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

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Abstract. Over the past decades, vegetation and climate have changed significantly 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 factors drive vegetation changes in the tundra ecosystem are still not sufficiently clear. In this study, the dynamic tundra vegetation model, NUCOM-tundra (NUTrient and COMpetition), was used to evaluate the consequences of climate change scenarios of warming and increasing precipitation for future tundra vegetation change. 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 16 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 were 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 increases in biomass of both graminoids and shrubs, with graminoids increasing in abundance. The simulations suggest that shrub

growth can be limited by very wet soil conditions and low nutrient supply, whereas graminoids have the advantage of being able to grow in a wide range of soil moisture conditions and have 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

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 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 CO₂ and CH₄ to the atmosphere (Dutta et al., 2006; McGuire et al., 2009). An increase in greenhouse gas release, including CO₂ and CH₄ (Christensen et al., 2004; Walter et al., 2006; Nauta et al., 2015; Schuur et al., 2015), from thawing permafrost 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 extremely low summer temperatures. Southwards, with increasing summer temperatures, graminoids 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 in 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 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; El-mendorf et al., 2012). However, besides climate, other factors such as herbivory, soil moisture and soil nutrient availability affect shrub growth as well, and it is therefore complex predicting the expansion of shrubs in the Arctic region (Myers-Smith et al., 2011, 2015). Increased abundance of shrubs might have important consequences for permafrost feedbacks. For example, an increase in 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 colonised 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, 2006; Turetsky et al., 2002; Christensen et al., 2004; 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 as a consequence drastically alter hydrological and soil processes, as well as in adjacent areas (Osterkamp et al., 2009; Nauta et al., 2015; Schuur et al., 2015).

The 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, b; 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 composition, and (2) explore the impacts of thaw pond formation due to local permafrost collapse.

