Final response to comments on "Simulating the effects of temperature and precipitation change on vegetation composition in Arctic tundra ecosystems" by H. van der Kolk et al.

Reply to comments by anonymous Referee #1

This paper is well written and logically structured. It presents a study with many potentially interesting insights on the High Arctic permafrost ecosystem dynamics (vegetation competition and succession) in response to future climate change, permafrost thawing, and lateral interaction in hydrology and thermokarst development. However, some major mechanisms behind the processes associated with the interaction between biotic and abiotic factors haven't been clearly demonstrated.

REPLY: We thank the referee for his/her constructive comments. We appreciate that the referee recognizes that the model has the potential to provide interesting insights in the response of tundra vegetation composition to climate change, gradual permafrost thawing and abrupt permafrost thaw (thermokarst). In our study the focus is on the vegetation modelling and we acknowledge that particularly for the abiotic factors there is room for improvement in the model. In the next phase of model development we plan to couple the vegetation model to a soil physics/methane emission model (e.g. Mi et al. 2014).

I suggest the issues the paper should address in the following phase.

(1) Nutrient availability and mobility. The N availability is determined by the rate of minimization and fixation of N in response to the extent of climate changes. Their net effects determine the nutrient constraint for different vegetation species. In addition, snow is another important aspect to influence the subsurface temperature and then the N cycling. The N mobility can be reflected by how dry ecosystems interacts wet ecosystems through water movement. These two issues have not been well investigated in the current modelling work, but they are fundamental in understanding how growth of plant function types are influenced by environmental changes.

REPLY: In general, growth of tundra plants is assumed to be limited by nitrogen availability and therefore simulation of nitrogen dynamics is essential for a dynamic tundra vegetation model. In our model, mineralisation of soil organic nitrogen is temperature-dependent, so will respond to climatic changes. The soil temperature dependence of nitrogen mineralisation is now explicitly mentioned on page 5, lines 7-8. In addition, atmospheric nitrogen deposition, nitrogen fixation, nitrogen leaching to deeper soil layers and denitrification of nitrogen are included in the model. The available nitrogen in the different soil layers influences competition between the deeper-rooted graminoids and shallower-rooted dwarf shrubs.

Indeed, snow influences the winter soil temperatures, which is not explicitly included in our regression-based soil temperature simulation, see further reply to comment 2. However, at our study site with an extremely harsh winter climate nitrogen mineralisation is always extremely low in winter.

In summer, water movement can indeed transport nitrogen from the elevated shrub patch to the sedge-dominated depression. This has been included in the model for the revised manuscript, and is mentioned on page 5, line 13 and described in S1.3.2. This nitrogen transport with water movement and the larger precipitation increase in the climate scenarios (comment 3) changed the results of the simulations, see further reply to comment 3.

(2) The model needs a thorough evaluation in the performance of simulating soil water, evapotranspiration and soil temperature, active layer depth, water table depth for the period the observations are available. This is the basis to convince the readers to believe the efficiency of the model. Particularly, the simulated soil temperature doesn't look correct in the 40, 80 cm.

REPLY: Indeed, the simulated soil temperature at 40 and 80 cm depth does not look good in winter. It has been acknowledged in the text that the soil temperature model is based on temperatures in the growing season only, as the below-zero temperature in winter hardly affects the model output (Supplement S1.3.4). We used a regression approach which is based on air temperature and does not take snow characteristics and phase changes into account. Still, realistic temperatures for the upper (most important for N mineralisation) soil layers in summer have been simulated, but there are (large) deviations for winter temperatures (Supplement Figure S1.3). These deviations did not affect the simulated periods of frozen and thawed soil, which were in agreement with the observations (Supplement page 29, lines 6-8). For broader applications of the model it will be necessary to couple the vegetation model to a more advanced soil physical model (page 11, lines 29-30). We added a new supplement section (S4.2) on the evaluation of soil temperature and active layer thickness to the revised manuscript. In the main text, the comparison with the soil temperature time series is mentioned on page 6, lines 14-15. The results of this evaluation have been summarized on page 8, lines 6-13.

New supplement section S4.2 also evaluates the simulated active layer thickness (ALT). Based on measured thawing depths on 20 dates, it appeared that the simulated and measured ALT were strongly correlated (new figure S4.2), but simulated ALT proved to be slightly too deep: average difference between simulated and measured ALT was 14 cm. Next, we assessed the consequences of too deep ALT for the simulated vegetation composition in a simulation where deep soil temperatures (and thus active layer thickness) were manually set back. The result is that too deep simulated ALT is to the advantage of graminoids (new figure S4.3). This can be explained by the fact that our vegetation model includes differential rooting depths for graminoids and shrubs. Graminoids are more capable of acquiring available nutrients in deeper soil layers, as they are deeper-rooted than the dwarf shrubs. The result implies that simulated graminoid biomass may be overestimated as a consequence of overestimated ALT. This is discussed in a new paragraph on page 11, lines 19-30. Although there is uncertainty regarding the simulated ALT and the amount of nutrients becoming available, the pattern of vegetation shifts in response to temperature and precipitation changes remained the same.

Unfortunately we have no time series of observations for soil moisture and water table depth for a thorough comparison with model outcome. The meteo tower at the Kytalyk field station does not measure soil moisture. Soil moisture and water table depth are extremely variable even at a small spatial scale in the tundra landscape. The wet depressions (resembling the wettest vegetation type in the model) are much wetter compared to the slightly elevated shrub patches. Therefore, we choose to simulate different vegetation types along a water movement gradient from relatively well-drained elevated shrub patches to downstream sedge-dominated depressions receiving water from their surroundings. Limited soil moisture measurements in graminoid, mixed and shrub dominated vegetation types (Wang et al. 2016) indicate clear trends that moisture during the growing season is high in graminoid but low in shrub dominated sites, similar as is simulated in the model. As described in the manuscript, the model simulates a build-up of the snow layer in winter, followed by a wet period in spring following snowmelt. In summer, the soil gradually dries as evapotranspiration (derived from measured latent heat flux) generally exceeds precipitation, the extent of drying depending on the amount of precipitation and temperature. This sequence and dependence on

precipitation matches with our personal observations at the study site in north-eastern Siberian tundra. We do have several point measurements of soil moisture for several years. However, these measurements are difficult to compare with the simulated soil moisture values as they represent different soil layers. Measurements using a Thetaprobe were taken from the top soil layer, i.e. the top 10cm including moss which easily dries out. Simulated soil moisture values represent the whole organic soil layer (which is 15-20cm deep). Therefore, the measured values show much more variation than the simulated values. Consequently, we could not reliably compare measured and simulated soil moisture data.

(3) I suggest use the percentage of increase to indicate the change of precipitation. For this study site, 45 mm/year, (i.e. 20% increase of annual precipitation) seems much lower than the IPCC CMIP5 prediction for the RCP8.5 scenario. For instance, http://www.nature.com/nature/journal/v509/n7501/pdf/nature13259.pdf

REPLY: We accepted this suggestion and used the percentage instead of the actual precipitation increase, which resulted in larger increases of precipitation in the climate scenarios and changed the outcome of the simulations. For the main climate change scenarios (RCP2.6, Intermediate, RCP8.5) graminoids performed relatively well in comparison to previous simulation. This improvement of graminoid performance can be attributed to increased precipitation in climate change scenarios (increased soil moisture content during growing season). As a consequence of these stronger precipitation effects, we highlighted the role of precipitation earlier in the discussion (page 11, lines 6-18) and had to adapt some text in the results (page 8, lines 31-32; page 9, lines 1-3).

Other minor issues:

The rate of biomass increase is suggested to use the unit "g m-2 yr-1".

REPLY: Sorry, it is not clear to us to which figure or part of the text the referee is referring to. Figures show biomass expressed in g m^{-2}.

How the development stages of thawing pond are evolved in different climate scenarios is suggested to demonstrate. For instance, the time series of water table depth in climate scenario runs.

REPLY: Suggestion accepted, we added the soil moisture content over time as an extra line to the thaw pond scenario graphs in the revised manuscript (Fig. ...).

The title should be catchier. The current one seems quite broad.

REPLY: We agree that the title "Simulating the effects of temperature and precipitation change on vegetation composition in Arctic tundra ecosystems" could be catchier. We changed the title to:

"Potential Arctic tundra vegetation shifts in response to changing temperature, precipitation and permafrost thaw"

An alternative could be: "A new Arctic tundra vegetation model for simulating vegetation shifts due to climate change and permafrost thaw"

Reply to comments by anonymous Referee #2

This is an interesting and relevant studied, which in my opinion deserves to be published in Biogeosciences. The paper presents in a clear and interesting way potential changes of Arctic tundra under warming/precipitation change/permafrost thaw. Especially, addressing 3 factors in combination, i.e. warming, precipitation and permafrost thaw is a relevant contribution to our understanding of tundra change.

REPLY: We thank the referee for his/her constructive comments. We appreciate that the referee recognizes that our study has the potential to provide interesting insights in the response of tundra vegetation composition to climate change, gradual permafrost thawing and abrupt permafrost thaw.

The paper is well written and the results are clearly presented. As this study represents a modelling approach, I would find it helpful if some modelling related issues could be clarified. In particular, many parameters in the NUCOM-tundra model were defined based on e.g. vegetation composition found in the field, so I was sometimes uncertain what I learned in the paper about mechanisms responsible for changes in the tundra.

REPLY: It is correct that some of the parameter values for the model have been derived from field measurements at our study site in north-eastern Siberian tundra, see further reply to comments below. From our field studies we have gained insights in the functioning of (dwarf) shrubs and graminoids which have been used for the model. For example, the graminoids are deeper-rooted than the shrubs which implies that the graminoids are better competitors for nutrients in the deeper soil layers. The model synthesizes own findings from field studies with knowledge on Arctic tundra ecosystem functioning from literature.

Also related to this issue: of course simplifications/assumptions need to be made for a model, especially if access to measured data is limited. However, I asked myself a few times if the simplification were justified.

A few examples. Abstract. L.24. The simulations suggest that shrubs are better light competitors... etc. If I understand the model right, shrubs are good competitors because they were defined as good competitors in the first place. Not that this would be incorrect. But several times I get the impression that findings are not necessarily a result of the model but a result of how the model was set up, which assumptions were made and which data were used to feed the model. Again, this is certainly an issue that can be said for all models. But I think the text needs some rephrasing to be clear about what is indeed a model outcome (e.g. increase of graminoids under wetter conditions) and what is not. To me the text seems to go too far, which mechanisms can actually explained by this model and which cannot. See related comments below.

REPLY: Of course a result of a model depends on how the model was set up, etc. This has the advantage that it is possible to trace back how a certain model outcome has been generated and provides a potential mechanism for the simulated vegetation change. It is correct that the mechanism is not independent of how the model was build and we agree that this should not be overstated. Still, we think that models are a helpful tool for exploring mechanisms of vegetation change.

We disagree that shrubs were defined as good competitors in the first place. Several plant traits (parameters values) are related to competition for light or nutrients. For light competition, leaf area and light extinction are important, which are influenced by parameters as specific leaf area, biomass allocation to leaves, leaf mortality and light extinction coefficient. Similarly, nutrient competition is influenced by parameters as specific root length, root distribution and nutrient requirements. This explanation is added to page 12, lines 17-23. Values for the parameters have been assigned independently, partly based on literature values and partly derived from own measurements. It is the combination of multiple plant traits and environmental conditions that determines which plant type is a good competitor. Based on our field observations, we assumed the (dwarf) shrubs and graminoids to be equally tall in the model. Therefore, the shrubs were not a-priori the better light competitor. We removed the sentence about shrubs being better light competitors (page 1, line 27), as it is not that clear from our simulations anyway.

Questionable assumption? p4 l21. Graminoids and dwarf shrubs are assumed to be equally tall. The authors may have their reasons to do so, but this is not entirely clear to me. Betula nana can grow easily 2.5 m tall (e.g. in parts of Alaska) and arctic graminoids don't. An incorrect assumption here could have a large influence on the results.

REPLY: Based on observations at our study site in north-eastern Siberian tundra we assumed the graminoids (*Eriophorum* spp.) and dwarf shrubs (*Betula nana*) to be equally tall, which is a simplification, but not unrealistic. Also in Alaska, in moist tussock tundra as in Toolik Lake, dwarf shrubs and graminoids are equally tall (Heijmans, personal observations). We acknowledge that in some other tundra areas the shrubs, including *B. nana*, can grow taller than the graminoids, although this may be limited to places with some additional nutrient supply. For a wider application of the vegetation model, i.e. to include transitions to tall shrub vegetation, a variable plant height up to a maximum would be required. We added this discussion to page 12, lines 27-31

Explaining mechanisms? P. 9 l16ff. The authors state that the NUCOM model was developed to assess which mechanisms are responsible for tundra change. I found this statement somewhat questionable because many very important mechanisms remain unknown when assumptions are made for models. The biomass example above is one such example. The issue that rooting depth in a warmer climate is not known is another example, but discussed later in the discussion. It might be helpful if the authors adapt their wording a bit. E.g. that they refer mechanisms to effects of warming vs. precipitation, which is the novel contribution of this paper.

REPLY: The focus of this modelling study was on exploring potential vegetation shifts in response to changes in temperature, precipitation and permafrost thaw, as is evident from the abstract. We agree that in parts of the main text the wording is a bit misleading with too much emphasis on mechanisms. We went through the whole text and adapted the wording in several places (e.g. page 1, lines 15, 18; page 4, line 1; page 10, lines 8-13).

So I suggest that the authors go through the entire manuscript another time and re-think carefully how to not over-sell their results. Apart from that, to state this again, I like the paper and find it helpful and novel.

