Recent spring warming limits near-treeline deciduous and evergreen alpine dwarf shrub growth

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Abstract. Warming may lead to a cover increase of tundra shrubs and a north- and upward shift of treelines. The latter may be inhibited by a densification of shrub stands. However, the climatic drivers of near-treeline shrub growth are relatively unexplored, especially that of shrub species from different functional groups growing intertwined, in competition for light and resources. We measured ring widths from two dominant dwarf shrubs species, the deciduous Betula nana and the evergreen Empetrum nigrum ssp. hermaphroditum from a near-treeline alpine ridge in the Central Norwegian Scandes, and tested the influence of on-site and regional climate, and changes therein, over the past 55 yr. Radial growth of B. nana was found to be negatively influenced by early summer (June–July) precipitation, possibly related to low amounts of photosynthetically active radiation and nitrogen leaching, and positively by July temperatures. That of E. hermaphroditum was positively correlated with late summer (July–August) temperatures. In recent decades, the influence of summer climate on both species’ growth has declined and been replaced by a negative influence of May temperatures. Rising spring temperatures in recent decades have likely advanced key phenology events in B. nana and E. hermaphroditum, such as budburst and flowering. This may have left the shrubs’ soft tissues vulnerable to late frost events, which in recent decades occur more frequently after the advanced start of the growing season, resulting in suppressed growth.

Key words: Alpine tundra; climate change; dwarf shrubs; frost damage; growth inhibition; phenology advance; Scandinavia; shrubs; spring warming; treeline.

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INTRODUCTION

Arctic and alpine ecosystems are sensitive to climate change (Settele et al. 2014), as the species which make up these ecosystems are adapted to the specific and harsh climatic conditions at high latitudes and elevations. Moreover, the rate of temperature change is greater at high latitudes and there is growing amount of evidence that warming is amplified with elevation (Pepin et al. 2015). As a consequence, further substantial changes in the boreal-Arctic system are to be expected (Settele et al. 2014). Increasing growing season temperatures may lead to a general northward and upward shift of the Arctic-alpine biome (Settele et al. 2014) and a greening through an increase in vegetation productivity and biomass has already been observed through satellite proxies over the past decades in some parts of the tundra (Goetz et al. 2011, Epstein et al. 2012). This increase in biomass has partly been attributed to an expansion of shrub cover or increase in shrub growth (Sturm et al. 2001, Tape et al. 2006, Myers-Smith et al. 2011, Elmendorf et al. 2012b, Macías-Fauria et al. 2012). In relatively warm Subarctic and Low Arctic tundra, shrub expansion has been linked to an increase in upright deciduous shrub species (Elmendorf et al. 2012a, Myers-Smith and Hik 2018), while in colder High Arctic tundra areas prostrate evergreen dwarf shrubs have been...
shown to rapidly respond with increased growth to higher summer temperatures in recent decades (Weijers et al. 2017, 2018a). However, shrub species growing at their southern range margin or in near-treeline Arctic-alpine tundra ecosystems might lose the competition for resources with other species, which can benefit more from increasingly favorable circumstances, and may ultimately be replaced. In contrast, a densification of near-treeline shrubs may inhibit the establishment of trees and slow down the upward shift of treelines (Liang et al. 2016). Still, many treelines have shifted north- or upward over the past century (Harsch et al. 2009). Up to now, relatively little is known of shrub growth responses of species living in the tundra near the upper Arctic-alpine treeline and it is thus largely unknown whether a treeline shift might be inhibited by a densification of shrub stands. In addition, in many studies on shrub growth responses to climate, only a single species is considered and possible differentiating responses of opposing species from different functional groups are ignored.

Here, we study the climate–growth relationships of two dwarf shrub species, the deciduous dwarf shrub Betula nana and the evergreen dwarf shrub Empetrum nigrum ssp. hermaphroditum, hereafter named E. hermaphroditum, at a near-treeline ridge in the low-alpine belt of the Central Norwegian Scandes. For this site, a long-term record (1994–2015) of micro-site-specific climate data exists. Both species are widespread in the southern Arctic and boreal zones and are circum-polar in distribution. Both have been found to increase their cover in the Scandes mountain range, although the expansion of B. nana may be inhibited by herbivory (Vowles et al. 2017). We compare the climate–growth relationships in, as well as between, these two dwarf shrub species. Through the construction of annually resolved ring-width chronologies, we aimed to pinpoint the particular climatic drivers of growth, how and if these drivers have recently changed, and how this may impact the species, and the ecosystem of which they form the backbone.

