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Climatic sensitivity of hydrology and carbon exchanges in boreal peatland ecosystems, with implications on sustainable management of reed canary grass (*Phalaris arundinacea*, L.) on cutaway peatlands

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Academic dissertation

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ABSTRACT

The aim of the study was to investigate the effects of climate change on soil hydrology and carbon (C) fluxes in boreal peatland ecosystems, with implications for the feasibility of cultivating reed canary grass (*Phalaris arundinacea, L*; RCG) as a way to restore the C sink in cutaway peatlands under Finnish conditions. *First*, hydrological models were developed for pristine peatland ecosystems and the cutaway peatlands under RCG cultivation. Concurrently, the hydrological responses to varying climatic forcing and mire types were investigated for these ecosystems. Thereafter, process-based models for estimating the seasonal and annual C exchanges were developed for the pristine mires and cutaway peatlands. The C models incorporated the hydrological models for corresponding ecosystems. Model simulations based on the climate scenarios (ACCLIM, developed by the Finnish Meteorological Institute, FMI) were further carried out to study the impacts of climate change on the C exchanges in the peatland ecosystems during the 21st century.

The simulation showed that the water table (WT) in the pristine Finnish mires would draw down slightly during the 21st century. Such a change in WT would be related to a decrease in the CO_2 sink but an increase in the CH_4 source at the country scale, as driven mainly by the rising temperature (*Ta*) and increasing precipitation (*P*). These changes in CO_2 / CH_4 fluxes would decrease the total C-greenhouse gas (GHG) sink (CO_2 equilibrium) by 68% at the country scale, and the changes would be more pronounced toward the end of the century. The majority of pristine fens in southern and western Finland and the pristine bogs near the coastal areas would become centurial CO_2 sources under the changing climate. On the other hand, the major distribution of fens in northern Finland would act to increase the CH_4 source at the country scale, whereas the CH_4 emission would tend to decrease with WT in the southern and western areas of Finland. Peat extraction and RCG cultivation tends to limit the influence of WT on the root-zone moisture content in a peatland ecosystem, resulting in a high sensitivity of soil moisture content to the regularity of summer rainfall. However, the phenological cycle of RCG may represent an adaptive feature of photosynthesis to the stochasticity of summer precipitation. By the end of the 21st century, climate change will decrease the CO_2 sequestration by 63% - 87% in a cutaway RCG peatland during a main rotation period of 12 years. Nevertheless, the site could sustain a net CO_2 sink, which is comparable to the pristine peatlands in the same region.

Keywords: Boreal peatlands, climate change, ecosystem modeling, reed canary grass, carbon-water exchange

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Finally, I would like to dedicate this thesis to my girlfriend, MSc. Linlin Sun, for her priceless love and support. I am especially grateful for my parents (Shuming Gong and Yufu Zhao) and all relatives for their continuous support. Last but not least, I would like to express my sincere gratitude to Joni Lappalainen, Katinka Käyhkö and my Chinese friends in Joensuu for their kind support and the joyful time we spent together.

LIST OF ORIGINAL ARTICLES

This thesis is based on the following four articles, which will be referred by the Roman numerals I - IV in the text. Articles I - II are reprinted with the kind permission of the publishers or with the rights retained as author, while Articles III - IV are the author version of the manuscript.

I Gong J., Wang K., Kellomäki S., Zhang C., Martikainen P.J., Surpali N. 2012. Modeling water table changes in boreal peatlands of Finland under changing climate conditions. Ecological Modelling 244: 65-78
doi: 10.1016/j.ecolmodel.2012.06.031

II Gong J., Kellomäki S., Wang K., Zhang C., Shurpali N., Martikainen P.J. 2013 Modeling CO_2 and CH_4 flux changes in pristine peatlands of Finland under changing climate conditions. Ecological Modelling 263: 64-80
doi: 10.1016/j.ecolmodel.2013.04.018

III Gong J., Shurpali N., Kellomäki S., Wang K., Salam M.M., Martikainen P.J. 2013. High sensitivity of peat moisture content to seasonal climate in a cutaway peatland cultivated with a perennial crop (*Phalaris arundinacea*, L.): a modeling study. Agricultural and Forest Meteorology 180: 225-235
doi: 10.1016/j.agrformet.2013.06.012

IV Gong J., Kellomäki S., Shurpali N., Wang K., Salam M.M., Martikainen P.J. Climatic sensitivity of CO_2 flux in a cutaway boreal peatland under cultivation of a perennial bioenergy crop (*Phalaris arundinaceae*, L.): beyond the diplotelmic modeling. (*manuscript*)

The present author had the main responsibility for modeling, analyzing and writing Articles I - IV. The co-authors contributed in implementation the research tasks and commenting on the writing.

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LIST OF ABBREVATIONS

ACCLIM: Climate extremes in present day climate and state of the art projections of climate change
C Carbon
C_a Atmospheric concentration of carbon dioxide
CH_4 Methane
CO_2 Carbon dioxide
EC Eddy covariance
ET Evapotranspiration
GPP Gross photosynthetic productivity
J_{max} Maximum rate of electron transport
Ks Saturated hydraulic conductivity
LE Latent heat flux
N Nitrogen
NEE Net ecosystem exchange of carbon dioxide
NPP Net primary productivity
P Precipitation
PPFD Photosynthetic photon flux density
RCG Reed canary grass
RE Respiration rate of living plant organs
SOM Soil organic matter
SVAT Soil-vegetation-atmosphere transportation
Ta Air temperature
V_{max} Maximum rate of carboxylation governed by Rubisco (ribulose 1,5-bisphosphate carboxylase-oxygenase)
WT depth of water table

1. INTRODUCTION

1.1 Boreal peatland ecosystems, climate change and sustainability of peatland management

Peatland ecosystems are terrestrial environments with a large deposit of partially decomposed organic matter or peat (Wieder et al., 2006). Approximately 80% of the peatlands in the world are in boreal regions. These peatlands cover approximately 2% of the global land surface, which contains approximately 500 Pg (10^{15} g) of organic carbon. This is approximately one-third of the world's soil carbon (C) pool (Gorham, 1991), which is an equivalent of 40 ppm in terms of the atmospheric CO_2 concentration (C_a) (Moore et al., 1998). This large amount of C was withdrawn from the atmosphere due to the net primary production (NPP) exceeding the decomposition of soil organic matter in these ecosystems. Under boreal conditions, the accumulation of peat mainly depends on the slow decay processes restricted by the low temperature and water-logged conditions of the soil (Turunen, 2008; Dorrepaal et al., 2009). A cool climate, low evapotranspiration rate and high effective moisture are essential for the formation and development of boreal peatlands in suitable geological settings (Yu et al., 2009).

Climate changes, specifically an increase in air temperature (*Ta*) and changes in precipitation (*P*), are associated with the increased atmospheric concentrations of C and other greenhouse gases (GHGs). These changes are estimated to be most pronounced at high latitudes (Prowse et al., 2006). A number of studies have suggested that the enormous C storage in peatland ecosystems could be highly sensitive to the changes in climatic conditions. For example, the increases in C_a and *Ta* are likely to increase the photosynthetic uptake of CO_2 due to the higher C_a, longer growing season and the increasing mineralization of nitrogen (e.g., Ge et al., 2012). Furthermore, the warming climate is likely to accelerate the emission of CO_2 and CH_4 (e.g., Ise et al., 2008; Bridgham et al., 2008; Dorrepaal et al., 2009). The C release via CH_4 efflux is currently less than 10% of the total C loss from peat to the atmosphere, but the impacts of CH_4 on radiative forcing are much greater (approximately 21 times for a centurial time horizon) than CO_2. The variability of the natural origin of mires, climate conditions and geographical settings among mire entities tend to lead to considerable variations in the mixing ratio of CH_4 and CO_2 fluxes (e.g., Laine et al., 1996; Alm et al., 2007; Minkkinen et al., 2002). As a result, the contributions of boreal peatlands to further changes of climate could be highly uncertain.

Anthropogenic disturbances on boreal peatlands, such as drainage and post-draining management, tend to further complicate the C exchanges in the ecosystems. In Northern Europe, especially in Finland, peatlands are drained extensively for forestry, agriculture and peat extraction for energy purposes (Turunen, 2008; Maljanen et al., 2010). In Finland, approximately 56% of the original peatlands have been drained since the 1950s. Only approximately 40% of the original peatlands are pristine, located mainly in northern Finland (Turunen, 2008).

The drainage of peatlands cuts off the surrounding hydrological influences on a mire system, lowers the ground water level (WT), aerates the catotelm peat, accelerates the heterotrophic soil respiration and reduces the methane effluxes (Nykänen et al., 1998). Furthermore, drained peatlands are likely to increase the C stock in trees and wooden materials in SOM, thus reducing the C loss from drained mire ecosystems (Maljanen et al., 2010). Long-term agriculture and peat extraction tend to enhance CO_2 emission, mainly because the repeated tillage keeps the topsoil in oxic conditions and enhances decomposition (Nykänen et al., 1995; Mäkiranta et al., 2007). In particular, cutaway peatlands are strong sources of CO_2 for decades after the cessation of peat extraction (e.g., Yli-Petäys et al., 2007). The area of such fields is increasing by 20 km^2 annually in Finland and Sweden (Maljanen et al., 2010). From 1970 to 2000, approximately 5.2 Tg of soil C was lost by gas emissions from the present and abandoned peat extraction sites (approximately 630 km^2) in Finland (Turunen, 2008).

