



**University of
Zurich**^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
University Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2017

Shrub growth rate and bark responses to soil warming and nutrient addition – A dendroecological approach in a field experiment

Iturrate-Garcia, Maitane ; Heijmans, Monique M P D ; Schweingruber, Fritz H ; Maximov, Trofim C ; Niklaus, Pascal A ; Schaepman-Strub, Gabriela

Abstract: Tundra shrubs are slow-growing species limited by low air temperature and scarce nutrient availability. However, shrub expansion has been widely observed in the Arctic during the last decades and attributed to climate warming. Shift in shrub growth, wood structure and abundance affects the surface albedo and permafrost thawing and these changes may feedback to climate. Despite the importance of shrub–climate feedbacks, uncertainties about shrub growth sensitivity to climate remain. Here, we explored the indirect effects of climate warming on shrub growth (vertical and radial), bark thickness, and bark investment in four arctic shrub species. We combined a field experiment addressing two suggested growth drivers – thawing depth and nutrient availability – with dendroecology in a Siberian tundra ecosystem. We used heating cables to increase the thawing depth. To enhance the nutrient availability, we fertilized the surface soil layers. We found that shrub growth was mainly limited by nutrient availability, as indicated by the fertilization treatment effects on shrub growth ring widths. We also found a bark thickness decrease with the combined soil heating and nutrient addition treatment and a negative correlation between bark investment and growth rate for two of the species. These findings suggest that tundra shrubs, especially deciduous species, will grow faster and taller driven by an increasing nutrient availability in the surface soil layers. However, shrubs might become more vulnerable to pests, herbivory, and climate extremes, such as frost or drought events, due to thinner bark and lower bark investment. Using dendroecological approaches in field experiments simulating projected climate scenarios for the Arctic, and an increasing number of study species and locations will reduce uncertainties related to shrub growth sensitivity to climate and other processes driving shrub dynamics.

DOI: <https://doi.org/10.1016/j.dendro.2017.07.001>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-144914>

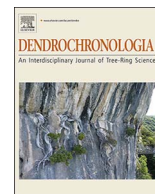
Journal Article

Published Version

Originally published at:

Iturrate-Garcia, Maitane; Heijmans, Monique M P D; Schweingruber, Fritz H; Maximov, Trofim C; Niklaus, Pascal A; Schaepman-Strub, Gabriela (2017). Shrub growth rate and bark responses to soil warming and nutrient addition – A dendroecological approach in a field experiment. *Dendrochronologia*, 45:12-22.

DOI: <https://doi.org/10.1016/j.dendro.2017.07.001>



Shrub growth rate and bark responses to soil warming and nutrient addition – A dendroecological approach in a field experiment



Maitane Iturrate-Garcia^{a,*}, Monique M.P.D. Heijmans^b, Fritz H. Schweingruber^c, Trofim C. Maximov^{d,e}, Pascal A. Niklaus^a, Gabriela Schaepman-Strub^a

^a Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

^b Plant Ecology Group and Nature Conservation, Wageningen University & Research, P.O. Box 47, 6700 AA Wageningen, The Netherlands

^c Swiss Federal Research Institute WSL, Zuercherstrasse 111, 8903 Birmensdorf, Switzerland

^d Institute for Biological Problems of the Cryolithozone, Siberian Branch, Russian Academy of Sciences, 41 Lenin Prospekt, Yakutsk, Republic of Sakha (Yakutia) 677980, Russian Federation

^e Institute for Natural Sciences of North Eastern Federal University, 58 Belinskogo st., Yakutsk, Republic of Sakha (Yakutia) 677000, Russian Federation

ARTICLE INFO

Keywords:

Arctic tundra
Bark investment
Bark thickness
Climate warming
Growth rings
Thawing depth

ABSTRACT

Tundra shrubs are slow-growing species limited by low air temperature and scarce nutrient availability. However, shrub expansion has been widely observed in the Arctic during the last decades and attributed to climate warming. Shift in shrub growth, wood structure and abundance affects the surface albedo and permafrost thawing and these changes may feedback to climate. Despite the importance of shrub–climate feedbacks, uncertainties about shrub growth sensitivity to climate remain. Here, we explored the indirect effects of climate warming on shrub growth (vertical and radial), bark thickness, and bark investment in four arctic shrub species. We combined a field experiment addressing two suggested growth drivers – thawing depth and nutrient availability – with dendroecology in a Siberian tundra ecosystem. We used heating cables to increase the thawing depth. To enhance the nutrient availability, we fertilized the surface soil layers. We found that shrub growth was mainly limited by nutrient availability, as indicated by the fertilization treatment effects on shrub growth ring widths. We also found a bark thickness decrease with the combined soil heating and nutrient addition treatment and a negative correlation between bark investment and growth rate for two of the species. These findings suggest that tundra shrubs, especially deciduous species, will grow faster and taller driven by an increasing nutrient availability in the surface soil layers. However, shrubs might become more vulnerable to pests, herbivory, and climate extremes, such as frost or drought events, due to thinner bark and lower bark investment. Using dendroecological approaches in field experiments simulating projected climate scenarios for the Arctic, and an increasing number of study species and locations will reduce uncertainties related to shrub growth sensitivity to climate and other processes driving shrub dynamics.

1. Introduction

Global air temperature is unequivocally increasing, more rapidly in the Arctic – where a temperature rise of 3 °C by the year 2100 is projected (emission scenario RCP4.5) – than in other regions (IPCC, 2013). As a consequence of this change, an increase in soil temperature is expected. Higher soil temperatures in the Arctic are associated with permafrost thawing (Osterkamp and Jorgenson, 2006; Schuur et al., 2008; Park et al., 2016). Permafrost thawing will release nutrients accumulated in the permafrost over decades due to adverse conditions for organic matter decomposition and leaching processes (Kokelj and Burn, 2003; Weintraub and Schimel, 2003; Schuur et al., 2009; Romanovsky

et al., 2010). This release may lead to the increase of nutrients (e.g. nitrogen) available for plants (Keuper et al., 2012). Furthermore, soil warming will stimulate soil microbial activity, which will accelerate soil organic matter mineralization rates and thus provide more nutrients to vegetation (Schmidt et al., 1999; Walther et al., 2002).

The enhanced nutrient availability will affect tundra vegetation diversity, species distribution, and plant traits (van Wijk et al., 2003; DeMarco et al., 2014; Edwards and Henry, 2016). These shifts in tundra vegetation might alter regional climate feedbacks (Chapin, 2003). Despite the importance of tundra vegetation–climate feedbacks and increasing efforts to understand species sensitivity to climate, the latter remains uncertain in terms of direction and spatial variability

* Corresponding author.

E-mail address: maitane.iturrate@ieu.uzh.ch (M. Iturrate-Garcia).

(Elmendorf et al., 2012; Myers-Smith et al., 2015a).

Tundra vegetation is adapted to harsh environmental conditions, such as extremely low temperatures, low precipitation, and scarce soil nutrient availability, and to a short growing season (< 3 months) (Billings and Mooney, 1968; Crawford, 2008). For that, tundra vegetation adopts a slow-growth strategy, with efficient use of resources (Chapin 1980; Reich et al., 1997; Cornelissen 1999). The low rate of tissue turnover allows these species to allocate resources to storage or defence structures (e.g. bark), conferring vegetation resistance to stress (Chapin et al., 1993). For example, wood and bark provide essential functions to shrubs such as mechanical support of aboveground tissues, conduction of sap, storage of resources, and protection against herbivory, pathogens, and frost damage (Vines, 1968; Paine et al., 2010; Francis and Vavrus, 2012; Poorter et al., 2014). Despite the slow-growth strategy adopted by tundra vegetation, shrub expansion has been reported in many arctic, subarctic, and alpine regions using repeat aerial photography, satellite imagery, and long-term monitoring plots (Sturm et al., 2001b; Tape et al., 2006, 2012; Myers-Smith et al., 2011).

Shrub expansion occurs through both lateral and vertical growth of individuals and new recruitment between existing patches and colonization of new areas, all which increase shrub cover or biomass (Myers-Smith et al., 2011). Arctic shrub expansion is spatially and temporally heterogeneous, which can partly be attributed to different shrub growth strategies and sensitivity to climate (Blok et al., 2010; Kremers et al., 2015; Myers-Smith et al., 2015a). Although summer air temperature is considered to be the main driver of shrub expansion (Bär et al., 2008; Forbes et al., 2010; Hallinger et al., 2010; Weijers et al., 2010; Blok et al., 2011a), other environmental factors have been proposed as growth drivers, such as soil moisture, thawing depth, and soil nutrient availability (Sturm et al., 2001b; Myers-Smith et al., 2015a; Li et al., 2016; Ackerman et al., 2017).

Shrub expansion may affect climate by altering the surface energy budget (e.g. decrease surface albedo) and the carbon cycle (e.g. decrease methane emission by permafrost protection through shading) among others (Eugster et al., 2000; Chapin, 2003; Beringer et al., 2005; Nauta et al., 2015). These shrub effects can be direct, through denser shrub cover and plant trait changes (Epstein et al., 2012; Juszak et al., 2016), but they can also be indirect by shifting community composition and diversity. Negative effects of shrub expansion on other plant functional types through resource competition and modification of local soil conditions may change community composition and diversity (Cornelissen et al., 2001; Startsev et al., 2008; Odland et al., 2015). Consequently, a better understanding of mechanisms driving shrub expansion is fundamental to improve the accuracy of projected shifts in tundra vegetation, ecosystem processes and consequences, and regional climate in the Arctic (Myers-Smith et al., 2011; Ackerman et al., 2017).

During the last decades, dendroecological methods have been adapted to shrub species to identify the drivers of shrub growth and expansion in tundra ecosystems (Rayback and Henry, 2005; Liang and Eckstein, 2009; Hantemirov et al., 2011; Schweingruber et al., 2013). However, a synthesis on climate sensitivity of arctic and alpine shrub growth summarizing the conducted dendroecological studies highlights the need of increasing the number of locations and species in order to better understand shrub growth responses to climate change (Myers-Smith et al., 2015a). Furthermore, to consider other plant traits (e.g. bark thickness) in dendroecological studies – in addition to growth ring width – may reduce the uncertainties of shrub growth and expansion sensitivity to climate.