**Methods**

**Study site**

On 28 September 2012 and 28 June 2013, 20 samples of the deciduous dwarf shrub Betula nana, and 20 samples of the evergreen species Empetrum nigrum ssp. hermaphroditum, were collected from an alpine ridge located near Vågamo, Oppland, Norway (61.8980° N, 9.1443° E, Fig. 1). The research site, named Vole, lies in the Central Norwegian Scandes mountain range in the low-alpine belt at 1100 m above sea level (a.s.l.). The treeline here is located at about 1050 m a.s.l. and is formed by Betula pubescens ssp. czerepanovii trees. It has largely been stable in recent decades (Rössler et al. 2008). Ridges in the area remain largely snow-free during winter, as strong winds redistribute snow to lower areas and leeward slopes (Löffler 2002). The vegetation at the site consists of lichen heath, with lichens forming the most abundant plant functional group, followed by dwarf shrubs (Löffler 2003). Alectoria ochroleuca and Cetraria nivalis are the most abundant lichen species, while B. nana and E. hermaphroditum are the dominant dwarf shrub species. Both shrub species grow decumbent and are low-statured, reaching heights up to ~30 cm. The species grow intertwined in patches, which are covered by lichens, and are in direct competition for light and resources. Shrubs were sampled randomly, but distances of at least 5 m between shrub patches were taken into account to prevent repeated sampling of the same genet. B. nana and E. hermaphroditum were sampled from the same patches.

**Climate**

We collected climate data from the on-site microclimate station, operative since June 1994, consisting of hourly measurements of air pressure, air temperatures, relative air humidity, wind direction, wind speed, and global radiation (total short-wave radiation); all measured at 2 m height. Furthermore, we collected air temperatures measured at 15 cm height, soil temperatures measured at 15 cm and 30 cm depth, and precipitation measured at 1 m height. We calculated daily and monthly means or sums (precipitation) for each climate parameter. Days with <24 measurements and months containing data for fewer than 20 d were excluded. This resulted in a continuous monthly microclimate dataset for the period June 1994–August 2015 for the parameters radiation, air temperature (at 2 m and 15 cm), and soil temperature at 15 cm depth. Precipitation data were only valid for months with predominantly liquid
precipitation (May–September). Soil moisture content was monitored at the site from August 2009 onwards. Photosynthetically active radiation (PAR) was monitored at the site between August 2012 and September 2014.

In addition, to allow for climate–growth analyses over longer periods, we obtained lapse rate adjusted interpolated monthly mean air temperature and monthly precipitation sums for the period 1957–2012, as modeled for the gridpoint nearest to our study site Vole (61.8979° N, 9.1466° W; 1099 m a.s.l.) from seNorge.no (seNorge.no 2017).

For a comparison with the modeled and on-site climate data, we obtained mean daily temperatures and daily precipitation sums from the eKlima database of the Norwegian Meteorological Institute (DNMI 2015) from the nearest weather stations, located about 25 km north-northeast from our study site: the Fokstua weather station (62.1167° N, 9.2833° E; 952 m a.s.l.; January 1940–May 1968) and the Fokstugu weather station (62.1133° N, 9.2862° E; 973 m a.s.l.; June 1968–December 2012). We calculated monthly mean temperatures and monthly precipitation sums based on these daily data to validate the gridded and microclimate data (cf. Appendix S1: Fig. S1).

The three climate datasets (Fig. 1c) show a mean annual temperature at the study site of around 0°C and a mean annual precipitation sum of ~450 mm. July is both the warmest and the wettest month,
with a mean temperature of 10.5°C (Fig. 1c) and mean precipitation sum of 69 mm, both measured on-site. February is the coldest month with a mean temperature of −8.3°C measured at 2 m height at the microclimate station at Vole.

