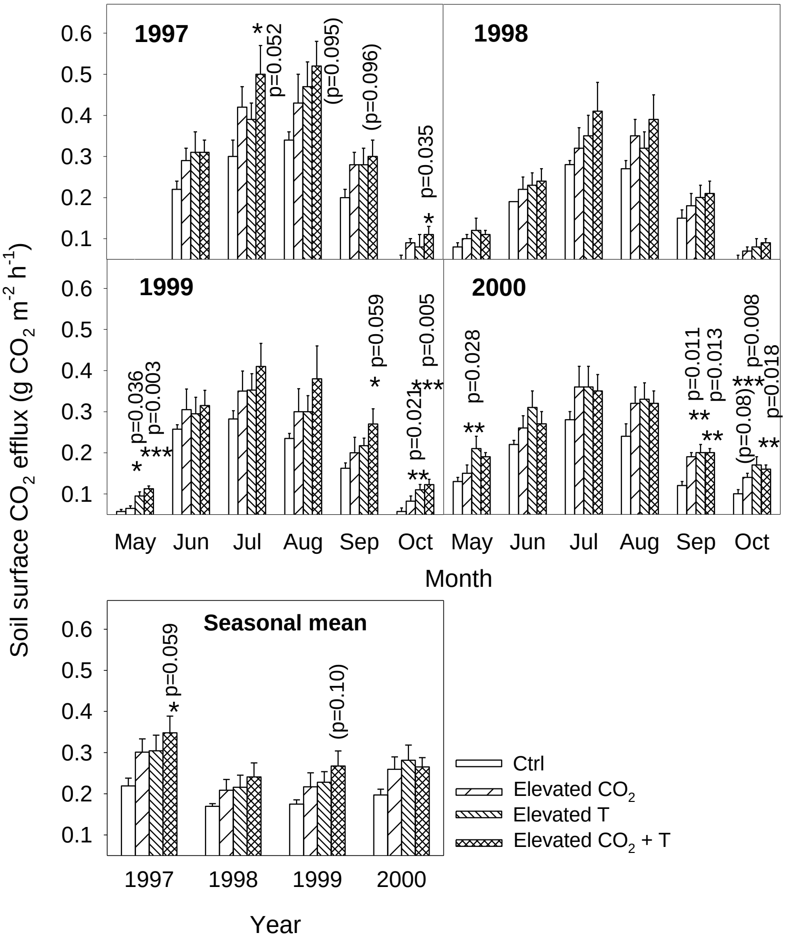

Fig. 5. Monthly and seasonal means (June–October in 1997, May–October in 1998–2000) +SE for soil surface CO_2 efflux. Asterisks denote differences relative to the controls in Dunnett's two-tailed test: $^*P<0.06$, $^{**}P<0.03$, $^{***}P<0.01$. (Figure originally published in Paper III, i.e. Niinistö et al. 2004)

In conclusion, elevated atmospheric CO_2 and air temperature consistently, but not always significantly, increased the forest soil CO_2 efflux during the 4-year study period. Their combined effect was additive, with no apparent interaction. Temperature elevation was a significant factor in the combined 4-year efflux data, whereas the effect of elevated CO_2 was not as evident (Paper III).

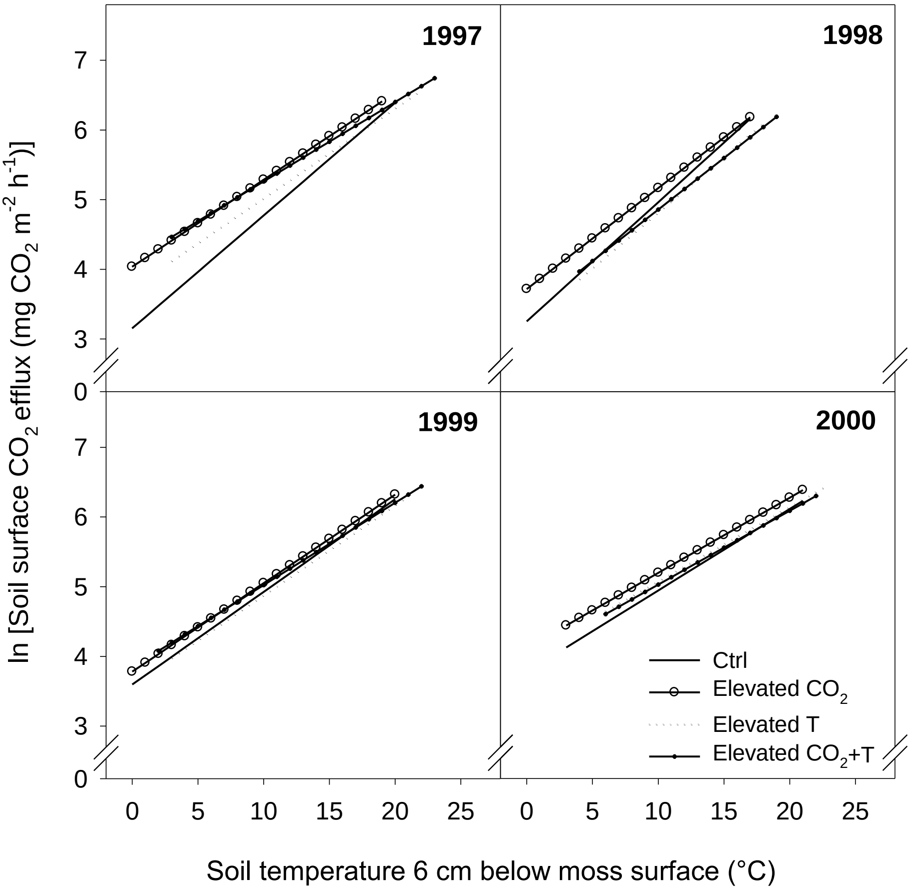

Fig. 6. Predicted natural logarithm of soil CO_2 efflux as a function of soil temperature in the controls and treatments in 1997–2000 (see Table 3 in III for the linear regression equations). (Figure originally published in Paper III, i.e. Niinistö et al. 2004)

4.5. Spatial variability of soil CO_2 efflux in boreal pine stands

Spatial variability of soil CO_2 efflux within the 20 x 20 m plots in four managed Scots pine stands was large from time to time; coefficient of variation (CV) ranged from 0.10 to 0.80 within the plots. The average CV for the snow-free period ranged between 0.22 and 0.36, depending on the plot, stand and year. Notably, the average CV of the small plot (0.7 x 0.7 m) was also within this range. In contrary, CV of plot averages, i.e. spatial variation between 20 x 20 m plots was small, or approximately 0.10 (Table 4; Paper IV).

