

RESEARCH ARTICLE

Spatiotemporal variability in precipitation-growth association of *Betula nana* in the Siberian lowland tundra

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Abstract

1. Shrubs are expanding across a warming Arctic, evident from range expansion and increases in biomass, stature and cover. This influences numerous aspects of Arctic ecosystems. While shrub growth is generally positively associated with summer temperature, tundra ecosystems are characterised by abiotic gradients on small spatial scales (metres), and the Arctic climate and its year-to-year variability are changing rapidly. Hence, it is often unclear to what extent climate-growth associations are scalable to future climate scenarios and across environmental gradients within ecosystems. Here, we investigate the stability of climate-growth associations of Arctic dwarf shrubs across small-scale (metre to kilometre) topographic gradients and decadal timescales.
2. We constructed ring width series (1974–2018) for a common Arctic dwarf shrub (*Betula nana*) for three representative types of subsites in the Siberian lowland tundra: higher elevation, lower elevation and thermokarst-affected (thaw ponds) terrain. We quantified decadal variability in climate-growth associations across subsites using partial least squares regression and a moving window approach.
3. We found consistently positive association of shrub radial growth with summer temperature, but substantial spatial and temporal variability in precipitation response. Association of shrub growth with summer rainfall increased in recent decades. Shrubs on elevated sites showed particularly strong response to rainfall following drier periods, and a negative association with recent snowfall extremes. Shrubs sampled from thaw ponds showed strong positive association with rainfall, followed by high shrub mortality after an extremely wet summer. This likely resulted from waterlogging due to thermokarst.
4. *Synthesis.* Our findings imply that the response of shrub growth to changes in Arctic precipitation regimes is regulated by (i) macro- (kilometre-scale) and

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micro-topographical (metre-scale) gradients, (ii) colimitation between temperature and moisture and (iii) potentially nonlinear responses to precipitation extremes. This suggests that the scalability of precipitation-growth relationships for Arctic shrubs across dynamic tundra landscapes and future climate scenarios is limited. We recommend that future climate-growth studies on Arctic tundra shrubs simulate future precipitation changes across spatial gradients and include detailed microsite and shrub physiological monitoring.

KEYWORDS

Arctic greening, *Betula nana*, dendrochronology, lowland tundra, precipitation, shrubs, Siberia

1 | INTRODUCTION

With air temperatures in the Arctic increasing several times faster than the global average (AMAP, 2021), Arctic ecosystems are subject to drastic ecological changes (AMAP, 2021; Box et al., 2019; Meredith et al., 2019). Shrubs in particular tend to respond positively to Arctic warming, and this 'shrubification' can manifest as a range expansion as well as increase in biomass or stature (Myers-Smith et al., 2011). Increases in shrub cover, height and biomass are evident from long-term monitoring sites (Bjorkman et al., 2020; Elmendorf, Henry, Hollister, Björk, et al., 2012; Heijmans et al., 2022; Martin et al., 2017), as well as warming experiments (Bjorkman et al., 2020; Elmendorf, Henry, Hollister, Björk, et al., 2012; Ercan et al., 2021; Hobbie & Chapin III, 1998; Walker et al., 2006). In addition, tree ring studies find positive associations between shrub radial growth and temperatures (Bär et al., 2008; Blok et al., 2011; Forbes et al., 2010; Hollesen et al., 2015; Myers-Smith, Elmendorf, et al., 2015), and satellite observations indicate range expansions of shrubs evident from aerial imagery or vegetation productivity indices (Forbes et al., 2010; Frost et al., 2014; Nitze & Grosse, 2016; Tape et al., 2006). Shrub expansion is mostly attributed to increases in taller deciduous genera (*Salix*, *Betula*, *Alnus*; Myers-Smith et al., 2011; Vowles & Björk, 2019), although prostrate evergreen shrubs also expand in a warming climate (Elmendorf, Henry, Hollister, Björk, et al., 2012; Vowles & Björk, 2019).

Increases in abundance, cover and height of shrub canopies affect ecosystems in multiple ways, which can result in complex and highly site-specific feedbacks (Heijmans et al., 2022; Loranty & Goetz, 2012). Increases in cover and height of tall deciduous shrubs in particular can affect the depth, density and duration of snow cover, which generally results in increased soil temperatures in winter (Kropp et al., 2021; Myers-Smith & Hik, 2013; Sturm et al., 2001; Wilcox et al., 2019). In contrast, shading of the ground surface, evapotranspiration and accumulation of organic layers generally lead to soil cooling in summer (Blok et al., 2010; Heijmans et al., 2022). Shrub growth may affect the tundra greenhouse gas balance through changes in carbon sequestration in shrub biomass (Elmendorf, Henry, Hollister, Björk, et al., 2012; Forbes et al., 2010; McGuire et al., 2018; Mekonnen et al., 2021; Tremblay et al., 2012;

Walker et al., 2006). Apart from changes in standing biomass, evergreen shrub expansion may promote soil carbon accumulation through production of poorly decomposable litter, while deciduous shrub expansion may enhance soil matter turnover due to production of decomposable litter and impacts on the soil microclimate (Vowles & Björk, 2019). Given these substantial ecosystem impacts, it is relevant to assess to what extent expansion of various shrub species can be expected across a heterogeneous and rapidly warming Arctic.

This study focuses on secondary stem growth in existing shrub communities as derived from tree rings. Across Arctic and Alpine ecosystems, shrub growth shows strong correspondence to summer temperature (Bär et al., 2008; Blok et al., 2011; Forbes et al., 2010; Myers-Smith, Elmendorf, et al., 2015). Beside direct influences of warming, shrub growth may be affected by lengthening of the growing season, advances in the timing of snow melt and deepening of the active layer in permafrost soils and resulting increases in nutrient availability (Myers-Smith et al., 2019; Oberbauer et al., 2013). The degree to which shrubs can respond to increasing summer temperatures may depend on soil temperatures, snow dynamics, nutrient availability and numerous other factors (Anadon-Rosell et al., 2018; Francon et al., 2020; Martin et al., 2017). A number of recent studies finds an important role of moisture availability in the temperature-growth response (Ackerman et al., 2017; Buchwal et al., 2020; Elmendorf, Henry, Hollister, Björk, et al., 2012; Myers-Smith, Elmendorf, et al., 2015; Opała-Owczarek et al., 2018; Piao et al., 2014; Tape et al., 2012; Tremblay et al., 2012) and expansion dynamics (Frost et al., 2013) of tundra shrubs. As a result, anticipated increases in Arctic precipitation and variability thereof (Bintanja et al., 2020) may be an important control on shrubs' temperature-growth response (Myers-Smith, Elmendorf, et al., 2015).

Snow conditions and temperature during winter provide additional controls on Arctic shrub growth. Continuous snow cover protects shrubs from frost damage during the cold season (Bjerke et al., 2017; Bokhorst et al., 2009; Phoenix & Bjerke, 2016; Treharne et al., 2019). Winter and spring warming can contribute positively to shrub growth (Fraser et al., 2014; Hollesen et al., 2015; Krab et al., 2018), likely as a result of earlier snowmelt and earlier drainage and warming of soils. This stimulates microbial decomposition and enhances nutrient availability in the following growing season (Fraser

et al., 2014; Hollesen et al., 2015; Sturm et al., 2005). However, if extreme winter warming or early spring thaw results in removal of protective snow cover, subsequent frost events can result in shrub damage and compromised growth (Bjerke et al., 2017; Bokhorst et al., 2009; Treharne et al., 2019). Timing of snowmelt affects the phenology of both evergreen and deciduous shrub species (Wipf & Rixen, 2010). However, the growth of relatively frost-tolerant deciduous species such as *Betula nana* may be predominantly positively affected by earlier onset of snowmelt, while evergreens with overwintering leaves (e.g. *Empetrum nigrum*, *Vaccinium vitis-idaea*) may show predominantly negative effects of early-season frost damage (Bokhorst et al., 2009; Dobbert et al., 2021a; Krab et al., 2018).

Climate-growth associations of Arctic shrub species can vary spatially and temporally. Spatial contrasts in climate-growth response have been identified in earlier dendrochronological and monitoring studies in a variety of shrub genera (Black et al., 2021; Dobbert et al., 2021b; Opała-Owczarek et al., 2018). Such spatial variability ranges from large-scale contrasts (thousands of kilometres) among Arctic regions associated with differential sea ice decline (Buchwal et al., 2020), to smaller scale regional contrasts (kilometre scale) among landforms (Ackerman et al., 2017; Ropars et al., 2015) and local-scale (metres to hundreds of metres) topographical and hydrological contrasts (Black et al., 2021; Dobbert et al., 2021b). Spatial divergence in temperature-growth responses of *Betula* and *Salix* species is often related to local differences in moisture availability (Ackerman et al., 2017; Buchwal et al., 2020; Myers-Smith, Elmendorf, et al., 2015; Ropars et al., 2015). Observations of differential expansion of various shrub genera in wetter and drier sites under warming treatments further suggest that moisture dependence of temperature response is likely species specific (Scharn et al., 2021). Species-specific divergences in climate-growth response have additionally been found under local (metres to hundreds of metres) contrasts in snow dynamics among species with variable frost tolerance and phenological plasticity (Dobbert et al., 2021b; Krab et al., 2018; Lawrence & Swenson, 2011; Loranty & Goetz, 2012; Ropars et al., 2015). Other sources of spatial heterogeneity in climate-growth response include microclimate variability, biotic interactions, permafrost dynamics and herbivory (Martin et al., 2017).