Monthly mean air temperatures (2 m) from the three datasets show good coherence (0.93 < r < 0.99, P < 0.001; Appendix S1: Fig. S1a). Correlations between the monthly precipitation sums of Fokstugu/Fokstua and those of the Vole grid are less strong (0.49 < r < 0.83, P < 0.001; Appendix S1: Fig. S1b). Monthly precipitation sums for the summer months June, July, and August, from the Vole microclimate station correlate strongly with those from the Vole grid (r = 0.82, r = 0.94, r = 0.89, respectively; P < 0.001), but less strongly with those from the Fokstugu station (r = 0.79, r = 0.72, r = 0.60, respectively; P < 0.01). Therefore, we used the Vole grid data to assess longer-term seasonal climate changes at our site. We defined November–March as winter and June–August as summer, as daily mean air temperatures (2 m) during these months are generally below and above 0°C, respectively (Appendix S1: Fig. S2). During spring (April–May) and autumn (September–October) months, daily mean temperatures fluctuate around the freezing point (Appendix S1: Fig. S2).

Mean temperatures have risen significantly in all seasons at our site over the period 1957–2012, except in autumn (Appendix S1: Fig. S3). The increase has been strongest in winter (r = 0.48, P < 0.001), followed by spring (r = 0.47, P < 0.001), and summer (r = 0.30, P < 0.05). The linear trends in seasonal precipitation sums (Appendix S1: Fig. S3) are not significant, except for the negative trend in autumn, during which precipitation has decreased (r = −0.37, P < 0.01). All calculations were carried out in R version 3.4.1 (R Core Team 2017).

Climate–growth analyses

As intra-plant radial growth variability both within B. nana (Meinardus et al. 2011, Hollesen et al. 2015) and E. hermaphroditum (Bår et al. 2006, 2007) is high, serial sectioning (Kolishchuk 1990) was applied on each processed shrub sample. In total, we quantified annual growth as ring width for 17 E. hermaphroditum shrubs and 13 B. nana shrubs and constructed site chronologies for both species. We used the signal-free multiple regional curve standardization (SF-MRCS) method to remove age-related growth trends before site chronology construction. This method has been shown to be effective for shrub growth chronologies (Weijers et al. 2017). See Appendix S1 for details on sample preparation, ring width measurement, detrending, and chronology construction and statistics calibration.

We tested the influence of climate on individual shrub growth through linear mixed models and that on the detrended mean site chronologies through correlation and response function analyses. In linear mixed models, individual (shrub) ring-width time series are analyzed hierarchically as response variables creating a population mean response for each site (see Myers-Smith et al. 2015 for more details). This differs from the correlation and response function analyses in which we explored the common climate signal of the mean ring-width series for each of the two studied species at the site level.

We used linear mixed model analyses, in which we compared climate–growth models over two different periods: 1958–2012 and 1995–2012. The length of these periods was determined by the length of the Vole grid and microclimate datasets, respectively. We used the R-package nlme (Pinheiro et al. 2017) for the mixed model analyses, with maximum likelihood estimation for model comparison and restricted maximum likelihood estimation for slope estimates (Crawley 2007).

Before the analyses, the climate and raw individual shrub ring-width chronologies were normalized through subtraction of the mean, followed by a division by the standard deviation. Annual ring widths of individual shrubs were included in the models as the response variable; climate variables were included as fixed effects. Furthermore, random intercepts were included in the models for year, next to an autoregressive structure (ARI, autoregressive process of order one). Conditional pseudo-R² values were calculated for each mixed model using the rsquaredGLMM function of the MuMIn package (Nakagawa and Schielzeth 2013).