The average efflux from a single measurement point ranged between 0.23 and 0.69 gCO_2 $m^{-2}h^{-1}$, depending on plot and year, the greatest average being about 1.5–2.5 times the smallest within a plot of 20 x 20 m. A positive spatial autocorrelation was indicated at short distances, i.e. at 3 to 8 meters, on several of the plots (Table 5). Similar correlation was found at 15 cm for the small plot of 0.7 x 0.7 m.

Thickness of organic humus layer emerged as a significant predictor of spatial variation of soil CO_2 efflux on different spatial scales. Approximately one third of the spatial variation in average soil CO_2 efflux was explained by the thickness of the organic humus layer in pooled data from four 20 x 20 m plots in three stands (Table 6). Findings from the small plot (0.7 x 0.7 m) with a homogenous moss cover supported this (Paper IV).

Soil CO_2 efflux was also found to correlate with the distance to the closest trees and root mass variables measured in the humus layer. In the pooled data from three stands, variation in thickness of the organic humus layer explained 28% of the variance of the average soil CO_2 efflux for the snow-free period of 1999, and together with the average distance to the three closest trees, as much as 40% of the variation was explained (Table 6). Soil temperature measured next to each collar did not correlate alone with soil CO_2 efflux. Yet, variation in the distance to the closest trees, multiplied with average tree diameter, and variation in temperature explained together as much as 50% of the variation in efflux in the middle-aged Scots pine stand (Fig. 7; Table 6).

Differences in soil CO_2 efflux between plots and stands were small, especially between plots adjacent to each other in Huhus and during the dry year. A statistically significant difference in average soil CO_2 efflux for the snow-free period was found only in the first year between the plots: the average efflux was higher in the 65-year old middle-aged stand than in the 40-year old pole-stage stand (Paper IV). The older stand had a larger standing stock of pines and total root mass (both trees and understory) in the upper soil. The younger, denser stand had, however, a greater mass of pine roots, which was compensated in the older stand with a greater mass of dwarf shrub (*Vaccinium* sp.) roots.

Table 4. Collar-specific mean soil CO_2 efflux and temperature and coefficients of variation (CV) of soil CO_2 efflux.

	Site			**Huhus**		**Mekrijärvi**		**Huhus**
	Plot		**H1**	**H2**	**H3**	**M1**	**M2[a]**	**H0.1**
Variable		**Year**						
Collar-specific mean soil CO_2 efflux, $gCO_2\ m^{-2}h^{-1}$ (May-Oct)	plot mean	1998	0.39	0.42	0.35	0.43	n.a.	n.a.
	(s.e.)		(0.030)	(0.029)	(0.018)	(0.036)		
		1999	0.38	0.39	0.38	0.50	0.54	0.29
			(0.032)	(0.024)	(0.016)	(0.033)	(0.053)	(0.010)
	minimum	1998	0.28	0.26	0.26	0.29	n.a.	n.a.
		1999	0.23	0.28	0.29	0.38	0.39	0.22
	maximum	1998	0.45	0.58	0.44	0.63	n.a.	n.a.
		1999	0.59	0.52	0.47	0.69	0.88	0.39
Soil temperature, °C (May-Oct)	mean	1998	10.1	9.9	9.9	8.7	n.a.	n.a.
		1999	10.4	10.2	10.2	12.5	13.9	13.6
	minimum	1998	9.7	9.6	9.3	8.4	n.a.	n.a.
		1999	10.0	10.0	9.6	11.9	13.5	12.4
	maximum	1998	10.5	10.2	10.7	9.0	n.a.	n.a.
		1999	10.9	10.5	10.7	13.1	14.9	15.2
CV of efflux (May-Oct)								
	mean	1998	0.32	0.26	0.23	0.36	n.a.	n.a.
		1999	0.32	0.26	0.22	0.26	0.37	0.22
	minimum	1998	0.13	0.14	0.11	0.15	n.a.	n.a.
		1999	0.20	0.1	0.10	0.11	0.16	0.16
	maximum	1998	0.55	0.38	0.44	0.84	n.a.	n.a.
		1999	0.63	0.61	0.57	0.48	0.57	0.29
Monthly means of CV								
	May	1998	0.26	0.31	0.26	0.29	n.a.	n.a.
	June		0.24	0.26	0.17	0.39	n.a.	n.a.
	July		0.29	0.25	0.23	0.34	n.a.	n.a.
	August		0.37	0.25	0.24	0.58	n.a.	n.a.
	September		0.37	0.23	0.21	0.31	n.a.	n.a.
	October		0.40	0.24	0.28	0.30	n.a.	n.a.
	May	1999	0.45	0.38	0.40	0.30	n.a.	0.28
	June		0.23	0.23	0.17	0.32	n.a.	0.28
	July		0.30	0.28	0.17	0.31	0.27	0.21
	August		0.32	0.26	0.22	0.24	0.28	0.29
	September		0.29	0.20	0.17	0.20	0.50	0.18
	October		0.37	0.20	0.20	0.18	n.a.	0.16
CV of efflux between plots H1-H3,M1								
		1998	0.09					
		1999	0.14					

N.B. Minima and maxima are the smallest and greatest collar-specific average efflux for May-Oct

[a] M2 was only measured from July to September 1999

[**] H0.1 has 25 measurement points, i.e. permanent collars on a 0.7m x 0.7m plot, other plots 10 permanent points on a 20m x 20m plot. H0.1 was measured once or twice a month May –October 1999, others twice a day on two days a week during the snow-free period, May–October, in 1998 and 1999.

Table 5. Mantel test and spatial correlogram analysis (Moran's I) on the average soil CO_2 efflux for the snow-free period 1999.

	Plot					
	H1	**H2**	**H3**	**M1**	**M2**	**H0.1**
Mantel correlation	0.14	**0.21**	0.12	**0.49**	**0.45**	-0.07
p-value	0.186	**0.040**	0.125	**0.009**	**0.016**	0.825
Distance class 1						
mean distance, m	3.4	3.7	**3.2**	3.2	2.8	**0.15**
number of pairs	4	20	15	6	7	40
Moran's *I*	0.28	−0.02	0.40	0.23	0.20	0.21
p	0.23	0.38	**0.04**	0.15	0.15	**0.05**
Distance class 2						
mean distance. m	**8.1**	7.9	**8.1**	**8.6**	8.0	0.26
number of pairs	13	42	34	10	10	62
Moran's *I*	0.40	−0.08	−0.33	0.51	0.20	−0.01
p	**0.005**	0.47	**0.05**	**0.006**	0.08	0.34
Distance class 3						
mean distance, m	13.0	13.0	12.4	12.5	12.6	**0.38**
number of pairs	13	30	33	18	13	86
Moran's *I*	−0.43	−0.19	−0.12	−0.17	−0.31	−0.25
p	0.08	0.21	0.34	0.37	0.16	**0.01**
Distance class 4						
mean distance, m	17.2	16.8	17.1	**17.5**	17.1	0.52
number of pairs	13	13	22	10	13	66
Moran's *I*	−0.45	0.14	0.11	−0.63	−0.28	−0.05
p	0.07	0.17	0.12	**0.01**	0.17	0.45

Table 6. Description of linear regression models (Ln(Efflux in $mgCO_2m^{-2}h^{-1}$) = $\beta_0 + \beta_1 \times x_1 + \beta_2 \times x_2 + ... + \beta_i \times x_i$) fitted to the measurements made in 1999.