The sustainable management of boreal peatlands should take advantage of both optimizing socio-economic utilization and protecting the C sink functions of peatland ecosystems. The cultivation of reed canary grass (*Phalaris arundinacea*, L.; RCG), a perennial bioenergy crop, provides a superior option (Lewandowski et al., 2003; Alm et al, 2011; Shurpali et al., 2013) compared with several other approaches, such as forestry (Mäkiranta et al., 2007), rewetting or the cultivation of barley and grasses (e.g., Nykänen et al., 1995; Maljanen et al., 2010). The benefits of RCG cultivation for cutaway peatlands include the purification of runoffs from peat extraction sites (Hyvönen et al, 2013) and the production of biomass for energy production (Shurpali et al., 2009). By cultivating RCG for energy biomass, C sinks can be recovered in cutaway boreal peatlands (e.g., Shurpali et al., 2009; Hyvönen et al., 2009; Järveoja et al., 2012). However, the net ecosystem CO_2 exchange (NEE) and the carbon-neutrality of RCG-based bioenergy are highly variable, even at an annual scale (Shurpali et al., 2009; 2010). Field studies (e.g., Shurpali et al., 2008; 2009; 2010) and greenhouse experiments (e.g., Zhou et al., 2011; Zhang et al., 2013) show that this variability is related to the variations in the growth of RCG, as affected by the climate variability and the moisture content in the rooting zone. Therefore, it is necessary to compare the climatic sensitivity of the C fluxes in the peatland ecosystems used to cultivate RCG with the fluxes from pristine peatlands to evaluate the sustainability of RCG cultivation in restoring the C-sink functions of cutaway peatlands and optimizing the bioenergy production through proper management strategies.

1.2 Hydrological controls on the C-flux changes in pristine peatlands under changing climate

Pristine peatlands are characterized by a diplotelmic structure determined by the water table (WT), i.e., an upper, oxic layer of less decomposed materials (acrotelm) and a deeper, anoxic layer of more decomposed peat (catotelm) (Ingram, 1978; Morris et al., 2011a). Consequently, many ecological and biogeochemical processes and structures co-vary with the changes in WT (e.g., Lafleur et al., 1994; Admiral et al., 2006; Alm et al., 2007; Price and Ketcheson, 2009). Meanwhile, the ecological functions of peatlands are also determinants of their hydrological settings. Plant litter contributes to peat accumulation, which shapes the microtopography (e.g., hummocks and hollows, Nungesser, 2003) and possibly elevates WT with the humification of organic materials and the enhancement of capillary flows (Belyea and Baird, 2006; Price and Ketcheson, 2009). Thus, understanding the changes in peatland hydrology and WT is important to investigating the C-flux changes under the changing climate (e.g., Bohn et al., 2007).

Several studies show that the expected climate change may draw down WT in boreal and subarctic peatlands by 10 - 20 cm (e.g., Roulet et al., 1992; Ise et al., 2008). Such estimations are mainly based on the possible increase in evapotranspiration (*ET*), which usually represents a major water loss in boreal peatlands. Based on these estimations, experimental studies (e.g., Bridgham et al., 2008; White et al., 2008; Updegrade et al., 2001) have emphasized a strong decrease in CH_4 emissions but an increase in CO_2 emissions under the changing climate. However, these WT fluctuations effectively regulate the water movement in the acrotelm (e.g., capillary rise) and the volumetric water content (θ) in the peat matrix (Price, 1997; Gnatowwski et al., 2002; Price and Ketcheson, 2009). The variation of θ further influences the WT changes, i.e., the water potential and hydraulic conductivity of peat are functions of θ (Price and Ketcheson, 2009). Such a θ-WT interaction is behind the self-regulatory features of peatland hydrology under climatic forcing (Ingram, 1983; Price and Ketcheson, 2009). As a result, there are uncertainties in the responses of WT in pristine peatlands to the changing climate regarding the self-regulatory features of peat hydrology.

At the regional scale, peatlands are discrete systems surrounded by mineral uplands that are weakly recharged by stream systems (e.g., Charman, 2002; Siegel and Glaser, 2006). These characteristics suggest that the hydrology and WT dynamics of peatlands at a regional scale depend mainly on the soil-vegetation-atmosphere transportation (SVAT) processes specific to each individual mire system in the area. Due to the topographical complexity of the regional landscape, the influences of lateral hydrology can be highly variable among mire entities. Such a hydrological variability is strongly correlated with the variations in other properties of mire entities, e.g., nutrient richness, vegetation, microtopology and soil texture, as represented by the classification of mire types. Typically, fens are minerotrophic (receive water and nutrients from both precipitation and their surroundings) and are dominated by vascular ground plants, whereas bogs are ombrotrophic (receive water and nutrients only from precipitation), have low pH and are dominated by non-vascular mosses (Igram, 1983). Such differences in the properties of mires indicate differences in the SVAT-based transportation of water-energy and the differences in hydrological responses to the changing climate among mire systems. Under artificial manipulations of WT and *Ta*, the responses of C-fluxes are found to be different in fens and bogs, due to the differences in the ecophysiology and biogeochemistry of ecosystems (e.g., Weltzin et al, 2000; Updegraff et al, 2001; Bridgham et al, 2008). The mire-type differences in hydrology, ecophysiology and biogeochemistry need to be addressed when studying the climatic sensitivity of the hydrology and C fluxes in pristine boreal peatlands.

The boreal peatlands in Finland cover approximately 30% of the country's territory, with a total C storage of approximately 5960 Tg (Turunen, 2008). A major fraction of these peatlands is fen, which dominate central and northern Finland. In contrast, the peatlands in southern Finland are rarer and ombrotrophic bog-dominated. On average, the peat deposits in these areas are older and thicker than in the mires in the north of the country (Turunen et al., 2002). Based on a 30-year (1981-2010) average of climate records, the interactions between *Ta* and *P* in Finland show a south-north gradient, i.e., the mean annual *Ta* varies from -2 °C in the north to +5 °C in the south, and the annual *P* varies from 400 mm in the north to 750 mm in the south. The climate change associated with the doubling of C_a by the end of the 21st century implies an increase of 2 to 6 °C in the annual mean *Ta* and 7 to 26% in the annual mean *P* (Jylhä et al, 2009), the changes being greater in winter than in summer. It is still poorly known how the changing climate may affect the exchanges of C gases in peatlands over the whole of Finland. This effect is closely related to the heterogeneity of mire types and changes in climate, which reduces the accuracy of GHG inventories of peatlands (Alm et al., 2007).

1.3 Influences of peat extraction and RCG cultivation on the C-water processes in boreal peatlands

Management strategies for peat extraction and RCG cultivation are likely to significantly modify the hydrology and C processes that are representative in pristine peatland ecosystems. In peat extraction, the acrotelm peat is removed, and old, highly decomposed peat previously preserved in the bottom catotelm is exposed. These peats are characterized by low porosity and saturated hydraulic conductivity (*Ks*) (Price, 1997) due to the consolidation, compression, shrinkage (Schlotzhauer and Price, 1999; Price and Whitehead, 2004) and oxidation (Waddington and Price, 2000) of peat after tillage and drainage. The cultivation of RCG drives the transformation process of organic matter, a process known as moorshification (Okruszko and Ilnicki, 2003). On the other hand, the accumulation of RCG litter in the topsoil tends to decrease the water retention capacity but increase the *Ks* of the surface peat. The growth of RCG rhizomes also increases the macropores in rhizospheric soil (Beven and Germann, 1982). These characteristics of soil tend to facilitate the gravity drainage of water from topsoil. However, the low permeability of the old peat layer could restrict the ability of the upward capillary flow to the surface. If the organic layer is thin and the WT is drained beneath the peat bottom, the θ-WT interaction could be further decoupled, especially if the subsoil is highly permeable (e.g., coarse sand) and has a low water retention capacity (e.g., Walczak et al., 2002). Consequently, the decoupling of the θ-WT interaction may modify the soil hydrology and its responses to the climatic forcing compared with pristine peatlands, where WT is generally regarded as a surrogate of θ and is related to multiple ecophysiological and biogeochemical processes. To date, little is known about the extent to which the flow mechanisms and climatic sensitivity of the soil hydrology could be affected by peat extraction and RCG cultivation.

The possible decoupling of the θ-WT interaction in RCG cutaway peatlands further implies that the core assumption of diplotelmic theory, in which the WT is a strong predictor of many variables relevant to peatland ecohydrology, may not apply in such ecosystems. Instead, the changing climate is likely to impact the C exchanges mainly through manipulating the root-zone moisture content and the C fixation of RCG (e.g., Shurpali et al., 2009; Zhou et al., 2011; Zhang et al., 2013). Moreover, such impacts tend to accumulate over the years due to several long-term feedbacks. For example, the accumulation of rhizome biomass could speed up the development of the RCG canopy during the early growing season (Asaeda and Karunaratne, 2000; Xiong and Kätterer, 2010). The accumulation of RCG litters and exudates gradually increases the labile substrates in the soil, improving the quality of the peat (e.g., Hobbie et al., 1995) and speeding up the decomposition of SOM, even for old, resistant materials (priming effect, Kuzyakov et al., 2000; Tavi et al., 2010). Due to the uncertainties regarding the hydrological responses and the complexity of plant ecophysiology, little is known about the extent to which the C exchanges may respond to the potential climatic changes in cutaway boreal peatlands with ongoing RCG cultivation and to which extent management has altered the climatic sensitivity of the C exchange in cutaway compared with pristine peatlands.