Potential Arctic tundra vegetation shifts in response to changing temperature, precipitation and permafrost thaw ~~Simulating the effects of temperature and precipitation change on vegetation composition in Arctic tundra ecosystems~~

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Abstract. Over the past decades, vegetation has changed significantly along with climatic changes in the Arctic. Deciduous shrub cover is often assumed to expand in tundra landscapes, but more frequent abrupt permafrost thaw resulting in formation of thaw ponds could lead to vegetation shifts towards graminoid dominated wetland. Which ~~mechanisms~~factors drive vegetation changes in the tundra ecosystem is still not sufficiently clear. In this study, the dynamic tundra vegetation model NUCOM-tundra was used to evaluate the consequences of climate change scenarios of warming and increasing precipitation for future tundra vegetation change~~, and to identify the mechanisms that drive these changes~~. The model includes three plant functional types (moss, graminoids and shrubs), carbon and nitrogen cycling, water and permafrost dynamics and a simple thaw pond module. Climate scenario simulations were performed for sixteen combinations of temperature and precipitation increases in five vegetation types representing a gradient from dry shrub dominated, to moist mixed and wet graminoid dominated sites. Vegetation composition dynamics in currently mixed vegetation sites was dependent on both temperature and precipitation changes, with warming favouring shrub dominance and increased precipitation favouring graminoid abundance. Climate change simulations based on greenhouse gas emission scenarios in which temperature and precipitation increases were combined showed ~~initial~~ increases in biomass of both graminoid~~s~~ ~~abundance followed by shrub~~ and shrubs, with graminoids increasing in abundance~~expansion with further climate change~~. The simulations suggest that ~~the~~ shrub~~s are better light competitors, but their~~ growth can be limited by very wet soil conditions and low nutrient supply. whereas. ~~G~~ graminoids have the advantage of being able to grow in a wide range of soil moisture conditions and having access to nutrients in deeper soil layers. Abrupt permafrost thaw initiating thaw pond formation led to complete domination of graminoids. However, due to increased drainage, shrubs could profit from such changes in adjacent areas. Both climate and thaw pond formation simulations suggest that a wetter tundra can be responsible for local shrub decline instead of shrub expansion.

1 Introduction

5   Tundra ecosystems in the Arctic are shaped by strong interactions between biological, hydrological and climatological factors (Hinzman et al., 2005). An important feature of the Arctic ecosystem is permafrost, which is the soil that is persistently frozen for at least two years. For the near future, global climate models project a further increase in temperature and precipitation with pronounced changes in the Arctic region (Johannessen et al., 2004; Vavrus et al., 2012; IPCC, 2014). Rising temperatures potentially result in increased seasonal thawing of the permafrost and thus in an increased thickness of

10   the active layer (the soil layer that thaws during the growing season) and drawback of near surface permafrost (Anisimov et al., 1997; Lawrence and Slater, 2005; Zhang et al., 2005). Given the large soil organic carbon stocks in permafrost (Zimov et al., 2006a; Tarnocai et al., 2009), there is a major concern that these stocks get decomposed and subsequently released as CO_2 and CH_4 to the atmosphere (Dutta et al., 2006; McGuire et al., 2009). An increase in greenhouse gas release, including CO_2 and CH_4 (Christensen et al., 2004; Walter et al., 2006; Nauta et al., 2015; Schuur et al., 2015), from thawing permafrost

15   could stimulate further warming and result in a positive feedback loop between temperature increase and greenhouse gas emission (Zimov et al., 2006b; Schuur et al., 2008; MacDougall et al., 2012; van Huissteden and Dolman, 2012; Schuur et al., 2015).

Climate change in the Arctic region affects tundra vegetation composition. The northernmost tundra is dominated by mosses and lichens due to the extreme low summer temperatures. Southwards, with increasing summer temperatures, graminoids

20   and dwarf shrubs increase in abundance (Walker et al., 2005). Climate change influences the tundra vegetation in multiple ways. Warming experiments in tundra ecosystems showed an increase of graminoids and deciduous shrubs in response to raised temperatures, while mosses and lichens and the overall species diversity decreased (Walker et al., 2006). Shrubs have been observed to expand with ongoing temperature increase presumably due to the increased availability of nutrients in the warmer soil (Tape et al., 2006; Myers-Smith et al., 2011). Several tree and shrub species, including dwarf birches (*Betula*

25   *glandulosa* and *Betula nana*), willows (*Salix* spp.), juniper (*Juniperus nana*) and green alder (*Alnus viridis*), have expanded and increased in abundance in the Arctic as a response to climatic warming (Sturm et al., 2001; Tape et al., 2006; Hallinger et al., 2010; Elmendorf et al., 2012). However, besides climate, other factors as herbivory, soil moisture and soil nutrient availability affect shrub growth as well and it is therefore complex to predict the expansion of shrubs in the Arctic region (Myers-Smith et al., 2011, 2015). Increased abundance of shrubs might have important consequences for permafrost

30   feedbacks. For example, an increase of low shrubs might slow down permafrost thaw as a result of the shadow they cast on

the soil (Blok et al., 2010). However, tall shrubs may increase atmospheric heating and permafrost thawing due to their lower albedo (Bonfils et al., 2012)

Another mechanism by which climate change affects tundra vegetation is abrupt thaw resulting in local collapse of the permafrost. Thawing of underground ice masses results in a collapse of the ground, by which water filled thermokarst ponds are formed. These ponds are first colonized by sedges and later by mosses (Jorgenson et al., 2006). Due to thaw pond formation, changes in northern permafrost landscapes from dry birch forests or shrub dominated vegetation towards ponds or wetlands dominated by graminoids may occur with climatic change in both discontinuous and continuous permafrost regions (Jorgenson et al., 2001; Turetsky et al., 2002; Christensen et al., 2004; Jorgenson et al., 2006; Nauta et al., 2015). In the continuous permafrost region, permafrost collapse can change the vegetation from shrub dominated towards a wet graminoid dominated stage within less than one decade. The thermokarst ponds might stimulate further soil collapse and consequently drastically alter hydrological and soil processes, also in adjacent areas (Osterkamp et al., 2009; Nauta et al., 2015; Schuur et al., 2015).

The ~~mechanisms~~factors that drive the observed tundra vegetation composition changes, especially shrub expansion, and their consequences are not yet well understood. Increased air temperatures lead to higher soil temperatures, especially in the shallow layers, and may thus promote microbial activity, thereby increasing nutrient availability in the soil. In tundra vegetation, shrubs are hypothesised to be best able to respond to such increased nutrient availability (Tape et al., 2006). It is, however, not known to what extent this and other shrub growth factors, including precipitation, growing season length and disturbances (Myers-Smith et al., 2011), will affect the competition between different plant functional types in the Arctic. As shrub expansion has important implications for land surface albedo and consequently climate feedbacks (Chapin et al., 2005; Pearson et al., 2013), it is crucial that we understand and are able to predict further vegetation change in the tundra.

One approach to better understand the interactions between plants in tundra landscapes is to use a dynamic vegetation model to analyse developments in vegetation composition in response to climatic changes. Tundra vegetation models that aim to predict the impacts of climate change on vegetation-substrate interactions should at least include the most important plant functional types, competition and permafrost feedbacks. Although several tundra vegetation models exist, these models do not take into account hydrological feedbacks, the formation of thaw ponds and~~ ~~vegetation-permafrost feedbacks or do not include mosses as separate plant functional type (e.g. Epstein et al., 2000; Wolf et al., 2008; Euskirchen et al. 2009). Therefore, in this study, the effects of climate change, including both temperature and precipitation change, on plant competition and vegetation composition were studied by developing a new model named NUCOM-tundra based on earlier NUCOM (NUtrient and COMpetition) models for other ecosystems (Berendse, 1994a, 1994b; van Oene et al., 1999; Heijmans et al., 2008, 2013). The new tundra vegetation model includes mosses, graminoids, dwarf shrubs, hydrological and soil processes, and permafrost dynamics. In this study, we simulated tundra vegetation changes under different climate change scenarios in order to (1) analyse the effects of future temperature and precipitation scenarios on tundra vegetation

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composition, ~~(2) identify important mechanisms that drive these vegetation changes,~~ and (~~3~~2) explore the impacts of thaw pond formation due to local permafrost collapse.

2 Methods

2.1 Brief model description

5 NUCOM-tundra has been developed to simulate long-term dynamics of vegetation composition in tundra landscapes for analysis of vegetation-permafrost-carbon feedbacks in relation to climate change and includes nitrogen and carbon cycling, permafrost and water dynamics (Fig. 1). An extensive model description and all equations are provided in Supplement Section S1.

NUCOM-tundra simulates the dynamics of three Plant Functional Types (PFTs), moss, graminoids (e.g. *Eriophorum*
10 *vaginatum*) and deciduous dwarf shrubs (e.g. *Betula nana*), on a local scale at the decadal timescale using a daily time step. NUCOM-tundra represents tundra landscapes, which are an alternation of shrub dominated, graminoid dominated and mixed vegetation types. The model is based on an area of 1 m². The biomass and nitrogen content of the vascular plant PFTs is separated into fine roots, woody plant parts (for shrubs) or rhizomes (for graminoids), and leaves. Mosses form a layer on top of the soil surface, with a thickness up to 4.5 cm. The soil profile is divided into an organic top soil layer with a variable
15 height and 10 deeper mineral soil layers each with a thickness of 10 cm. The fine roots of vascular plants are distributed throughout the active soil profile, with graminoids rooting deeper in comparison to dwarf shrubs (Shaver and Cutler, 1979; Nadelhoffer et al., 1996; Iversen et al., 2015). The thickness of the active layer depends on the soil temperature profile (Supplement Section S1). The thickness of the organic layer, which consists solely of moss, leaf, stem and root litter, generally increases over time, depending on the balance between litter input and litter decomposition. The mineral soil layers
20 contain initial soil organic carbon and nitrogen pools as well. During the simulations, only fine root litter is added to the mineral soil layers and decomposed there. The other litter types become part of the soil organic layer. Decomposition rates depend on soil temperature and differ among PFTs and plant organs (leaves, stems and fine roots).

Plant growth (net primary production) is determined by temperature, light availability, nutrient availability and moisture conditions (Supplement Section S1). In the model, there are temperature thresholds for plant growth thus excluding growth
25 during the winter season. Graminoids and dwarf shrubs compete for the incoming light based on their leaf area. It is assumed that graminoids and dwarf shrubs are equally tall. The moisture content in the upper 10 cm of the soil can strongly reduce PFT growth as both graminoids and dwarf shrubs have an optimum growth only in part of the range of possible soil moisture conditions. Dwarf shrubs prefer drier conditions, and cannot grow if the soil is completely water saturated. The graminoids in the model do not grow well under dry conditions, but can grow on water-saturated soils.

Mosses acquire nitrogen by nitrogen fixation from the atmosphere and can absorb available nitrogen from the upper cm of the soil profile. Vascular plant nitrogen uptake is determined by the fine root length of both graminoids and dwarf shrubs present in each layer and the amount of nutrients available. At the start of the growing season, when the air temperature is above the threshold for growth but the soil is still mostly frozen, the plants can use nitrogen from an internal storage, which

5 is filled by nitrogen reallocated from senescing leaves and roots. Dying plant material enters the soil organic carbon and nitrogen litter pools. Soil organic carbon is lost by microbial decomposition, whereas the mineralised nitrogen from soil organic nitrogen becomes available for plant uptake. The rate of decomposition and nitrogen mineralisation depends on soil temperature. Subsequently, pPart of thise pool of available nitrogen can be lost by denitrification under high soil moisture conditions (Supplement Section S1).

10 A simple hydrological module is included in NUCOM-tundra, which simulates the volumetric water content of the organic and mineral soil layers (Supplement Section S1). Water from snowmelt, rainfall and inflow from a neighbouring vegetation type (Fig. 2) fills up the pore space in the soil layers. Evapotranspiration, surface runoff, and lateral drainage out of the moss and organic layer lower the water content. The lateral drainage includes transport of dissolved nitrogen. The hydrological processes follow a seasonal pattern. A snow layer accumulates during the winter season, and snowmelt occurs with positive

15 air temperatures at the start of the growing season. During this period, the shallow active layer becomes water saturated and the excess of water runs off over the soil surface. During the growing season, evapotranspiration generally exceeds precipitation, resulting in gradual drying of the soil.

2.2 Parameter values and model input

Parameter values for plant properties such as root characteristics, mortality, reallocation and decomposition have been

20 derived from literature or have been calibrated using field data collected at the Chokurdakh Scientific Tundra Station, located 70° 49′ N, 147° 29′ E, altitude 10m (Supplement Section S2). The Chokurdakh Scientific Tundra Station, also known as Kytalyk field station, is located in the lowlands of the Indigirka river, north-eastern Siberia, which is in the continuous permafrost zone and the Low Arctic climate zone. The vegetation is classified as tussock-sedge dwarf-shrub moss tundra (vegetation type G4 on Circumpolar Arctic Vegetation Map; Walker et al., 2005). The parameter values are provided in

25 Appendix A.

NUCOM-tundra requires daily temperature and precipitation data as input for the model simulations. Weather data from Chokurdakh Weather Station (WMO station 21946, located 70˚ 62‘ N, 147˚ 88‘ E; altitude 44.0m) for the years 1954 to 1994 obtained through the KNMI climate explorer tool (Klein Tank et al., 2002, http://climexp.knmi.nl) were input to the model. Initial values of the model simulations are provided in Supplement Section S3. The biomass start values were based

30 on field measurements at the Chokurdakh Tundra Station.

2.3 Vegetation types

We defined five initial vegetation types representing a gradient from relatively dry to wet sites for the climate change simulations in NUCOM-tundra. These initial vegetation types represent five landscape positions, ranging from relatively well-drained shrub patches to waterlogged graminoid-dominated wetland (Fig. 2). The first vegetation type represents dry shrub-dominated vegetation. Vegetation types 2, 3 and 4 represent moist mixed vegetation from relatively dry to wet sites. Vegetation type 5 represents a wet graminoid-dominated vegetation downslope which receives water from the neighbouring cell. In vegetation type 1, only outflow of both surface water and water in the organic layer occur, whereas moist sites are characterized by having both water inflow and water outflow. The water flow into a downslope landscape position is the actual water outflow from the adjacent upslope located simulation cell. This water movement over the gradient includes transport of dissolved nitrogen from the elevated shrub patch to the sedge-dominated depression.