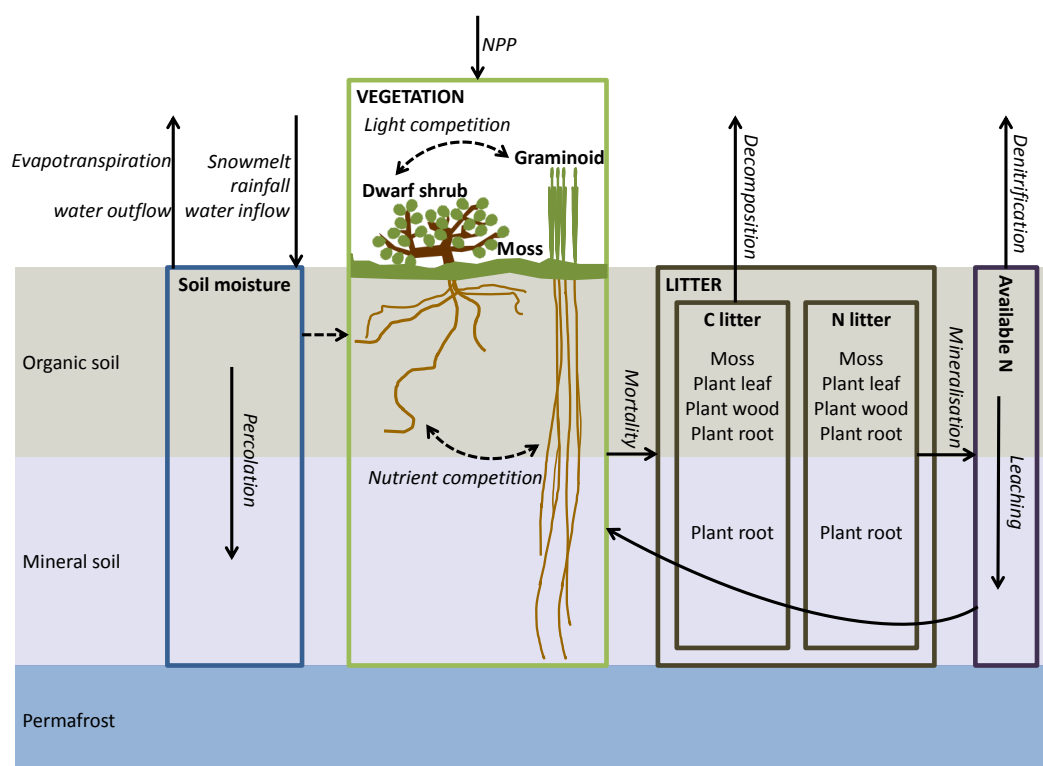


Figure 1. Schematic presentation of NUCOM-tundra, including the main processes simulated in organic and mineral soil layers and the effects of moisture and available nitrogen on vegetation. Air temperature influences many of these processes, including active layer depth, plant growth, evapotranspiration, snowmelt, decomposition, mineralisation and denitrification. The mineral soil is divided into 10 layers, each 10 cm in height.

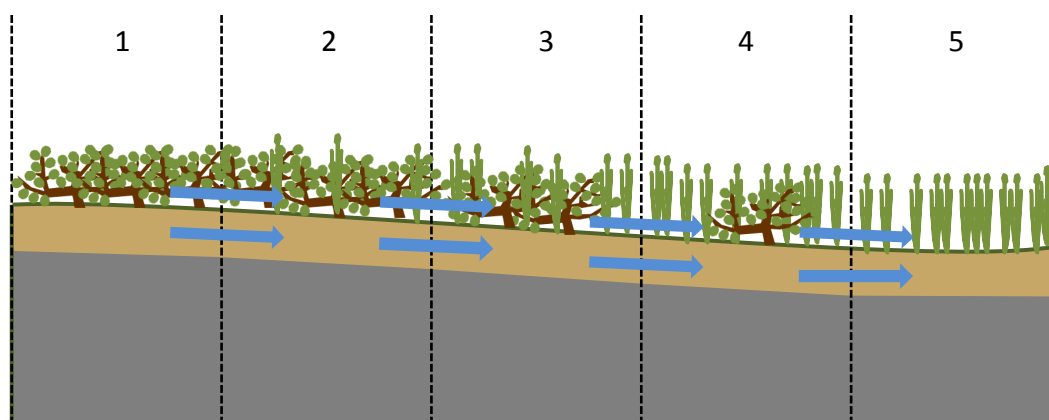


Figure 2. Vegetation types used in simulations of NUCOM-tundra. The vegetation types represent landscape positions, ranging from relatively dry shrub-dominated (1) to wet graminoid-dominated (5) vegetation. Blue arrows indicate water flows.

2 Methods

2.1 Brief model description

NUCOM-tundra has been developed to simulate long-term dynamics of vegetation composition in tundra landscapes for analysis of vegetation–permafrost–carbon feedbacks in rela-

tion 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 the Supplement, Sect. S1.

NUCOM-tundra simulates the dynamics of three plant functional types (PFTs), moss, graminoids (e.g. *Eriophorum vaginatum*) and deciduous dwarf shrubs (e.g. *Betula nana*),

on a local scale and in 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 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 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 (Sect. 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 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 (Sect. S1). In the model, there are temperature thresholds for plant growth thus excluding growth 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 centimetre 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 is filled by reallocated nitrogen 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. Part of the pool

of available nitrogen can be lost by denitrification under high soil moisture conditions (Sect. S1).

A simple hydrological module is included in NUCOM-tundra, which simulates the volumetric water content of the organic and mineral soil layers (Sect. 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 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 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 10 m (Sect. 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 the Circumpolar Arctic Vegetation Map; Walker et al., 2005). The parameter values are provided in 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 m) 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 Sect. S3. The biomass start values were based on field measurements at the Chokurdakh Scientific 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 characterised 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 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 the comparison of 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 Sect. S4.