1.4 Modeling tools for the C-water cycle in boreal peatland ecosystems

Understanding C-water changes under the changing climate requires investigation of the very mixed effects of changes in ecohydrology, soil thermal loading, photosynthetic efficiency and SOM quality (Shannon and White, 1994; Moore et al., 1998; White et al., 2008). There is a clear need for analytical models capable of reproducing the ecosystem cycles of C, nutrients, water and energy. A number of hydrological models at the point scale have been developed over the past two decades for the SVAT-based water transportation in boreal peatlands (e.g., Letts et al., 2000; Comer et al., 2000). Many of these models emphasize WT controls on the *P-ET* balance (Roulet et al., 1992; Rouse, 1998) and the effects of vegetation type on surface resistance schemes (SWAPS model, Spieksma et al., 1997). Moreover, Nungesser (2003) suggested the importance of microtopology (i.e., hummocks and hollows) to the soil water capacity and evaporation. Several models have also described the effects of peat water retention capacity (Weiss et al., 2006) and ditching (Koivusalo et al., 2008) on WT changes.

The recent peatland C models incorporate the processes of ecohydrology, ecophysiology and biogeochemistry with respect to seasonal (e.g., Frolking et al., 2001; 2002; Zhang et al., 2002; St-Hilaire et al., 2008) and long-term dynamics (e.g., Ise et al., 2008). Efforts have also been made to extrapolate the C-water processes from the point scale to the regional scale by considering the spatial heterogeneities of lateral hydrology and vegetation (e.g., Govind et al., 2011; Tague and Band, 2004; Chen et al., 2005; Bohn et al., 2007; Devito et al., 2005). However, many models omit the fen-bog differences in ecohydrology, ecophysiology and biogeochemistry. On the other hand, the diplotelmic theory, which is one of the core assumptions behind the current peatland models, may not apply in peatlands disturbed by the extraction of peat and the cultivation of RCG on cutaway peatlands. For these reasons, the mire-type effects should be included in modeling tools supporting the assessment of the climatic sensitivity of hydrology and C fluxes in pristine peatlands. For cutaway RCG peatlands, the diplotelmic theory should be tested and the C-water processes specified in the modeling tools regarding the influences of peat extraction and RCG cultivation on the hydrology and ecophysiology of mire ecosystems.

1.5 Aims of the study

The aim of this study was to investigate the effects of climate change on soil hydrology and C fluxes in boreal peatland ecosystems, with implication for the feasibility of RCG cultivation as a way to restore the C-sink functions of cutaway peatlands under the Finnish conditions. Modeling approaches were employed to carry out the specific research tasks, which are listed as follows:

1. Modeling the changes in WT and water balance in boreal peatlands in Finland under the changing climate (Article I).
2. Modeling the changes in CO_2 and CH_4 fluxes in pristine peatlands in Finland under the changing climate (Article II).
3. Modeling the climatic sensitivity of soil moisture content in a cutaway peatland cultivated with a perennial bioenergy crop (*Phalaris arundinacea*, L.) (Article III).
4. Modeling the climatic sensitivity of ecosystem carbon exchanges in a cutaway peatland under the cultivation of a perennial bioenergy crop (*Phalaris arundinacea*, L.) (Article IV).

For tasks 1 and 2, the diplotelmic theory was employed in the development of the modeling tools. The mire-type differences in lateral hydrology, ecophysiology and biogeochemistry, i.e., fens *vs.* bogs, were hypothesized to lead to different hydrological responses to the changing climate, and such differences were assumed to differentiate the climatic sensitivity of the ecosystem fluxes of CO_2 and CH_4. In task 3, management systems for peat extraction and RCG cultivation were hypothesized to modify the diplotelmic hydrology in the cutaway peatlands, and such changes were further related to the C-exchange responses of the ecosystem to the changing climate (task 4).

2. MATERIALS AND METHODS

2.1 General outlines

The research tasks of this study follow the schematic procedure shown in Figure 1. A series of process-based models were developed to perform a point level (stand level) simulation of the hydrology and energy balance of a site under climatic forcing in pristine (Article I) and cutaway RCG peatland ecosystems (Article III). The hydrology and energy balance models were further incorporated within the C models (Articles II, IV) to simulate the annual and seasonal dynamics of C exchanges (g C m^{-2} $timestep^{-1}$). For the pristine peatland ecosystems, the models were developed based on the diplotelmic theory, and the differences in hydrological, ecophysiological and biogeochemical processes between fens and bogs were highlighted (Articles I & II). The models for cutaway peatlands cultivated with RCG are non-diplotelmic, and the influences of multiple management practices (e.g., site preparation, cultivation, fertilization and harvesting) were highlighted in the water, energy, C and N cycles (Articles III & IV).

The models were used to investigate the sensitivities of soil hydrology and C exchanges of mire ecosystems to the changes in climatic factors (i.e., C_a, *Ta* and *P*). The hydrological responses of pristine peatlands were represented by the changes in WT (Article I), which further affected the response of CO_2 and CH_4 fluxes through multiple feedbacks among the water, energy, C and N cycles (Article II). For cutaway peatlands under RCG cultivation, the sensitivities of root-zone moisture content to the changes in WT and *P-ET* balance were also tested (Article III). The climate change scenarios developed by the Finnish Meteorological Institute (FMI) for the 21st century were employed to simulate the mixed effects of the changes in C_a, *Ta* and *P* on the hydrology and C exchanges (Articles I, II & IV). In Articles I & II, the changes in C-water cycling were simulated for the pristine peatlands across the territory of Finland. Mapping data from SRTM remote sensing, the National Land Survey of Finland, the European Soil Bureau and the Finnish Meteorological Institute were used in the country-scale simulations. In Articles III and IV, the modeling and simulations were performed at the mire unit level (Linnansuo, 62°30'N, 30°30'E).

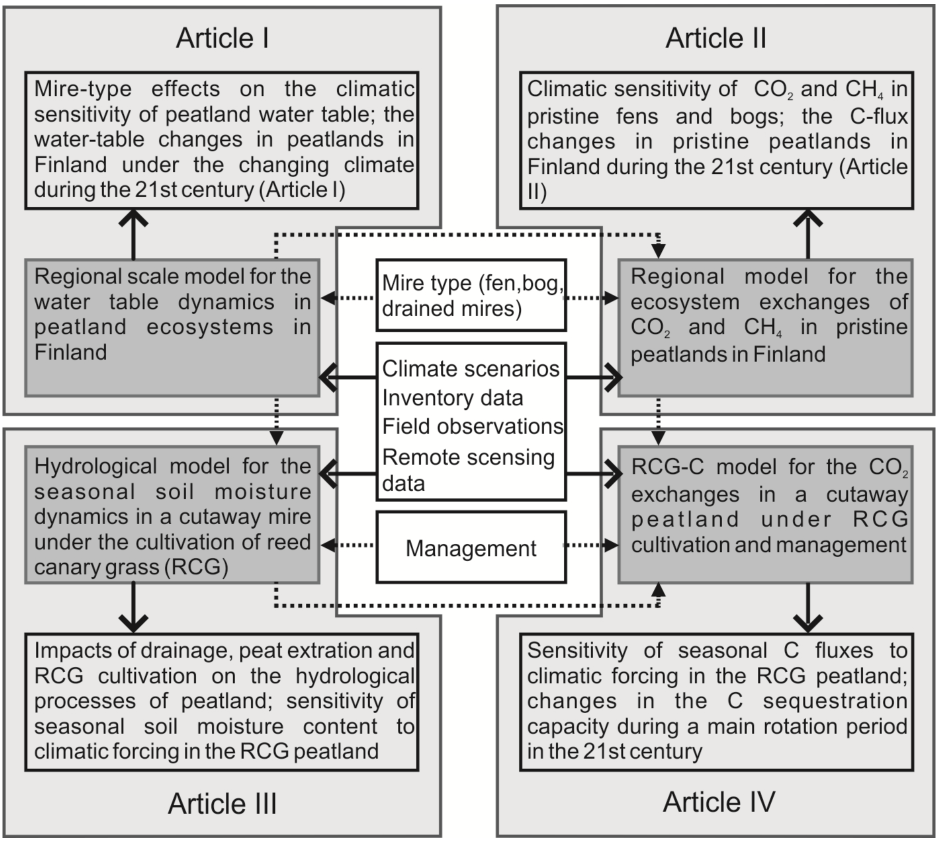

Figure 1. Outline of the study. The dashed arrows represent the effects or processes included in the model.

