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Influence of larval outbreaks on the climate reconstruction potential of an Arctic shrub

Martin Wilmking[a,*], Allan Buras[a,1], Jiří Lehejček[b], Jelena Lange[a], Rohan Shetti[a], Ernst van der Maaten[a,2]

[a] Institute of Botany and Landscape Ecology, University Greifswald, Soldmannstr. 15, 17487 Greifswald, Germany
[b] Department of Environmental Security, Faculty of Logistics and Crisis Management, Tomas Bata University in Zlín, nám. T.G. Masaryka 5555, 760 01 Zlín, Czech Republic

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ABSTRACT

Arctic shrubs have a strong potential for climate and environmental reconstructions in the chronically understudied regions of the high northern latitudes. The climate dynamics of these regions are important to understand because of large-scale feedbacks to the global climate system. However, little is known about other factors influencing shrub ring growth, possibly obscuring their climate signal. For example, as of yet we are not able to differentiate between herbivory or climatically induced growth depressions. Here, we use one of the most common Arctic shrubs, *Alnus viridis* as a test case to address this question. We sampled *Alnus* in Kobbefjord, Greenland, measured shrub-ring width and cell wall thickness and built site chronologies of each parameter. We analysed climate-growth relationships, tested their stability over time and employed a pointer-year analysis to detect growth depressions. We employed bootstrapped transfer function stability tests (BTFS) to assess the suitability of our shrub chronologies for climate reconstruction. Correlations with climate data showed strong significantly positive and stable correlations between summer temperature and ring-width with the exception of the recent decade. A climate reconstruction model failed stability tests, when the complete period of record was used for calibration and verification. Wood anatomy analysis uncovered the occurrence of unusual cell structure (very thin cell walls) in the exceptionally narrow ring of 2004, a recorded insect outbreak year in other parts of Greenland. When excluding the affected ring and a recovery period, the reconstruction model passed all tests, suggesting that the unusual 2004 ring was not climate driven, but rather the result of an insect attack. When combining anatomical analysis with traditional ring-width measurements, we move a step further in potentially distinguishing small rings caused by insect attacks from small rings formed in climatically challenging years. While this study does not provide unambiguous evidence, it does provide potential useful methodological combinations to enable more robust climate reconstructions in areas where climatic records are extremely sparse.

1. Introduction

Temperatures in the Arctic are rising faster than any other region worldwide, because of several feedback mechanisms related to temperature gradients, sea-ice cover, water vapor and albedo (Chapin et al., 2005; Pithan and Mauritsen, 2014; Serreze and Barry, 2011). A spatially explicit, longer-term perspective of that temperature rise is difficult to assess however, because climate stations are sparsely spread and not many stations have been operating for longer than a few decades (Cowtan and Way, 2014). Spatially explicit past and projected variability of climate change in the Arctic is mainly a result of modeling exercises (e.g. see CRU data set) and surrounded by relatively high error estimates (Hodson et al., 2013).

Arctic shrubs can help fill this gap, because they can be found in large parts of the Arctic, can live to considerable ages and form annual growth rings, like trees. Since temperatures are usually limiting growth at these high latitudes, the link between Arctic shrub growth and climate is often strong (Bär et al., 2008; Beil et al., 2015; Blok et al., 2011; Buchwal et al., 2013; Forbes et al., 2010; Gamm et al., 2017; Hallinger et al., 2010; Hallinger and Wilmking, 2011; Hollesen et al., 2015;

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* Corresponding author.
E-mail address: wilmking@uni-greifswald.de (M. Wilmking).
[1] Current address: Forest Ecology and Forest Management, Wageningen University and Research, Droevendaalsesteg 3a, 6708 PB Wageningen, The Netherlands.
[2] Current address: Forest Growth and Woody Biomass Production, TU Dresden, Pienner Str. 8, 01737 Tharandt, Germany.

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Jørgensen et al., 2015; Myers-Smith et al., 2015a; Rozema et al., 2009; Weijers et al., 2017; Young et al., 2016), generally qualifying shrubs for climate and environmental reconstructions (Buras et al., 2012, 2017a; Rayback and Henry, 2006; Rayback et al., 2012; Weijers et al., 2010, 2013). While shrub ring width variability over time has been linked to temperature variability (Havstrom et al., 1995), wood anatomical studies (e.g. using cell wall thickness or vessel lumen area) have recently provided additional insights into the relationship between shrub growth and climate drivers or other environmental parameters such as glacier melt (Buras et al., 2017a; Lehejček et al., 2017; Nielsen et al., 2017), opening up new avenues to interpret the shrub ring record.