We tested 30 climate models for the period 1958–2012 with monthly and seasonal temperature means and precipitation sums derived from the Vole grid data as fixed effects together with a null model for each species. Climate models included means and sums from 11 individual
months (June to October of the previous year and April to September of the current year), and four seasons (autumn of the previous year, winter, spring, and summer). We did not test climate models with individual winter months (previous year November to current year March), as climate of individual months during the dormant period is less likely to strongly impact ring-width formation. Furthermore, this reduced the numbers of models compared and thus the chance that models come up by chance having a lower Akaike information criterion (AIC) value than the related null model (Weijers et al. 2018). The null model was identical to the other models, but with a constant mean (i.e., 1) instead of the climate variables as fixed effect. For the recent period (1995–2012), we tested 75 climate models and a null model for both species. The same months and seasons were tested over this period, but with the air temperatures at 2 m and 15 cm, soil temperatures at 15 cm depth, and radiation, as measured at the microclimate station, and the modeled precipitation sums of the Vole grid. In a first step, we selected climate models that performed better than the null model over the corresponding period, based on the AIC, that is, models with ΔAIC > 2. Thereafter, we calculated Akaike weights for the selected models. Akaike weights are a relative weight of evidence for each model (Johnson and Omland 2004).

In addition, we tested climate–growth relationships between the detrended site chronologies and monthly and seasonal climate parameters through the calculation of Pearson’s correlation coefficients and response coefficients. This was done with seasonal and monthly precipitation sums and mean temperatures, as modeled for the Vole grid over the period 1958–2012. Monthly parameters from June to October prior to the year of ring formation and April to September of the current year were included in the analyses, as were the four seasons (autumn of the previous year, winter, spring, and summer). Over the same period and with the same monthly and seasonal parameters, we calculated Pearson’s correlation coefficients and response coefficients over 18-yr moving windows (which equals the length of the recent period 1995–2012), but separately for mean temperatures and precipitation sums. The significance of each correlation coefficient and each response coefficient was determined through the calculation of a 1000 bootstrapped iterations. Response function analysis takes the multicollinearity between climate parameters into account, through the regression of ring width chronologies against principal components of these parameters (Zang and Biondi 2015). The correlation and response analyses were performed with the package treeclim in R (Zang and Biondi 2015, R Core Team 2017). Ring widths formed in 2013 were not included in any of the climate–growth analyses, as ring formation was not completed at the time of sampling in June 2013 (S. Weijers, personal observation).

RESULTS

The age of the 13 Betula nana shrubs varied between 50 and 80 yr, and of the 17 Empetrum nigrum ssp. hermaphroditum shrubs between 28 and 93 yr (Fig. 2). Both species showed comparatively strong individualistic radial growth patterns over time, as expressed by the relatively low mean interseries correlation coefficients (rbar) and EPS values (Table 1). Mean ring width of B. nana (0.86 μm) was found to be greater than that of E. hermaphroditum (0.47 μm; P < 0.001). The Gini coefficients of ~0.2 for both species (Table 1) indicate reasonable variability of radial growth and are intermediate values compared to those of tree ring chronologies from mesic to xeric sites (Biondi and Qeadan 2008). The mean chronologies of both species are characterized by some positive first-order autocorrelation (ar1), which decreased for B. nana and increased for E. hermaphroditum after SF-MRCS standardization (Table 1). The SF-MRCS standardization furthermore revealed that the oldest parts of B. nana, those closer to the root–shoot boundary, contained the widest rings, while in E. hermaphroditum, these parts contain the narrowest rings.

We observed a negative linear trend in the raw mean ring width chronology of B. nana (r = −0.3, P < 0.05; 1958–2012), but no trend in the raw E. hermaphroditum chronology. There was a positive linear trend in the standardized mean ring width chronology of E. hermaphroditum (r = 0.3, P < 0.05), but no trend in the standardized B. nana chronology. Mean standardized radial growth of the species was largely uncorrelated (r = 0.25, P = 0.06) over the period of climate–growth analyses (1958–2012).

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Climate–growth analyses

The variation in annual radial growth of both species is best explained by summer climate parameters, when tested over the period 1958–2012 (Table 2). Summer precipitation is the best climate model for *B. nana* over this period, and had a negative influence on radial growth of this species. The mean July temperature model is the best model for

![Graphs of ring width and ring width index chronologies for Betula nana and Empetrum nigrum ssp. hermaphroditum](image)

Fig. 2. Individual shrub (gray lines) with bi-weight robust mean ring width and ring-width index chronologies (black lines) of *Betula nana* (a) and (b), respectively, and *Empetrum nigrum* ssp. *hermaphroditum* (c) and (d), respectively. The gray areas at the bottom of each graph show the corresponding sample depths (right y-axes).