2.2 Outlines of modeling tools (Articles I - IV)

2.2.1 Hydrological tools (Articles I & III)

Figure 2 shows the framework of the hydrological tools (Articles I & III). In these tools, the changes in soil water storage (*dW*) at the point scale are driven by the balance among the *P*, *ET* and water flow in the soil, e.g., discharge and recharge, as indicated by Equation (1). The changes in the volumetric moisture content in the peat profile (divided by 10-cm layers) lead to multiple water-energy feedbacks to the water balance via *ET* and discharges (Figure 2). The calculation of *ET* covers snow-covered and snow-free seasons. During the snow-free season, *ET* is calculated as the total water loss through canopy transpiration, evaporation of the intercepted rainfall and evaporation from the ground. The discharge is calculated as the sum of seepage (*Ws*) and overland flow (*Wo*). The recharge consists of melting snow (W_{melt}) and the inflowing water from the upstream areas (*Wf*). During the snow-covered season, *ET* is calculated as the evaporation from snow, ignoring the variations in soil moisture content and WT. In the calculations, *Ws*, *Wo* and *ET* are negative (water is flowing out from the stand), whereas *Wf*, W_{melt} and *P* are positive (water is flowing into the stand).

$$dW = P + ET + Ws + Wo + Wf + W_{melt} \tag{1}$$

In the pristine peatland ecosystems, the change in soil water storage drives the fluctuation of WT based on an empirical water retention function. The fen-bog differences in the water balance at the stand level are represented by the different *Wf* calculation schemes in the pristine fens. The value of *Wf* depends on the water budget in the upstream areas of the stand, whereas the recharge from the surroundings is ignored in the water-balance calculation for the pristine bogs. The SVAT-based transportation of water-energy is also specified for the pristine fens and pristine bogs regarding the differences in the vegetation types, surface resistance features and microtopography.

In the cutaway peatlands occupied by RCG, the hydrological influence from the surroundings is ignored due to the drainage. The soil layers, which represent distinctive anthropogenic and ecobiological features, are separated (Figure 1, Article III). The water transportation between soil layers of dissimilar hydraulic properties is calculated as the sum of Darcy's flow and turbulent flow through micropores. The transpirative uptake of water from each soil layer is related to the distribution of fine roots in the soil profile. The phenological cycle of RCG influences the seasonality of *ET* demand by affecting the canopy morphology, surface energy partitioning, rainfall interception and surface aerodynamic features. The surface energy balance is also affected by the development of snowpack, the soil thermal properties and the thaw-frost dynamics of the soil water content.

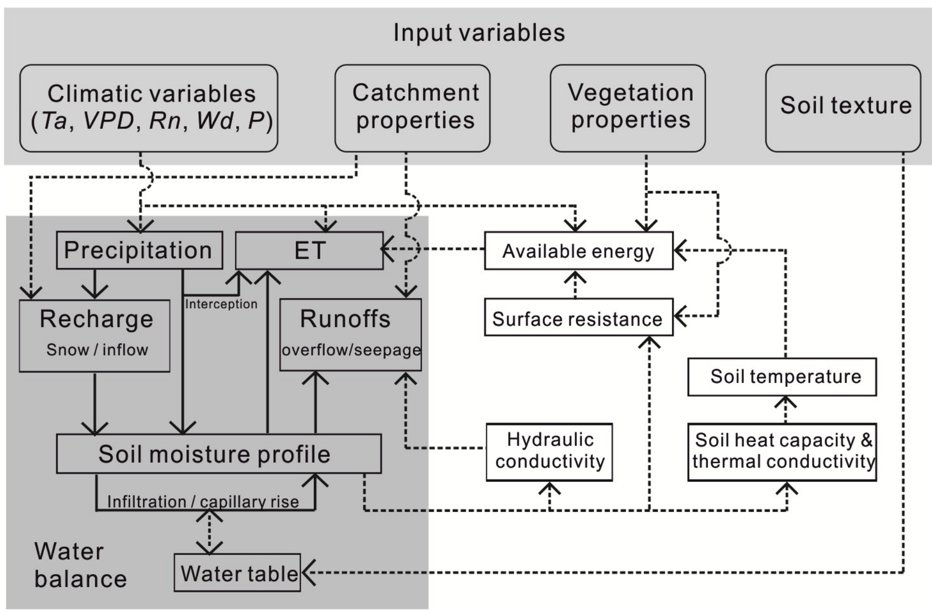

Figure 2. Framework of the hydrological tools for the pristine (Article I) and drained peatland ecosystems (Article III). The solid arrows indicate the water flow in the ecosystems. The dashed arrows indicate the information flow between the model variables.

2.2.2 C-flux tools (Articles II & IV)

Figure 3 shows the framework of the C-flux tools (Articles II & IV). The C-flux tools calculate the net C exchanges of the peatland ecosystems by simulating the simultaneous input and output of C, i.e., photosynthesis (*GPP*) *vs.* respiration for CO_2 (*AR*), and methanogenesis (*Ra*) *vs.* methanotrophy (*RO*) for CH_4:

$$F_{CO2} = GPP + AR + RO \tag{2}$$

$$C_{CH4} = Ra - RO \tag{3}$$

where *AR* includes the CO_2 loss via the respiration in the living plant organs (*RE*) and the CO_2 respired from the decomposition of SOM (*Ro*). In the calculation, *GPP* is negative (C is flowing into the system), whereas *RE*, *Ro*, *RO* and *Ra* are positive (C is flowing out of the system).

The simulation of the C processes at the mire-entity scale is based on a combination of sub-models (Figure 3) that are linked by multiple feedbacks to represent the complex interactions among the C, N, water and energy cycles in the soil-plant-atmosphere continuum. The hydrological tools for the pristine peatlands (Article I) and the cutaway peatland (Article III) are incorporated in the C models for corresponding ecosystems as the sub-models of soil water (iii, see Figure 3) and soil temperature (iv, see Figure 3). The dynamics of soil moisture content, energy balance and soil temperature calculated in these sub-models further regulate the rates of photosynthesis and respiration in the sub-models for vegetation (i), decomposition (ii) and peat texture (v) (Figure 3).

In the vegetation sub-model, the rate of photosynthesis (*GPP*) is calculated as a function of biochemical parameters (i.e., maximum carboxylation velocity (V_{max}), maximum rate of electron transport (J_{max})), leaf nitrogen content (N_{leaf}), climatic variables (i.e., radiation, *Ta* and C_a) and stomatal conductance (Farquhar et al., 1980). A temporal and spatial scaling scheme is used to integrate the diurnal irradiative cycle and the distribution of sunlit (LA_{sun}) and shaded leaf area (LA_{shade}) within dense upper canopies. The stomatal conductance is further subject to independent stress scalars of photosynthetic photon flux density (*PPFD*), *Ta*, vapor pressure deficit (D_a) and the moisture content in the root-zone soil. The CO_2 loss via the respiration in plant organs (*RE*) depends on the biomass and the air and soil temperatures. The net primary production (NPP), which is the balance between *GPP* and *RE*, is further regulated by the availability of mineral N, and it drives the accumulation of biomass in plant organs. Litter falling from the plant organs is added to the soil organic matter (SOM) and is subjected to the decay process.

In the sub-model for decomposition, the rates of aerobic / anaerobic decay are calculated based on the vertical profile of peat temperature and moisture content. The rate of decomposition at a certain point in the peat profile is calculated based on multiple SOM components of characteristic decomposability and N concentrations. The decomposition process is constrained by multiple environmental factors, i.e., soil temperature, soil moisture, pH, availability of mineral N and the C:N ratio of SOM. The CH_4 efflux is subject to the balance between methanogenesis in the anoxic soil layers and the methanotrophy during the transportation process. The emission of CO_2 from soil comprises the CO_2 produced in methanotrophy and respired from belowground biomass as well as the decomposition of SOM. The balance between litter accumulation and SOM decomposition drives the changes in the thickness and bulk densities of the peat layers. These changes further feed back to the water-energy exchange in the soil (see the peat texture sub-model, Articles II & IV).

For the pristine peatlands, the differences in ecosystem processes between the fen-type and bog-type peatlands are emphasized in the C-flux tool (Article II). These differences mainly emphasize the differences in hydrology (Article I), plant-mediated C sequestration and N cycling and the mineral N input from the upstream areas (Article II). For the cutaway RCG peatland, the C-flux tool (Article IV) entails the influences of seasonal soil moisture on the canopy morphology, the allometric scheme of biomass, the photosynthetic intrinsics (i.e., V_{max} and J_{max}) and the phenological cycle of RCG. The rhizome biomass also affects the growth of RCG at the start of a growing season. In addition, the effects of management practices, i.e., drainage, fertilization and harvesting, are related to the soil hydrology, N cycling and litter returning, respectively.

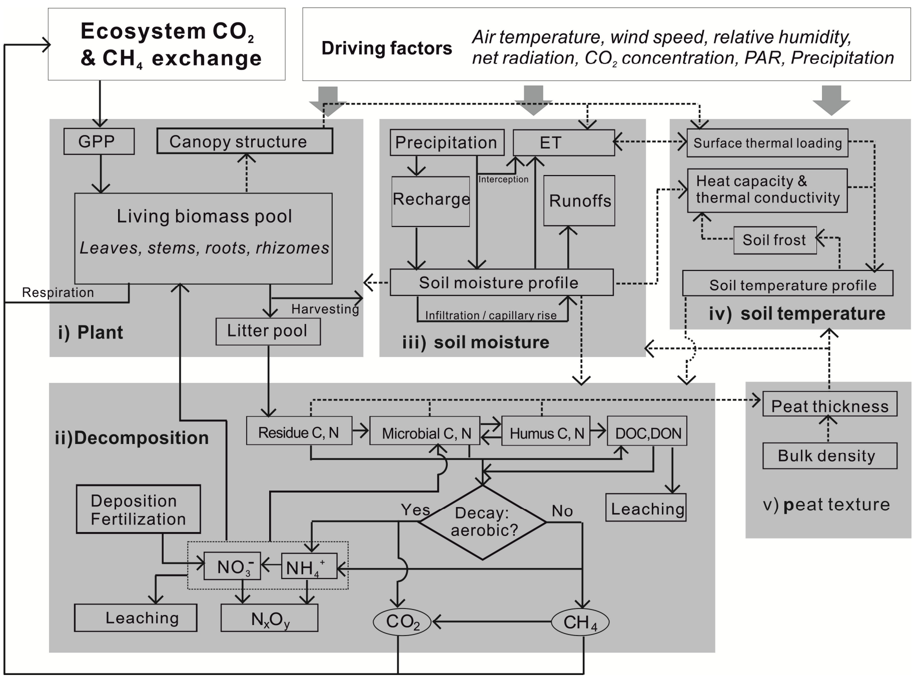

Figure 3. Framework of the C-flux tools for the pristine peatlands (Article II) and the drained peatland under RCG cultivation (Article III). The solid arrows indicate the flows of mass and energy. The dashed arrows indicate the information flow between model variables.

