

Individual white spruce (*Picea glauca* (Moench) Voss)  
growth limitations at treelines in Alaska

I n a u g u r a l d i s s e r t a t i o n

zur

Erlangung des akademischen Grades eines

Doktors der Naturwissenschaften (Dr. rer. nat.)

der

Mathematisch-Naturwissenschaftlichen Fakultät

der

Universität Greifswald

vorgelegt von

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Greifswald, 18.06.2018

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**Tag der Promotion:** 16.10.2018

*"Gauss's conversation turned to chance,  
the enemy of all knowledge,  
and the thing he had always wished to overcome.  
Viewed from up close, one could detect the  
infinite fineness of the web of causality  
behind every event.  
Step back and the larger patterns appeared:  
Freedom and Chance were a question of distance,  
a point of view."*

- Daniel Kehlmann, Measuring the World



## Abstract

White spruce (*Picea glauca* (Moench) Voss) is one of the most common conifers in Alaska and various treelines mark the species distribution range. Because treelines positions are driven by climate and because climate change is estimated to be strongest in northern latitudes, treeline shifts appear likely. However, species range shifts depend on various species parameters, probably most importantly on phenotypic plasticity, genetic adaptation and dispersal. Due to their long generation cycles and their immobility, trees evolved to endure a wide variety of climatic conditions. In most locations, interannual climate variability is larger than the expected climate change until 2100. Thus treeline position is typically thought of as the integrated effect of multiple years and to lag behind gradual climate change by several decades. Past dendrochronological studies revealed that growth of white spruce in Alaska can be limited by several climatic variables, in particular water stress and low temperatures. Depending on how the intensity of climate warming, this could result in a leading range edge at treelines limited by low temperatures and trailing treelines where soil moisture is or becomes most limiting.

Climate-growth correlations are the dendrochronological version of reaction norms and describe the relationship between an environmental variable and traits like tree-ring parameters (e.g. ring width, wood density, wood anatomy). These correlations can be used to explore potential effects of climate change on a target species. However, it is known that individuals differ with respect to multiple variables like size, age, microsite conditions, competition status or their genome. Such individual differences could be important because they can modulate climate-growth relationships and consequently also range shifts and growth trends. Removing individual differences by averaging tree-ring parameters of many individuals into site chronologies could be an oversimplification that might bias estimates of future white spruce performance. Population dynamics that emerge from the interactions of individuals (e.g. competition) and the range of reactions to the same environmental drivers can only be studied via individual tree analyses. Consequently, this thesis focuses on factors that might alter individual white spruce' climate sensitivity and methods to assess such effects. In particular, the research articles included explore three topics:

1. First, clones were identified via microsatellites and high-frequency climate signals of clones were compared to that of non-clonal individuals. Clonal and non-clonal individuals showed similar high-frequency climate signals which allows to use clonal and non-clonal individuals to construct mean site chronologies. However, clones were more frequently found under the harsher environmental conditions at the treelines which could be of interest for the species survival strategy at alpine treelines and is further explored in the associated RESPONSE project A5 by David Würth.
2. In the second article, methods for the exploration and visualization of individual-tree differences in climate sensitivity are described. These methods represent a toolbox to explore causes for the variety of different climate sensitivities found in individual trees at the same site. Though, overlaying gradients of multiple factors like temperature, tree density and/or tree height can make it difficult to attribute a single cause to the range of reaction norms (climate growth correlations).

3. Lastly, the third article attempts to disentangle the effect of age and size on climate-growth correlations. Multiple past studies found that trees of different ages responded differently to climatic drivers. In contrast, other studies found that trees do not age like many other organisms. Age and size of a trees are roughly correlated, though there are large differences in the growth rate of trees, which can lead to smaller trees that are older than taller trees. Consequently, age is an imperfect proxy for size and in contrast to age, size has been shown to affect wood anatomy and thus tree physiology. The article compares two tree-age methods and one tree-size method based on cumulative ring width. In line with previous research on aging and wood anatomy, tree size appeared to be the best predictor to explain ontogenetic changes in white spruce' climate sensitivity. In particular, tallest trees exhibited strongest correlations with water stress in previous year July.

In conclusion, this thesis is about factors that can alter climate-growth relationships (reaction norms) of white spruce. The results emphasize that interactions between climate variables and other factors like tree size or competition status are important for estimates of future tree growth and potential treeline shifts. In line with previous studies on white spruce in Alaska, the results of this thesis underline the importance of water stress for white spruce. Individuals that are taller and that have more competitors for water appear to be most susceptible to the potentially drier future climate in Alaska. While tree ring based growth trends estimates of white spruce are difficult to derive due to multiple overlaying low frequency (>10 years) signals, all investigated treeline sites showed highest growth at the treeline edge. This could indicate expanding range edges. However, a potential bottleneck for treeline advances and retreats could be seedling establishment, which should be explored in more detail in the future.



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## Contributions to this thesis and the research articles

- *Abstract* – Solely written by Mario Trouillier.
- *Introduction* – Solely written by Mario Trouillier.
- *Chapter I* – Martin Wilmking led the writing of the manuscript and analyzed the data together with Alan Buras. Pascal Eusemann, Martin Schnittler, Mario Trouillier, David Würth, Jelena Lange, Marieke van der Maaten-Theunissen, and Glenn Patrick Juday collected and managed the respective data, discussed and commended on the manuscript.
- *Chapter II* – Mario Trouillier analyzed the data and led the writing of the manuscript. Marieke van der Maaten-Theunissen, Jill E. Harvey, David Würth, Martin Schnittler, and Martin Wilmking discussed methodologies and commented on the manuscript.
- *Chapter III* – Mario Trouillier analyzed the data and led the writing of the manuscript. Samples and data were collected by Mario Trouillier, David Würth, Andreas Burger, and others. Mario Trouillier, Marieke van der Maaten-Theunissen, Tobias Schwarnweber, David G. Würth, Andreas Burger, Martin Schnittler and Martin Wilmking discussed methodologies and wider implications of the findings and commented on the manuscript.
- *Synthesis* – Solely written by Mario Trouillier.
- *Conclusions and Outlook* – Solely written by Mario Trouillier.

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## Scope of this thesis

The increasing temperatures due to climate change will result in species specific responses. Reactions of white spruce in Alaska do not only affect the species own future viability, but could have a variety of consequences: White spruce distribution-range edges often mark the biome transition-zone between tundra and taiga, which might shift. This also could affect the global carbon cycle, alter the albedo and thus feedback loops to climate change and shift the habitat for other species. White spruce is also an important forestry species. To study the response of white spruce to climate change it is necessary to assess traits that vary with respect to the changing climate variables. This link between the respective trait and climatic variables is often referred to as the reaction norm and allows to hypothesize about the future growth-performance of the species.

This thesis is part of the graduate college RESPONSE of the German Research Foundation (DFG) and the main objective in the first generation was to identify and critically evaluate traits and reaction norms of the respective species. Tree-ring parameters like width, wood density or wood anatomical parameters are traits that are known to be sensitive to the climatic conditions. However, which climate variable (e.g. spring temperature or summer precipitation) is 'recorded' in tree-ring chronologies depends on the species and the site conditions. Furthermore there is an ongoing discussion on the temporal stability of climate-growth correlations (reaction norms) as well as on individual differences in climate sensitivity and growth trends. Consequently, to investigate these difficulties regarding tree's reaction norms, this thesis focuses particularly on effects that modulate individual tree's climate sensitivity. Such effects would impede simple linear extrapolations from white spruce growth in the past to its future growth and distribution-range dynamics.

In particular this thesis focuses on the effects of tree size, age and competition on climate-growth correlations of white spruce in Alaska. Furthermore, in collaboration with David Würth from the RESPONSE project A5 genetic, methods are deployed to identify clones and compare their growth and climate signal to that of non-clonal individuals.

# 1 Introduction

## 1.1 Tree responses to climate change

All species require certain environmental conditions to survive, grow and to produce offspring. For trees, species-specific temperature, moisture and soil nutrient conditions are particularly important, but the biotic environment (e.g. competition, facilitation, pathogens, and predation) affects tree's population-viability too. Earth's climatic conditions vary widely across the globe and result in diverse ecosystems with species adapted to local conditions. The ecological niche concept describes under which conditions different species can survive and maximize their fitness, which then shapes species' spatial distribution range (MacArthur 1972, Hannah 2014, Pocheville 2015). When environmental conditions are relatively stable and only show regular diurnal and seasonal dynamics, and when fundamental niche does not change due to evolution, species distribution-ranges should be stable in time apart from certain stochastic variations. However, due to anthropogenic greenhouse-gas emissions climate is changing very fast and species' optimal conditions for survival are shifting spatially (Pachauri et al. 2014). One approach to explore range dynamics are species distribution models, specifically bioclimatic envelope models (Hampe 2004, Elith and Leathwick 2009). These models assess potential future distribution ranges based on the climate within the current distribution range of a species and various climate change scenarios. While this approach certainly helps to understand and predict range shifts, the accuracy is limited because of necessary simplifications of the highly complex response of species to climate change (Araújo and Peterson 2012).

When facing unprecedented climatic conditions, trees, as other organisms, will react in one of three general ways: 1) adaptation to the new environment, 2) migration to more favorable environments or 3) extinction (Aitken et al. 2008, Hannah 2014). One of the reasons why trees could be particularly vulnerable to climate change is their immobility in combination with their longevity and the length of generation cycles: Neither can trees move directly to more favorable climatic conditions, like many animals can, nor can they produce multiple generations within a few decades and thus move comparatively fast via seed dispersal as annual or biennial plants. The speed of climate change could thus be too fast to track for some tree species and cause distribution-ranges that lag behind the potential distribution range. For example it has been estimated for sitka spruce (*Picea sitchensis* (Bong.) Carr.) that 1°C per generation would be the fastest tolerable speed of climate change over a longer time period, which is insufficient to keep up with current rates of climate change (Aitken et al. 2008). Probably the most common dispersal mechanism of trees is seed dispersal. While pollination can be counted as dispersal too, it is essentially 'just' the transport of genetic material and does not allow range expansions (Koenig and Ashley 2003). Seed dispersal is often modelled with dispersal kernels based on more or less empirical observations (Vittoz and Engler 2007). However, these dispersal kernels mostly cover distances below 100m, with the exception of zoochory and anthropochory (Vittoz and Engler 2007). There is only little knowledge regarding long-distance dispersal, which might be particularly important in the response to climate change, while it is estimated that rare long-distance dispersal events can have large impacts (Aitken et al. 2008, Taleb 2008, Nathan et al. 2008).

Because trees cannot migrate directly and seed dispersal beyond the current range might be limited too, adaptation is an important option for trees to cope with climate change. Phenotypic plasticity as well as genotypic adaptation are powerful mechanisms that can facilitate the survival of species. The longevity of trees affects how these mechanisms are functioning: During the potentially century-long life of a tree a wide range of climates is experienced, potentially including dry and wet summers, different vegetation period length and extreme events like late frosts. To survive such variable conditions, phenotypic plasticity facilitates relatively fast adaptations. Generally, passive and active plasticity can be distinguished, as well as reversible and irreversible plasticity (Begon et al. 2006, Valladares et al. 2006, Merilä and Hendry 2014). Apart from ontogenetic changes, tree-ring width and other proxies for woody biomass production vary passively, which means trees will grow more or less depending on the favorability of environmental conditions (Fritts 1976, Cook and Kairiukstis 1990). Series of very narrow rings can be the result of a series of climatically unfavorable years and show the remarkable levels of resilience that trees can exhibit (Lloret et al. 2011, Príncipe et al. 2017). Even missing rings are frequently reported in dendrochronological studies (Cook and Kairiukstis 1990). In contrast to traits like tree-ring width that change passively and might be seen as proxy traits, other traits show active adaptations to the environment. Changes in wood anatomical properties likely belong to the most important active adaptation mechanisms for trees. Wood anatomy has become increasingly important to study phenotypic plasticity in trees, as it might show how trees can actively react to more or less stressful environments. For example, tracheids in conifers serve as pipelines for water transport, and to keep hydraulic resistance low it would be favorable to increase the lumen diameter (Ryan and Yoder 1997, Ryan Michael G. et al. 2006). However, tracheids with a large lumen diameter are prone to drought induced cavities, thus trees face a tradeoff concerning wood anatomy between water conductivity and other functions such as stability and drought resistance (Hacke et al. 2001, Sperry et al. 2008, Cuny et al. 2014). Trees can actively alter their wood anatomy in response to environmental cues like spring drought, allowing insights into tree's survival strategies and how they might be affected by climate change (Fonti et al. 2009). While wood anatomical phenotypic plasticity is irreversible, the continuous secondary growth (stem and branch diameter-increment) of trees with each successive vegetation period allows trees to repeatedly update their adaptation and thus increase their fitness and survival chances. Sometimes, this adaptation is even actively managed by humans: In one of the few fields of applied dendrochronology, phenotypic plasticity of wood anatomy is actively managed in viticulture: Irrigation in spring can be used to increase the vessel size during secondary growth in spring. In this way, trees are more susceptible to drought later that year, which can be favorable, as to a certain extent drought stress will result in more aromatic grapes for wine production (personal communication Schweingruber et al. 2015).

Next to phenotypic plasticity, trees show genetic adaptation to environmental conditions. This means that often local genotypes (ecotypes) exist, whose genetic composition is favorable for the local conditions. Such ecotypes evolved through the local selection pressure. Common garden experiments with different provenances have often been used to demonstrate such genetic adaptation to local site conditions (Savolainen et al. 2007, Merilä and Hendry 2014). However, these experiments do not give any information

on the speed of the adaptation spreading to where it might be needed most (Hoffmann and Sgrò 2011). Consequently, assisted migration is frequently debated (McLachlan et al. 2007, Vitt et al. 2010). On the local scale, gene flow is typically high and differences in growth performance cannot be attributed to genetic differences (King et al. 2013, Kruse et al. 2018). While one study by Heer et al. (2018) could link differences in single nucleotide polymorphisms (SNPs) with photosynthesis and drought stress, the effect sizes are relatively low. This could be because a large variety of genes is involved in adaptations and these adaptations are only of use in stressful years (Aitken et al. 2008), while adaptations typically come at a price and require additional resources (Allen Orr 2000, Botero et al. 2015). Hence, the ‘genetic signal’ in tree-ring series might be relatively low compared to effects like climate and competition, which cause much larger inter-individual variations in secondary growth.

To summarize, trees rely on various mechanisms to cope with climate variability and long-term changes in climate. One mechanism cannot be said to be more important than another. It is the magnitude and time scale of environmental change that determines which mechanism is best suited, while the transition from one mechanisms to another can mark evolutionary tipping points and an increased thread to population viability (Botero et al. 2015). This can for example be the case when phenotypic plasticity slows down genetic adaptation by reducing selection pressure (Botero et al. 2015). In this thesis, as well as in the related work of David Würth, phenotypic plasticity (Chapter II & III) and genetic effects (Chapter I) of white spruce are explored.

## 1.2 Treelines

Treelines are popular sites in research, in particular for the exploration of abiotic growth-limiting factors for trees and species distribution ranges (Körner 2012). In contrast to closed canopy forests, treelines typically consist of only one tree species, gradually declining tree density and canopy closure, altered tree morphology (‘Krummholz’) or tree islands (Harsch and Bader 2011). In closed canopy forests mostly competition for light limits tree growth and interannual differences in light limitation are low. Hence trees in a forest are often more ‘complacent’, i.e. they show weaker climate-growth correlations. On the other side, tree-ring chronologies from treelines are often more sensitive to climate variables like temperature or precipitation that vary significantly between years and are thus less complacent. Consequently, to increase the signal to noise ratio, treelines sites are preferably sampled (Fritts 1976, Cook and Kairiukstis 1990). Climatically-controlled growth makes treeline sites particularly suitable to study climate-change effects on individual trees and tree ecosystems. Moreover, treelines are not just borders of species distribution ranges but also mark a transition between very different ecosystems, typically from taiga to tundra. If climate warming shifts these transition zones this can have important consequences for global carbon models (Pan et al. 2011), species depending on respective habitats and albedo, which is an important feedback loop in climate change (Bonan 2008, Euskirchen et al. 2016).

Mechanisms that have been hypothesized to explain temperature driven treeline positions are controversially debated. Two contrasting hypotheses in particular have been tested and discussed repeatedly in the literature: the carbon-source and carbon-sink

limitation hypotheses. The carbon-source hypothesis proposes that photosynthesis, the source of tree's carbohydrates, is more temperature limited and thus inhibits tree growth. In contrast, carbon-sink limitation suggests that cambial activity (cell division) is most temperature. This would mean that trees cannot grow despite the availability of carbohydrates. A strong case has been built in favor of the carbon-sink hypothesis by showing that the concentration of non-structural carbohydrates (NSC) increases with elevation for many alpine treelines worldwide (Hoch and Körner 2012, Fajardo et al. 2012). Since it were mainly starch and not sugar concentrations that increased, it does not appear to be an osmotic adjustment to protect for frost damage. Furthermore, in evergreen plants photosynthesis often does not even completely stop at 0°C air temperature, which appears to ensure NSC supply even at low temperatures (Grace et al. 2002). It also has been argued that the existence of shrubs, Krummholz and other plants beyond the treeline appears to contradict the temperature limitation of photosynthesis. However, some studies do indicate that temperature-limited photosynthesis could also be involved in determining the treeline location, and by that support the source-limitation hypothesis. In particular low soil temperatures might affect photosynthesis indirectly (Wieser 2012), for example by reduced nutrient mineralization and resulting lower nitrogen availability for leaves and thus reduced photosynthesis (Sveinbjörnsson et al. 2002, 2010, McNown and Sullivan 2013). Furthermore, the same finding of increasing NSC concentrations towards the treeline that has been used to support carbon sink limitation, was also used to advocate in favor of the source limitation hypothesis: While higher NSC contents could mean that trees cannot utilize available carbon for tree growth, it could also be that trees actively increase NSC storage at the cost of reduced growth as survival strategy (Sala et al. 2012, Wiley and Helliker 2012, Dietze et al. 2014), which is supported by a variety of studies with respect to temperature and water limited growth (Canham et al. 1999, Gleason and Ares 2004, Achard et al. 2006). In contrast, others consider NSC storage the lowest priority C-sink (Hartmann et al. 2018). Generally it was argued by Sveinbjörnsson et al. (2010) that one should not jump to the conclusion that tree growth is sink limited simply by showing that growth is likely not source limited. This appears particularly true when considering that (above-ground) wood production is highly plastic and not necessarily larger than other carbon sinks like respiration, seed production, active NSC storage, litter production or below ground carbon allocation (Ryan et al. 2004, Dietze et al. 2014, Klein and Hoch 2015, Hartmann and Trumbore 2016, Hartmann et al. 2018).

Despite this disagreement how exactly temperatures limits tree survival, there is general agreement regarding the importance of temperature for the location of alpine treelines. Around the world, mean growing season temperature of alpine treeline is about 6.6°C (Hoch and Körner 2012). However, treelines can vary in shape, depending on how temperature affects trees directly or indirectly. In particular diffuse, abrupt, island and Krummholz treelines can be distinguished, and it has been hypothesized that these treeline shapes are the result of different mechanisms, namely direct growth limitation, seedling mortality, dieback and facilitation (Harsch and Bader 2011). Increase in temperature due to climate change will thus likely cause different responses in these different treeline types. In fact, many treelines do not yet show a spatial shift, while infilling is observed more frequently (Körner 2012). Krummholz treelines might see a change in the shape of trees from



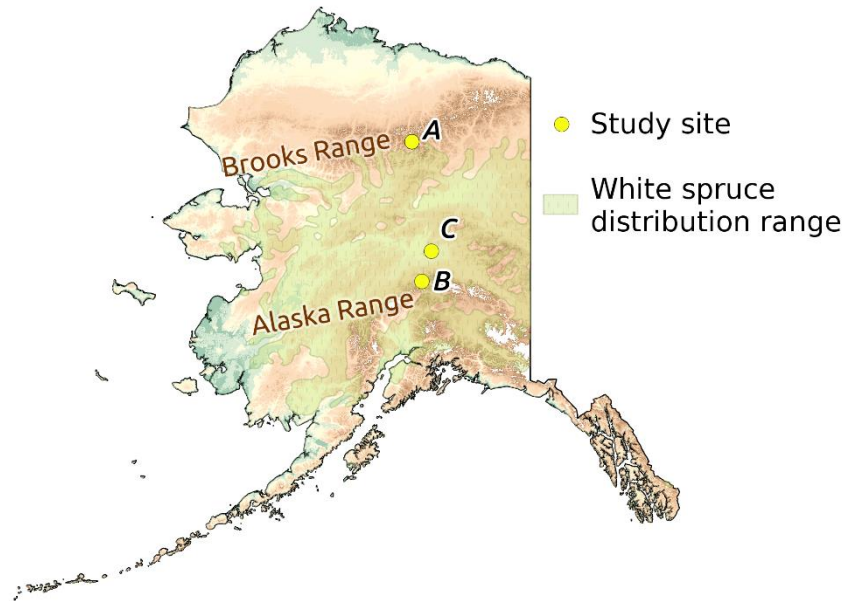
multi stemmed creeping individuals to single stemmed erect trees (Devi et al. 2008). As argued before, treeline shifts are of interest because they mark the border of a species distribution-range and shifts could indicate if the dispersal can keep up with the speed of climate change. But trees' response to climate change is inherently slow and impeded by their ecology. This can also be explained by the aforementioned model on evolutionary tipping points by Botero et al. (2015), which estimates at what speed of environmental change species react with plasticity or genetic adaptation: Due to trees longevity and interannual differences in climate, evolutionary selection favored high levels of plasticity to allow survival under the various climatic conditions trees experience in their life. In probably most ecosystems around the world trees experience interannual differences in climate that are much larger than current levels of climate change. Trees could not persist if they were not able to withstand single years or even series of years of relatively unfavorable climate, because stochastically such events are likely to happen on a regular scale within centuries. Because of this, treeline position is the product of integrated effects of at least a couple of decades and treeline shifts will inherently lag behind climate change (Paulsen et al. 2000, Aitken et al. 2008). This argument is further supported by the fact that alpine treelines typically stretch over less than 100m in elevation, which corresponds to a relatively small temperature difference of 0.6°C. This difference is typically much smaller than interannual temperature differences (Paulsen et al. 2000). Further, more specific reasons for slow treeline shifts are listed by Körner (2012) and highlight the importance of 1) the matching of masting years and favorable climate for seedling establishment, 2) slow growth rates at treelines, 3) cold-induced dieback, 4) warmer winters rather than warmer/prolonged vegetation periods, 5) seedlings that require shelter, and 6) competition with heat and shrub vegetation.

While tree growth at alpine treelines is strongly related to low temperatures, low precipitation can additionally limit tree growth. The continental climate in the boreal zone does not have an explicit dry season, but annual precipitations is still frequently below 400mm (Peel et al. 2007). The main difference in the growth-limiting factors temperature and water is that temperature affects all individuals similarly while water is a resource for which trees can compete. Consequently, treeline gradients are potentially also competition gradients and water stress might decrease with tree density along the treeline (Choler et al. 2001, Wang et al. 2016, Jochner et al. 2017). Water limitation at alpine treelines has been shown for white spruce treeline sites in Alaska (Lloyd Andrea H. 2005, Ohse et al. 2012) and might become more important in the future because climate warming also increases the evapotranspiration.

### 1.3 The ecology of white spruce in Alaska

White spruce is a plastic species with a relatively wide ecological niche that is controlled by various abiotic variables in Alaska (Burns and Honkala 1990). Temperature, precipitation, as well as nutrient limitations have been shown to directly affect white spruce growth. However, climate drives more processes in Alaska's boreal forest and treeline ecosystems than just individual tree's biomass production. For example, successional trajectories, including changes in species interactions and wildfire dynamics are also expected to change

(Johnstone et al. 2010, Mann et al. 2012, Euskirchen et al. 2016, Trugman et al. 2018). The primary and secondary succession in Alaska resulted in a multitude of forest types with different species compositions (Viereck et al. 1992). White spruce is mainly growing on comparatively warm soils without permafrost and can be found in most parts of Alaska but not in the very north (Figure 1).