2.5 Climate scenario simulations

For all vegetation types, a period of 40 years was simulated to initialise the model using precipitation and temperature data from the Chokurdakh weather station from 1 August 1954 to 31 July 1994 as input. This period excludes the most pronounced warming that took place over the last few decades. Annual precipitation was, however, variable with both increasing and declining trends in the 40-year time period (Sect. 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 °C and precipitation changes of 0, 15, 30 or 45 % increase over 100 years. In the Arctic region, increases of 2.5 °C and 15 % precipitation are expected under emission scenario

Thaw pond simulation grid

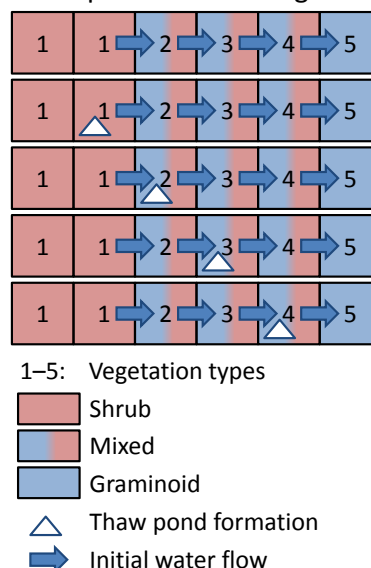


Figure 3. Simulation grid used to simulate thaw pond initiation in the vegetation types 1–4. Water flows at the start of the simulation are as indicated in the diagram. After the local permafrost collapse, the water flow from the cell with the thaw pond formation to the following downslope cell is stopped (see Fig. 8 for the consequences).

RCP2.6 and increases of 8 °C and 45 % precipitation are expected over the 21st century under emission scenario RCP8.5 (IPCC, 2014). A scenario with 5 °C increase and 30 % precipitation increase 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 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 is the average number of days per year at which the temperature threshold for vascular plant growth was exceeded.

2. Soil moisture is the average soil moisture content in the upper 10 cm of the soil profile during the growing season.
3. Light competition is the average percentage of light intercepted by graminoids and shrubs during the growing season.
4. Moisture conditions are the percentage of time in the growing season with optimal soil moisture content for growth of graminoids and dwarf shrubs.
5. Nutrient limitation is the limitation of the growth of graminoids and dwarf shrubs due to insufficient availability of nutrients in the growing season, expressed as the percentage of potential growth realised.

2.6 Thaw pond simulations

Thaw pond initiation was simulated for dry and moist 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 through 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 Sect. S4). Simulated timing of accumulation and melt of the snow layer between 1944 and 2008 was in agreement with observations of snow depth at the Chokurdakh weather station. Simulated shallow soil temperatures were in agreement with observations from the Kytalyk meteorological 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). This deeper active layer thickness resulted in an overestimation of graminoid biomass, as was

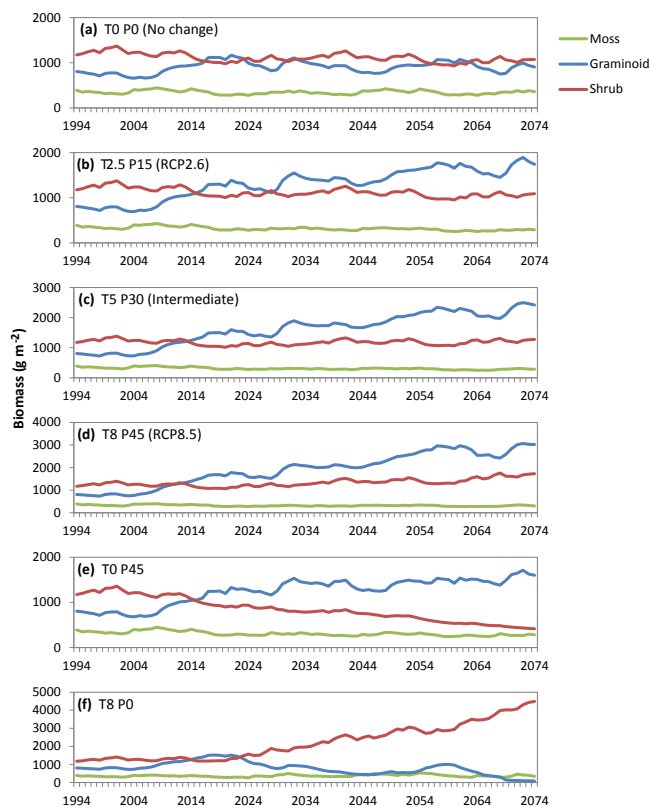


Figure 4. Simulated summer biomass of moss, graminoids and dwarf shrubs between 1994 and 2074 under different temperature (T , °C increase) and precipitation (P , % increase) change scenarios over the 21st century.

demonstrated by simulations with lowered active layer thickness (Fig. S4.3 in the Supplement). 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 did 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.