2.3 Model parameterization, calibration and validation (Articles I - IV)

2.3.1 Models for pristine peatland ecosystems (Articles I & II)

The parameterization of the hydrological and the C-flux tools for the pristine peatland ecosystems is based on 10 km×10 km spatial grids, which capture the heterogeneities of climate, catchment conditions and C storage across Finland. At the grid scale, the models are parameterized for fens and bogs based on 1 km×1 km patches. The SRTM digital elevation model and multivariate data from SYKE, National Land Survey of Finland and European Soil Bureau, are used to parameterize the distribution of pristine fens and pristine bogs in Finland, including the hydrological properties of catchments. In the pristine bogs, the atmospheric deposition of nitrates is the only outside source of N input. In the fens, nutrients are also available from upland areas in addition to the atmospheric input of N, i.e., the N deposition is related to the ratio of fen area to the upstream area that contributes nutrients to a particular fen. The values of the other parameters, such as peat thickness and texture (e.g., Turunen et al., 2002), plant communities (e.g., Aurela et al., 2002), canopy structure (e.g., Repola, 2009) and surface resistance (e.g., Raddatz et al., 2009) are from previous publications.

Table 1. Validation and sensitivity analysis of the models for pristine peatland ecosystems.

	Model validation	Sensitivity analysis
Hydrological tool	The simulated *ET* was compared with the measured potential evaporation from seven evaporation stations across Finland. The Priestley-Taylor coefficient was estimated and compared with previous studies. The modeled monthly WT for each mire type was compared with the values measured from three spatial grids (Lakkasuo, Mekrijävi and Vaisjeäggi areas).	The sensitivity of WT to 15 scenarios (0, +2 °C and +6 °C in *Ta*, and -20%, -10%, 0, +10% and +20% in *P*) were tested for pristine fens and bogs based on 5 grid areas from southern Finland to Lapland. The parameter sensitivity of WT was tested by manipulating peat thickness, peat hydraulic conductivity, water retention capacity, hollow area, hollow depth or the surface resistance for *ET*.
C-flux tool	The modeled monthly and annual exchanges of CO_2 were compared with EC records from the Kaamanen mire complex over a six-year period. The modeled soil emissions of CO_2 and CH_4 were further validated based on the data measured from two grid areas (Lakkasuo and Mekrijävi areas), which include a variety of fen- and bog-type sites.	The sensitivity of the modeled C fluxes to the variations of several land-surface parameters was tested. These parameters include peat thickness, C:N ratio of the peat, hydraulic conductivity, DBH of trees, leaf area of ground vegetation and hollow depth. The model sensitivities to the changes in climatic factors were tested based on 25 climate scenarios. These scenarios combine five increases in annual *Ta* (0, +1 °C, +3 °C, +5 °C and +7 °C) and five increases in annual *P* (0, +5%, +10%, +15%, +20% and +25%) under elevated C_a (700 ppm).

In addition to the previous studies regarding the validity of the model (Table 3, Article I; Table 2, Article II), the validity of the models were further tested utilizing the WT and C flux data measured from several sites across Finland (Table 1). These sites were located in the grids from southern to northern Finland, and they represent a variety of pristine fens and bogs. The model sensitivities to several land-surface parameters were tested (Table 1). Based on the validated model, the sensitivity of the soil WT and the CO_2/CH_4 fluxes to the changes in the climatic factors (i.e., *Ta*, *P* and C_a) were tested based on multiple grid areas (Table 1).

2.3.2 Models for cutaway peatlands under RCG cultivation (Articles III & IV)

The parameterization of the modeling tools for cutaway RCG peatlands was based on the Linnansuo site (62°30'N, 30°30'E), which is located in eastern Finland in a transition zone between southern and mid-boreal climatic conditions. The area is well drained by ditches, and the RCG cultivation began in 2002 after peat extraction ceased. The soil profile is characterized by multiple layers representing distinctive anthropogenic and ecobiological features (Article III). The dissimilar properties of the layers, i.e., thickness, bulk density, C and N contents and microbial biomass, were parameterized based on soil-core samples from the field (Articles III & IV). The water retention curves of the soil and the effects of macropores on the rate of infiltration were fitted based on the measured soil-moisture changes during several rain events (Article III). The influence of soil moisture conditions on the canopy morphology, i.e., canopy height (*hc*) and leaf area (*LA*), were parameterized by a set of environment-controlled experiments (Article IV). The influence of drought on the photosynthetic parameters (e.g., V_{max} and J_{max}) and the phenological cycle of RCG were also investigated by calibrating the modeled NEE to the measured values during a wet year (2009) and a very dry year (2010) (Article IV).

Table 2 lists the validation and sensitivity analysis based on the hydrological tool and the C-flux tool based on the Linnansuo site (Articles III & IV). The hydrological tool was validated by comparing the simulated daily values of the latent heat flux (LE) and the soil temperature and soil moisture profiles with the values measured during 2009-2010 (Article III). The sensitivity of the soil moisture profile to artificial manipulations of the WT and *P-ET* balance were tested (Article III). The modeled CO_2 flux was tested by contrasting the simulated daily vapor flux and NEE values to the values measured during a 6-year period (2005-2010) representing the 4th - 9th year of cultivation. The climatic sensitivity of the CO_2 exchanges was further tested by manipulating the *Ta*, *P* and C_a values in the simulations (Article IV).

2.4 Climate change scenarios (Articles I, II & IV)

The simulations of climate-change effects on the hydrology and C-fluxes of the ecosystems employed the ACCLIM climate change scenarios provided by the Finnish Meteorological Institute (Jylhä et al., 2009). In the ACCLIM scenarios, the climatic gradient in Finland was captured by daily climatic data from 318 stations, each of which represents the central point of a 0.5°×0.5° area throughout the country. The changing climate scenario was based on the A1B GHG scenario given in the studied periods, i.e., 2000-2019 (Period I), 2020-2059

(Period II) and 2060-2099 (Period III). The increases in the climatic factors (i.e., C_a, *Ta* and *P*) were predicted to be more pronounced in Period III than in Periods I and II. Furthermore, the changes in *Ta* and *P* were more pronounced in winter than in summer (Figure 4). The effects of climate change on the WT and the C fluxes were represented by the differences in the values under the changing climate and the current climate.

To simulate the changes in WT and the C fluxes in pristine peatland ecosystems across Finland, the ACCLIM climate scenarios were averaged to monthly values and interpolated to 10 km × 10 km grids (the universal Kriging method) (Articles I & II). These simulations covered the 2000-2099 period. To simulate the C-flux changes in the cutaway RCG peatland, climate change scenarios were constructed for the period between the 4th - 15th years since cultivation, considering the common rotation length of 10 - 15 years in the Nordic countries (Elbersen et al., 2000). The climatic variables measured during 2005-2010 (from an age of 4 to 9 years) were used as the current climate (CU) and were repeated for an age of 10 to 15 years. The changes in the daily values of *Ta* and *P* were extracted from the ACCLIM scenarios for Periods I-III from the site (62°46'N, 30°58'E) closest to the Linnansuo peatland (Figure 4). The trends of these changes were added to CU to represent the changing climate (CC). The changes in the CO_2 flux were calculated for RCG the period from 4 to 15 years of age for Periods I-III.

Table 2. Validation and sensitivity analysis of the models for drained peatland cultivated with RCG.

	Model validation	Sensitivity analysis
Hydrological tool	The modeled soil moisture content and soil temperature was compared with the values measured at multiple depths of the Linnansuo site during 2009-2010. The modeled daily *ET* was also compared with the values measured using the EC technique.	The sensitivity of the modeled soil moisture content was tested with ±25% manipulations of the effective moisture (*P* minus *ET*) and change in the regularity of summer rainfall. The model sensitivity to the manipulation of WT was also tested by disregarding the seasonal fluctuation of WT and decreasing the WT by 50 cm.
C-flux tool	The modeled daily exchanges of latent heat and CO_2 were compared with the EC records during a six-year period (2005-2010).	The sensitivity of the modeled CO_2 exchange was tested for potential changes in the climatic factors (i.e., *Ta*, *P* and C_a). These changes were based on the ACCLIM climate change scenarios, and the changes in *Ta*, *P* and C_a were given for 2000-2019 (Period I), 2020-2059 (Period II) and 2060-2099 (Period III).