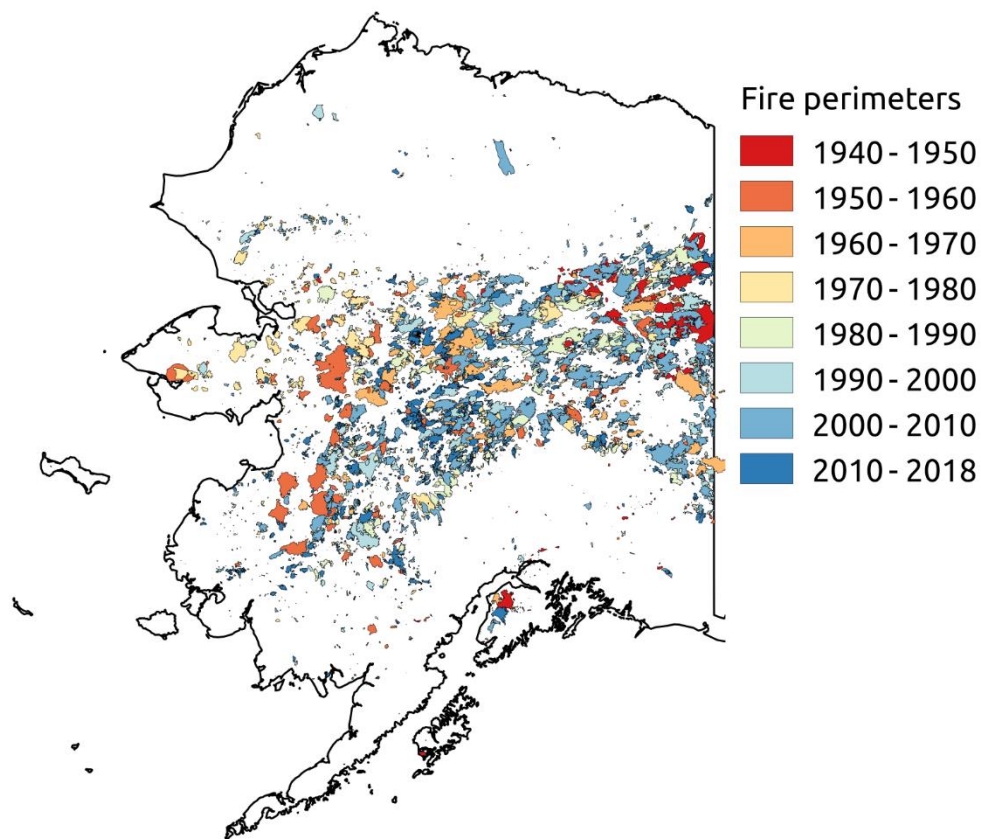
**Figure 1** The distribution range of white spruce in Alaska (Prasad and Iverson 2003) and the location of the three study sites of this thesis in the Brooks Range (A), Denali National (B) Park, and Interior Alaska (C).

Black spruce (*Picea mariana* Mill.), on the other hand, is often growing on permafrost, while broad leafed species like aspen (*Populus tremuloides* Michx.) are typically found as pioneer species and on the warmest soils.

Regarding direct climatic effect on white spruce growth in Alaska, dendrochronological studies most frequently reported negative correlations between tree growth and summer temperatures, which is typically attributed to temperature-induced drought stress (Barber et al. 2000, D'Arrigo et al. 2004, Driscoll et al. 2005, Yarie and Van Cleve 2010, Beck et al. 2011, Juday et al. 2015). Interestingly, even at treeline and floodplain sites along rivers, summer precipitation appears to be important (Wilmking and Juday 2005, Yarie 2008, Ohse et al. 2012). However, despite studies reporting correlations between summer temperature/drought and tree growth, the negative effect of regional warming on long-term growth trends in white spruce has recently been questioned (Sullivan et al. 2017, Cahoon et al. 2018). Naturally, increasing temperatures do not only induce drought stress but can also be favorable for growth in the subarctic climate of Alaska. In particular at colder sites or in colder years, white spruce growth appears to be limited by low temperatures (Williams et al. 2011).

More indirectly, climate effects ecosystem succession. Chapin et al. (2006) aptly describe the multitude successional trajectories after wildfires as a maze. Similarly, the conceptual framework on climate change effects on the boreal forest in Alaska by Wolken et al. (2011) highlights a multitude of interacting processes. Soil substrate, permafrost, topography, competition, herbivory and pest outbreaks (spruce budworm - *Choristoneura*

*spec.*, and aspen leaf miner - *Phyllocnistis populiella*, Chambers) all can have profound impacts on forest structure and succession (Burns and Honkala 1990, Chapin et al. 2006). One of the most prominent drivers of succession in Interior Alaska are wildfires, to which particularly black spruce and white spruce forests are susceptible because of their high fuel loads. Extensive fires are very frequent in Interior Alaska with fire return intervals of 80 to >250 years depending on the local climate. Consequently, fires frequently disturb otherwise very slow successional processes and ecosystem states (Payette 1992, Chapin et al. 2006). Hardly any area in Interior Alaska was not affected by fire in the last decades as can be seen from fire monitoring since 1940 (Figure 2).



**Figure 2** Monitoring since 1940 shows the frequency and size of wildfires in Alaska.

Data: <https://fire.ak.blm.gov> ; 13.05.2018.

Fire return intervals and the size of burned area per year is affected by forest management and climate (Calef et al. 2015). On longer time scales the Pacific Decadal Oscillation (PDO) appears to affect fire dynamics by periodically drier and moister weather (Duffy et al. 2005). While fires are frequent in Interior Alaska, the Brooks Range and the Alaska Range hardly experience wild fires.

In conclusion, white spruce growth and distribution range depends on how climate affects growth directly, as well as on indirect climatic effects like wild-fire dynamics and forest succession.



## 1.4 Climate-change effects on white spruce in Alaska

Temperature increases in Alaska due to climate change are expected to be higher than the global average. Northern latitudes, including Alaska, will likely experience a warmer and potentially drier climate (van Oldenborgh et al. 2013, Wang et al. 2014, Huang et al. 2017). The medium CO<sub>2</sub> emission scenario RCP 4.5 forecasts mean annual temperature increases of 3°C in the period 2081 to 2100, compared to 1986-2005 (Pachauri et al. 2014). Until now, the temperatures in Fairbanks rose by about 1.4°C and the vegetation period prolonged by 45% within the last ~100 years and this trend might proceed (Wendler and Shulski 2009). Regarding precipitation trends most frequently dryer climate is anticipated in the future (Bieniek et al. 2014), but significant uncertainties exist regarding future precipitation trends in Alaska (McAfee et al. 2014). This means that the climate in Alaska might become drier because of temperature-induced increases in evapotranspiration if precipitation is not increasing sufficiently to keep up. In the past, the boreal forest in Alaska already experienced considerable climate variability and showed high levels of resilience (Chapin et al. 2010). However, the recent climate change is unprecedented and significant uncertainties exist regarding how trees, taiga and tundra will react (Chapin et al. 2010). Generally, there will be direct and indirect effects of climate change on white spruce:

Direct effect include changes in the growth performance due to more or less favorable climate, but also effects fructification. Various dendroecological studies explored how white spruce responded to past climate and often found negative correlations with summer temperature. Understanding white spruce growth limitations can help to predict future changes in forest productivity, which is important for local forestry as well as for global carbon models. However, correctly identifying long term growth trends from tree-ring data is challenging, even without considering successional cycles and wild-fire dynamics. Bowman et al.(2013) describe multiple effects that can bias growth-trend estimates that are typical for dendrochronological datasets. The general problem is that tree growth is the sum or function of a variety of different factors, including climate, tree size, genetics and competition, as described in the linear aggregated model for tree-ring series (Fritts 1976, Cook 1985, Cook and Kairiukstis 1990, Speer 2010). Even though dendrochronologists try to correct for some biases with the '*dark art of detrending*' (Rob Wilson at TRACE 2018 conference), long-term growth trends often remain uncertain (Bowman et al. 2013, Peters et al. 2015).

In case of white spruce in Alaska, changes in climate sensitivity have been observed at various sites and sprouted concerns regarding future growth. This decrease or increase in the strength of climate-growth correlations is often been referred to as the divergence problem (Driscoll et al. 2005, D'Arrigo et al. 2008, Williams et al. 2011, Ohse et al. 2012). This phenomenon raised concerns because it could be interpreted as a violation of the Uniformitarian Principle, which would mean that one cannot deduce tree growth from climate data or vice versa. However, this concern appears unreasonable since all empirical science relies on the assumption that past experiments and observations would lead to the same outcome if they were repeated. Consequently, it appears more likely that the divergence problem rather reflects an insufficient understanding of tree growth (Wilmking et al. 2017). Typically dendrochronologists follow Liebig's Law of the Minimum and assume that the most limiting environmental variable controls the growth rate at a point in time

(Speer 2010). Hence the loss of sensitivity to one climate variable could either indicate that conditions improved and the factor that limited the growth rate in the past lost its importance, or it could indicate that another environmental variable is now even more limiting than the previous factor. Hence no conclusion regarding climate-change induced growth trends can be drawn from the observation of the divergence problem alone. The general link between (linear) climate-growth correlations and the complexity of the tree growth-process is discussed in detail in section 3.1 in the synthesis of this thesis.

Fructification of white spruce is characterized by masting years, which might change in intensity and frequency. Depending on local site conditions and climate, white spruce is masting every 2-6 up to 6-12 years (Burns and Honkala 1990). Because certain climatic conditions are required to trigger masting as well as for the establishment of the seedlings in the successive years, the specific combinations of climatically favorable years for regeneration are not happening very often. When series of years with favorable weather occur, recruitment waves can be observed (Miller et al. 2017) but it is uncertain if these weather conditions are becoming more or less frequent under a climate change scenario. Altered white spruce regeneration is also linked to treeline shifts in Alaska. Recruitment beyond the current treelines appears to benefit from warmer climate at temperature-limited alpine treelines, while increased evapotranspiration might decrease seedling survival (Miller et al. 2017), particularly at local south-exposed bluffs.

Apart from these direct effects, climate change will likely also affect white spruce indirectly via changes in wildfire dynamics or shifts in biotic interactions (competition, pest outbreaks). Increased fire frequency might favor post-fire successional stages and thus it was hypothesized that angiosperms (mainly paper birch - *Betula papyrifera* and balsam poplar - *Populus balsamifera*) might benefit from climate change, even though angiosperms might suffer from more frequent and/or intense insect outbreaks (Trugman et al. 2018, Cahoon et al. 2018). Another indirect consequence of climate change could be increased competition for water. Increasing tree density at treelines from the tundra to the taiga also poses a competition gradient. It has been shown that competition can modulate climate-growth correlations, affect forest and treeline dynamics by increased self-thinning, as well as drought resistance and resilience (Wang et al. 2016, Alam et al. 2017, Bottero et al. 2017, Trugman et al. 2018).

In conclusion, climate change is likely to have a variety of impacts on white spruce ecosystems by affecting various processes. Not just direct effects on tree growth are to be expected, but also changes in forest-succession processes, including fire dynamics, pest outbreaks and competition. While the full complexity of these dynamics cannot yet be assessed in holistic models, in this thesis tree-ring datasets are assessed, including tree metadata, because they pose useful tools to shed light on some of the key processes in Alaska's boreal forest.

## 1.5 Methods, sites and samples to study white spruce dynamics

Because of the long generation times and the size of mature white spruce, experimental setups where all environmental variables are controlled are difficult to implement. Instead, dendrochronology makes use of the fact that tree rings can be century long records of past growth, and collects wood cores directly in nature. Because such field ecological methods

have the disadvantage that the environmental variables cannot be controlled, statistical analysis is often impeded by the multitude of abiotic and biotic variables that do affect tree growth. Furthermore, often only climate data from the nearest weather station or gridded climate data is available, but no data on microsite differences in soil or competition. However, the multitude of varying factors in nature can potentially be important because they cover cumulative effects of several parameters and effect interaction that might have been overlooked in laboratory experiments. In dendroecology the majority of variance in tree-ring parameters often remains unexplained. This unexplained variance or 'noise' impedes the detection of factors with smaller effect sizes. However, the technological advancement, from remote sensing to computational power, has made observational ecology more popular again, in particular when large spatial and temporal scales are concerned that cannot be manipulated and controlled. (Sagarin and Pauchard 2010).

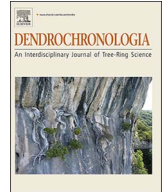
This thesis is largely based on dendrochronological data sets of white spruce collected at three treeline sites in Alaska (Figure 1): 1) An latitudinal and elevational treeline in the Brooks Range (67.95°N, 149.75°W), 2) an elevational treeline in the Denali National Park and Reserve (63.74°N, 149.01°W), and 3) a local treeline on a steep south-exposed bluff in Interior Alaska close to the city of Fairbanks (64.70°N, 148.31°W). All sites are based on south-exposed slopes and the treelines indicate an abiotic gradient that limits tree growth (Fritts 1976, Cook and Kairiukstis 1990). The three sites exemplarily cover different types of treelines and thus potentially different growth limitations and different responses to climate change. The surface of wood cores that were collected in the field were prepared with a core microtome (Gärtner and Nievergelt 2010) and ring width was measured digitally (see Chapter II and III for details). Before the research-question specific analyses in Chapter II and III, tree-ring data as well as climate data were detrended with a 30 years cubic smoothing spline and 50% frequency cutoff via the dplR package (Bunn 2008) for R (R Core Team 2015). Additionally autocorrelation was removed from tree-ring data. This cautious approach attempts to avoid spurious correlations due to long-term trends in time-series data. Such trends are likely the effect of multiple climatic and non-climatic variables and should thus not be attributed to one factor alone. Consequently this approach might underestimates correlation strength but was a good foundation for the assessment of effects that modulate individual climate-growth correlations, as outlined in the scope of this thesis.

## 2 Published articles and submitted manuscripts

**Chapter I** of this thesis explores vegetative reproduction of white spruce in Alaska to compare climate sensitivity and general growth performance of clones and non-clones. **Chapter II** outlines four methods to assess if and which individual tree parameters can modulate climate-growth correlations (reaction norms) and might thus play a role in for growth trends and range dynamics. Lastly, **Chapter III** attempts to disentangle age and size effects on tree's climate sensitivity. The manuscript compares exemplarily for a white spruce dataset age and size dependent methods to evaluate effects of tree's ontogenetic development. It appeared most likely that tree size alters climate-growth correlations, not tree age. Consequently the cumulative ring-width method is best suitable to assess ontogenetic changes in climate sensitivity (reaction norms) by calculating stem diameters retrospectively from tree rings.

## Chapter I

Wilmking, M., A. Buras, P. Eusemann, M. Schnittler, M. Trouillier, D. Würth, J. Lange, M. van der Maaten-Theunissen, and G. P. Juday. 2017. **High frequency growth variability of White spruce clones does not differ from non-clonal trees at Alaskan treelines.** *Dendrochronologia* 44:187–192.



## ORIGINAL ARTICLE

# High frequency growth variability of White spruce clones does not differ from non-clonal trees at Alaskan treelines



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## ARTICLE INFO

## Keywords:

*Picea glauca*  
Reproduction  
Dendroclimatology  
Dendroecology

## ABSTRACT

Northern and elevational treelines are classic sites for dendroclimatological studies. At these marginal sites only one climate parameter is usually considered growth limiting and trees from these sites are therefore used to reconstruct that parameter back in time. Marginal sites are also those sites within a species range, where clonal reproduction is most frequent. Clonal growth can ensure plant species survival and growth under stressful conditions or if the environmental conditions do not allow sexual reproduction, e.g. by layering, by stems resprouting after damage, or through the exchange of resources between different clone ramets ("stems"). We literally stumbled across clonal and non-clonal growth forms of White spruce growing intermingled with each other at two Alaskan treeline sites. The two growth forms could not be distinguished a priori in the field. After sampling and detection of clones we thus asked whether clonal ramets and non-clonally grown trees (singletons) showed similar growth patterns. Clones were identified by identical multilocus genotypes in a SSR microsatellite genotyping analysis and radial growth was analyzed using traditional tree ring width methods. High-frequency growth patterns were very similar between singletons and clonal ramets in Alaskan treeline White spruce, thus posing no problem in including both reproductive strategies in a classic dendroclimatological investigation.

## 1. Introduction

Treelines represent impressive examples of clearly visible edges of a species' geographical distribution, where usually one environmental factor is considered growth limiting. Often this factor is inferred to be climatic and in the case of northern and elevational treelines, is generally known or suspected to be growing season temperature (Holtmeier, 2009; Körner, 1998, 2012). Treeline systems are often assumed to react strongly and directly to climate change, and in fact the climate sensitivity of treelines and treeline advance in reaction to climate warming is well documented (Lloyd and Fastie, 2002; Esper and Schweingruber, 2004; Wilmking et al., 2004; Harsch et al., 2009). Treelines have thus been extensively used to reconstruct past climatic dynamics using tree rings (e.g. ring width, density, isotopes) as climate archives (Esper, 2002; Grudd, 2008; Grudd et al., 2002; Helama et al., 2009; Linderholm and Gunnarson, 2005; Linderholm et al., 2014; McCarroll et al., 2013; Porter et al., 2013, 2014).

As an ecological question, much research has been conducted on treeline dynamics and the processes that govern treeline formation (for an extensive review see Körner, 2012). Many treeline systems include upright single trees as well as krummholz and tree islands, the latter being generally clonally in origin (Holtmeier, 2009). Clonality in trees is often associated with stressful or disturbed habitats, because it enhances a genotype's probability of survival in such habitats by producing multiple descendants of a single zygote (Eriksson and Jerling, 1990) and may increase the quality of the micro-environment by facilitation effects (Scott and Hansell, 2002; Holtmeier and Broll, 2010). Clonality also enhances a plant's ability to regenerate from damage (Peterson and Jones, 1997) and allows more efficient foraging for resources and sharing of resources among several connected ramets (Hutchings and De Kroon, 1994). Therefore, clonality generally increases towards the edge of a species' geographical distribution range (Klimešová and Doležal, 2011; Silvertown, 2008), where species-specific stress is typically higher.

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In northern Alaska, a region where temperatures have been rising faster than almost anywhere else on the globe during recent decades (Bekryaev et al., 2010; Walsh et al., 2014), treelines are formed mainly by White spruce (*Picea glauca* (Moench) Voss). White spruce normally regenerates through sexual reproduction via seeds. The species can also reproduce vegetatively through layering, resulting in at least temporarily connected ramets, which might affect radial growth patterns through resource exchange between them. Clonal growth forms in White spruce treelines have been shown to exist in the northern Canadian lowlands, usually associated with continuous permafrost conditions (Walker et al., 2012; Scott and Hansell, 2002). There, clonal growth forms can make up a considerable proportion of a population's individual trees at the tundra-treeline ecotone (Walker et al., 2012). During a study focusing on population genetics at Alaskan treelines, we found clonal growth in White spruce at several upland, non-permafrost locations in northern and Interior Alaska, classic sites for dendroclimatological investigations. At these sites, clonal and non-clonal growth forms co-exist under the same environmental conditions and we therefore asked the basic but important question: Do the two differing reproductive strategies result in similar growth patterns?

2. Material and methods

2.1. Study species

*Picea glauca* (Moench) Voss (White spruce) is one of the signature tree species of the North American boreal forest. It occurs across the entire continent from Newfoundland and Labrador in the east to Alaska in the west, forming the northern treeline in the western part of North America (Lloyd et al., 2005; Payette and Filion, 1985). Its vertical distribution ranges from sea level to 1520 m (Burns and Honkala, 1990), often forming the elevational treeline. The species is widely used in forestry in Canada and the United States and is one of the most important commercial species in the North American boreal forest (Burns and Honkala, 1990).

2.2. Study areas and sample collection

We established two study areas at White spruce treeline in Alaska, at classic dendroclimatological sampling sites at the presumably temperature limited range edge of that species (Fig. 1), one at northern

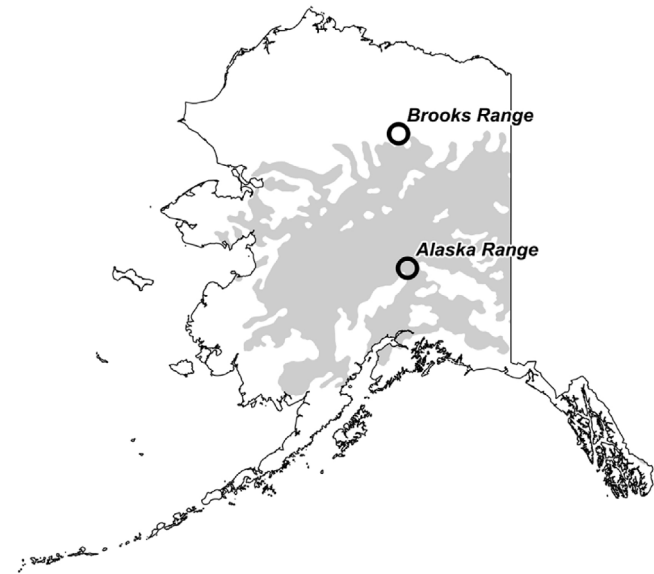


Fig. 1. Location of the study sites, grey shading indicating the range of White spruce in Alaska (Little, 1971). The Brooks Range site represents the northern treeline, while the Alaska Range site is an elevational treeline.

Table 1  
Description of study sites.