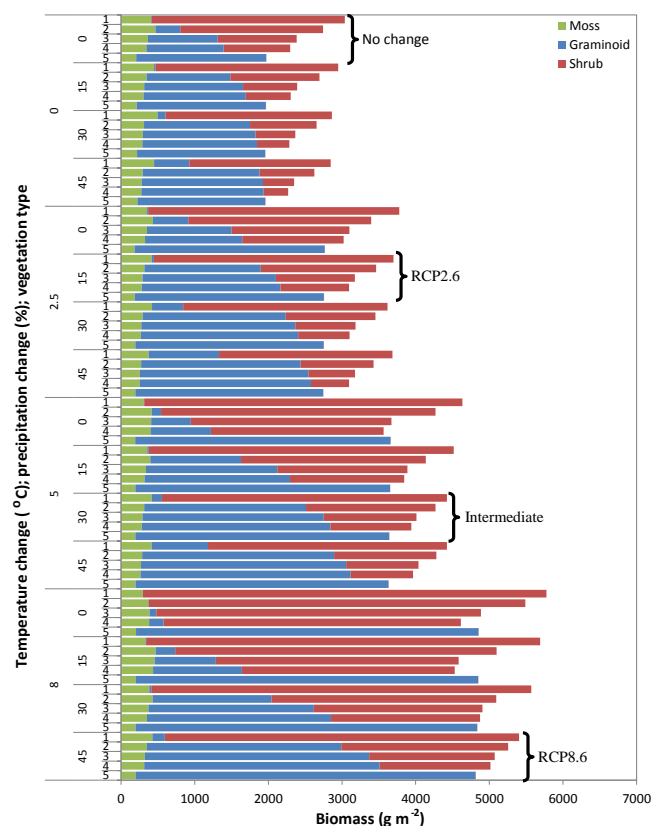


Figure 5. Simulated summer biomass of moss, graminoids and shrubs averaged over 2065–2074 for 16 climate scenario simulations in five vegetation types representing a gradient from relatively dry to wet conditions. Temperature and precipitation changes were based on 21st century RCP climate change scenarios. Biomass is total biomass (above and belowground).

3.2 Climate scenario simulations: vegetation changes

In the “No 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–d). Considering all combinations of temperature and precipitation scenarios in all vegetation types, 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 1970 to 3037 g m⁻² with no temperature change, whereas total biomass ranged between 4815 and 5402 g m⁻² with a gradual increase of 8 °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 (type 1) and wet graminoid-dominated vegetation (type 5) did not change under any of the climate change scenarios (Fig. 5). In mixed vegeta-

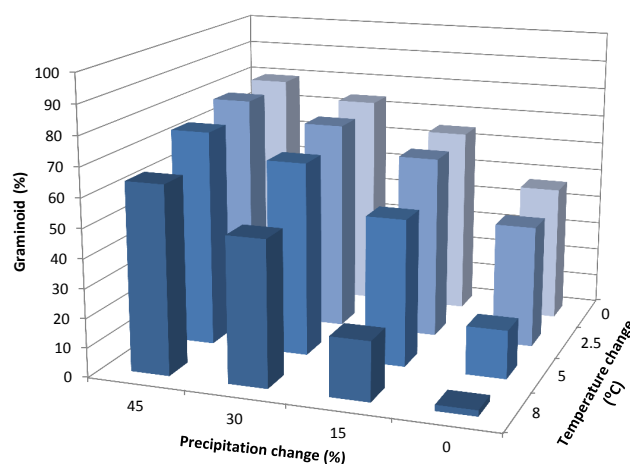


Figure 6. Percentage of graminoid biomass in the vascular plant community biomass, averaged over 2065–2074, for vegetation type 3 (initial moist mixed vegetation) for 16 temperature and precipitation scenarios in the 21st century.

tion (type 3), graminoids increased in abundance with the RCP2.6 scenario (2.5 °C temperature and 15 % precipitation increases over the 21st century), “Intermediate” and RCP8.5 scenario (8 °C temperature and 45 % precipitation increases over the 21st century; Figs. 4b–d, 6). 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 (Figs. 4e, 6). In contrast, graminoids were outcompeted by shrubs by the end of simulations of initially mixed vegetation sites under a scenario with 8 °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 (Figs. 4, 5).