In addition, dendroclimatological studies over longer timescales reveal nonstationarity in climate-growth associations (D'Arrigo et al., 2008; Francon et al., 2020, 2021; Hollesen et al., 2015; Wilmking et al., 2005). The strength and direction of climate-growths can vary over decadal timescales, for instance due to nonlinear growth responses, increasing climate variability or colimitation processes (Buchwal et al., 2020; Gamm et al., 2018; Jevšenak & Levanič, 2016). Colimitation is defined here as situations in which plant growth responds more strongly or only to the combined increase of two (or potentially more) independent limiting factors (Harpole et al., 2011). For example, precipitation-growth association of *Betula nana* may be stronger in warm years compared to colder years (Li et al., 2016), and temperature response of shrub growth may vary among wetter and drier Arctic regions (Buchwal et al., 2020). Quantitative assessment of local-scale controls on Arctic shrub climate-growth

relations over longer time periods at a spatial scale representative for tundra ecosystem heterogeneity (i.e. as small as metres) remains a key knowledge gap that hampers projection of future shrub expansion rates (Martin et al., 2017; Mekonnen et al., 2021; Myers-Smith et al., 2020). Data from the Russian Arctic are particularly scarce in this context (Martin et al., 2017).

Here, we study the scalability of climate-growth associations in the deciduous Arctic shrub *Betula nana* in a North-Eastern Siberian tundra site across kilometre to metre scale landscape heterogeneity over a time period of 45 years using a dendrochronological approach. Dendrochronology, the study of tree rings, offers a standardised way to study annual dynamics of radial stem growth of woody species across Arctic environments (Cook & Kairiukstis, 2013; Fritts, 2012; Myers-Smith, Hallinger, et al., 2015). Radial stem growth generally corresponds to increases in above-ground shrub biomass (Le Moullec et al., 2019). We investigated whether climate-growth associations of *Betula nana* in our study area showed:

1. colimitation effects of summer temperature and water availability?
2. variability across macro- (kilometres) and micro-topographical (metres) gradients?
3. nonstationarity over decadal timescales?

We expected that (1) the temperature-growth response of *Betula nana* would be lower in periods with little rainfall or moisture availability, indicated by a positive interactive effect of summer temperature and rainfall. Furthermore, we expected that climate-growth associations would differ (2) among both macro- and micro-topographical gradients, and (3) across decadal timescales with different baseline climatic conditions. With this study, we aim to better account for interactions between multiple climatic influences over longer timescales (Mekonnen et al., 2021), and to assess to what extent general relations between climate and shrub growth can be scaled across heterogeneous tundra landscapes and to future climate scenarios.

2 | MATERIALS AND METHODS

2.1 | Study site and species description

We conducted our dendrochronological study at the Chokurdakh Scientific Tundra station (70°49' N, 147°29' E) in the North-Eastern Siberian lowland tundra (Indigirka Lowlands; Figure 1a). On a larger scale (kilometres), the study area is characterised by thaw lakes, floodplains, overlapping drained thaw lake basins ('alases') of various ages and low ridges representing erosion remnants of late Pleistocene Yedoma deposits, with typical areas of approximately 1–10 km² (van Huissteden et al., 2021, Figure 1b,c). The study area shows an elevational range of 8–35 m a.m.s.l. (Figure 3d, Porter et al., 2018). The area is characterised by continuous ice-rich permafrost with a shallow active layer of approximately 40–50 cm

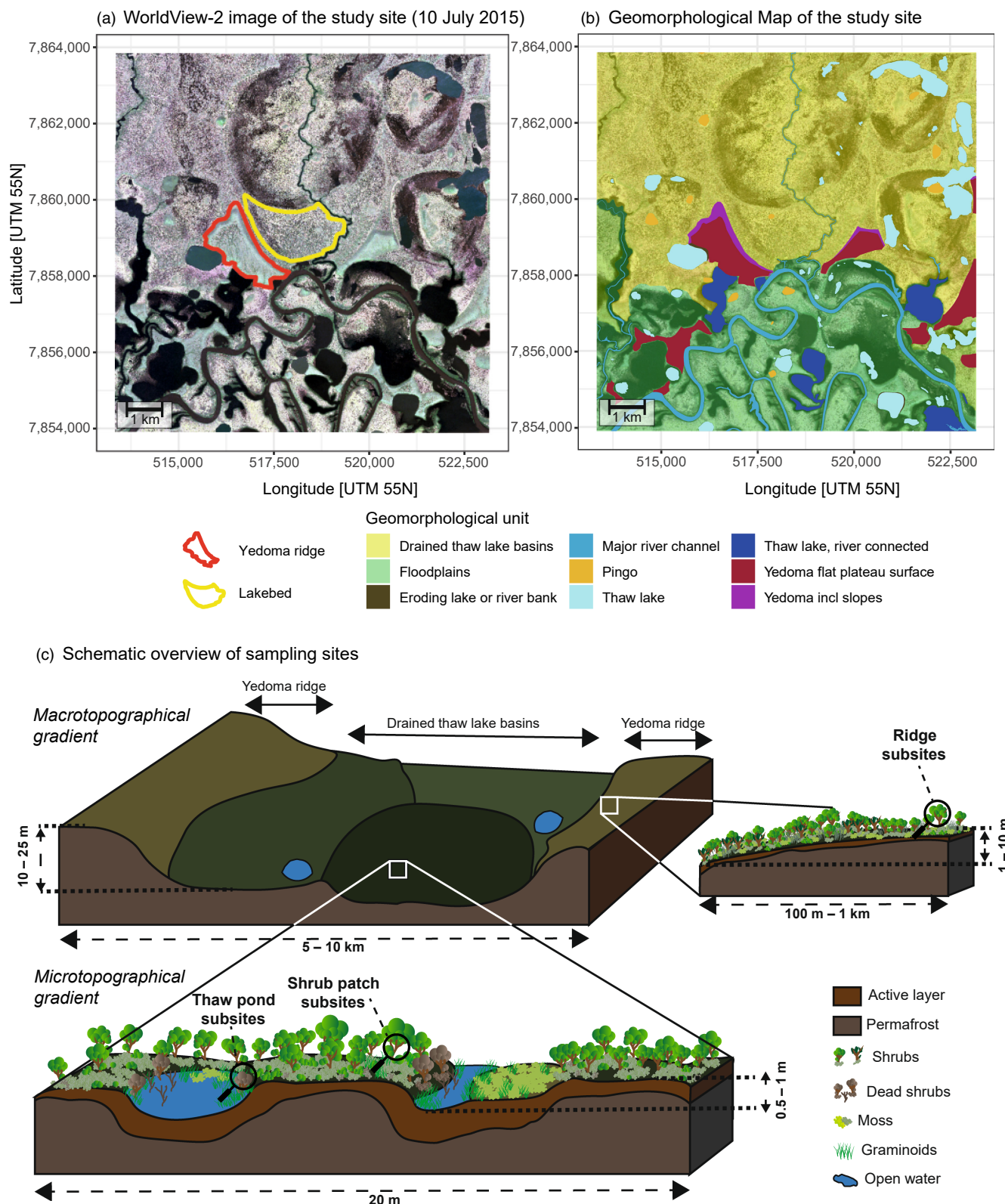


FIGURE 1 Site overview. (a) 10×10km WorldView-2 image (July 2015) of the study site. WorldView 2 © MAXAR, 2019. (b) Geomorphological map of the study site by van Huissteden and Beileli Marchesini (2014), with WorldView-2 image as background. In (a, b), the yellow polygon represents the drained thaw lake basin and the red polygon indicates the Yedoma ridge. (c) Schematic overview of the spatial scales and subsites considered in the sampling design.

(CALM, 2021). Mean annual temperature and precipitation are -12.7°C and 189 mm, average July temperature and precipitation are 10.6°C and 22 mm (1990–2020; RIHMI-WDC, 2020). The peak growing season is July–August (Van der Molen et al., 2007). Higher elevation sites such as Yedoma ridges and pingos generally feature mixed tussock-sedge (*Eriophorum vaginatum*) and dwarf shrub vegetation. On smaller spatial scales (metres, Figure 1c), low lying areas such as drained thaw lake basins feature slightly elevated shrub patches dominated by *Betula nana*, lichens and mosses, alternating with waterlogged depressions with standing water, aquatic sedges (e.g. *Eriophorum angustifolium*, *Carex* spp.) and peat moss (*Sphagnum*

spp.), with typical areas of several to several 100m^2 (Magnússon et al., 2021; Siewert et al., 2015). Soil properties generally vary on similarly local scales, and show some correspondence with vegetation composition (Table 1; Bartholomeus et al., 2012). Fieldwork and sampling were carried out under a memorandum of understanding with the Directorate of Biological Resources and Protected Areas, Ministry of Nature Protection of Republic of Sakha (Yakutia), Russian Federation.