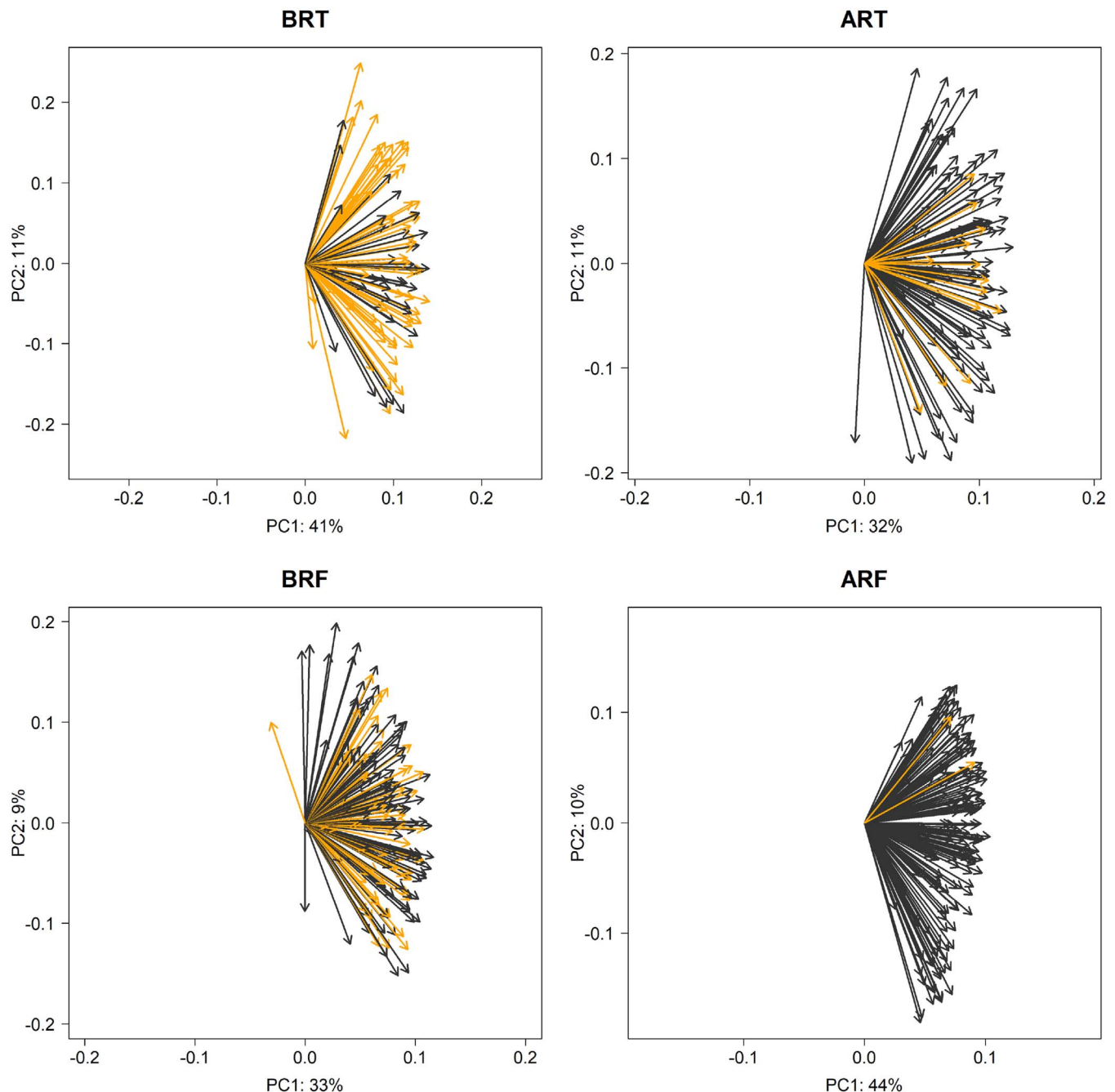
	BRT	BRF	ART	ARF
Latitude	67.95	67.95	63.74	63.72
Longitude	−149.74	−149.75	−149.01	−149.01
Elevation [m a.s.l.]	923	876	1008	802
n individual stems	358	470	313	380
n singletons analyzed (sample depth of the singleton chronology)	34	110	113	168
n clones	23	27	10	10
n clonal ramets analyzed (sample depth of the clonal chronology)	64	59	13	2

Latitude, longitude and elevation refer to the center point of each plot. “n individual stems” is the total number of visual tree-like structures or individual stems in the plot (clone ramets or singletons), “n singletons analyzed” is the number of singletons used in the analyses (=sample depth of singleton chronology), “n clones” is the total number of clones (comprised of several ramets each) in the respective plot and “n clonal ramets analyzed” is the total number of ramets (belonging to different clones) which we analyzed in a respective plot.

treeline in the Central Brooks Range (67°56'N, 149°44'W) (BR) and one at elevational treeline in the Alaska Range (Denali National Park and Preserve, 63°43'N, 149°00'W) (AR). Growing on south-facing slopes, White spruce forms the local treeline at an elevation of about 960 m and 1050 m a.s.l., at the two sites respectively, undisturbed by human activity. Due to the southern exposure, soils at both sites are usually completely unfrozen during the summer down to the bedrock (pers. observation during numerous field campaigns and measurements over three years with soil temperature loggers). Within each area, we selected two plots of roughly one ha each of nearly monospecific White spruce stands including the current upper limit of the treeline ecotone (treeline plot, T) and closed canopy forest areas below (forest plot, F). The two plots bordered each other in the Brooks Range, while in the Alaska Range the two plots were separated by about 1 km of nearly flat terrain. This set-up resulted in four plots, two in each study area (Brooks Range treeline, BRT; Brooks Range forest, BRF; Alaska Range treeline, ART; Alaska Range forest, ARF). Needles for DNA extraction were collected from all living trees inside the plots, dried and stored on silica gel. Tree height and, if the tree was tall enough, diameter at breast height (dbh) were recorded from all trees and saplings using a Suunto PM-5 clinometer and a measuring tape. Tree cores were collected from all trees with a dbh larger than 5 cm, usually two cores were taken perpendicular to each other as low as possible to the ground.

2.3. Genotyping

Dry needles were powdered in a Retsch ball mill MM301 (Retsch, Germany). Approximately 70 mg of needle tissue was used for DNA extraction with the Invisorb Spin Plant Mini Kit (Stratec, Birkenfeld, Germany) following the manufacturer's protocol. DNA concentration was measured with NanoDrop Lite (Thermo Fisher Scientific, Waltham, MA, USA), adjusted to 5 ng and used as template DNA for microsatellite analysis in three different multiplex reactions (Eusemann et al., 2014). Clones were determined by identification of identical multilocus genotypes (MLG) using GenAEx 6 (Peakall and Smouse, 2006). To account for scoring errors (see Schnittler and Eusemann, 2010) we allowed a threshold of two deviating loci within an MLG, i.e. a putative clone. As genetic diversity measures we calculated clonal diversity  $R = (G-1)/(N-1)$  with G being the number of genotypes and N the number of sampled trees and its opposite parameter, clonality  $C = 1-R$  (Dorken and Eckert, 2001), as well as the proportion of clonally derived trees within the stand. Probability of Identity (PID) was calculated using GenAEx 6, and null allele frequencies were calculated using GenePop'007 (Rousset, 2008). Apart from the clonality estimations, all population genetic



**Fig. 2.** PCGA (Principal Component Gradient Analysis) is not able to differentiate between clonal ramets (orange) and singletons (black) suggesting similar growth patterns independent of reproductive strategy. Each arrow represents one individual tree or clonal ramet. Also visible is the high percentage of clonal ramets in the BRT site, the climatically most stressful site at northern treeline. Axes numbers reflect the amount of variance explained by the respective principal component. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

calculations were performed on a genet basis, i.e. after exclusion of clonal duplicates from the data set. Percental clonal growth was defined as the number of ramets belonging to clones at a site versus the total amount of stems/ramets at that site. Non-clonally grown stems were called “singletons”.

#### 2.4. Tree-ring analysis

All tree cores were air dried and then glued transverse side up onto wooden sample holders. Surfaces were prepared with either a core-microtome (WSL, Switzerland; Gärtner and Nievergelt, 2010) or by progressively finer sanding until cellular structures became visible. Tree cores were then either measured for ring width using a LINTAB 5 table

(1/1000 mm resolution) and the TSAPWin Software (Frank Rinn, Heidelberg, Germany), or scanned on a flatbed scanner (Epson Perfection V700 Photo) with 3200 dpi and subsequently measured using CoReRecorder (v. 7.7, Cybis Elektronik & Data AB, Sweden) with 1/1000 mm precision. Crossdating was done visually using CDendro (v. 7.7, Cybis Elektronik & Data AB, Sweden) and verified using COFECHA and the dplR package (Bunn, 2008) of the R programming software v. 3.1.1 (R Foundation for Statistical Computing). To reduce effects of different age cohorts, we restricted our analyses to all trees that had established until 1976. We chose 1976 as it demarcates an important year with respect to the shift of a locally important climate mode, i.e. the Pacific Decadal Oscillation (Ohse et al., 2012). We also used subsets of trees (e.g. all trees established before 1947, another shift



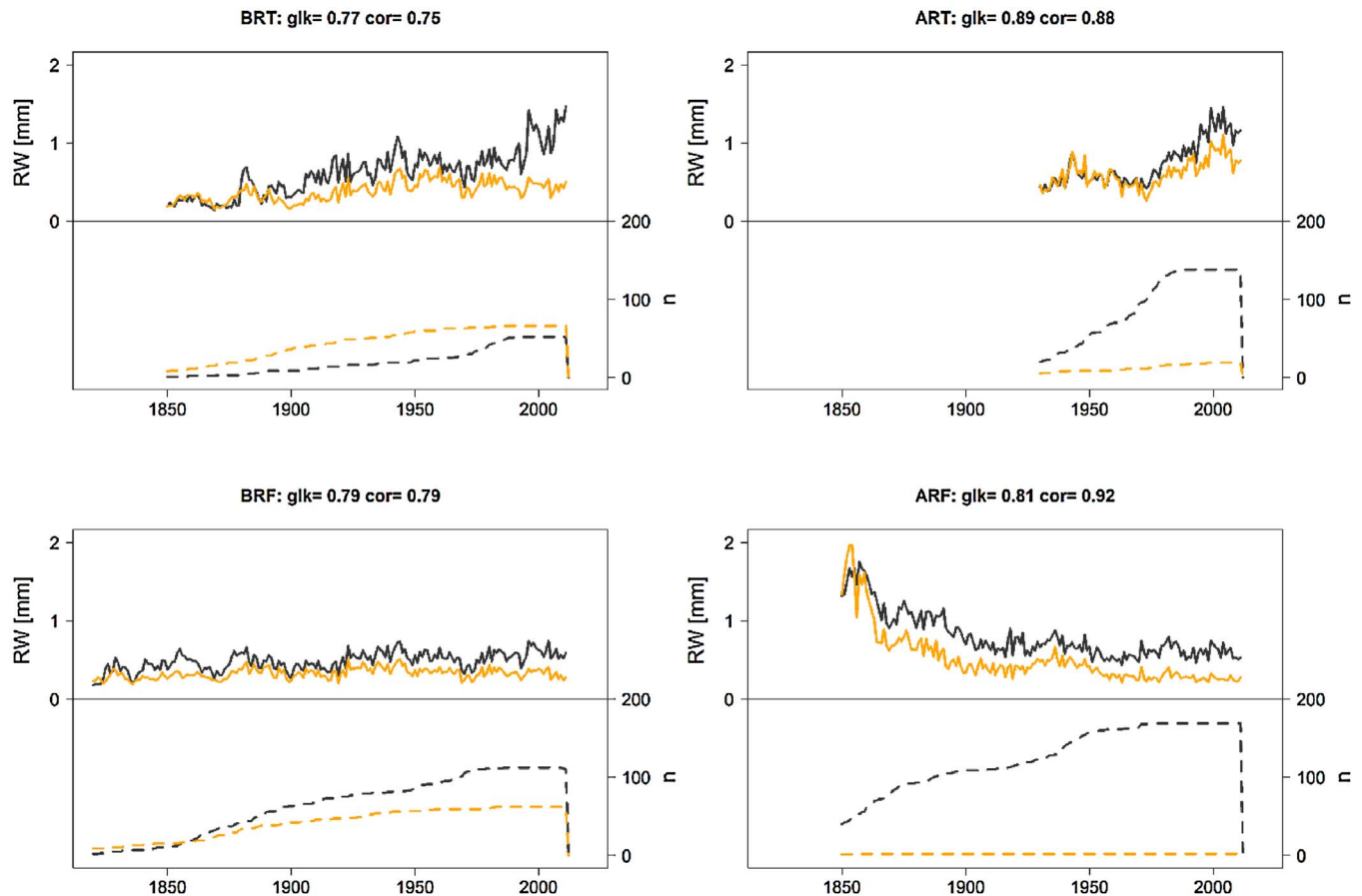


Fig. 3. Singletons (black curve) generally outperform clone ramets (orange curve) in terms of absolute radial growth, but high-frequency growth variability is very similar. Sample sizes delineated by dashed lines and right y-axis. Glk: Gleichläufigkeit, cor: Pearson correlation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of the PDO) and all trees in the analyses, but the results were always very similar. Raw ring width was individually detrended using a 50-year cubic smoothing spline with 50% frequency cut-off (dplR-package, Bunn, 2008) for visualizing and comparing the growth patterns of the two groups (clonal vs. seed-derived ramets/stems) over time. Detrended ring-widths were used in a Principal Component Gradient Analysis (PCGA, Buras et al., 2016) to explore whether clone ramets and singletons expressed specific and differing growth variability. For the PCGA, detrended ring-widths were variance-scaled and only the common overlap period was considered in the analysis, i.e. the period from 1976 to 2012. To compare absolute growth (represented by raw ring-widths) as well as detrended growth between clone ramets and singletons, we computed respective master chronologies per site using a biweight robust mean. Gleichläufigkeit (Eckstein and Bauch, 1969; Buras and Wilmsking, 2015) and (Pearson) correlations between master chronologies were computed per site, reflecting growth similarity between ramets and singletons. We repeated all analyses with BAI, the results were similar and we opted to only present the raw and RWI chronologies.

### 3. Results and discussion

In the field, we were unable to distinguish clonal ramets from singletons. Only the genetic analyses showed a higher frequency of clonal growth towards the range margins of White spruce. Clonality is generally higher in the northern treeline (Brooks Range) than the Central Alaska elevational treeline site (Denali NP). Within each site, clonality is generally higher in treeline versus forest plots (Table 1).

The pattern of higher clonality in more stressful habitats is consistent with the literature (Klimešová and Doležal, 2011; Silvertown,

2008; Honnay and Bossuyt, 2005). Although clonal growth forms have not been extensively documented in White spruce, clonality can be high in White spruce stands on permafrost soils, such as in the northern Canadian lowlands close to Churchill, Manitoba (Scott and Hansell, 2002) or the Mackenzie delta (Walker et al., 2012). Our analysis appears to be one of the first, if not the first, to show White spruce clones on upland, non-permafrost soils. We can only speculate about the mechanism, but layering, or ingrowth of low hanging branches, seems the main mechanism responsible. Since layering results, at least for a period of time, in a connection of the different ramets facilitating resource exchange between them, radial growth patterns might be affected by clonality.

Our PCGA-analysis has shown, however, that growth patterns of clone ramets and singletons could not be separated (Fig. 2). At all four sampling plots, the range of clone ramet growth variability is well within the spectrum of growth variability of the singletons (but notice the low sample size in ARF). This suggests that climate-growth relationships of clone ramets and singletons do not differ systematically, since PCGA-gradients have been reported to reflect gradients of climate-growth relationships (Buras et al., 2016). While singletons generally outperform single clone ramets in terms of absolute radial growth (Fig. 3), the detrended time series of ring width show virtually no difference between clonal ramet and singleton growth chronologies (Fig. 4). We also tested subsets of data related to different PDO phases, the results (not shown) are the same: The similarity in growth forms is consistent through time and across different PDO phases. Gleichläufigkeit between the two chronologies per plot was high and varied between 0.77 and 0.89 for the raw ring width and 0.80 and 0.86 for the detrended chronologies. Correlation between the two chronologies per plot was high as well, and varied between 0.75 and 0.92 for the raw

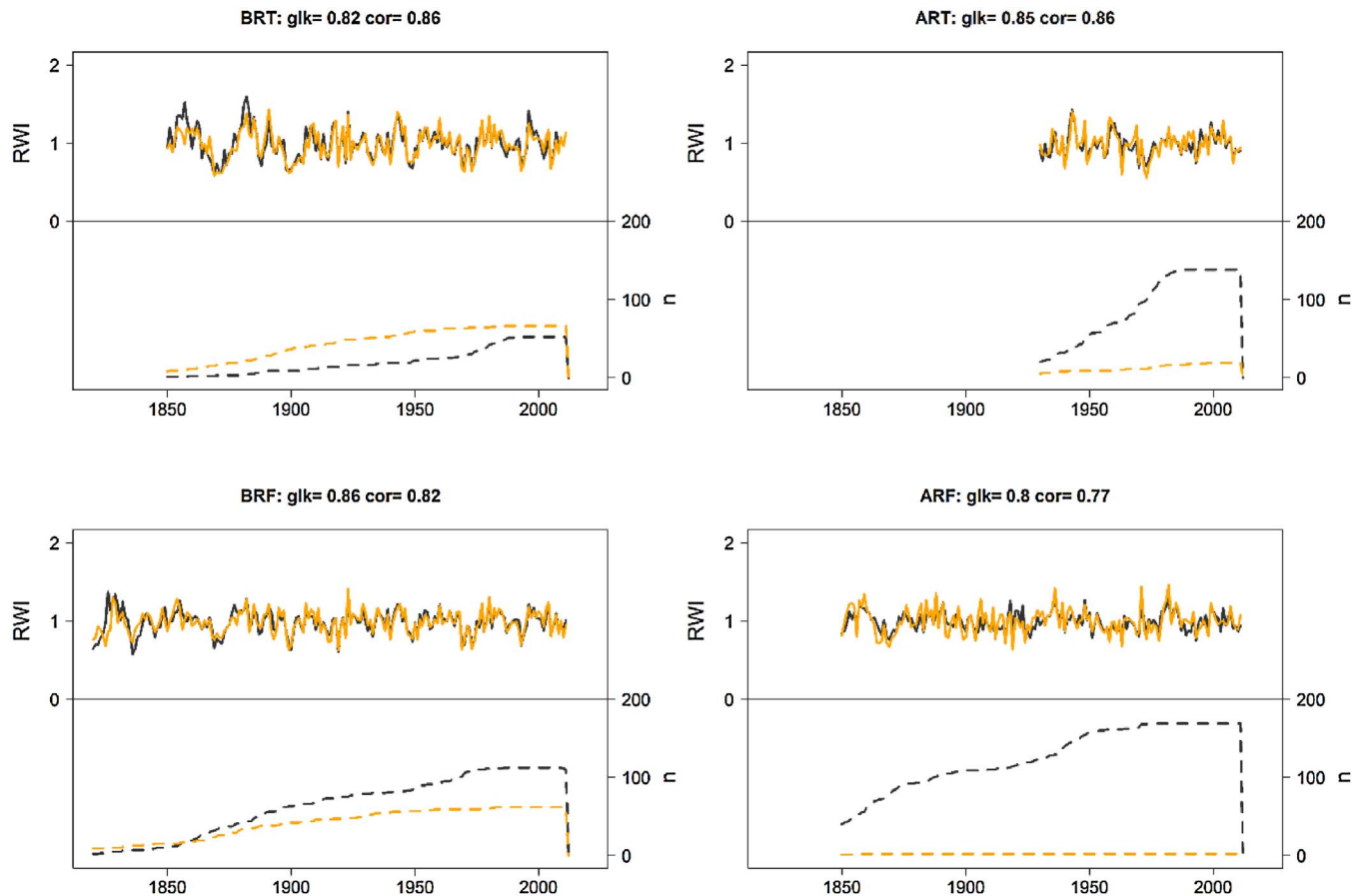


Fig. 4. High-frequency growth variability of clonal ramets (orange curve) is very similar to that of singletons (black curve) White spruce in every plot, shown here 50-year spline detrended data. Sample sizes delineated by dashed lines and right y-axis. Glk: Gleichläufigkeit, cor: Pearson correlation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ring width and 0.77 and 0.86 for the detrended chronologies.

While it is beyond this study to speculate about the generally higher absolute radial growth in the singletons when compared to the clone ramets, clearly, in terms of growth variability over time, clonal ramets and the non-clonally grown singletons safely can be regarded as similar.

#### 4. Conclusions

We found clones of White spruce growing mixed with non-clonal White spruce at typical treeline sites in two Alaskan mountain ranges. Clone frequency increased towards climatically more stressful sites: More clones occurred at northern than elevational treeline sites and generally there were more clones at local treeline than in a forest site below. While singletons generally outperformed single clone ramets in terms of absolute radial growth, high-frequency growth variability of clones and non-clonal trees was very similar thus posing no problem in including chronologies from both reproductive strategies in a classic dendroclimatological investigation.

#### Acknowledgements

This study was supported by DFG EU 132/1-1 and DFG WI 2680/8-1. Data were analyzed and paper was written within the Research Training Group RESPONSE (DFG RTG 2010).

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## Chapter II

Trouillier, M., M. van der Maaten-Theunissen, J. Harvey, D. Würth, M. Schnittler, and M. Wilmking. 2018. **Visualizing Individual Tree Differences in Tree-Ring Studies**. *Forests* 9:216.

## Article

# Visualizing Individual Tree Differences in Tree-Ring Studies

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Received: 29 March 2018; Accepted: 16 April 2018; Published: 19 April 2018



**Abstract:** Averaging tree-ring measurements from multiple individuals is one of the most common procedures in dendrochronology. It serves to filter out noise from individual differences between trees, such as competition, height, and micro-site effects, which ideally results in a site chronology sensitive to regional scale factors such as climate. However, the climate sensitivity of individual trees can be modulated by factors like competition, height, and nitrogen deposition, calling attention to whether average chronologies adequately assess climatic growth-control. In this study, we demonstrate four simple but effective methods to visually assess differences between individual trees. Using individual tree climate-correlations we: (1) employed jitter plots with superimposed metadata to assess potential causes for these differences; (2) plotted the frequency distributions of climate correlations over time as heat maps; (3) mapped the spatial distribution of climate sensitivity over time to assess spatio-temporal dynamics; and (4) used t-distributed Stochastic Neighborhood Embedding (t-SNE) to assess which trees were generally more similar in terms of their tree-ring pattern and their correlation with climate variables. This suite of exploratory methods can indicate if individuals in tree-ring datasets respond differently to climate variability, and therefore, should not solely be explored with climate correlations of the mean population chronology.

**Keywords:** climate–growth relationships; averaging; individual based; dendrochronology

## 1. Introduction

### 1.1. Background

One of the most fundamental methods used in tree-ring studies involves averaging yearly tree-ring measurements from multiple individuals. The resulting chronology is often referred to as the site, population, or master chronology [1,2]. As is the case in many other disciplines, averaging replicated measurements serves to reduce individual noise and avoids pseudoreplications in statistical analyses [1–5]. Tree-ring variables, including width, density, and/or isotope concentration, are affected by various biotic and abiotic parameters, and when combined are often referred to as the ‘principle of aggregated tree growth’ [2,3,6,7]. Therefore, the chronology of each individual tree is the unique product of multiple signals. Differences between trees can originate from competition, microsite differences, age, size, physical damage, or asynchronous masting [2,3,8]. Therefore, it appears desirable

to average measurements from multiple trees to reduce this within-site variance and filter out the population-level signal(s). Particularly on the regional and landscape scale, or along large-scale environmental gradients like latitude, such mean chronologies are of great value to assess drivers of tree growth [9–11]. In such studies, it seems reasonable to assume that climate parameters affect all trees in a population similarly, and that the population signal largely contains climate signals.

It is desirable to quantify the effect of all parameters on tree growth; however, this is not yet possible. Explanatory variables of soil, micro-site conditions, root systems, or competition, available in a sufficient spatial and temporal resolution, are often not documented, nor are all the resultant physiological processes associated with tree-ring formation understood. Additionally, statistics require large sample sizes to detect small effects, which is critical if tree growth is the sum of many small effects [3,7]. Lastly, environmental variables often interact and can have ambiguous effects on different physiological processes, for example, higher temperatures might increase the speed of chemical processes in radial tree growth, but conversely, can cause drought stress by increasing evapotranspiration. Even though tree growth appears highly complex, few research fields outside tree-ring science can access samples from specimens that yield century-spanning records of individualistic reactions to the environment. Such valuable datasets should be evaluated as thoroughly as possible; therefore, in this manuscript, we outline four methods to visualize and explore individual tree differences.

### 1.2. Sampling and Data Processing

Various methods and principles have been established to build and evaluate population chronologies. Each study begins with selection of the sampling design, which inherently depends on the research question. It has been both criticized and defended that trees and sites are frequently selected systematically and non-randomly [2,12]. Generally, trees with high ring-width variability indicate that the growth-limiting factor varies between years, for example, climate. Such trees are preferred over complacent trees [3], which might rather be limited by a factor that does not vary greatly interannually, for example, light. Less sensitive trees might require a higher sample size per site than just 20–30 individuals [2]. It is common practice in dendrochronology to sample only specific sites or individuals. For example, treeline sites are often preferred because climate conditions at these sites are assumed to impose greater limitations on growth than competition [13]. On the individual level, tall, old, and dominant trees are often preferentially sampled. Generally, these sampling procedures, just as the averaging of multiple trees, serve to filter out individual ‘noise’. Similarly, individuals that do not correlate well with the rest of the population are often excluded when creating a population chronology with the intention to reduce ‘noise’. Next, the resulting population chronology is often described with various statistical measures to quantify the signal–noise ratio (SNR) [14], the mean sensitivity (MSX) [15], the shared growth variance of trees—subsample signal strength (SSS), or the commonly used expressed population signal (EPS), with its debated threshold of 0.85 [14,16,17]. Apart from reporting these statistical measures, these values cannot directly enhance the interpretation of analyses like climate correlations. This is because these measures relate to the cumulative effect of all biotic and abiotic variables on tree growth, not just single variables. Additionally, the underlying data distributions of these statistical measures or causes of high and low values are rarely explored.