Table 1. Descriptive statistics of the raw and detrended ring-width chronologies.

| Statistic            | Betula Ring width | RWI | Empetrum Ring width | RWI |
|----------------------|-------------------|-----|---------------------|-----|
| No. shrubs/micro-sections | 13/122            |     | 13/122              |     |
| Timespan             | 1934–2013         |     | 1921–2013           |     |
| Mean                 | 86 (µm)           | 0.882| 47 (µm)            | 0.847|
| SD                   | 33                | 0.315| 15                 | 0.302|
| Gini                 | 0.209             | 0.200| 0.180              | 0.197|
| ar1                  | 0.482             | 0.442| 0.095              | 0.252|
| rbar                 | 0.192             | 0.174| 0.263              | 0.281|
| EPS                  | 0.71              | 0.68 | 0.78               | 0.79 |
| EPS (1994–2013)      | 0.87              | 0.86 | 0.94               | 0.93 |
| $r$                  | 0.32              | 0.30 | 0.38               | 0.43 |

*Note: RWI, ring width index; mean, robust bi-weight mean; SD, standard deviation; Gini, Gini coefficient; ar1, first-order autocorrelation; rbar, mean interseries correlation; EPS, expressed population signal; $r$, mean correlation of each shrub series with the mean chronology derived from all other series.*
annual radial growth of *E. hermaphroditum*, but the mean summer temperature model is also supported (Akaike weights of 0.39 and 0.23, respectively, Table 2). Both models have a positive slope.

Over the recent period (1995–2012), with microclimate models included, the July precipitation model is the best model for *B. nana* growth, but there is almost equal support for the mean May temperature (at 2 m) model; both models have negative slopes (Table 2). There is also support for the June and spring precipitation models, both with negative slopes, explaining *B. nana* growth. For *E. hermaphroditum*, radial growth is best explained by May temperature models, the best model being that of mean May temperatures at 15 cm, but with almost equal support for May temperatures at 2 m, both with a negative slope.

These effects were largely confirmed by the results of the correlation and response function analyses. We found negative correlations between precipitation sums of previous June, current year June, July, and summer, and radial growth of *B. nana* over the period 1958–2012 (Appendix S1: Fig. S6a). In contrast to the mixed model analyses, we also found a positive correlation between mean July temperatures and *B. nana* growth (Appendix S1: Fig. S6a), which remains significant when multicollinearity within the monthly climate data is taken into account (Appendix S1: Fig. S6b). Radial growth of *E. hermaphroditum* was
positively correlated to mean July, August, and summer temperatures (1958–2012; Appendix S1: Fig. S6c). In addition, we found a positive correlation with previous June precipitation sums. The response function analysis showed that *E. hermaphroditum* growth responded significantly to both mean July and summer temperatures (Appendix S1: Fig. S6d).

The moving correlation analyses (Fig. 3) show that the majority of correlations tested display temporal fluctuations. The most prominent correlations found between *B. nana* ring widths and monthly climate are the negative correlations with sum monthly precipitation sums, June–August in the earlier decades (1958–1993) and July in recent decades (1987–2012). Furthermore, we found positive correlations with mean temperatures of July (1986–2012) and August (1958–1985). May temperatures were negatively associated with *Betula* growth in recent decades (1985–2012). Other distinct features consist of the positive influence during earlier decades of previous year mean August and September temperatures (1958–1992) and previous autumn precipitation sums (1958–1993). In addition, spring precipitation had a positive influence on *B. nana* growth during a large part of the record (1964–2001). For *E. hermaphroditum* radial growth, the correlation with mean July temperature is the most stable one found. This correlation is, however, no longer significant, when measured over the last two decades (1994–2012). Instead we also