Dependent variable	Model	Independent variables x_i	F_{model}	df_{model}	df_{error}	RMSE	R^2	Estimates β_0	 β_1	 β_2
Models for the middle-aged stand i.e. Plots H1 +H2 combined in Huhus										
Dependent: Mean efflux for snow-free period 1999										
	1	distance_trees	6.365^{*}	1	18	0.204	0.26	6.350	−0.141	
	2	distance_trees _x_DBH	8.002^{**}	1	18	0.198	0.31	6.295	−0.657	
	3	distance_trees _x_DBH, Tsoil	8.535^{***}	2	17	0.173	0.50	1.551	−0.866	0.473
Models for the combination of the two young stands and the middle-aged stand (i.e. Plots H1, H2, H3 and M1) in Huhus and Mekrijärvi										
Dependent: Mean efflux for snow-free period 1999										
	4	thickness_humus	14.84^{***}	1	38	0.197	0.28	5.728	0.096	
	5	thickness_humus, distance_trees	12.49^{***}	2	37	0.182	0.40	5.950	0.083	−0.085
Models for the combination of all four stands (i.e. Plots H1, H2, H3, M1, and M2[a] in Huhus and Mekrijärvi										
Dependent: Mean efflux for Jul-Aug[a] 1999										
	6	distance_trees, thickness_humus	6.456^{**}	2	47	0.208	0.22	6.419	−0.082	0.048

[a] Plot M2 in the old stand in Mekrijärvi was measured only in July-September 1999.

Abbreviations of variables and units used: distance_to_trees = average distance to the 3 closest trees (m), DBH= diameter at breast height, at 1.3 m (cm), distance_to_trees _x_DBH (cm x cm), thickness_humus = thickness of humus layer (cm), Tsoil= soil temperature measured next to each collar (°C)

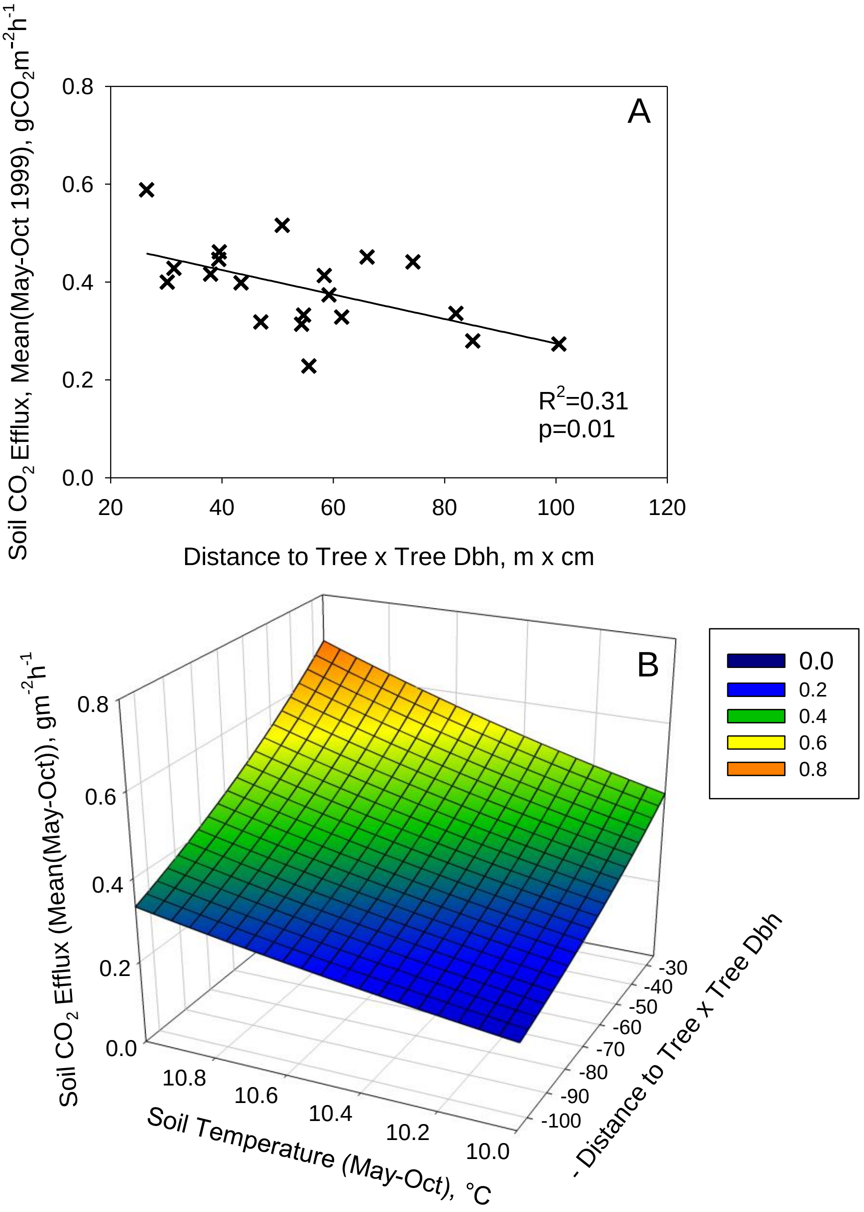

Fig. 7. A. Regression between the average soil CO_2 efflux in a measuring point for the snow-free period (May–Oct 1999) and the average distance to the three closest trees multiplied by the average tree diameter (Dbh) on Plots H1 and H2 in the 65-year old thinned stand in Huhus. **B.** Regression between soil CO_2 efflux in a measuring point and the average distance to the three closest trees multiplied by the average tree diameter (Dbh) and with soil temperature (T_{soil}). A stepwise regression model was formulated as the following: LnEfflux (mean efflux for May–Oct 1999) = 1.551 − 0.009×average distance to the 3 closest trees × average diameter of the 3 closest trees + 0.473×T_{soil}(mean for May–Oct 1999), R^2=0.50, p=0.003, n=20 permanent measuring points.