3.3 Nutrient availability, light competition and moisture conditions

In comparison to the “No change” scenario, the growing season was on average 39 days longer in the years 2065–2074 in simulations with an 8 °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, “In-

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

<i>T</i> change ^a (°C)	<i>P</i> change ^a (%)	Growing season length ^b (days)	Soil moisture (vol. %)	Graminoids			Shrubs		
				Light ^c (%)	Moisture ^d (%)	Nutrients ^e (%)	Light ^c (%)	Moisture ^d (%)	Nutrients ^e (%)
0	0	101	62.1	4.9	78.0	89.3	8.6	49.5	40.2
0	15	101	63.8	7.8	82.5	87.4	4.1	42.7	41.1
0	30	101	64.9	9.3	86.1	86.3	1.7	36.0	41.3
0	45	101	65.7	10.1	87.8	85.4	0.6	32.6	41.6
2.5	0	115	58.3	5.0	66.8	87.1	14.7	63.7	37.4
2.5	15	115	61.5	9.8	73.7	84.0	7.9	49.5	39.1
2.5	30	115	62.9	11.8	77.5	82.3	4.9	45.1	40.0
2.5	45	115	64.0	13.3	81.1	81.1	2.7	39.2	40.6
5	0	128	52.8	0.6	45.7	86.9	25.8	70.7	36.1
5	15	128	58.6	7.7	67.4	83.9	15.6	61.1	36.5
5	30	128	61.3	12.6	73.4	81.1	9.3	49.1	38.1
5	45	128	62.7	14.8	75.1	79.4	6.3	44.7	39.0
8	0	140	45.6	0.0	38.9	89.1	33.7	77.5	36.5
8	15	140	53.2	1.4	47.0	86.0	28.0	69.5	35.8
8	30	140	58.3	8.7	66.5	82.8	18.9	60.7	36.0
8	45	140	60.9	13.7	72.3	80.1	12.9	49.3	37.3

^a Temperature (*T*) and precipitation (*P*) change scenarios 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. ^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).

termediate” and RCP8.5 scenario, moisture conditions became slightly less favourable for graminoid growth and remained unchanged for shrub growth in comparison to the “No change” scenario.

In general, shrubs were able to intercept 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 °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 (Figs. 7, 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 stabilised 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 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.

4 Discussion

The effects of climate change on tundra vegetation are complex since temperature and precipitation drive changes in hydrology, active layer depths, nutrient availability and growing season length, which interact with each other (Serreze et al., 2000; Hinzman et al., 2005). NUCOM-tundra has been developed to explore future changes in the Arctic tundra vegetation composition in response to climate scenarios, thereby taking changes in soil moisture, thawing depth and nutrient availability into account.