**Fig. 3.** Moving correlation coefficients, calculated over 18-yr windows, between the detrended *Betula nana* and *Empetrum hermaphroditum* site chronologies and monthly and seasonal precipitation sums (a, c) as well as mean monthly and seasonal temperatures (b, d) as modeled for the Vole grid over the period 1958–2012. pJun: June prior to the year of ring formation. Asterisks (*) indicate significant correlations ($P < 0.05$).
found a negative correlation between \(E.\ \text{hermaphroditum}\) growth and May temperatures in recent decades (1989–2012). Besides the positive correlations with July and, to a lesser extent August, temperatures, we also found positive correlations with previous autumn and current year September precipitation throughout large periods of the record. In addition, we found negative correlations between \(E.\ \text{hermaphroditum}\) growth and September temperatures in recent decades. The moving response function analyses gave a similar impression of the climate–growth relationships over time in \(B.\ nana\) and \(E.\ \text{hermaphroditum}\) (Appendix S1: Fig. S7).

Summarizing, we found a continuous negative influence of summer precipitation on radial growth of \(B.\ nana\), as well as a positive effect of July temperatures. In recent decades, we observed a negative link with May temperatures. High summer temperatures, mainly in July, generally have had a positive impact on radial growth of \(E.\ \text{hermaphroditum}\). We also observed a positive influence of precipitation in June and October in the year prior to growth. In recent decades, higher May temperatures have had a negative effect on \(E.\ \text{hermaphroditum}\) growth.

**DISCUSSION**

We have shown that radial growth of the deciduous dwarf shrub \(B.\ nana\) as well as that of the evergreen dwarf shrub \(E.\ \text{nigrum}\) at a near-treeline alpine ridge site has been driven by summer climate over the period 1958–2012. In recent decades, however, the influence of summer climate on the growth of both species has declined and been replaced by a negative impact of temperatures in May.

We found some evidence for a positive influence of summer temperature on radial growth of both examined species. This was previously demonstrated for \(B.\ nana\) from a low-alpine mixed depression and ridge site ~100 km southwest of our site (Meinardus et al. 2011). In the lowland tundra of north-eastern Siberia, \(B.\ nana\) growth correlated best with early summer, mid-June to mid-July, temperatures (Blok et al. 2011). For \(E.\ \text{hermaphroditum}\) growing in the middle alpine belt near our site, a positive response to summer temperatures was found, irrespective of the micro-topographic position of the shrubs (Bär et al. 2007, 2008). Moreover, \(E.\ \text{hermaphroditum}\) has been found to increase its shoot length growth and biomass in response to experimental warming of the understorey of a birch forest in Subarctic Sweden (Parsons et al. 1994), as well as in the High Arctic tundra in Svalbard (Buizer et al. 2012). In contrast, Campioli et al. (2012) found no growth response of \(B.\ nana\) and \(E.\ \text{hermaphroditum}\) after 22 yr of experimental warming in a Subarctic treeline heath near Abisko, Sweden. June temperatures were previously found to positively influence growth of \(E.\ \text{hermaphroditum}\) on north-facing slopes and ridges, but not on south-facing slopes in the middle alpine belt in our research area (Bär et al. 2007, 2008). At our site, a low-alpine ridge, we only found some evidence for a positive influence of June temperatures in recent decades (1986–2009; Fig. 3d). In earlier decades, the relationship with June temperatures has been negative (1968–1987, Fig. 3d). The latter may be similar to the negative response to May temperatures found in recent decades (see Discussion section below).

