



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



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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

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(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 $-13.1\text{ }^{\circ}\text{C}$, with minimum monthly means of $-33.5\text{ }^{\circ}\text{C}$ in January and maximum of $11.3\text{ }^{\circ}\text{C}$ 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 (Schirrmeyer 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 ($\text{pH} < 6.5$) 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 $1.5 \times 1.5\text{ m}$ placed at randomly chosen locations within each block. We randomly assigned the six treatment combinations (3 soil warming \times 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 $1\text{ }^{\circ}\text{C}$ 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 $3.7\text{ g K m}^{-2}\text{ y}^{-1}$) 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*

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