In this study, we explored the effects of increased thawing depth and enhanced surface soil nutrient availability on tundra shrub growth and traits. We hypothesized that under simulated environmental conditions expected with climate warming (i.e. increased thawing depth and nutrient availability) (i) arctic shrubs will grow faster and taller and (ii) bark investment will be lower as a consequence of faster growth. To test our hypotheses, we ran a four-year soil warming and fertilization experiment in northeastern Siberia (Wang et al., 2016a). We measured

growth ring widths of the four years before the experiment started and the four years of treatment application. In the last year of experiment, we also measured height, total aboveground and wood biomass, xylem diameter, bark thickness, and bark investment in four tundra shrub species.

2. Material and methods

2.1. Study area and species

The study area is located in the Kytalyk nature reserve, in the Indigirka lowlands, Yakutia, northeastern Siberia (70°49'N, 147°28'E, 10 m.a.s.l.), in the continuous permafrost arctic region. The mean annual air temperature is −13.1 °C, with minimum monthly means of −33.5 °C in January and maximum of 11.3 °C in July, and the mean annual precipitation is 210 mm (1980–2013, WMO station 21946, Chokurdakh, monthly summaries of GHCN-D, NOAA National Climatic Data Center), which mainly occurs during the growing season months (about mid-June to end-August).

The experimental plots were placed on a Pleistocene yedoma hill (Schirrmeister et al., 2012), in a tussock-sedge tundra area. The soil is classified as Gelisol following the USDA soil taxonomy (Wang et al., 2016a). The yedoma soil is slightly acidic (pH < 6.5) and has high organic matter content and a silty-clay texture. The mean carbon to nitrogen ratio is 22 and the cellulose to lignin ratio 2.4, indicating low soil organic matter decomposition. The mean active layer thickness is 35 cm at mid-growing season and about 50 cm by the end of the season. The main vegetation comprises sedges (mainly *Eriophorum vaginatum*), abundant deciduous and evergreen dwarf shrubs, bryophytes and lichens, and has a maximum canopy height of 25 cm (Iturrate-García et al., 2016).

We studied four shrub species that are dominant in the test site: *Betula nana* ssp. *exilis* (Sukazcev) Hultén and *Salix pulchra* Cham., which are deciduous, and *Ledum palustre* ssp. *decumbens* (Aiton) Hultén and *Vaccinium vitis-idaea* L., which are evergreen. The species were present in all the plots in similar abundance, except for *S. pulchra*, that was less abundant than the rest. *L. palustre* was originally sampled, but not included in the growth rate analysis because the growth rings of this species were undistinguishable.

2.2. Experimental design and sampling

We ran a fully factorial soil warming and fertilization experiment from 2011 to 2014 in the study area. The experiment had five blocks and two treatments (soil warming and fertilization) applied to six plots of 1.5 × 1.5 m placed at randomly chosen locations within each block. We randomly assigned the six treatment combinations (3 soil warming × 2 fertilization treatments) to the plots within blocks. Heating cables powered by solar panels were buried at 15 cm depth in order to rise soil temperature to increase the thawing depth. We included a cable without heating to account for possible disturbance effects caused by burying the cables. In total, the warming treatment had three levels: no cable, unheated cable, and heated cable. The soil temperature rose by 1 °C at 15 cm depth during the growing season on heated cable plots, which increased the thawing depth by 7 cm on average when comparing with unheated cable plots (Appendix A, Tables A1 and A2). For the nutrient addition treatment, we applied slow-release NPK fertilizer tablets with micronutrients (Osmocote Exact Tablet, Scotts International, Heerlen, the Netherlands) to the surface soil layers at the start of the experiment and two years later. The fertilization treatment was nutrient addition (approximately 5.6 g N, 1.4 g P and 3.7 g K m^{−2} y^{−1}) and no addition.

We followed the protocol described in Pérez-Harguindeguy et al. (2013) to sample and transport the plant samples. At mid-growing season in 2014, we randomly selected six healthy-looking individuals (< 20% leaf damage) of each species in every plot, except for *S. pulchra*

for which fewer individuals were present (one to four individuals per plot). We cut off the selected individuals 4 cm below the root collar after measuring shrub height. Then, we cut 2 cm above and below the root collar of every individual to obtain samples for dendroecological analysis. These samples were preserved in ethanol (40% vol. aqueous solution) until laboratory processing.

2.3. Height, biomass, and wood fraction

We measured shrub height before individual sampling as the vertical distance from the tallest vegetative tissue of each individual to the ground.

We separated main stem and branches from other aboveground structural parts (i.e. leaves, buds and flowers) and weighed them before (wet weight) and after oven-drying (dry weight, 60 °C, 72 h). Aboveground wood biomass was the sum of stem and branch dry weights, while leaf biomass was the dry weight of the leaves. To estimate wood fraction, we divided aboveground wood biomass dry weight by dry weight of all aboveground structural parts (total aboveground biomass). Leaf fraction was estimated as the ratio between leaf and total aboveground biomass dry weights.

2.4. Shrub growth rate

Thin sections of 20–30 µm were obtained using a GSL1 sledge microtome (Gärtner et al., 2014) from disks cut along the root collar of the main stem. We put the micro-sections on microscope slides, adding a drop of glycerine:distilled water mixture (4:1). Only the samples used for illustration (Fig. 1a,b) were stained following standard methods (Gärtner and Schweingruber, 2013). We used a camera (AxioCam MRC, Carl Zeiss MicroImaging GmbH, Göttingen, Germany) connected to a microscope (Axioskop2 plus, Carl Zeiss Microscopy GmbH, Jena, Germany) to photograph the samples with a 200× magnification and measured the annual growth ring widths (AxioVision SE 64 v4.8.4., Carl Zeiss MicroImaging GmbH, Göttingen, Germany). Due to the

growth eccentricity of shrubs, growth ring widths were measured along the longest axis of the micro-sections (Fig. 1). Shrub growth rate was the average annual growth ring width of the four years previous to the experiment (growth rate before experiment) or the four experimental years (growth rate during experiment).

2.5. Stem traits

To measure the xylem diameter and bark thickness, we used the same slices and set-up as for the shrub growth rate. In this case, pictures were taken with a 10× magnification (50× for *V. vitis-idaea*). We measured the xylem diameter along the longest axis of the slice (Fig. 1a). Bark thickness was estimated by averaging the measurements taken along three different radii for each slice (Fig. 1b). We divided the bark thickness by the xylem radius to obtain the bark investment.

2.6. Data analysis

To test whether shrub growth was affected by the soil warming and fertilization treatments, we analysed growth rate as a function of treatments, species, and their interaction with a linear mixed-effect model (ASReml, 3.0, VSN International Ltd., UK). The mean growth rate of the experimental years was log-transformed to account for size differences among species. The fixed terms of the model were block (factor with five levels), log-transformed mean growth rate of the four years prior to the experiment (allometric correction standardizing the response variable by individual size within species), and the interaction among warming treatment, fertilization treatment and species. Random terms were plot (factor with 30 levels) and the interaction of plot and species. Permafrost thawing (heated cable) and cable disturbance (unheated cable) effects were tested by splitting the three-level warming factor into two contrasts of one degree of freedom (i.e. presence of cable and heating). We tested permafrost thawing effects by fitting cable followed by heating and cable effects by fitting heating followed by cable. To explore the treatment effects on other traits (height, total

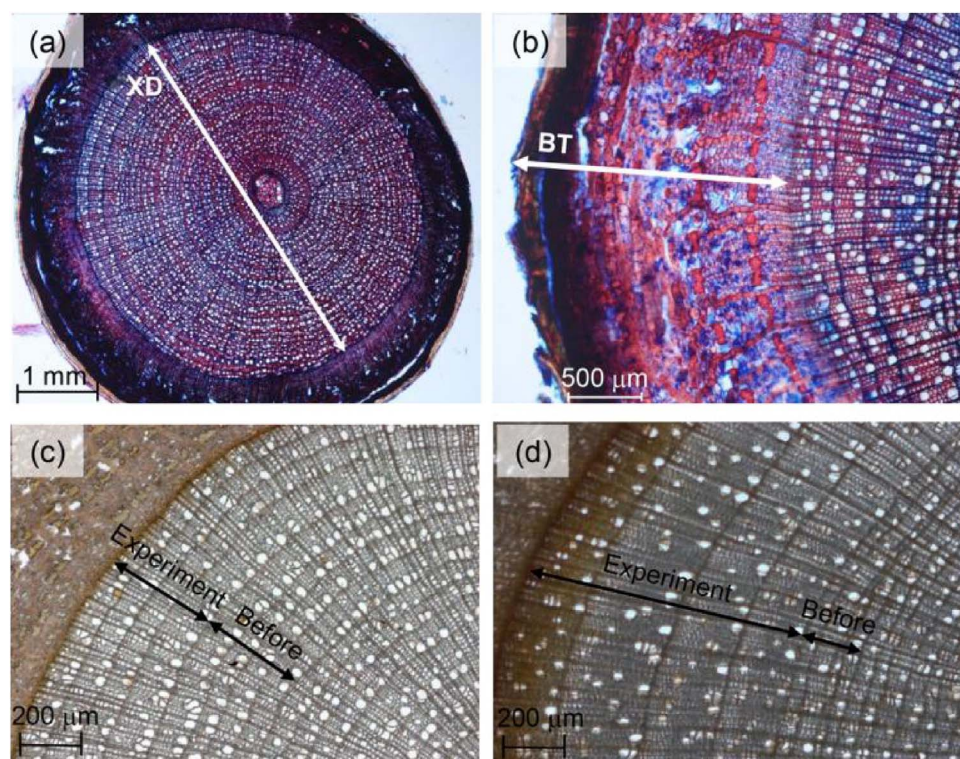


Fig. 1. Micro-sections of *Salix pulchra* showing xylem diameter (XD) (a), bark thickness (BT) (b), and growth ring width of the four years previous to the experiment and the four years of experiment in a control plot (c) and in a treatment plot (soil warming × fertilization) (d).

aboveground and wood biomass, wood and leaf fractions, bark thickness, and bark investment), we used a similar model to the one described for growth rate, but without applying the allometric correction. The response variables wood and leaf fractions and bark investment were not log-transformed.

To test for significant differences between growth rates before and during the experiment, we used a linear mixed-model where the response variable was the growth rate difference before and during the experiment. Block and the interaction between warming and fertilization treatment were the fixed terms of the model and individuals the random term.

To explore the relationship of bark thickness and growth rate with shrub age – using xylem diameter as a proxy of age – and between bark investment and growth rate, we used a similar linear mixed-effect model to the one used to test the treatment effects on growth rate, but without applying the allometric correction. Outliers were detected based on model residual values more than three times and a half the median absolute deviation (Leys et al., 2013). We removed seven outliers ($n = 595$ observations) prior to analysing the significance of the linear relationships between variables using Pearson's correlation coefficients in addition to the linear mixed-effect models.

