Chapter VI

General discussion
The aim of this thesis was to evaluate the responses of permafrost peatland vegetation at the community and the plant level (for both vascular and bryophyte plants) to several important aspects of climate change. Vegetation responses to direct effects of climate change (warming, increased precipitation, Chapter 2 and 3) as well as to indirect effects (increased nutrient availability as a result of permafrost thawing, Chapter 5) were investigated. In Chapter 4, the potential amount of plant-available N that can be released from thawing permafrost peatlands was presented, which is essential information for estimating the potential impact of permafrost thawing on tundra vegetation.

In this general discussion, the relative impacts of the investigated direct (warming, precipitation) and indirect effects (increased nutrient availability) of climate change on permafrost peatland vegetation will be analysed and compared. By means of conversion of the observed vegetation responses to units of carbon uptake, an answer is provided to the question: what is the relative contribution of the studied climate factors to changes in C-uptake by peatland vegetation (through changes in species specific growth and vegetation biomass) in northern permafrost peatlands? Moreover, an attempt is made to relate the findings presented in this thesis to the grand overarching climate change question: “what do these vegetation responses mean for the carbon sink-function of northern permafrost peatlands?”

1. Estimation of climate impacts on C-uptake

1a. Warming

In Chapter 2, we showed that our permafrost peatland vegetation community was more stable in response to manipulations of spring and summer temperature than is typically observed in other (sub-)arctic experiments (Elmendorf et al., 2012). Even after eight years of climate manipulations we observed no changes in total vascular plant abundance, nor in individual species abundances, Shannon’s diversity or evenness. These findings suggest that changes in carbon-sequestration through changes in species composition (differing in carbon turnover times) are unlikely for this system, which makes this system particularly different from other tundra ecosystems where often increases in shrub abundance are observed. Such changes may lead to increased C-storage in wood (Myers-Smith et al., 2012). In our system, the proposed mechanism through which the stability was achieved is ‘a race for space’: increased growth of both vascular plants as well as the peatmoss. Hence, total biomass increased although this was not reflected in vascular plant community composition. Thus, despite community stability in response to the experimentally altered climate, carbon sequestration most likely did increase, as all separately measured individual species showed increased productivity at the individual plant level. Vascular plant biomass production increased by up to approximately 130 %, based on the average increase in aboveground *E. hermaphroditum* and *B. nana* productivity as weighted by their contribution to total aboveground vascular biomass. This would lead to an annual increase in C-uptake of 20 g C m⁻², which, when extrapolated to all permafrost peatland area, adds up to 70 Mt C annually (Box 1 and 2). Moreover, bryophyte (*Sphagnum fuscum*) productivity responses to higher summer temperatures increased with approximately 200% (based on vertical growth measurements, Chapter 2), leading to an impressive annual increase in C-uptake of 150 g C m⁻² (based on an observed ambient productivity of 75 g C m⁻² which is lower than but comparable to *S. fuscum* productivity values of 112 g C m⁻² observed by Street (2012). When extrapolated to all permafrost peatland area, this adds up to 535 Mt C annually¹ (Box 1 and 2).
1b. Increased precipitation

In Chapter 3, we showed that the vegetation of the studied permafrost peatland was irresponsive (both in terms of vascular and bryophyte biomass and of species composition) to doubling of the ambient summer precipitation. Precipitation in the sampling area (Abisko) in the years of sampling (2008 and 2009) was lower than the long-term average, with 2009 being the 11th driest year since 1913 (Callaghan et al., 2010, Olefeldt et al., 2012). During dry years, an experimental increase in summer precipitation would have had a maximum effect on growth of the vegetation, yet no effect was observed. Moreover, our results for permafrost peatlands are in line with the established pattern of negligible tundra plant productivity responses to experimentally increased summer precipitation (Dormann & Woodin, 2002). Thus, in terms of carbon currency, no effects of increased precipitation are expected on vegetation performance of permafrost peatlands.

