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Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia

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Summary

- Shrub expansion in alpine and arctic areas is a process with possibly profound implications for ecosystem functioning. The recent shrub expansion has been mainly documented by remote sensing techniques, but the drivers for this process largely remain hypotheses.
- Here, we outline a dendrochronological method, adapted to shrubs, to address these hypotheses and then present a mechanism for the current shrub expansion by linking recent climate change to shrub growth performance in northern Sweden.
- A pronounced increase in radial and vertical growth during recent decades along an elevational gradient from treeline to shrubline indicates an ongoing shrub expansion. Age distribution of the shrub population indicates the new colonization of shrubs at high elevations.
- Shrub growth is correlated with warm summers and winter snow cover and suggests the potential for large-scale ecosystem changes if climate change continues as projected.

Introduction

In contrast to the long tradition of tree-line research, the examination of changes in the cover and position of shrub vegetation in the treeless tundra regions has just begun. In 2001, Sturm *et al.* reported on increasing shrub abundance in the Alaskan Arctic, where shrub-dominated vegetation had partly doubled during the last 50 yr, over an area of *c.* 320 km^2. In 2006, evidence from time series of aerial photography in arctic Alaska indicated that shrub cover was expanding over an area of *c.* 200 000 km^2 (Tape *et al.*, 2006), and the pan-Arctic trend of increasing photosynthetic activity of herbaceous and shrub vegetation types suggests a similarly widespread shrub expansion (Jia *et al.*, 2004; Bunn *et al.*, 2007). This shrub expansion is commonly attributed to climate warming (Forbes *et al.*, 2009) whose current rate in the arctic (of *c.* 0.5°C per decade) is five times faster than the global average (Serreze *et al.*, 2000; ACIA, 2005). However, the exact role of summer or winter temperatures, snow cover or the change in growing season length remains unclear (Sturm *et al.*, 2005a; Tape *et al.*, 2006) and so the actual mechanisms and processes behind the current shrub expansion merit examination. Although there are estimates of tundra shrub colonization rates derived from repeat photography, no *in situ* quantification of the growth rates of tundra shrubs has been achieved.

Shrubs are likely to take full advantage of the current climate warming, because they profit from climate-induced ecosystem changes, such as soil disturbances or shifts in nutrient availability, more than other plant functional types (Lantz *et al.*, 2009). Most shrubs produce highly decomposable litter (Lett & Knapp, 2003) and shrubs have the highest resource uptake potential of all tundra plants (Sturm *et al.*, 2005b). Once established, shrubs thrive and dominate the lower vegetation by canopy shading (Bret-Harte *et al.*, 2002; Mack *et al.*, 2004), leading to widespread changes in tundra-ecosystems.

A change in shrub cover could alter the hydrology of the tundra by influencing the active layer depth through increasing summer transpiration and accumulation of winter snow (Sturm *et al.*, 2005b). An increased accumulation of snow in winter would also alter soil thermal regimes leading to warmer soil temperatures, whereas shading in the summer could possibly reduce summer soil temperatures.

Shrub expansion will also change the carbon balance of tundra ecosystems: more carbon will be sequestered by increased growth of existing shrubs and colonization of former shrub free areas (Oechel *et al.*, 2000; Sturm *et al.*, 2005a) but carbon losses might also occur from greater soil microbial activity because of easily decomposable litter, increased nutrient supply and generally warmer soil temperatures resulting in faster soil carbon turnover rates (Mack *et al.*, 2004; Chapin *et al.*, 2005; Sturm *et al.*, 2005a). In permafrost areas sensitive to thaw, the additional warming resulting from higher snow accumulation in winter could possibly tip the scale to a large-scale release of old carbon currently stored in the frozen ground (Michaelson *et al.*, 1996; Sturm *et al.*, 2005b) further amplifying global warming. Evidence also suggests a reduction of albedo: in summer, solar radiation will be absorbed to a greater extent by the darker surface of the shrub canopies compared with the brighter tundra vegetation (Beringer *et al.*, 2005). In winter, those shrubs that protrude above the snow surface might further add to the absorption of solar radiation (Chapin *et al.*, 2005; Sturm *et al.*, 2005a). Both processes will reduce albedo and lead to regional warming (Sturm *et al.*, 2005a). A full conversion of arctic tundra to shrub tundra would increase summer atmospheric heating. The resulting energy fluxes are estimated to be twice as high as those resulting from a potential doubling of the present CO_2 concentration in the atmosphere (Chapin *et al.*, 2005).

Shrub expansion has three characteristics: (1) an increasing shrub density, that is, the infilling of shrub patches, (2) an increase of shrub size (radial and vertical growth) and (3) the new colonization of formerly shrubless areas (Tape *et al.*, 2006). Here, we outline a strategy to apply methods of dendrochronology – the analysis of tree or shrub rings – as a tool to examine the current shrub expansion.