5. DISCUSSION

5.1. Soil CO_2 efflux in current climate

The level and temporal range of plot averages of soil CO_2 efflux, from 0.04 to 0.90 $gCO_2\ m^{-2}\ h^{-1}$ in Huhus and 0.05 to 1.12 $gCO_2\ m^{-2}\ h^{-1}$ in Mekrijärvi during the snow-free period (Papers I, III), was within the range reported for other boreal Scots pine forests (e.g. Shibistova et al. 2002b; Bhupinderpal-Singh et al. 2003; Pumpanen 2003; Kolari et al. 2009). The snow-free period was covered with over 5000 measurements during three consequent snow-free periods in Huhus, of which the data from two latter years were used to model efflux and thus estimate annual efflux (Paper I). The annual estimates, 1750 and 2050 $gCO_2\ m^{-2}$, corresponded previous estimates for some boreal coniferous forests (e.g. Kurganova et al. 2003; Wang et al. 2003) but were smaller than in some other studies (e.g. Morén and Lindroth 2000; Rayment and Jarvis 2000; Pumpanen et al. 2003a; Domisch et al. 2006; Laganière et al. 2012).

The range of soil CO_2 efflux, 0.044–0.134 $gCO_2\ m^{-2}\ h^{-1}$ measured in Huhus in winter was similar to the range of winter emissions in other boreal forests (Winston et al. 1997; Kurganova et al. 2003; Pumpanen et al. 2003a) but smaller than in some (e.g. Domisch et al. 2006). There was some uncertainty in winter CO_2 efflux because of the low frequency of measurements in winter (Paper I). This did not, however, considerably increase the uncertainty of annual estimate of soil CO_2 efflux, because typically only a small proportion, from 5 to 25 %, has been estimated to be emitted in wintertime in boreal forests with an equally long snow-covered period (Strömgren 2001; Kurganova et al. 2003; Wang et al. 2003; Domisch et al. 2006, Paper I).

In addition to the temporal coverage of measurements, spatial coverage and type of the measurement system affect the reliability of the soil CO_2 efflux estimates. In general, different measurement principles have different limitations, or advantages and disadvantages (Norman et al. 1997; Davidson et al. 2002). Contrary to the hypothesis that differences in accuracy would be related to the measurement principle, the reliability of the chambers to measure soil CO_2 efflux was not related to the measurement principle *per se*. Variable results were obtained even with the same chambers in our study (Paper II).

The type of measurement system used in our field measurements introduced an overestimation which could be estimated to be 5% in average for mineral soil in 1999 and smaller than that in 1998, assuming a linear correlation between the overestimation and the air-filled porosities. Although our system comparison study (Paper II) did not test organic substrates, overestimation for the topmost organic humus and mineral soil layer in Huhus could be estimated to be 10% on average for the dry snow-free period of 1999. Overestimation was presumably smaller in the wet year 1998 for which water content measurements of the organic/surface soil layer were not available and air and water-filled porosities could thus not be estimated. Turbulence created by the chamber fan, together with tightly sealed soil, most likely caused a mass flow of CO_2 from soil which led to an overestimation of efflux in our system (LeDantec 1999, Paper II). This overestimation could have diminished, to some degree, the negative effect of drought on the true soil CO_2 efflux in the dry year because of the effect of greater air-filled pore space in the dry soil, thus leading to greater overestimation. However, the type of chamber system would not affect the comparisons between pine stands or between different climate change treatments, between which the differences in soil moisture and thus in air-filled pore space were small.

Differences within the range of 5 to 27%, as measured for this type of chamber in the comparison study, are not rare; field comparisons on forest soils have shown differences up to 50% between different measurement techniques or chamber designs (e.g. Norman et al. 1997; Le Dantec 1999; Janssens et al. 2000; Shibistova et al. 2002b; Pumpanen et al. 2003a). Even the measurement system developed by LiCor that has been concluded to yield consistent measurements and has several advantages over other closed dynamic systems (e.g. Norman et al. 1997) gave a 10% overestimation of the controlled efflux with one exactly similar version of the measurement system, but not with another one (Paper II). However, over- or underestimations smaller than 10% were not considered statistically significant in our comparison study. On the whole, comparisons against known fluxes are valuable as they concentrate on the differences in measurements without the additional discrepancies created by differences in spatial or temporal coverage of measurements in field (e.g. Drewitt et al. 2002; Shibistova et al. 2002b).

In addition to the effect of chamber, inclusion of the dark respiration of moss cover in field added to the soil efflux, by some 10% on the average (Paper I). Keeping the living moss or lichen cover was yet assessed necessary to avoid disturbance to the litter and humus layers as well as to avoid artefacts such as reduced moisture retention in the organic layer which could have affected both heterotrophic and autotrophic respiration.

Spatial variability of soil CO_2 efflux complicates the comparisons between forests or developmental stages of tree stands. Within plots, standard deviation was on the average one third of the plot mean, which corresponds well to similar variance reported in other forest ecosystem studies (Pumpanen et al. 2003a; Saiz et al. 2006; Ohashi and Gyokusen 2007; Kelsey et al. 2012). Differences of 100% between measurement locations within a plot in momentary, seasonal or semiannual efflux such as observed in our study, have been typical in previous studies as well (e.g. Ohashi and Gyokusen 2007; Martin and Bolstad 2009).

Contrary to the within plot variation, coefficients of variation for spatial variation between plots in the average soil CO_2 efflux were small, approximately 0.10. Despite the differences between plots in tree volume and root mass, differences in soil CO_2 efflux between plots were small especially within the forested area in Huhus (Paper IV). In general, differences in soil CO_2 efflux between stands of different age and developmental stage have often proven difficult to detect with feasible sampling (e.g. Irvine and Law 2002).

5.2. Effect of environmental variables on temporal variability and modelling

Soil temperature

Soil temperature was a strong and dominant predictor of soil CO_2 efflux during the snow-free period as observed in other studies in boreal forests (e.g. Russell and Voroney 1998; Morén and Lindroth 2000; Pumpanen et al. 2003a; Kelsey et al. 2012; Laganière et al. 2012). Variation in the temperature of the organic humus layer and in its square explained over 75% of the temporal variation in ln-transformed plot averages (Paper I), which confirmed our initial hypothesis of the significance of temperature as a predictor of temporal variation in soil CO_2 efflux.