Chronology averaging also makes the assumption that frequency distributions of social status, age classes, and tree density per area do not significantly change over time. The interactions of individual trees are also lost through averaging, when in theory, emergent properties develop from interacting elements within a system that cannot be explained by the sum or mean of the elements. For example, in tree-ring studies, individual trees interact via competition or facilitation, which can lead to subsequent changes in forest structure (e.g., tree density, crown shape, above/below ground biomass allocation) [18–21], and further confound the explanation of tree-growth variability. Single trees are rarely the main focus of dendrochronological or dendroclimatological studies, with the possible



exception of very old individuals or individuals, such as the “Loneliest Tree in the World” [22,23], however, increasingly, studies do analyze individual tree differences [21,24–31].

Of course, mean population chronologies remain a useful tool to explore how a population reacts on average to an environmental variable, but invariably, information might be lost or become biased in the process of noise reduction. A common saying, sometimes attributed to the mathematician Edward W. Ng, goes “one man’s noise is another man’s signal”. Two types of noise can be distinguished in tree-ring studies. First, as described by the principle of aggregated tree growth [3,7], tree-ring properties are the product of multiple factors. Investigating only one of these factors without accounting for the others means every other factor contributes to the ‘noise’. For example, the effect of nitrogen deposition is seen as noise when a drought signal is investigated, even though it has been shown that nitrogen deposition alters drought sensitivity [32]. Second, sensitivity to the same environmental factor can differ between individuals or different time periods [33–35]. Micro-site differences or competition not only have a direct effect on tree growth, but also indirectly modulate growth by altering the sensitivity of trees to other factors [6,19,20,32,36]. We therefore argue for utilization of the ‘noise’ and the exploration of individual growth differences.

### 1.3. Individual Based Assessments

The arguments above indicate that individual-based assessments of tree growth can potentially reveal additional insights into forest and treeline growth. For example, when climate correlations are explored, the frequency distribution of correlation coefficients can show if a few trees show a strong response or many trees show a medium response. Investigating the spatial distributions of trees with higher and lower correlation coefficients could identify site heterogeneities. Recently, temporally unstable climate correlations, termed the ‘divergence problem’, have been reported more frequently [35–37]. Of course, it would be of interest if this temporal phenomenon was distributed spatially (e.g., along temperature or moisture gradients). For example, at treeline sites the individual response to the divergence phenomenon might differ along the forest–tundra gradient [38]. Tree-level metadata, such as information on the spatial position of trees within a plot, tree height, crown-base height, crown diameter, social status, vitality, age, or competition indices, enhances individual-based analyses and can often easily be recorded directly in the field. Even though it requires considerable work and additional expertise, genetic analyses can provide data that can be used to identify clones [39], or a link between tree-ring traits and specific genes [40]. However, the genetic effect on growth within a site is likely low compared to the environmental variables [41].

The purpose of this study is to demonstrate, using an exemplary white spruce (*Picea glauca* (Moench) Voss) dataset, that individual-based assessments can offer additional insights into tree growth and ecosystem dynamics. We outline four simple but effective individual-based methods for the visual assessment of tree-ring datasets that describe tree and forest growth, as well as their environment control, in more detail than mean population chronologies can provide.

## 2. Materials and Methods

### 2.1. Site, Sampling and Data

To assess the possibilities of various individual tree assessment-methods, we used data from a white spruce (*Picea glauca* (MOENCH) Voss) treeline site at a steep (12–34°) south exposed bluff near Fairbanks, Alaska (64.70° N, 148.31° W). We hypothesized that the steep angle of incidence causes higher evapotranspiration, and consequently, water limited tree growth. A 1 ha plot was established in 2015 where all trees ( $N = 327$ ) with a diameter at breast height (DBH) > 5 cm were sampled by extracting two cores per tree, or one core for small trees (DBH < 10 cm), to reduce damage to the tree. Cores were then mounted on wooden lathes and the surface was prepared with a core microtome [42]. Ring widths were measured from optical scans (Epson Perfection V700 Photo flatbed scanner, Nagano, Japan, 3200 dpi) with CooRecorder and were cross-dated visually with CDendro 8.1 (Cybis Elektronik

& Data AB, Saltsjöbaden, Sweden) [43]. Measurements of cores from the same tree were averaged. In addition, metadata for each tree was recorded in the field, including, tree height, DBH, crown diameter, crown base height, vitality (1 = best to 5 = dead), social status (open grown, dominant, codominant, intermediate, and suppressed), and spatial position (S100, SunNav Technology Co., Ltd., Tianjin, China, Differential Global Navigation System). The tree coordinates and DBH were used to calculate a neighborhood competition index (NCI, [44]) for each tree.

Monthly climate data (precipitation sum, mean temperature, mean potential evapotranspiration (PET), and vapor pressure) were downloaded from the Scenarios Network for Alaska and Arctic Planning (SNAP) for the period 1901–2009 [45], and the standardized precipitation evapotranspiration index (SPEI, [46]) was calculated from this data with the R package SPEI [47] for 6 (SPEI6) and 9 (SPEI9) months. Because we only intended to investigate climate sensitivity and not reconstruct climate or model tree growth, we detrended both tree-ring and climate data with a 30-year cubic smoothing spline using the *dplR* package [48] in R 3.2.3 [49]. The resulting tree-ring indices (TRI) and climate indices preserve the high-frequency signal (year–year variability) for the assessment of climate–growth correlations, and reduce spurious correlations due to non- or weakly-connected long-term trends in radial growth and climate. Autocorrelation was removed from the tree-ring series (prewhitening) by utilizing the *detrend* function with the *Ar* method within *dplR*.

## 2.2. Climate Correlations

Whole period and moving window climate correlations were computed for all individual tree chronologies. Correlations were computed with the six climate variables for all months of the previous year and January–September of the current year (21 months), resulting in  $6 \times 21 = 126$  correlation values per tree. Running the same correlations with a moving window (20 years width, one year offset) over the period where climate data was available (109 years) resulted in up to  $6 \times 21 \times (109 - 30) = 9954$  correlations per tree; though less for trees younger than the climate records. Given several hundred trees per site, this huge number illustrates why calculating arithmetic means as an intermediate step is warranted to make the results interpretable. With the methods described below, we attempt to supplement such averaging with individual analyses.

## 2.3. Jitterplots of Climate Correlations

Monthly climate correlations are often illustrated with the month on the *x*-axis and the correlation coefficients on the *y*-axis, sometimes including confidence intervals. Analogue to such figures, for example, are those produced by the *dcc* function in the R package *treeclim* [50]; jitter plots can be used to show the correlation values of all individual trees [24]. In addition to showing how frequent certain correlation values are, jitter plots also facilitate using metadata, such as age or competition index, as color. This allows the identification of trees that are more (or less) sensitive to a climate variable. The *geom\_jitter* function in the R-package *ggplot2* [51] is one way to implement this concept in R.

## 2.4. Individual Tree Moving Window Correlations

Temporally unstable climate correlations, sometimes called the divergence problem [37], have been reported by various studies and its causes are still unclear [34,37,52]. Divergent growth can be assessed using methods such as moving window correlations (described above). While normal histograms show the frequency distribution of correlation values in one period, heat maps with a color scale for these frequencies are required to demonstrate how these frequency distributions change over time. The advantage of using moving window correlations with a single mean population chronology is that temporal changes in the variance of correlation values among individuals can become evident.



## 2.5. Spatial Distribution Maps

Recording tree coordinates within a plot is advantageous because it facilitates assessment of the spatial distribution of individual-tree climate sensitivity. Most sites can be assumed to have some microsite differences, even though they might not be obvious in the field. Microsite variability is caused by multiple factors, including, soil depth differences, above- or below- ground water runoff, organic matter accumulation in depressions, distribution of other competitive or symbiotic organisms, the effect of shading on photosynthetically active radiation, temperature, and evapotranspiration. Environmental gradients, such as the treeline datasets used in this study, are also particularly suitable for spatial analyses, because they cover environmental gradients. Furthermore, the incorporation of moving window climate correlations adds a time component to examine temporal variability in spatial patterns of climate sensitivity. In print, multiple maps are required to visualize spatio-temporal dynamics properly, however, in digital media, plots of multiple time windows can be combined into a video or animation.

## 2.6. The t-SNE Method to Assess Tree Similarities

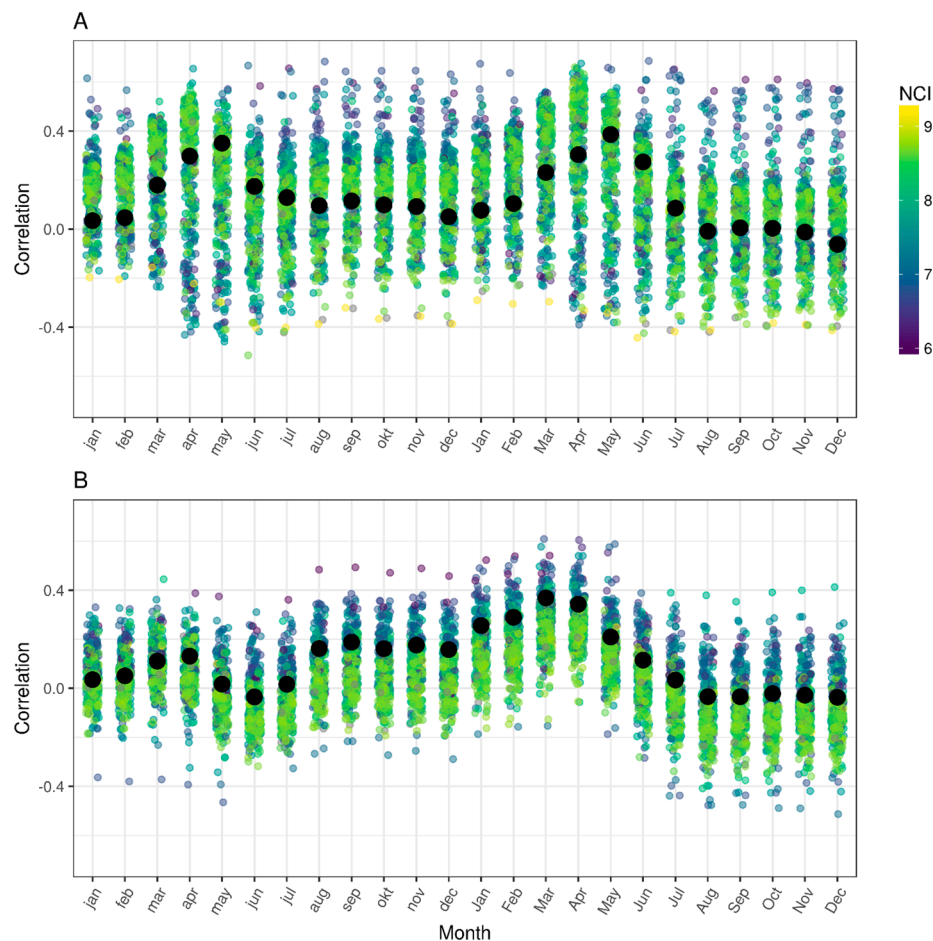
Most scientific plots only use two dimensions ( $x$  and  $y$  axis), as more than four dimensions, after adding a  $z$ -axis and colors, are almost impossible to display within one plot. However, many datasets that describe more than four properties of any individual or item would require more dimensions to be plotted. For example, the ring width of one year can be interpreted as one trait and would require one dimension per year if not plotted as a time series. Similarly, climate growth correlations for multiple climate variables would require more dimensions to be plotted (e.g., 126 dimensions/climate variables in this study). Many correlations are appropriate because tree growth is a process that takes place over the whole vegetation period; winter months also affect growth via snow fall, snow melt water, and extreme events, and even the months of previous years can affect reserves (non-structural carbohydrates, NSCs), buds formed for the next year, or needles persisting multiple years, in the case of evergreen conifers. Thus, it can be desirable to identify trees with similar tree ring patterns or similar climate responses to identify what makes trees more similar or different. Clustering methods are an approach to assess similarity. Common clustering methods, like the  $k$ -means algorithm [53], require users to predefine a (more or less meaningful) discrete number of clusters. Principal component analyses (PCA), on the other hand, assesses commonality between variables, which is often employed just to visualize the first two principal components in biplots, resulting in the loss of individual information. However, developments like the principal component gradient analysis [31] show the utility of such methods and validate the interest of the tree-ring community in intra-site differences in climate sensitivity.

$t$ -distributed Stochastic Neighbor Embedding ( $t$ -SNE [54]), which originated from machine learning algorithms to reduce multi-dimensional data and create 2D plots, could be a more suitable method to assess why certain trees have similar climate responses. Points corresponding to trees with more similar tree-ring patterns or climate responses are plotted closer to each other. Thus, trees are not assigned to discrete clusters, but the distance between two points/trees in a  $t$ -SNE plot reflects their similarity on a continuous scale. We created  $t$ -SNE plots with the R-package *Rtsne* [55] using the TRI data and the 126 climate correlations for each tree.  $t$ -SNE plots based on TRI will highlight which trees have similar year–year variability in tree-ring width (high-frequency signal). Analogous to TRI,  $t$ -SNE plots based on the climate correlations of each tree will illustrate which trees have similar climate sensitivity. As with PCAs, the  $t$ -SNE method cannot handle missing values, therefore, a tradeoff decision between including younger trees and including tree-ring data over a longer time period had to be made. We chose to exclude the youngest 10% of the trees in the TRI  $t$ -SNE analysis, and we only used the climate-growth correlations of the last moving windows (1980–2009) for the respective climate sensitivity  $t$ -SNE analysis.

### 3. Results

#### 3.1. Jitterplots

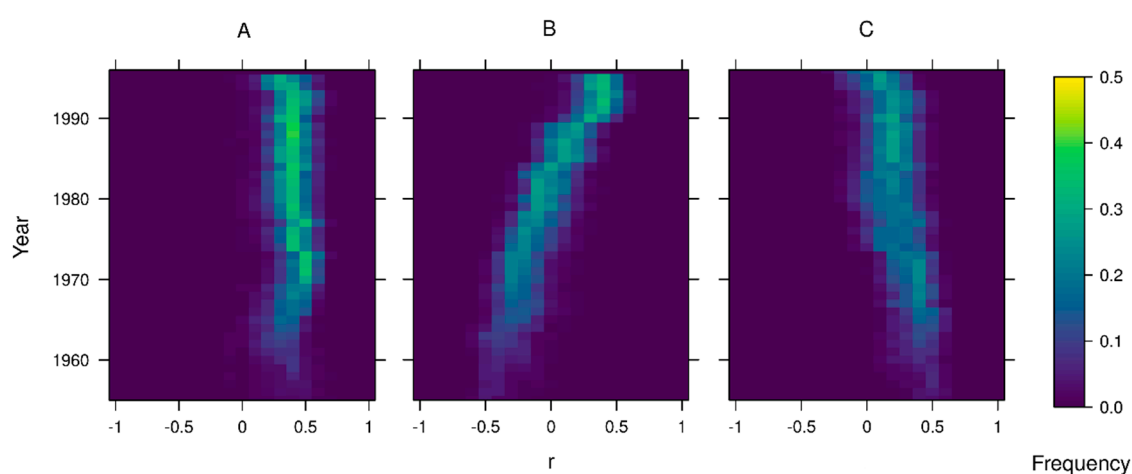
The correlations between climate and individual trees varied significantly for most climate variables, but often ranged between  $-0.5$  and  $+0.5$  (Figure 1A). Detrending procedures (30-year cubic smoothing spline and prewhitening) reduced this variance significantly (Figure 1A,B). Correlation coefficients of the mean population chronology mostly indicated stronger correlations than would be expected by the mean individual tree coefficients. Indicated by the color gradients in Figure 1, differences between the sensitivity of individual trees to April SPEI9 appeared to be related to competition (NCI). We observed that the detrending of the tree-ring width and climate data switched which trees were most sensitive to April SPEI9, and in many cases even switched the sign of the correlation (Figure 1A,B). After detrending, trees with a lower NCI, i.e., trees closer to the treeline edge with fewer neighbors, were most sensitive. The effect of detrending on the climate–growth correlations is discussed in Supplementary Material Figure S1.



**Figure 1.** Jitterplot of (A) Pearson correlation coefficients of the raw tree-ring width with the SPEI9 for individual trees (small colored points) and for the mean population chronology (big black points). The neighborhood competition index (NCI) was used as color scale for individual trees; (B) the same correlations as in (A), but using detrended ring width (tree-ring indices (TRI)) and SPEI9 time-series (30-year cubic smoothing spline and ring width was additionally prewhitened).

### 3.2. Individual Tree Moving Window Correlations

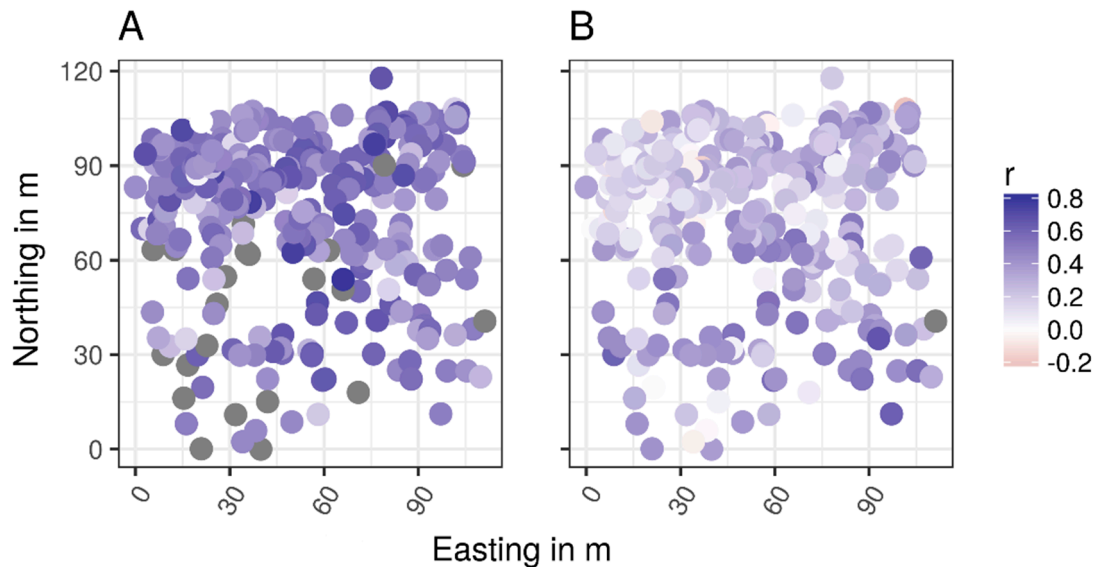
Heat maps were used to assess ‘individual tree moving window climate correlations’, and described the frequency distribution of correlation values in each time window (3D histograms). Figure 2 shows three examples of the general patterns that heatmaps can provide, in particular, stability over time, changes over time, and variance differences between climate variables. For example, climate correlations were comparatively strong and stable over time, showing no changes in mean, variance, and skewness of the distributions for April SPEI9 (Figure 2A). However, more frequently, these distribution parameters changed over time (e.g., June temperature, Figure 2B). Typically, these distributions were normally distributed at mean correlation values around zero, and became skewed toward zero at higher or lower mean values. The variance can also differ slightly between climate variables, as shown in Figure 2A,C, though much larger variances can be found at other sites (not shown).



**Figure 2.** Frequency distributions (3D histograms) of individual tree correlation values with climate variables over time (30 year moving window). (A) correlation of individual TRI with April SPEI9; (B) correlations with June temperature; (C) correlations with previous year August SPEI6.

### 3.3. Spatial Distribution Maps

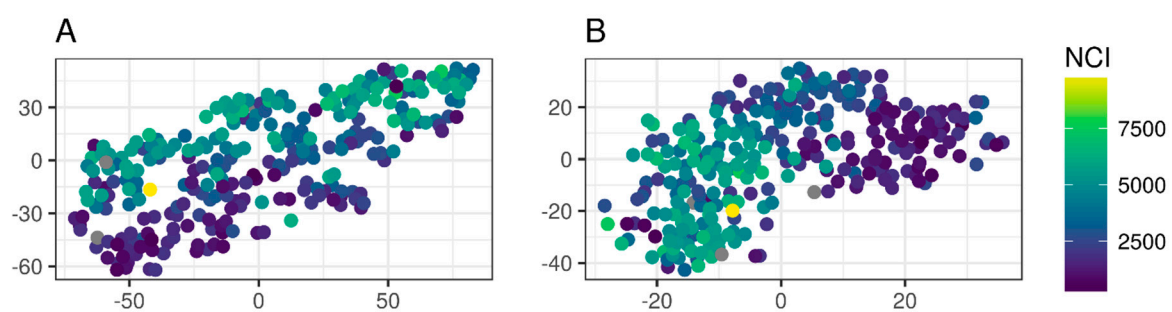
The climate sensitivity of individual trees displayed a random spatial distribution in the plots for most climate variables. However, in some cases spatio-temporal patterns emerged. By comparing Figure 3A,B, the initial absence of spatial patterns is visible in the period 1969–1988 when all trees showed a similar sensitivity to April SPEI9. Interestingly, between 1989–2008, further away from the treeline edge, and particularly for trees growing at more northerly locations, sensitivity to April SPEI9 declined (Figure 3). This corresponds to the drought gradient anticipated by the treeline formation. Spatio-temporal dynamics for April SPEI9 and all other climate variables are also visualized as videos in Supplementary Material Video S1.



**Figure 3.** Spatial distribution of the correlation coefficients of individual TRI with April SPEI9. (A) shows the correlation for the period 1969–1988 and (B) for the period 1989–2008. Grey dots show trees for which no climate correlations could be calculated due to young age and thus insufficient data in the respective time period.

### 3.4. Similar Tree Ring Patterns and Climate Sensitivity

The t-SNE method visualizes trees which were more similar or more different regarding their TRI pattern and climate correlations, with more similar trees plotted closer to each other. Similarity between individual-tree ring-width patterns and climate-growth correlations of the 126 climate variables varied, but did not exhibit distinct groupings. However, superimposing the t-SNE plot with color scales based on tree metadata reveals the parameters that contribute to tree growth and climate sensitivity. The t-SNE plots show that trees with a similar TRI pattern or similar climate sensitivity also had a similar crowding index (Figure 4). However, there are some exceptions where several trees with a low NCI have a climate sensitivity more similar to that of trees with a high NCI.



**Figure 4.** t-distributed Stochastic Neighbor Embedding (t-SNE) plots for (A) TRI patterns and (B) climate correlations with each point representing one tree. Points of more similar trees are plotted closer together and the neighborhood competition index (NCI) was used as color scale. Axes in t-SNE plots are dimensionless.

## 4. Discussion

The tree-ring patterns of individual trees differ at the site-level, which appears to be partly caused by differences in individual responses to climate variability. Depending on the target research question(s) and spatial scale of application, it can be useful to remove these differences by averaging

all individuals, or, as demonstrated here, various methods can explore these differences systematically and aid the ecological interpretation of the results. Our research highlights that tree metadata, like age, height, crowding indices, or microsite differences can be used to assess climatic growth-drivers in more detail.