This study focuses on the response of the Arctic dwarf birch (*Betula nana*) to a warming Arctic. *Betula nana* is one of the most widespread Arctic shrub species and may be found in Arctic tundra

TABLE 1 Differences in abiotic conditions (mean $\pm$ standard deviation) and vegetation composition among different types of sampling locations.

			Drained thaw lake basin		
Variable	Date measured	Yedoma ridge (YR)	Thaw ponds (TP)	Shrub patches (SP)	References
Elevation	Various	20–35 m a.m.s.l.	9–11 m a.m.s.l.		ArcticDEM Porter et al. (2018)
	July 2018	—	Ponds 30 to 50 cm lower than shrub patches		Magnússon et al. (2020)
Soil moisture (top 5 cm)	July 2007	39.0±7.4 vol-%	—	30.0±6.8 vol-%	Blok et al. (2010)
	July 2008	21.0±7.8 vol-%	—	17.5±5.4 vol-%	Blok et al. (2010)
	July 2012	—	85.0±8.5 vol-% ^a	47±14.6 vol-%	Nauta et al. (2015)
	August 2018	—	88.7±23.1 vol-%	17.4±9.3 vol-%	Magnússon et al. (2020)
Snow height	May 2008	30.2±6.7 cm	—	29.5±6.9 cm	Blok et al. (2010)
	April 2012	—	35.0±4.4 cm ^a	24.8±1.7 cm	Nauta et al. (2015)
Soil type	August 2012	Turbels	Histoturbels (Histels locally)		Siewert et al. (2015)
	Summer 2008	Soil stratigraphy varies on microscale (metres) based on topography and wetness			Bartholomeus et al. (2012)
Organic layer depth	August 2012	12.3±8.6 cm ^b	20.6±5.7 cm ^b	19.5±4.0 cm ^b	Siewert et al. (2015) ^b
	August 2019	—	24.7±5.2 cm	21.7±3.7 cm	Magnússon et al. (2020)
Thaw depth	July 2007	33.1±4.4 cm	—	22.4±2.9 cm	Blok et al. (2010)
	July 2010	28.4±5.3 cm	—	22.7±1.9 cm	Blok et al. (2010)
	August 2012	38±11.7 cm ^b	43±10.3 cm ^b	33.0±8.1 cm ^b	Siewert et al. (2015)
	July 2018	—	40.3±10.5 cm	23.5±7.2 cm	Magnússon et al. (2020)
Landscape composition	Various	Homogeneous, with frost boils, and ice wedges several metres wide	Heterogeneous, polygons or irregular frost mounds and with waterlogged depressions		Wang et al. (2016) and Siewert et al. (2015)
Vegetation composition	July 2019	Mixed vegetation: tussock sedges (<i>Eriophorum vaginatum</i>), dwarf shrubs (<i>Betula nana</i> , <i>Salix pulchra</i> , <i>Salix glauca</i> , <i>Rhododendron tomentosum</i> , <i>Vaccinium vitis-idaeae</i> , <i>Vaccinium uliginosum</i> , <i>Dryas octopetala</i>), mosses and lichens (a.o. <i>Polytrichum</i> spp., <i>Dicranum</i> spp., <i>Flavocetraria cucullata</i> , <i>Cladonia</i> spp., <i>Hylocomium splendens</i>)	Drowned shrubs, standing water, sedges (predominantly <i>Eriophorum angustifolium</i> and <i>Carex aquatilis</i>) and <i>Sphagnum</i> (mainly <i>S. subsecundum</i> and <i>S. squarrosum</i>) in older ponds	Dwarf shrubs (mainly <i>Betula nana</i> , <i>Salix pulchra</i>), moss and lichen understory (a.o. <i>Polytrichum</i> spp., <i>Dicranum</i> spp., <i>Flavocetraria cucullata</i> , <i>Cladonia</i> spp., <i>Peltigera</i> spp.)	Magnússon et al. (2021)

^aNauta et al. (2015) measured abiotic conditions in very recently formed thaw ponds whose formation was triggered by shrub removal.

^bSiewert et al. (2015) measured abiotic conditions in the landscape subclasses 'tussock tundra', 'sedge fen' and 'dwarf shrub fen', generally equivalent to our sampling site subdivision.

as well as alpine environments (GBIF, 2021). Its growth form varies from low (around 5 cm) and decumbent in high Arctic sites to more erect (around 30 cm) under more favourable environmental conditions (De Groot et al., 1997; Myers-Smith, Hallinger, et al., 2015). *Betula nana* is associated with moist, acidic and nutrient poor sites with thick organic layers, but does not tolerate prolonged waterlogging (De Groot et al., 1997). Its photosynthetic optimum lies around 10–13°C. Growth starts rapidly after the thawing of the frozen topsoil and shoot growth continues until mid-summer (De Groot et al., 1997). In our study area, shrubs generally reach a height of around 20 cm and establish both as seedlings and ramets (vegetative clones; Li et al., 2016). With its wide circumarctic distribution and presence at various topographical positions within our study region, *Betula nana* is a strategic focus species for our research aim.

2.2 | Dendrochronological data

2.2.1 | Sampling

In late summer 2018 and 2020, 79 shrub ramets were sampled across a macro- and micro-topographical gradient in the study area (Figure 1c). The macro-topographical (kilometre-scale) gradient is represented by a drained thaw lake basin and an elevated (10–25 m) Yedoma ridge. The micro-topographical (metre-scale) gradient is nested within the drained thaw lake basin, consisting of slightly elevated (0.5–1 m) shrub patches and small (<100 m²) thaw ponds formed within shrub patches through thermokarst. Shrubs from shrub patches and thaw ponds were sampled in 2018 (Magnússon et al., 2020), and shrubs from the Yedoma ridge were sampled in 2020. Most shrubs sampled from thaw ponds were dead or showed signs of compromised growth (small and discoloured leaves), but the stem was generally sufficiently intact to discern tree rings. This allowed for identification of potential contrasts in shrub radial stem growth under progressive thermokarst relative to intact shrub-dominated areas. No further micro-topographical subdivision was made for the Yedoma ridge, since it showed few thermokarst depressions and comparatively homogeneous vegetation (Table 1, Figure 1c). This resulted in three distinct subsites: a higher elevation Yedoma ridge (YR; 20 shrubs), slightly elevated shrub patches (SP; 30 shrubs) and thaw ponds (TP; 29 shrubs), the latter two situated within a drained thaw lake basin. To mitigate imbalances in sample availability among subsites, ring width series from three shrubs growing at the YR site were added from Blok et al. (2011), available from the ShrubHub database (Myers-Smith, Elmendorf, et al., 2015), resulting in 82 shrubs. Using a GPS, shrub locations were recorded with approximately 2 m accuracy. Samples were taken from relatively large, undamaged shrubs where possible. We sampled ramets at distances of at least 2 m from each other (usually >100 m) and dug out part of the root to avoid sampling of clonal individuals as much as possible. We visually identified the root collar (transition between stem and root) from the partially dug out roots. Three stem segments (2 cm length) were sampled along the main stem at the

root collar, at the moss surface and just below the first above-ground branch (generally <10 cm above the moss surface; Blok et al., 2011; Li et al., 2016). Segments were kept in a 1:3 solution of glycerol and alcohol (vodka). For all YR shrub samples and a subset of SP and TP shrubs, the above-ground length of the stem was measured along the longest branch prior to cutting stem fragments.

2.2.2 | Ring width measurement and chronology development

Ring widths of shrubs from thaw ponds and shrub patches were measured and cross-dated earlier by Magnússon et al. (2020) for the purpose of age determination of shrubs. Samples from the Yedoma ridge were analysed according to the same protocol. Cross-dating of ring width series of individual shrubs was carried out separately per subsite to account for potential spatial variability in climate–growth associations.

Serial sectioning on the three stem segments collected for each shrub ramet was used to detect missing rings (Hallinger et al., 2010; Kolischuk, 1990; Myers-Smith, Elmendorf, et al., 2015; Myers-Smith, Hallinger, et al., 2015; Wilmking et al., 2012). A full description is available in Text S1. Shrub ring widths were measured in CooRecorder v. 9.0 (Cybis, 2019) on high-resolution images of radial micro sections (20–30 µm) of sampled shrubs along two to four (usually three) radii per section. Visual cross-dating was carried out in WinTSAP v. 4.70d (RINTECH, 2017). Partially missing rings were inserted manually by first visually cross-dating and inspecting radii within a section. Radii were then averaged to a section ring width series. Next, sections within a shrub were visually cross-dated against other shrubs in the same subsite and checked for continuous missing rings. From the 82 available shrubs, 11 were omitted during ring width measurement due to poorly discernible rings, lack of visual fit among sections or radii or extensive damage, resulting in a selection of 22 YR shrubs, 25 SP shrubs and 24 TP shrubs that were used for statistical cross-dating and chronology development.