The soil CO_2 efflux was found to be higher at a given temperature later in the snow-free period (August and September) than in spring and early summer (May and June) (Paper I). A similar hysteresis-type of pattern in the temperature response over the course of snow-free period has been observed in other forest studies with single-depth measurements of soil temperature (e.g. Morén and Lindroth 2000; Drewitt et al. 2002). The peak CO_2 efflux occurred in July–August as observed in many previous studies in boreal coniferous forests (e.g. Morén and Lindroth 2000; Högberg et al. 2001; Shibistova et al. 2002a; Domisch et al. 2006; Kolari et al. 2009). The highest soil CO_2 efflux at 10°C was found in August as well and the lowest in May, similar to the temperature response pattern observed in a Siberian Scots pine forest (Shibistova et al. 2002a). The observed seasonality of temperature response in monthly models corresponded also well to the pattern reported for a temperate forest (Janssens and Pilegaard 2003), with greater Q_{10}'s and lower base respiration (i.e. constant) at low temperatures for spring and autumn months but smaller Q_{10}'s and higher base respiration for the summer or early autumn (June, August and September).

Inclusion of a seasonality index, degree days, improved the accuracy of temperature response model that covered the entire snow-free period, as has been reported for ecosystem respiration and soil CO_2 efflux in other boreal forests (Goulden et al. 1997; Lavigne et al. 1997; Richardson et al. 2006). Similarly to another Finnish pine forest study by Kolari et al. (2009), the efflux during the peak period in July–August was consistently underestimated with the models for the snow-free period, with or without degree days. Variation in soil moisture did not explain the seasonality of the temperature response (Paper I).

The seasonal pattern of root growth as well as the rapid growth of external mycelium of ectomycorrhizal fungi during the second part of the snow-free period could explain the failure of models to predict magnitude of efflux during the peak efflux from mid-July to August. The fine root biomass and root growth in Scots pine forests of our region have been observed to peak late in the summer or early autumn, in July– September (Makkonen and Helmisaari 2001; Helmisaari et al. 2009). In a Scots pine stand at the same latitude in Sweden, the peak root and mycorrhizal respiration was observed to occur similarly in August (Högberg et al. 2001; Bhupinderpal-Singh et al. 2003). External mycelium of ectomycorrhizal fungi, a significant part of microbial biomass in our conditions, has also been detected to grow most rapidly from July to September or October in similar boreal coniferous forests (Wallander et al. 1997, 2001).

Soil CO_2 efflux measured in July showed no clear response to temperature or to soil moisture, contrary to the findings from a Siberian Scots pine stand (Kelliher et al. 1999). Also others have found a weak or no correlation between CO_2 efflux from forest soil and soil temperature during the peak period of efflux in summer (Russell and Voroney 1998; Kelliher et al. 1999; Curiel Yuste et al. 2004) or between efflux and soil temperature and moisture (Schlentner and Van Cleve 1985). In our case, differences in the width of the temperature range did not clearly explain the lack of an apparent temperature response in July: The temperature range in the combined data for July (8–26 °C) was not narrower than for the other months of the snow-free period but represented the high end of the temperature range. The apparent temperature insensitivity observed in July, the month of peak photosynthesis, could be explained by the importance of root-associated respiration, especially by the influence of flux of photosynthates through roots, which has been observed to be proportionally largest in the middle of the growing period (e.g. Savage et al. 2013). Recent aboveground weather conditions affecting photosynthesis may, hence, have had an effect on root-associated respiration during that time (Russell and Voroney 1998; Ekblad et al. 2005; Savage et al. 2013).

The difference between spring and late autumn in the level of soil CO_2 efflux is most likely due to differences in temperatures within the soil column during warming and cooling (Reichstein et al. 2005) and to differences in size of the volume of soil that is active, i.e. not waterlogged or frozen (Rayment and Jarvis 2000). An auxiliary analysis with temperatures measured at a depth of 7 cm in mineral soil indicated that use of temperature of the organic humus layer contributed for the most part to the observed greater level of CO_2 efflux at a given temperature in October compared to May (see Paper I). In addition, seasonally variable factors such as substrate availability and size and composition of the microbial population could have contributed to the differences, through a greater respiring mass of ectomycorrhizal fungi in autumn, for instance.

A possible discrepancy between the soil layer from which most of the CO_2 originates and the layer in which temperature is measured could be avoided by the use of a set of temperatures at different depths or with a multi-layer approach (e.g. Morén and Lindroth 2000; Pumpanen et al. 2003b; Reichstein et al. 2005; Davidson et al. 2006b). In our study, the underestimation of soil CO_2 efflux during the peak efflux in July–August and its overestimation in spring and early summer, i.e. in May and June, persisted also when the temperatures in the organic humus layer and topmost mineral soil layer were both included as predictors. Temperature of the topmost mineral layer did not appear to be a better predictor than the temperature of the organic humus layer which has previously been identified as a significant and even dominating source of CO_2 in temperate and boreal forest soils (Kähkönen et al. 2002; Risk et al. 2002; Pumpanen et al. 2003b, Reichstein et al. 2005; Davidson et al. 2006b).

Soil moisture

Results from the two snow-free periods that differed greatly in precipitation showed different patterns in relationship between soil CO_2 efflux and soil moisture, similar to the observations by Davidson et al. (1998); in spring and early summer of both years, decreasing soil moisture was associated with increasing soil CO_2 efflux. During the dry late summer and early autumn of the second year, decreasing soil moisture was, in contrast, associated with a decrease in soil CO_2 efflux. This decline in efflux was not explained by a decline in soil temperature.

Negative effects of dry conditions on soil CO_2 efflux have been observed in temperate and boreal forests in other studies as well (Davidson et al. 1998; Savage and Davidson 2001; Subke et al. 2003; Kolari et al. 2009). The effect of drought was not, however, carried over to our models that covered the entire snow-free period. Yet, the effect was evident when shorter periods of time were compared. The large difference (50%) between the two years in cumulative precipitation over the snow-free period most likely helped to discern the effect of drought on the efflux in September of the dry year, which was preceded by the driest August in 30 years (Drebs et al. 2002).

It was estimated unlikely that the production processes of CO_2 were hindered by high soil water content in Huhus (see Discussion in Paper I). Therefore the negative relationship between the soil CO_2 efflux and soil moisture in spring and early summer could have been an artifact, reflecting the influence of some other covarying factor, such as temperature (Carlyle and Than 1988; Davidson et al. 1998). On the other hand, slower transportation of gases in moist soils could have contributed to this effect (e.g. Pumpanen et al. 2003b).

A weak and negative relationship between soil CO_2 efflux and moisture has been observed in some other temperate and boreal forests as well (Davidson et al. 1998; Morén and Lindroth 2000; Lavoie et al. 2012). In our case, the strong correlation in multivariable models between time and soil moisture during the first half of the snow-free period suggested that soil moisture could have been a surrogate for time, i.e. progress of the growing season and associated processes. Correspondingly, a similar temporal pattern of soil moisture (a steady decrease after snow-melt) and a negative correlation between soil moisture and coniferous root growth have been observed in Canada (Steinaker et al. 2010). Yet, distinction between the effects of soil moisture and the time/stage of the growing season, or between soil moisture and temperature, is difficult to make based on observations of soil CO_2 efflux and soil moisture in unmanipulated field conditions (Schlesinger 1977; Davidson et al. 1998; Kane et al. 2003; Kelsey et al. 2012).