#### 4.1. Variances

The frequency distributions of climate correlations gradually highlighted that some climate variables correlated with all trees similarly and continuously throughout time, indicating that this climate parameter influences the growth of all trees at a site (e.g., April SPEI9, Figure 2A). In contrast, we also found that climate sensitivity can vary significantly over time (e.g., June temperature, Figure 2B [35–37]) or show a higher variance (e.g., previous year August SPEI6, Figure 2C). Highly variable climate sensitivity can be caused by differences in microsite conditions and individual-tree parameters like age, height, or competition [25,56,57]. Climate correlations with population chronologies do not consider these individual differences and provide only one correlation value. Thus, as with all averaging procedures, the underlying distribution of the data is lost. Our results indicate that skewness in the distribution of correlation values increases with the mean value. In this case, climate sensitivity may be underestimated by climate correlations with population chronologies. Interpreting population-level climate-correlations with respect to population statistics like the SSS [14,17] does not solve this problem either, because these measures are not directly linked to single environmental variables, but the overall variance between individuals. The variability in the climate sensitivity of individual trees generally calls for further analyses to determine potential causes.

#### 4.2. Individual Metadata Effects on Climate Sensitivity

Variability in individual tree growth, as pointed out above, emphasizes the importance of collecting tree-level metadata. In this study, metadata that quantified individual differences provided valuable information on the causes of different climate sensitivities. The jitter plots (Figure 1) indicated the variables that could affect climate sensitivity, such as the neighborhood competition index NCI at our study site (Figure 1). On the downside, multicollinearity between metadata variables can complicate these investigations. In our case, trees with a higher crowding index were also taller, likely because vertical growth is promoted by competition for light [58,59].

The spatial distribution of the climate correlations of individual trees does indicate an environmental gradient at the site (Figure 3). In other studies, such maps might not just indicate gradients, but also local spots or groups of trees with different climate sensitivity. Furthermore, metadata was crucial for the t-SNE method. t-SNE plots, based on TRI and climate correlation values, did not show discrete clusters (i.e., a group of trees separated far from other trees). However, the distribution of trees in the t-SNE plots indicated that trees did differ regarding their TRI pattern and their climate sensitivity, with variability expressed continuously and not in discrete clusters. Superimposing metadata color-scales in the t-SNE plots revealed potential variables that could make trees more similar or different. As already indicated by the jitter plots, the crowding index appeared to affect climate sensitivity at our study site (Figure 4B). The t-SNE plots based on TRI are potentially useful in the absence of strong climate–growth relationships and can help identify what factors limit tree growth. Furthermore, t-SNE plots based on many climate correlations, as in Figure 4B, can be used to illustrate an individual-tree climate-sensitivity fingerprint. This can be used to identify trees that are generally more sensitive to drought related parameters due to their root system, wood anatomy, or microsite. Such trees will likely not just show a higher sensitivity to one monthly climate variable, but a whole set of moisture related variables.

Various potential mechanisms could explain why climate sensitivity varies along certain metadata gradients. For example, competition for resources, like water, could modulate climate sensitivity. In particular, asymmetric competition, meaning that the competitive power scales under or over-proportional to tree-size, could vary individual water availability [60–62]. As trees



grow taller with age, their wood anatomy changes (conduit tapering [56,57,63]), which increases hydraulic resistance, and thus, could also increase drought susceptibility [64,65]. In theory, genetic or epigenetic differences could also alter climate sensitivity, although, this has usually only been shown in provenance trials [40], not for natural within-site genetic variation [41].

#### 4.3. Potential Further Analyses

Some of the differences in tree-level climate sensitivity can be explained, and should not necessarily be treated as noise. Earlier studies have shown that parameters like competition, nitrogen deposition, and tree-height-related wood anatomical changes affect climate sensitivity [19–21,32,59,66]. In this study, we demonstrated how to visually detect potential causes of different climate sensitivities. We suggest that more advanced statistical analyses and tree-growth models are needed to describe climate-growth relationships more realistically. As the principal of aggregated tree growth already indicates, there is an almost infinite number of variables that directly affect tree growth [2,3], which are often modulated by other variables. Additionally, ‘complete’ tree growth models would have to account for the various physiological processes within a tree, e.g., photosynthesis and cambial activity, and separate how each process affects tree-ring parameters. Such models are not yet possible, leaving scientists to use more basic methods, like climate correlations with mean chronologies. However, increasing sample sizes and newer statistical methods allow for analyses that include the individual variables visualized in our study.

One advantage of simply averaging multiple individual tree chronologies is that it avoids pseudoreplications in statistical analyses. However, methods exist that can account for pseudoreplications while not relying on the computation of mean values. Mixed models can accomplish this via random effects [5,67], and have successfully been applied to tree-ring datasets [30]. For example, tree IDs can be used as random intercepts in mixed models. These random intercepts, sometimes called the nuisance variable, can consider that some trees grow more or less without exactly knowing why. More complex mixed models might also incorporate random slopes [5], which could be used to account for individual climate-sensitivities. Generally, variable interactions can be used in various model types to account for modulations of climate sensitivity by additional variables like tree height or crowding indices. Lastly, process based and agent based models (ABM) are promising tools that have become increasingly popular. Process based models can be used to model the growth rate/process over the course of the year, though they can be difficult to fit [68,69]. Agent based models can be particularly suitable to account for interactions between individuals (agents), such as competition for light and water [70,71].

## 5. Conclusions

This article addresses the principle of aggregated tree growth and the accumulating evidence that various parameters influence the climate sensitivity of individual trees, such as, competition [21,25,66], age [29,57], and height [56,59]. The methods described here highlight individual tree differences and potential causes. In tree-ring science applications, inferring the general effects of climate on overall tree growth from single individuals is not possible [24], nor appropriate, thus, the principle of sample replication has become extremely important in tree-ring studies. However, tree metadata is becoming increasingly available, and as sample sizes increase, site-level may not be the best methodological option anymore. Thus, we agree with the assessment of Lloyd et al. [6], who argued for the integration of dendrochronology with other disciplines that can provide metadata. The methods described in this article are therefore intended to promote individual-based analyses of tree-ring datasets and the exploitation of tree metadata, with the ultimate goal of contributing to a better understanding of tree growth and its driving factors.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/1999-4907/9/4/216/s1>. Figure S1: (A) mean annual growth and the respective trend-line for trees with a lower and a higher neighborhood

competition index (NCI). (B) time-series of the April SPEI9 with its trend-line, Videos S2: Spatio-temporal dynamics of climate sensitivity shown for all climate variables.

**Acknowledgments:** This project was funded by the German Research Foundation (DFG) within the Research Training Group RESPONSE (DFG RTG 2010). We thank Glenn Juday, Ryan Jess, and Jamie Hollingsworth for supporting our work and their expertise. In addition, we would like to thank Jelena Lange, Renate Hefner, Franziska Eichhorn, Brook Anderson, and Tobias Scharnweber for their help during fieldwork.

**Author Contributions:** M.T., D.W., M.S. and M.W. conceived the plot setup and collected the samples with the help of others (see acknowledgements). M.T. analyzed the data with the help of M.W. and M.v.d.M.-T.; Methods and ecological implications were discussed by M.T., M.v.d.M.-T., J.E.H., D.W., M.S. and M.W.; M.T. drafted the original manuscript together with J.E.H., M.W. and M.v.d.M.-T.; all authors revised and refined the final manuscript.

**Conflicts of Interest:** The authors declare no conflicts of interest.

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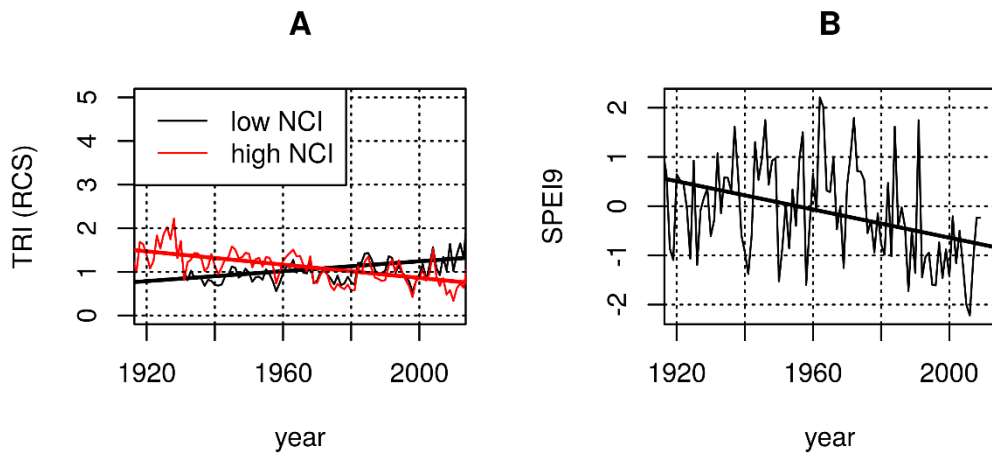
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## Supplementary material Figure S1

Figure 1 A&B in the main article show different growth responses to April SPEI9 for raw and detrended tree-ring data. The differences are likely caused by different long-term trends in the tree-ring as well as in the climate data. For comparison of growth trends we split trees into two groups based on the median NCI (7.9), removed potential age-effect biases with regional curve standardization (RCS) and averaged all trees per group to assess average growth-trends (Figure S1. A). Trees closer to the tundra edge and with a lower NCI show a slightly increasing growth trend ( $R^2 = 0.20$ ,  $p < 0.001$ ,  $DF = 83$ ). On the contrary, decreasing trends were observed for trees with a higher NCI ( $R^2 = 0.34$ ,  $p < 0.001$ ,  $DF = 98$ ), as well as for April SPEI9 (Figure S1 A,B). Thus, because both show decreasing trends, non-detrended data showed that trees with a high NCI correlated more strongly with April SPEI9. After the trend is removed, climate-growth analyses only correlates the high frequency signals and most sensitive trees were those at the treeline edge (low NCI). In the method description we thus argued for the detrending of tree-ring as well as climate data, because long term trends are unlikely to be the product of single monthly climate variables.



**Figure S1. A)** Mean annual growth and the respective trend-line for trees with a lower and a higher neighborhood competition index (NCI). **B)** Time-series of the April SPEI9 with its trend-line.

### Chapter III

Trouillier, M., M. van der Maaten-Theunissen, T. Scharnweber, D. Würth, A. Burger, M. Schnittler, and M. Wilmking. 2018. **Comparison of three methods to assess age and size dependent climate sensitivity of trees** [submitted to 'Trees - Structure and Function' on June 3<sup>rd</sup> 2018]

**Title**

Size matters – A comparison of three methods to assess age and size dependent climate sensitivity of trees

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## **Abstract**

Climate affects tree growth but the effect size can be modulated by other variables, including tree's age and size. To assess how climate sensitivity changes over the life of a tree, previous studies mostly stratified trees into age classes, while cambial ring-age stratification (age band decomposition) was less frequently used. However, trees do not age as other organisms and arguably age is mainly a proxy for size, which in contrast to age has been shown to affect wood anatomy and physiology. Stem diameter classes, calculated from cumulative ring width, could thus facilitate a more direct assessment of size effects. Here we compare these three methods, which differ regarding how they stratify data into age/size classes.

We found that using age band decomposition and cumulative ring-width classes had major advantages over the tree-age method: a) Age and size are decoupled from other temporal changes, like atmospheric CO<sub>2</sub> concentration or nitrogen deposition, which excludes potential biases. b) Shifts in climate sensitivity occur earlier than estimated by the tree-age method. c) Younger/smaller classes can be assessed. Furthermore, direct comparison supports that size, rather than age, alters climate sensitivity. Therefore, the cumulative ring-width method appears the best approach to assess the effect of ontogenetic changes on tree's climate sensitivity.

Understanding how climate sensitivity changes when trees get older and larger is important for forest ecology and management, climate reconstructions, global carbon models and can help to study age and height limitations of trees.

**Key message** Changes in tree's climate sensitivity during their ontogenetic development is best assessed with stem-diameter classes, which can be calculated retrospectively from the cumulative ring width.

**Keywords:** dendrochronology, climate sensitivity, tree age, tree height, hydraulic limitation hypothesis



## **Introduction**

### *Tree-age related development*

Age appears to have no direct effect on tree physiology, or at least aging of trees is very different from aging in many other organisms (Bond 2000; Thomas 2002). In particular, the cambial meristem does not show signs of tissue senescence, as it was shown with reciprocal-grafting experiments: Transplanting shoot tips from young to old trees and vice versa showed that the shoot tips adopt the characteristics of the rootstock (Bond et al. 2007). Similarly, size not cellular senescence, is responsible for declining growth with age (Mencuccini M. et al. 2005). Instead of aging, trees develop continuously, through stages of seedlings, juveniles, mature and old growth (Thomas 2002). Next to changes in the root systems and stem diameter, height growth is probably the most apparent developmental change of trees. Because of that, previous studies also used size-related parameters, instead of age, to consider the effect of ontogenetic development in the assessment of long-term growth trends (Luis et al. 2009; Bontemps and Esper 2011). Evolutionary, height growth developed because it is a selective advantage for plants in the competition for light. However, this competitive advantage appears to come with a trade-off cost (King 1990; Koch et al. 2004). Various physiological and morphological changes occur related to height growth, for example leaf morphology (Koch et al. 2004) or annual primary growth (shoot length) (Day et al. 2002). One of the main costs of increased height is increased hydraulic resistance (Ryan and Yoder 1997; Ryan Michael G. et al. 2006). Wood anatomy in particular seems to play an important role in height related changes in the hydraulic conductivity of the xylem (Carrer et al. 2015a). As first described in 'Sanio's law' (Sanio 1872), conduit area increases with distance from apex. Mencuccini et al. (2007) evaluated 'Sanios law' and developed a model that accounts for the xylem construction costs relative to the photosynthetic gain, to describe wood anatomical changes with tree height. This illustrates why tree height, rather than age is of interest when physiological processes are studied and why wood anatomy has recently seen recognizable methodological advances (Rossi et al. 2006; Gärtner and Nievergelt 2010; von Arx and Carrer 2014). Tree height thus plays an important role for tree physiology, but long time series of

height increment data is rarely available to study its effect directly. Stem diameter and age on the other side can be easily calculated retrospectively from tree-rings and are useful proxies for tree height and allow to study how height modulates environmental effects on tree growth.

### *Climatic effects on tree growth*

Because tree height affects tree physiology, it also affects climate-growth relationships of trees. Climate-growth correlations are studied with various backgrounds, for example tree growth under past climate is studied to estimate future tree growth under climate change and effects of the global carbon cycle (Jump et al. 2006; Babst et al. 2014; Zhang et al. 2015; Price et al. 2015; Sullivan et al. 2017). Inversely, climate-growth relationships can be used to reconstruct past climate before instrumental records (Fritts 1976; Cook and Kairiukstis 1990; Briffa et al. 1998). Both research fields are based on the fact that climate affects the processes which are directly and indirectly involved in radial tree growth, for example cambial activity, photosynthesis or seed production (masting). Being able to quantify the effect of climate on tree-ring parameters, like tree-ring width (TRW), late wood density (MXD), wood anatomical properties or isotope concentration is thus of high priority for various studies. However, as it was formulated so elegantly by Briffa et al. (1996), “*trees are not thermometers or raingauges*”, which emphasizes the high complexity of tree growth. Even though this complexity has long been recognized (Cook and Kairiukstis 1990; Vaganov et al. 2006), many studies still assume that trees show the same climate sensitivity in the past as they do in the present, often referred to as the 'uniformitarian principle' (Fritts 1976; Cook and Kairiukstis 1990). However, as argued by Wilmking et al. (2017b), frequently reported changes in climate sensitivity, the so called ‘divergence problem’ (D’Arrigo et al. 2008; Williams et al. 2011), rather reflect an incomplete understanding of tree growth, not the invalidity of this principle. Recently, there has been an increase in the number of studies that report modulations of tree's climate sensitivity by competition (Wang et al. 2016; Gleason et al. 2017), nitrogen deposition (Ibáñez et al. 2018) and CO<sub>2</sub> concentration (Nicolussi et al. 1995). However, long time-series of competition (forest structure) or nutrient status

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are rarely available which makes studying their effect difficult. Tree-height effects on the other side can be studied by using age or stem diameter data, obtained from tree-rings, as proxies.

In conclusion, significant structural changes happen to a tree as it develops continuously over time. These changes can have important ecological implications for the study of tree growth, survival, reproduction, carbon sequestration models as well as for climate reconstructions. Here we present a comparison of three methods to stratify tree-ring data according to age and size and show their effect on the assessment of climate-growth relationships.

## Materials and Methods

### *Tree-ring data*

Assessing age- and size-dependent climate sensitivity requires large data sets, ideally with several hundred trees. We took advantage of a large white spruce (*Picea glauca* Moench Voss) treeline dataset from the Brooks Range, Alaska, originally sampled in 2012 (Eusemann et al. 2016) and updated in 2015 and 2016 (Wilmking et al. 2017a) summing up to 452 individual trees. For this data set, all trees in a plot of 100x200m with a diameter at breast height (DBH) of >5cm were cored at the lowest possible height (~ 40 cm). One or two cores were extracted from each tree and DBH, diameter at coring height (DCH), tree height, and coring height were recorded. Along two 110m transects, diameter at the root-shoot boundary and height was measured of all seedlings and saplings (DBH <5cm). Additionally, we collected 20 disks (cookies) of five different height classes each (0-30cm, 31-60,...,121-150cm). Cores from trees sampled in 2012 and seedling cookies were sanded with increasingly finer grits, while the surface of cores sampled in 2015 was prepared with a core microtome (Gärtner and Nievergelt 2010). Samples were then scanned with an Epson Perfection V700 Photo flatbed scanner with 3200dpi and ring widths were measured with Coorecorder 8.1 (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). The measurements were cross-dated visually and with CDendro 8.1 (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). Ring-width measurements were then loaded into R 3.1 (R Core Team 2015) with the *dplR* package (Bunn 2008)

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and detrended with a 30-year cubic smoothing spline with a 50% frequency cut-off to create a dimensionless tree-ring index (TRI). Additionally we removed autocorrelation ('prewhitening'). Ring ages were corrected for coring height based on the age-height relationships of the sampled seedlings. Similarly, stem diameters in each year, that were calculated from cumulative ring width, were corrected for coring height based on the seedling age and stem diameter at the root-shoot boundary. To assure that our plot setup did not pose a bias we assessed age, DBH and tree height distribution along the treeline gradient.

#### *Age and size class methods*

In this study, we compare three methods for the assessment of age- and size-related changes in climate sensitivity. The methods differ in how they stratify the tree-ring data, which is either based on 1) tree age, 2) cambial ring age, also known as age band decomposition (ABD) and 3) stem diameters calculated from the cumulative ring width (CRW). 4) For the direct comparison of size- and age-effects we combined cambial ring age and cumulative ring width methods by distinguishing fast and slow growing trees:

1) The first approach, that is most frequently applied to assess age modulated climate sensitivity, calculates tree age from the number of tree rings and then divides all trees into age classes (Carrer and Urbinati 2004; Yu et al. 2008; Esper et al. 2008; Vieira et al. 2009; Rozas et al. 2009). This means that in each year the same tree subset is used to calculate the class average. 2) Briffa et al. (2001) introduced age-band decomposition (ABD), which uses the cambial ring age to create age classes. Despite the apparent similarity to the tree-age method, ABD leads to a fundamentally different data subset for each age class, because ABD selects for each year tree-rings from a different subset of trees, illustrated in Fig. 1. 3) Similar to ABD, we created stem diameter classes based on the cumulative ring width, similar to size-class isolation used for the assessment of long term growth-trends (Bowman et al. 2013; Peters et al. 2015). Analogue to the ABD method, tree rings rather than trees are used to create classes. Often cores did not hit the pith and no pith-offset estimates were

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included in the dataset. Thus we used the diameter at coring height and calculated CRW classes backwards from bark to pith. 4) Lastly, size and age cannot directly be compared because they use different scales. Therefore, to facilitate a direct comparison of age and size methods, we created size data-subsets of age subsets based on cambial ring age and cumulative ring width. This allows to compare climate sensitivity of small and large trees of the same age, by accounting for different growth speeds. Fast and slow growing trees were split based on the slope of the linear regression between cambial ring age and cumulative ring width.

For each of the methods we created overlapping classes of 20 year or 20mm width with an offset of one year or one mm (1-20, 2-21, 3-22,...). We used a minimum sample size of 15 trees for each class and year, which resulted in 144 tree-age classes, 147 ABD classes and 151 CRW classes. Because of large sample size requirements when creating CRW classes within ABD classes (4), we had to use 30 year windows and a minimum sample sizes of  $n=10$ . We then calculated class chronologies (yearly averages) from the detrended tree-ring data in each class, which we then used for the climate-growth correlations.

#### *Climate data and climate-growth correlations*

Because of limited climate station data in Alaska, particularly in the Brooks Range and in the first half of the 20th century, we used gridded monthly climate data for the period 1950 till 2009, which was provided by the Scenarios Network for Alaska and Arctic Planning (SNAP 2016). On top of the available data on precipitation, temperature, potential evapotranspiration (PET) and water-vapor pressure, we calculated the standardized precipitation evapotranspiration index SPEI (Vicente-Serrano et al. 2009) including a ‘memory’ of 6 and 9 previous months (hereafter SPEI6 and SPEI9 which represent drought on different time-scales) with the R package SPEI (Beguería and Vicente-Serrano 2013). Analogue to the tree-ring data, we detrended climate data with a 30-year cubic smoothing spline. Detrending ring width as well as climate data avoids erroneously lower/higher correlation coefficients between both variables because of similar/opposite long term trends in

climate and radial tree growth time-series data. We argue that long-term growth trends can hardly be attributed to single monthly climate-variables, because such trends likely exist in multiple climate variables as well as in other environmental variables like atmospheric CO<sub>2</sub> concentration or nitrogen deposition. Therefore only high-frequency signals were correlated for our analyses.

Similar to the host of studies analyzing climate effects on tree growth, we computed climate-growth correlations (Pearson correlation coefficients) for all climate variables of the previous and the current year and all age and size-class chronologies. In addition to these 'static' correlations, we assessed how climate sensitivity changed over time for each age/size class with moving window correlations (window width = 31 years, one year offset).

## Results

The three methods differ in their assessment on how climate sensitivity of trees changes as trees get older and larger. First, the tree age and ABD methods disagree at what age the climate sensitivity changes. In particular, the ABD method finds that these shifts happen at a younger age (Fig. 2 a,b). This age lag approximates half the length of the climate-data period used in the climate correlations and is connected to the fact that with the tree-age method age in the selected classes increases with time, contrary to the ABD and CRW methods. For the same reason the tree age method appears to be able to assess older age classes than the ABD method. The youngest age classes on the other hand are not covered by the tree-age method. This is important because pronounced changes in climate sensitivity were mostly detected in younger/smaller classes. The CRW method appears to perform very similar to the ABD method (Fig. 2 b,c). However, in direct comparison the CRW method generally appears to be a slightly better predictor of changes in climate-growth correlations: Fig. 3 directly compares climate sensitivity of small (slow growing) and large (fast growing) trees of the same age. In particular, larger trees showed stronger correlations with previous July temperature than smaller trees of the same age. This indicates that climate sensitivity changes are more likely size- than age-related.



Climate-growth correlations with previous July temperature were stable over time but varied for other climate variables like previous year May temperature (supplementary Fig. S1d). This could be due to changes in the growth limiting factor ('divergence problem') or due to low quality of the climate data, particularly further back in time when fewer climate stations were available. Lastly we thus assessed a potential divergence problem with double moving window correlations over 1) CRW classes and 2) calendar years. Fig. 4 shows exemplarily for previous year July temperature that correlations with tree growth were relatively strong and stable throughout time for larger CRW classes while correlations for smaller classes were not significant.