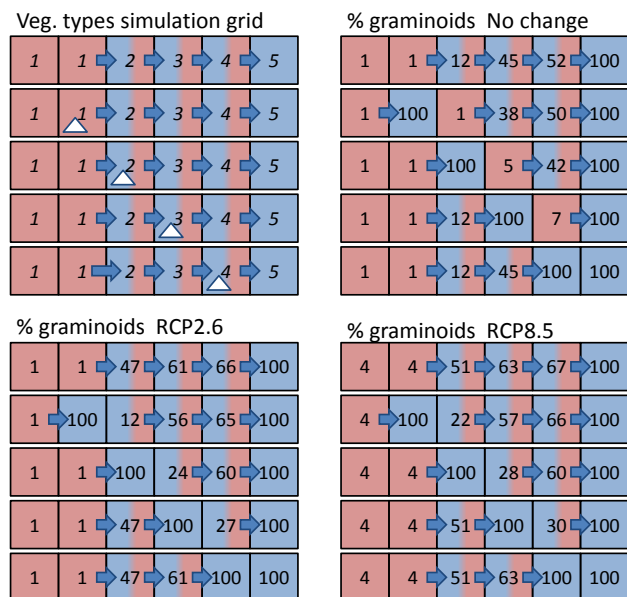


Figure 7. Results of thaw pond simulations: simulation settings (top left panel) in which vegetation types (numbers), initial water flows (arrows) and permafrost collapse sites are indicated. The other grids show the percentage of graminoids in total vascular plant biomass during the summers of 2065–2074 and the altered water flows for “No change”, RCP2.6 and RCP8.5 climate scenarios. Red cells: shrub-dominated, blue cells: graminoid-dominated, both blue and red cells: mixed vegetation.

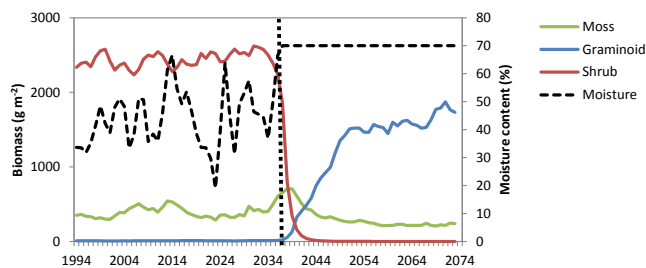


Figure 8. Biomass of moss, graminoids and shrubs and organic layer moisture content during the thaw pond formation simulation in an initially dry shrub-dominated vegetation type (1) under the “No change” scenario. The dotted line indicates the moment of ice wedge collapse.

4.1 Effects of increases in temperature and precipitation

Our climate scenario simulations suggest a significant increase in biomass with continuing climate change, and especially, increased graminoid abundance under scenarios with different magnitudes of climate change. For modest and strong emission scenarios (“Intermediate” and RCP8.5), both shrub and graminoid biomass increased. These simulations are in line with biomass increases in both shrubs and graminoids that have been observed during the past decades

in Arctic tundra landscapes as a response to temperature increase (Dormann and Woodin, 2002; Walker et al., 2006; Hudson and Henry, 2009). Shrub expansion has been observed in many places in the Arctic (Sturm et al., 2001; Tape et al., 2006; Myers-Smith et al., 2011), but is not explicitly simulated by NUCOM-tundra for the RCP-based climate change scenarios which combine temperature and precipitation increases.

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, likely due to their shallow rooting systems. Compared to shrubs, graminoids root relatively deeply (Wang et al., 2016). As a consequence, 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 mineralisation takes place (Björk et al., 2007). Nevertheless, it is likely that growing season lengthening and increased microbial mineralisation of soil organic matter improve growing conditions for both shrubs and graminoids, as also graminoids have been shown to respond strongly upon fertilisation (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 (Sect. S2). Higher summer temperatures increase potential evapotranspiration, and thus lead to drier soils, if precipitation remains unchanged. Consequently, the area of relatively dry sites characterised by dense dwarf shrub vegetation might increase. A similar imbalance 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 graminoids especially 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 in 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 (Sect. S1.3.4). Especially for deeper soil layers, this module lacks accuracy in precisely predicting changes in active layer thickness for different temperature change scenarios, which results in uncertainty in both the depth of the active layer and the amount of nutrients that becomes 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.

Previously, the effectiveness of shrubs in dealing with increased nutrient levels has been proposed as an explanation for 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 stem growth (Shaver et al., 2001). However, *Betula nana* is also known to respond to increased temperatures and fertilisation 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 several plant traits (parameters values). For light competition, leaf area and light extinction are important, which are influenced by parameters such as specific leaf area, biomass allocation to leaves, leaf mortality and light extinction coefficient. Similarly, nutrient competition is influenced by parameters such 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 into the mineral soil layers. Based on our observations at our study site in the 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 be-

comes more important. In parts of the tundra area, shrubs, including *Betula nana*, can grow taller than 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.