For our study, we chose the alpine tundra area of Northern Sweden, near Abisko. Evidence of shrub expansion there relies on early observations that have not been quantified (Sandberg, 1963). Similar to many Arctic areas (Serreze *et al.*, 2000), winter and summer warming around Abisko has been pronounced in recent decades, leading to a significant lengthening of the growing season within the last decade (Kohler *et al.*, 2006). We chose *Juniperus nana* as our study species for three reasons: (1) the species is generally not browsed and thus the influence of browsing on growth performance can be neglected; (2) it is possible to sample single individuals without apparent concurrence effects, as induced by growth in thickets; (3) it is the only medium-size shrub species existing from treeline all the way up the mountain slopes to form the highest shrub communities. Our research questions were: Has there been an increase in shrub size (radial and vertical shrub growth) over recent decades? Which climatic parameters (if any) drive shrub growth? How do climate–growth relationships change over an elevational gradient? Do distinct age classes exist along an elevational gradient as a possible indication for an elevational shrubline advance?

Materials and Methods

Study area

The study area is situated in the Northern Swedish Scandes near Abisko (68°21′ N, 18°49′ E) with a mean annual temperature of 0.7°C and, because of the rain shadow of the Scandes, a mean annual precipitation of 310 mm (1913–2000). Over 40% of the annual precipitation occurs in summer (June–August) and July is both the warmest and wettest month (Kohler *et al.*, 2006). Tree line in this area is formed by mountain birch (*Betula pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman), and reaches upper elevations of between 670 m above sea level (asl) on northern and 780 m asl on southern mountain slopes. Above the tree line until *c.* 850 m asl there is a vegetation belt dominated by medium sized shrubs (0.2–1.8 m) including various willow species (*Salix* sp.), dwarf birches (*Betula nana* L.) and prostrate junipers (*Juniperus nana* Willd.). At higher elevations, the vegetation cover comprises dwarf shrub heath- and meadow communities and shrubs retreat to sheltered microsites. *Juniperus nana* is the only medium-sized shrub on the southern mountain slopes, ascending from tree line, where it grows in its erect form, to *c.* 1100 m asl, where it grows in its prostrate growth form. It is a dioecious evergreen shrub with a circumpolar subcontinental and subalpine distribution that can reach ages of up to 850 yr and stem diameters of 18 cm (Shiyatov *et al.*, 2002). No signs of herbivory were found in the study area, but seeds of *J. nana* are distributed by birds that feed on the blue berries.

In *Juniperus* trees, differences in resource allocation among different genders can influence mean ring width, because of long-term differential reproductive costs (Rozas *et al.*, 2009). To exclude the possibility of the influence of gender related growth differences in *Juniperus* shrubs, we sampled only male shrubs. Three female shrubs at 770 m asl were sampled to test for differences in mean ring width and growth trend. Sampling plots were placed on the south slope (180° ± 10°) of Mount Slåttatjocka, *c.* 3 km west of Abisko. Starting at the *J. nana* shrubline at 1100 m asl we sampled five to eight shrubs (a total of 35) every 100 m (1100, 1000, 900, 800 m asl) of elevation until above the tree line at 770 m asl. Sampling plots were placed on a straight transect with slope angles of *c.* 20°. If possible, complete individuals, including the root and the whole branch system, were extracted from the soil. The main stem (the one with the biggest diameter), including the root, was retained for further analysis. In cases where this was not possible, the main stem was cut just below the root collar. To be accepted as sample, shrubs had to be spatially distinct, and in larger mats only one sample was taken to prevent collection of the same genotype twice. Large vital shrubs, indicated by many green needles and intact stems, were collected, as well as two dead individuals. The length of the main stem, the maximum diameter and the zone with adventitious roots of each individual was measured.

Climate data

Temperature, precipitation and snow depth have been measured at Abisko Scientific Research Station (385 m asl) since 1913 (Kohler *et al.*, 2006). The research station is located *c.* 3 km away from the sampled shrub plots. Since 1956, average annual temperature in Abisko has been rising at an average of 0.2°C per decade. Winter temperatures (December, January, February) have increased 0.6°C per decade, spring temperatures (March, April, May) 0.3°C per decade and summer temperatures (June, July, August) 0.1°C per decade, accompanied by a lengthening of the vegetation period since 1997 (Kohler *et al.*, 2006). Warmer winters have caused an increase in snowfall (*c.* 4 cm per decade) since the 1930–40s. We used snow depth data from a newly digitized record provided by Kohler *et al.* (2006). For years with incomplete or missing measurements (11 yr between 1930 and 1956), values from a snow depth-model for Abisko were inserted (Kohler *et al.*, 2006).

Ring-width measurements

Ring-width measurements were performed to measure radial and vertical growth, to track growth changes over time, to age the shrub individuals and to correlate annual shrub growth with climate. Key challenges of dealing with growth rings of shrubs are small annual ring widths (0.3–0.01 mm), rings that are absent in parts of the stem and rings that are wedging out in a stem disk because of the failure of cambial activity. Because of the wavy growth of subalpine shrubs, the pith of shrub stems is often not found in the centre of a stem disk, which present difficulties for the measurement of radii, which ideally should comprise the same number of growth rings.

All shrub stems were treated and analysed according to the serial sectioning technique (Kolishchuk, 1990), advised for shrub ring analysis. Each main stem was dissected with a saw every 10 cm into stem disks with a height of typically 2–3 cm. As it was sometimes very difficult to visually distinguish the root from the stem, in most cases the whole stem of each individual was dissected, including the root system. The retrieved disks were labelled according to their former position on the stem, sanded with sandpapers of increasingly finer grain size and finally polished with sand paper of 800 grit. Between four and 12 stem disks were chosen from each individual, depending on its total length, so that ring-width measurements along the entire stem could be analysed in regular intervals. Disks with stem wounds or extremely eccentric growth were excluded from the dendrochronological analysis.

