Summary

Strong climate warming and altered precipitation regimes are predicted to occur at higher latitudes this century, with potentially major consequences for vegetation productivity and carbon sequestration. Although northern permafrost peatlands contain one-third of the world’s soil organic carbon, little is known about responses of their vascular plant communities to climatic changes. Both direct effects, of warming and altered precipitation, as well as indirect effects, through permafrost thawing and increased nutrient-availability, are expected. In this thesis I aimed to investigate how short- to long-term experimental climate manipulations, relevant to different predicted future climate scenarios, affect vascular plant productivity and species composition in permafrost peatlands. Specifically, answers were sought to the following research questions: (1) How do spring- and summer warming, and increased snow cover affect species-specific growth responses and species composition in northern permafrost peatlands; (2) How does increased summer precipitation affect species-specific growth responses and species composition in northern permafrost peatlands; and (3) Can permafrost thawing affect species-specific growth responses and species composition in northern permafrost peatlands through a release of plant-available N? To answer these questions three experiments were performed, investigating vegetation responses to: (a) spring- and summer warming and a thicker snow cover (Chapter 2); (b) increased summer precipitation (Chapter 3); and (c) increased nutrient availability at the permafrost thaw front (Chapter 5). Moreover, the amount of plant-available nitrogen (N) that can be released from thawing permafrost into these peatlands in the near-future was quantified (Chapter 4). All experiments were performed on Sphagnum fuscum-dominated permafrost peatlands the Abisko area, northern Sweden. The increased summer precipitation experiment (Chapter 3) was complemented by a sister-experiment in the Kytalyk Reserve in north-eastern Siberia.

I found that in response to 8 years of experimental spring- and summer warming, and (moderately) thicker snow cover, vascular plant species composition of Sphagnum fuscum-dominated permafrost peatlands was more resistant than is typically observed in (sub)arctic experiments: neither changes in total vascular plant abundance, nor in individual species abundances, Shannon’s diversity or evenness were found in response to the climate manipulations. For three key species (Empetrum hermaphroditum, Betula nana and S. fuscum) it was also determined whether the treatments had a sustained effect on plant length growth responses and how these responses interacted. Contrasting with the stability at the community level, both key shrubs and the peatmoss showed sustained positive growth responses to the climate treatments. However, a higher percentage of moss-encroached E. hermaphroditum shoots and a lack of change in B. nana net shrub height indicated encroachment by S. fuscum, resulting in long-term stability of the vascular community composition. These findings show that in a warmer world, vascular species of subarctic peat
bogs appear to just keep pace with growing *Sphagnum* in their ‘race for space’. They contribute to general ecological theory by demonstrating that community resistance to environmental changes does not necessarily mean inertia in vegetation response (Chapter 2).

Secondly, vegetation responses to three years of experimentally increased summer precipitation in two tundra types were investigated, in (a) *B. nana*-dominated shrub tundra (northeast Siberia) and (b) a dry *S. fuscum*-dominated bog (northern Sweden). These tundra types were not previously addressed in increased precipitation studies. Positive responses to approximately doubled ambient precipitation (an increase of 200 mm yr$^{-1}$) were observed at the Siberian site, for *B. nana* (30% larger length increments), *Salix pulchra* (leaf size and length increments) and *Arctagrostis latifolia* (leaf size and specific leaf area), but none were observed at the Swedish site. Total biomass production did not increase at either of the sites. This work corroborates studies in other tundra vegetation types and shows that despite regional differences at the plant-level, total tundra plant productivity is, at least at the short or medium-term, largely irresponsible to experimentally increased summer precipitation (Chapter 3).