Although the response function analysis suggests that mean July temperatures are the dominant factor controlling mean site-level \(B.\ nana\) growth, the linear mixed model analysis suggests a stronger negative influence of summer precipitation on growth of \(B.\ nana\) individuals, especially that of June and July over the period 1958–2012. This negative effect of summer precipitation comes also forward from the (moving) correlation analyses (Fig. 3a; Appendix S1: S6a) and the moving response function analysis (Appendix S1: Fig. S7a). As moist rather than wet conditions persist throughout the growing season at the study site (Appendix S1: Fig. S8), it is unlikely that summer precipitation has had a negative impact on \(B.\ nana\) growth through the creation of temporary anoxic conditions. Moreover, \(B.\ nana\) responded with increased growth in response to an experimental doubling in summer of the mean annual precipitation to 400 mm in a lowland tundra heath in north-eastern Siberia (Keuper et al. 2012), which experiences similar summer temperatures as our site. It is more likely that photosynthesis and, consequently, radial growth is slowed down due to a reduction in photosynthetically active radiation.
(PAR) resulting from cloudy weather which accompanies wet summers. \textit{B. nana} may be sensitive to reduced PAR-availability, as it is a shade-intolerant species, which has been shown to reduce its growth in reaction to 22 yr of experimental shading (Campioli et al. 2012). Monthly mean global radiation as measured at the Vole microclimate station (1994–2015) was indeed negatively correlated with monthly precipitation in July \((r = -0.64, P < 0.01)\) and August \((r = -0.59, P < 0.01)\), but not in June \((r = -0.37, P = 0.09)\). Still, the climate model with mean global radiation of summer (months) was not selected in the linear mixed model analysis for the period 1995–2012 \((\Delta AIC < 2)\). However, mean daily radiation was not correlated with mean daily PAR over the summer months between August 2012 and September 2014 (June: \(r = 0.23, P = 0.08; August: r = 0.06, \text{n.s.)\), except in July \((r = 0.47, P < 0.001)\), and global radiation may thus be a relatively poor measure for PAR.

An additional, or alternative, explanation for the negative influence of early summer precipitation on \textit{B. nana} growth could be that high summer precipitation may lead to an increase in nitrogen loss due to downslope leaching. Ackermann et al. (2013), for example, found greater losses of added nitrogen in our research area at ridges in the middle alpine belt (1400 m a.s.l.), receiving greater amounts of precipitation, compared to those at lower elevations. Moreover, growth of \textit{B. nana} may be strongly limited by nitrogen availability, as it can greatly increase its production (Bret-Harte et al. 2001), and may dominate in tussock tundra in response to long-term fertilization (Bret-Harte et al. 2002, Mack et al. 2004).

Previous October precipitation was found to be an important (co-)driver of radial growth of \textit{E. hermaphroditum}, except in the first decade of the record (before 1967; Fig. 3). The latter may be explained by the fact that autumn precipitation has decreased over the period of study (Appendix S1: Fig. S3). Likewise, we found some support for a positive effect of previous September-October precipitation on \textit{B. nana} growth (Table 2, Fig. 3). Similarly, Bår et al. (2008) found a positive effect of high precipitation in September/October on vessel growth in the following year of \textit{E. hermaphroditum} growing at ridge positions in the middle alpine belt in our research area. Previous year autumn precipitation has earlier been found to be beneficial for growth of the evergreen dwarf shrub \textit{Cassiope tetragona} in High Arctic Svalbard (Weijers et al. 2010) and could support late season glucose storage when photosynthesis may become more moisture-limited as a result of lower soil moisture levels in autumn (Appendix S1: Fig. S8). Short periods of snow cover may also support the initiation of autumnal hardening in \textit{E. hermaphroditum} and thus prevent frost damage by early critically low temperatures, as the onset of dormancy is under photoperiod control (Körner 2016). Moreover, autumn precipitation may act as a water reservoir as it freezes in soils and might support growth the following year after thaw (cf. Appendix S1: Fig. S8). This could also explain the positive effect on vessel area of \textit{E. hermaphroditum} of previous year autumn precipitation found by Bår et al. (2008). A comparison of hydrogen and oxygen isotope fractionation in autumn precipitation and shrub rings may confirm this hypothesis.

Only a small proportion of radial growth of both species studied could be explained by monthly or seasonal climate parameters (Table 2, Fig. 3), and we observed high intra- and interspecific radial growth variability (Table 1), which might be a result of strong competition between and within species for nutrients and light. Arctic-alpine ecosystems are generally nitrogen-limited, especially at warmer lower elevations and latitudes (Havström et al. 1993), and both \textit{B. nana} and \textit{E. hermaphroditum} increased their biomass in response to greater nitrogen availability in the Alaskan tundra (Chapin and Shaver 1985, 1996). Higher competition for nutrients in the low-alpine belt may also explain the weaker response to summer temperature of \textit{E. hermaphroditum} found in our study compared to those reported in the middle alpine belt in the same research area (Bår et al. 2007, 2008).