On each stem disk, a minimum of two and a maximum of four radii were measured with a precision of 0.001 mm, using a ring-width measuring stage (LINTAB 5; Rinn, 1996). One radius comprised the thicknesses of all annual growth rings in a line between the pith and the bark of a shrub disk. Depending on the length of the stem, and thus the number of shrub disks analysed, between 6 and 24 radii per individual plant were measured.

Chronology development

First, all radii of one disk (one height level of the stem) were averaged after accounting for missing or wedging rings in parts of the disk. Then, the radii of all disks of one individual plant were cross-dated and averaged. The successive overlap of the disk averages (here referred to as ring-width curves) from the top to the basal part of the stem ensured the correct assignment of each ring-width curve to the correct period in time (Kolishchuk, 1990). The ring-width curves of all individual shrubs were then cross-dated among each other (Holmes, 1983; Rinn, 1996) to confirm their correct dating. Eleven ring-width curves without any missing outer rings served as the reference for this procedure. Only one subfossil individual (found dead without green needles) of 322 yr could not be dated and was excluded from further analysis.

Next, the dated ring-width curves were standardized by removing any age-related growth trend, as well as part of the variance at very low frequencies to eliminate physiologically induced trends in the data that could obscure the climate signal (Fritts, 1976; Cook, 1985; Cook & Kairiukstis, 1990). For that purpose, a horizontal line through the mean (n = 29), a linear regression line (with negative slope; n = 4) or a negative exponential curve (n = 1) was fitted to the ring-width curves. The measured ring widths were then divided by the fitted regression functions producing dimensionless index series, which were averaged to form chronologies (Cook, 1985; Cook & Kairiukstis, 1990). Standard chronologies were established, as well as residual chronologies, with the first-order autocorrelation removed, thus eliminating the influence of previous year's growth on the growth of the next years (Cook & Holmes, 1986). These analysis steps were conducted for all shrub ring-width curves, giving the main chronology, and for a subset of ring-width curves from the five elevational levels (five to eight individuals per elevation), giving the five elevational chronologies.

Radial and vertical shrub growth

The standardized ring widths were also used to assess radial growth changes of individuals over time by dividing the arithmetic mean of the annual growth increment of the first

25 yr of the life of a shrub by the average annual growth increment of the last 25 yr. Thus, our calculations were rather conservative, as ring growth during 1981–2006 was compared with the, usually strong, growth of the individual as a sapling. The 25-yr period was chosen as some of the youngest shrubs were *c.* 50 yr old and climate warming was pronounced during the last 25 yr (Kohler *et al.*, 2006), thus making it possible to quantify the effect of the warming on radial growth. For shrubs with an age of < 50 yr (three individuals), the average for the full period 1981–2006 was compared with the average of the remaining years before 1981 AD.

Generally, the long-term pattern of shrub radial growth of the whole population could be best modelled with a third-order polynomial. Polynomial growth curves are commonly used to model plant growth (Snipen, 1998) and northern latitude temperatures during the 20th century (Grudd *et al.*, 2002; ACIA, 2005).

Vertical growth rates were calculated by dividing the length (cm) of the stem section between consecutive disks by the number of years separating the onset of growth between the disks. Vertical growth rate changes were calculated comparably to the radial growth rate changes by dividing the average vertical shrub growth of 1981–2006 by the individual's average vertical growth as a sapling (first 25 yr).

Climate–growth analysis

Climate–growth relationships were assessed with the DENDROCLIM2002 program (Biondi & Waikul, 2004), which uses bootstrapped confidence intervals to estimate the significance of correlation function coefficients. Mean monthly temperatures, total monthly precipitation and mean monthly snow depth were the predictor variables. We computed simple correlations for all chronologies and a moving correlation analysis for the main chronology to assess the temporal stability of climate–growth relationships. Correlation coefficients were calculated and reported for the residual main chronology, and the residual elevational chronologies. Correlations with the respective shrub standard chronologies were computed as control.

Results

The key findings of our study were that shrubs at the highest elevations are comparatively young and show the strongest relative radial growth increase compared with shrubs at other elevational levels. For the whole slope at all elevational levels, average radial growth and average vertical growth have increased over the last 25 yr. Shrub growth correlated positively with summer temperatures but frequently also with winter snow, winter precipitation and winter temperatures.

Chronology quality and shrub ring growth patterns

In all chronologies, autocorrelation and (inter-) serial correlation was comparatively high and mean sensitivity low (Fritts, 1976). Expressed population signal (EPS) values of the main chronology exceeded 0.85 from 1920 onwards, indicating, as a standard measure of chronology goodness, a strong common signal within the chronology.