\[1\text{ Although we did not measure bulk density of the Sphagnum carpet, this could be negatively affected by the warming treatment (Dorrepaal, 2004). However, even when taking into account a potential decrease in bulk density of 20\% (Dorrepaal, 2004), warming would still lead to an extra uptake of approximately 430 Mt C annually.}\]
1c. Permafrost thaw induced increase in N-availability

In Chapter 4, we showed that thawing permafrost of subarctic peatlands can release plant-available N (up to 1.3 g N m\(^{-2}\) in the near-future). In contrast with the irresponsiveness of the permafrost peatland vegetation to experimentally increased precipitation, a rather large increase in total biomass production (up to 20\%) of the vascular vegetation was observed in response to deep (40 cm) below-ground fertilization (Chapter 5). Note should be taken that this is a maximum value, as the amount of fertilizer added experimentally was higher than what can be expected to be released from thawing permafrost\(^2\) (Chapter 4). However, although vegetation responses to a release of nutrients in deeper soil layers such as presented in this thesis cannot be inferred in a straightforward manner from studies where fertilizer was applied at the soil surface,

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**Box 2. Carbon-comparisons for sink and source strength of permafrost peatlands**

Assumptions about C-sink strength in a changing climate

<table>
<thead>
<tr>
<th>Total permafrost peatland area</th>
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<tr>
<td>1. 3.5 x 10(^{12}) m(^2) (Tarnocai 2009)</td>
</tr>
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</table>

**Maximum effect of warming (Ch. 1)**

| 2. Total area x effect on vascular C uptake [Box 1] = 70 Mt C yr\(^{-1}\) |
| 3. Total area x effect on bryophyte C uptake [Box 1] = 535 Mt C yr\(^{-1}\) |

**Maximum effect of permafrost thaw (indirect, via increased thaw-front N, Ch. 5)**

| 4. Total area x effect on vascular C uptake [Box 1] = 18 Mt C yr\(^{-1}\) |

Assumptions about C-source strength in a changing climate

| 1. Maximum C-source strength in response to warming: |
| 100 Mt C yr\(^{-1}\) (Dorrepaal 2009) |

| 2. Permafrost thaw induced C-source strength: |
| 1000-2000 Mt C yr\(^{-1}\) (Schuur 2011) |

Comparisons C-uptake by vegetation with C-source strength

1. In response to warming, C-uptake by vegetation (70 + 535 Mt C yr\(^{-1}\)) is **6 times larger** than C-release by the deeper soil layers.

2. The **N-availability related effect of permafrost thawing** on C-uptake by vegetation (18 Mt C yr\(^{-1}\)) is approximately **50-100 times smaller** than C-release by permafrost thawing.
the observed positive response in vegetation productivity (up to 20% increase) to increased nutrient availability is in line with many fertilization experiments that were carried out in subarctic tundra (Haugwitz & Michelsen, 2011, Lamb et al., 2011, Parsons et al., 1994, Shaver et al., 2001). In carbon currency, 20% higher permafrost peatland vegetation productivity would mean an increased C-uptake of 5 g C m⁻² yr⁻¹ (18 Mt C yr⁻¹ for all permafrost peatlands) (Box 1 & 2).

2. Permafrost peatlands and climate change: comparison of sink and source strengths

2a. Direct effects

The values for increased C-uptake (carbon sink function) through increased vegetation productivity in response to spring- and summer warming (yearly 70 Mt C for vascular plants and 535 Mt C for bryophytes), easily offset the predicted increase in carbon (CO₂) emissions based on measurements in the same experiment, for which the maximum given value is an annual increase of 100 Mt C per year (Dorrepaal et al., 2009) (Box 2). No direct effect of warming on methane (CH₄) emission is expected in permafrost peatlands without a groundwater table and with relatively mild redox conditions (Dorrepaal et al., 2009, Roulet et al., 1992). In wetter (permafrost) peatlands, temperature is one of the primary factors influencing CH₄ emission (Moore et al., 2011) and can have a direct positive impact of up to 40% (based on Q₁₀ ranging between 2 and 3) (Svensson & Rosswall, 1984, Williams & Crawford, 1984), although large variation exists in observed Q₁₀ for the direct effect of warming on methane emission (Segers, 1998, van Hulzen et al., 1999). Even so, estimations based on four warming scenarios (part of the IPCC fifth assessment report) show that most of the released carbon will be in the form of CO₂, with only about 2.7% in the form of CH₄ (Schuur et al., 2011). In line with this, Lee et al. (2012) conclude that the direct potential effect on climate from permafrost C release is greater under aerobic (dry) conditions than under anaerobic (wet) conditions, even when taking the higher greenhouse warming potential of CH₄ into account. Hence, the net direct effect of warming on C-uptake and release suggests that climatic warming will increase the carbon sink-strength of permafrost peatlands.