Individual sections' ring widths were detrended for age-related growth effects using C-method detrending (Biondi & Qeadan, 2008) in R using the DPLR package (Bunn, 2008). Next, sections within a shrub were retained and averaged if they showed significant ($p < 0.05$) correlation among sections and otherwise omitted from analysis (see Text S1). Then, samples with significant correlation coefficients compared to average detrended ring width of the rest of the dataset and a series length of at least 30 years were selected to develop a residual chronology. Exceptions were made for shrubs with shorter ring width series (25–30 years) but significant and very strong visual correlation towards the rest of the dataset, or shrubs with very long ring width series ($n > 60$) but near significant correlation ($p < 0.1$). After selection of shrubs, the first 5 years of each ring width series were removed to reduce the effect of irregular juvenile growth. Residual chronologies were developed for the overall study area (based on cross-dating of samples from all three sites) and for each subsite separately, based on averaged residuals of the

first-order temporal autoregressive model fits per individual shrub, expressed as a dimensionless ring width index (RWI). We used a minimum sample depth of six shrubs. We compared the different residual chronologies using lagged correlations to check for missing rings and did not find indications thereof in any of the chronologies. Comparison of resulting chronologies with earlier dendrochronological work at the study site indicated strong correlations among the different chronologies of this study, and significant correlations with chronologies developed during earlier studies (Blok et al., 2011; Li et al., 2016; Figure S1). This suggests that any potential bias due to the separate measurement and initial visual cross-dating process for the different sets of samples is limited.

Additionally, we exported residual RWI series for each individual shrub that was included for chronology development. Using averaged raw ring width measurements of individual shrubs, we calculated the age, final stem diameter (excluding bark tissues), average annual basal-area increment and average basal-area increment during the first 10 years of growth (here including the first 5 years of juvenile growth). Raw ring width measurements and ages were used to derive diameter-age curves per individual shrub. These age, diameter, length and growth associations were used to assess potential differences in shrub growth strategy among the three subsites.

2.3 | Remote sensing time series

To gain a better understanding of spatial differences in vegetation phenology, soil moisture and presence of surface water and snow, we extracted several coarse to very high-resolution time series of remote sensing products for the study area. To approximate temporal dynamics in growing season soil moisture, we downloaded daily EUMETSAT scatterometer root zone soil moisture (RZSM) data (Datasets H141 and H142) (HSAF, 2020). These coarse resolution data (10×10 km) are available for 1992–2020 and were extracted for the topsoil layer (0–7 cm). To assess potential variability in snow cover dynamics and phenology on smaller spatial scales, we selected 10 m resolution cloud-free Sentinel-2 top-of-atmosphere reflectance (TOAR) (2016–2018) and surface reflectance (SR) (2019–2020) images from May to September from Google Earth Engine (earlier Sentinel-2 images are not available). For these images, we calculated the normalised difference vegetation index (NDVI) and Pixel Snow Probability using standard Sentinel scene classification algorithms (Main-Knorn et al., 2017; see Text S2). We extracted pixel NDVI and Snow Probability values in May and June for each shrub sample site and visualised these values against the day of year and site type (ridge, shrub patch or pond) to visually assess whether snow dynamics and early growing season phenology differed among site types. Since wetness can vary on very small spatial scales in this ecosystem (Magnússon et al., 2020), we used two WorldView-2 satellite images (2 m resolution) to visually assess small-scale spatial variability in surface wetness. Images were corrected with surface reflectance using MAXAR's ACOMP algorithm and were collected on 10 July 2015 and 1 August 2019. Average normalised difference

water index (NDWI) values were used as an approximation of small-scale variability in terrain wetness. Since these high-resolution images were acquired at different seasonal timings, we did not derive a high-resolution WorldView-2 NDVI. Lastly, we used the 2 m resolution ArcticDEM (Porter et al., 2018) to extract elevation above mean sea level for each shrub sampling location, and a geomorphological map of the study area (van Huissteden & Beletti Marchesini, 2014).

2.4 | Statistical analysis

2.4.1 | Climate data and trends

Climate data for the site were retrieved for the Chokurdakh Meteorological Station (WMO code 29146, ±27 km Northeast from the site) from the AISORI database (<http://aisori-m.meteo.ru/waisori/>) of the All-Russia Research Institute of Hydrometeorological Information-World Data Centre (RIHMI-WDC, 2020). Daily data of average, minimum and maximum temperature, total precipitation, snow height and snow extent are available for 1944–2020. We used monthly averages of average daily temperatures, monthly sums of total daily precipitation and monthly maxima of daily snow height visually assess changes in weather conditions over the period 1948–2020. We selected the period 1948–2020 due to frequently missing data in the first years of the record.

We used a moving window correlation analysis with flexible windows size as implemented in the DENDROTOOLS package in R (Jevšenak & Levanič, 2018) to explore during which periods *Betula nana* shows sensitivity to the available daily climate variables (average temperature, total precipitation and snow height). Sensitivity was expressed as Pearson correlation between RWI and a daily climate variable, using a 95% bootstrap ($n=100$) adjusted confidence interval to determine significance (Jevšenak & Levanič, 2018). Moving window analysis was performed for climate variables in the current as well as previous year. We used these moving window correlations (Figure S3) as well as evidence from earlier climate–growth studies of *Betula nana* from the study site (Blok et al., 2011; Li et al., 2016) to identify main periods of climate sensitivity.

In addition, we screened earlier studies of climate–growth response of *Betula nana* from our site and evidence from other Arctic environments to preselect additional climate variables relevant for annual radial stem growth (Table 2). The resulting climate dataset includes summer (June–July; Blok et al., 2011; Li et al., 2016) and winter (November–April) temperature (Hollesen et al., 2015), summer precipitation (June–July) (Blok et al., 2011; Li et al., 2016) and snow height (rather than winter precipitation; Bokhorst et al., 2009), for year of growth as well as previous years (Figure S3; Blok et al., 2011). The summer season was restricted to June–July, based on earlier findings of Blok et al. (2011) and Li et al. (2016) and moving window correlations presented in Figure S3, which shows the absence of climate–growth correlation in later summer months. To approximate interannual variation in the duration and integrated temperature over the growing season, we derived the date of snowmelt and

TABLE 2 Overview of climate variables potentially relevant in climate–growth associations of *Betula nana*.

Variable	Abbreviation	Description
Mean temperature June–July	T–summer	Mean of average daily temperatures in June and July (=early summer)
Previous year's mean temperature June–July	T–prev.summer	T–summer of previous year
Total precipitation June–July	P–summer	Sum of total daily precipitation in June and July
Previous year's total precipitation June–July	P–prev.summer	P–summer of previous year
Mean temperature winter	T–winter	Mean of average daily temperatures in November–April
Previous year's mean temperature winter	T–prev.winter	T–winter of previous year
Max snow height April–May	S–spring	Maximum observed snow height in April and May
Previous year's max snow height April–May	S–prev.spring	S–spring of previous year
Date of snowmelt	Melt date	First day with no snow cover in May–June
12-month Standardised Precipitation Evapotranspiration Index (SPEI) June–July	SPEI12–summer	Mean SPEI (calculated over 12-month period) for June–July (Vicente-Serrano et al., 2010), using Hargreaves equation for potential evapotranspiration
Snow-free thawing degree days	SFTDD	Sum of temperatures >0°C on days with no snow cover in May–July ^a
Growing degree days >5°C	GDD	Sum of temperatures >5°C in May–July ^a
Spring frost events	Spring Frost	Sum of temperatures <0°C occurring at least 5 days after snowmelt in May–July ^a
Winter warming events*	Winter warming	Sum of temperatures >0°C in November–April ^b
Interaction summer temperature and precipitation	int(T,P)–summer	Product of standardised T–summer and P–summer
quadratic term for summer temperature	T ² –summer	Squared standardised T–summer

^aTemperatures above zero degrees did not occur prior to May.

^bWinter warming events were not observed over the study period and were not considered in further statistical analysis.

several degree day products from the Chokurdakh record (Table 2). We defined the date of snowmelt as the first day on which no snow cover was recorded in May or June. We computed snow-free thawing degree days (SFTDDs, following Francon et al., 2020) as the sum of temperatures above zero degrees Celsius on days with no snow cover in May–July. Growing degree days were defined as the sum of temperatures over 5 degrees Celsius (GDD) in May–July (Ercan et al., 2021; Wipf et al., 2006). Temperatures above zero degrees did not occur in April or earlier months. The 12-month Standardised Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010) over summer (June–July) was added to represent moisture availability during the growing season (Buchwal et al., 2020; Li et al., 2016). Spring frost events (total freezing degree days in June and July occurring at least 5 days after snowmelt; Wheeler et al., 2014) and winter warming events (quantified here as thawing degree days in November–April prior to snowmelt) were added to represent potential frost damage prior to the growing season (Bjerke et al., 2017; Bokhorst et al., 2009; Treharne et al., 2019; Wheeler et al., 2014).