With increasing elevation, average total ring width decreased almost linearly (Table 1) from a maximum of 0.370 mm at 800 m asl to a minimum of 0.050 mm at 1100 m asl, thus, a negative correlation between average ring width and elevation existed ($r = -0.75$; $P < 0.01$). No differences between different genders in mean ring width or general growth trend could be found and therefore the three female shrubs were included in the chronologies. Eccentric piths and locally missing rings (especially on the shorter radii) were a common feature in *J. nana.*

Serial sectioning revealed that the biggest diameter of the stem did not always comprise the most number of years and that there often was a more or less continuous loss of the outer, most recent, shrub rings, proceeding from the tip of the plant towards the root collar. In two out of three cases, the outermost ring measured at the stem base did not refer to the last year of growth. Instead, the actual date of the formation of the outermost ring was up to 82 yr ago. On average, 10 consecutive annual rings were absent at the root collar. The occurrence of consecutively missing outer rings was not correlated with stem size below and above ground, shrub age or the length of the zone along the stem with adventitious roots. The average radial growth did not significantly decrease with shrub age (linear regression: $r^2 = -0.06$). The average age of the shrubs was 84 (SE = 7) yr.

Age classes

Grouped by elevation, average ages increased from 65 yr at 770 m asl to 97 yr at 1000 m asl, and then decreased to 73 yr at 1100 m asl. The latter, highest elevation shrubs were > 30 yr younger than predicted by a simple linear extrapola-

Table 1 Average radial growth increases at five different elevational levels, comparing the first 25 yr with the last 25 yr (1981–2006) of individual shrub growth

Elevation (m asl)	Radial growth increase (%)	Average ring width (mm)
770	18	0.321
800	60	0.251
900	59	0.183
1000	54	0.161
1100	73	0.117

One outlier removed from calculation (at 770 m above sea level (asl), with an increase of 228%). Average ring-width decreases with increasing elevation as expected.

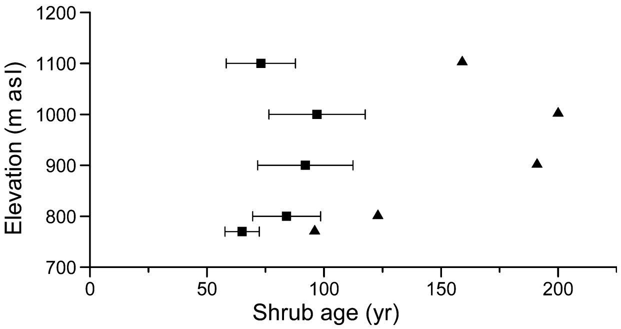

Fig. 1 Average shrub ages (squares) along the elevational gradient do not follow the expected linear extrapolation of increasing age with increasing elevation (standard errors shown with horizontal lines). The highest shrub communities at 1100 m above sea level (asl) are *c.* 30 yr younger than expected, suggesting recent shrub expansion up the slope. Maximum shrub ages (triangles) show the same pattern.

tion of average age vs elevation (Fig. 1). Maximum shrub ages over the elevational gradient followed the same trend, first increasing from 96 yr (770 m asl) to 200 yr (1000 m asl), then decreasing to 159 yr at the shrubline. At the highest elevations, we also observed a lot of shrub saplings compared with the small total number of mature individuals present.

Main climate–growth relationships

All correlations reported in this section were significant at the 0.05 level. The strongest correlations between ring width of the main chronology and climate variables were those with June and July temperatures ($r = 0.31$; $r = 0.33$). Correlations with June and July temperature were temporally stable over the whole period of the climate record (1913–2004). June and July temperatures combined (JJ) correlated with the main chronology at $r = 0.40$. In addition, there was a positive correlation with December temperature and a negative relationship with June snowfall. A substantial amount of snow in June occurred in 5 yr. Also, the correlation with June snowfall was unstable through time. For the main chronology, no significant correlations with precipitation values were observed. Correlations with August temperature were weak at the beginning of the 20th century, but consistent and significantly positive over the 2nd half of the 19th century and of a similar magnitude as the JJ temperatures. The correlation with December temperatures faded out *c.* 1995, although it had been constantly stable before. Around the same time, a positive correlation with November snow started to influence growth.

Climate–growth relationships and elevational gradients

Shrubs at lower elevations had positive correlations with late summer temperatures (August), while shrubs at higher elevations had positive correlations with early summer temperatures (July and June). The 770-m chronology showed positive correlations with November temperature of the year before growth ($r = 0.20$), August temperature of the year of growth ($r = 0.23$) and April snow depth ($r = 0.20$). A negative correlation with September precipitation of the previous year ($r = -0.19$) was observed (Fig. 2). The 800-m chronology showed positive correlations with summer temperatures (July, $r = 0.20$; and previous August, $r = 0.26$) as well as previous December ($r = 0.25$) temperatures and March precipitation ($r = 0.24$; Fig. 2). The 900-m chronology showed a strong positive correlation