As a confirmation to our initial hypothesis and earlier work in northern forests (e.g. Lessard et al. 1994, Russell and Voroney 1998, Morén and Lindroth 2000, Borken et al. 2002), the effect of soil moisture on soil CO_2 efflux appeared small and with little impact on cumulative efflux for longer periods of time, such as the snow-free period. Differences in annual estimates between years with contrasting precipitation patterns were small as previously noted by Pumpanen et al. (2003a) under similar Finnish conditions. Discovery of the negative effect of drought in a dry year on a shorter time-scale highlighted, however, the possible influence of soil moisture in the boreal forests in Fennoscandia, even if they are often thought not to be water-stressed (Bergh et al. 2005). In future, soils are predicted to be drier in our region during the snow-free period (Kellomäki et al. 2005; IPCC 2013), which could increase the frequency of drought conditions similar to the ones observed in our study.

5.3. Effect of environmental variables on spatial variability

No clear spatial autocorrelation was found in the soil CO_2 efflux within plots or within combination of plots of the same stand (Paper IV). Only at short distances, i.e. three or eight meters, some spatial correlation was detected on plots with trees of variable age, size and spacing. Previous studies have either found no spatial correlation within stands (Raich et al. 1990, Thierron and Laudelot 1996) or found it to occur on various scales from less than one meter to some 40 meters (Rayment and Jarvis 2000, Tedeschi et al. 2006, Ohashi and Gyokusen 2007). Some of the studies that have found spatial autocorrelation, have studied it along a natural gradient such as a slope (e.g. Ohashi and Gyokusen 2007). On the flat terrain of our sites, with relatively great number of trees compared to measurement locations, we did not, however, expect to find such gradients of environmental variables that could have produced spatial autocorrelation throughout a plot or a stand.

Yet, several variables were identified to spatially correlate with soil CO_2 efflux; thickness of the organic humus layer emerged as the single most effective predictor of soil CO_2 efflux across all plots of our study, similarly to findings from a chronosequence of temperate spruce stands (Saiz et al. 2006). Correlation between soil CO_2 efflux and organic layer attributes has also been found in other studies in northern forests (e.g. Rayment and Jarvis 2000; Scott-Denton et al. 2003; Martin and Bolstad 2009). The organic humus layer is both the source of substrate for the microbial respiration as well as a significant rooting zone of trees and understorey vegetation, and is thus identified as the dominant source of the soil CO_2 emissions in Finnish boreal pine stands (Makkonen and Helmisaari 1998; Pumpanen et al. 2003b, Saiz et al. 2006).

The distance to the closest trees complemented the thickness of the organic humus layer as a predictor of soil CO_2 efflux in the present study (Paper IV), something which confirmed our initial hypothesis about the influence of standing stock of trees on the spatial variability of soil CO_2 efflux. Soil CO_2 efflux was also found to correlate with root variables, especially of those measured in the organic humus layer. Similarly, several studies have reported a negative correlation with the distance to the trees and either a weak, moderate or strong correlation between root variables such as total root mass and volume and forest soil CO_2 efflux (Scott-Denton et al. 2003; Wieser 2004; Wiseman and Seiler 2004; Saiz et al. 2006; Martin and Bolstad 2009; Katayama et al. 2009). However, in some stands, correlation between efflux and distance to the trees or between efflux and root variables has not been confirmed (e.g. Gough and Seiler 2004; Saiz et al. 2006; Ngao et al. 2012).

Differences in soil CO_2 efflux between stands were small in our study (Paper IV). Thus, linking spatial variability of soil CO_2 efflux between plots to differences in tree stand characteristics was difficult, although variation within plots and variation in the pooled plots were partly explained by the variation associated with tree stand characteristics such as by the distance to the closest trees and root mass. In general, differences in forest soil CO_2 efflux related to stand age or developmental or successional stage may not be derived only from the differences in standing tree stock, but can reflect actual differences in other factors or their combination. Such factors may include micro-climate, current or past litter inputs (such as logging residues), ground cover or vegetation, contribution of root respiration, and hydrological conditions, which in turn can be greatly influenced by the management and other disturbances (see references and discussion in Paper IV).

5.4. Climate change experiment

Effect of elevated CO_2

Average soil CO_2 efflux for the snow-free period was observed to be 23–37% greater under enrichment of atmospheric CO_2, without warming, than in the control chambers during the four years of our study. The magnitude of the increase corresponded well to the initial increases in two long-term FACE experiments, one in a temperate pine forest (King et al. 2004) and another in alpine mixed forest (Hagedorn et al. 2013). However, it was smaller than the increase measured in another boreal whole-tree chamber experiment (Comsted et al. 2006, Table 1). The seasonal pattern of the CO_2-enrichment response in our study was consistent with Andrews and Schlesinger (2001), who found the greatest relative increases late in the growing season in a temperate pine forest, whereas Comstedt et al. (2006) observed the greatest increases both early and late in the season in a boreal spruce forest. On the average, CO_2 enrichment without nutrient addition has been found to increase soil CO_2 efflux by 17% in temperate and boreal forests, according to the meta-analysis by Dieleman et al. (2010).

In our study, the differences in monthly or six-month averages of soil CO_2 efflux were not statistically significant between elevated CO_2 alone and the control chambers (Paper III). However, an analysis of the temperature response revealed the impact of CO_2 enrichment; a greater soil CO_2 efflux at a given soil temperature was detected under the elevated CO_2 treatment than in the control chambers which is supported by findings in other forest experiments (King et al. 2004). In addition, CO_2 enrichment, with or without warming, was a statistically significant factor in the analysis of variance, especially for the first year of the experiment. A strong initial response has been reported for other, longer-term studies of CO_2 enrichment as well (Table 1; King et al. 2004; Bernhardt et al. 2006). Some results suggest that the effect of elevated CO_2 may, however, persist even for a decade (Jackson et al. 2009; Hagedorn et al. 2013).