The data analysis was performed using R.3.2.5. (<http://r-project.org>).

3. Results

3.1. Growth rate

Growth rates of the three shrub species examined increased with the fertilization but not with the soil warming treatment (Fig. 2). Neither the interaction between treatments nor the disturbance caused by burying the heating cables was significant for shrub growth rate. The net effect of nutrient addition was a significant increase of the growth rate of *B. nana* ($F_{1,29} = 21.2$, $P < 0.001$), *S. pulchra* ($F_{1,29} = 16.2$, $P < 0.001$), and *V. vitis-idaea* ($F_{1,29} = 9.8$, $P < 0.01$) (Fig. 2).

During the four experimental years, the mean growth rate increased compared to the four years before the experiment (Fig. 3). However, this increase was significant only in the fertilized plots ($F_{1,29} = 43.3$ (*B. nana*), 20.0 (*S. pulchra*), 16.3 (*V. vitis-idaea*), $P < 0.001$) (Fig. 3).

3.2. Bark thickness and investment

Bark thickness decreased with the soil heating and fertilization treatment combination for *B. nana* ($F_{1,25} = 4.54$, $P < 0.05$) and *L. palustre* ($F_{1,25} = 8.15$, $P < 0.01$). For *B. nana*, the bark decrease was 24% relative to the soil heating treatment alone and 25% relative to the nutrient addition treatment alone and 25% and 21% respectively for *L. palustre*. Soil heating or nutrient addition alone did not affect bark

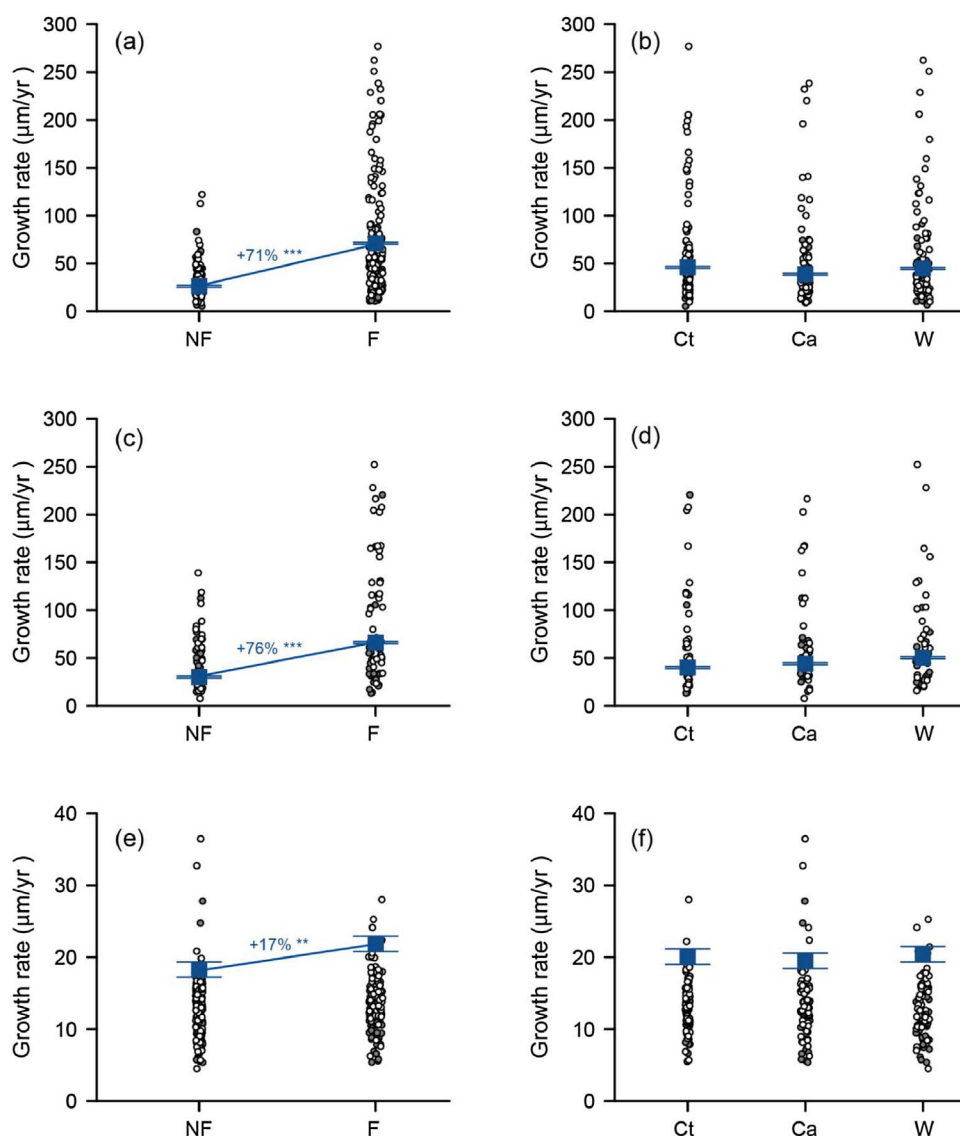


Fig. 2. Fertilization (left) and warming (right) treatment effects on the growth ring width of the four experimental years for *Betula nana* (a, b), *Salix pulchra* (c, d), and *Vaccinium vitis-idaea* (e, f). Only the fertilization effect was significant (*** $P < 0.001$, ** $P < 0.01$). Circles show measured growth rates before the experiment (grey circles) and during the experiment (open circles). Blue squares show predictions of the model for each treatment and error bars, the standard error of the predictions. The fertilization treatment levels are no nutrient addition (NF) and nutrient addition (F), and the warming treatment levels are no cable (Ct), unheated cable (Ca), and heated cable (W). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

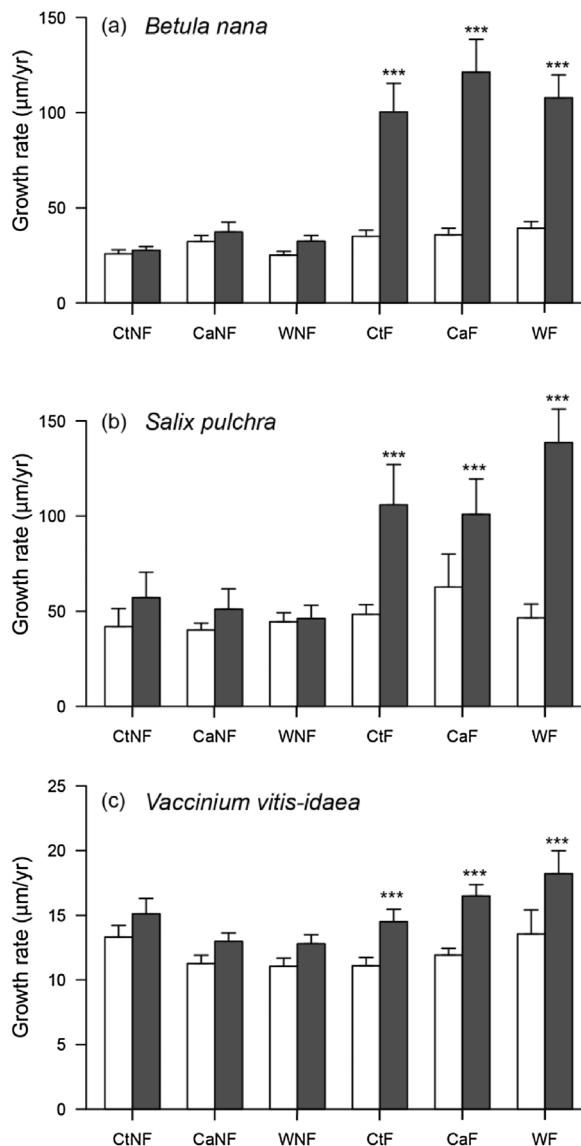


Fig. 3. Mean growth rate of the four years before the experiment (white bars) and the four years of experiment (grey bars) (a–c). The treatment combinations are no-nutrient addition × no-cable (CtnF), no-nutrient addition × unheated cable (CaNF), no-nutrient addition × heated cable (WNF), nutrient addition × no-cable (CtF), nutrient addition × unheated cable (CaF), and nutrient addition × heated cable (WF). Error bars indicate the standard error ($n = 5$ blocks). Significant differences in the growth rate of the years before and during the experiment are indicated by asterisks (***) ($P < 0.001$).

thickness and bark investment (Table 1).

Shrub bark thickness was positively related to xylem diameter for *B. nana*, *S. pulchra*, and *V. vitis-idaea* (Fig. 4). This relationship was also significant and positive for *L. palustre* ($r = 0.66$, $P < 0.001$; data not shown). Although weak, we found a negative correlation between bark investment and growth rate for *B. nana* and *V. vitis-idaea*, but not for *S. pulchra* (Fig. 4). These relationships were similar in plots with and without nutrient addition.

3.3. Other traits

Height of the four species increased with nutrient addition (Table 1). Wood fraction decreased significantly, suggesting a higher leaf fraction of the total aboveground biomass, for all the species except for *V. vitis-idaea* ($P = 0.1$) (Table 1). However, leaf fraction increase was only significant for *B. nana* and *S. pulchra* (Table 1). Wood biomass of *L. palustre* was negatively affected by the disturbance through the buried cables ($F_{1,25} = 10.6$, $P < 0.01$). Total aboveground biomass of

L. palustre responded to the heating treatment, but it was also negatively affected by the disturbance through the buried cables (Table 1). Xylem diameter of *V. vitis-idaea* was also affected by this disturbance, but only in the fertilized plots ($F_{1,25} = 5.43$, $P < 0.05$). For the rest of traits, cable disturbance and treatment interaction (heating × nutrient addition) were not significant.

4. Discussion

We explored the effects of permafrost thawing and increased surface soil nutrient availability on radial and vertical growth, wood biomass, and bark thickness and investment of four tundra shrub species. Our findings show that all the species grew faster (radially and vertically) with the fertilization but not with the soil warming treatment, contrary to our hypothesis. We also found a weak but significant negative correlation between bark investment and growth rate for some of the species. These results suggest that shrubs will grow faster and taller in a changing climate, but might be more vulnerable to pests, herbivory, and climate extremes (e.g. frost events, drought) due to a reduced investment in bark.