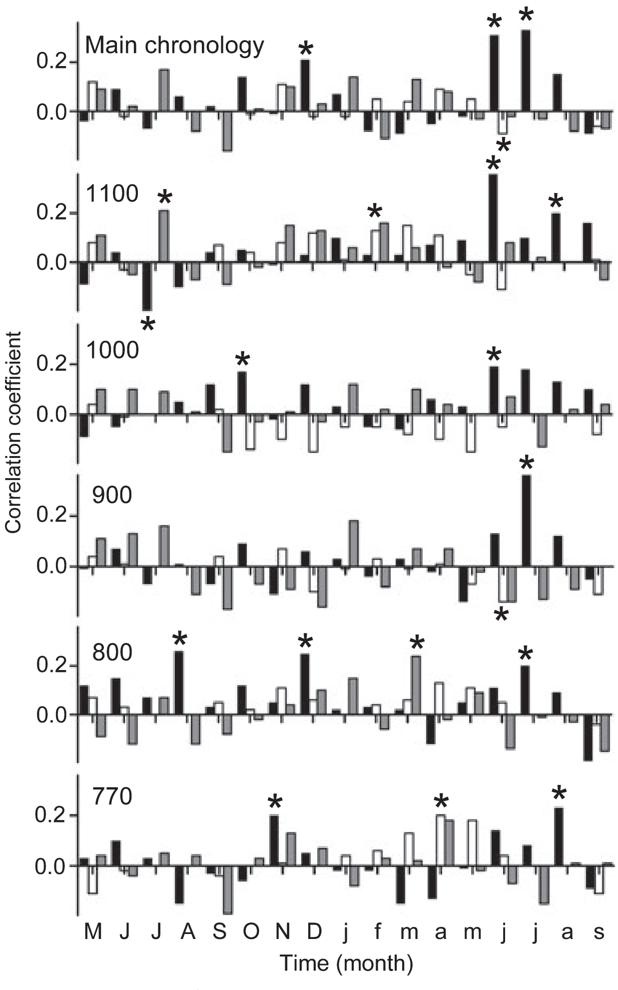

Fig. 2 Correlations of shrub radial growth (ring width) with monthly climate data of the main and elevational chronologies from May of the year before growth (capital letters: M, J, J…, etc.) to September of the year of growth (small letters:…j, a, s). Asterisks indicate significant ($p < 0.05$) correlation coefficients. Note that the highest correlation with summer temperatures shifts from August to June with increasing elevation. Also note significant positive correlations with snow, winter precipitation and winter temperatures. Black bars, correlations with mean monthly temperature; white bars, correlations with total monthly snowfall; grey bars, correlations with total monthly precipitation.

with July temperature ($r = 0.46$) and a weak negative correlation with June snow cover ($r = -0.14$; Fig. 2). The 1000-m chronology showed positive correlations with October temperatures of the previous year ($r = 0.17$) and June temperatures of the current year ($r = 0.19$; Fig. 2). The 1100-m chronology showed positive correlations with June and August temperature ($r = 0.42$; $r = 0.20$) and snow depth in February ($r = 0.16$; Fig. 2). The previous year's July temperature was negatively ($r = -0.24$) correlated with growth while the precipitation correlated positively ($r = 0.21$; Fig. 2).

Changes in radial growth over time

Individual shrub growth rates showed a distinct recent increase in growth. Both differences in measured (raw, as well as indexed) ring width of individual shrubs as well as the general radial growth trend displayed by the main chronology clearly showed this increase. The result for the standardized values, accounting for the possibly decreasing ring width with increasing stem diameter, was a mean increase of 61% during the last 25 yr, with 74% of all shrubs showing an increase. The individual growth changes ranged from an increase in ring width of 240% to a decrease of 25%. The average values for the positive growth changes of the last 25 yr rose with elevation, with a maximum at 1100 m asl (73%; Table 1). Between 1886 and 1946, shrub growth of the whole population (standard chronology) increased and the only marked decrease in growth from 1940–60 was followed by a distinct increase from 1970 until 2006 (Fig. 3). The average measured ring width increased over time from 0.110 mm in the 1850s to 1860s to 0.215 mm from 1980 to 2006. Total average ring width was 0.127 mm. Increases in growth were not restricted to younger individuals only, as almost all *J. nana* individuals older than 100 yr increased their annual radial growth substantially over the last three decades.

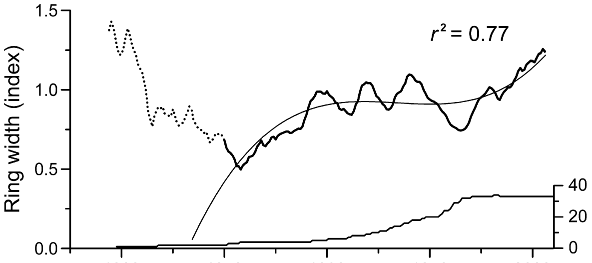

Fig. 3 Indexed radial growth of the main chronology smoothed with a 10-yr filter (broken and solid black lines, left y-axis) and sample size (grey line, right y-axis) over time. Radial growth is best modelled ($r^2 = 0.77$) with a third-order polynomial indicated by a thick black line. The growth model was only calculated for a sample of four or more shrubs (1850–2006). Before 1850 (broken line), sample size is too small and ring width in the chronology therefore too variable to reliably model shrub growth. Note the growth decrease in the middle of the 20th century and the subsequent radial growth increase.

Changes in vertical growth over time

The highest average vertical growth rates occurred at 770 m asl (2.9 cm yr^{-1}), followed by 900 m asl and 800 m asl (2.1 cm yr^{-1}) and 1100 m asl (1.9 cm yr^{-1}). Shrubs at 1000 m asl had the lowest vertical growth rate (1.6 cm yr^{-1}).