Analysis of several field studies suggests that a large part of the stimulation of soil CO_2 efflux may be due to increased root respiration (Lukac et al. 2009). Results from enrichment with ^{13}C-labelled CO_2 also indicated that an increase in soil CO_2 efflux in a spruce stand mostly resulted from increased root and rhizosphere respiration of recently fixed carbon (Comstedt et al. 2006). Correspondingly, fine and coarse root biomass and production have been found to increase under elevated CO_2 in various forest experiments (e.g. Pregitzer et al. 2008; Jackson et al. 2009; Lukac et al. 2009; Dieleman et al. 2010) but not in some (e.g. Dawes et al. 2013). Aboveground biomass and litterfall have been found to increase (Lichter et al. 2008; Jackson et al. 2009; Dieleman et al. 2010). In some cases such an increase aboveground has occurred in conjunction with a similar increase belowground (e.g. Pregitzer et al. 2008), but often to a lesser degree (Dieleman et al. 2010; 2012). Root biomass or production were not monitored during our experiment but results from root sampling at the end of the experiment, as well as from a seedling study carried out during the second year, showed a tendency for a greater fine root biomass and a greater number of mycorrhizal root tips under the elevated CO_2 compared to the control (Leinonen 2000; Helmisaari et al. 2007). Elevated CO_2 also increased the diameter growth of trees in our experiment, both in ambient as well as in elevated temperature (Peltola et al. 2002; Kilpeläinen et al. 2005).

Effect of warming

Air warming without atmospheric CO_2 enrichment increased on the average the mean soil CO_2 efflux of the snow-free periods by one third during the four years of our study, which is similar to the effect of the first years of soil warming experiments in temperate forests (McHale et al 1998; Melillo et al. 2002). Meta-analyses of data from several biomes have showed lower average increases in different warming treatments, or 9 to 20 % (Rustad et al. 2001; Wu et al. 2011; Lu et al. 2013). In both temperate and boreal forests, the impact of soil and ecosystem warming is reported to range from a 31% decrease to a 58% increase in annual or growing season average efflux. A positive effect was observed on soil CO_2 efflux in the majority of these studies (Table 1).

More experience has been gained from field experiments of warming forest soil only than from experiments in which air is heated and as a consequence the soil is warmed as well (Table 1). Despite the trend for a higher temperature elevation in soil warming experiments compared to air warming experiments, conclusions on the treatment effects on soil CO_2 efflux have generally supported each other (Table 1; Lu et al. 2013). Yet, the only experiment in which soil was heated separately with cables, with and without air warming, resulted in an increase in forest soil CO_2 efflux under soil warming, but a decrease under soil and air warming (Bronson et al. 2008). The decrease, however, was not evident in the following years (Vogel et al. 2014). Although treatment effects can be similar in these two types of experiments, warming of the aboveground vegetation can influence soil CO_2 efflux to a greater extent, e.g. through higher assimilation because of longer growing season than under soil only warming or through changes in aboveground litter quantity and quality (Conant et al. 2011; Chung et al. 2013). Our experiment included warming of the trees, which most likely contributed to the response of soil CO_2 efflux.

A larger warming impact on soil CO_2 efflux in spring and in autumn, when the temperature elevation was set to be greater in our study, are supported by soil warming studies in which temperature elevation was not dependent on season (e.g. Strömgren 2001; Contosta et al. 2011). A declining trend of the warming effect with time (e.g. Rustad et al. 2001; Melillo et al. 2002) was not clear in our study, but the duration of our experiment was shorter than in the longest-term experiments (Table 1). Interannual variation in weather, i.e. warm growing seasons versus cooler and wetter, could have also influenced the size of the treatment effect in different years in our case. The analysis of the temperature response of the first year showed, however, a tendency for a higher level of soil CO_2 efflux at a given soil temperature in both warming treatments, with or without CO_2 enrichment. This was interpreted to be most likely a result of the direct effect of elevated temperature through enhanced oxidation of most labile soil carbon in the first year (as in Peterjohn et al. 1994). The higher nitrogen content per unit of organic matter in the soil organic layer in heated treatments (our unpublished results), also supported the interpretation of a strong decomposition response during the first year of the experiment. Indirect effects of warming, such as an increase in carbon assimilation of the trees and subsequent increases in root respiration and carbon inputs to the soil could also have contributed to the effect. Warming had, indeed, mainly a positive effect on diameter growth, especially during the first year

(Peltola et al. 2002), although how this was reflected in root growth was not quantified at the time. Fine root biomass has been observed to increase under warming (e.g. Rustad and Fernandez 1998; Majdi and Öhrvik 2004; Leppälammi-Kujansuu et al. 2013) although not in all soil warming experiments (e.g. Jarvi and Burton 2013). In our study, there was a tendency for a greater root mass in the heated chambers at the end of the experiment (Helmisaari et al. 2007).

A decrease in temperature sensitivity of soil CO_2 efflux, so called "acclimatization" of soil CO_2 efflux (Luo et al. 2001) was observed in the second year, in both elevated temperature treatments (with or without CO_2 enrichment) which conformed well to the patterns previously reported for boreal forests (Pajari 1995 for our site; Strömgren 2001 for a Swedish spruce site) and a temperate grassland (Luo et al. 2001). This decrease in temperature sensitivity could be explained by a smaller pool of labile soil organic carbon (SOC) after the first year of warming, during which the enhanced decomposition may have diminished it. Correspondingly, oxidation of soil organic matter has been observed to be enhanced by over 100% at the beginning of a warming experiment, but only by a moderate 10% during the following year (Lin et al. 2001). Labile SOC pools have, indeed, been observed to be lower in heated soils than in control in a long-term soil warming experiment of a temperate forest (Bradford et al. 2008), but results from air warming of a temperate grassland site suggest the opposite (Luo et al. 2009). Note should be made that results from soil warming alone might not, however, be directly comparable with air or ecosystem warming experiments because of the possible differences in treatment effects on amounts of carbon inputs to the soil, especially in the long term.

The decrease in the apparent temperature sensitivity of soil CO_2 efflux under both warming treatments in the present study could also be caused partly by thermal acclimation or adaptation of the root or microbial respiration (Atkin et al. 2000; Bradford et al. 2008). Adjustment of respiration rates of soil microbes to temperature could imply either adjustment of specific respiration rates per unit microbial biomass or adjustment of total rates (e.g. Bradford et al. 2008). Results from soil warming in temperate forests and grasslands suggest that the effect of thermal adaptation/acclimation of microbial respiration could be small. Substrate availability and direct effects of temperature to microbial growth could instead be significant in mediating such a response to warming (Hartley et al. 2007; Bradford et al. 2008; Rousk et al. 2012).

A drop in the level of soil CO_2 efflux at a specific temperature in the following years could also be partly attributed to a lower soil water content often observed in the warming experiments (e.g. Peterjohn et al. 1994; Rustad and Fernandez 1998; Rustad et al. 2001; Allison et al. 2010). However, this interpretation was not supported by soil warming study in a temperate grassland site (Luo et al. 2001) or in an irrigated boreal forest (Strömgren 2001). Warming and drying has also been observed to suppress microbial activity and carbon cycling in boreal forest soils (Allison and Treseder 2008). Our closed-top chambers were irrigated, but with a similar amount regardless of the treatment. The negative impact of air warming on soil water content of the mineral soil was small. The warming may have, however, dried the surface litter in the warmed chambers (as in Verburg et al. 1999). In the fourth year of our study, temperature sensitivity of soil CO_2 efflux under elevated temperature was no longer below that of the control chambers which could be due to a greater respiring root biomass and greater carbon inputs to the soil originating from the greater above- and belowground growth as measured at the end of the experiment (Peltola et al. 2002; Helmisaari et al. 2007).