4.1. Dendroecology in arctic tundra

Dendroecological approaches have been adapted and increasingly applied to arctic tundra shrubs in order to explore their sensitivity to climate (Woodcock and Bradley, 1994; Schweingruber and Poschold, 2005; Bär et al., 2006; Young et al., 2016). However, shrub growth rings can be difficult to identify due to eccentric growth, narrow growth ring widths, and wedging, incomplete, or missing rings, which can lead to erroneous results (Myers-Smith et al., 2015b). Furthermore, these approaches are mainly observational (dendrochronology) and therefore difficult to discern whether the correlation between growth and climatic factors is driven by direct effects of the factor or by other mechanisms associated to its indirect effects (Liang and Eckstein, 2009; Hallinger et al., 2010; Buchwal et al., 2013; Hollesen et al., 2015; see exceptions: Bret-Harte et al., 2002; Rixen et al., 2010). Here, we combined dendroecological and experimental approaches to identify drivers of shrub growth. This combination requires the identification of fewer growth rings than for dendrochronology (only growth rings of the experimental years and the same number of years before the experiment). Thereby, analysing time is shortened and the probability of finding missing, incomplete or wedging rings may decrease. Moreover, the experimental design allows us to identify the actual drivers of shrub growth among the manipulated environmental factors which, in our case, were permafrost thaw depth and soil nutrient content.

4.2. Shrub growth under climate warming

We hypothesized that greater thawing depth and surface soil nutrient addition would increase shrub radial growth. However, our findings showed that shrub growth responded to enhanced nutrient availability, but not to the increased thawing depth. Similar effects were observed on the vertical growth of the four shrub species. These growth responses are in agreement with other experimental manipulations showing growth and biomass increase with fertilization, but shrub unresponsiveness or weak responses to experimental warming (van Wijk et al., 2003; Walker et al., 2006; Hudson and Henry, 2010; Zamin and Grogan, 2012; Wang et al., 2016a). Shrub growth unresponsiveness to the soil warming treatment might be explained by their rooting depth. Most of the root biomass of the study species occurs in soil layers above the depth where the heating cables were buried (Churchland et al., 2010; Wang et al., 2016a,b). Therefore, shallow-rooted shrubs may not benefit from indirect effects of greater thawing depths, through enhanced deep nutrient and water availability. Contrary to shrubs, deeper-rooted graminoids have access to those resources, thus increasing their aboveground biomass (Wang et al.,

Table 1

Effects of fertilization (Fert), cable disturbance (Ca) and soil heating (H) on structural and bark traits of each shrub species (*B. nana* (Betn), *S. pulchra* (Salp), *L. palustre* (Ledp) and *V. vitis-idaea* (Vacv)). Treatment columns show the average and standard error of the response variables for no-fertilization (NFert), fertilization (Fert), no-heating cables (Ct), unheated cables (Ca) and heated cables (H). LMM (linear mixed-effect model) columns show the Wald test outputs for our models (*** $P < 0.001$, ** $P < 0.01$ and * $P < 0.05$). Significant effects are in bold. Effect of the soil heating and fertilization treatment combination was not included as it was significant only for bark thickness of Betn and Ledp ($F_{1,25} = 4.54$, $P < 0.05$; $F_{1,25} = 8.15$, $P < 0.05$).

	Treatment					LMM		
	Fertilization		Warming			Fert	Ca	H
	NFert	Fert	Ct	Ca	H	$F_{1,29}$	$F_{1,28}$	$F_{1,28}$
Height (cm)								
Betn	14.0 ± 0.5	20.2 ± 0.6	16.7 ± 0.8	16.2 ± 0.6	18.5 ± 0.9	35.6***	0.00	2.00
Salp	14.8 ± 0.7	19.2 ± 1.0	16.7 ± 1.1	16.8 ± 1.3	17.8 ± 1.2	12.3**	0.10	0.20
Ledp	11.2 ± 0.4	14.2 ± 0.4	12.4 ± 0.4	12.3 ± 0.5	13.5 ± 0.6	36.4***	0.20	2.60
Vacv	3.9 ± 0.1	5.9 ± 0.2	4.4 ± 0.2	5.0 ± 0.3	5.3 ± 0.2	42.1***	3.34	0.54
Total aboveground biomass (g)								
Betn	3.23 ± 0.42	5.41 ± 0.76	5.27 ± 0.99	3.39 ± 0.56	4.30 ± 0.71	4.50*	1.49	0.91
Salp	3.67 ± 0.53	5.54 ± 0.72	4.27 ± 0.73	3.88 ± 0.74	4.24 ± 0.91	0.53	0.01	0.05
Ledp	1.33 ± 0.16	1.57 ± 0.23	1.82 ± 0.31	0.98 ± 0.16	1.53 ± 0.21	0.98	20.5***	12.2**
Vacv	0.13 ± 0.01	0.21 ± 0.03	0.12 ± 0.01	0.16 ± 0.02	0.22 ± 0.04	2.98	0.71	1.19
Wood biomass (g)								
Betn	2.68 ± 0.37	4.15 ± 0.63	4.22 ± 0.83	2.64 ± 0.46	3.39 ± 0.57	2.61	0.24	0.91
Salp	3.05 ± 0.44	3.54 ± 0.61	3.52 ± 0.63	3.06 ± 0.64	3.35 ± 0.76	0.05	0.00	0.07
Ledp	0.86 ± 0.12	1.02 ± 0.19	1.19 ± 0.24	0.74 ± 0.18	0.92 ± 0.17	0.04	10.6**	3.96
Vacv	0.02 ± 0.00	0.04 ± 0.01	0.02 ± 0.00	0.03 ± 0.01	0.04 ± 0.01	4.34	1.13	0.41
Wood fraction								
Betn	0.79 ± 0.01	0.73 ± 0.01	0.77 ± 0.02	0.75 ± 0.01	0.76 ± 0.01	13.5**	0.70	0.70
Salp	0.79 ± 0.01	0.73 ± 0.01	0.74 ± 0.02	0.76 ± 0.02	0.77 ± 0.01	11.4**	1.80	0.00
Ledp	0.60 ± 0.02	0.53 ± 0.02	0.60 ± 0.02	0.56 ± 0.03	0.55 ± 0.02	5.90*	1.71	0.04
Vacv	0.16 ± 0.01	0.18 ± 0.01	0.17 ± 0.01	0.18 ± 0.01	0.17 ± 0.01	4.32	1.08	0.60
Leaf fraction								
Betn	0.18 ± 0.01	0.24 ± 0.01	0.20 ± 0.01	0.22 ± 0.02	0.21 ± 0.01	10.9**	0.77	0.31
Salp	0.20 ± 0.01	0.26 ± 0.01	0.25 ± 0.02	0.23 ± 0.02	0.22 ± 0.01	8.92**	2.14	0.02
Ledp	0.39 ± 0.02	0.44 ± 0.02	0.38 ± 0.02	0.43 ± 0.03	0.43 ± 0.02	3.22	2.29	0.00
Vacv	0.84 ± 0.01	0.81 ± 0.01	0.83 ± 0.01	0.81 ± 0.01	0.82 ± 0.01	2.40	0.40	0.20
Bark thickness (mm)								
Betn	0.60 ± 0.02	0.61 ± 0.02	0.63 ± 0.03	0.63 ± 0.03	0.5 ± 0.03	0.14	0.02	1.47
Salp	1.04 ± 0.05	1.04 ± 0.06	1.02 ± 0.06	1.12 ± 0.08	0.98 ± 0.06	0.05	0.52	1.08
Ledp	0.18 ± 0.01	0.19 ± 0.01	0.19 ± 0.01	0.19 ± 0.02	0.18 ± 0.09	0.13	0.24	0.08
Vacv	0.12 ± 0.00	0.12 ± 0.00	0.12 ± 0.00	0.13 ± 0.00	0.12 ± 0.01	0.78	0.54	0.36
Bark investment								
Betn	0.23 ± 0.01	0.22 ± 0.01	0.24 ± 0.01	0.23 ± 0.01	0.21 ± 0.01	1.43	0.49	1.34
Salp	0.32 ± 0.01	0.31 ± 0.01	0.33 ± 0.01	0.32 ± 0.01	0.30 ± 0.01	0.29	0.01	1.03
Ledp	0.11 ± 0.00	0.12 ± 0.00	0.11 ± 0.00	0.11 ± 0.01	0.11 ± 0.01	0.01	0.11	0.74
Vacv	0.28 ± 0.01	0.26 ± 0.01	0.27 ± 0.01	0.28 ± 0.01	0.27 ± 0.01	1.04	0.17	0.51

2016a). As a consequence of this increase, shrubs might be out-competed by graminoids for light through shade effects (Shaver and Chapin, 1991; Shaver et al., 1998). Although shrubs can respond rapidly to environmental changes and some studies reported positive growth responses in four-year experiments, the short term of our experiment might additionally contribute to explain the lack of growth response to the soil warming treatment (Arft et al., 1999; Bret-Harte et al., 2002; Hallinger and Wilkening, 2011).

Previous dendroecological studies in the area revealed early summer temperature as the most important factor influencing the annual growth variation in *B. nana* and *S. pulchra* (Blok et al., 2011a; Li et al., 2016). However, those studies did not include soil temperature as an explanatory variable and the positive correlation between air temperature and shrub growth found in the dendrochronological studies might be explained by indirect effects of air temperature (Weih and Karlsson, 2001; Zamin and Grogan, 2012). Rising air temperature can increase soil temperature, permafrost thawing, and soil organic matter mineralization, enhancing in all cases the nutrient availability (Schmidt et al., 1999; Walther et al., 2002; Schuur et al., 2009). However, these indirect effects are difficult to identify in the dendrochronological studies, because only temporal series of air temperature are used, but not series of soil temperature, active layer thickness or soil nutrient concentrations.

4.3. Bark thickness and investment

Shrub woody tissues conduct and store water and nutrients, provide biomechanical support, and, especially the bark, play an important role in the defence against frost damage, drought, herbivory, and pathogens (Kozłowski, 1992; Rowe and Speck, 2005; Lens et al., 2011; Paine et al., 2010). We found a positive correlation between shrub bark thickness and xylem diameter for all the species, showing that bark thickness is age-dependent. As bark thickens with age, older individuals may be better protected and therefore can allocate more resources to functions other than defence (e.g. growth, reproduction) than younger ones (Payette et al., 2010; Poorter et al., 2014; Arco Molina et al., 2016). However, tundra shrubs (even the younger individuals) are expected to invest more in growth with climate warming, as suggested by our results. As a consequence of the growth–defence trade-off, shrubs may allocate fewer resources to defence, which might reduce their stress resistance (Chapin et al., 1993; Westoby et al., 2002; Grime, 2006; Chave et al., 2009; Reich, 2014). The weak but significant negative correlation between bark investment and growth rate found for *B. nana* and *V. vitis-idaea* might be the result of a growth–defence trade-off.