Average vertical growth increased by 77% after 1981 with highly variable individual changes, ranging from a more than threefold increase (from 2.1 to 7.2 cm yr^{-1}) to a maximum decrease of −75% (from 2.6 to 0.6 cm yr^{-1}; Fig. 4). A marked increase in vertical growth (shoot elongation) existed during recent decades at all elevational levels. This increase started in 1970 and was most prominent at higher elevations (Fig. 4). There, maximum shrub growth rates in the last three decades were as high as shrub growth rates formerly only found in low-elevation shrubs (770 m asl).

Discussion

To study the effects of climate on shrub growth, shrubs have typically been exposed to experimental treatments (Serreze *et al.*, 2000; Bret-Harte *et al.*, 2002). Experimental studies are very useful to assess plant responses to various possible changes in (micro-) climate induced by climate change over short observational periods. Results suggest that increased temperatures and increased levels of nutrients will promote shrub growth (Bret-Harte *et al.*, 2002).

In this study, we have used dendrochronological methods, developed mostly to study tree growth and, with one additional step (serial sectioning), applied them to shrubs. We found that the warming climate has indeed increased shrub growth over the last decades to centuries in natural shrub populations. In the following, we will first discuss the dendrochronological method necessary to analyse shrub growth changes. We will then discuss the rates of shrub size increase, the starting period of shrub expansion, the possibility of ongoing elevational shrubline dynamics and the climatic factors responsible for the shrub expansion.

Dendrochronology applied to shrubs

The method of serial sectioning, as advised by Kolishchuk (1990), was necessary because two-thirds of all samples were missing outer, recent rings at the stem base. Without serial sectioning, the radii of two-thirds of all shrubs would have been assigned to the wrong period of time, thus making the chronologies erroneous.

The most probable reasons for continuously missing outer rings at lower stem sections are the short growing seasons and limited resource availability during certain years.

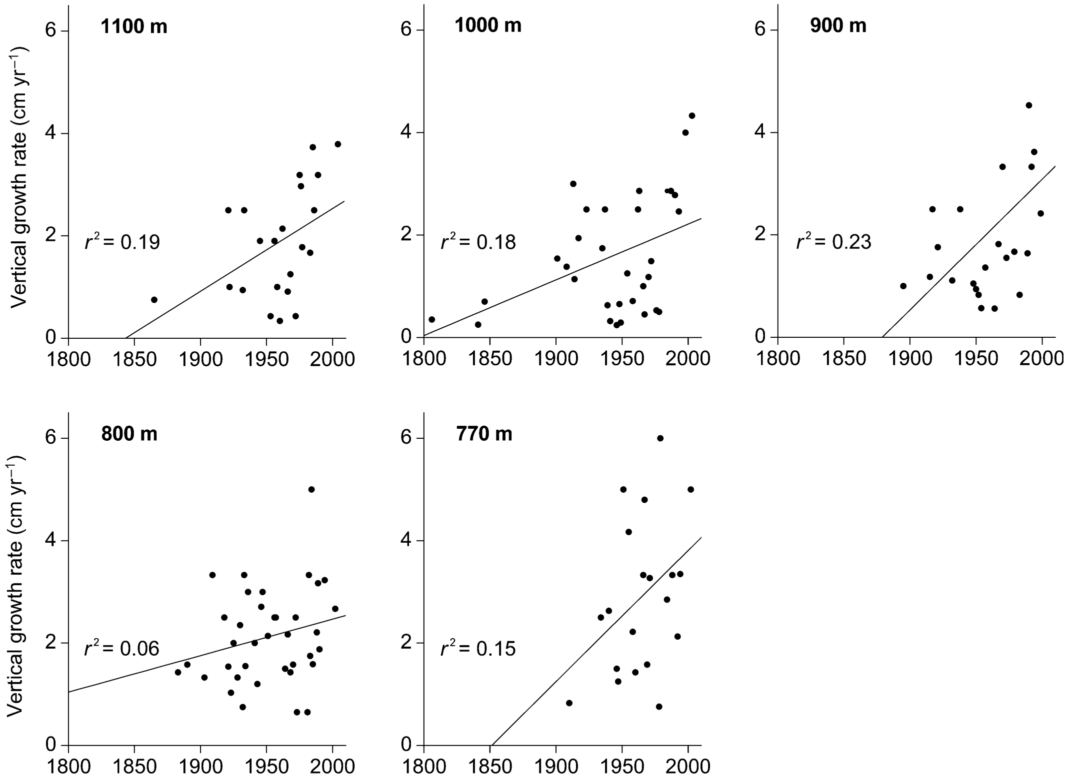

Fig. 4 Vertical growth rates and growth trends at the five elevational levels over time indicate recent growth increases. Absolute vertical growth rates are lowest at 1100 m above sea level (asl) and increase steadily with decreasing elevation until 770 m asl. Relative vertical growth rate increases over time were most prominent at higher elevations, where shrubs currently grow with growth rates formerly restricted to lower elevations only.

Shrub growth is initiated by the apical buds shedding the hormone auxin (Forest *et al.*, 2006), causing the cambium to become active and produce cells (Kolishchuk, 1990; Sitte *et al.*, 1991). With increasing age, the stem gets longer, the growth-stimulating cells move further away from the root collar, and thus hormones probably need more time to reach the lower stem parts. In years with unfavourable growing conditions (cold growing season), hormones may not reach lower stem portions and/or the amount of resources might not be sufficient for the shrub to produce cell layers along the whole length of the plant. In these years, the cambium in the basal part of the stem remains inactive (F. Schweingruber, pers. comm.) and growth occurs only in the upper part of the stem.