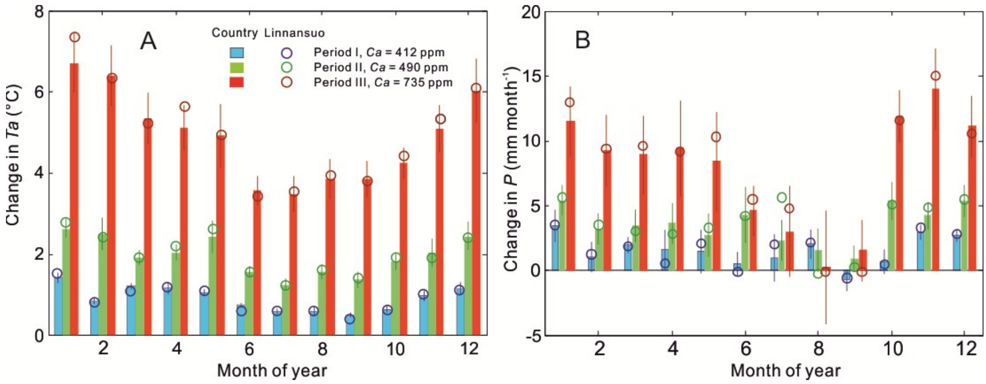

Figure 4. Changes in monthly *Ta* (A) and *P* (B) in peatlands in Finland over the 21st century (ACCLIM climate scenarios). Period I: 2000-2019; Period II: 2020-2059; Period III: 2060-2099. The error bars represent the standard deviations of the changes based on 10 km × 10 km spatial grids.

3. RESULTS

3.1 Climatic sensitivity of hydrology and C fluxes in pristine peatland ecosystems (Articles I & II)

3.1.1 Model validity

In general, the simulated values of the WT, CO_2 and CH_4 fluxes were strongly correlated with the values measured at the grid scale. The hydrological model explained more than 85% of the variations in the grid-based WT measured at the Lakkasuo, Mekrijärvi and Vaisjeäggi mire-complexes (Article I). The C-flux tool explained more than 80% of the variations in the monthly soil emissions of CO_2 and CH_4 measured from the pristine fen sites at the Lakkasuo and Mekrijärvi areas (Article II). For the pristine bog sites in these areas, the model explained 77% and 42% of the variations in the measured soil CO_2 and CH_4 fluxes, respectively (Article II). The C-flux tool also showed no significant deviations in describing the monthly and annual NEE trends of the Kaamanen mire complex (Article II).

The tests for the parameter sensitivities showed that the hydrological tool was more sensitive to the variations in the surface resistances compared with the land-surface parameters, including the peat thickness, soil hydraulic conductivity, hollow area and hollow depth (Article I). On the other hand, the C-flux tool was more sensitive to the variations in hollow area and hollow depth compared with the others (Article II). In addition, the CH_4 emission in the pristine bogs was also sensitive to the increased C:N ratio (Article II).

Table 3. General responses of water table, soil temperature and C exchanges in pristine peatland ecosystems in Finland to increases in *Ta*, *P* and C_a. Downward arrows represent the decrease in parameter values, whereas upward arrows represent the increase in parameter values. A greater number of arrows indicates the higher sensitivity of a parameter to the changes in a climate variable.

Parameters	C_a	*Ta*	*P*
WT	n.a.*	↓	↑
Soil temperature (10 cm depth)	n.a.*	↑↑↑	n.c.**
CH_4 source	↑	↓	↑
NPP	↑	↑	↑
AR	↑	↑↑↑	↓
NEE	↑	↓↓↓	↑

* Not available. ** The change is unclear.

3.1.2 Sensitivity of WT and C fluxes in pristine peatlands to the changes in the climatic factors

Table 3 lists the general responses of the WT and C fluxes in the pristine mires to the changes in climatic factors (i.e., *Ta*, *P* and C_a). Increasing *Ta* and constant *P* tended to draw down the WT (Article I) and raise the soil temperature but reduce the CH_4 emissions (Article II). On the other hand, an increasing *P* and constant *Ta* tended to raise the WT (Article I) and increase the CH_4 emissions but slightly decrease the soil temperature (Article II). The WT and CH_4 emission in the pristine fens showed greater sensitivity to the manipulation of climatic factors compared with that in the pristine bogs (Articles I & II). In both fens and bogs, the NEE would increase along with rising *P* and C_a, whereas a rising *Ta* would decrease the NEE by enhancing AR more than NPP (Article II). The NEE was more sensitive to the changes in *Ta* compared with the changes in *P*. The NEE of the pristine fens showed greater *Ta* sensitivities but less *P* sensitivity compared with the pristine bogs, whereas an increase in *Ta* tended to shift bogs from a CO_2 sink to CO_2 sources more easily than the fens.

3.3.3 Changes in WT and C fluxes in pristine peatland ecosystems in Finland during the 21st century

In response to climate change, the simulation showed that the WT at the country scale would draw down mainly in the spring months (i.e., April - May), whereas the WT drawdown tended to be weaker in the summer and autumn months (June - September). During Period I (2000-2019), the WT drawdown occurred mainly in the southwestern part of the aapa-mire region and the western parts of the raised-bog region. This drawdown in WT tended to become greater and to expand southward and northward in Periods II and III. The WT drawdown was also more pronounced in the pristine fens than in the pristine bogs, particularly in the southwestern parts of the aapa-mire region (Figure 5).

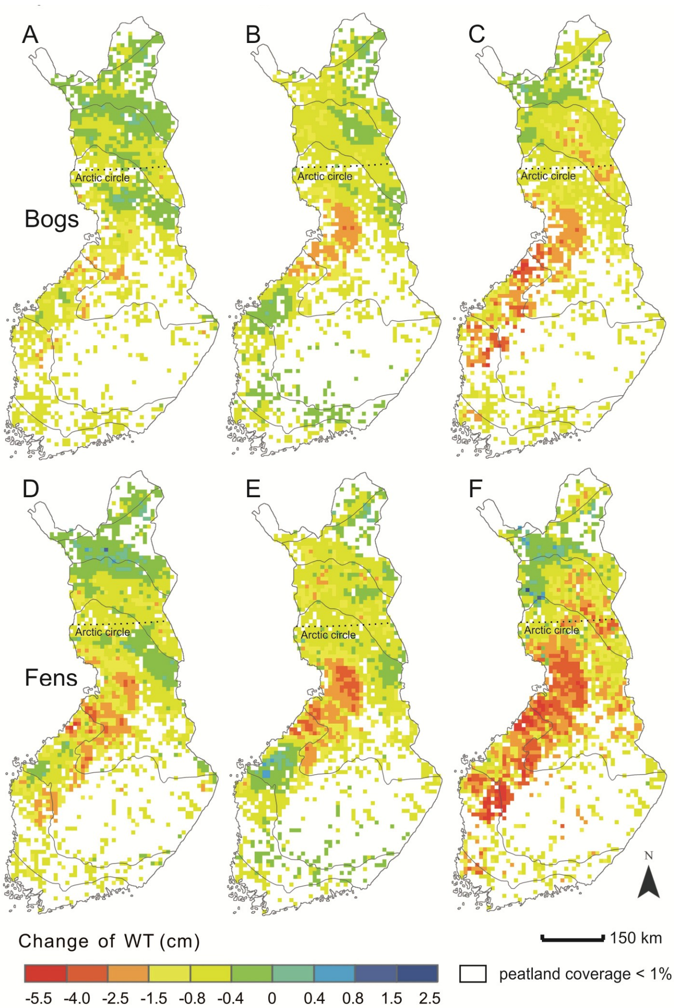

Figure 5. Spatial variation in the WT changes in the pristine bogs (A-C) and pristine fens (D-F) during Periods I (2000-2019, A and D), II (2020-2059, B and E) and III (2060-2099, C and F). A negative value of WT change indicates a drawdown of WT.

At the country scale, the climate changes tended to decrease the CO_2 sink by 21.5 ± 5.4 g C m^{-2} a^{-1} but to increase the CH_4 emission by 0.7 ± 0.3 g C m^{-2} a^{-1} in the pristine peatlands during the 21st century. These changes tended to be the most pronounced in Period III (2060-2099) compared with Periods I (2000-2019) and II (2020-2059). In the southwestern part of Finland, the climate changes tended to decrease the CH_4 emissions from the pristine peatlands, mainly in the Periods II and III, along with the WT drawdown in these areas. On the other hand, the peatlands tended to become greater CH_4 sources over time in the northwestern parts of Finland (Article II). Compared with the pristine fens, the reduction of the CO_2 sink function in the pristine bogs was smaller in Period III (Article II). In most parts of the raised-bog region and the western part of the southern aapa-mire region, the pristine fens are likely to turn from a net C sink to a weak source under the changing climate by the end of this century. The transition of the bogs from C sinks to sources will bemost notable near the coastal areas (Figure 6).