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2 An exact value can not be provided here because the fertilizer was added in the form of ‘slow release grains’, of which the exact release rate is not known. The inserted amount was equivalent to 8 g N m⁻².

3 The permafrost peatlands studied in this thesis are ombrotrophic peatlands, which, by definition, do not have a groundwater table. Unfortunately, the available global area coverage data which are generally used for upscaling results of permafrost peatlands (Walker 2004; Tarnocai 2009; Gorham 1991) do not distinguish between ombrotrophic and non-ombrotrophic peatlands, nor is the dominant type of peatmoss specified. This is a major uncertainty in the calculations presented in this chapter. Fortunately, for the response to warming specific C-source data were available from the same experimental site (Dorrepaal 2009). However, for the C-source strength in response to permafrost thawing, I chose to use an educated guess provided by the permafrost community in Schuur (2004), which is not ombrotrophic peatland specific. I could have used 19% of this educated guess number, to represent the percentage of permafrost area that is covered by peatlands (Tarnocai 2009), but as most greenhouse gas emissions are expected to come from soils with high organic carbon contents, this correction would most likely give an underestimation. Hence, under the assumption that the main part of the C-source strength of permafrost will come from permafrost peatlands, I used the number provided by Schuur (2011).

4 CH₄ has a greater global warming potential (GWP CH₄ = 25) than CO₂ (GWP = 1) over a 100-year time period (IPCC, 2007).
2b. Indirect effects

The value for C-uptake by vegetation as a result of increased N-availability in response to permafrost thawing (18 Mt C per year, Box 2) is approximately 50 to 100 times smaller than the estimate for the increase in total C-emissions as a result of permafrost thaw (faster release of CO₂, CH₄ and DOC) based on an educated guess from the permafrost community (Schuur et al., 2011). This estimation of carbon release from permafrost degradation was 30 billion to 63 billion ton of carbon by 2040 (equal to approximately 1000-2000 Mt C yr⁻¹) (Box 2). Hence, apart from being one order of magnitude smaller than the direct effect of warming, the effects of increased N-availability through permafrost thawing on the sink strength of permafrost peatlands would, according to these simple calculations, most likely not counteract a shift from sink to source function of permafrost peatlands as a result of permafrost thawing.

2c. Factors potentially affecting the calculations

The carbon calculations presented here are fairly crude. Firstly, vegetation changes were not observed within the scope of the performed experiments, and thus not taken into account in the calculations in Box 1 (purely based on the work performed in this thesis). However, in response to warming for example, vegetation changes may occur on the longer term in permafrost peatlands with a more dense vascular cover, where the here observed bryophyte-driven stability in the vascular community (Chapter 2) does not take place (Elmendorf et al., 2012). Unfortunately, detailed information about vegetation density and bryophyte cover is not yet available for all area covered by permafrost peatlands (Walker et al., 2005). For this reason, it remains challenging to upscale the experimental findings or estimate the longer-term implications for C-uptake of either vegetation changes or the observed bryophyte-vascular community interaction (Chapter 2) for permafrost peatlands. Another potential driver of longer-term vegetation shifts on the longer term which was beyond the scope of this thesis, is degrading palsa structure due to disappearance of the physical support provided by permafrost, and associated changes in hydrology. Accompanying shifts to a graminoid-dominated vascular community could lead to mildly increased C-sequestration by the vegetation of up to 4 g C m⁻² yr⁻¹ (7.3 %) (Malmer et al., 2005). However, such changes in hydrology are also associated with faster CO₂ and CH₄ release and increased outflow of dissolved organic C from permafrost peatlands (Christensen et al., 2004, von Deimling et al., 2012). Moreover, such changes in hydrology could increase outflow of plant available N from permafrost peatlands (Frey & McClelland, 2009, McClelland et al., 2007) and thus negatively affect our estimations of potential increased C-uptake by vegetation as a result of increased N-availability through thawing of permafrost soil.