Consecutively missing outer rings might be the reason for a stem diameter in *J. nana*, whose dimensions, unlike in trees, remained constant over long parts of the basal stem. These findings are in accordance with the studies of Kolishchuk (1990) on *Pinus mugo*, where no age-related radial growth trend was apparent. Similarly, *Salix arctica* from northeast Greenland did not show a visible growth trend (Schmidt *et al.*, 2006), suggesting that this growth pattern might be characteristic for high latitude or altitude shrubs.

Three lines of evidence for shrub expansion

The first line of evidence for a shrub expansion is the observed distinct, sometimes even exponential increase, in radial growth at all elevational levels since the 1970s. Individual shrubs showed a strong increase in radial growth (61% increase on average), when the first 25 yr and the last 25 yr of growth were compared (Table 1). While the lowest average increase occurred at 770 m asl (18%, one outlier removed), the highest relative radial growth increase occurred at 1100 m asl (73%), suggesting that shrubs at highest elevations profit most in relative radial growth from recent warming.

Radial growth over time could be best modelled by a third-order polynomial (Fig. 3). This growth model sets the onset of the shrub expansion right after 1860, when shrub radial growth was at its minimum. Because of a very small sample size before 1850 of less than four individuals and EPS values approaching zero (indicating diverse responses of those four or less individual shrubs), the growth model could not be extended with reasonable confidence further into the past. However, it still makes sense to assume the start of the shrub expansion at *c.* 1860, as it coincides with the end of the little ice age in Scandinavia (Grudd *et al.*, 2002). Thus, the expansion predates the current climate warming, a conclusion that is confirmed by the most extensive Alaskan shrub expansion study so far. There, the shrub expansion has been modelled to have begun similarly early, between 1875 and 1925, and was probably also connected with the end of the little ice age and the subsequent warming (Tape *et al.*, 2006).

Generally, long-term radial growth dynamics in shrubs at our sample site covary with average annual temperatures in Abisko and ring width in the Torneträsk pine chronology from the same area (Grudd *et al.*, 2002). All those time-series can be best modelled by a third-order polynomial, which is the typical trend approximation underlying northern latitude temperatures since the beginning of the 19th century (ACIA, 2005). This coherence in curve shape and timing further suggests links between climate and vegetation dynamics since the little ice age.

The second line of evidence for a shrub expansion is the increased vertical shrub growth since the 1970s, which is simultaneous with the radial growth increase. While the highest total growth rates were found among the 770–800 m asl shrubs, the greatest relative vertical growth increases were found at higher elevations, concurrent with the changes in radial shrub growth (Fig. 4, Table 1). Because temperature limitation is more severe at higher elevations, shrubs there might profit most from warming temperatures.

The third line of evidence for an ongoing shrub expansion in the area is the comparatively young average age and young maximum age of the highest shrub population and the presence of a fairly large number of shrub saplings there. Woody plants at high elevations often grow much older than at lower elevations because of the severe growing conditions that result in slow but prolonged growth (Fritts, 1976; Schweingruber & Poschlod, 2005; Bär *et al.*, 2006, 2008). Thus, the average age of shrubs commonly increases with elevation (Schweingruber & Poschlod, 2005; Bär *et al.*, 2006). In our study however, this relationship existed only from 770 m asl up to 1000 m asl. If we assume this general trend of increasing age with increasing elevation to be valid, shrubs at 1100 m asl should have had an average age of > 100 yr (Fig. 1), but instead they showed an average age of 73 yr, suggesting recent colonization.

We have to keep in mind that another reason for the observed age trend could be an oscillatory pattern of young shrubs establishing at high elevations during favourable conditions, just to be killed-off during periods of unfavourable conditions. However, maximum ages of up to 159 yr and average ages of 73 yr at the highest elevation make a short-term oscillation of the shrubline unlikely. We also did not find any dead individuals preserved at 1100 m asl as evidence for this explanation. We thus conclude that climate conditions might have become suitable for shrub growth at higher elevations in our study area, concurrent with the general trend of climate warming.

Main chronology climate–growth relationships: the possible mechanism

The main chronology had marked and significant positive correlations with early summer temperature (JJ) that were stable over time. This finding and the similar shape and timing of longer-term temperature trends and long-term vegetation dynamics (our shrub records, Fig. 3 and Grudd *et al.*, 2002) point towards a causal relationship between warmer temperatures and the ongoing shrub expansion in our study area.

The main chronology also had significant positive correlations with December temperature that were stable for much of the record. Positive correlations with winter temperatures have been rarely reported so far, but have recently been identified as potential co-drivers for shrub growth (Sturm *et al.*, 2005a).

Warmer winters in Abisko have been associated with an increase in winter mean snow depth (2 cm per decade 1913–2004; Kohler *et al.*, 2006). A greater snow cover is thought to provide better insulation and thus to increase temperatures and promote microbial life under the snow, resulting in an increased nutrient supply for shrubs at the beginning of the growth period of the following year (Mack *et al.*, 2004; Chapin *et al.*, 2005). This positive feedback loop may be one of the reasons for the currently observed shrub expansion (Sturm *et al.*, 2005a). The correlation with December temperature might therefore further support the beneficial influence of snow cover on shrub growth and viability (Sturm *et al.*, 2005b).