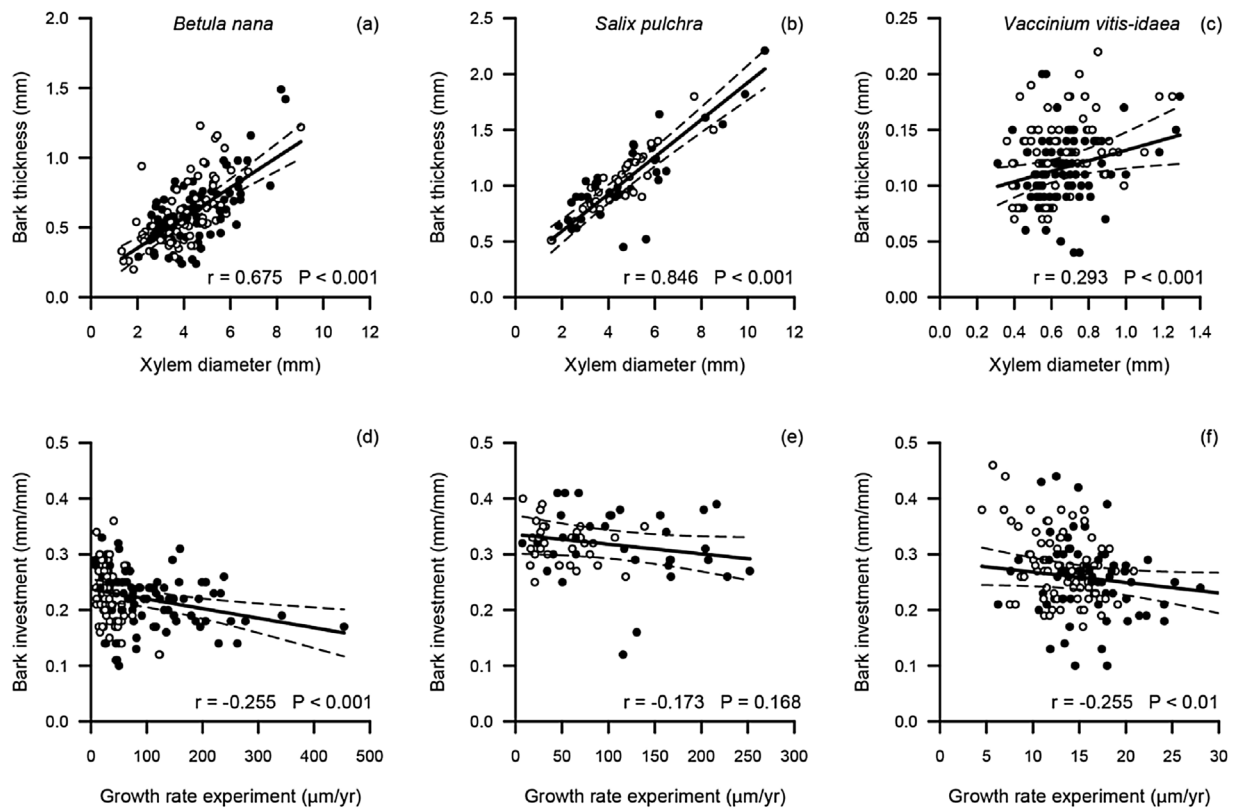


Fig. 4. Correlations between bark thickness and xylem diameter (a–c) and bark investment and growth rate of the years of experiment (d–f) for *Betula nana*, *Salix pulchra*, and *Vaccinium vitis-idaea*. White circles show values from unfertilized plots and black circles from fertilized plots. Solid lines are the values predicted by the linear mixed-effect model and dashed lines are the upper and lower limits of the confidence interval after removing the seven outliers detected. Pearson's correlation coefficient (r) and p-value (P) of data without outliers are indicated in each panel.

4.4. Shrub growth–climate feedbacks

Tundra shrubs are expected to grow faster with the increase of available nutrients in soil, especially in the shallower soil layers, associated with climate warming (Nadelhoffer et al., 1991; Schuur et al., 2009). Our findings show greater growth rates and taller shrubs with nutrient addition. Furthermore, the wood fraction decrease and leaf fraction increase shown by the deciduous species in our results suggest that resources may be allocated to leaf production under climate warming. These changes in shrub growth and traits may in turn affect climate by altering the surface radiation partitioning (e.g. decrease albedo) among others (Eugster et al., 2000; Pearson et al., 2013). For example, greater leaf to wood ratio and denser canopies (e.g. > 20% increased cover) will reduce the albedo, especially during melting periods, and the amount of radiation transmitted to the soil surface (Beringer et al., 2005; Blok et al., 2011b; Loranty et al., 2011; Juszak et al., 2014; Juszak et al., 2017). In summer, the decrease of radiation transmitted to the soil due to canopy shading may result in lower soil temperature and thawing depth (Blok et al., 2010; Marsh et al., 2010; Bonfils et al., 2012). During the winter, taller shrubs expected with climate warming may trap more snow leading in turn to higher soil temperature (snow-shrub hypothesis), which might enhance the nutrient availability and promote a positive feedback to shrub growth (Sturm et al., 2001b; Myers-Smith and Hik, 2013). Furthermore, shrubs buried under the resulting thicker snow layer will not affect winter albedo (Sturm et al., 2005). However, a decrease in snow cover is projected for the Arctic over the next decades (RCP4.5; IPCC, 2013). Taller shrubs expected with climate warming might be exposed to winter desiccation and frost damage as the snow layer might be insufficient to provide protection (Sturm et al., 2001a; Myers-Smith and Hik, 2013). Moreover, shrub stems and branches extended above the snowpack will reduce albedo (Sturm et al., 2005).

Tundra shrubs might also affect climate by altering species composition. Faster growing shrubs may outcompete other shallow-root species and cryptogam species, through use of light and nutrients, which might

alter the surface radiation budget and the water cycle (Cornelissen et al., 2001; Startsev et al., 2008; Odland et al., 2015). But in communities with abundant deep-root graminoids, which will benefit from greater thawing depth, shrubs may be likewise outcompeted (Wang et al., 2016a), affecting also the surface radiation budget and the water cycle.

5. Conclusions

In this study, we explored indirect effects of climate warming on shrub growth, bark thickness, and bark investment by combining experimental manipulation of two suggested environmental drivers of shrub growth – thawing depth and nutrient availability – with dendroecology. Our results showed that shrub growth was mainly limited by surface soil nutrient availability and not by thawing depth, at least in the short-term. Furthermore, the decrease of bark thickness and bark investment found for some of the species, suggests that shrubs might become more vulnerable to climate extremes (frost or drought events), herbivory, and pathogens under climate warming conditions. The combination of dendroecological and experimental methods, manipulating environmental factors in order to simulate projected climate scenarios for the Arctic (e.g. precipitation increase or snow layer decrease), together with increasing number of study shrub species and locations, might reduce the uncertainties related to shrub growth sensitivity to climate. In turn, the better understanding of shrub growth will provide insight into shrub–climate feedbacks in arctic tundra ecosystems.

Acknowledgement

This study was supported by the University Research Priority Program on Global Change and Biodiversity of the University of Zurich (URPP-GCB), the Swiss National Foundation (SNSF project grant 140631), and the Netherlands Organisation for Scientific Research (NWO-ALW, VIDI grant 864.09.014). T.C. Maximov was supported by the Russian Basic Foundation Project No 15-54-71003 Арктика_a.

Appendix A

See Tables A1–A3.

Table A1

Mean soil temperature (standard deviation) of the five experimental blocks for each treatment combination (no-cable (Ct), unheated cable (Ca), heated cable (W), no nutrient addition (NF), and nutrient addition (F)). Temperature is expressed in degrees Celsius.

	CtNF	CaNF	WNF	CtF	CaF	WF
Annual						
0 cm	−7.6 (11.6)	−7.5 (11.6)	−6.8 (10.7)	−7.8 (11.2)	−7.9 (11.1)	−6.8 (10.6)
5 cm	−7.6 (9.6)	−7.6 (9.8)	−6.5 (9.2)	−7.9 (9.1)	−7.8 (9.3)	−6.6 (9.0)
15 cm	−7.8 (8.0)	−7.8 (8.3)	−6.6 (8.0)	−8.0 (7.7)	−7.9 (7.9)	−6.7 (7.8)
25 cm	−7.7 (7.4)	−7.8 (7.8)	−6.7 (7.5)	−8.0 (7.4)	−7.8 (7.5)	−6.8 (7.3)
Growing season (June–August)						
0 cm	+8.9 (2.0)	+8.7 (2.2)	+8.8 (2.3)	+7.9 (1.8)	+7.9 (1.8)	+8.0 (2.0)
5 cm	+5.2 (1.9)	+5.4 (2.3)	+5.5 (2.1)	+3.8 (1.6)	+4.3 (1.9)	+5.0 (1.9)
15 cm	+1.6 (1.2)	+2.1 (1.7)	+2.7 (1.8)	+0.7 (1.2)	+1.3 (1.4)	+2.1 (1.5)
25 cm	+0.3 (1.0)	+0.9 (1.5)	+1.4 (1.6)	−0.1 (1.1)	+0.3 (1.2)	+1.0 (1.4)
No-growing season (September–May)						
0 cm	−13.1 (7.4)	−12.9 (7.4)	−11.6 (7.1)	−13.1 (7.2)	−13.1 (7.1)	−11.7 (7.0)
5 cm	−11.8 (6.9)	−11.9 (7.1)	−10.5 (6.8)	−11.8 (6.8)	−11.8 (6.9)	−10.4 (6.7)
15 cm	−10.9 (6.7)	−11.1 (6.9)	−9.7 (6.7)	−10.9 (6.7)	−10.9 (6.7)	−9.6 (6.7)
25 cm	−10.4 (6.6)	−10.7 (6.8)	−9.5 (6.6)	−10.6 (6.6)	−10.6 (6.6)	−9.4 (6.5)

Table A2

Mean thawing depth (standard deviation) in centimetres of the five experimental blocks for each treatment combination (no-cable (Ct), unheated cable (Ca), heated cable (W), no nutrient addition (NF), and nutrient addition (F)). Thawing depth was measured by introducing vertically a metal rod with centimetre scale until hitting the frozen soil at five points in each plot.