The influence of summer climate on radial growth of both species at our site has declined in recent decades, while the influence of May temperatures increased. Concurrently, the start of the growing season has advanced at our site with about three weeks over the studied period, from late to early May. Meanwhile the timing of the last frost day has remained stable, usually taking place at the end of May (Fig. 4). A similar negative response to spring temperatures in recent decades
was previously observed for *B. nana* in West Greenland (Young et al. 2016). *E. hermaphroditum* immediately starts flowering after snowmelt in High Arctic Svalbard (S. Weijers, personal observation) and as soon as February in coastal dune ecosystems in the Netherlands (Buizer et al. 2012). Snowmelt defines the start of the growing season in many Arctic and alpine regions (Wipf 2010) including our research area (J. Löfﬂer, personal observation). Photosynthesis in evergreen species may even start under snow before snowmelt is completed (Starr and Oberbauer 2003). Flowering on snow-free ridges in Swedish Lapland was found to start around the same date each year in a 10-yr study, possibly linked to photoperiod and temperatures (Molau et al. 2005). The same study showed that flowering phenology of species with a predominantly boreal distribution, such as *B. nana* and *E. hermaphroditum*, was more strongly triggered by temperature than that of pure tundra species. Moreover, bud break in *B. nana* was found to be controlled by warm spring temperatures (Pop et al. 2000). Therefore, we assume that high temperatures (early) in May could have triggered the onset of phenology events. This has left soft tissue of both species vulnerable to freezing in late spring, causing reduction in annual growth, as lost tissue has to be compensated for by regrowth (Körner 2016). Similarly, winter warming events followed by frost have been shown to have damaging effects on *E. hermaphroditum* in the Subarctic, strongly reducing its growth in the following summer (Bokhorst et al. 2009). Late spring frost can also lead to collapse of developing xylem cells, and the formation of frost rings, when warm temperatures after frost increase transpiration while the root system is still frozen, thereby causing high tension in the xylem (Schweingruber 2007, Schweingruber et al. 2008). Frost rings consist of a narrow band of collapsed xylem cells, a wider callus band, and bent rays (Schweingruber et al. 2008), but were practically absent in both species studied. Likewise, Bär et al. (2006) did not find any frost rings in *E. hermaphroditum* shrubs from the same ridge in the low-alpine belt, in contrast to shrubs from an adjacent low-alpine south-facing slope and from a south-facing slope and ridge in the adjacent middle alpine belt. The absence of frost rings suggests that xylem formation is adapted to freeze–thaw cycles at low-alpine ridges in our research area. Shrubs can adapt to freeze–thaw cycles by reducing their vessel size...
and grouping, which decreases the risk of cavitation (Nielsen et al. 2017).

An alternative explanation for the observed negative response in recent decades of shrub growth to warm May temperatures could be increased drought stress. Growth of Juniperus pinigii var. wilsonii shrubs in the central Tibetan Plateau was for example found to be limited by drought stress in May and June (Liang et al. 2012), and its recruitment was negatively associated with summer temperatures (Wang et al. 2015). Drought stress at the onset of the growing season is however less likely at our site, where soil moisture content increases sharply in spring after water in soils has melted (Appendix S1: Fig. S8).

**CONCLUSIONS**

We have shown that, over the past 55 yr at a near-treeline alpine ridge site, radial growth of the shade-intolerant deciduous dwarf shrub Betula nana has been negatively influenced by early summer (June–July) precipitation, which may be linked to low PAR and nitrogen leaching, while that of the evergreen dwarf shrub Empetrum nigrum ssp. hermaphroditum has partly been driven by late summer (July–August) temperatures. In recent decades the influence of summer climate on the growth of both species has declined and been replaced by a negative impact of May temperatures. Rising spring temperatures may have advanced phenology events, such as budburst and flowering, on snow-free ridges, where such events are not delayed by snowmelt, leaving the shrubs’ soft tissue vulnerable to late frost events.

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**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2328/full