However, there can be a tipping point, when the amount of snow becomes so much that the advantage of better insulation is outweighed by the disadvantage of a shortening of the vegetation period. Then, snow has a negative effect on growth, as reported for *Salix arctica* in Greenland (Schmidt *et al.*, 2006). The very weak negative correlation with June snow observed in the main and the 900 m chronology has to be interpreted with caution, as there were only 5 yr with snow cover in June within the whole record. However, a delay in the onset or an interruption of the growing period by snowfall in June would certainly be detrimental to any plant growth (Schmidt *et al.*, 2006).

The stronger correlations with snow depth of the standard chronologies (not shown) compared with the residual chronologies indicate that several year's snow depth influences the ring width of 1 yr. Thus, the influence of snow on shrub growth seems a highly autocorrelated process. However, one has to keep in mind that all correlations with winter snow depth or winter precipitation (which both refer to snow), are based on data from Abisko valley and exposure and topography might have altered the spatial distribution of precipitation, snowfall and especially snow depth considerably. Therefore, at this stage, we suggest that the observed correlations provide an indication that snow cover is likely to influence shrub growth mostly in a positive way (Sturm *et al.*, 2005b).

Elevational levels: influence of climate and environment

The significant correlation coefficients of the elevational chronologies with climate data shifted from late summer temperatures (August) at low elevations to early summer temperatures (June) at high elevations (Fig. 2). This might reflect the importance for woody plants at high elevations to experience a warm early summer and thereby an immediate onset of the growing period (Körner, 2003). For *J. nana* shrubs at lower elevations, however, the late summer temperature and the length of the growing season seems more important. Shrubs at lower elevations may therefore additionally benefit from a significant lengthening of the growing season since 1997 that has been observed for Abisko (Kohler *et al.*, 2006).

In the future, other processes and mechanisms might play an increasing role as shrubs colonize formerly shrub-free high-elevation sites. For example, the 1100-m chronology showed a negative correlation with temperature and a positive correlation with precipitation of the previous July, suggesting drought sensitivity of *J. nana* on the shallow-soiled, lichen-covered, stony slope.

This finding, together with the strong decline in ring width with increasing elevation, might indicate that the elevational advance of *J. nana* might come to a halt at 1200–1300 m asl, as the ring size would approach zero under current conditions. The lowest average annual ring width (0.05 mm) of a *J. nana* shrub found at 1100 m asl is among the lowest values that have ever been reported for coniferous species and equals typical average values for dwarf shrubs such as *Loiseleuria procumbens* (Schweingruber & Dietz, 2001).

However, these restrictions for growth might only be relevant for high-elevation shrubs today and in the long run a warming climate and the presence of suitable microsites could allow the permanent establishment of shrubs also at elevations of 1200 m asl and above.

Conclusion

We documented a distinct increase in radial and vertical growth rates of *J. nana* shrubs during recent decades in the subalpine zone of North Sweden. The age structure of shrubs along the elevational gradient provides evidence that an upslope advance of the altitudinal shrubline is underway. We observed significant, strong and stable correlations between annual ring width and summer temperatures (June, July, August). The acceleration of radial and vertical growth since 1970 also coincides with the recent three decades of rising arctic air temperatures (Overpeck *et al.*, 1997) and the warming trend of 0.2°C per decade for the average temperature since 1956 at Abisko (Kohler *et al.*, 2006). While numerous experimental studies showed the effect of artificial warming on shrub growth (Serreze *et al.*, 2000; Bret-Harte *et al.*, 2002), dendrochronology enabled us to establish and confirm the mechanistic link between actual climate warming and the observed shrub expansion and to quantify shrub growth rates *in situ.* There is mounting evidence that shrubs are expanding into alpine and arctic areas because of climate warming, and that this expansion occurs in both evergreen and deciduous shrub types (Forbes *et al.*, 2009).

The implications of a pan-Arctic shrub increase would be substantial and would include important consequences for the hydrology, the energy balance and the carbon budget of high-latitude ecosystems (Chapin *et al.*, 2005; Sturm *et al.*, 2005a; Tape *et al.*, 2006). A large-scale conversion of tundra into boreal forest is unlikely to happen in the near future because of lag effects in seed distribution (Rupp *et al.*, 2001). Shrubs, however, are already present in most tundra ecosystems and highly responsive to environmental changes, increasing the likelihood of a large-scale range margin expansion (Bret-Harte *et al.*, 2002; Epstein *et al.*, 2004). Whereas the findings presented here add evidence to the postulated pan-Arctic shrub expansion (Tape *et al.*, 2006) it would be desirable to further corroborate our conclusions. This could be done by expanding the dendrochronological approach to include different shrub species and study sites, or by combining remote sensing and repeat aerial photography approaches with the *in situ* technique of dendrochronology. In light of the increasing evidence for a climatically driven shrub expansion into tundra areas, the regional and global feedbacks resulting from this alteration (Chapin *et al.*, 2005; Sturm *et al.*, 2005a) will have to be included in future models of climate change.

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