2.4 Comparison with field data

The performance of several model parts was evaluated by comparing outputs with data from the Kytalyk field station and Chokurdakh Tundra Station and Weather Station. The simulated timing of snow accumulation and snowmelt was compared with snow height data from the Chokurdakh Weather Station between 1944 and 2008. Time series of soil temperature at different depths and measurements of thawing depth were used to evaluate the soil temperature calculations. Furthermore, simulated PFT total biomass, biomass partitioning among leaves, woody parts, rhizomes and fine roots and vertical root distribution were compared with field data. Field biomass collections were done for both graminoids and dwarf shrubs in graminoid dominated, mixed and dwarf shrub dominated vegetation sites at the tundra field site in north-eastern Siberia (Wang et al., 2016). Roots were collected over different depths, enabling to compare the field data with simulated root distribution over depth. These field data were compared with simulations that were run with climate input from the Chokurdakh Weather Station. A detailed description of these comparisons of simulated and field data is provided in Supplement Section S4.

2.5 Climate scenario simulations

For all vegetation types a period of 40 years was simulated to initialize the model, using precipitation and temperature data from the Chokurdakh weather station from 1 August 1954 till 31 July 1994 as input. This period excludes the most pronounced warming that took place over the last decades. Annual precipitation was, however, variable with both increasing and declining trends in the 40-year time period (Supplement Section S2). After the initialisation phase, 16 different climate change scenarios were run for all five vegetation types for the period 1 August 1994 – 31 July 2074. Inspired by the RCP emission scenarios over the 21st century, we combined four temperature increases with four precipitation increases to simulate climatic changes over this 80-year period. The combinations include temperature increases of 0, 2.5, 5 or 8 $^{\circ}$C and precipitation increaseschanges of 0, 15, 30 or 45 % increase overmm per 100 years. In the Arctic region, an increase of

2.5 °C and 15mm% precipitation increase is expected under emission scenario RCP2.6 and an increase of 8 °C and 45 mm% precipitation increase are expected over the 21st century under emission scenario RCP8.5 (IPCC, 2014). A scenario with 5°C and 30 mm% precipitation changeincrease is regarded here as an 'Intermediate' scenario.

The weather data series over the period 1 August 1954 – 31 July 1994 from the Chokurdakh weather station was used twice to create a baseline (no climate change) for the climate scenario simulations between 1994 and 2074. For all climate change scenarios, temperature and precipitation were gradually increased over this 80 year simulation period. For precipitation, only the intensity of rainfall was increased and not the number of days at which rainfall occurred.

To evaluate the effects of climate change on the vegetation composition, we compared the biomass of moss, graminoids and dwarf shrubs on 31 July, averaged over the last 10 years of the simulation (corresponding with 2065-2074). Furthermore, several factors that influenced plant growth and competition were evaluated using the simulations for moist mixed vegetation sites (vegetation type 3) in which all three PFTs co-occur. The following factors were evaluated for the last 10 years of the simulations:

1) *Growing season length*: The average number of days per year at which the temperature threshold for vascular plant growth was exceeded;

2) *Soil moisture*: Average soil moisture content in the upper 10cm of the soil profile during the growing season;

3) *Light competition*: The average percentage of light intercepted by graminoids and shrubs during the growing season;

4) *Moisture conditions*: Percentage of time in the growing season with optimal soil moisture content for growth of graminoid and dwarf shrub;

5) *Nutrient limitation*: Limitation of growth of graminoid and dwarf shrub due to insufficient available nutrients in the growing season, expressed as percentage of potential growth realised.

2.6 Thaw pond simulations

Thaw pond initiation was simulated for dry and moist vegetation types (vegetation types 1-4) under three different climate change scenarios: no change, RCP2.6 and RCP8.5. Thaw pond collapse was simulated by imposing a sudden alternation of water flows. Upon a collapse event, water inflow, including surface runoff and lateral drainage through the soil organic layer, doubled whereas water outflow stopped. To evaluate the effects of thaw pond collapse on downslope vegetation sites, simulations were performed in series that included all five vegetation types (Fig. 3). Thaw pond formation was initiated at a fixed time step halfway the simulation (corresponding to 31 July 2034). The change in vegetation composition after collapse was evaluated by determining the abundance of graminoids (in %) in the vascular plant community biomass in the last 10 summers of the simulation (31 July in the years 2065-2074), when the vegetation is at its peak biomass.

3 Results

3.1 Comparison with field data

Simulated snow height, soil temperature, active layer thickness, total PFT biomass, biomass partitioning and vertical root distribution were compared with observations from Chokurdakh Scientific Tundra Station or Weather Station (detailed description in Supplement Section S4). Simulated timing of accumulation and melt of the snow layer between 1944 and 2008 was well in agreement with observations of snow depth at the Chokurdakh Weather Station. Simulated shallow soil temperatures were in agreement with observations from the Kytalyk meteo tower, but simulated deep soil temperatures were higher than observed, resulting in simulated thawing depths that were on average 14 cm higher than observed thawing depths (Fig. S4.2). ~~Furthermore,~~This deeper active layer thickness result~~ed~~ in an overestimation of graminoid biomass, as was demonstrated by simulations with lowered active layer thickness (Figure S4.3). However, the patterns of changing graminoid biomass ~~among~~ the main climate change scenarios remained when the active layer thickness was lowered, indicating that the uncertainty about the simulated deep soil temperatures d~~o~~id not significantly affect the vegetation composition changes for the climate change scenario simulations.

NUCOM-tundra simulated total biomass for graminoids and dwarf shrubs within the range of biomass values obtained for shrub, mixed and graminoid vegetation types at the field site. Simulated biomass partitioning over leaves, stems and fine roots was comparable to the partitioning observed in the field with high total biomass, although the simulated biomass partitioning was rather constant and did not change with increasing total biomass, as observed in the field. Fine root vertical distribution patterns were similar between observed and simulated data as NUCOM-tundra took into account the different rooting patterns of graminoids and dwarf shrubs, and variations in active layer thickness.

3.2 Climate scenario simulations: Vegetation changes

In the No climate change scenario, the total vegetation biomass was rather stable throughout the simulation in all vegetation types (Fig. 4A for vegetation type 3, data not shown for other vegetation types). Gradual biomass increases between 1994 and 2074 were simulated under the three climate change scenarios based on the RCP scenarios (Fig. 4B, 4C, 4D). Considering all combinations of temperature and precipitation scenarios in all vegetation types, ~~shows that the~~ simulated total biomass of the vegetation responded strongly to increased temperature (Fig. 5). The average total (aboveground and belowground) summer biomass between 2065 and 2074 ranged from ~~1544~~ 1970 g m^{-2} to ~~2428~~ 3037 g m^{-2} with no temperature change, whereas total biomass ranged between ~~3702~~ 4815 g m^{-2} to ~~4483~~ 5402 g m^{-2} with a gradual increase of 8 ^{o}C over the 21st century. In contrast, precipitation change did not affect the total vegetation biomass.

The vegetation composition in relatively well-drained sites dominated by shrub vegetation (vegetation type 1) and wet graminoid-dominated vegetation (vegetation type 5) did not change under any of the climate change scenarios (Fig. 5). In mixed vegetation (vegetation type 3), graminoids ~~slightly~~ increased in abundance with the RCP2.6 scenario (2.5 ^{o}C temperature and ~~15mm~~ 15% precipitation ~~year^{-1}~~ increase over the 21st century), intermediate and RCP8.5 scenario (8 ^{o}C

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temperature and 45 % precipitation increase over the 21st century) (Fig. 4B-D; Fig. 6). ~~However, under scenario RCP8.5 (8 ^{0}C temperature and 45 mm precipitation year^{-1} increase over the 21st century), shrubs became more dominant by 2065-2074 after an initial increase in graminoid abundance (Fig. 4D).~~ In other climate change scenarios, the magnitude of both precipitation and temperature change determined changes in vegetation composition in currently mixed vegetation sites (Fig. 6). The proportion of graminoids in the vascular plant community increased in simulations with more pronounced precipitation changes and lower temperature changes (Fig. 4E; Fig. 6). In contrast, graminoids were outcompeted by shrubs by the end of simulations of initially mixed vegetation sites under a scenario with 8^{0}C temperature increase but no precipitation change over the 21st century (Fig. 4F).

Simulated moss biomass was in general lowest in wet graminoid dominated vegetation sites (Fig. 5), and showed little variation among the climate scenario simulations (Fig. 4; Fig. 5).

3.3 Nutrient availability, light competition and moisture conditions

In comparison to the scenario for no climate change, the growing season was on average 39 days longer ~~between 1~~in the ~~years~~ ~~August 1964 and 31 July 1974~~2065-2074 in simulations with an 8 ^{0}C temperature increase scenario (Table 1). During the same time period, the averaged soil moisture at mixed vegetation sites was higher in simulations with more pronounced precipitation change and lower temperature changes (Table 1). Consequently, soil moisture conditions became more favourable for graminoids under these scenarios, whereas moisture conditions became more favourable for shrubs with large changes in temperature and small changes in precipitation. For the RCP2.6, intermediate and RCP8.5 scenario, moisture conditions became slightly less favourable for graminoid growth and ~~more favourable~~remained unchanged for shrub growth in comparison to the scenario for no climate change.

In general, shrubs were able to intercept~~ed~~ more light in comparison to graminoids in pronounced climate change scenarios (Table 1). Both graminoids and shrubs intercepted more light when moisture conditions became more favourable. The effect of temperature changes on light interception differed between graminoids and shrubs. Shrubs intercepted more light when temperature changes were more pronounced. Light interception in graminoids, however, decreased under scenarios with 8 ^{0}C temperature increase and less pronounced precipitation increase over the 21st century. Nutrients limited shrub growth under all climate scenarios (Table 1). For both graminoids and shrubs, nutrients became less limiting under less suitable growth conditions.

3.4 Thaw pond simulations

All thermokarst events (initiated in 2034) led to the complete domination of graminoids over shrubs within 15 years after initiation of thaw pond development (Fig. 7; Fig. 8). The vegetation composition on collapsed sites became similar to the composition on wet graminoid dominated sites (vegetation type 5). After abrupt permafrost thaw, bryophytes took advantage of the decreased vascular plant leaf area, but stabilized later at a biomass that was equal to the moss biomass in non-collapsed wet graminoid dominated vegetation sites (Fig. 8). When a collapse occurred in vegetation type 1, 2 or 3, the

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collapse enhanced shrub expansion in the next grid cell. The thermokarst pond acted as a water sink, due to which water flows into the next grid cell were halted. Consequently, the grid cell adjacent to the thermokarst pond became drier which favoured shrub growth (Fig. 7). Similar patterns for the thaw pond simulations were observed for No change, RCP2.6 and RCP8.5 climate scenarios.

5   ## 4. Discussion

The effects of climate change on tundra vegetation are complex since <u>temperature and precipitation drive changes in</u> hydrology, active layer depths, nutrient availability and growing season length<u>, which</u> interact with each other (Serreze et al., 2000; Hinzman et al., 2005). ~~Climate warming might alter vegetation composition by increasing nutrient availability due to faster mineralization rates and increasing active layer depths (Mack et al., 2004). It remains, however, unclear which factors~~

10   ~~are most decisive with respect to the observed expansion of shrubs at the expense of graminoids (Myers-Smith et al., 2011).~~ NUCOM-tundra ~~was~~<u>has been</u> developed to explore future Arctic tundra vegetation composition changes in response to climate scenarios<u>, thereby taking changes in soil moisture, thawing depth and nutrient availability into account.</u> ~~and to assess which mechanisms are responsible for these changes.~~

4.1 ~~Vegetation Composition Changes~~<u>Effects of increases in temperature and precipitation</u>

15   Our climate scenario simulations suggest a significant increase in biomass with continuing climate change, and ~~eventually~~ <u>especially</u> increased ~~shrub~~<u>graminoid</u> abundance under scenarios with ~~strong~~<u>different magnitudes of</u> climate change~~, such as the RCP8.5 emission scenario~~. For ~~the~~ modest <u>and strong</u> emission scenarios (~~RCP2.6, +2.5 ⁰C and +15mm~~<u>%</u> ~~precipitation increase over the 21ˢᵗ century~~<u>Intermediate and RCP8.5</u>), ~~particularly~~<u>both shrub and</u> graminoid biomass increased. These simulations are in line with biomass increases in both shrubs and graminoids that have been observed during the past

20   decades in Arctic tundra landscapes as a response to temperature increase (Dormann and Woodin, 2002; Walker et al., 2006; Hudson and Henry, 2009). ~~In addition, s~~<u>S</u>hrub expansion ~~, as predicted by the model for strong climate change scenarios,~~ has been observed in many places in the Arctic (Sturm et al., 2001; Tape et al., 2006; Myers-Smith et al., 2011)<u>, but is not explicitly simulated by NUCOM-tundra for the</u> ~~main~~<u>RCP-based</u> climate change scenarios <u>which combine temperature and precipitation increases</u>.

25   As nutrient availability limits plant growth in tundra landscapes (Shaver et al., 2001), a positive effect of warming on nutrient availability is a likely explanation for biomass increase observed in tundra vegetation (Hudson and Henry, 2009). Climate warming might influence nutrient availability positively by lengthening of the growing season, active layer deepening and increased microbial activity. In our simulations, nutrients were especially limiting for the shrubs, <u>likely</u> due to their shallow rooting systems. Compared to shrubs, graminoids root relatively deep <u>(Wang et al. 2016)</u>. As a consequence,

30   active layer deepening is expected to favour especially graminoids. It is, however, unclear how plant root morphology

responds to climate warming. An experimental warming study in dry tundra demonstrated that plants do not necessarily root deeper in response to warmer temperatures, but instead may concentrate their main root biomass in the organic layer where most nutrient mineralization takes place (Björk et al., 2007). Nevertheless, it is likely that growing season lengthening and increased microbial mineralization of soil organic matter improve growing conditions for both shrubs and graminoids, as also graminoids have been shown to respond strongly upon fertilization (e.g. Jonasson, 1992).