Shrub growth can be influenced by a combination of climate and environmental factors, and disentangling these different factors is often challenging, since they might act at different time scales, for different time periods or only episodically. One widespread example of an environmental factor affecting shrub growth with varying periodicity or only episodically in the Arctic is herbivory. Herbivory in Arctic shrubs can be the result of animal species ranging from large vertebrates such as moose (Tape et al., 2016), caribou, reindeer or muskox (Post and Pedersen, 2008; Vowles et al., 2017) to snowshoe hares (Ewacha et al., 2014), and birds such as ptarmigan (Tape et al., 2010) (for a review see Christie et al., 2015), or invertebrates (Barrio et al., 2017; Kozlov and Zvereva, 2017; Young et al., 2016 and references therein). In the case of insects, larval stages e.g. from *Epirrita autumnata, Operophtera brumata* or *Eurois occulta* can episodically defoliate large areas of subarctic and arctic vegetation, which has been documented for Fennoscandia and Greenland (Dahl et al., 2017; Tenow et al., 2007; Young et al., 2016). Generally, herbivory in the Arctic leads to the (partial) loss of foliage, a reduced photosynthetic apparatus, and subsequent lower growth resources, which might result in lower net ecosystem productivity (Lund et al., 2017) and lower radial growth of stems. When then using shrub stem growth as proxy of past climate variability, the subsequent logical question becomes: How to differentiate between narrow rings caused by climate and those caused by herbivory?

This study has therefore two main aims:

1) To investigate the climate signal and climate reconstruction potential in a widespread Arctic shrub, using *Alnus viridis* ssp. *crispa* (mountain alder) as an example.
2) To explore the potential of wood anatomy to disentangle climatic influences on mountain alder shrub growth from herbivory induced growth depressions.

2. Methods

2.1. Sample species

Alnus viridis has a near circumpolar northern distribution and can be found in large parts of the Subarctic and Low Arctic. It is generally a mid to large size shrub growing along small water courses or in moist habitats. It can defend its twigs and buds with the toxins pinosylvin and pinosyl, making it less palatable at least to snowshoe hares (Bryant et al., 1987). *Alnus viridis* has the ability to grow rapidly, while at the same time investing in effective antibrowsing defenses, likely a consequence of its capacity to fix nitrogen (Hendrickson et al., 1991 in Christie et al., 2015). The species can be subdivided in several subspecies which are ecologically very similar. In Northeastern North America and Greenland, our sample region, the subspecies is *Alnus viridis* ssp. *crispa* (hereafter alder). Its distribution in Greenland is concentrated on the south-western coastal areas to approximately 68°N (Fig. 1).

2.2. Field site

Our field site was in Kobbefjord, Greenland, close to the Kobbefjord Research Station (64.136578°N, 51.380204°E). The vegetation in the research area was generally low arctic tundra with several shrub species such as *Salix glauca*, *Betula nana*, *Juniperus communis* and, as the largest shrub, alder. Alder in the area reached canopy heights of up to 3 m in thickets and could be found mainly on the south facing slopes.

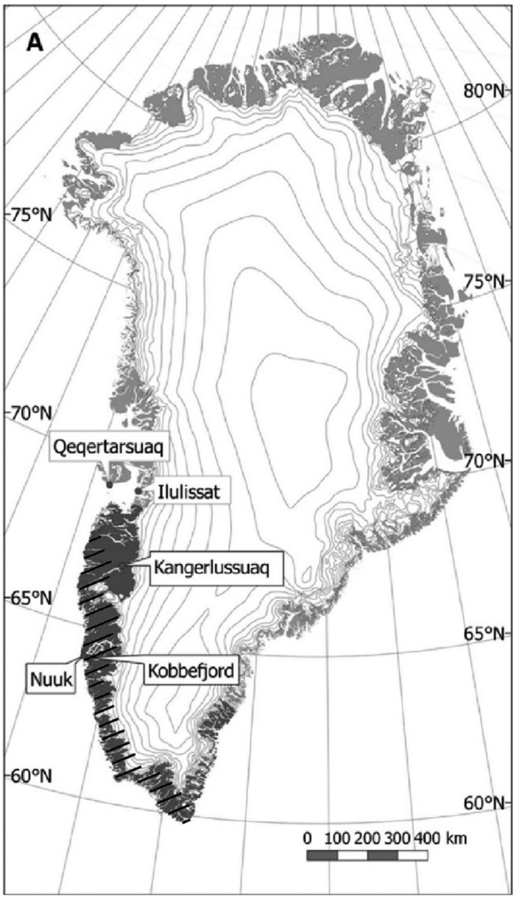

Fig. 1. Map of Greenland modified after Lund et al. (2017) with distribution *of Alnus viridis* ssp. *crispa* (hatched) and the moth *Eurois occulta* (in dark grey).

2.3. Sampling

We employed a nested sampling design which combined intensive and extensive sampling strategies for alder shrubs (Table 1). First, we intensively sampled alder in August of 2012 in a relatively restricted area in an elevational belt between 200 and 240 m above sea level (m.a.s.l.) on a slope with south to southwest exposure. From each individual shrub, we selected the thickest and/or highest stem and cut it as low as possible, often at the root collar. We selected three to five stem sections along the length of that stem, according to the serial sectioning technique (Kolishchuk, 1990; Myers-Smith et al., 2015b; Wilmking et al., 2012). All sampled shrubs were dominant (except one, which was co-dominant) and all had erect stem forms and full foliage. Stem length varied between 135 and 350 cm. Second, we extensively sampled alder in 2013 at different elevations and at several locations on

Table 1
Metadata for shrub sampling and analysis.

	intensive sampling	extensive sampling	total
n shrubs	20	22	42
n stem sections	62	22	84
n radii measured	156	22	178
n shrubs crossdated	20	18	38
n shrubs used	19	18	37