A second simplification in our calculations is the omission of potential changes in belowground biomass. Since approximately 80% of vascular plant biomass in northern tundra ecosystems resides below-ground (Chapin & Ruess, 2001), not taking into account potential changes in this carbon pool is a major oversight (van Noordwijk et al., 1998). This is most likely especially true for permafrost affected ecosystems, where plant root growth is restricted by the depth of the active layer (Billings et al., 1976) that will increase as a result of permafrost thawing (Akerman & Johansson, 2008). If aboveground-belowground allometry remains stable (or decreases), increased belowground biomass (Chapter 5) and concomitant C-uptake can be expected. Hence,
not taking potential changes in belowground biomass into account may lead to a conservative estimate of C-uptake by the vegetation in response to climatic changes by permafrost peatlands.

Overall, the discussed interactions between different elements of the permafrost peatland system (plant-plant; plant-microbe; plant-permafrost soil) can be affected by climatic changes in ways that were not addressed in this thesis. Further, unforeseen feedback mechanisms may occur on the longer term and either increase or decrease C-sequestration. Yet, the calculations presented in this chapter are, to our knowledge, the first calculations specifically about the vegetation productivity component of the carbon balance of permafrost peatlands. Moreover, the straightforward comparison between C-uptake in response to specific experimental manipulations relevant to current climate change scenarios is, to our knowledge, unique. Hence, the insight these calculations provide in the sink-strength of these climate sensitive ecosystems is, albeit crude, highly relevant in order to direct future research.

My recommendations for future research include a stronger focus on belowground processes, both plant-root as well as microbe related. Moreover, ongoing research in long-term experiments is essential for detecting longer-term changes in vegetation community and microbial activity as a result of climatic changes. And lastly, since according to the calculations provided here (Box 1 & 2) the peatmoss *Sphagnum fuscum* can play a crucial role in the carbon-sink function of permafrost peatlands, more research should be performed on total land area coverage and on factors affecting the productivity of this ‘living soil’.

3. Conclusions

In summary, the work presented here suggests that the direct effect of warming, and the indirect effect of thawing of permafrost soil via a release of plant available nutrients, will have a greater impact on carbon-uptake (sink-function) of permafrost peatland vegetation than an increase in summer precipitation. The sum of the here discussed direct effects (623 Mt C yr⁻¹) and indirect effects (18 Mt C yr⁻¹) of climate change on the C-sink value of permafrost peatlands is large enough to offset approximately half the predicted release of carbon from thawing permafrost (1000-2000 Mt C yr⁻¹, Schuur 2011). Hence, in depth understanding of the underlying processes of changes in carbon uptake as a result of climate change, as provided in this thesis⁵, is of major importance to estimate future impacts of climatic changes on the terrestrial carbon balance.

⁵ Note: according to the latest IPCC report (2007), the anthropogenic C-source strength is approximately 13.4 x 10³ Mt C yr⁻¹. This is at minimum one order of magnitude larger than the projected climate driven release of greenhouse gases from permafrost soils and at least two orders of magnitude larger than the in this chapter presented maximum value for increased C-uptake by peatland vegetation in response to climatic changes. Hence, “despite the massive amount of carbon stored in permafrost soils, emissions from these soils are unlikely to overshadow those from the burning of fossil fuels, which will continue to be the main source of climate forcing” (Schuur, 2011). Increased C-uptake by permafrost peatland vegetation will not easily offset this.