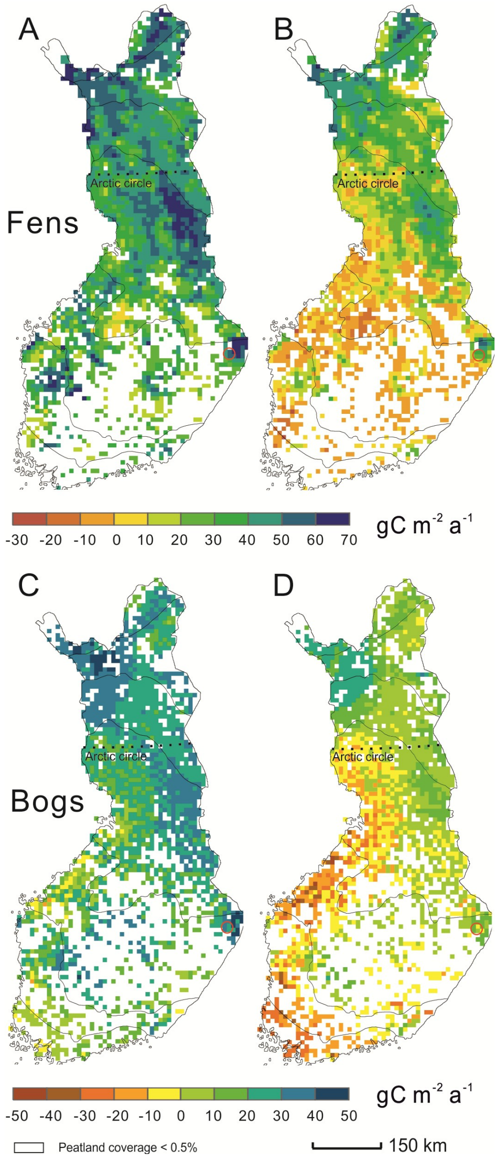

Figure 6. Spatial variation of C accumulation in the pristine fens (A-B) and the pristine bogs (C-D) during the 21st century under the current (A and C) and changing climate (B and D). A negative value indicates a net C source. The red circles represent the Linnansuo sites (B and D).

3.2 Climatic sensitivities of soil hydrology and CO2 flux in a cutaway peatland cultivated with RCG (Articles III & IV)

3.2.1 Model parameters and validity

The environment-controlled experiments showed that lowering moisture content in the rooting zone decreased the leaf-stem ratio of the RCG and limited the canopy development (Figure 5, Article IV). The hydrological model calibration showed that the water retention capacity was greater but that the saturated hydraulic conductivity was smaller deeper in peat profile (Article III). Moreover, more than 80 % of the rain water could be transported through the topsoil via flashy turbulent flows mediated by macropores (Table 1, Article III). On the other hand, calibrating the RCG-C showed that the Julian day for the growth commencement and the temperature sum required by the whole phenological cycle did not clearly differ between a wet year (2009) and a very dry year (2010). Moreover, the variations in the dry-wet climate conditions in the calibration years slightly affected the V_{max} and J_{max} values and the allometric pattern of photosynthetic assimilates between the above- and below-ground mass (Table 4, Article IV). The spring harvest removed 66.8 % of the above-ground mass inherited from the previous autumn. Stems were more efficiently removed in the harvest than leaves (Figure 4, Article IV).

The hydrological tool validation based on the years 2009-2010 showed that the model explained 70.3 % of the variance in the measured latent heat flux (LE) (Figure 5, Article III). On the other hand, the model explained more than 90 % of the seasonal variations in the soil temperature at depths of 2 cm, 6 cm and 16 cm (Figure 6, Article III). The model also captured well the seasonal trends of soil moisture changes in the peat profile (e.g., at depths of 2.5 cm, 10 cm and 30 cm) during 2009-2010, and it explained 90.3 % of the overall variations in the soil moisture measured (Figure 7, Article III). Validating the RCG-C model using the six-year eddy-covariance records showed that the model explained 81.0% of the variations in the measured daily NEE. The RMSE of the simulated NEE was 0.834 g C m^{-2} day^{-1}, which is approximately one order lower than the seasonal variations (Figure 7, Article IV). The simulated values of the total CO_2 sequestration, rhizome biomass growth and litter layer accumulation were also close to the measured values (Table 5 and Figure 7, Article IV).

3.2.2 Sensitivities of soil moisture content to water table manipulations and changing P-ET balance

The sensitivity analysis showed that the simulated moisture content in the unsaturated peat was not sensitive to the WT level in the cutaway peatland cultivated with RCG. The low sensitivity of the soil moisture content to the changing WT was associated with the dominance of the downward water flux from the organic layer to the sandy layer underneath. The soil moisture content in the shallow peat (e.g., 2.5 cm and 10 cm deep) was more sensitive to such changes than that in the NT layer (Table 3 & Figure 8, Article III). Increasing *ET* by 25 % or decreasing *P* by 25 % reduced the soil moisture content mainly at the 2.5 cm and 10 cm depths, whereas the changes at the 30 cm depth were weaker. A 25 % decrease in *P* showed a greater influence on the soil moisture changes than the 25 % increase in *ET*, regardless of the year. The downward water flux increased with the drawdown of WT but decreased with the reduction in P and the increase in *ET* (Table. 2).

The sensitivity of the water flux and soil moisture content to the changes in *ET* and *P* was significantly greater in the wet year (2009) than in the dry year (2010) (Table 3, Article III).

3.2.3 Sensitivity of CO_2 exchanges to the climate change scenarios

Several responses of the CO_2 exchanges to the changes in the climatic factors were clear. *First*, the increase in *Ta* decreased the CO_2 sequestration during the rotation period, whereas the increase in C_a increased the CO_2 sequestration. *Second*, the increase in *P* slightly decreased the ecosystem CO_2 sequestration, whereas such an effect is irrelevant compared with the effect of the increase in *Ta* or C_a. *Third*, under the increasing *Ta*, the changes in the CO_2 sink were greater ($p < 0.001$) during the period from 4 to 9 years of age compared with the period from 10 to 15 years. The magnitude of the decrease in the CO_2 sink under the rising *Ta* was also greater than the magnitude of the increase in CO_2 sink under the increasing C_a (Figure 9, Article IV).

The simulations showed that the climate change in Period I (2000-2019) may slightly decrease the CO_2 sink function of peatland occupied by RCG during a main rotation period, i.e., during the period representing the age of cultivation from 4 to 15 years since establishment. However, the CO_2 sink function tended to decrease extensively under the climate changes in Periods II (2020-2059) and III (2060-2099). Under the changing climate, the total CO_2 sequestration in Period III would decrease by 63% - 87% during a main rotation period (Article IV).

4. DISCUSSION AND CONCLUSIONS

4.1 Evaluation of the modeling tools

In this work, a series of process-based models were developed, parameterized and validated to study the effects of climate changes on the soil hydrology and C fluxes in boreal peatland ecosystems under Finnish conditions (Articles I - IV). The results showed that the diplotelmic models included the key mechanisms that control the hydrology and seasonal C exchanges in the pristine peatlands (Articles I & II). The model also described ecosystem processes specific to fens and bogs, thus making it possible to include the heterogeneity of the different mire types in the regional simulations. At the study scale, the mire-type effects mainly affected the heterogeneities of the hydrology and C fluxes, whereas the spatial variations of the water table and C fluxes for a certain mire type were more stochastic. In this context, stochastic modeling could be helpful to further improve the model performance in describing the heterogeneity at the sub-grid scale. The sensitivities of the parameters suggested that the main uncertainties in the hydrology and C-flux models may be related to the control on the canopy resistance and the hummock-hollow structures. It also should be noted that the agreement of the modeled CH_4 flux with the measured values was relatively weak in the pristine bogs. This may be due to the relatively strong variations of WT in the pristine bogs leading to a low CH_4 oxidation stability. Thus, considering the water table's influence on the stability of the CH_4 oxidation may be helpful to improve the model's ability to predict the methane flux in ombrotrophic mires.

In the cutaway peatland cultivated with RCG, the hydrological tool captured well the variations in *ET* and the moisture content during the wet year (2009) and in the very dry year (2010) (Article III). This finding implies that the model could account for the key hydrological processes in peatland ecosystems similar to the Linnansuo site. Based on the hydrological tool, the daily NEE simulated by the RCG-C model agreed well with the measured values during a six-year period (2005-2010) (Article IV). The total CO_2 sequestration simulated for the years 2005-2010 (638 g C m^{-2}) was very close to that (643 g C m^{-2}) measured at the site. An increase in the peat layer thickness was also found to be in accordance with the measured changes. Therefore, RCG-C could be able to serve as a quantitative tool to simulate the CO_2 flux in cutaway RCG peatlands similar to the Linnansuo site under varying climatic conditions.

4.2 Evaluation of the simulation results

4.2.1 Climatic sensitivity of water table and C fluxes in pristine peatland ecosystems across Finland (Articles I & II)

The results showed that under the changing climate, the WT in the pristine peatlands decreased across Finland, with the relative decrease becoming more pronounced toward the end of the 21st century. This result suggests that the predicted increase in *P* was unlikely to offset the increase in water loss driven by the warming climate. Usually, climate change is thought to draw down WT by increasing *ET*, and such a change in WT is considered a key forcing in the C exchanges in boreal and subarctic peatlands (e.g., Gorham, 1991; Roulet et al., 1992; Ise et al., 2008). With the drawdown of WT, the reduction of CH_4 emissions is regarded as helpful in offsetting the increase in C-GHG emissions under the warming climate (e.g., Strack and Waddington, 2007; Lain et al., 2009).

The changes in *ET* and WT were found to be much weaker than those estimated previously. The small magnitudes of the changes in *ET* and WT may be due to the multiple water-energy feedbacks that exist among the water balance components and the "mismatch" of seasonal water-energy availabilities under the changing climate (Article I). Related to the low climatic sensitivity of WT, the changes in the CO_2 sink of the Finnish mires would be affected mainly by the *Ta* sensitivities of photosynthesis and respiration. Furthermore, the CH_4 source from the country-scale pristine peatlands was predicted to increase under the changing climate (Article II).