The association between age, DBH and tree height was analyzed to assess if age and stem diameter generally are appropriate proxies for tree height, because tree height is assumed to have a direct effect on tree growth. Generally DBH and tree height were closer associated with each other than with tree age (Supplementary Figure S2), indicating that trees have different growth speeds, and that rather stem diameters (like CRW) should be used as proxy for tree size and height.

## **Discussion**

### *Method comparison*

The ABD and the CRW methods had three major advantages over the most frequently applied tree-age method: 1) Arguably most importantly, the ABD and CRW methods quantify only the pure age/size effect on climate sensitivity because these methods decouple aging and size increment from the temporal change of other variables like CO<sub>2</sub> concentration or additional climate variables. Other variables can thus not overlay and bias these effects. 2) The ABD method more correctly identifies a shift in climate sensitivity at a younger age than the tree-age method, most likely, because the tree-age method does not decouple age from time. For example, correlating age class 80-100 with 50 years of climate data actually means that in the beginning of the 50 year long climate time series the trees within this age class are only 30-50 years old. Consequently the tree age-method erroneously stretches shifts in climate-growth correlations towards an older age. This delay approximates half the length of

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the climate data, in our example 25 years. 3) The tree-age method cannot compute climate-growth correlations for age classes younger than the length of the climate data. For example, one cannot correlate tree-ring chronologies of 30-year old trees with 50 years of climate data, because it would require to drop 20 years from the correlation. Because of this effect only few studies using the tree-age method considered age classes below 100 years (Konter et al. 2016), where a lot of ontogenetic development takes place. The ABD and CRW method are not affected by this bias and can assess even youngest ages/sizes. This is particularly important because in the first decades of a tree, height growth is strongest (Ryan Michael G. et al. 2006) and the described height related changes in climate sensitivity thus appears likely.

Our direct comparison supports previous studies that found size, not age, to be the cause of physiological changes in trees: At the same age, larger trees showed stronger climate-growth correlations in cases where climate sensitivity increased with age and weaker correlations in case correlations decreased with age. In our analysis this effect appears relatively weak (difference in Pearson's  $r$  of about 0.1). However, because of sample size limitations we only could separate two size classes per age (fast and slow growing trees). It thus appears likely that the most extreme growth speed differences, like 5% quantiles, would show much stronger differences in climate sensitivity of trees with the same age. We thus conclude that cumulative ring width should be used in future studies to explore size effects. This also is the logical consequence from previous studies that showed how tree height affects wood anatomy (Mencuccini et al. 2007; Carrer et al. 2015b) and thus tree physiology and the fact that stem diameter (CRW) is closely related to tree height (supplementary Fig. S2).

#### *Size and age related changes in climate sensitivity*

Climate correlations can either increase or decrease with size and age (Carrer and Urbinati 2004; Rozas et al. 2009; Konter et al. 2016), which points towards different mechanisms driving such changes. Higher climate sensitivity of taller and older trees is mostly found with moisture-related

parameters like precipitation, SPEI or temperature-induced drought stress (Carrer and Urbinati 2004; Bond et al. 2007; Linares et al. 2013). This increased sensitivity of old trees to drought stress is in line with wood anatomical studies (Mencuccini et al. 2007; Petit et al. 2011) and the 'hydraulic limitation hypothesis' (Ryan and Yoder 1997; Ryan Michael G. et al. 2006), reporting an increasing hydraulic resistance with height. In addition changes in the position of a tree within a stand might lead to such effects (Mérian and Lebourgeois 2011). Once understory trees reach the canopy position their more exposed crown might cause a higher drought susceptibility. However in the sparse boreal forest of our study this effect is probably rather small.

Higher climate sensitivity of smaller and younger trees on the other side could be related to prolonged vegetation periods reported for smaller trees (Bond 2000; Day et al. 2002; Deslauriers et al. 2003; Rossi et al. 2008; Rathgeber et al. 2011; Zeng et al. 2018). This is also supported by our white spruce dataset, where young/small trees showed stronger correlations with shoulder season climate (e.g. previous year May temperature, supplementary Fig. S1). However, further research with more species and climatic regions is required to come to general conclusions regarding climate signal size-effects. Likely these effects are highly species and site dependent. For example, under dry climate but at sites with ground water access, small trees might show higher correlations with precipitation because they have shallower root systems and no access to the groundwater yet.

### *Methodological challenges and potential biases*

The ABD and CRW methods require large sample sizes that might impede the use of these methods. To some extent both methods can be adjusted for lower sample sizes by using wider age classes (20 years in this study) and lower minimum sample sizes ( $n=15$  in this study), though, this will of course reduce the accuracy of the explored age and size effects. We thus recommend that future field-work campaigns that aim at exploring age and size effects should sample several hundred, ideally  $>500$  trees per site, including seedlings, saplings and dead trees. When using the ABD or CRW methods to explore age and size effects samples should be corrected for coring height based on sampled seedlings

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and for pith offset, either based on offset-estimates or stem diameters at coring height. Not accounting for this will bias any correlation towards the correlation values of younger/smaller classes.

Even though the ABD and CRW method decouple age from other temporal changes, for example in climate or atmospheric CO<sub>2</sub> concentration, there are still potential biases left, in particular environmental gradients within study sites like the treeline in our study site. Supplementary Fig. S3 shows that the oldest and largest trees are only found towards the forest edge of the plot. Because climate sensitivity is usually assumed to be highest at the tree-line edge (Fritts 1976; Cook and Kairiukstis 1990), old tree-line edge trees could be underrepresented. However, this age and size gradient is relatively weak and mainly caused by a few old trees and a few trees at the tundra edge, thus we assume this to have little effect on our results.

## **Applications**

Our findings support that size rather than age affects tree's climate sensitivity. Consequently cumulative ring-width classes appear to be a promising tool for various research questions: Forest management techniques that aim to reduce competition for water (Callaway and Walker 1997; Allen et al. 2010; Bottero et al. 2017; Gleason et al. 2017) by reducing stem density already consider tree sizes, not age. In unmanaged forests self-thinning due to water stress (Wang et al. 2016) should be studied in relation to tree size. Research on treeline shifts related to climate change (Harsch and Bader 2011; Körner 2012; Jochner et al. 2017), can benefit from better understanding size specific climate-sensitivity by identifying which size classes are suffering or profiting the most from unprecedented climate. Old forests are reported to be carbon sinks (Knobl et al. 2003; Luyssaert et al. 2008), but the role of tree height on carbon accumulation is less clear. Climate reconstructions crucially depend on stable climate-growth correlations, thus shifts in the tree size distribution of the samples over time could bias climate reconstructions (Carrer and Urbinati 2004). On the other side the climate signal could potentially be increased and reconstruction accuracy improved by only using the most sensitive

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CRW classes. In conclusion, the CRW method appears to be a very promising tool to explore a variety of different research questions related to trees, forests and climate change.

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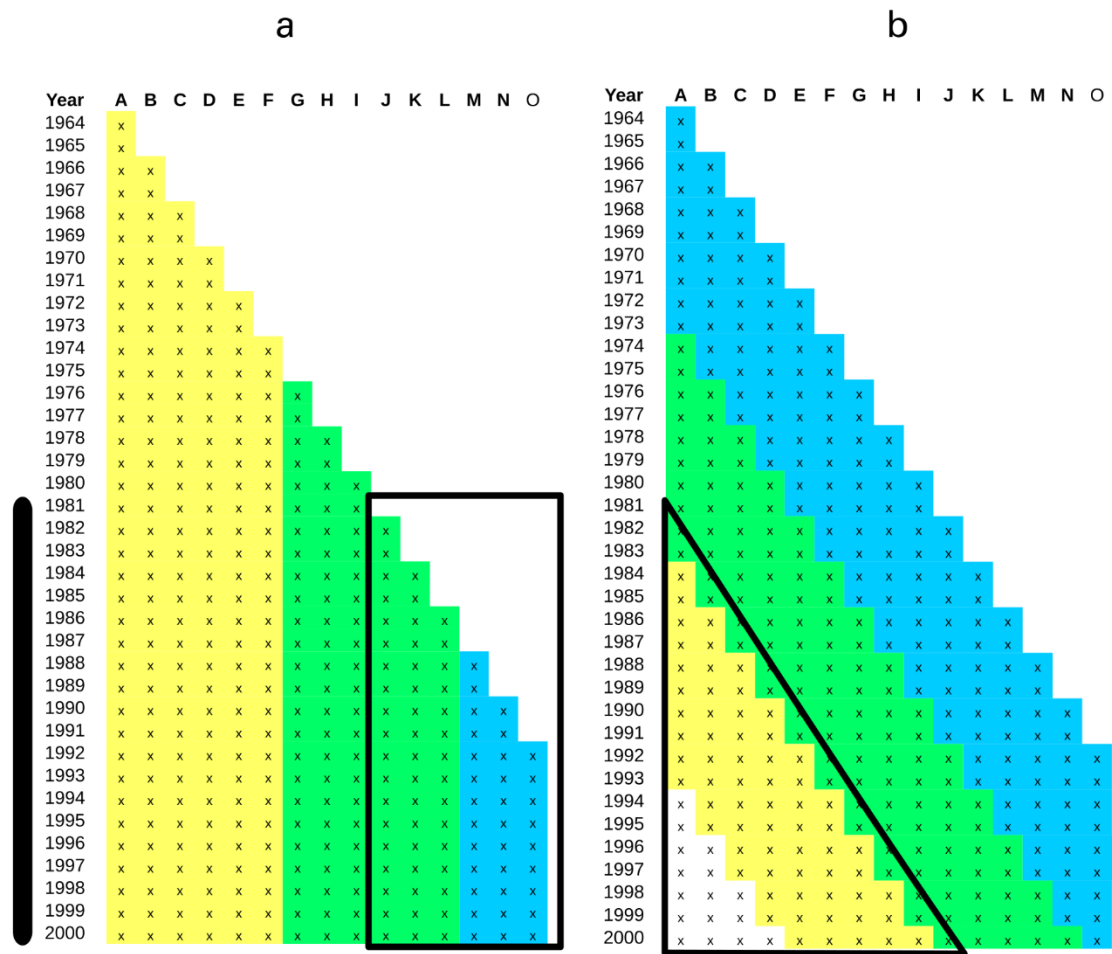
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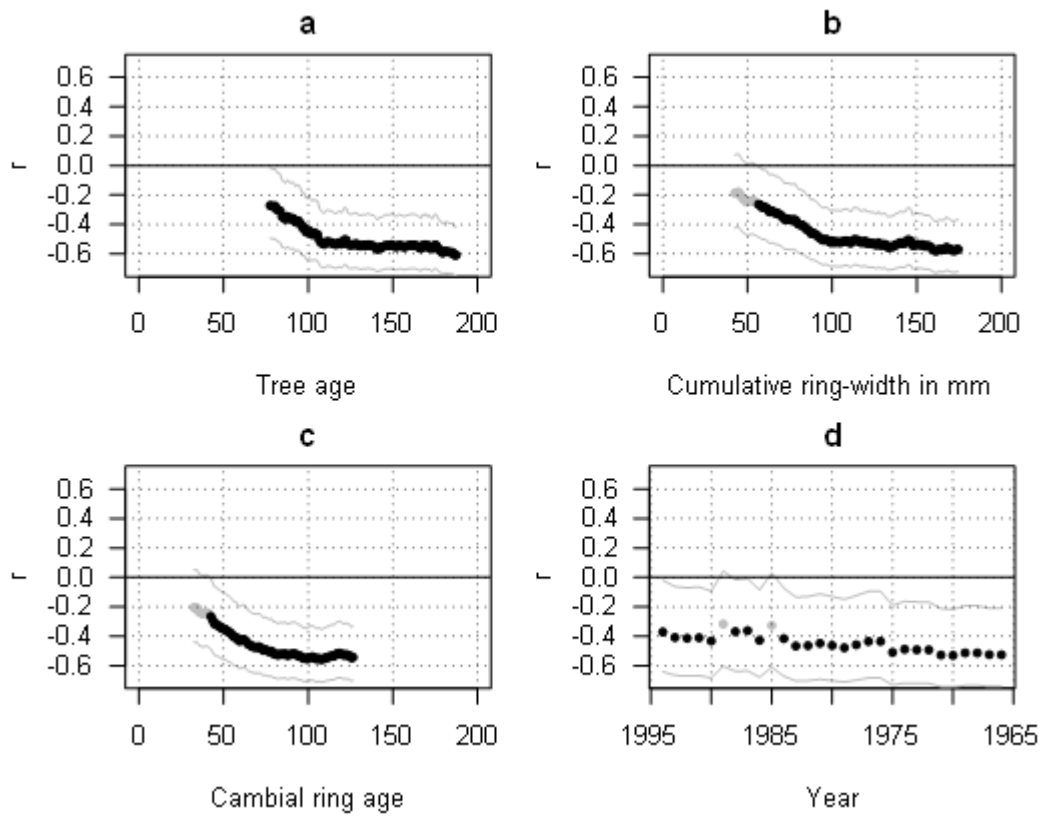
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Figures

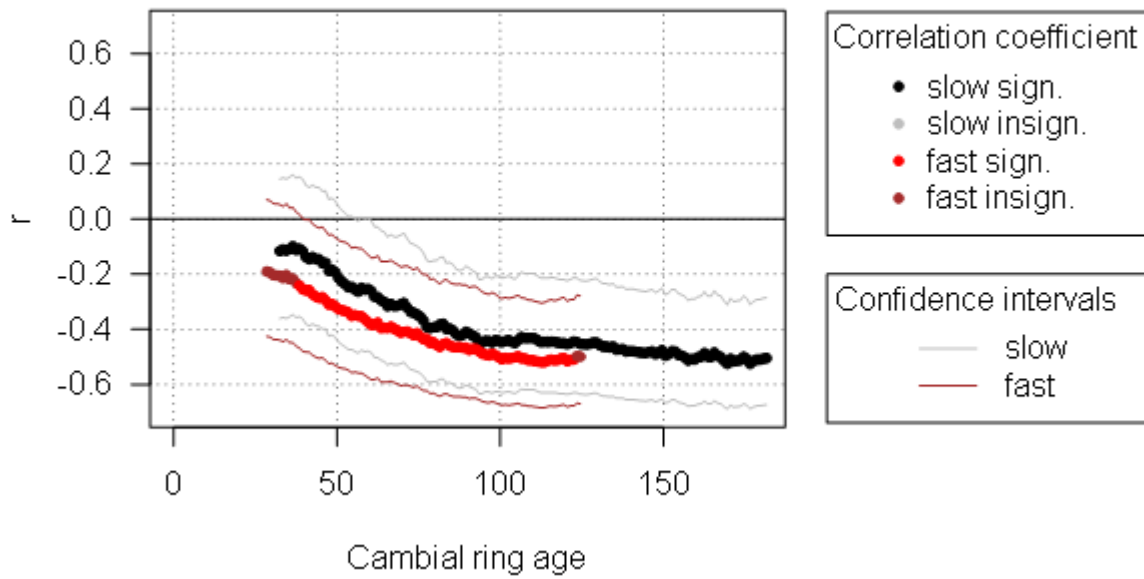


**Figure 1** Schematic illustration of the difference in the subsamples taken to create age-chronologies: a) tree-age method, b) cambial-ring-age method. Individual trees are in columns A to O. The ‘×’ marks the years with ring-width measurements available. The first ‘×’ in each column thus marks the year of the pith and tree age is decreasing from left to right. If climate-growth correlations are calculated with climate data since 1981 (indicated by the black bar on the left) the data in the black frames is dropped.

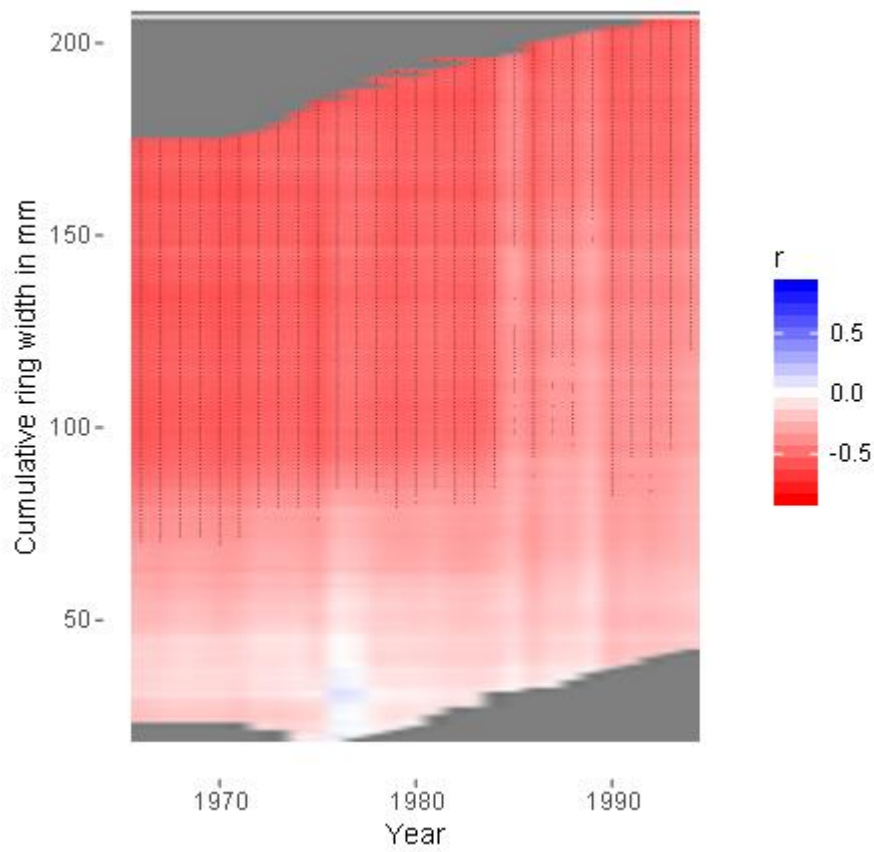


**Figure 2** Correlations between previous July temperature and the tree-ring index of age and size classes based on tree age (a), CRA (b) and ABD (c). Tree age and ABD method are plotted above each other to allow a direct comparison of the timing when age-effects are observed. Lastly (d), moving window (31 years) climate-growth correlations for the mean site chronology, including all age/size classes. Black points indicate significant correlations ( $p < 0.05$ ), grey points insignificant correlations. Grey lines mark the confidence intervals.





**Figure 3** Direct comparison of correlations between tree-ring indices with previous year July temperature of thicker (fast growing) and thinner (slow growing) trees of the same age. At the same age, larger trees show stronger climate correlations.



**Figure 4** Correlation matrix showing CRW-class specific sensitivity to previous year July temperature in each time period. Black dots mark significant correlations ( $p < 0.05$ ) and show that larger CRW classes showed relatively stable climate-growth correlation over time.

### **Author's contributions**

MT, TS, DW, AB and others collected the data. MT ran all analyses and drafted the first manuscript version. All authors discussed methodological details and the wider implications of age- and size-related climate sensitivity. All authors contributed to the draft and gave final approval for publication.

### **Acknowledgments**

This project was funded by the German Research Foundation (DFG) within the Research Training Group RESPONSE (DFG RTG 2010). We would like to thank Glenn Juday, Ryan Jess, and Jamie Hollingsworth for supporting our work and their expertise. Furthermore we thank Jelena Lange, Renate Hefner, Franziska Eichhorn and Brook Anderson for their help during fieldwork.

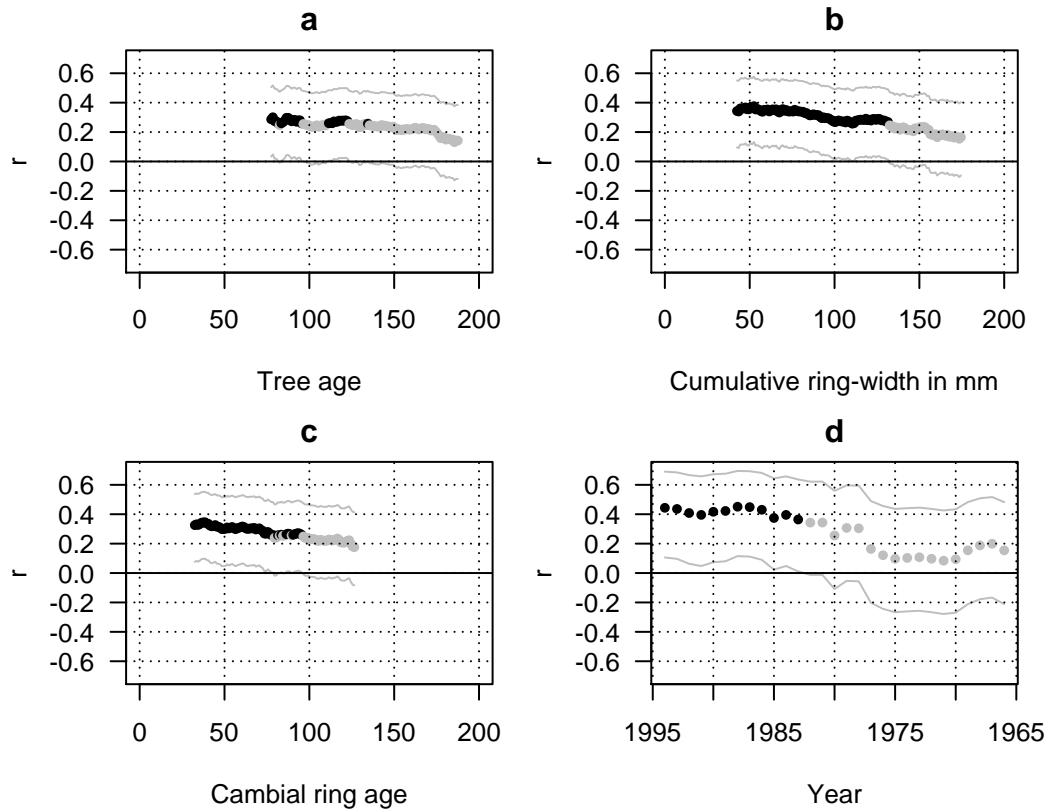
### **Data archiving**

All data will be uploaded to the international tree-ring data base (ITRDB).

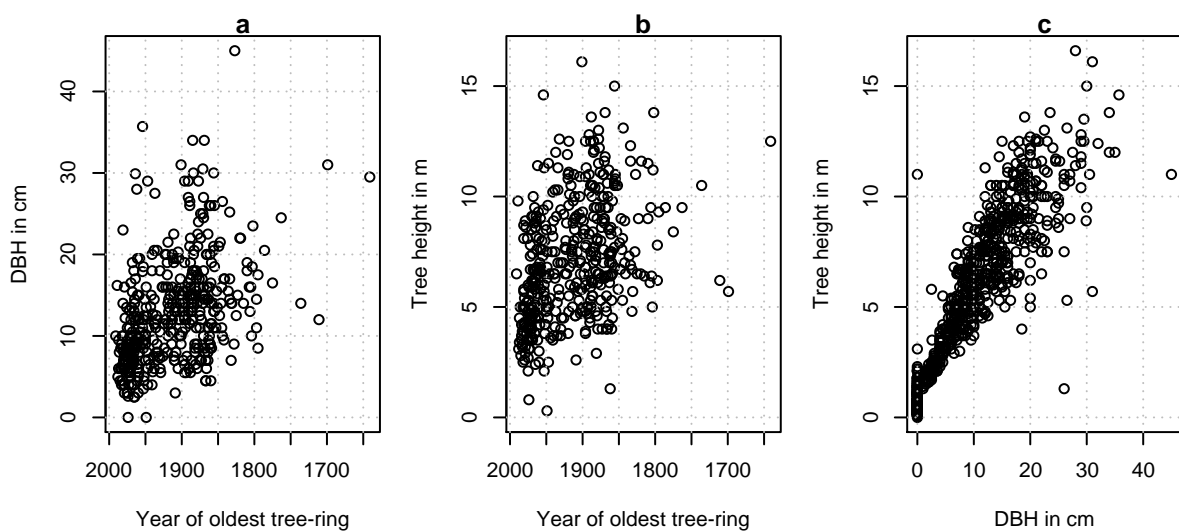
### **Conflicts of Interest**

We declare that there are no conflicts of interest.