2.4.2 | Climate–growth associations

As an exploratory analysis, we quantified Pearson correlation coefficients for selected (Table 2) climate variables and RWI values for the *Overall* chronology and *Yedoma Ridge*, *Thaw Ponds* and *Shrub Patches* chronologies, visualised as scatter matrices. Climate data were

standardised prior to correlation analysis (mean-centred and unit-variance scaled). Based on visual inspection (Figure S6), linear relations with RWI were used in principle. However, following from our research aim and previous findings, we added an interaction term for summer temperature and precipitation to represent potential colimitation of temperature and moisture availability during the growing season (Buchwal et al., 2020; Li et al., 2016), and a quadratic term for summer temperature to represent potential effects of extremes and diminishing growth returns under increasing summer temperature (Ackerman et al., 2017) to further statistical analyses (Table 2).

Next, orthogonalised partial least squares (OPLS) regression analysis was used to quantify associations between climate variables and radial stem growth of *Betula nana*, including all previous year's climate variables, selected interactions and quadratic terms based on literature screening (Table 2). OPLS regression was chosen because of its efficient handling of large numbers of multicollinear variables, and limited number of observations relative to explanatory variables. Partial least squares (PLS) regression is a multivariate regression method that quantifies association between a predictor matrix *X* and response matrix (or variable) *Y* by decomposing *X* and *Y* into latent factors based on linear recombinations of original variables. Contrary to principal component regression, PLS decomposes both *X* and *Y* into latent factors in such a way that the (multidimensional) variance in *Y* that is explained by multidimensional components in *X* is maximised (Wold, 1980). OPLS regression is an extension to PLS in which orthogonal signal correction is used to separate variation in *X* into variation that is nonorthogonal (correlated) to *Y* and variation

that is orthogonal to Y (non-correlated; Bylesjö et al., 2006; Trygg & Wold, 2002). While PLS and OPLS are identical in terms of predictive performance, OPLS allows for better characterisation of predictive versus nonpredictive variation in X (Bylesjö et al., 2006). (O)PLS methods are widely used in chemometrics, bioinformatics and industrial fields, but have gained popularity in other fields owing to their ability to analyse dataset with few observations relative to the number of predictors and datasets with multicollinear predictors and their lack of distributional assumptions (Wold, 1980). PLS has been successfully applied to ring width indices (Kalela-Brundin, 1999) and dendrometer measurements (Dobbert et al., 2021b; Löffler & Pape, 2020) to characterise climate–growth associations.

Here, we employ OPLS regression as implemented in the `opls()` function in the `ROPLS` package in R (Thévenot, 2016) to quantify associations between detrended ring width indices (Y) and a large set of standardised (mean-centred and unit-variance scaled) annual climate statistics (X) (Table 2). The `opls()` function performs cross-validation to select the optimal number of latent components and uses permutation tests to provide model diagnostics. As a measure of influence of individual X variables on Y , `opls()` provides estimates of regression coefficients based on the NIPALS algorithm (Thévenot, 2016; Thévenot et al., 2015). Using an OPLS model with the optimised number of components we performed bootstrapping ($n=200$) to derive standard errors, 95% confidence intervals and p -values for each regression coefficient estimate. This resulted in estimates, significance and confidence intervals of regression coefficients for each X variable for the *Overall* chronology over the time period 1974–2018.

2.4.3 | Spatiotemporal variation in climate–growth associations

To assess spatiotemporal variability in climate–growth associations, we extended our analysis by performing OPLS climate–growth regression separately for the three subsite chronologies using a moving window approach. This resulted in separate OPLS models over individual 30-year time periods with a 5-year time step for each subsite chronology. We do not consider potential variability in RWI among shrubs within a chronology, since only averaged RWI for the *Overall* and each subsite chronology is used, as is common practice in dendroclimatological studies (Fritts, 2012).

We further explored spatial heterogeneity in climate–growth associations by comparing differences in sensitivity to the main climate factors among individual shrubs to shrub characteristics and site factors (Trouillier et al., 2018). OPLS regression coefficient estimates were obtained for climate–growth associations of individual shrubs' RWI curves over a common time period (1980–2006). This selected common period is a compromise between the number of shrubs that could be included and length of the common period. We only included those climate variables that showed significant associations with any of the site chronologies in OPLS analysis. This resulted in separate estimated coefficients for climate variables for each individual shrub. We then

assessed Pearson correlations between these estimated coefficients, shrub age, shrub growth rates and local abiotic conditions, extracted from remote sensing products using sampling site coordinates. Extracted remote sensing products included two-summer average WorldView NDWI (July 2015, August 2019) and elevation (ArcticDEM). Shrub growth rates included average radial stem growth rate and average radial stem growth rate for the first 10 years of shrub growth. Shrub age was defined as the mean age of each shrub in the selected time period (1980–2006). Using Pearson correlation matrices among these different datasets we assess whether individual shrubs' climate response and growth rates show any relation to their age or selected abiotic site conditions.

2.4.4 | Analysis of pointer years and extreme weather conditions

Lastly, we analysed temporal patterns of pronouncedly poor and good growth years for all three subsites using pointer years. Pointer years are years that show extremely high or low RWI in a chronology. We quantified pointer years for the three subsite chronologies over the period 1959–2018 as years in which at least 50% of individuals showed RWI scores higher or lower than 1, 1.28 or 1.645 standard deviations away from the mean as weak, strong and extreme pointer years respectively (Neuwirth et al., 2007). We used the `POINTRES` package in R (van der Maaten-Theunissen et al., 2015) to identify pointer years. We then compared standardised annual climate variables for pointer years (Bär et al., 2006), restricting the comparison to those climate variables that showed correlation with at least one of the chronologies in the OPLS analysis. We tabulated RWI scores for the three subsites in the 3 years that showed the highest and lowest standardised scores for each significant climate variable from OPLS analysis to qualitatively assess which climatic conditions are associated with distinctly strong or poor growth years across subsites. Throughout all statistical analyses a significance criterion of $\alpha=0.05$ was used.

3 | RESULTS

3.1 | Climate trends

Mean annual temperature at the study site shows a warming trend of 0.3°C per decade since the start of the record in 1948. Warming is particularly evident after 1980 (0.7°C per decade, Figure 2a, Table S5) and driven more by winter warming than by summer warming (Figure 2a,b, Table S5). November and April in particular show strong recent warming (Figure S11a). Growing degree days and snow-free thawing degree days (GDD, SFTDD) have increased (Figure 2e,f) mostly in early (June) and late (August) summer (Figure S11d,e). Precipitation shows high year-to-year variability and an apparent trend of decreasing summer rainfall (Figure 2c)