Date	CtNF	CaNF	WNF	CtF	CaF	WF
26/06/ 2013	12.4 (1.3)	15.0 (1.4)	19.6 (2.2)	12.6 (1.8)	13.6 (2.4)	18.0 (1.9)
06/07/ 2013	17.4 (4.2)	21.9 (2.9)	29.5 (1.6)	17.3 (3.0)	19.5 (3.2)	27.7 (2.7)
17/07/ 2014	31.7 (6.7)	39.0 (5.2)	46.0 (4.9)	27.8 (5.7)	33.3 (2.9)	42.8 (2.2)
27/07/ 2014	39.3 (6.0)	46.6 (5.6)	52.1 (4.3)	35.6 (6.9)	42.6 (3.2)	49.8 (1.0)

Table A3

Growth rate during experiment, structural trait, and stem trait means (standard error) for each species (*B. nana* (Betn), *S. pulchra* (Salp), *L. palustre* (Ledp), and *V. vitis-idaea* (Vacv)) and treatment combination (no-cable (Ct), unheated cable (Ca), heated cable (W), no nutrient addition (NF), and nutrient addition (F)).

	CtNF	CaNF	WNF	CtF	CaF	WF
Growth rate ($\mu\text{m yr}^{-1}$)						
Betn	27.7 (2.0)	37.3 (5.1)	32.5 (3.0)	100.5 (15.0)	121.3 (17.3)	107.9 (12.0)
Salp	57.1 (13.4)	51.0 (10.6)	46.2 (6.9)	105.9 (21.2)	100.9 (18.6)	138.6 (17.6)
Vacv	15.1 (1.2)	13.0 (0.6)	12.8 (0.7)	14.5 (1.0)	16.5 (0.9)	18.2 (1.8)
Wood fraction (g g^{-1})						
Betn	0.79 (0.04)	0.54 (0.03)	0.54 (0.03)	0.52 (0.02)	0.53 (0.02)	0.53 (0.02)
Salp	0.76 (0.04)	0.53 (0.03)	0.61 (0.03)	0.52 (0.02)	0.56 (0.03)	0.54 (0.03)
Ledp	0.45 (0.01)	0.48 (0.03)	0.50 (0.04)	0.46 (0.01)	0.44 (0.02)	0.43 (0.01)
Vacv	0.52 (0.05)	0.51 (0.05)	0.51 (0.05)	0.53 (0.06)	0.52 (0.05)	0.52 (0.04)
Xylem diameter (mm)						
Betn	3.86 (0.25)	4.13 (0.32)	4.04 (0.21)	4.59 (0.28)	4.46 (0.28)	4.18 (0.17)
Salp	4.91 (0.44)	4.44 (0.54)	4.15 (0.30)	4.04 (0.50)	5.42 (0.79)	5.25 (0.53)
Ledp	2.80 (0.17)	2.81 (0.17)	3.22 (0.21)	3.06 (0.19)	3.07 (0.25)	3.01 (0.18)
Vacv	0.85 (0.12)	0.61 (0.03)	0.65 (0.04)	0.62 (0.03)	0.68 (0.03)	0.69 (0.04)
Bark thickness (mm)						
Betn	0.57 (0.05)	0.61 (0.05)	0.64 (0.04)	0.71 (0.04)	0.64 (0.04)	0.49 (0.03)
Salp	1.13 (0.10)	1.01 (0.08)	0.96 (0.05)	0.95 (0.07)	1.23 (0.13)	0.99 (0.10)
Ledp	0.18 (0.01)	0.17 (0.01)	0.19 (0.01)	0.19 (0.01)	0.21 (0.01)	0.16 (0.01)
Vacv	0.14 (0.02)	0.12 (0.01)	0.13 (0.01)	0.11 (0.00)	0.13 (0.01)	0.11 (0.01)
Bark investment (mm cm^{-1})						
Betn	0.23 (0.01)	0.24 (0.01)	0.24 (0.01)	0.24 (0.01)	0.22 (0.01)	0.19 (0.01)
Salp	0.32 (0.01)	0.32 (0.01)	0.32 (0.01)	0.34 (0.01)	0.32 (0.01)	0.28 (0.02)
Ledp	0.12 (0.00)	0.11 (0.01)	0.11 (0.00)	0.11 (0.00)	0.12 (0.00)	0.10 (0.01)
Vacv	0.26 (0.01)	0.29 (0.01)	0.29 (0.01)	0.26 (0.01)	0.28 (0.01)	0.24 (0.02)