Thirdly, the amount of plant-available nitrogen that can be released by near-surface permafrost soil of permafrost peatlands was quantified (Chapter 4), and how such a release can affect species-specific growth responses and species composition in northern permafrost peatlands was investigated (Chapter 5). Plant-available N-pools and -fluxes in near-surface permafrost soil samples (taken 0-10 cm below the thaw front) were compared to those taken from a current rooting zone layer (5-15 cm depth) across five representative permafrost peatlands in subarctic Sweden. A range of complementary methods was used: extractions of inorganic and organic N, inorganic and organic N-release measurements at 0.5 and 11 °C (over 120 days, relevant to different thaw-development scenarios) and a bioassay with *Poa alpina* test-plants. All extraction methods, across all peatlands, consistently showed up to seven times more plant-available N in near-surface permafrost soil compared to the current rooting zone layer. These results were supported by the bioassay experiment, with an eight-fold larger plant N-uptake from permafrost soil than from other N-sources such as current rooting zone soil or fresh litter substrates. Moreover, net mineralisation rates were much higher in permafrost soils compared to soils from the current rooting zone layer (273 mg N m$^{-2}$ and 1348 mg N m$^{-2}$ per growing season for near-surface permafrost at 0.5 °C and 11 °C respectively, compared to -30 mg N m$^{-2}$ for current rooting zone soil at 11 °C). Hence, these results demonstrate that near-surface permafrost soil of subarctic peatlands can release a biologically relevant amount of plant available nitrogen, both directly upon thawing as well as over the course of a growing season through continued microbial mineralisation of organically bound N (Chapter 4). However, being plant-available does not necessarily imply that peatland plant species will be able to take up this N at the thaw front. Therefore, I identified the potential impact of increased N-availability due to thawing permafrost on subarctic peatland plant production and species composition. This impact was compared to the effect of increased nutrient availability in shallower layers (e.g. through enhanced N-mineralization due to climatic warming). To achieve this, $^{15}$N-labeling of the thaw front was applied and a full-factorial belowground fertilization experiment (deep-fertilization at the thaw front at 45 cm depth and shallow-fertilization at 10 cm depth) was performed. I found that only particular species (e.g. *Rubus chamaemorus*) have active roots at the thaw front. Further, once supplied with nitrogen at the thaw front, these species had higher aboveground biomass and N-content, whereas this was not the case for shallower-rooting species (e.g. *E. hermaphroditum* and *Andromeda polifolia*). Moreover, the effects of increased nutrient availability
at the thaw front on total aboveground biomass production were similar in magnitude to the effects of increased nutrient availability in shallower layers. Additionally, nutrient limitation of plant growth in subarctic peatlands appeared to be strong enough for the effects of increased deep and shallow nutrient availability on biomass production to be additive. Altogether, these results show that plant-available N released from thawing permafrost can be considered a true ‘new’ N source for deep-rooting sub-arctic plant species, which will increase their biomass production. As this is not the case for shallow-rooting species, the release of plant-available N from thawing permafrost has the potential to alter species composition on the long-term by benefitting specific deep-rooting species only (Chapter 5).

This thesis was concluded by a comparison of response sizes to the different investigated direct and indirect effects of climate change on permafrost peatlands. The comparison was based on potential responses, expressed using carbon-uptake as a unifying currency. The largest response in carbon-uptake by permafrost peatland vegetation is to be expected from warming (approximately 170 g C m$^{-2}$ yr$^{-1}$), mainly through increased productivity of the peatmoss *Sphagnum fuscum* (approximately 150 g C m$^{-2}$ yr$^{-1}$), followed by the vascular vegetation responses to increased nutrient availability through thawing permafrost (5 g C m$^{-2}$ yr$^{-1}$). No effects of increased precipitation are expected on vegetation performance of permafrost peatlands. Based on an estimated permafrost peatland area of 3.5 x 10$^{12}$ m$^{2}$ (Tarnocai 2009), the potential increase in C-sink strength as a result of increased vegetation productivity calculated on the findings presented in this thesis would be at approximately 600 Mt C yr$^{-1}$ in response to warming, and 18 Mt C yr$^{-1}$ in response to increased nutrient availability as a result of permafrost thawing. Although these increases in C-sink strength are about halve the total global expected C-source strength as a result of permafrost thawing (1000-2000 Mt C yr$^{-1}$, Schuur *et al.* 2011), they are about 6 times higher than the projected increased C-source strength of permafrost peatlands in response to warming, for which the maximum given value is an annual increase of 100 Mt C yr$^{-1}$ (Dorrepaal *et al.*, 2009). Therefore, further in depth understanding of the underlying processes of changes in carbon uptake as a result of climate change, as provided in this thesis, is of major importance for estimating future impacts of climatic changes on the terrestrial carbon balance.