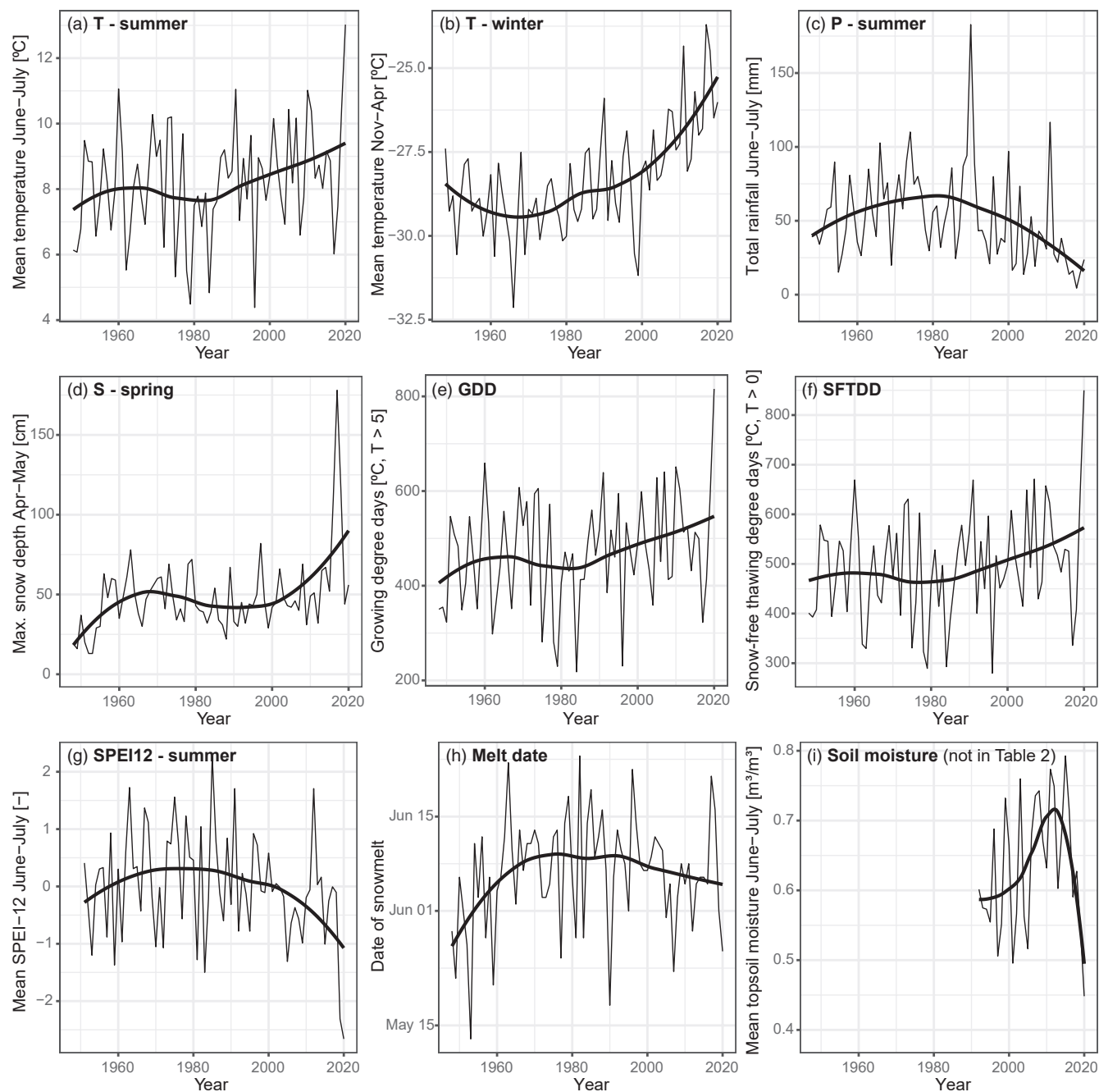


FIGURE 2 Annual Climate Variables from 1948 to 2020, derived from the Chokurdakh Meteorological Station (WMO code 29146). Data retrieved from the AISORI database (RIHMI-WDC, 2020). For an overview of the selected climate variables, see Table 2. Spring frost and winter warming events are not shown due to low occurrence. Previous years' variables and derived terms (quadratic, interaction) not depicted. Solid lines represent LOESS fits, thinner lines represent annual values. (a) Average of daily mean temperatures in summer (June–July). (b) Average of daily mean temperatures in winter (November–April). (c) Sum of precipitation in summer (June–July). (d) Maximum snow height in spring (April–May). (e) GDD (sum of all temperatures $> 5^{\circ}\text{C}$ in May–July). (f) Total SFTDD (snow-free thawing degree days, sum of all temperatures $> 0^{\circ}\text{C}$ on days with no snow cover in May–July). (g) Average SPEI12 in summer (June–July). (h) Date of snowmelt (first day of the year with zero snow height). (i) We additionally show summer (June–July) soil moisture as derived from EUMETSAT scatterometer data for a $10 \times 10 \text{ km}$ surrounding the study site. data (HSAF, 2020).

and decreasing SPEI12 in June–July (Figure 2g) since 1990 (except for individual very wet years such as 2011). Snow height in spring fluctuates between 25 and 75 cm, but was exceptionally high (100–200 cm) in 2016–2018 (Figure 2d). Snowmelt typically occurs around early June, but shows high year-to-year variability, with a trend

for later snowmelt until approximately 1980 and a weak trend for earlier snowmelt since 1980 (Figure 2h). Scatterometer data suggest average topsoil volumetric moisture contents of 40%–80% in June–August (Figure 2i) with a strong decline in recent dry summers (Figure 2c,i).

3.2 | Abiotic contrasts among sampling sites

Sampling locations in the lakebed ranged from approximately 9–11 m in elevation a.s.l., whereas those from the ridge generally ranged from 20 to 35 m (Figure 3d,e). No substantial differences in WorldView-2 based wetness index (NDWI, 2 m resolution) were evident, except for occasionally higher wetness in ponds (Figure 3c,f). Field observations do indicate large contrasts in wetness between

generally dry shrub patches and waterlogged ponds (Table 1). Sampling locations on the ridge tended to show earlier snow-free conditions (Figures 3b and 4a) and earlier greening (Figures 3a,g and 4b) during the start of the growing season, as derived from 10 m resolution Sentinel-2 NDVI. This was especially evident on the top-most sites on the ridge (Figure 3a). Within the lakebed sites (thaw ponds and shrub patches), no distinction in snow and vegetation dynamics was visible from WorldView-2 and Sentinel-2 data.

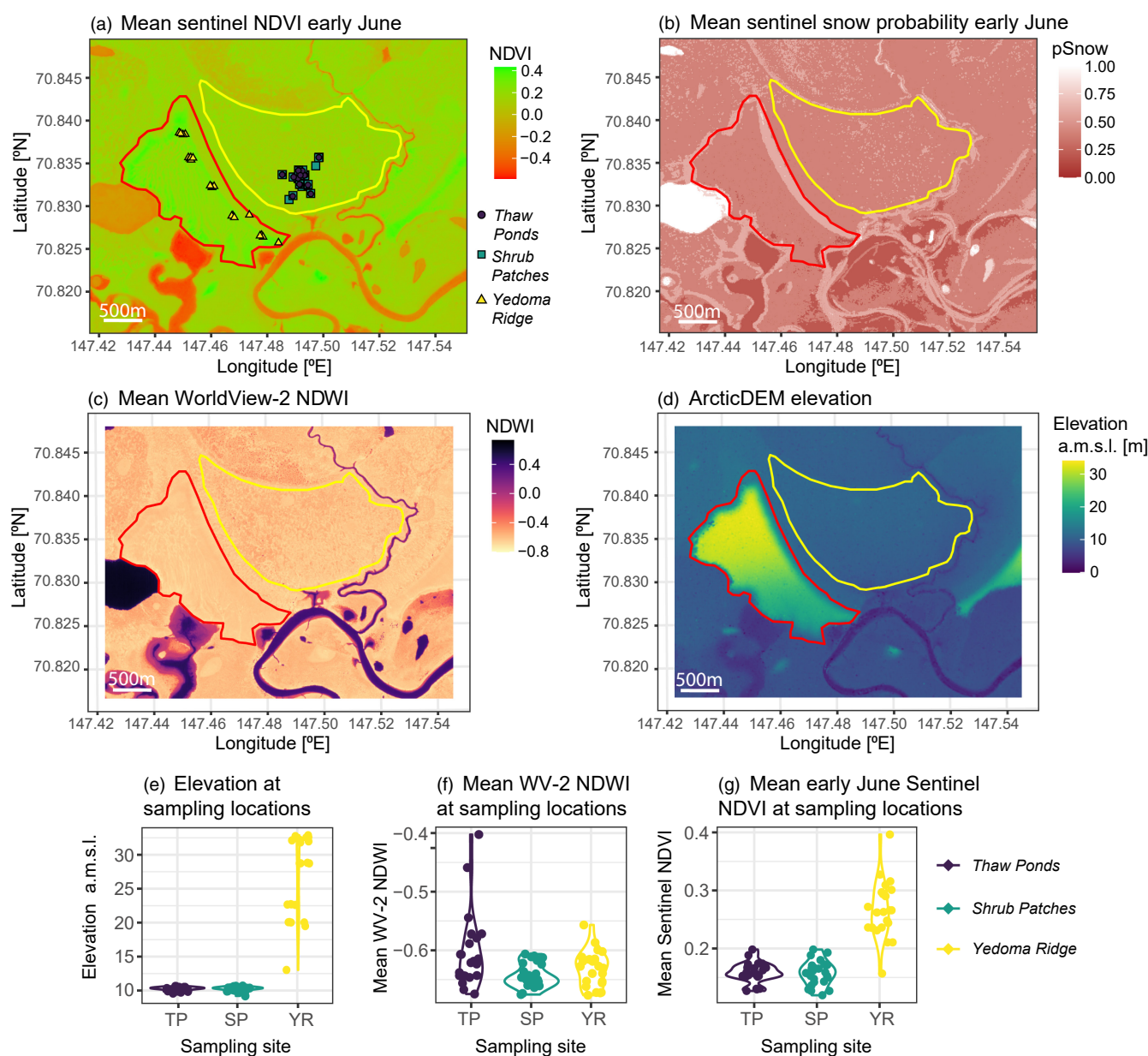


FIGURE 3 Spatial patterns of early June (3 June–12 June) snow and NDVI dynamics, wetness and topography. (a) Mean Sentinel-2 (2016–2020) early June NDVI. Points indicate sampling sites of shrubs selected for chronology development. Some overlap in points occurs due to proximity of sampling locations. (b) Mean Sentinel-2 (2016–2020) early June pixel Snow Probability (0–1). (c) Multiyear (2015, 2019) mean WorldView-2 NDWI. WorldView 2 © MAXAR, 2019. (d) ArcticDEM elevation above mean sea level. In (a, d), the red polygon indicates the Yedoma ridge. The yellow polygon indicates the drained thaw lake basin. (e) Elevation per sampling location of shrubs selected for chronology development. (f) WorldView-2 NDWI per sampling location of shrubs selected for chronology development. (g) Mean early June Sentinel-2 NDVI per sampling location of shrubs selected for chronology development.