Effects of elevated CO_2 and temperature

Results of our study supported our initial hypothesis, according to which all three treatments in the climate change experiment would result in greater soil CO_2 efflux compared to the control. The combined treatment of atmospheric CO_2 enrichment and air warming resulted in greater soil CO_2 efflux compared to the controls, similarly to other experiments (Dieleman et al. 2012; Table 1). It generally yielded the highest soil CO_2 effluxes in the first three years, with the strongest treatment effect of +59% in the first year (Paper III).

The effects of elevated CO_2 and elevated temperature were more or less additive and no significant interaction was found in our study or in previous studies (e.g. Edwards and Norby 1999; Lin et al. 2001; Dieleman et al. 2012). Responses of plant productivity under the combined treatment have resembled more those in the elevated CO_2-only treatment than those in the warming only treatment (Dieleman et al. 2012). Similarly, the effect of elevated CO_2 was evident in diameter growth of the trees in our experiment, both in ambient as well as in elevated temperature, whereas the effect of warming was not as notable (Peltola et al. 2002; Kilpeläinen et al. 2005). With four-year data on soil CO_2 efflux, however, temperature elevation emerged as a significant factor in the analysis of variance under the treatments (Paper III). Correspondingly, the year-to-year pattern of temperature response of soil CO_2 efflux under the combined treatment resembled the pattern under the warming-only treatment.

6. CONCLUSIONS AND FUTURE RESEARCH

Temperature was a strong and dominant predictor of the temporal variability of soil CO_2 efflux in the boreal Scots pine stands. Many other environmental factors and ecosystem processes that can influence the substrate supply to soil respiration varied in concert with temperature and were thus indirectly included in the temperature response. Such factors include e.g. solar irradiation, carbon uptake, root growth and partly soil moisture (e.g. Jassal et al. 2008; Savage et al. 2013). Model evaluation with independent data showed that a regression model with temperature and degree days as predictors simulated well the soil CO_2 efflux, with a 15% difference on the average between the measured and predicted efflux. However, the models did not capture all seasonal variation; soil CO_2 efflux remained underestimated during the peak efflux period from mid-July to August.

In future modelling, a distinction between the primary effects of temperature and soil water content and their secondary effects due to interactions with substrate availability will be essential (e.g. Davidson et al. 2006a). Irrigation experiments could help to distinguish between the effects of soil temperature and moisture and between soil moisture and stage of the growing season (e.g. Kelsey et al. 2012). Under conditions of pronounced seasonal variation, as occurs in boreal forests, separate models for shorter time periods or for different phenological phases could also increase the accuracy of predictions of short-term soil CO_2 efflux (e.g. Janssens and Pilegaard 2003; DeForest et al. 2006) and help to correct for the consistent underestimation observed in this study during the period of peak efflux.

Our findings on the correlation between the soil CO_2 efflux and a tree needle mass and the distance to the three closest trees, highlights the link between soil CO_2 efflux and the CO_2 assimilating component of the ecosystem. Models of soil CO_2 efflux could, thus, be further developed to include dynamic substrate supply and links to aboveground processes, such as phenological patterns in canopy processes (Irvine et al. 2005; Sampson et al. 2007) and dynamics of root and mycorrhizal fungi production (Savage et al. 2013). Temporal variation in root and/or mycorrhizal fungi production most likely contributed to the underestimation by the models during the peak efflux in our study. On the other hand, interannual variation in phenology of different processes as well as time-lags associated with supply of substrates are difficult to define. Moreover, because the within-plot spatial variation in soil CO_2 efflux was found to be partly explained by variation in site characteristics, such as thickness of the organic humus layer and tree density in the vicinity, inclusion of that kind of site/stand characteristics into efflux models could further improve estimates of the soil CO_2 efflux in forests.

Similarly to the findings under current climate, temperature was found to be the dominant driver for soil CO_2 efflux in our climate change experiment according to the analysis of variance on soil CO_2 efflux. However, changes in soil CO_2 efflux occurring in a changing climate will also depend strongly on the assimilating component of the forest ecosystem, as illustrated by our findings on the relationship between soil CO_2 efflux and needle area of the treatment trees. However, the observed decrease in the temperature sensitivity of soil CO_2 efflux in the elevated temperature treatments after the first year, suggested that some response mechanisms in the soil were independent of the aboveground component of the forest ecosystem.

There are not yet enough experimental data for firm conclusions about the long-term effects of both warming and atmospheric CO_2 enrichment on soil CO_2 efflux or on the mechanisms behind results obtained in different experiments so far. Substrate availability will regulate the responses of roots, microorganisms and soil organic matter pools to elevated CO_2 and temperature, and other limiting/influencing factors for tree growth, such as nitrogen availability or forest management actions, will influence the efflux responses and the potential for carbon storage (Pendall et al. 2004; Hyvönen et al. 2007; Sigurdsson et al. 2013). In the future, more manipulation studies are needed that combine field and laboratory experiments and the responses of above- and belowground components of the forest ecosystem, to further clarify the multiple mechanisms and interactions influencing soil CO_2 efflux and soil carbon pools under changing climate.

The climate will change gradually instead of the step-wise approach used in manipulation experiments so far, which may possible induce transient stages and acclimation of ecosystem processes (e.g. Oechel et al. 2000). In addition, carbon cycling in terrestrial ecosystems will be affected by the changing variability of climate (Medvigy et al. 2010). Already studies from recent years and decades have suggested that annual carbon budgets of boreal forest ecosystems can be notably influenced by early thaw in spring or warmer than usual autumns (Goulden et al. 1998; Piao et al. 2008; Bjarnadottir et al. 2009), the latter through an increase in ecosystem respiration. Longer-term or delayed effects of these variations are not clear yet, such as the effects on the level of soil CO_2 efflux in the following years (e.g. Vesala et al. 2010). Based on our work as well as on work of others (e.g. Liski et al. 1999; Strömgren 2001; Davidson and Janssens 2006; Allison and Treseder 2011; Lu et al. 2013), it seems unlikely that climate warming will generate any large positive feedback from upland mineral soils of boreal forests to the atmosphere. Yet, the overall response of soil CO_2 efflux will strongly depend on the response of the assimilating component of the boreal forest ecosystem.

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