Strikingly, the climate simulations in this study show that shifts in vegetation composition are not only dependent on temperature change, but are strongly affected by precipitation changes as well. Simulated soil moisture contents decreased with higher temperature and lower precipitation scenarios. Evapotranspiration is an important hydrological process determining soil moisture during the growing season. Throughout the growing season, the top soil layer dries out as evapotranspiration exceeds precipitation during this period, which is in agreement with observations at our study site (Supplement Section S2). Higher summer temperatures increase potential evapotranspiration, and thus lead to drier soils, if precipitation remains unchanged. Consequently, the area of relatively dry sites characterized by dense dwarf shrub vegetation might increase. A similar misbalance of temperature and precipitation change between 1950 and 2002 has been proposed by Riordan et al. (2006) as one of the possible causes for drying of thermokarst ponds in Alaska. A second mechanism for tundra drying with higher temperatures is increased water drainage enabled by gradual deepening of the active layer or permafrost degradation. The latter mechanism is especially important in the discontinuous permafrost zone, where climate change may cause loss of permafrost at thermokarst sites and subsequently lead to increased drainage to adjacent areas (Yoshikawa and Hinzman, 2003).

Whereas NUCOM-tundra predicts that especially graminoids benefit under the main climate change scenarios, other Arctic vegetation models mainly simulate shrub expansion (e.g. Epstein et al., 2000; Euskirchen et al., 2009; Yu et al., 2011). As moisture conditions did not differ much between the combined climate change scenarios (Table 1), the relatively large increase of graminoids in those scenarios is likely enabled by active layer deepening. Nutrients that become available in deeper soil layers are easily accessible by graminoids which are able to root throughout the whole active layer, whereas shrubs rely on the nutrient availability in the top soil layers as their root system is confined to that region. It is important to note that NUCOM-tundra currently uses a simple soil temperature soil module, which calculates soil temperature based on air temperature (Supplement S1.3.4). Especially for deeper soil layers, this module lacks accuracy to precisely predict changes in active layer thickness for different temperature change scenarios, which results in uncertainty in both the depth of the active layer and the amounts of nutrients becoming available. These processes influence graminoid growth more than shrub growth. Coupling NUCOM-tundra to an advanced soil temperature model is needed to simulate the physical soil processes more accurately. The climate simulations in this study show that shifts in vegetation composition are not only dependent on temperature change, but are strongly affected by precipitation changes as well. Simulated soil moisture contents decreased with higher temperature and lower precipitation scenarios. Evapotranspiration is an important

hydrological process determining soil moisture during the growing season. Throughout the growing season, the top soil layer dries out as evapotranspiration exceeds precipitation during this period, which is in agreement with observations at our study site (Supplement Section S2). Higher summer temperatures increase potential evapotranspiration, and thus lead to drier soils, if precipitation remains unchanged. Consequently, the area of dry vegetation sites characterized by their dense dwarf shrub
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10 adjacent areas (Yoshikawa and Hinzman, 2003).

Previously, Tthe effectiveness of shrubs to deal with increased nutrient levels has been proposed as an explanation that shrubs can expand in a warmer climatefor observed shrub expansion in the Arctic (Shaver et al., 2001; Tape et al., 2006). *Betula nana* responds to higher nutrient availability by increasing its biomass, which is mainly due to increased secondary
15 stem growth (Shaver et al., 2001). However, *Betula nana* is also known to respond to increased temperatures and fertilization by growing taller and by producing more shoots and tillers, thereby increasing its ability to compete for light with other species (Chapin and Shaver, 1996; Hobbie et al., 1999; Bret-Harte et al., 2001; Shaver et al., 2001). In NUCOM-tundra, competition for light or nutrients is determined by a combination of Sseveral plant traits (parameters values) are related to competition for light or nutrients. For light competition, leaf area and light extinction are important, which are influenced by
20 parameters as specific leaf area, biomass allocation to leaves, leaf mortality and light extinction coefficient. Similarly, nutrient competition is influenced by parameters as specific root length, root distribution and nutrient requirements. Although tiller production is not explicitly included in NUCOM-tundra, shrubs had an advantage in the competition for light as they have a higher specific leaf area and higher light extinction coefficient than the graminoids. Yet, this advantage for shrubs was in the combined climate change scenarios overruled by the advantageous ability of graminoids to root deep in the
25 mineral soil layers. Although tiller production is not explicitly included in NUCOM-tundra, shrubs clearly had an advantage in the competition for light as they have a higher specific leaf area and higher light extinction coefficient than the graminoids. Based on our observations at our study site in north-eastern Siberian tundra and at Toolik Lake moist tussock tundra, we assumed the (dwarf) shrubs and graminoids to be equally tall in the model. With warming-induced increases in aboveground biomass for both graminoids and shrubs, the competition for light becomes more important. In parts of the
30 tundra area shrubs, including *B. nana*, can grow taller than the graminoids. For a wider application of the vegetation model, i.e. to include transitions to tall shrub vegetation, a variable plant height up to a maximum would be required.

The climate simulations in this study show that shifts in vegetation composition are not only dependent on temperature change, but are strongly affected by precipitation changes as well. Simulated soil moisture contents decreased with higher temperature and lower precipitation scenarios. Evapotranspiration is an important hydrological process determining soil moisture during the growing season. Throughout the growing season, the top soil layer dries out as evapotranspiration

5 exceeds precipitation during this period, which is in agreement with observations at our study site (Supplement Section S2). Higher summer temperatures increase potential evapotranspiration, and thus lead to drier soils, if precipitation remains unchanged. Consequently, the area of dry vegetation sites characterized by their dense dwarf shrub coverage might increase. A similar misbalance of temperature and precipitation change between 1950 and 2002 has been proposed by Riordan et al. (2006) as one of the possible causes for drying of thermokarst ponds in Alaska. A second mechanism for tundra drying with

10 higher temperatures is increased water drainage enabled by gradual deepening of the active layer or permafrost degradation. The latter mechanism is especially important in the discontinuous permafrost zone, where climate change may cause loss of permafrost at thermokarst sites and subsequently lead to increased drainage to adjacent areas (Yoshikawa and Hinzman, 2003).

Predicted increases in total biomass and expansion of shrubs are not unique for NUCOM tundra, but have also been

15 simulated by other Arctic vegetation models (e.g. Epstein et al., 2000; Euskirchen et al., 2009; Yu et al., 2011). OOverall, our results from the climate change scenarios mainly, however, highlight the importance of changes in annual precipitation, as they have a large influence on the water table and thus on the tundra vegetation composition. Precipitation, especially in summer, compensates for evapotranspiration water losses, thereby having a direct positive influence on soil moisture and water table position. Climate models predict considerable precipitation increases for the Arctic region (IPCC, 2014) as the

20 retreat of sea ice in the Arctic Ocean results in strongly increased evaporation and precipitation (Bintanja and Selten 2014). In agreement with these predictions, significant increases in precipitation over the last decades have been demonstrated for several Arctic weather stations (Hinzman et al., 2005; Urban et al., 2014). Changes in precipitation are, however, less consistent in comparison to climate warming (Urban et al., 2014). In Chokurdakh, the location used for the model simulations, precipitation has not increased along with temperature change between 1981 and 2010 (Temperature +0.0565 ^{o}C

25 year^{-1}; Precipitation -1.127 mm year^{-1}) (climexp.knmi.nl/atlas; Li et al., 2015). Continuation of the climate trends observed in Chokurdakh between 1981 and 2010 would lead to a scenario that most resembles a temperature increase of 5°C and no precipitation change by the end of this century. This scenario would imply that currently mixed vegetation will shift towards shrub dominated vegetation in the near future due to tundra drying.

4.2 Thaw Pond Formation

30 Formation and expansion of shrub vegetation might be set back by the degradation and collapse of ice wedges in the permafrost. Even in dry vegetation type simulations, the initiation of thermokarst led, as a result of water accumulation in thaw ponds, to complete replacement of shrubs by graminoids. The simple thaw pond module in NUCOM-tundra simulated

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a peak of moss biomass shortly after ground collapse and before significant colonization of graminoids. After the collapse, the shrubs were dying because of the water-saturated soil, while the graminoids had not yet colonized the new thaw pond, and the mosses took advantage of the increased light availability. At the Siberian field site we observe that mosses mostly drown as well and the first colonizers of thaw ponds are mostly graminoids, for example *Eriophorum angustifolium*
5   (Jorgenson et al., 2006), although also mosses can be first colonizers. NUCOM-tundra does not (yet) take surface water depth into account for the calculation of plant and bryophyte growth, due to which drowning of mosses could not be simulated. The model is also not able to simulate further vegetation succession in thaw ponds. Most likely, after graminoid and moss establishment, an organic layer starts to accumulate, shrubs recolonize the collapsed sites, after which permafrost aggradation can take place. Water runoff out of collapsed sites is expected to increase when the organic layer accumulates,
10   probably aided by newly developing ice structures which lift the surface.

Simulated thermokarst events favoured shrub growth in adjacent grid cells due to increased drainage. Although graminoids become dominant in thaw ponds, ice wedge collapses may provide opportunities for shrub growth on the pond margins due to small scale changes in water flows. Such a mechanism was observed in Alaska, where shrubs became dominant around thermokarst spots as a result of increased drainage from shrub-dominated patches to the new ponds (Osterkamp et al., 2009).
15   These results further reveal that tundra drying is an important mechanism for shrub expansion in the Arctic. Thermokarst ponds, however, may also act as a heat source and thereby stimulate further permafrost collapse (Li et al., 2014). Overall, permafrost degradation should be recognized as an important potentially graminoid stimulating factor when studying climate change in Arctic landscapes (Jorgenson et al., 2006). Rapid expansion of shrubs might be partly compensated by the formation of graminoid dominated thaw ponds, particularly in poorly drained lowland tundra.

20   The inclusion of thaw pond formation is a new but not yet fully developed element of NUCOM-tundra. There are models that simulate tundra vegetation change (ArcVeg (Epstein et al., 2000); TEM-DVM (Euskirchen et al., 2009); LPJ-Guess (Wolf et al., 2008; Zhang et al., 2013)), and models that simulate thaw lake cycle dynamics (van Huissteden et al., 2011). Taking into account the formation of thaw ponds and the subsequent vegetation succession is, however, essential for a full analysis of climate change effects on tundra ecosystem (Van Huissteden & Dolman, 2012). This model feature should
25   therefore receive special attention with further model developments.

Appendix A: Parameter values in NUCOM-tundra

References

Berendse, F.: Litter decomposition - a neglected component of plant fitness, Journal of Ecology, 82, 187-190, 1994a.

Berendse, F.: Competition between plant populations at low and high nutrient supplies, Oikos, 71, 253-260, 1994b.

Bintanja, R., and Selten, F. M.: Future increases in Arctic precipitation linked to local evaporation and sea-ice retreat, Nature, 509, 479-482, 2014.

Björk, R. G., Majdi, H., Klemedtsson, L., Lewis-Jonsson, L., and Molau, U.: Long-term warming effects on root morphology, root mass distribution, and microbial activity in two dry tundra plant communities in northern Sweden, New Phytologist, 176, 862-873, 2007.

Blok, D., Heijmans, M. M. P. D., Schaepman-Strub, G., Kononov, A. V., Maximov, T. C., and Berendse, F.: Shrub expansion may reduce summer permafrost thaw in Siberian tundra, Global Change Biology, 16, 1296-1305, 2010.

Bonfils, C. J. W., Phillips, T. J., Lawrence, D. M., Cameron-Smith, P., Riley, W. J., and Subin, Z. M.: On the influence of shrub height and expansion on northern high latitude climate, Environmental Research Letters, 7, doi: 10.1088/1748-9326/7/1/015503, 2012.

Bret-Harte, M. S., Shaver, G. R., Zoerner, J. P., Johnstone, J. F., Wagner, J. L., Chavez, A. S., Gunkelman IV, R. F., Lippert, S. C., and Laundre, J. A.: Developmental plasticity allows Betula nana to dominate tundra subjected to an altered environment, Ecology, 82, 18-32, 2001.

Chapin, F. S., Van Cleve, K., and Tieszen, L. L.: Seasonal nutrient dynamics of tundra vegetation at Barrow, Alaska, Arctic and Alpine Research, 7, 209-226, 2975.

Chapin, F. S., and Shaver, G. R.: Physiological and growth responses of arctic plants to a field experiment simulating climatic change, Ecology, 77, 822-840, 1996.

Chapin, F. S., Bret-Harte, M. S., Hobbie, S. E., and Zhong, H.: Plant functional types as predictors of transient responses of arctic vegetation to global change, Journal of Vegetation Science, 7, 347-358, 1996.

Chapin, F. S., Sturm, M., Serreze, M. C., McFadden, J. P., Key, J. R., Lloyd, A. H., McGuire, A. D., Rupp, T. S., Lynch, A. H., Schimel, J. P., Beringer, J., Chapman, W. L., Epstein, H. E., Euskirchen, E. S., , L. D., Jia, G., Ping, C.-L., Tape, K. D.,
5 Thompson, C. D. C., Walker, D. A., and Welker, J. M.: Role of land-surface changes in Arctic summer warming, Science, 310, 657-660, 2005.

Christensen, T. R., Johansson, T., Åkerman, H. J., Mastepanov, M., Malmer, N., Friborg, T., Crill, P., and Svensson, B.H.: Thawing sub-arctic permafrost: Effects on vegetation and methane emissions, Geophysical research letters, 31, doi: 10.1029/2003GL018680, 2004.