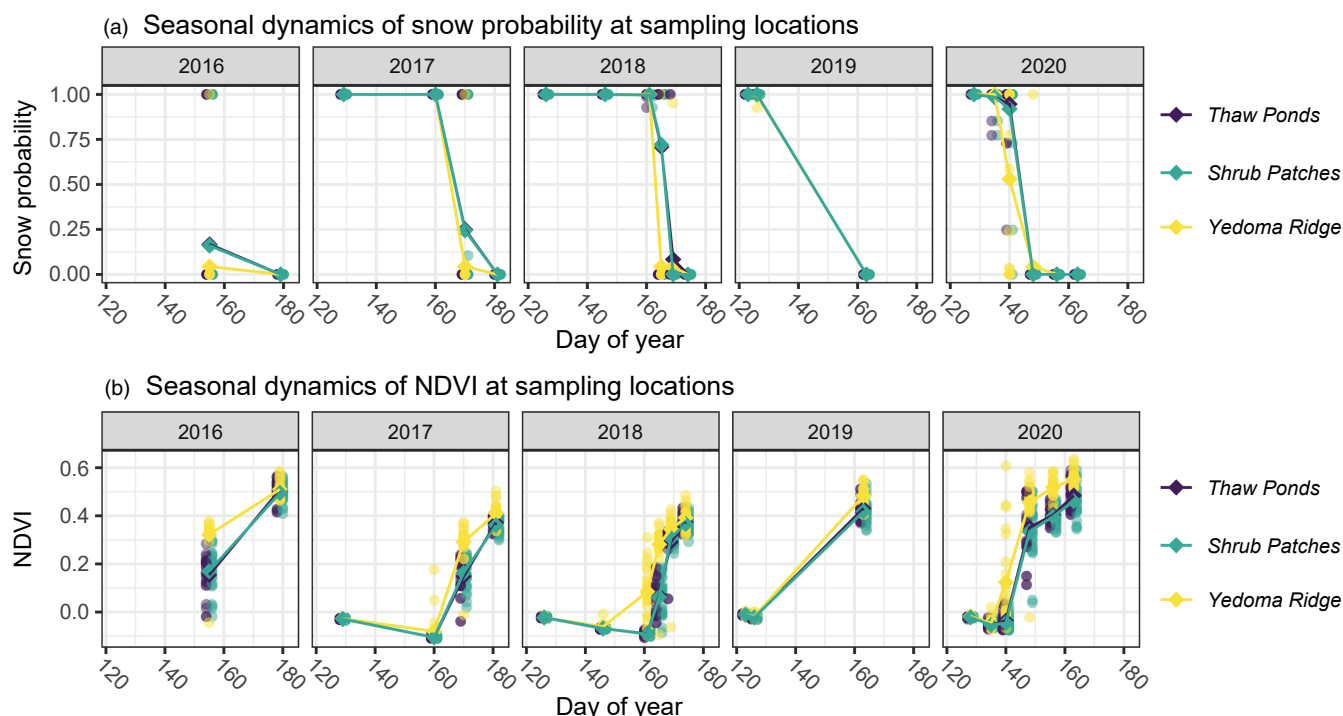


FIGURE 4 Snow and NDVI dynamics for sampling sites. (a) Timeseries of Sentinel-2 TOAR/SR pixel Snow probability at sampling locations of selected shrubs for early summer (1 May–1 July) 2016–2020. (b) Timeseries of Sentinel-2 TOAR/SR NDVI at sampling locations of selected shrubs for early summer (1 May–1 July) 2016–2020. Data are shown only for cloud-free images. Transparent dots indicate individual pixels, opaque dots and lines indicate subsite average. Day of year 120 corresponds to 1 May and day of year 180 corresponds to 30 June (in nonleap years).

Chronology	Mean correlation	Number of individuals	Rbar	Expressed population signal	Signal to noise ratio	AR1
Overall	0.432	57 ^a	0.243	0.896	8.654	0.401
Yedoma Ridge	0.465	16	0.288	0.740	2.844	0.441
Thaw Ponds	0.454	19	0.305	0.792	3.805	0.365
Shrub Patches	0.456	21	0.254	0.782	3.585	0.351

Note: Mean correlation indicates the mean interseries correlation based on correlations of each shrub with a chronology based on all other shrub series (based on a leave-one-out principle); Rbar indicates the mean correlation between shrubs series; Expressed population signal indicates the explanatory power of a finite sample compared to the theoretical population chronology (Wigley et al., 1984); Signal-to-noise ratio indicates the relative strength of the common variance signal present in the chronology relative to the total variance of series in the dataset (Cropper, 1982); AR1: mean first-order autoregression coefficient for shrub ring width series. Final RWI is corrected using a first-order autoregressive model.

^aThe Overall chronology included 15 ridge shrubs, 21 shrub patch shrubs and 20 ponds shrubs. Cross-dating was carried out separately for each established chronology (see Paragraph 2.2.2 and Text S1) to account for potential subsite-specific responses. Hence, the total number of individuals in the Overall chronology deviated from the sum of individuals in the subsite chronologies.

TABLE 3 Dendrochronological statistics of Overall and subsite chronologies.

3.3 | Overall site chronology and subsite chronologies

Four chronologies were developed; an Overall site chronology including shrubs from the three subsites in roughly equal proportions, a Yedoma Ridge chronology for shrubs sampled on the Yedoma ridge,

a Thaw Ponds chronology for shrubs sampled in thaw ponds and a Shrub Patch chronology for shrubs sampled in shrub patches in the drained thaw lake basin (Table 3). The chronologies generally showed similar RWI dynamics (Figure 5). Yedoma Ridge shrubs showed higher radial stem growth in particular years (1980–1981, 1999, 2001–2002) and particularly high growth in the relatively wet summers of

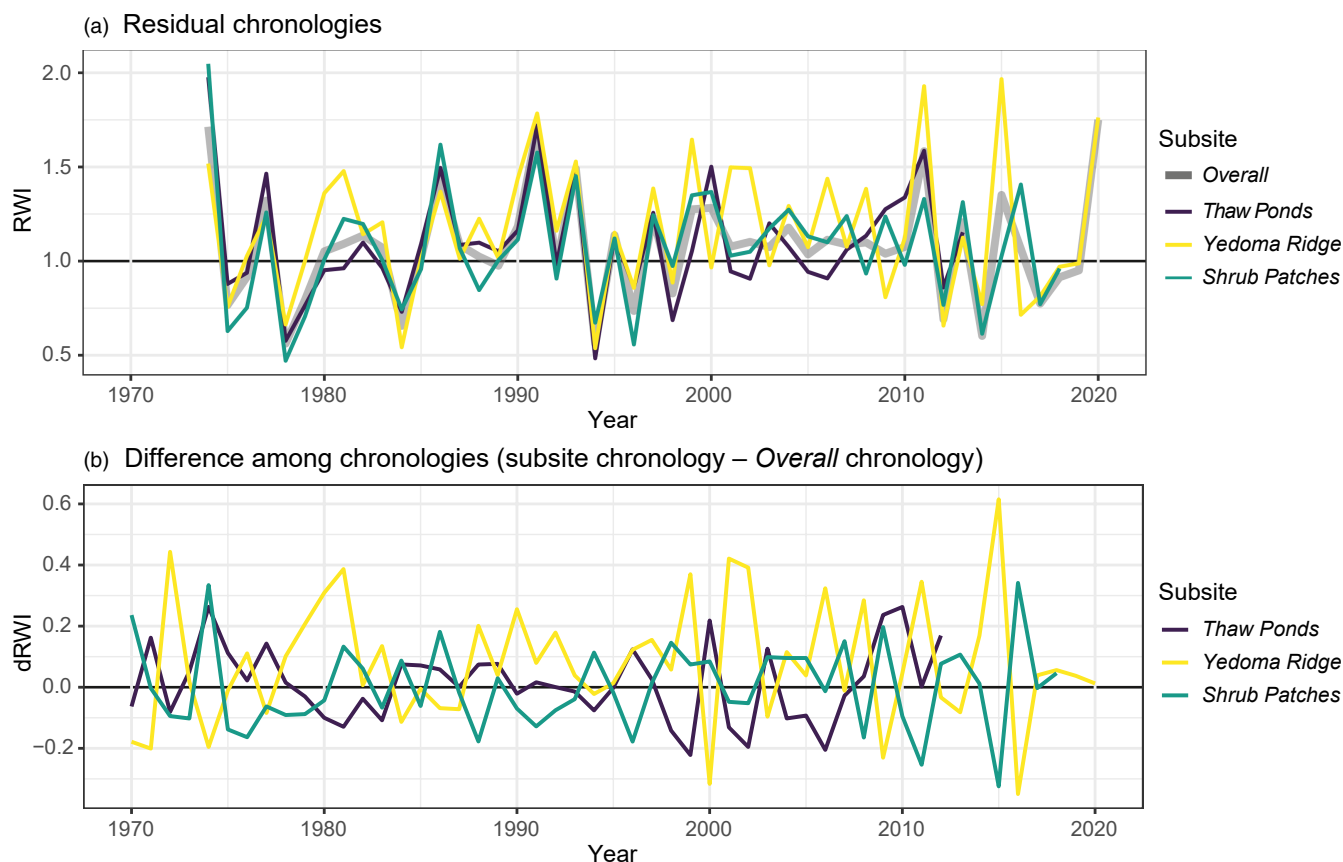


FIGURE 5 Ring width chronologies. (a) Overall residual chronology and subsite residual chronologies after C-method detrending and correction for first-order temporal autocorrelation, based on a sample depth of at least six individuals. The chronology for *Thaw Ponds* shows a shorter record due to the fact that many shrubs in thaw ponds were dead and showed no more rings in recent years. (b) Difference among subsite chronologies, visualised as the difference between each individual subsite chronology and the Overall chronology.