References

- Ackerman, D., Griffin, D., Hobbie, S.E., Finlay, J.C., 2017. Arctic shrub growth trajectories differ across soil moisture levels. *Glob. Chang. Biol.* 1–9. <http://dx.doi.org/10.1111/gcb.13677>.
- Arco Molina, J.G., Hadad, M.A., Patón Domínguez, D., Roig, F.A., 2016. Tree age and bark thickness as traits linked to frost ring probability on *Araucaria araucana* trees in northern Patagonia. *Dendrochronologia* 37, 116–125. <http://dx.doi.org/10.1016/j.dendro.2016.01.003>.
- Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., Gugerli, F., Henry, G.H.R., Jones, M.H., Hollister, R.D., Jonsdóttir, I.S., Laine, K., Levesque, E., Marion, G.M., Molau, U., Molgaard, P., Nordenhall, U., Raszhivin, V., Robinson, H., Starr, G., Stenstrom, A., Stenstrom, M., Totland, O., Turner, P.L., Walker, L.J., Webber, P.J., Welker, J.M., Wookey, P.A., 1999. Responses of tundra plants to experimental warming: meta-analysis of the International Tundra Experiment. *Ecol. Monogr.* 69, 491–511. <http://www.jstor.org/stable/2657227>.
- Bär, A., Bräuning, A., Löffler, J., 2006. Dendroecology of dwarf shrubs in the high mountains of Norway – A methodological approach. *Dendrochronologia* 24, 17–27. <http://dx.doi.org/10.1016/j.dendro.2006.05.001>.
- Bär, A., Pape, R., Bräuning, A., Löffler, J., 2008. Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. *J. Biogeogr.* 35, 625–636. <http://dx.doi.org/10.1111/j.1365-2699.2007.01804.x>.
- Beringer, J., Chapin, F.S., Thompson, C.C., McGuire, A.D., 2005. Surface energy exchanges along a tundra-forest transition and feedbacks to climate. *Agric. For. Meteorol.* 131, 143–161. <http://dx.doi.org/10.1016/j.agrformet.2005.05.006>.
- Billings, W.D., Mooney, H.A., 1968. The ecology of arctic and alpine plants. *Biol. Rev.* 43, 481–529.
- Blok, D., Heijmans, M.M.P.D., Schaepman-Strub, G., Kononov, A., Maximov, T.C., Berendse, F., 2010. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Glob. Chang. Biol.* 16, 1296–1305. <http://dx.doi.org/10.1111/j.1365-2486.2009.02110.x>.
- Blok, D., Sass-Klaassen, U., Schaepman-Strub, G.D., Heijmans, M.M.P., Sauren, P., Berendse, F., 2011a. What are the main climate drivers for shrub growth in Northeastern Siberian tundra? *Biogeosciences* 8, 1169–1179. <http://dx.doi.org/10.5194/bg-8-1169-2011>.
- Blok, D., Schaepman-Strub, G., Bartholomeus, H., Heijmans, M.M.P.D., Maximov, T.C., Berendse, F., 2011b. The response of Arctic vegetation to the summer climate: relation between shrub cover, NDVI, surface albedo and temperature. *Environ. Res. Lett.* 6, 35502. <http://dx.doi.org/10.1088/1748-9326/6/3/035502>.
- Bonfil, C.J.W., Phillips, T.J., Lawrence, D.M., Cameron-Smith, P., Riley, W.J., Subin, Z.M., 2012. On the influence of shrub height and expansion on northern high latitude climate. *Environ. Res. Lett.* 7, 15503. <http://dx.doi.org/10.1088/1748-9326/7/1/015503>.
- Bret-Harte, M.S., Shaver, G.R., Chapin III, F.S., 2002. Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change. *J. Ecol.* 90, 251–267. <http://dx.doi.org/10.1046/j.1365-2745.2001.00657.x>.
- Buchwal, A., Rachlewicz, G., Fonti, P., Cherubini, P., Gärtner, H., 2013. Temperature modulates intra-plant growth of *Salix polaris* from a high Arctic site (Svalbard). *Polar Biol.* 36, 1305–1318. <http://dx.doi.org/10.1007/s00300-013-1349-x>.
- Chapin III, F.S., Autumn, K., Pugnaire, F., 1993. Evolution of suites of traits in response to environmental stress. *Am. Nat.* 142, 78–92.
- Chapin III, F.S., 1980. The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* 11, 233–260.
- Chapin III, F.S., 2003. Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Ann. Bot.* 91, 455–463. <http://dx.doi.org/10.1093/aob/mcg041>.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. *Ecol. Lett.* 12, 351–366. <http://dx.doi.org/10.1111/j.1461-0248.2009.01285.x>.
- Churchland, C., Mayo-Bruinsma, L., Ronson, A., Grogan, P., 2010. Soil microbial and plant community responses to single large carbon and nitrogen additions in low arctic tundra. *Plant Soil* 334, 409–421. <http://dx.doi.org/10.1007/s11104-010-0392-4>.
- Cornelissen, J.H.C., Callaghan, T., Alatalo, J.M., Michelsen, A., Graglia, E., Hartley, A.E., Hik, D.S., Hobbie, S.E., Press, M.C., Robinson, C.H., Henry, G.H.R., Shaver, G.R., Phoenix, G.K., Jones, D.G., Jonasson, S., Chapin III, F.S., Molau, U., Neill, C., Lee, J.A., Melillo, J.M., Sveinbjörnsson, B., Aerts, R., 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *J. Ecol.* 89, 984–994. <http://dx.doi.org/10.1046/j.1365-2745.2001.00625.x>.
- Cornelissen, J.H.C., 1999. A triangular between leaf size and seed size relationship among woody species: allometry, ontogeny, ecology and taxonomy. *Oecologia* 118, 248–255. <http://dx.doi.org/10.1007/s004420050725>.
- Crawford, R.M.M., 2008. Cold climate plants in a warmer world. *Plant Ecol. Divers.* 1, 285–297. <http://dx.doi.org/10.1080/17550870802407332>.
- DeMarco, J., Mack, M.C., Bret-Harte, M.S., Burton, M., Shaver, G.R., 2014. Long-term experimental warming and nutrient additions increase productivity in tall deciduous shrub tundra. *Ecosphere* 5, 1–22. <http://dx.doi.org/10.1890/ES13-00281.1>.
- Edwards, M., Henry, G.H.R., 2016. The effects of long-term experimental warming on the structure of three High Arctic plant communities. *J. Veg. Sci.* 27, 1–10. <http://dx.doi.org/10.1111/jvs.12417>.
- Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Björkman, A.D., Callaghan, T.V., Collier, L.S., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Fossaa, A.M., Gould, W.A., Grétarsdóttir, J., Harte, J., Hermandutz, L., Hik, D.S., Hofgaard, A., Jarrad, F., Jónsdóttir, I.S., Keuper, F., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lang, S.I., Loewen, V., May, J.L., Mercado, J., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Pieper, S., Post, E., Rixen, C., Robinson, C.H., Schmidt, N.M., Shaver, G.R., Stenström, A., Tolvanen, A., Totland, Ø., Troxler, T., Wahren, C.H., Webber, P.J., Welker, J.M., Wookey, P.A., 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecol. Lett.* 15, 164–175. <http://dx.doi.org/10.1111/j.1461-0248.2011.01716.x>.
- Epstein, H.E., Reynolds, M.K., Walker, D.A., Bhatt, U.S., Tucker, C.J., Pinzon, J.E., 2012. Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. *Environ. Res. Lett.* 7 (12). <http://dx.doi.org/10.1088/1748-9326/7/1/015506>.
- Eugster, W., Rouse, W.R., Pielke SR, R.A., McFadden, J.P., Baldocchi, D.D., Kittel, T.G.F., Chapin, F.S., Liston III, G.E., Vidale, P.L., Vaganov, E., Chambers, S., 2000. Land-atmosphere energy exchange in Arctic tundra and boreal forest: available data and feedbacks to climate. *Glob. Chang. Biol.* 6, 84–115. <http://dx.doi.org/10.1046/j.1365-2486.2000.06015.x>.
- Forbes, B.C., Fauria, M.M., Zetterberg, P., 2010. Russian Arctic warming and greening are closely tracked by tundra shrub willows. *Glob. Chang. Biol.* 16, 1542–1554. <http://dx.doi.org/10.1111/j.1365-2486.2009.02047.x>.
- Francis, J.A., Vavrus, S.J., 2012. Evidence linking Arctic amplification to extreme weather in mid-latitudes. *Geophys. Res. Lett.* 39, 1–6. <http://dx.doi.org/10.1029/2012GL051000>.
- Gärtner, H., Schweingruber, F.H., 2013. *Microscopic Preparation Techniques for Plant Stem Analysis*. Verlag Dr. Kessel, Remagen-Oberwinter (78 pp).
- Gärtner, H., Lucchinetti, S., Schweingruber, F.H., 2014. New perspectives for wood anatomical analysis in dendrosciences: the GSL1-microtome. *Dendrochronologia* 32, 47–51. <http://dx.doi.org/10.1016/j.dendro.2013.07.002>.
- Grime, J.P., 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *J. Veg. Sci.* 17, 255–260. <http://dx.doi.org/10.1111/j.1654-1103.2006.tb02444.x>.
- Hallinger, M., Wilms, M., 2011. No change without a cause – why climate change remains the most plausible reason for shrub growth dynamics in Scandinavia. *New Phytol.* 189, 902–908. <http://dx.doi.org/10.1002/9780470650158.ch3.Key>.
- Hallinger, M., Manthey, M., Wilms, M., 2010. Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytol.* 186, 890–899. <http://dx.doi.org/10.1111/j.1469-8137.2010.03223.x>.
- Hantemirov, R., Shiyatov, S., Gorlanova, L., 2011. Dendroclimatic study of Siberian juniper. *Dendrochronologia* 29, 119–122. <http://dx.doi.org/10.1016/j.dendro.2010.05.001>.
- Hollesen, J., Buchwal, A., Rachlewicz, G., Hansen, B.U., Hansen, M.O., Stecher, O., Elberling, B., 2015. Winter warming as an important co-driver for *Betula nana* growth in western Greenland during the past century. *Glob. Chang. Biol.* 21, 2410–2423. <http://dx.doi.org/10.1111/gcb.12913>.
- Hudson, J.M.G., Henry, G.H.R., 2010. High Arctic plant community resists 15 years of experimental warming. *J. Ecol.* 98, 1035–1041. <http://dx.doi.org/10.1111/j.1365-2745.2010.01690.x>.
- IPCC, 2013. *Climate Change 2013: The Physical Science Basis*. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. <http://dx.doi.org/10.1017/CBO9781107415324>.
- Iturrate-García, M., O'Brien, M.J., Khitun, O., Abiven, S., Niklaus, P.A., Schaepman-Strub, G., 2016. Interactive effects between plant functional types and soil factors on tundra species diversity and community composition. *Ecol. Evol.* 6, 8126–8137. <http://dx.doi.org/10.1002/ece3.2548>.
- Juszkak, I., Erb, A.M., Maximov, C., Schaepman-Strub, G., 2014. Arctic shrub effects on NDVI, summer albedo and soil shading. *Remote Sens. Environ.* 153, 79–89. <http://dx.doi.org/10.1016/j.rse.2014.07.021>.
- Juszkak, I., Eugster, W., Heijmans, M.M.P.D., Schaepman-Strub, G., 2016. Contrasting radiation and soil heat fluxes in Arctic shrub and wet sedge tundra. *Biogeosciences* 13, 4049–4064. <http://dx.doi.org/10.5194/bg-13-4049-2016>.
- Juszkak, I., Iturrate-García, M., Gastellu-Etcheberry, J.-P., Schaepman, M.E., Maximov, T.C., Schaepman-Strub, G., 2017. Drivers of shortwave radiation fluxes in Arctic tundra across scales. *Remote Sens. Environ.* 193, 86–102. <http://dx.doi.org/10.1016/j.rse.2017.02.017>.
- Keuper, F., Parmentier, F.J.W., Blok, D., Van Bodegom, P.M., Dorrepaal, E., Van Hal, J.R., Van Logtestijn, R.S.P., Aerts, R., 2012. Tundra in the rain: differential vegetation responses to three years of experimentally doubled summer precipitation in Siberian shrub and Swedish bog tundra. *Ambio* 41, 269–280. <http://dx.doi.org/10.1007/s13280-012-0305-2>.
- Kokelj, S.V., Burn, C.R., 2003. Ground ice and soluble cations in near-surface permafrost, Inuvik, Northwest Territories, Canada. *Permafrost. Periglac. Process.* 14, 275–289. <http://dx.doi.org/10.1002/ppp.458>.
- Kozłowski, T.T., 1992. Carbohydrate sources and sinks in woody plants. *Bot. Rev.* 58, 107–222.
- Kremers, K.S., Hollister, R.D., Oberbauer, S.F., 2015. Diminished response of arctic plants to warming over time. *PLoS One* 10, 1–13. <http://dx.doi.org/10.1371/journal.pone.0116586>.
- Lens, F., Sperry, J.S., Christman, M.A., Choat, B., Rabaey, D., Jansen, S., 2011. Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus *Acer*. *New Phytol.* 190, 709–723. <http://dx.doi.org/10.1111/j.1469-8137.2010.03518.x>.
- Li, B., Heijmans, M.M.P.D., Berendse, F., Blok, D., Maximov, T., Sass-Klaassen, U., 2016. 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. <http://dx.doi.org/10.1007/s00300-015-1847-0>.