10 Dormann, C. F., and Woodin, S. J.: Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments, Functional Ecology, 16, 4-17, 2002.

Dutta, K., Schuur, E. A. G., Neff, J. C., and Zimov, S. A.: Potential carbon release from permafrost soils of Northeastern Siberia, Global Change Biology, 12, 2336-2351, 2006.

Eissenstat, D. M., Wells, C. E., Yanai, R. D., and Whitbeck, J. L.: Research view: Building roots in a changing environment:
15 Implications for root longevity, New Phytologist, 147, 33-42, 2000.

Elmendorf, S. C., Henry, G. H., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Dorrepaal, E., Elumeeva, T. G., Gill, M., Gould, W. A., Harte, J., Hik, D. S., Hofgaard, A., Johnson, D. R., Johnstone, J. F., Jónsdóttir, I. S., Jorgenson, J. C., Klanderud, K., Klein, J. A., Koh, S., Kudo, G., Lara, M., Lévesque, E., Magnússon, B., May, J. L., Mercado-Díaz, J. A., Michelsen, A., Molau, U., Myers-Smith, I. H., Oberbauer, S. F.,
20 Onipchenko, V. G., Rixen, C., Schmidt, N. M., Shaver, G. R., Spasojevic, M. J., Þórhallsdóttir, Þ. E., Tolvanen, A., Troxler, T., Tweedie, C. E., Villareal, S., Wahren, C., Walker, X., Webber, P. J., Welker, J. M., and Wipf, S.: Plot-scale evidence of tundra vegetation change and links to recent summer warming, Nature Climate Change, 2, 453-457, 2012

Epstein, H. E., Walker, M. D., Chapin, F. S., and Starfield, A. M.: A transient, nutrient-based model of arctic plant community response to climatic warming, Ecological Applications, 10, 824-841, 2000.

25 Euskirchen, E. S., McGuire, A. D., Chapin, F. S., Yi, S., and Thompson, C. C.: Changes in vegetation in northern Alaska under scenarios of climate change, 2003-2100: implications for climate feedbacks, Ecological Applications, 19, 1022-1043, 2009.

Hallinger, M., Manthey, M., and Wilmking, M.: Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia, New Phytologist, 186, 890-899, 2010.

Heal, O. W., and French, D. D.: Decomposition of organic matter in tundra. Soil organisms and decomposition in tundra, Tundra Biome Steering Committee, Stockholm, pp. 279-309, 1974.

5 Heijmans, M. M. P. D., Arp, W. J., and Chapin, F. S.: Carbon dioxide and water vapour exchange from understory species in boreal forest, Agricultural and Forest Meteorology, 123, 135-147, 2004.

Heijmans, M. M. P. D., Mauquoy, D., van Geel, B., and Berendse, F.: Long-term effects of climate change on vegetation and carbon dynamics in peat bogs, Journal of Vegetation Science, 19, 307-320, 2008.

Heijmans, M. M. P. D., van der Knaap, Y. A., Holmgren, M., and Limpens, J.: Persistent versus transient tree encroachment 10 of temperate peat bogs: effects of climate warming and drought events, Global change biology, 19, 2240-2250, 2013.

Heinen, M.: Simplified denitrification models: overview and properties, Geoderma, 133, 444-463, 2006.

Hinzman, L. D., Bettez, N. D., Bolton, W. R., Chapin, F. S., Dyurgerov, M. B., Fastie, C. L., Griffith, B., Hollister, R. D., Hope, A., Huntington, H. P., Jensen, A. M., Jia, G. J., Jorgenson, T., Kane, D. L., Klein, D. R., Kofinas, G., Lynch, A. H., Lloyd, A. H., McGuire, A. D., Nelson, F. E., Nolan, M., Oechel, W. C., Osterkamp, T. E., Racine, C. H., Romanovsky, V. 15 E., Stone, R. S., Stow, D. A., Sturm, M., Tweedie, C. E., Vourlitis, G. L., Walker, M. D., Walker, D. A., Webber, P. J., Welker, J. M., Winker, K. S., and Yoshikawa, K.: Evidence and implications of recent climate change in northern Alaska and other Arctic regions, Climatic Change, 72, 251–298, 2005.

Hobbie, S. E.: Temperature and plant species control over litter decomposition in Alaskan tundra, Ecological Monographs, 66, 503-522, 1996.

20 Hobbie, S. E., Shevtsova, A., and Chapin, F. S.: Plant responses to species removal and experimental warming in Alaskan tussock tundra, Oikos, 84, 417-434, 1999.

Hobbie, S. E., and Gough, L.: Litter decomposition in moist acidic and non-acidic tundra with different glacial histories, Oecologia, 140, 113-124, 2004.

Hudson, J. M., and Henry, G. H. R.: Increased plant biomass in a High Arctic heath community from 1981 to 2008, Ecology, 25 90, 2657-2663, 2009.

IPCC: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R. K. Pachauri and L. A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp, 2014.

Iversen, C. M., Sloan, V. L., Sullivan, P. F., Euskirchen, E. S., McGuire, A. D., Norby, R. J., Walker, A. P., Warren, J. M., and Wullschleger, S. D.: The unseen iceberg: plant roots in arctic tundra, New Phytologist, 205, 34-58, 2015.

Johannessen, O. M., Bengtsson, L., Miles, M. W., Kuzmina, S. I., Semenov, V. A., Alekseev, G. V., Nagurnyi, A. P., Zakharov, V. F., Bobylev, L. P., Pettersson, L. H., Hasselmann, K., and Cattle, H. P.: Arctic climate change: Observed and modelled temperature and sea-ice variability, Tellus A, 56, 328-341, 2004.

Jonasson, S.: Plant responses to fertilization and species removal in tundra related to community structure and clonality, Oikos, 63, 420-429, 1992.

Jorgenson, M. T., Racine, C. H., Walters, J. C., and Osterkamp, T. E.: Permafrost degradation and ecological changes associated with a warming climate in central Alaska, Climatic change, 48, 551-579, 2001.

Jorgenson, M. T., Shur, Y. L., and Pullman, E. R.: Abrupt increase in permafrost degradation in Arctic Alaska, Geophysical Research Letters, 33, doi: 10.1029/2005GL024960, 2006.

Klein Tank, A. M. G., Wijngaard, J. B., Können, G. P., Böhm, R., Demarée, G., Gocheva, A., Mileta, M., Pashiardis, S., Hejkrlik, L., Kern-Hansen, C., Heino, R., Bessemoulin, P., Müller- Westermeier, G., Tzanakou, M., Szalai, S., Pálsdóttir, T., Fitzgerald, D., Rubin, S., Capaldo, M., Maugeri, M., Leitass, A., Bukantis, A., Aberfeld, R., Van Engelen, A. F. V., Forland, E., Mietus, M., Coelho, F., Mares, C., Razuvaev, V., Nieplova, E., Cegnar, T., Antonio López, J., Dahlström, B., Moberg, A., Kirchhofer, W., Ceylan, A., Pachaliuk, O., Alexander, L. V., and Petrovic, P.: Daily dataset of 20th-century surface air temperature and precipitation series for the European Climate Assessment, International journal of climatology, 22, 1441-1453, 2002.

Lang, S. I., Cornelissen, J. H., Klahn, T., Van Logtestijn, R. S., Broekman, R., Schweikert, W., and Aerts, R.: An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species, Journal of Ecology, 97, 886-900, 2009.

Lawrence, D. M., and Slater, A. G.: A projection of severe near-surface permafrost degradation during the 21st century, Geophysical Research Letters, 32, doi: 10.1029/2005GL025080, 2005.

Li, S., Zhan, H., Lai, Y., Sun, Z., and Pei, W.: The coupled moisture-heat process of permafrost around a thermokarst pond in Qinghai-Tibet Plateau under global warming, Journal of Geophysical Research: Earth Surface, 119, 836-853, 2014.

Li, B., Heijmans, M. M. P. D., Berendse, F., Blok, D., Maximov, T. C., and Sass-Klaassen, U.: The role of summer precipitation and summer temperature in establishment and growth of dwarf shrub Betula nana in northeast Siberian tundra, Polar Biology, doi: 10.1007/s00300-015-1847-0, 2015.

Lundberg, A., and Beringer, J.: Albedo and snowmelt rates across a tundra-to-forest transition. In Proceedings of the 15 northern research basins international symposium and workshop, Department of Water Resources Engineering, Lund University, pp. 1-10, 2005.

MacDougall, A. H., Avis, C. A., and Weaver, A. J.: Significant contribution to climate warming from the permafrost carbon feedback, Nature Geoscience, 5, 719-721, 2012.

Mack, M. C., Schuur, E. A., Bret-Harte, M. S., Shaver, G. R., and Chapin, F. S.: Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization, Nature, 431, 440-443, 2004.

Marion, G. M., and Miller, P. C.: Nitrogen mineralization in a tussock tundra soil, Arctic and alpine research, 287-293, 1982.

McGuire, A. D., Anderson, L. G., Christensen, T. R., Dallimore, S., Guo, L., Hayes, D. J., Heimann, M., Lorenson, T. D., Macdonald, R. W., and Roulet, N.: Sensitivity of the carbon cycle in the Arctic to climate change, Ecological Monographs, 79, 523-555, 2009.

Murphy, M. T., McKinley, A., and Moore, T. R.: Variations in above-and below-ground vascular plant biomass and water table on a temperate ombrotrophic peatland, Botany, 87, 845-853, 2009.

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L. S., Weijers, S., Rozema, J., Rayback, S. A., Schmidt, N. M., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C. B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H. E., and Hik, D. S.: Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities, Environmental Research Letters, 6, doi: 10.1088/1748-9326/6/4/045509, 2011.

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S. A., Wilmking, M., Hallinger, M., Blok, D., Tape, K. D., Rayback, S. A., Macias-Fauria, M., Forbes, B. C., Speed, J. D. M., Boulanger-Lapointe, N., Rixen, C., Levesque, E., Schmidt, N. M., Baittinger, C., Trant, A. J., Hermanutz, L., Collier, L. S., Dawes, M. A., Lantz, T. C., Weijers, S., Jorgensen, R. H.,

Buchwal, A., Buras, A., Naito, A. T., Ravolainen, V., Schaepman-Strub, G., Wheeler, J. A., Wipf, S., Guay, K. C., Hik, D. S., and Vellend, M.: Climate sensitivity of shrub growth across the tundra biome, Nature Climate Change, 5, 887–91, 2015.

Nadelhoffer, K., Shaver, G., Fry, B., Giblin, A., Johnson, L., and McKane, R.: 15N natural abundances and N use by tundra plants, Oecologia, 107, 386-394, 1996.

5 Nauta, A. L., Heijmans, M. M. P. D., Blok, D., Limpens, J., Elberling, B., Gallagher, A., Li, B., Petrov, R. E., Maximov, T. C., van Huissteden, J., and Berendse, F.: Permafrost collapse after shrub removal shifts tundra ecosystem to a methane source. Nature Climate Change, 5, 67-70, 2015.

Osterkamp, T. E., Jorgenson, M. T., Schuur, E. A. G., Shur, Y. L., Kanevskiy, M. Z., Vogel, J. G., and Tumskoy, V. E.: Physical and ecological changes associated with warming permafrost and thermokarst in interior Alaska, Permafrost
10 Periglacial Process, 20, 235–256, 2009.

Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S., Damoulas, T., Knight, S. J., and Goetz, S. J.: Shifts in Arctic vegetation and associated feedbacks under climate change, Nature Climate Change, 3, 673-677, 2013.

Pettersson, R., McDonald, A. J. S., and Stadenberg, I.: Response of small birch plants (Betula pendula Roth.) to elevated CO_2 and nitrogen supply, Plant, Cell and Environment, 16, 1115-1121, 1993.

15 Riordan, B., Verbyla, D., and McGuire, A. D.: Shrinking ponds in subarctic Alaska based on 1950–2002 remotely sensed images, Journal of Geophysical Research: Biogeosciences, 111, doi: 10.1029/2005JG000150, 2006.

Saxton, K. E., and Rawls, W. J.: Soil water characteristic estimates by texture and organic matter for hydrologic solutions, Soil Science Society of America Journal, 70, 1569-1578, 2006.

Schuur, E., Bockheim, J., Canadell, J., Euskirchen, E., Field, C., Goryachkin, S., Hagemann, S., Kuhry, P., Lafleur, P., and
20 Lee, H.: Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle, BioScience, 58, 701-714, 2008.

Schuur, E. A. G., McGuire, A. D., Schädel, C., Grosse, G., Harden, J. W., Hayes, D. J., Hugelius, G., Koven, C. D., Kuhry, P., Lawrence, D. M., Natali, S. M., Olefeldt, D., Romanovsky, V. E., Schaefer, K., Turetsky, M. R., Treat, C. C., and Vonk, J. E.: Climate change and the permafrost carbon feedback, Nature, 520, 171-179, 2015.

25 Serreze, M. C., Walsh, J. E., Chapin, F. S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W. C., Morison, J., Zhang, T., and Barry, R. G.: Observational evidence of recent change in the northern high-latitude environment, Climatic Change, 46, 159-207, 2000.

Shaver, G. R., and Chapin, F. S.: Production: biomass relationships and element cycling in contrasting arctic vegetation types, Ecological Monographs, 61, 1-31, 1991.

Shaver, G. R., and Cutler, J. C.: The vertical distribution of live vascular phytomass in cottongrass tussock tundra, Arctic and Alpine research, 11, 335-342, 1979.

5   Shaver, G. R., Bret-Harte, M. S., Jones, M. H., Johnstone, J., Gough, L., Laundre, J., and Chapin, F. S.: Species composition interacts with fertilizer to control long-term change in tundra productivity, Ecology, 82, 3163-3181, 2001.

Sturm, M., Racine, C., and Tape, K.: Climate change: increasing shrub abundance in the Arctic, Nature, 411, 546-547, 2001.