The climatic sensitivities of the WT and C exchanges in the pristine peatlands were also related to the mire type at the site. Compared with the pristine bogs, the WT is usually higher and the runoff events are more regular in the pristine fens (Lafleur, 1994; Price and Maloney, 1994). As a result, an increase in *ET* and a decrease in the recharge water from upstream ecosystems (see also Ge et al., 2010) is likely to lead to a greater drawdown of WT in the pristine fens compared with the pristine bogs, as found in this study (Article I). The significant drawdown of WT in southwestern Finland could decrease the strength of the CH_4 source in such areas under changing climate (Article II). On the other hand, the relatively low WT in the pristine bogs may lead to a strong methanotrophic effect and thus constrain the change in the CH_4 source of such ecosystems.

Compared with the pristine fens, the peat of the pristine bogs could be more easily heated up under the increase in *Ta*, whereas the increase in NPP was more limited. The relatively low *Ta*-sensitivity of NPP in the bogs may be due to the ombrotrophic condition and tight N-cycle in such ecosystems. Such fen-bog differences are likely to contribute to a greater decrease in NEE in the pristine bogs than in the pristine fens. However, the results showed that the *Ta*-sensitivity of NEE in the pristine fens was similar to that in the pristine bogs (Article II), which may be due to the low N availability and the low decomposability of plant litters (Limpens et al., 2006). This effect tends to constrain the enhancement of decomposition under the warming climate. Because the NEE in the bogs was relatively lower than that in the fens, the loss of SOM in the bogs could be faster at the annual level than in the fens. The decreasing stock of labile SOM could, in turn, limit the decomposition in the long run. As a result, the NEE in the bogs would be less sensitive to climate change than in the fens at a centurial timeframe, although the climatic sensitivity of the NEE in the fens would be greater than that in the bogs at a decadal scale (Article II).

The simulations indicated that both the climatic gradient and the mire-type pattern would strongly affect the spatiality of the C-water responses to the changing climate at regional scales. Compared with the southwestern parts of Finland, the drawdown of WT was relatively weak in northern Finland because the greater *P* increase there could partially offset the WT drawdown (Article I). This would enable the pristine fens, which are common in northern Finland, to act as greater CH_4 sources under the changing climate. On the other hand, the climate is warmer and the estimated WT drawdown would be greater in peatlands in the southern parts of Finland. This would yield a greater decrease in the CO_2 sink in the south than in the north under the warming climate (Article II). The dominance of bogs in southern Finland may, to some extent, mitigate such a change in the C sink during the second half of this century. This is because the long-term *Ta* sensitivity of C sequestration would be lower in the bogs than that in the fens. In general, the pristine Finnish peatlands may persist as CO_2 sinks under climate change during the 21st century. However, the total CO_2 sink equilibrium would decrease by 68% (Article II).

4.2.2 Climatic sensitivities of hydrology and C fluxes in a cutaway peatland cultivated with RCG (Articles III & IV)

The results of this study showed that anthropogenic disturbances such as drainage, peat extraction and RCG cultivation, may critically change the C-water processes in the boreal peatlands. The seasonal variation of the moisture content of peat in the Linnansuo site was weakly affected by the fluctuation of WT. On the other hand, the capillary rise of water from WT was found to contribute marginally to the water-storage changes in the unsaturated peat during both the wet year (2009) and the dry year (2010) (Article III). These findings are counter to many previous findings representing undrained and drained organic soils, emphasizing that the position of the WT and the capillary water rise critically influence the water exchanges in the unsaturated soil (e.g., Price, 1991; Lafleur and Roulet, 1992; Schwärzel et al., 2006; Price and Ketcheson, 2009). Such a change in the soil hydrology in the Linnansuo site could be due to the intensive drainage and the changes in the hydraulic properties of unsaturated soil, which facilitated the downward gravity drainage of pore water but constrained the upward capillary flows from the WT (Article III). As a result, the seasonal variations of the peat moisture content in such a peatland could be driven mainly by the *P-ET* balance, particularly by the regularity of summer rainfalls. This finding implies that WT may not be among the key factors mediating the C-water responses to climate change in boreal peatlands similar to the Linnansuo site. In addition, peatland models based on diplotelmic hydrology may not be applicable to the simulation of C exchanges under the changing climate in such ecosystems.

The strong influence of WT on capillary rise and root-zone moisture content are essential to the self-regulatory features of the peatland WT and C balance under climatic forcing (Price and Ketcheson, 2009; Morris et al., 2011b). This is the case especially for pristine boreal mires, where the variability of annual NEE depends more on the decomposition than the productivity of plant biomass (Alm et al., 2007; Vourlitis and Oechel, 1999). However, such adaptive features could be largely absent in a cutaway peatland cultivated with RCG (Article III). Drought pressure could severely limit the photosynthetic efficiency (e.g., V_{max}, J_{max}) and LAI of RCG (Ge et al., 2012; Xiao et al., 2011) and depress the GPP, which mainly controls the NEE in such an ecosystem (Shurpali et al., 2010). In this study, the V_{max} and J_{max} values and the temperature sum required by the phenological cycle did not clearly differ between the wet year (2009) and the very dry year (2010) (Article IV). This may be due to the adaptive feature of the RCG phenology, which allows fast vegetative growth during the spring season when the soil is wet and the *ET* demand is relatively low. As a result, the drought influences on the canopy growth can be minimized and the potential of photosynthesis can be maximized during the period when the irradiance and *Ta* are most favorable.

The sensitivity analysis showed a low sensitivity of NEE in the Linnansuo site to the *P* changes due to climate change (Article IV). This may be due to the weak changes in the summer *P*, the adaptive feature of GPP to the variations in wet-dry summers and the increase in N leaching associated with the increase in *P*. Increasing C_a could enhance the CO_2 sequestration cumulatively via accelerating the accumulation of rhizome biomass. However, the predicted increase in *Ta* would deteriorate the rhizome growth, limit the canopy development and GPP and lead to further deterioration. During Period III (2060-2099), the *Ta* effect was found to offset the C_a effect, causing the CO_2 sink of the Linnansuo site to decrease by 63% - 87% at an annual rate of 13 - 27 g C m^{-2} yr^{-1} (Article IV). These values are comparable to the mean annual CO_2 sinks estimated for the pristine mires in the neighboring areas (Figure 3 B and D). Because climate change would decrease the CO_2 sinks more in Period III than in Periods I and II (Article II), the Linnansuo site would become an even stronger CO_2 sink than those in the pristine mires. In addition, the CH_4 emission from the RCG peatland (approximately 0.33 g m^{-2} a^{-1}, Hyvönen et al., 2009) was much lower than the values measured from the pristine mires in this region (e.g., Nykänen et al., 1998). Therefore, RCG cultivation could be a suitable way to restore C sinks in cutaway peatlands similar to the Linnansuo site under climate change, while supporting the biomass demand for bioenergy production.

4.3 Conclusions

In this study, a series of process-based models were developed to investigate the climatic sensitivities of hydrology and C exchanges in pristine mires and cutaway peatlands under RCG cultivation in Finland. For pristine peatland ecosystems, the models highlighted the close relationship between the dynamics of WT and CO_2 / CH_4 fluxes and the fen-bog differences in C-water cycling. Based on the ACCLIM climate scenarios for the 21st century, the WT of the Finnish pristine mires was predicted to draw down slightly, as constrained by multiple water-energy feedbacks in the ecosystems. Such a small change in WT would be related to a decrease in the CO_2 sink but an increase in the CH_4 source in the country-scale peatlands driven mainly by the rising *Ta*. These responses of CO_2 / CH_4 fluxes are likely to decrease the total C-GHG sink by 68% at the country scale. The WT drawdown tends to be more pronounced in the peatlands in the southern and western areas of the country. Accordingly, the CH_4 emission and the CO_2 sequestration tended to decrease significantly in these areas. The mire-type pattern also strongly affected the spatial variation of the regional C-flux changes. The major distribution of fens in northern Finland would increase CH_4 emissions at the country scale. On the other hand, the majority of pristine fens in the south and the west of Finland and the pristine bogs near the coastal areas would become centurial C sources under the changing climate. Because the C exchange in bogs is less sensitive to climate change than that in fens over the long term, the dominance of bogs in the pristine peatlands in southern Finland may limit the C-sink changes toward the end of the 21st century.

Peat extraction and RCG cultivation are likely to critically change the C-water cycling in boreal peatland ecosystems. WT is no longer a strong control on the root-zone moisture content in a cutaway peatland cultivated with RCG. Instead, the root-zone moisture content is highly sensitive to the regularity of summer rainfalls. The phenological cycle of RCG may represent an adaptive feature of such species to the stochasticity of summer precipitation. Climate change during Period III (2060-2099) tended to decrease the NEE by 63% - 87% for a main rotation period, mainly because of the deterioration in rhizome growth under the warmer climate. Nevertheless, the Linnansuo site could sustain a net CO_2 sink comparable to the pristine mires in neighboring areas. Therefore, RCG cultivation could be a suitable way to restore C sinks in cutaway peatlands similar to the Linnansuo site under climate change and bioenergy production.

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