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ORIGINAL ARTICLE

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

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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 re-sprouting 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; Lindholm 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 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.

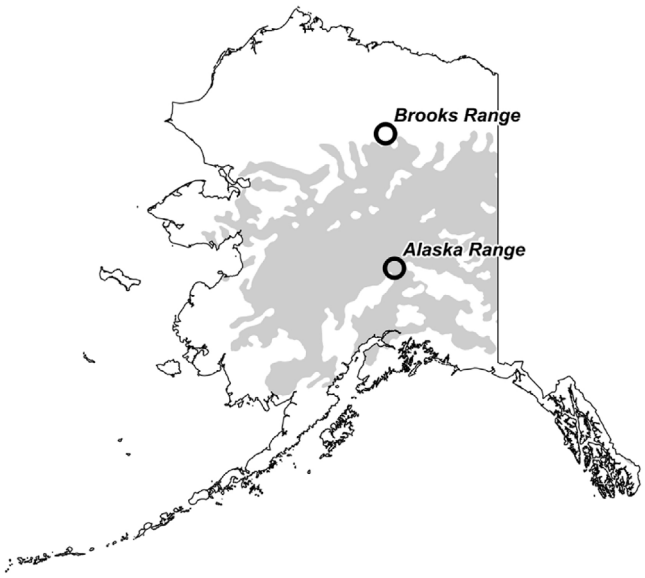

Fig. 1. Location of the study sites, grey shading indicating the range of White spruce in Alaska (Little, 1971). The Brooks Range site represents the northern treeline, while the Alaska Range site is an elevational treeline.

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.

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 GenAlEx 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 GenAlEx 6, and null allele frequencies were calculated using GenePop'007 (Rousset, 2008). Apart from the clonality estimations, all population genetic