Tape, K. E. N., Sturm, M., and Racine, C.: The evidence for shrub expansion in northern Alaska and the Pan-Arctic, Global Change Biology, 12, 686-702., 2006.

10   Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G., and Zimov, S.: Soil organic carbon pools in the northern circumpolar permafrost region, Global biogeochemical cycles, 23, 2009.

Turetsky, M. R., Wieder, R. K., and Vitt, D. H.: Boreal peatland C fluxes under varying permafrost regimes, Soil Biology and Biochemistry, 34, 907-912, 2002.

Urban, M., Forkel, M., Eberle, J., Hüttich, C., Schmullius, C., and Herold, M.: Pan-arctic climate and land cover trends
15   derived from multi-variate and multi-scale analyses (1981–2012), Remote Sensing, 6, 2296-2316, 2014.

van Huissteden, J., Berrittella, C., Parmentier, F. J. W., Mi, Y., Maximov, T. C., and Dolman, A. J.: Methane emissions from permafrost thaw lakes limited by lake drainage, Nature Climate Change, 1, 119-123, 2011.

van Huissteden, J., and Dolman, A. J.: Soil carbon in the Arctic and the permafrost carbon feedback, Current Opinion in Environmental Sustainability, 4, 545-551, 2012.

20   van Oene, H., Berendse, F., and de Kovel, C. G.: Model analysis of the effects of historic CO_2 levels and nitrogen inputs on vegetation succession, Ecological applications, 9, 920-935, 1999.

van Wijk, M. T.: Predicting ecosystem functioning from plant traits: results from a multi-scale ecophysiological modeling approach, Ecological modelling, 203, 453-463, 2007.

Vavrus, S. J., Holland, M. M., Jahn, A., Bailey, D. A., and Blazey, B. A.: Twenty-first-century Arctic climate change in
25   CCSM4, Journal of Climate, 25, 2696-2710, 2012.

Walker, D. A., Raynolds, M. K., Daniels, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., and Yurtsev, B. A.: The circumpolar Arctic vegetation map, Journal of Vegetation Science, 16, 267-282, 2005.

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H. E., Jonsdottir, I. S., Klein, J. A., Magnusson, B., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., Suding, K. N., Thompson, C. C., Tolvanen, A., Totland, O., Turner, P. L., Tweedie, C. E., Webber, P. J., and Wookey, P. A.: Plant community responses to experimental warming across the tundra biome, Proceedings of the National Academy of Sciences of the United States of America, 103, 1342-1346, 2006.

Walter, K. M., Zimov, S. A., Chanton, J. P., Verbyla, D., and Chapin, F. S.: Methane bubbling from Siberian thaw lakes as a positive feedback to climate warming, Nature, 443, 71-75, 2006.

Wang, P., Mommer, L., van Ruijven, J., Berendse, F., Maximov, T. C., and Heijmans, M. M. P. D.: Seasonal changes and vertical distribution of root standing biomass of graminoids and shrubs at a Siberian tundra site. Plant and Soil, in press DOI 10.1007/s11104-016-2858-5, 2016.

Wolf, A., Callaghan, T. V., and Larson, K.: Future changes in vegetation and ecosystem function of the Barents Region, Climatic change, 87, 51-73, 2008.

Yoshikawa, K., and Hinzman, L. D.: Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near Council, Alaska, Permafrost and Periglacial Processes, 14, 151-160, 2003.

Yu, Q., Epstein, H. E., Walker, D. A., Frost, G. V., and Forbes, B. C.: Modeling dynamics of tundra plant communities on the Yamal Peninsula, Russia, in response to climate change and grazing pressure, Environmental Research Letters, 6, doi: 10.1088/1748-9326/6/4/045505, 2011.

Zhang, T., Frauenfeld, O. W., Serreze, M. C., Etringer, A., Oelke, C., McCreight, J., Barry, R. G., Gilichinsky, D., Yang, D. Q., Ye, H. C., Ling, F., and Chudinova, S.: Spatial and temporal variability in active layer thickness over the Russian Arctic drainage basin, Journal of Geophysical Research: Atmospheres, 110, D16101, doi: 10.1029/2004JD005642, 2005.

Zhang, W., Miller, P. A., Smith, B., Wania, R., Koenigk, T., and Döscher, R.: Tundra shrubification and tree-line advance amplify arctic climate warming: results from an individual-based dynamic vegetation model, Environmental Research Letters, 8, 2013.

Zheng, D., Hunt Jr, E. R., and Running, S. W.: A daily soil temperature model based on air temperature and precipitation for continental applications, Climate Research, 2, 183-191, 1993.

Zimov, S. A., Davydov, S. P., Zimova, G. M., Davydova, A. I., Schuur, E. A. G., Dutta, K., and Chapin, F. S.: Permafrost carbon: Stock and decomposability of a globally significant carbon pool, Geophysical Research Letters, 33, doi: 5 10.1029/2006GL027484, 2006a.

Zimov, S. A., Schuur, E. A., and Chapin, F. S.: Permafrost and the global carbon budget, Science, 312, 1612-1613, 2006b.