- Liang, E., Eckstein, D., 2009. Dendrochronological potential of the alpine shrub *Rhododendron nivale* on the south-eastern Tibetan Plateau. *Ann. Bot.* 104, 665–670. <http://dx.doi.org/10.1093/aob/mcp158>.
- Lorant, M.M., Goetz, S.J., Beck, P.S.A., 2011. Tundra vegetation effects on pan-Arctic albedo. *Environ. Res. Lett.* 6 (7). <http://dx.doi.org/10.1088/1748-9326/6/2/029601>.
- Marsh, P., Bartlett, P., MacKay, M., Pohl, S., Lantz, T., 2010. Snowmelt energetics at a shrub tundra site in the western Canadian Arctic. *Hydrol. Process.* 24, 3603–3620. <http://dx.doi.org/10.1002/hyp.7786>.
- Myers-Smith, I.H., Hik, D.S., 2013. Shrub canopies influence soil temperatures but not nutrient dynamics: an experimental test of tundra snow-shrub interactions. *Ecol. Evol.* 3, 3683–3700. <http://dx.doi.org/10.1002/ece3.710>.
- Myers-Smith, I.H., Forbes, B.C., Wilkming, 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., Schaeppman-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., Hik, D.S., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ. Res. Lett.* 6 (045509). <http://dx.doi.org/10.1088/1748-9326/6/4/045509>. (15 pp.).
- Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S.A., Wilkming, 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., Schaeppman-Strub, G., Wheeler, J.A., Wipf, S., Guay, K.C., Hik, D.S., Vellend, M., 2015a. Climate sensitivity of shrub growth across the tundra biome. *Nat. Clim. Chang.* 5, 887–891. <http://dx.doi.org/10.1038/nclimate2697>.
- Myers-Smith, I.H., Hallinger, M., Blok, D., Sass-Klaassen, U., Rayback, S.A., Weijers, S.J., Trant, A., Tape, K.D., Naito, A.T., Wipf, S., Rixen, C., Dawes, M.A., Wheeler, J.A., Buchwal, A., Baittinger, C., Macias-Fauria, M., Forbes, B.C., Lévesque, E., Boulanger-Lapointe, N., Beil, I., Ravolainen, V., Wilkming, M., 2015b. Methods for measuring arctic and alpine shrub growth: a review. *Earth-Sci. Rev.* 140 (10.1016/j.earscirev.2014.10.004), 1–13.
- Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R., Laundre, J.A., 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. *Ecology* 72, 242–253.
- 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., Berendse, F., 2015. Permafrost collapse after shrub removal shifts tundra ecosystem to a methane source. *Nat. Clim. Chang.* 5, 67–70. <http://dx.doi.org/10.1038/nclimate2446>.
- Odland, A., Reinhardt, S., Pedersen, A., 2015. Differences in richness of vascular plants, mosses, and liverworts in southern Norwegian alpine vegetation. *Plant Ecol. Divers.* 8, 37–47. <http://dx.doi.org/10.1080/17550874.2013.862751>.
- Osterkamp, T.E., Jorgensen, J.C., 2006. Warming of permafrost in the arctic national wildlife refuge. *Alaska. Permafrost. Periglacial Process.* 17, 65–69. <http://dx.doi.org/10.1002/ppp.538>.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschold, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 61, 167–234. <http://dx.doi.org/10.1071/BT12225>.
- Paine, C.E.T., Stahl, C., Courtois, E.A., Patiño, S., Sarmiento, C., Baraloto, C., 2010. Functional explanations for variation in bark thickness in tropical rain forest trees. *Funct. Ecol.* 24, 1202–1210. <http://dx.doi.org/10.1111/j.1365-2435.2010.01736.x>.
- Park, H., Kim, Y., Kimball, J.S., 2016. Widespread permafrost vulnerability and soil active layer increases over the high northern latitudes inferred from satellite remote sensing and process model assessments. *Remote Sens. Environ.* 175, 349–358. <http://dx.doi.org/10.1016/j.rse.2015.12.046>.
- Payette, S., Delwaide, A., Simard, M., 2010. Frost-ring chronologies as dendroclimatic proxies of boreal environments. *Geophys. Res. Lett.* 37, 1–6. <http://dx.doi.org/10.1029/2009GL041849>.
- Pearson, R.G., Phillips, S.J., Lorant, M.M., Beck, P.S., Damoulas, T., Knight, S.J., Goetz, S.J., 2013. Shifts in Arctic vegetation and associated feedbacks under climate change. *Nat. Clim. Chang.* 3, 673–677. <http://dx.doi.org/10.1038/nclimate1858>.
- Poorter, L., McNeil, A., Hurtado, V.H., Prins, H.H.T., Putz, F.E., 2014. Bark traits and life-history strategies of tropical dry- and moist forest trees. *Funct. Ecol.* 28, 232–242. <http://dx.doi.org/10.1111/1365-2435.12158>.
- Rayback, S.A., Henry, G.H.R., 2005. Dendrochronological potential of the arctic dwarf shrub *Cassiope tetragona*. *Tree-Ring Res.* 61, 43–53. <http://dx.doi.org/10.3959/1536-1098-61.1.43>.
- Reich, P.B., Walters, M.B., Ellsworth, D.S., 1997. From tropics to tundra: global convergence in plant functioning. *Ecology* 94, 13730–13734. <http://dx.doi.org/10.1073/pnas.94.25.13730>.
- Reich, P.B., 2014. The world-wide fast-slow plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301. <http://dx.doi.org/10.1111/1365-2745.12211>.
- Rixen, C., Schwoerer, C., Wipf, S., 2010. Winter climate change at different temporal scales in *Vaccinium myrtillus*, an Arctic and alpine dwarf shrub. *Polar Res.* 29 (10.1111/j.1751-8369.2010.00155.x), 85–94.
- Romanovsky, V.E., Smith, S.L., Christiansen, H.H., 2010. Permafrost thermal state in the polar northern hemisphere during the international polar year 2007–2009: A synthesis. *Permafrost. Periglacial Process.* 21, 106–116. <http://dx.doi.org/10.1002/ppp.689>.
- Rowe, N., Speck, T., 2005. Plant growth forms: an ecological and evolutionary perspective. *New Phytol.* 166, 61–72. <http://dx.doi.org/10.1111/j.1469-8137.2004.01309.x>.
- Joint Russian-German polygon project East Siberia 2011–2014: the expedition Kytalyk 2011. In: Schirmer, L., Pestryakova, L., Wetterich, S., Tumskey, V. (Eds.), Reports on Polar and Marine Research. <http://hdl.handle.net/1013/epic.40369>.
- Schmidt, I.K., Jonasson, S., Michelsen, A., 1999. Mineralization and microbial immobilization of N and P in arctic soils in relation to season, temperature and nutrient amendment. *Appl. Soil Ecol.* 11, 147–160. [http://dx.doi.org/10.1016/S0929-1393\(98\)00147-4](http://dx.doi.org/10.1016/S0929-1393(98)00147-4).
- Schuur, E., Bockheim, J., Canadell, J., Euskirchen, E., Field, C.B., Goryachkin, S.V., Hagemann, S., Kuhry, P., Lafleur, P.M., Lee, H., Mazhitova, G., Nelson, F.E., Rinke, A., Romanovsky, V.E., Shiklomanov, N., Tarnocai, C., Venevsky, S., Vogel, J.G., Zimov, S.A., 2008. Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. *Bioscience* 58, 701–714. <http://dx.doi.org/10.1641/b580807>.
- Schuur, E.A.G., Vogel, J.G., Crummer, K.G., Lee, H., Sickman, J.O., Osterkamp, T.E., 2009. The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature* 459, 556–559. <http://dx.doi.org/10.1038/nature08031>.
- Schweingruber, F., Poschold, P., 2005. Growth rings in herbs and shrubs: life span: age determination and stem anatomy. *For. snow Landsc. Res.* 79, 195–415.
- Schweingruber, F.H., Hellmann, L., Tegel, W., Braun, S., Nievergelt, D., Büntgen, U., 2013. Evaluating the wood anatomical and dendroecological potential of arctic dwarf shrub communities. *IAWA J.* 34, 485–497. <http://dx.doi.org/10.1163/22941932-00000039>.
- Shaver, G.R., Chapin III, F.S., 1991. Production: biomass relationships and element cycling in contrasting arctic vegetation types. *Ecol. Monogr.* 61, 1–31.
- Shaver, G.R., Johnson, L.C., Cades, D.H., Murray, G., Laundre, J.A., Rastetter, E.B., Nadelhoffer, K.J., Giblin, A.E., 1998. Biomass and CO₂ flux in wet sedge tundra: responses to nutrients temperature, and light. *Ecol. Monogr.* 68, 75–97.
- Startsev, N., Lieffers, V.J., Landhäusser, S.M., 2008. Effects of leaf litter on the growth of boreal feather mosses: implication for forest floor development. *J. Veg. Sci.* 19, 253–260. <http://dx.doi.org/10.3170/2008-8.18367>.
- Sturm, M., McFadden, J.P., Liston, G.E., Stuart Chapin, F., Racine, C.H., Holmgren, J., 2001a. Snow-shrub interactions in Arctic Tundra: a hypothesis with climatic implications. *J. Clim.* 14, 336–344. [http://dx.doi.org/10.1175/1520-0442\(2001\)014<0336:SSIIAT>2.0.CO;2](http://dx.doi.org/10.1175/1520-0442(2001)014<0336:SSIIAT>2.0.CO;2).
- Sturm, M., Racine, C., Tape, K., 2001b. Climate change. Increasing shrub abundance in the Arctic. *Nature* 411, 546–547. <http://dx.doi.org/10.1038/35079180>.
- Sturm, M., Douglas, T., Racine, C., Liston, G.E., 2005. Changing snow and shrub conditions affect albedo with global implications. *J. Geophys. Res.* 110, 1–13. <http://dx.doi.org/10.1029/2005JG000013>.
- Tape, K., Sturm, M., Racine, C., 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Glob. Chang. Biol.* 12 (10.1111/j.1365-2486.2006.01128.x), 686–702.
- Tape, K.D., Hallinger, M., Welker, J.M., Ruess, R.W., 2012. Landscape heterogeneity of shrub expansion in arctic Alaska. *Ecosystems* 15, 711–724. <http://dx.doi.org/10.1007/s10021-012-9540-4>.
- Vines, R.G., 1968. Heat transfer through bark, and the resistance of trees to fire. *Aust. J. Bot.* 16, 499–514.
- 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., Jónsdóttir, I.S., Klein, J.A., Magnússon, B., Molau, U., Oberbauer, S.F., Rewa, S.P., Robinson, C.H., Shaver, G.R., Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, Ø., Turner, P.L., Tweedie, C.E., Webber, P.J., Wookey, P.A., 2006. Plant community responses to experimental warming across the tundra biome. *Proc. Natl. Acad. Sci. U. S. A.* 103, 1342–1346. <http://dx.doi.org/10.1073/pnas.0503198103>.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395. <http://dx.doi.org/10.1038/416389a>.
- Wang, P., Limpens, J., Mommer, L., Ruijven, J., Van Nauta, A.L., Berendse, F., Schaeppman-Strub, G., Blok, D., Maximov, T.C., Heijmans, M.M.P.D., Science, E., 2016a. Above and belowground responses of four tundra plant functional types to deep soil heating and surface soil fertilization. *J. Ecol.* <http://dx.doi.org/10.1111/1365-2745.12718>.
- Wang, P., Mommer, L., van Ruijven, J., Berendse, F., Maximov, T.C., Heijmans, M.M.P.D., 2016b. Seasonal changes and vertical distribution of root standing biomass of graminoids and shrubs at a Siberian tundra site. *Plant Soil* 407, 55–65. <http://dx.doi.org/10.1007/s11104-016-2858-5>.
- Weih, M., Karlsson, P.S., 2001. Growth response of mountain birch to air and soil temperature: is increasing leaf-nitrogen content an acclimation to lower air temperature? *New Phytol.* 150 (10.1046/j.1469-8137.2001.00078.x), 147–155.
- Weijers, S., Broekman, R., Rozema, J., 2010. Dendrochronology in the High Arctic: July air temperatures reconstructed from annual shoot length growth of the circumpolar dwarf shrub *Cassiope tetragona*. *Quat. Sci. Rev.* 29, 3831–3842. <http://dx.doi.org/10.1016/j.quascirev.2010.09.003>.
- Weintraub, M.N., Schimel, J.P., 2003. Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in arctic tundra soils. *Ecosystems* 6, 129–143. <http://dx.doi.org/10.1007/s10021-002-0124-6>.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* 33, 125–159. <http://dx.doi.org/10.1146/annurev.ecolsys.33.010802.150452>.
- Woodcock, H., Bradley, R.S., 1994. *Salix arctica* (Pall.): its potential for dendroclimatological studies in the high arctic. *Dendrochronol* 12, 11–22.
- Young, A.B., Watts, D.A., Taylor, A.H., Post, E., 2016. Species and site differences influence climate-shrub growth responses in West Greenland. *Dendrochronologia* 37,

- 69–78. <http://dx.doi.org/10.1016/j.dendro.2015.12.007>.
- van Wijk, M.T., Clemmensen, K.E., Shaver, G.R., Williams, M., Callaghan, T.V., Chapin III, F.S., Cornelissen, J.H.C., Gough, L., Hobbie, S.E., Jonasson, S., Lee, J.A., Michelsen, A., Press, M.C., Richardson, S.J., Rueth, H., 2003. Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Glob. Chang. Biol.* 10, 105–123. <http://dx.doi.org/10.1046/j.1529-8817.2003.00719.x>.
- Zamin, T.J., Grogan, P., 2012. Birch shrub growth in the low Arctic: the relative importance of experimental warming, enhanced nutrient availability, snow depth and caribou exclusion. *Environ. Res. Lett.* 7, 34027. <http://dx.doi.org/10.1088/1748-9326/7/3/034027>.