Overall, our results from the climate change scenarios mainly 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 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 few 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 $+0.0565^{\circ}\text{C yr}^{-1}$; precipitation -1.127 mm yr^{-1} ; <http://climexp.knmi.nl/atlas>; Li et al., 2016). 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

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 a peak of moss biomass shortly after ground collapse and before significant colonisation of graminoids. After the collapse, the shrubs were dying because of the water-saturated soil, while the graminoids had not yet colonised the new thaw pond, and the mosses took advantage of the increased light availability. At the Siberian field site we also observe that mosses mostly drown and the first colonisers of thaw ponds are mostly graminoids, for example *Eriophorum angustifolium* (Jorgenson et al., 2006), although mosses can also be the first colonisers. 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 recolonise 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, 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). 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 recognised 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.

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 the tundra ecosystem (Van Huissteden and Dolman, 2012). This model feature should, therefore, receive special attention with further model developments.

5 Data availability

Data are available upon request.

Appendix A: Parameter values in NUCOM-tundra

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	15 660			Heijmans et al. (2004)
maxheight	maximum height of moss layer	m	0.045			Blok et al. (2010)
minheight	minimum 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 and 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}	minimum volumetric soil water content for growth	%	20	20	0	
w _{low}	lowest volumetric soil water content for optimal growth	%	40	40	10	
w _{high}	highest volumetric soil water content for optimal growth	%	70	70	65	
w _{max}	maximum volumetric soil water content for growth	%	70	70	70	
T _{min}	minimum air T for growth	°C	0	1	1	
T _{low}	lowest air T for optimal growth	°C	3	4	4	
N _{min}	minimum N concentration for growth	g N g ⁻¹	0.0102	0.0122	0.0172	Hobbie (1996)
N _{max}	maximum 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 in stems to storage	–		0	0	Heijmans et al. (2008)
Kreal	reallocation of N in 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	150 000	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 mineralisation	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 maximum denitrification		1	
Q ₁₀	denitrification increase factor with 10 °C increase		2	Heinen (2006)
T _{ref}	reference temperature(for denitrification)	°C	20	Heinen (2006)
DDF	degree day factor for snowmelt	mm °C ⁻¹ day ⁻¹	5.3	Lundberg and Beringer (2005)
FieldCap _{org}	volumetric water content at field capacity in organic layer	mm mm ⁻¹	0.36	Zotarelli et al. (2010)
MaxCap _{org}	maximum volumetric water content in organic layer (saturation)	mm mm ⁻¹	0.70	
FieldCap _{min}	volumetric water content at field capacity in mineral layer	mm mm ⁻¹	0.42	Saxton and Rawls (2006)
MaxCap _{min}	maximum volumetric 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	

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References

- Anisimov, O. A. and Nelson, F. E.: Permafrost zonation and climate change in the northern hemisphere: results from transient general circulation models, *Climatic Change*, 35, 241–258, 1997.
- Berendse, F.: Litter decomposition – a neglected component of plant fitness, *J. Ecol.*, 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., Klemmedtsson, 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 Phytol.*, 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, *Glob. Change Biol.*, 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, *Environ. Res. Lett.*, 7, 015503, 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, *Arct. Alp. Res.*, 7, 209–226, 1975.
- 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, *J. Veg. Sci.*, 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., J. D., Jia, G., Ping, C.-L., Tape, K. D., 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, *Geophys. Res. Lett.*, 31, L04501, doi:10.1029/2003GL018680, 2004.
- Dormann, C. F. and Woodin, S. J.: Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments, *Funct. Ecol.*, 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, *Glob. Change Biol.*, 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: Implications for root longevity, *New Phytol.*, 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., Onipchenko, V. G., Rixen, C., Schmidt, N. M., Shaver, G. R., Spasojevic, M. J., Þórhallsdóttir, P. 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, *Ecol. Appl.*, 10, 824–841, 2000.
- 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, *Ecol. Appl.*, 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 Phytol.*, 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, 279–309, 1974.
- Heijmans, M. M. P. D., Arp, W. J., and Chapin, F. S.: Carbon dioxide and water vapour exchange from understory species in boreal forest, *Agr. Forest Meteorol.*, 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, *J. Veg. Sci.*, 19, 307–320, 2008.
- Heijmans, M. M. P. D., van der Knaap, Y. A., Holmgren, M., and Limpens, J.: Persistent versus transient tree encroachment of temperate peat bogs: effects of climate warming and drought events, *Glob. Change Biol.*, 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. 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, *Ecol. Monogr.*, 66, 503–522, 1996.
- 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*, 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, edited by: Core Writing Team, Pachauri, R. K., and Meyer, L. A., 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 Wulfschleger, S. D.: The unseen iceberg: plant roots in arctic tundra, *New Phytol.*, 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, *Geophys. Res. Lett.*, 33, L02503, 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., Miletus, 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, *Int. J. Climatol.*, 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, *J. Ecol.*, 97, 886–900, 2009.
- Lawrence, D. M. and Slater, A. G.: A projection of severe near-surface permafrost degradation during the 21st century, *Geophys. Res. Lett.*, 32, L24401, 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, *J. Geophys. Res.-Earth*, 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 Biol.*, 39, 1245–1255, doi:10.1007/s00300-015-1847-0, 2016.
- 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, 1–10, 2005.
- MacDougall, A. H., Avis, C. A., and Weaver, A. J.: Significant contribution to climate warming from the permafrost carbon feedback, *Nat. Geosci.*, 5, 719–721, 2012.
- Marion, G. M. and Miller, P. C.: Nitrogen mineralization in a tussock tundra soil, *Arct. Alp. Res.*, 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, *Ecol. Monogr.*, 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, *Environ. Res. Lett.*, 6, 045509, 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., Lévesque, 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, 887–891, 2015.