Zotarelli, L., Dukes, M. D., and Morgan, K. T.: Interpretation of soil moisture content to determine soil field capacity and avoid over-irrigating sandy soils using soil moisture sensors, 2010.
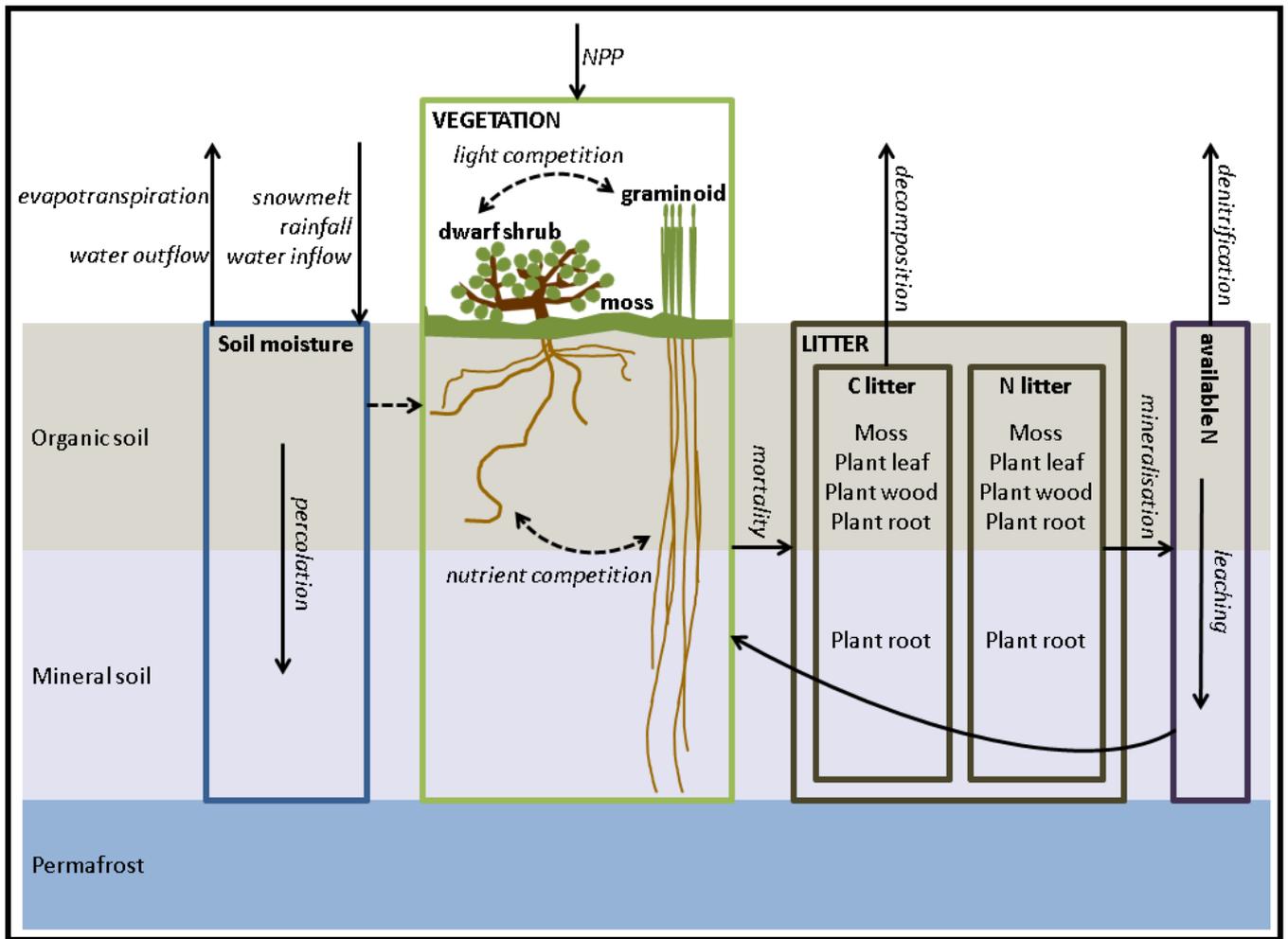
Figure 1. Schematic presentation of NUCOM-tundra, including the main processes simulated in organic and mineral soil layers and the effects of moisture and available nitrogen on vegetation. Air temperature influences many of these processes, including active layer depth, plant growth, evapotranspiration, snowmelt, decomposition, mineralisation and denitrification. The mineral soil is divided into 10 layers of 10 cm height each.
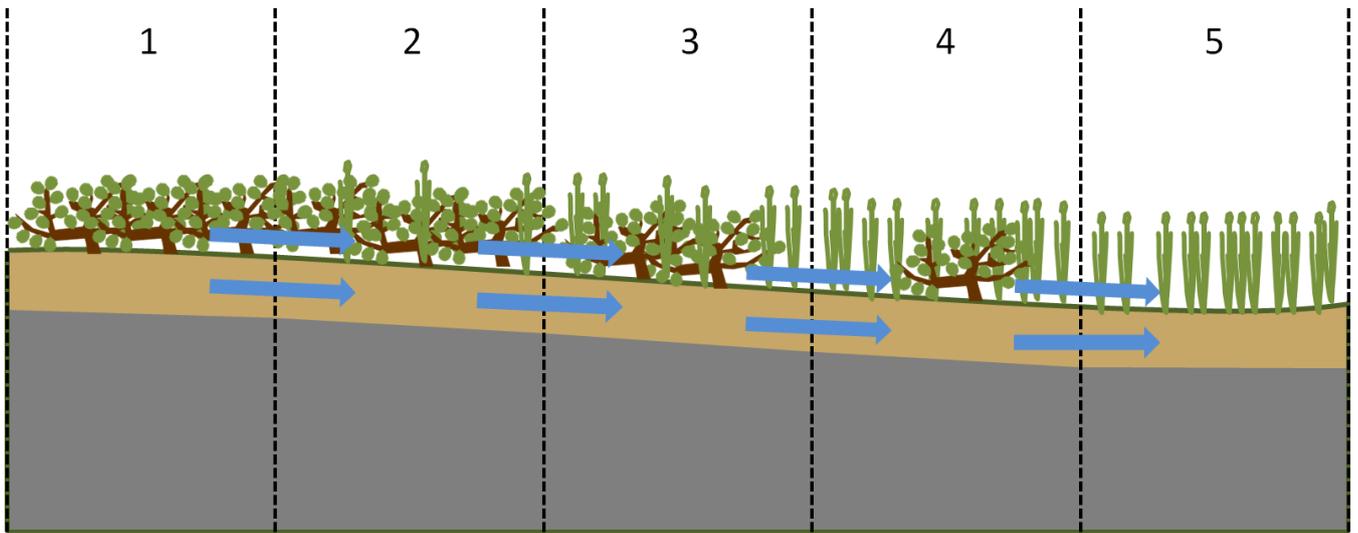
Figure 2. Vegetation types used in simulations of NUCOM-tundra. The vegetation types represent landscape positions, ranging from relatively dry shrub dominated to wet graminoid dominated vegetation. Blue arrows indicate water flows.
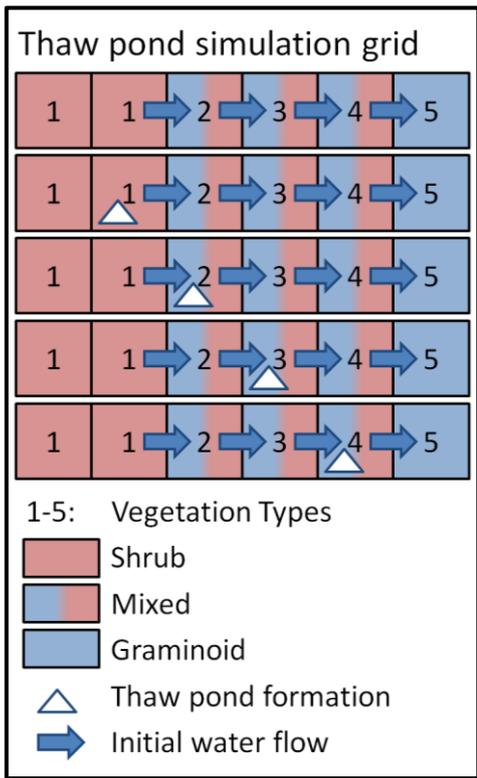
Figure 3. Simulation grid used to simulate thaw pond initiation in four different vegetation types. Water flows at the start of the simulation are as indicated in the diagram. After the local permafrost collapse the water flow from the cell with the thaw pond formation to the following downslope cell is stopped (see Figure 6 for the consequences).
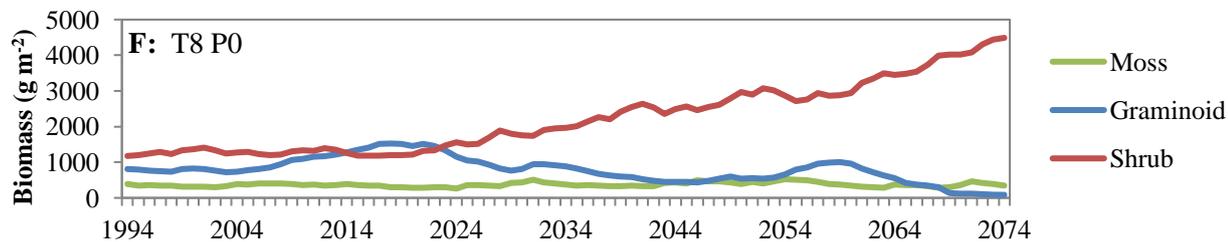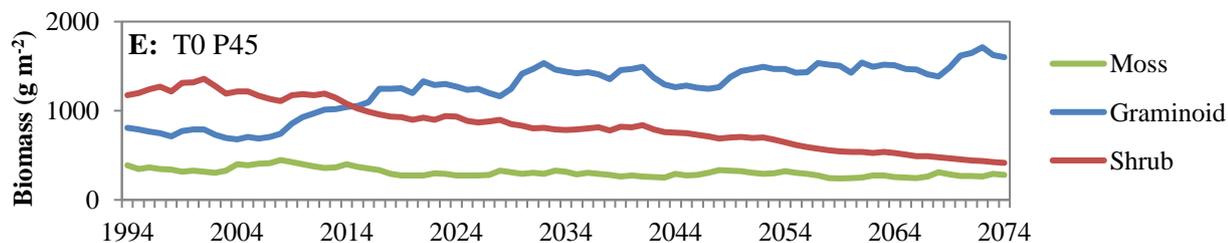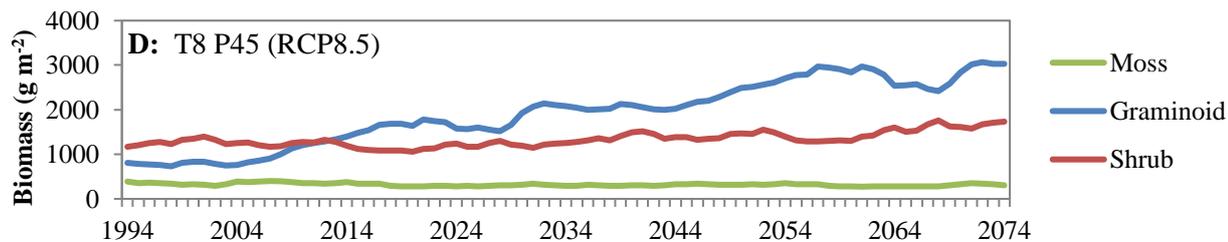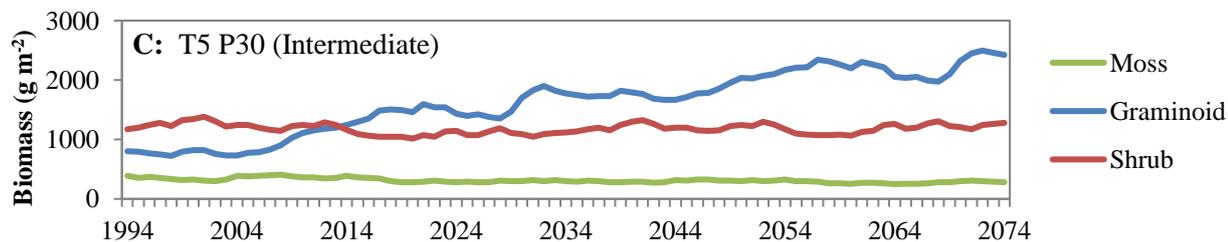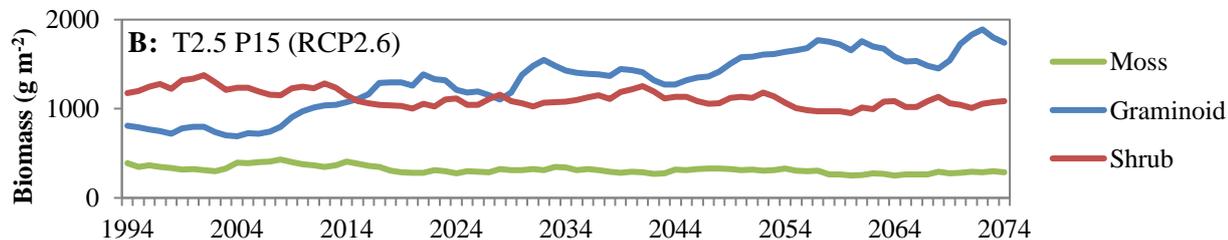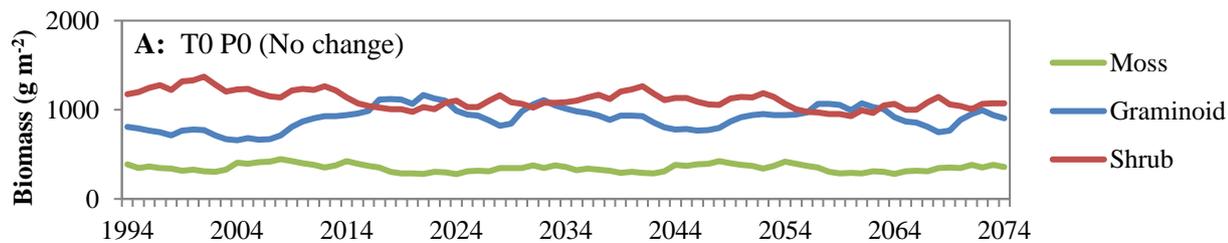
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Figure 4. Simulated summer biomass of moss, graminoids and dwarf shrubs between 1994 and 2074 under different temperature (T, ^{0}C) and precipitation (P, mm year^{-1}) change scenarios over the 21st century.
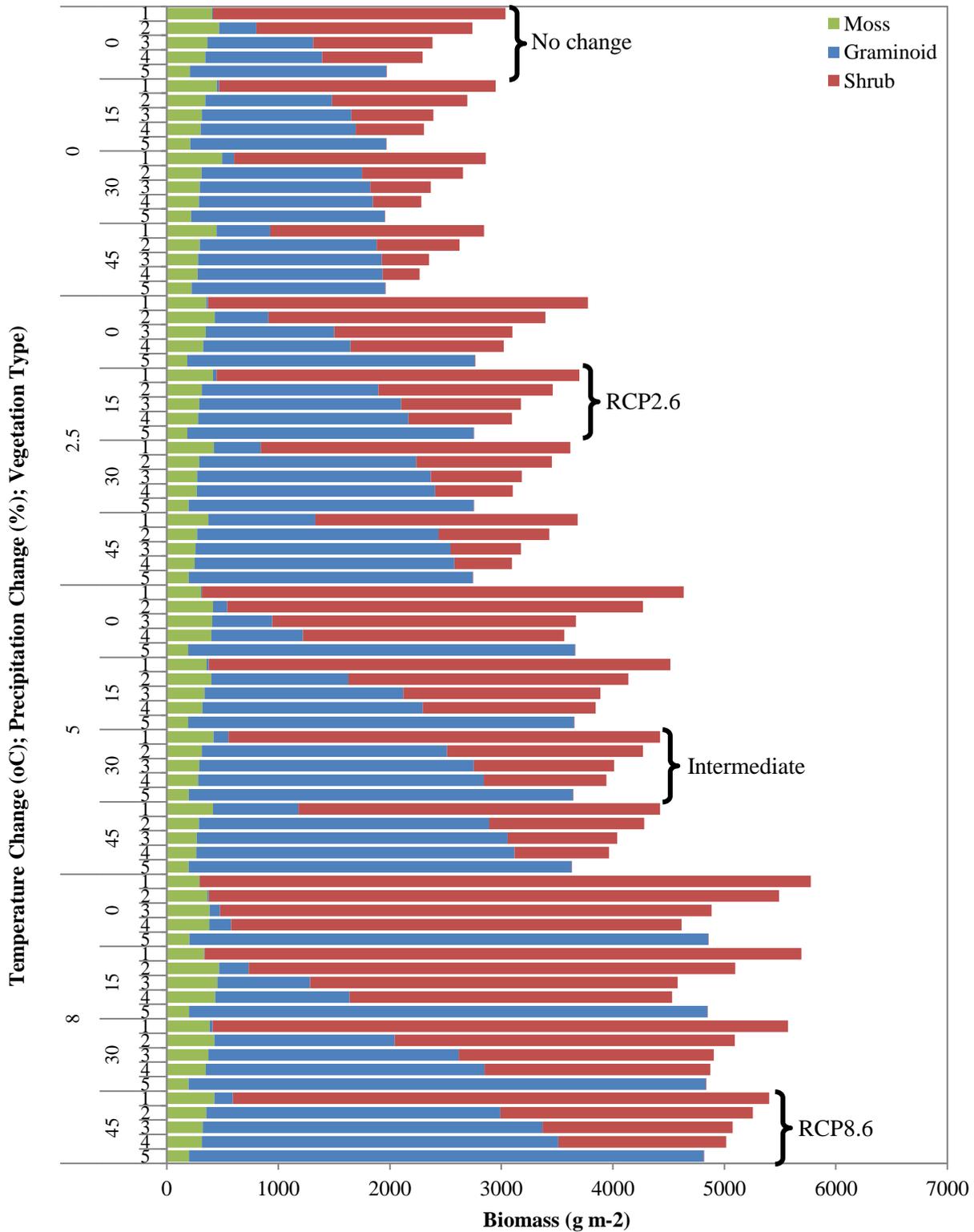
Figure 5. Simulated summer biomass of moss, graminoids and shrubs averaged over 2065-2074 for sixteen climate scenario simulations in five vegetation types representing a gradient from relatively dry to wet conditions. Temperature and precipitation changes were based on 21st century RCP climate change scenarios. Biomass is total biomass (above and belowground).

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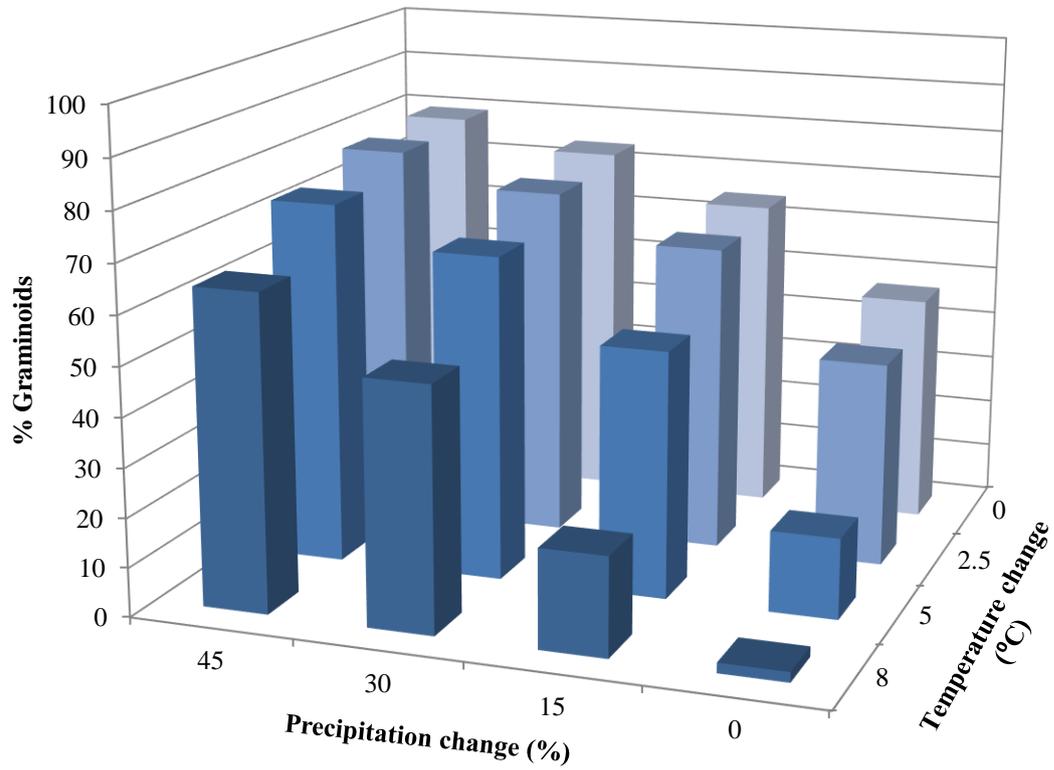
Figure 6. Percentage of graminoid biomass in the vascular plant community biomass, averaged over ~~2064~~2065-2074, for vegetation type 3 (initial mixed moist vegetation) for sixteen temperature and precipitation scenarios for the 21st century.
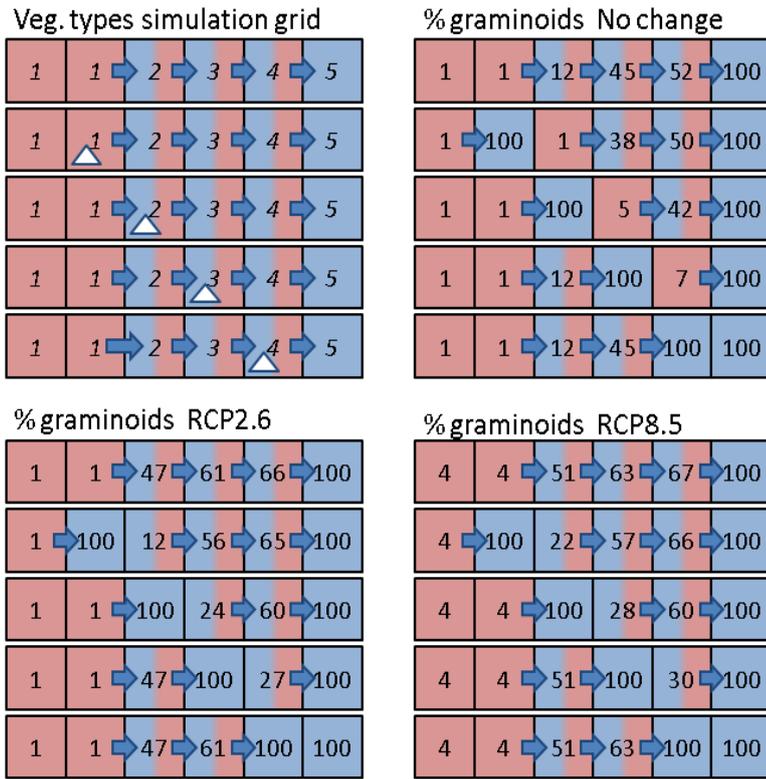
Figure 7. Results of thaw pond simulations: simulation settings are in the top left, in which vegetation types (numbers), initial water flows (arrows) and permafrost collapse sites are indicated. The other grids show the percentage of graminoids in total vascular plant biomass during the summers of 2065-2074 and the altered water flows for No change, RCP2.6 and RCP8.5 climate scenarios. Red cells indicate shrub dominated, blue graminoid dominated and both blue and red mixed vegetation.
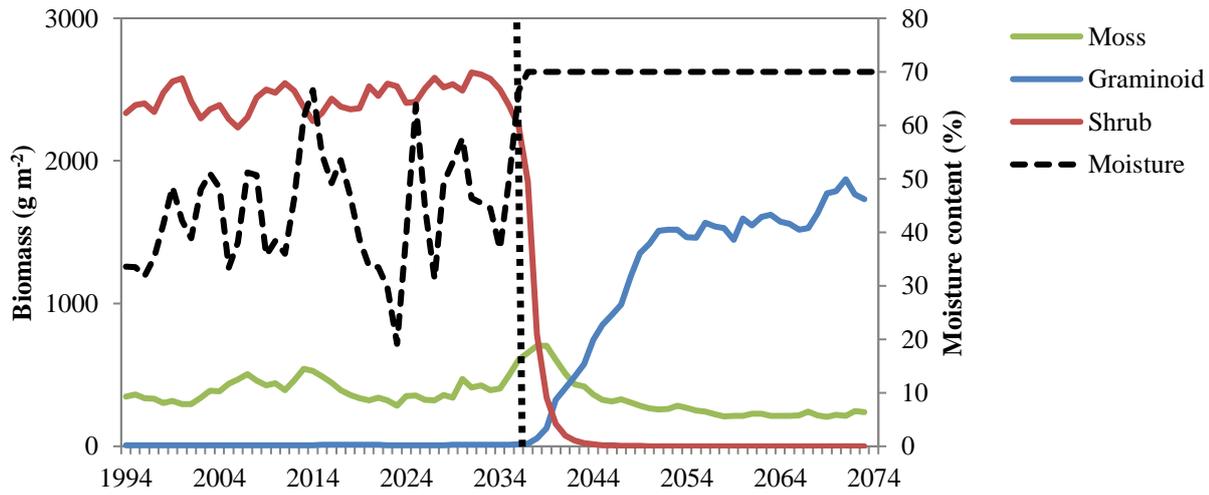
Figure 8. Biomass of moss, graminoids and shrubs and organic layer moisture content during a thaw pond formation simulation in an initially dry shrub dominated vegetation type (vegetation type 1) under the No change scenario. The ~~interrupted~~ dotted line indicates the moment of ice wedge collapse.