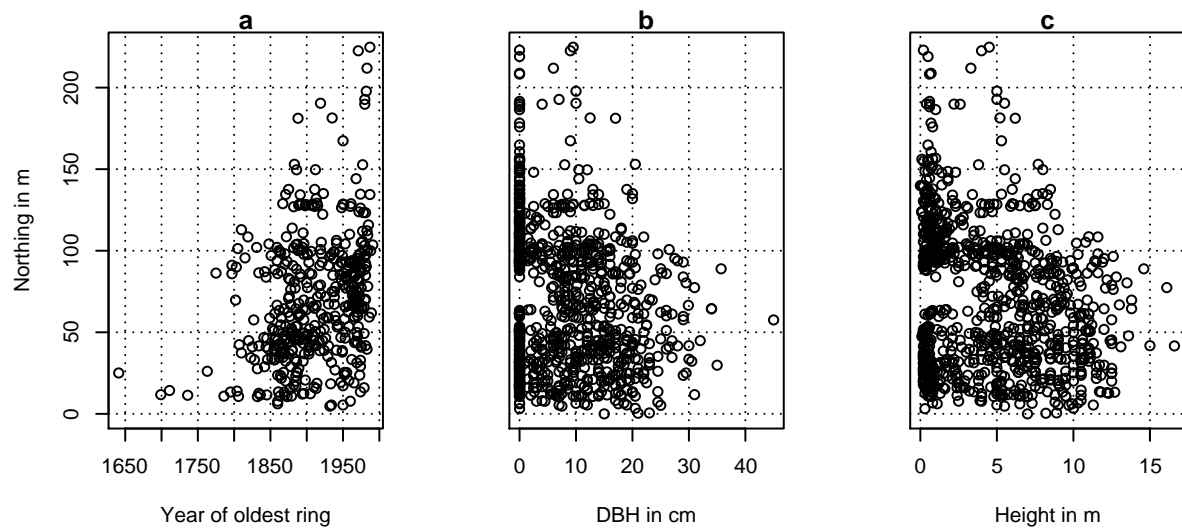
## Supplementary material



**Fig. S1** Correlations between tree-ring indices of age and size classes and previous year May temperature for a) the tree-age, b) age band decomposition, and c) cumulative ring width method. Sensitivity of trees appears to decrease with age and size. However, the correlations with the mean site chronology (no age or size classes) are not significant before 1983, as shown by the moving window (31 years) climate-growth correlations (d).



**Fig. S2** Association between tree's age, height and diameter at breast height (DBH).



**Fig. S3** Age, DBH and tree height are relatively even distributed throughout the plot and gradients are mainly the result of few trees in the very north of the plot and oldest/largest trees in the south of the plot.

### 3 Synthesis

The aim of this thesis was to critically assess the suitability of white spruce tree-rings as a trait for reaction norms, in particular: climate-growth correlations. Such correlations are important because they might facilitate insights into future growth trends and range dynamics of white spruce in Alaska. Consequently effects on individual climate growth correlations like the affiliation to a clonal colony (genet, Chapter I), competition status (Chapter II) and tree size and age (Chapter III) were explored.

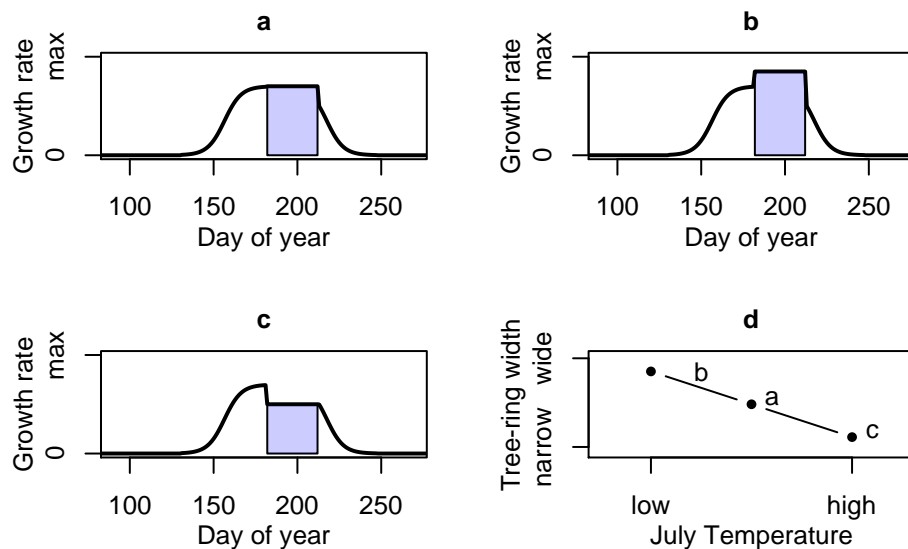
The results from the analyses in Chapter I showed no significant differences in the high frequency climate signal of clones and non-clones, which allows to include clones when calculating mean site chronologies. Clones appeared to grow less, which could not be explained in this article but is discussed further in section 3.1. Chapter II outlines various methods for the visualization of individual white spruce differences regarding their climate signal or tree-ring pattern. While these methods generally appear useful, at each site multiple gradients are overlaid (e.g. temperature, tree density and tree height), which can make it difficult to identify causal relationships and disentangle effects from multiple factors. Lastly, Chapter III compares three methods to assess the ontogenetic change in tree's climate sensitivity, in particular age and size. In agreement with wood anatomical studies and grafting experiments, it appears to be tree size that matters, while age is not or less important. For white spruce in the Brooks Range, increasing susceptibility to previous year summer temperature and drought with tree size were found.

Hereafter the methods, findings and the overall research within the RESPONSE project B2 are discussed from two perspectives. The first part (3.1) focuses on the theoretical link between climate-growth correlations and the growth process. This represents the underlying theoretical framework behind this thesis. In particular, this section follows the scope of the first RESPONSE generation by discussing if using a single reaction norm could be a too strong generalization that neglects the large range of individual reaction norms. In the second part of this synthesis potential consequences of the findings for the future growth of white spruce in Alaska under climate change are discussed. Of course using dendrochronological datasets from three treeline sites in Alaska has only limited potential to make conclusions regarding the growth dynamics and potential range shifts of white spruce in general. Particularly because mainly the growth of trees beyond the seedling and sapling stage was investigated, limited conclusions can be drawn regarding the regeneration dynamics. The investigated dendrochronological datasets nonetheless allow to hypothesize which processes and effects could play an important role in future white spruce growth under climate change and findings are discussed in the context of other recent research articles.

### 3.1 Climate-growth correlations from the perspective of continuous tree-growth

*'[...] trees are not thermometers or raingauges.'*  
- Briffa et al. 1996

One of the main tools in dendrochronology are climate-growth correlations, typically between a mean site tree-ring chronology (master chronology) and climate variables on a monthly or seasonal resolution. However, tree growth is a continuous process. Hence, there is a certain discrepancy between the data, which integrates a certain time period (ring width per year, climate variables per month/season), and continuous tree growth. Climate-growth correlations essentially aim at quantifying the relative variance in tree-ring width (TRW) that is caused by a single climate variable. Thus, when the growth rate is plotted as a line over the course of the year, the area under the curve (integral) represents the tree-ring width (Figure 3a). According to the limiting factor principle, only one factor at a point in time is limiting the growth rate. Thus, if during a specified time period only one factor limits growth, the area under the growth rate curve in this time period is proportional to the value of the climate variable. Figure 3 illustrates such a climate-growth correlations for three years with different July temperatures, assuming that high temperatures in July are negatively correlated with TRW, as found for the Brooks Range site (Chapter III).



**Figure 3** Simplified illustration of a) average, b) low and c) high July temperatures and the effect on tree-growth rates. The respective linear climate-growth relationship is shown in d) where the point labels refer to the other panel IDs (a-c) of this figure.

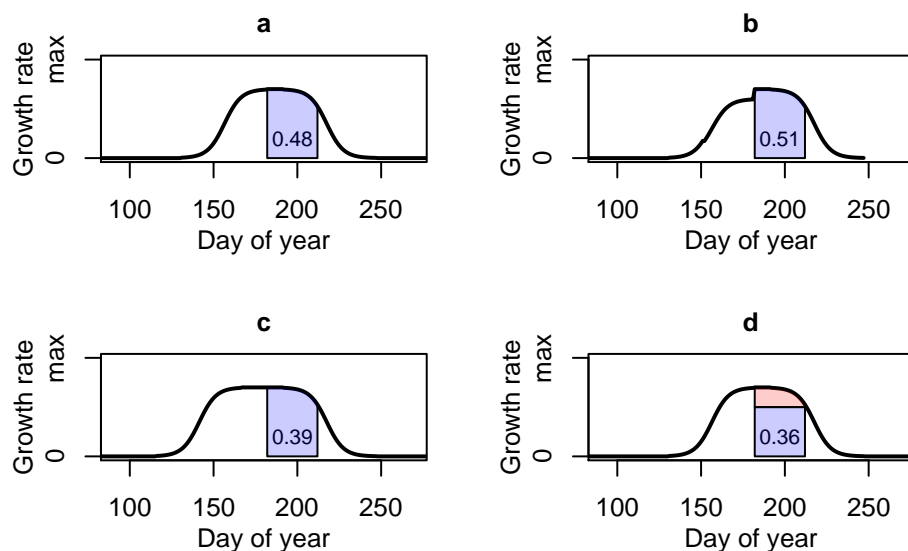
This idealized example assumes that no other variables affect tree growth and that the effect of July temperature on TRW is perfectly linear, hence 100% of the variance would be explained. Of course other variables do affect tree growth, which results in considerable 'noise' in climate-growth correlations and often brings the Pearson correlation coefficient down to values below 0.5.



Noise, i.e. unexplained variance, in linear climate-growth correlations can have a variety of causes. Hereafter some of the most important factors are listed, though a fully comprehensive list may yet be impeded by our incomplete understanding of tree growth.

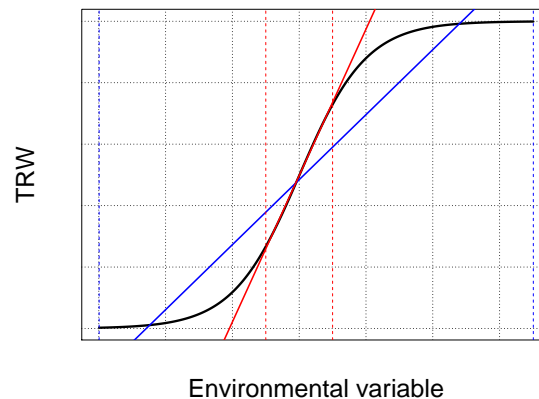
1) Climate in other months also shows interannual variability and affects the final tree-ring width at the end of the year. This means that the relative proportion of tree growth within a year that is related to a single climate variable (e.g. July temperature) depends on how much the tree grew over other parts of the vegetation period. Figure 4b,c shows this exemplarily for decreased growth in June and an earlier onset of the vegetation period, which both affects the relative growth effect of July climate.

2) During some parts of a month, other variables than the one used in a correlation analysis can limit tree growth. For example, growth during one month might first be limited by low temperatures, but after temperatures have increased and do not limit growth anymore, water availability might limit tree growth (Figure 4d). This example still follows the limiting factor principle: While this principle states that only the most limiting factor controls the growth rate at one specific point in time, it leaves the possibility that the growth-limiting factors might switch frequently. Within one month multiple factors can thus limit tree growth.



**Figure 4** The plots show different annual growth rate curves, where the area under the curve (integral) is proportional to the TRW. Different causes for variance in TRW do lower correlations with a single monthly climate variable, exemplarily shown for July temperature. The blue shaded area and the respective number therein depict the proportion of the final TRW that can be attributed to July temperature in the respective year: a) Shows the baseline scenario where July temperature explains all of July growth and 48% of the overall annual growth (TRW). In b) a year with reduced growth in June is shown, which resulted in a lower TRW but a higher relative proportion of July growth. Years with a prolonged vegetation period (c) can increase the TRW but will lower the relative proportion of growth in July. Finally, other variables than temperature can limit growth within July (red shaded area). Consequently July temperature contributes less to the TRW in this year.

3) Pearson correlations only assess linear relationships between two variables. This linearity might be far from nature and bell-shaped, logistic, exponential or logarithmic relationships between processes like growth and environmental variables might be more realistic. Hence, linear relationships are likely only appropriate within a certain range of an environmental variable response (Figure 5). Importantly, even at the quasi-linear parts of any non-linear relationship (red dashed lines in Figure 5) the fit of a linear model can be low when the observed values in the environmental variable range beyond this linear part (e.g. the environmental range marked by the blue dashed line).



**Figure 5** Describing non-linear relationships between environmental variables and TRW (black line) with linear models (solid red and blue lines) will systematically cause systematic over or underestimations of TRW depending on the range of the observed variance (dashed red and blue line respectively to the lines of the linear models) in the environmental variable.

4) Parts of the restrictions of the limiting factor principle were already described in (2), i. e. the temporal switch in growth-limiting factors. However, even the fundamental claim of this principle could be flawed. While it likely remains a useful generalization for statistical analyses, it is questionable if environmental variables do not have any effect on tree growth, as long as they are not the most limiting factor. In particular the concept of co-limitation contrasts the limiting factor principle. It was hypothesized that adaptations regarding resource-allocation should equalize growth limitation by all resources (Bloom et al. 1985). In particular because adaptation comes at a price and because there is no selection pressure towards efficiency if a factor is not limiting anyway, multiple factors could limit growth equally. This lead to the formulation of the 'Law of the minimum paradox', stating that '*if for a randomly chosen pair "organism–environment" the Law of the Minimum typically holds, then in a well-adapted system, we have to expect violations of this law*' (Gorban et al. 2011). In fact, various studies did find co-limitation in plants and thus a violation of the limiting factor principle (Taylor and Terry 1984, Andersen and Pedersen 2002, Garcia et al. 2013). Three types of co-limitation can be distinguished: 1) truly independent co-limitation, 2) biochemical substitution and 3) biochemically dependent co-limitation where one resource is required to obtain another resource (Saito et al. 2008). Theoretically co-limitation could occur at white spruce treelines in Alaska, for example when increasing atmospheric CO<sub>2</sub> levels would increase the water use efficiency in a water stressed tree. This effect was already shown with free-air CO<sub>2</sub> enrichment (FACE) experiments and carbon isotope studies (Drake et al. 1997, Ainsworth and Rogers 2007, Frank et al. 2015). Plants close their

stomata to reduce water loss, which also prohibits CO<sub>2</sub> uptake. Consequently both, increased CO<sub>2</sub> levels as well as increased precipitation, could increase plant growth. However, simply showing that CO<sub>2</sub> or NPK fertilization promotes growth in natural systems like treelines is insufficient to support either theory. This is because Liebig's Law of the Minimum only refers to a point in time and environmental conditions are changing constantly in nature, thus improved growth could also be explained by temporal switches in growth limitation (see 2).

5) Lastly, intrinsic effects could add to the noise in simple climate-growth relationships. Even under exactly the same environmental conditions, tree growth can vary. Chapter II and III outline that individual tree parameters like competition status and tree size affect climate-growth correlations. Thus, if these effects are not accounted for and their frequency in the population changes over time, biases in mean site chronologies are to be expected. Autocorrelation in tree-ring data is another important internal source for noise: A year with extremely unfavorable climate for tree growth will result in a wider ring when the previous years were more favorable and a narrower ring when previous years were also very limiting for tree growth. Such effects can have multiple causes: Parameters like tree and crown size usually do not change drastically between two years, hence a tree should have a very similar photosynthetic capacity between successive years, resulting in significant autocorrelation in tree-ring series (Fritts 1976, Cook and Kairiukstis 1990). Evergreen conifers like white spruce also keep multiple generations of needles, similarly increasing autocorrelation (Hom and Oechel 1983) by affecting the photosynthetic capacity. Non-structural carbohydrates, the reserves of a tree, will also affect autocorrelation. However, the mobility of non-structural carbohydrates can be very high or low (Richardson et al. 2013) and generally little is known on how trees allocate carbon into secondary growth, reserves, seed production and other compartments (Lacointe 2000, Dietze et al. 2014, Hartmann and Trumbore 2016, Hartmann et al. 2018). These uncertainties also contribute to the controversy around carbon source and sink limited tree growth described in the introduction. Carbon allocation to different compartment and process can vary significantly between years, for example in species that exhibit masting behavior, as white spruce does. During masting years considerably more resources are needed for seed production, which appears to leave less resources for secondary growth and has thus been linked to narrower tree rings (Roland et al. 2014, Hacket-Pain et al. 2015). For example in beech (*Fagus sylvatica*), the majority of autocorrelation in TRW is caused by masting (Hacket-Pain et al. 2015). It is possible to study carbon allocation with carbon isotopes but this is often impeded by the large efforts, size of mature trees, destructive methods and difficulties in accessing below ground biomass (Epron et al. 2012).

The described effects of tree's intrinsic physiology, carbon dynamics and autocorrelation cumulatively lower correlation values in the analysis of tree's climate sensitivity. Only the average effect sizes of masting or autocorrelation can be estimated, while its interannual variability is barely understood. These uncertainties in estimates of such carry-over effects could easily sum up over time (Markov chain), which also makes predictions of future tree growth more difficult.

Further intrinsic effects that add unexplained variance in climate-growth correlations are genetic differences between trees. However, studies that did investigate genetic effects

either found no effects at all or only low effect sizes (King et al. 2013, Heer et al. 2018, Kruse et al. 2018). Similarly our study on the high frequency growth variability between clones and non-clones found no differences (Chapter I). While we did find narrower rings for clones, this does not automatically imply that clonality causes reduced growth. Other factors that appear equally or even more likely to be responsible for narrower rings of clones are the higher average age of clones and that clones were more frequent at the harsher climate of the treeline edge, compared with the edge of closed forest.

All the above listed mechanisms that affect climate-growth correlations illustrate the complexity of tree growth and why the formula for the linear aggregated model for tree-ring series (Cook 1985, Speer 2010) is intentionally left vague, representing a concept rather than exactly describing tree physiology:

$$R_t = f(G_t, C_t, D1_t, D2_t, E_t) \quad (1)$$

In each year ( $t$ ),  $R_t$  is the tree-ring width (or another biomass increment proxy),  $G_t$  is the size/age-related growth trend,  $C_t$  is the climatic effect,  $D1_t$  and  $D2_t$  are endogenous and exogenous site effects and  $E_t$  is the error term covering all other variables. This formula can be adapted to describe how a single monthly climate variable affects tree-ring width (similar to the reaction norm in Figure 5). To do so, first tree-ring width or biomass increment has to be described as the integral of the growth rate  $r$ :

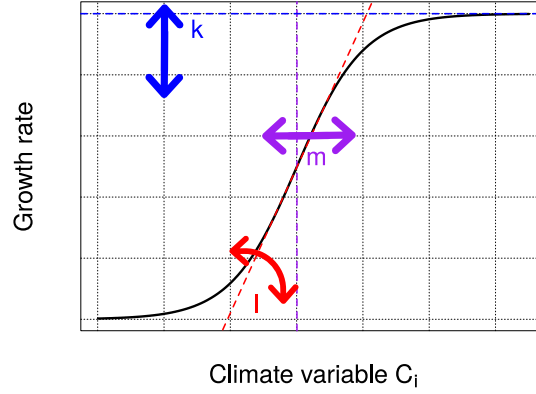
$$r = f(G, Cn, D1, D2, E) \quad (2)$$

$$RC_{iab} = \int_a^b r = \int_a^b f(G_{ab}, Cn_{ab}, D1_{ab}, D2_{ab}, E_{ab}) \quad (3)$$

This formula describes the fraction of the tree-ring width  $RC_{iab}$  that is attributed to climate variable  $C_i$  ( $i$  out of  $n$  climate variables) in the time period from  $a$  to  $b$ . In contrast to the original formula, the function  $f$  describes the tree-ring width not directly but the growth rate. Thus the integral of  $r$  in the time period  $a$ - $b$  represents the ring-width increment (see Figure 3 and 4). It is important to understand that  $RC_{iab}$  does not only depend on the single climate variable  $C_i$ , as outlined in the list above. Instead, a multitude of variables determines the shape of response curves. Consequently, a response curve should be seen as a simplification and a realistic figure would require as many dimensions as there are independent variables, resulting in a hypervolume which is impossible to illustrate. Nonetheless, such response curves remain useful even though they only show the effect of one variable under average or fixed values of all other variables. To link the limitation of response curves to the tree growth model above, the following logistic formula and Figure 6 for the growth rate  $r$  exemplarily shows how a multitude of independent variables could affect different properties of a response curve:

$$r = \frac{k}{1 + e^{-l(C_i - m)}} \quad (4)$$

While parameter  $k$  represents the maximum growth rate (upper asymptote),  $l$  determines the maximum slope angle and  $m$  the horizontal position.



**Figure 6** Example of a simplified logistic function and effects of the parameters a) maximum growth rate, b) maximum growth increase per change in the climate-variable, and c) climate-variable value at the inflection point.

While this formula could simply replace linear functions, the true complexity of tree growth arises from parameter interactions. In this case, the parameters  $k$ ,  $l$  and  $m$  would in fact again be functions of all other environmental and intrinsic variables:

$$r = \frac{k(G_{ab}, Cn_{ab}, D1_{ab}, D2_{ab}, E_{ab})}{1 + e^{-l(G_{ab}, Cn_{ab}, D1_{ab}, D2_{ab}, E_{ab})(C1 - m(G_{ab}, Cn_{ab}, D1_{ab}, D2_{ab}, E_{ab}))}} \quad (5)$$

At this point it is already impossible to fit a growth rate model because the large number of parameters and parameter interactions reduces the degrees of freedom so drastically that it would require an impossibly huge data set with time-series data of all environmental and endogenous variables. For simplification here a symmetric logistic function is used while asymmetric bell shaped functions would probably be more realistic. Furthermore, nature's complexity does not just stop there but tree growth could be further divided into different processes, like cambial activity, stomata regulation, photosynthesis and even single enzymatic activities (Pallardy 2010). At this point we come back to the introductory quote of this thesis which refers to the '*infinite fineness of the web of causality*', and perfectly describes tree physiology. The '*large patterns*' that arises from this complexity is the interannual variability of tree growth.

Hence, the challenge for dendroecology in general and treeline research in particular is to find appropriate simplifications to describe climate-growth relationships for the data that is available. While the five listed effects certainly do contribute to noise in climate-growth correlations, they likely differ in their importance or effect size. Typically significant climate-growth correlations are found for more than just one month or variable. Thus it appears likely that a significant proportion of 'noise' in the correlations between a single monthly climate variable and tree-ring width originates from the interannual growth-rate variability in other months (Figure 4b,c), as well as years where other climate variables than



the investigated one are more limiting to growth (Figure 4d). In addition, the work related to this thesis indicates that effects like tree size (Chapter II) or competition (Chapter II) between trees can also significantly alter climate-growth correlations, which corresponds to the endogenous effects ( $D_1$ ) in the original aggregated tree growth model. This highlights that individual tree differences in size or competition status should be considered. Thereby this thesis is in line with a series of recent research articles that found modulations of tree's climate sensitivity by age/size (Carrer and Urbinati 2004, Konter et al. 2016), competition (Choler et al. 2001, Wang et al. 2016, Alam et al. 2017, Gleason et al. 2017), mast years (Hacket-Pain et al. 2015), or nitrogen deposition (Ibáñez et al. 2018) and emphasizes the benefits from integrating various tree metadata in dendroecological analyses (Lloyd et al. 2017). But maybe most importantly, as dendrochronologists we need to be aware of the limitations of our own discipline and openly discuss the uncertainties regarding our data and analyses, thus fostering '*a culture of humility in tree-ring science*' (Biermann and Grissino-Mayer 2018).