- Nadelhoffer, K., Shaver, G., Fry, B., Giblin, A., Johnson, L., and McKane, R.: ^{15}N natural abundances and N use by tundra plants, *Oecologia*, 107, 386–394, 1996.
- 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 Tumskey, V. E.: Physical and ecological changes associated with warming permafrost and thermokarst in interior Alaska, *Permafrost 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 Environ.*, 16, 1115–1121, 1993.
- Riordan, B., Verbyla, D., and McGuire, A. D.: Shrinking ponds in subarctic Alaska based on 1950–2002 remotely sensed images, *J. Geophys.-Res.Bioge.*, 111, G04002, 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 Sci. Soc. Am. J.*, 70, 1569–1578, 2006.
- Schuur, E., Bockheim, J., Canadell, J., Euskirchen, E., Field, C., Goryachkin, S., Hagemann, S., Kuhry, P., Lafleur, P., and 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.
- 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, *Ecol. Monogr.*, 61, 1–31, 1991.
- Shaver, G. R. and Cutler, J. C.: The vertical distribution of live vascular phytomass in cottongrass tussock tundra, *Arct. Alp. Res.*, 11, 335–342, 1979.
- 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, *Glob. Change Biol.*, 12, 686–702, 2006.
- 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 Biogeochem. Cy.*, 23, GB2023, doi:10.1029/2008GB003327, 2009.
- Turetsky, M. R., Wieder, R. K., and Vitt, D. H.: Boreal peatland C fluxes under varying permafrost regimes, *Soil Biol. Biochem.*, 34, 907–912, 2002.
- Urban, M., Forkel, M., Eberle, J., Hüttich, C., Schmullius, C., and Herold, M.: Pan-arctic climate and land cover trends derived from multi-variate and multi-scale analyses (1981–2012), *Remote Sens.*, 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.
- 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, *Ecol. Appl.*, 9, 920–935, 1999.
- van Wijk, M. T.: Predicting ecosystem functioning from plant traits: results from a multi-scale ecophysiological modeling approach, *Ecol. Modell.*, 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 CCSM4, *J. Climate*, 25, 2696–2710, 2012.
- Walker, D. A., Reynolds, 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, *J. Veg. Sci.*, 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, *P. Natl. Acad. Sci. USA*, 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 Soil*, 407, 55–65, 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 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 graz-

- ing pressure, *Environ. Res. Lett.*, 6, 045505, 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, *J. Geophys. Res.-Atmos.*, 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, *Environ. Res. Lett.*, 8, 034023, doi:10.1088/1748-9326/8/3/034023, 2013.
- 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, *Geophys. Res. Lett.*, 33, L20502, doi: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, University of Florida Cooperation Extension Services, AE460, 2010.