5

Table 1. Simulated growth-limiting factors for the vascular plant PFTs in vegetation type 3 under different climate change scenarios. Growing season length, soil moisture and light, moisture and nutrient conditions, all during the growing season, were averaged for years 2064 – 1974.

				Graminoids			Shrubs		
T change[a] (°C)	P change[a] (mm year⁻¹)	Growing Season Length[b] (days)	Soil Moisture (vol. %)	Light[c] (%)	Moisture[d] (%)	Nutrients[e] (%)	Light[c] (%)	Moisture[d] (%)	Nutrients[e] (%)
0~~0~~	0~~0~~	101~~101~~	62.1~~57.8~~	4.9~~7.2~~	78.0~~79.4~~	89.3~~84.3~~	8.6~~15.7~~	49.5~~48.6~~	40.2~~41.6~~
0~~0~~	15~~15~~	101~~101~~	63.8~~59.2~~	7.8~~10.3~~	82.5~~82.6~~	87.4~~80.9~~	4.1~~11.2~~	42.7~~45.5~~	41.1~~44.9~~
0~~0~~	30~~30~~	101~~101~~	64.9~~60.2~~	9.3~~12.3~~	86.1~~84.4~~	86.3~~79.3~~	1.7~~8.1~~	36.0~~41.7~~	41.3~~46.6~~
0~~0~~	45~~45~~	101~~101~~	65.7~~61.1~~	10.1~~13.9~~	87.8~~85.9~~	85.4~~78.2~~	0.6~~5.4~~	32.6~~38.2~~	41.6~~49.3~~
2.5~~2.5~~	0~~0~~	115~~115~~	58.3~~52.8~~	5.0~~6.5~~	66.8~~68.6~~	87.1~~83.2~~	14.7~~28.5~~	63.7~~61.5~~	37.4~~33.1~~
2.5~~2.5~~	15~~15~~	115~~115~~	61.5~~55.9~~	9.8~~11.7~~	73.7~~73.7~~	84.0~~77.2~~	7.9~~20.6~~	49.5~~52.2~~	39.1~~36.6~~
2.5~~2.5~~	30~~30~~	115~~115~~	62.9~~57.2~~	11.8~~15.1~~	77.5~~75.4~~	82.3~~74.2~~	4.9~~15.7~~	45.1~~48.6~~	40.0~~38.7~~
2.5~~2.5~~	45~~45~~	115~~115~~	64.0~~58.1~~	13.3~~17.1~~	81.1~~77.9~~	81.1~~72.7~~	2.7~~13.0~~	39.2~~46.4~~	40.6~~40.3~~
5~~5~~	0~~0~~	128~~128~~	52.8~~46.1~~	0.6~~0.6~~	45.7~~47.1~~	86.9~~100~~	25.8~~47.1~~	70.7~~69.4~~	36.1~~33.5~~
5~~5~~	15~~15~~	128~~128~~	58.6~~49.8~~	7.7~~5.9~~	67.4~~59.3~~	83.9~~87.1~~	15.6~~37.9~~	61.1~~66.1~~	36.5~~32.1~~
5~~5~~	30~~30~~	128~~128~~	61.3~~53.4~~	12.6~~11.1~~	73.4~~69.4~~	81.1~~79.7~~	9.3~~30.7~~	49.1~~58.5~~	38.1~~33.4~~
5~~5~~	45~~45~~	128~~128~~	62.7~~55.6~~	14.8~~16.6~~	75.1~~72.9~~	79.4~~74.9~~	6.3~~23.4~~	44.7~~51.6~~	39.0~~35.9~~
8~~8~~	0~~0~~	140~~140~~	45.6~~40.1~~	0.0~~0.1~~	38.9~~39.7~~	89.1~~100~~	33.7~~61.4~~	77.5~~70.4~~	36.5~~36.7~~
8~~8~~	15~~15~~	140~~140~~	53.2~~43.9~~	1.4~~0.2~~	47.0~~43.4~~	86.0~~100~~	28.0~~58.2~~	69.5~~64.2~~	35.8~~36.8~~
8~~8~~	30~~30~~	140~~140~~	58.3~~46.9~~	8.7~~2.6~~	66.5~~50.9~~	82.8~~95.6~~	18.9~~51.3~~	60.7~~67.0~~	36.0~~33.8~~
8~~8~~	45~~45~~	140~~140~~	60.9~~50.6~~	13.7~~9.3~~	72.3~~62.2~~	80.1~~83.9~~	12.9~~42.4~~	49.3~~64.9~~	37.3~~32.9~~

5

a) Temperature and Precipitation change scenario over the 21st century

b) Growing season length is defined as the number of days with mean temperature above 0 °C

c) Percentage of incoming light absorbed during the growing season

10 d) Percentage of time at which soil moisture conditions were optimal for growth during the growing season (100% = optimal soil moisture conditions during the whole growing season)

e) Percentage of realised potential growth (100% = no nutrient limitation)

Table A1. Plant Functional Type parameter values in NUCOM-tundra.

Parameter	Description	Unit	Moss	Gram.	Shrub	Source
BD_m	bulk density moss	$g\ m^{-3}$	15660			Heijmans et al., 2004
maxheight	max. height of moss layer	m	0.045			Blok et al., 2010
minheight	min. height of moss layer	m	0.005			
minleafarea	minimum leaf area	$m^2 m^{-2}$		0.001	0.001	
Kext	light extinction coefficient	-		0.5	0.6	Heijmans et al., 2008 (Gram.)
SLA	Specific Leaf Area	$m^2 g^{-1}$		0.0060	0.0139	Shaver & Chapin, 1991
B	rooting depth coefficient	-		0.938	0.850	Murphy et al., 2009 (Gram.); van Wijk, 2007 (Shrub)
SRL	specific root length	$m\ g^{-1}$		37.5	141.0	Eissenstat et al., 2000 (Gram.); Pettersson et al., 1993 (Shrub)
Gmax	maximum growth	$g\ m^{-2}\ day^{-1}$	12.0	29.0	32.5	calibrated
seedbiom	daily seed biomass input	$g\ m^{-2}\ day^{-1}$	0.000033	0.000033	0.000033	
w_{min}	min. vol. soil water content for growth	%	20	20	0	
w_{low}	lowest vol. soil water content for optimal growth	%	40	40	10	
w_{high}	highest vol. soil water content for optimal growth	%	70	70	65	
w_{max}	max. vol. soil water content for growth	%	70	70	70	
T_{min}	minimum air T for growth	^oC	0	1	1	
T_{low}	lowest air T for optimal growth	^oC	3	4	4	
N_{min}	min. N concentration for growth	$g\ N\ g^{-1}$	0.0102	0.0122	0.0172	Hobbie, 1996
N_{max}	max. N concentration for N uptake	$g\ N\ g^{-1}$	0.0184	0.0352	0.0278	Hobbie, 1996
Kallor	Allocation of growth to fine roots	-		0.30	0.33	calibrated (Gram.); Shaver and Chapin, 1991 (Shrub)
Kallos	allocation growth towards stems	-		0.24	0.14	calibrated (Gram.); Shaver and Chapin, 1991 (Shrub)
Kallol	allocation growth towards leaves	-		0.46	0.53	calibrated (Gram.); Shaver and Chapin, 1991 (Shrub)
Krear	reallocation of N in roots to storage	-		0.30	0.10	Heijmans et al., 2008
Kreas	reallocation of N stems to storage	-		0	0	Heijmans et al., 2008
Kreal	reallocation of N leaf to storage	-		0.34	0.25	Chapin et al., 1975 (Graminoid)
$mort_{moss}$	mortality moss	day^{-1}	0.000914			Chapin et al., 1996
$mort_r$	mortality root	day^{-1}		0.000825	0.001015	calibrated
$mort_s$	mortality stems	day^{-1}		0.000232	0.000067	calibrated
$mort_l$	mortality leaf	day^{-1}		0.007315	0.010790	calibrated
$maxmort_s$	maximum mortality stems	day^{-1}		0.002500	0.002500	
kdec_m	decomposition moss litter	day^{-1}	0.001560			Lang et al., 2009
kdec_r	decomposition root litter	day^{-1}		0.001691	0.000946	Heal and French , 1974
kdec_s	decomposition stems litter	day^{-1}		0.000758	0.001256	Heal and French , 1974
kdec_l	decomposition leaf litter	day^{-1}		0.001564	0.002167	Hobbie and Gough, 2004

Table A2. Parameter values related to the soil profile, microbial processes and hydrology in NUCOM-tundra.

Parameter	Description	Unit	Value	Source
maxlayer	number of mineral layers	-	10	
layerdepth	thickness of mineral layer	m	0.10	
BD_{org}	organic matter density	$g\ m^{-3}$	150000	Marion and Miller, 1982
Nfixation_m	nitrogen fixation rate (by moss)	$g\ N\ day^{-1}$	0.00025	
Ndeposition	nitrogen deposition rate	$g\ N\ day^{-1}$	0.00027	
NCcrit	critical N:C ratio for mineralization	$g\ N\ g\ C^{-1}$	0.008	
e^{asseff}	microbial assimilation efficiency	-	0.2	Heijmans et al., 2008
α	optimal denitrification rate	day^{-1}	0.1	Heinen, 2006
S_{tres}	minimum fraction of water filled pores for denitrification		0.9	
S_{max}	fraction of water filled pores for max. denitrification		1	
Q_{10}	denitrification increase factor with 10°C increase		2	Heinen, 2006
T_{ref}	reference temperature (for denitrification)	^oC	20	Heinen, 2006
DDF	Degree Day Factor for snowmelt	$mm\ ^oC^{-1}\ day^{-1}$	5.3	Lundberg & Beringer, 2005
$FieldCap_{org}$	vol. water content at field capacity in organic layer	$mm\ mm^{-1}$	0.36	Zotarelli et al., 2010
$MaxCap_{org}$	max. vol. water content in organic layer (saturation)	$mm\ mm^{-1}$	0.70	
$FieldCap_{min}$	vol. water content at field capacity in mineral layer	$mm\ mm^{-1}$	0.42	Saxton and Rawls, 2006
$MaxCap_{min}$	max. vol. water content in mineral layer (saturation)	$mm\ mm^{-1}$	0.50	Saxton and Rawls, 2006
runoffr	surface water runoff	day^{-1}	0.10	
interflowr	Lateral drainage of water through organic layer	day^{-1}	0.01	
evaporation	fraction evaporation of total evapotranspiration	-	0.5	
evapodepth	Soil depth over which evaporation occurs	cm	10	
wheight	height of the upper soil layer for moisture calculation	cm	10	
leachr	fixed nitrogen leach rate to deeper soil layer	day^{-1}	0.00163	
$leachr_{max}$	maximum nitrogen leach rate	day^{-1}	0.00747	