## 3.2 White spruce responses to climate change in Alaska

### 3.2.1 Water-stress effects

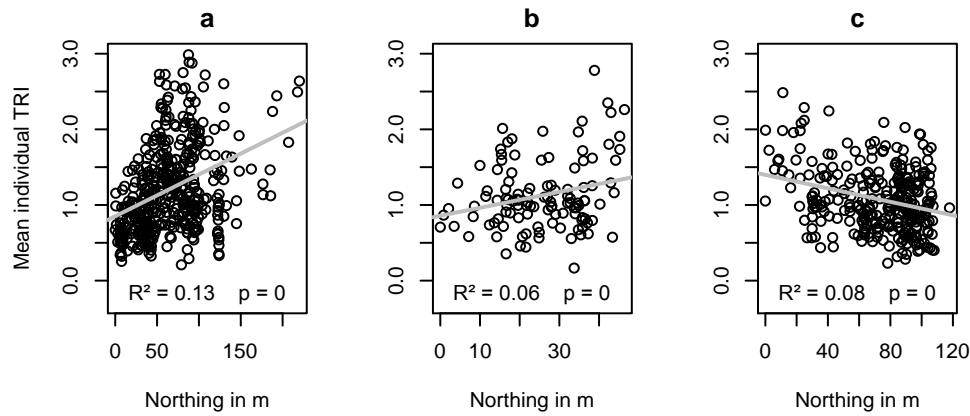
Future white spruce growth dynamics are of interest to estimate the impact of climate change on the boreal forest ecosystem, local forestry, as well as global carbon models and feedback loops to climate change. As outlined in the previous chapter, tree-ring studies and datasets have certain limitations. Nonetheless even comparatively simple methods like climate-growth correlations can shed light on several important factors that drive white spruce growth in Alaska and potential treeline shifts. Two important factors that were explored in this thesis are tree size and competition (Chapter II, III). These individual tree parameters are both connected to the xylem anatomy and water stress and illustrate that trees have to balance contrasting adaptations regarding wood anatomical traits to optimize their fitness: On the one hand, physical stability and resistance against embolisms due to drought is highest with smaller lumen diameters and thicker cell walls (Tyree and Zimmermann 2002, Ryan Michael G. et al. 2006). However, this tracheid morphology also requires more carbohydrates for construction, given that the cumulative hydraulic diameter of the tracheids stays constant (Tyree and Zimmermann 2002, Schweingruber 2007). In contrast, tracheids with larger lumen diameters have a lower physical strength but also a lower hydraulic resistance and thus ensure a more efficient water transport (Tyree and Zimmermann 2002, Ryan Michael G. et al. 2006). Thus wood anatomy nicely exemplifies that adaptation to one factor often comes for a price (Allen Orr 2000, Botero et al. 2015). Additionally, tracheid lumen-diameters also increase with the distance from the apex as described in Sanio's law (Sanio 1872, Mencuccini et al. 2007, Anfodillo et al. 2013). This could make tall trees potentially more susceptible to water stress, which is in line with our findings of higher sensitivity of tall trees to previous year July temperature in the Brooks Range (Chapter III). It could even be hypothesized that the non-linear change of climate sensitivity with tree size is linked to the power-function relationship between conduit diameter and tree height (Anfodillo et al. 2013), but more research is needed to support this hypothesis. Of course height-growth also has its advantages. In fact it is the result of selection pressure,

because higher trees have an advantage in the competition for light, which also plays a role in the boreal forest (King 1990, Koch et al. 2004).

Moisture is not just important for white spruce in Interior Alaska (e.g. positive correlations with drought index SPEI (Vicente-Serrano et al. 2009) in spring), but also at the alpine treelines in the Brooks Range and the Denali National Park and Preserve (negative correlations with previous summer temperatures and SPEI). Analogue, a range of other studies on white spruce growth in Alaska found similar correlations with moisture-related climate variables (Barber et al. 2000, D'Arrigo et al. 2004, Beck et al. 2011, Ohse et al. 2012, Sullivan et al. 2017). Consequently the three factors competition for water, height growth and wood anatomy could change at all sites in response to a potentially drier climate in Alaska (van Oldenborgh et al. 2013, McAfee et al. 2014). It has been hypothesized that increased competition for water might reduce tree density and accelerate self-thinning (Wang et al. 2016). Self-thinning in general describes the decrease in stem density as individual above-ground biomass increases (Bartsch and Röhrig 2016). In addition to self-thinning, individual growth rates could decline due to lower individual water availability. After the controversy around universal self-thinning functions like the  $3/2$  power rule (Zeide 1987, Lonsdale 1990, Hamilton 1995) there appears to be a considerable research gap regarding the link between growth trends and self-thinning. Generally self-thinning is mostly linked to competition for light (Bartsch and Röhrig 2016), but it has been shown that the self-thinning function can be modulated by other variables like soil moisture (Deng et al. 2006). In the past it has been observed that white spruce stands with lower tree density often showed lower moisture sensitivity and higher growth rates (Wilmking and Juday 2005, Beck et al. 2011, Sherriff et al. 2017, Buechling et al. 2017). This could point at a phenomenon where negative individual tree growth-trends are offset by increased self-thinning. However, a systematic analysis of this topic does not yet exist, which adds uncertainty to any estimates of future white spruce growth.

At treelines, stem density also decreases but is more typically attributed to stochastic effects like micro-site differences (Körner 2012). Nonetheless gradual treelines do also feature competition gradients (Choler et al. 2001, Sveinbjörnsson et al. 2002, Körner 2012, Gleason et al. 2017). It could thus be hypothesized that white spruce is less negatively affected by potentially drier climate at the very edge to the tundra. Particularly at temperature limited alpine treelines where precipitation is low too, there could be a steep gradient where trees at the tundra edge benefit from climate change due to warming while trees growth at the forest edge experience higher water stress and thus grow less. This could explain the counter intuitive growth differences along the investigated treeline gradients: wider tree rings at the tundra edge than at the forest edge (Figure 7). Typically it is assumed that growth conditions at the tundra edge are more limiting because of the harsher climate. However, increasing individual growth towards the tundra edge were also reported for other white spruce sites and appears to be linked to the benefits of increased temperatures (Rupp et al. 2001, Lloyd and Fastie 2002, Hinzman et al. 2005). Such increased growth of mature white spruce at treelines could hint treeline shifts. However, seed production, germination and seedling survival are arguably even more crucial to treeline dynamics and climatic effects on these processes are of highest interest.





**Figure 7** Mean age-trend corrected (RCS method) TRI per individual along the tree line gradients at a) the Brooks Range site, b) the Denali National Park site and c) the Interior Alaska bluff. The tundra edge is in the north for a) and b), but in the south for c). Thus linear models (grey line) for all sites indicate that trees at the tundra edge grow better than those at the forest edge.

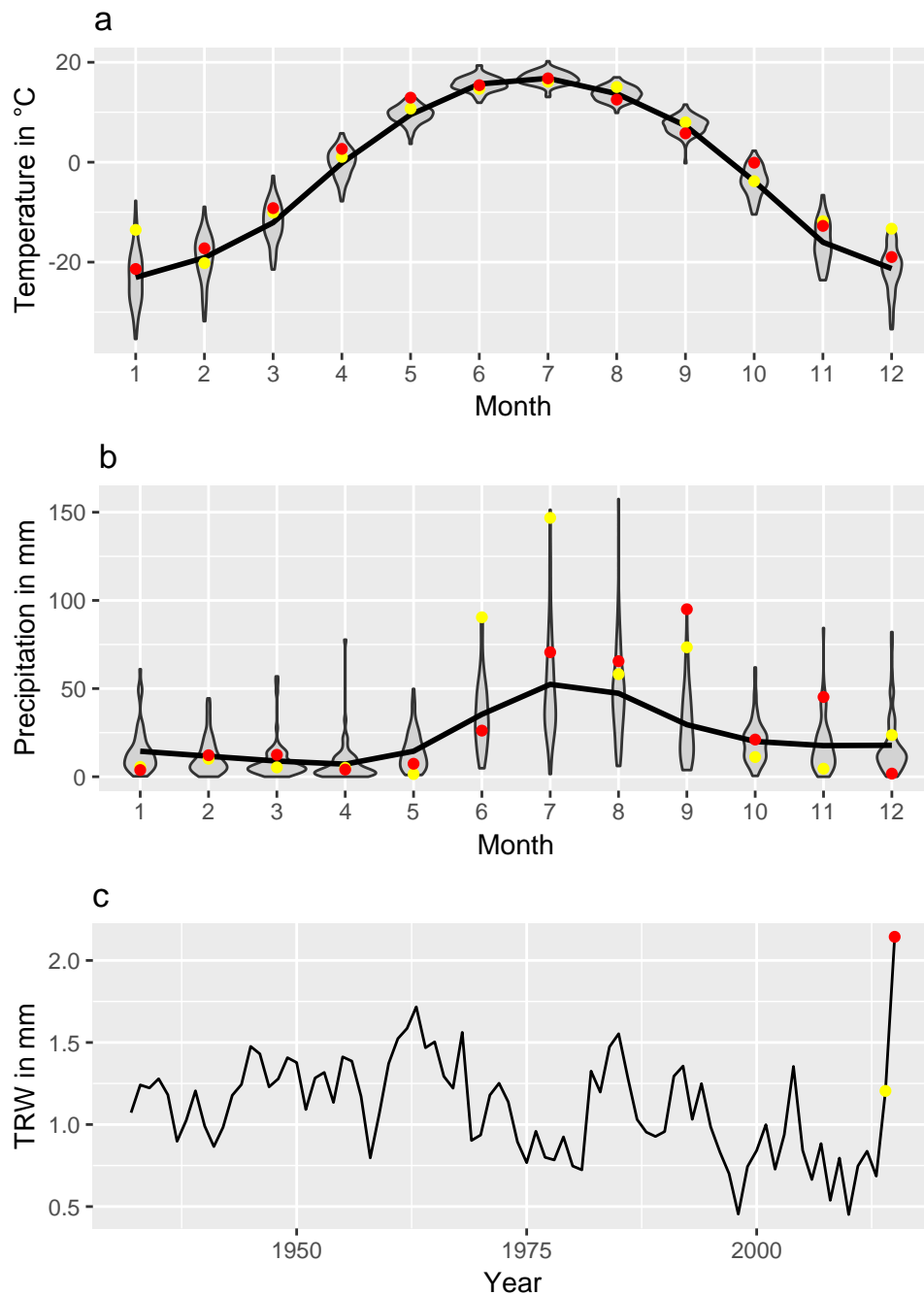
### 3.2.2 Frequency of climatically outstanding years

In future climatically exceptional years and periods of uncommon climate could play a crucial role with regard to masting years, survival probabilities of seedlings, as well as for white spruce growth in general. Globally, climate extremes appear to become more frequent (Fischer and Knutti 2015, Stott 2016), which could play a crucial role for the future of white spruce in Alaska. Generally, perennial plants are required to endure a wide variety of climates because climate can vary considerably between years. Stochasticity alone will lead to single years and series of years that are much drier, moister, warmer or colder than average years. If species would not have been able to cope with this variability they would have gone extinct in the past (Aitken et al. 2008). Nonetheless this interannual climatic variability does have an effect. In the introduction it was already described that the treeline position is the integrated effect of climate on a decadal scale and that treeline shifts will thus likely show a lagged responses to climate change (Paulsen et al. 2000, Körner 2012). Similarly, the frequency, and intensity of masting years in white spruce are connected to interannual climate variability (Kelly 1994). In particular, white spruce seed fall is positively correlated with summer precipitation and negatively correlated with summer temperature, while seed viability is higher when summers were warm (Roland et al. 2014). For successful recruitment after a masting year seeds need favorable climate for germination and establishment. Prolonged vegetation periods, i.e. early snow melt and high growing degree days (GDD) appear to be particularly favorable for seedlings (Barbeito et al. 2011, Miller et al. 2017). Furthermore, moss cover on the ground, previous fires and competition affect white spruce regeneration (Callaway and Walker 1997, Zhang et al. 2015, Sherriff et al. 2017). The multitude of factors that have to align to create favorable years and conditions for white spruce regeneration indicates why recruitment might happens infrequently and could explain why recruitment waves are observed (Miller et al. 2017). Age distributions at the investigated study sites also indicate recruitment waves, in particular the bimodal distribution in the Brooks Range and Denali National Park or the post-fire recruitment at the Interior Alaska bluff site and the resulting even aged stand structure (Figure 8).



**Figure 8** Age distribution at the three study sites showing bimodal distributions at the Brooks Range site (a) and the Denali National park site (b) and the comparatively young tree ages resulting from the post-fire succession at the Interior Alaska bluff (c).

Very favorable but infrequent weather conditions do not just affect regeneration, but also growth directly. Lloyd et al. (2013), linked good growth of white spruce at bluff sites to uncommon climatic conditions, in particular a period with comparatively moist and cool summers. The probability of favorable years for regeneration and growth of white spruce appears to be connected to large scale and long-term climate variability. In the past, the Pacific Decadal Oscillation (PDO) has been linked to low frequency (>10 years) black and white spruce growth-variability (Barber et al. 2004, Wilmking and Myers-Smith 2008, Ohse et al. 2012) and possibly also recruitment waves. It is uncertain to what extent climate change will increase or decrease the frequency distribution of extremely favorable or unfavorable climatic episodes, which adds considerable uncertainty regarding future white spruce performance. TRW time series from the Interior Alaska bluff site show a good example of the direct impact of outstanding favorable climatic conditions due to high summer precipitations (2014 and 2015, Figure 9). However, assessing the impact of rare events statistically is often impaired by the low sample size, even though the potentially large impact of unlikely events is generally accepted (Taleb 2008). Thus experimental setups have been proposed to study extreme events (Jentsch and Beierkuhnlein 2008), which also appears suitable for white spruce seedlings.



**Figure 9** Violin plots showing the distribution of the temperature (a) and precipitation (b) data recorded at the Fairbanks International Airport since 1950 and the mean tree-ring width (TRW) at the Interior Alaska bluff site near Fairbanks. The years 2014 (yellow) and 2015 (red) are highlighted because of the excessive growth in 2015 (c), which appears to be the result of excessive precipitation in the summer 2014. Climate data source: <http://akclimate.org> ; 30.05.2018.

### 3.2.3 White spruce growth trends

Long-term growth trends of white spruce in Alaska due to climatically exceptional years could play an important role, but it is of course also the gradual change of average climatic conditions that affect these trends. In the past ‘boreal browning’, i.e. a reduction in the normalized difference vegetation index (NDVI), has been observed in Interior Alaska’s

boreal forest (Verbyla 2008, Beck and Goetz 2011), which could indicate reduced growth but browning is also affected by insect infestations or wildfires. Even though tree-ring datasets appear to allow an easy assessment of past trends in tree growth, this assessment is hindered by effects like the ‘modern sample bias’, ‘big tree selection-bias’ and the ‘pre-death suppression bias’ (Briffa and Melvin 2011, Brien Roel J. W. et al. 2012, Bowman et al. 2013). Recently two publications reported that white spruce in Alaska does indeed often show negative correlations with summer temperatures but found little evidence for a negative growth trend over the last decades (Sullivan et al. 2017, Cahoon et al. 2018). However, both studies detrended data with multiple regional curves, which is supposed to remove age trends in tree growth while accounting for faster and slower growing trees. As outlined by Briffa and Melvin (2011), the use of multiple RCS curves requires that trees in the past grew under similar climate as today, else growth trends could be reduced or even removed. Essentially this effect describes that RCS curves are likely not stable over time. The fact alone that separate RCS curves are usually developed for each individual site shows that there is no universal age-trend curve and that disentangling age trends from other long term growth trends is challenging. Consequently growth-trend assessments should be treated with caution since there are methodological challenges and uncertainties, not just regarding future, but also regarding past growth trends of white spruce in Alaska. Biases in assessing growth trends are best avoided by assessing how the annual increments per stem diameter class vary over time (Bowman et al. 2013, Peters et al. 2015). However, these methods require larger sample sizes of several hundred trees, uneven aged forests, and asynchronous small scale disturbances (e.g. no fires or pest outbreaks).

## 4 Conclusions and outlook

This thesis focused on growth limitations of white spruce on the individual tree level. In particular it was explored if and how size, age, competition and cloning can affect climate growth correlations. On a meta-level this means that white spruce reaction-norms to one environmental variable are also a function of other intrinsic (e.g. height, genetics) or extrinsic (e.g. other climate variables or competition) variables. Estimating future white spruce range dynamics and growth trends is impeded by this complexity. However, dendrochronology allows to identify some of the most important climatic growth-drivers and thus provides rough estimates of white spruce responses to environmental change. In Alaska, water stress could play an increasingly prominent role for future white spruce growth dynamics. Though, more research is needed to better understand when moisture stress results in negative growth trends, in altered tree size and age distributions, altered wood anatomy and/or reduced tree densities.

Tree physiology still eludes our understanding in many aspects. Particularly carbon allocation and NSC dynamics appear to be important mechanisms that are not yet well understood. Correlations between pre-whitened (i.e. after autocorrelation was removed) TRW and previous year climate variables (e.g. previous year July temperature at the Brooks Range site) shows that interannual NSC dynamics do play an important role for white spruce in Alaska. Such interannual and multi-year effects are also particularly interesting for treeline dynamics because trees can survive several unfavorable years and their survival

is often rather bound to the long term climate (decades to centuries) (Paulsen et al. 2000), though extreme events can also have a large impact (Jentsch and Beierkuhnlein 2008).

The increasing interest in wood anatomy results from its link to tree physiology, for example hydraulic conductivity, embolism susceptibility, and the physical stability of the trees are linked to lumen diameter and cell wall thickness of tracheids (Cuny et al. 2014, Carrer et al. 2015, Rathgeber et al. 2016). Furthermore, wood anatomy is particularly promising because it allows insights into intra-annual tree growth and thus offers a higher temporal resolution of tree growth data, though collection of multiple micro cores within a year (Rossi et al. 2006) or dendrometer are required for exact timing (Deslauriers et al. 2007). Particularly once wood anatomical methods become more efficient to facilitate larger sample sizes, our understanding on tree growth will likely greatly benefit.

Lastly, statistical analysis are getting more complex and powerful than traditional climate-growth correlations with single climate variables. Mixed model for example already facilitate to assess multiple climatic and individual tree variables and their interactions (Zuur 2009). However, the complexity of tree growth as outlined in section 3.1 hints that even these models will likely have their limitations. The human mind is already challenged with four dimensions, while mathematically there is no limit to describing relationships of multiple variables and their interactions. Ultimately dendroecology could thus benefit from utilizing machine learning. Specialized machine-learning R-packages for dendrochronology have already been published (Jevšenak and Levanič 2018) and similar approaches are being developed for the parametrization of the Vaganov-Shashkin growth-rate model (pers. com. Ivan Tychkov). On the downside, large high-resolution datasets are required and results from machine-learning methods like artificial neural networks often are a 'black box', thus determining exact mechanisms and drivers for tree growth becomes more difficult with such methods.

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## List of other scientific contributions

### Conference contributions

- **Trouillier, M.**, M. van der Maaten-Theunissen, M. Wilmking (2016) Individual climate sensitivity of *Picea glauca* at water and temperature limited tree-lines in Alaska. poster presentation, Annual conference of the Ecological Society of Germany, Austria and Switzerland (GfÖ).
- **Trouillier, M.**, M. van der Maaten-Theunissen, M. Wilmking (2017) White spruce at its limits?. Oral presentation, annual conference of Tree Rings in Archaeology, Climatology and Ecology (TRACE).
- **Trouillier, M.**, M. van der Maaten-Theunissen, M. Wilmking (2018) Four methods to visualize individual tree differences in climate sensitivity. poster presentation, annual conference of Tree Rings in Archaeology, Climatology and Ecology (TRACE).

### Coauthored manuscripts

- Wilmking M., M. van der Maaten-Theunissen, E. van der Maaten, T. Scharnweber, A. Buras, C. Biermann, M. Gurskaya, M. Hallinger, J. Lange, R. Shetti, M. Smiljanic, **M. Trouillier** (2018) Non-stationarity dominates the relationship between climate and tree growth around the globe. in preparation.
- Würth, D. G., P. Eusemann, **M. Trouillier**, A. Buras, A. Burger, M. Wilmking, C. A. Roland (2018) Environment drives spatio-temporal patterns of clonality in white spruce (*Picea glauca*) in Alaska. Submitted to: Canadian Journal of Forest Research.
- La, C., T. Anfodillo, S. Pandey, G. Petit, P. Eusemann, **M. Trouillier**, M. Wilmking, A. Maritan (2018) Trees prioritize crown growth in height as latitude increases. Submitted to: Global Ecology and Biogeography.
- Thomas, H.J.D., I. H. Myers-Smith, T.T. Høye, M. Petit Bon, J. Lembrechts, E. R. Walker, K. Björnsdóttir, I. C. Barrio, I. S. Jónsdóttir, S. Venn, J. M. Alatalo, J. L. Baltzer, C. A. Wallace, D. Ackerman, L. Gough, J. Prevey, C. Rixen, M. Carbognani, A. Petraglia, C. T. Christianen, D. W. Inouye, J. E. Ogilvie, **M. Trouillier**, M. Wilmking, R. Treharne, S. Angers-Blondin, C. Urbanowicz, J. von Oppen, S. Wipf, M. Doyle, S. Suzuki, S. Serikova, A. D. Bjorkman, D. Blok, J. Sarneel. Drivers of decomposition across the tundra biome. in preparation.

## Eigenständigkeitserklärung

Hiermit erkläre ich, dass diese Arbeit bisher von mir weder an der Mathematisch-Naturwissenschaftlichen Fakultät der Universität Greifswald noch einer anderen wissenschaftlichen Einrichtung zum Zwecke der Promotion eingereicht wurde. Ferner erkläre ich, dass ich diese Arbeit selbstständig verfasst und keine anderen als die darin angegebenen Hilfsmittel und Hilfen benutzt und keine Textabschnitte eines Dritten ohne Kennzeichnung übernommen habe.

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Mario Trouillier

## Erklärung zur Abgabe einer elektronischen Kopie der Dissertation

Mathematisch-Naturwissenschaftliche Fakultät

Einverständniserklärung nach § 4 Abs. 1 Nr. c Promotionsordnung

Hiermit erkläre ich, dass von der Arbeit eine elektronische Kopie gefertigt und gespeichert werden darf, um unter Beachtung der datenschutzrechtlichen Vorschriften eine elektronische Überprüfung der Einhaltung der wissenschaftlichen Standards zu ermöglichen.

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Mario Trouillier

## Acknowledgements

I would like to thank all the people who helped and supported me during the years of my PhD. I am particularly grateful to Martin, who was a great mentor and who not just guided me through the winding path of doing a PhD in dendrochronology, but also impressively mastered all the non-scientific challenges in fieldwork, the graduate college RESPONSE and motivating an ever questioning student. To Marieke I am especially grateful for her constant kind support and her scientific expertise whenever I was running into problems. Generally I am grateful to all the people in the working group, the good atmosphere and all the inspiring scientific and non-scientific debates. To René, Ilka, Ulrich, Kathrin, Angelika and Christof I am grateful because they keep the institute's infrastructure running while they often only hear from us when things do not work.

To Birthe, my Family and my Friends I am grateful for supporting and encouraging me and I apologize for spending too much time in the office and too little time with you.

Special thanks goes to all the great people who support and contribute to the various open source and open access projects.