2011 and 2015 (Figures 2 and 5a). Chronologies showed relatively unsynchronised and undifferentiated growth between 2000 and 2010 (Figure 5a). All chronologies showed significant first-order autocorrelation (Table 3, Figure S10). Partial autocorrelation analysis indicates that shrubs growing on the ridge showed weak but significant second-order autocorrelation as well (Figure S10), indicating that growth was positively associated with growth up to 2 years earlier.

Analysis of individual shrubs' annual basal-area increment and shoot length measurements revealed no substantial differences in growth patterns among the three subsites (Figures S4 and S5). Shrubs from the three subsites tended to fall in the same range of diameter–age, length–diameter and length–age ratios and showed similar ranges of average basal-area increment. *Yedoma Ridge* shrubs tended to show relatively low initial basal-area increments in the first 10 years of growth, compared to shrubs from shrub patches and thaw ponds in the lakebed (Figure S5).

3.4 | Spatiotemporal variability in climate–growth associations

OPLS regression analysis shows a relatively consistent association with temperature among subsites, but several site-specific contrasts

in association with precipitation. Due to high correlation between summer temperature (T_{summer}) and the two degree day variables (GDD and SFTDD; Pearson's $r > 0.96$, Figure S6), only summer temperature was considered in OPLS regression. OPLS models for chronologies generally showed good fits and significant predictive performance based on permutation tests ($pQ^2 < 0.05$; Table S1). Overall, shrub radial stem growth shows positive association with summer temperature, summer precipitation and their interactive term, and a negative association with date of snowmelt and winter snow height (Figure 6a). Associations with rainfall (i.e. summer rainfall, previous summer's rainfall and the interaction of summer rainfall and temperature) appear strongly driven by *Thaw Ponds* shrubs. The *Yedoma Ridge* chronology shows particularly negative association with snow height in spring (Figure 6b). Exploratory Pearson correlation analysis (Figure S6) showed similar differences in patterns of climate–growth association across subsites.

Using a moving window approach (Figure 7), we evaluated whether climate–growth associations differed over time in the sampling subsites. We found a generally consistent response to summer temperature over 1974–2018, with somewhat lower temperature sensitivity for shrubs from *Thaw Ponds* and the *Yedoma Ridge* in 1979–2008. In contrast to *Thaw Pond* shrubs, *Shrub Patch*

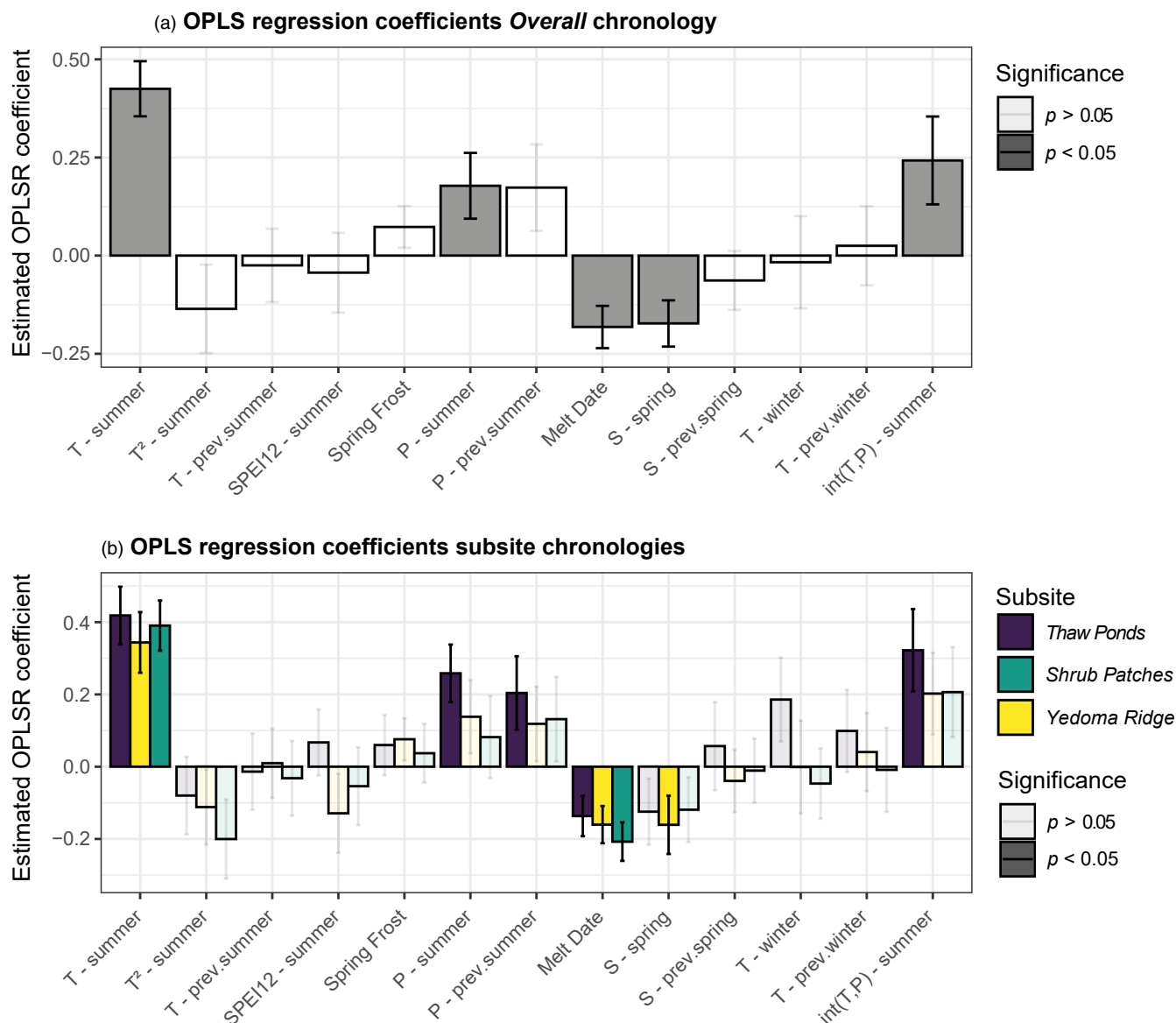


FIGURE 6 Estimated OPLSR coefficients for climate variables for (a) Overall and (b) subsite chronologies. Abbreviations and definitions of the selected climate variables are summarised in Table 2: T=temperature, P=precipitation, S=snow height. sum=summer (June–July), win=winter (November–April), spr=spring (April–May), prev=previous year. int(T,P)–sum indicates an interactive term between summer temperature and precipitation. T–sum² indicates a quadratic term for summer temperature. Solid bars represent significant estimated coefficients, transparent bars represent insignificant estimated coefficients. Height of the bars indicates estimates and 95% confidence intervals for OPLS regression coefficients based on bootstrapping ($n = 200$).

shrubs and Yedoma Ridge shrubs show no positive association with summer rainfall in the period from 1974 to 2008, but a tendency for increasingly positive association afterwards. This coincides with a prolonged period of low summer precipitation between 2000–2010 and 2018–2019 (Figure 2c). Response to interactive effects of summer rainfall and temperature appear variable across time periods (Figure 7), with higher degrees of association generally coinciding with individual summers with high temperature and rainfall (Figure 2, Figure S8). All subsites show a decrease in association with the date of snowmelt, against a trend of advancing snowmelt date after 1980 (Figure 2h). The three subsites show some association with precipitation of the previous summer season, particularly

in earlier decades. Associations between shrub growth and spring snow height seem to be influenced strongly by extreme snowfall in 2016–2018 (Figure 2d, Figure S8).

3.5 | Response of individual shrubs to climate variables

OPLS regression of individual shrubs' RWI series against climate variables that were identified as significant for shrub growth (shown in Figure 7) generally yielded poor OPLS model fits ($pQ^2 > 0.05$). In addition, the available common time period (26 years) and sample

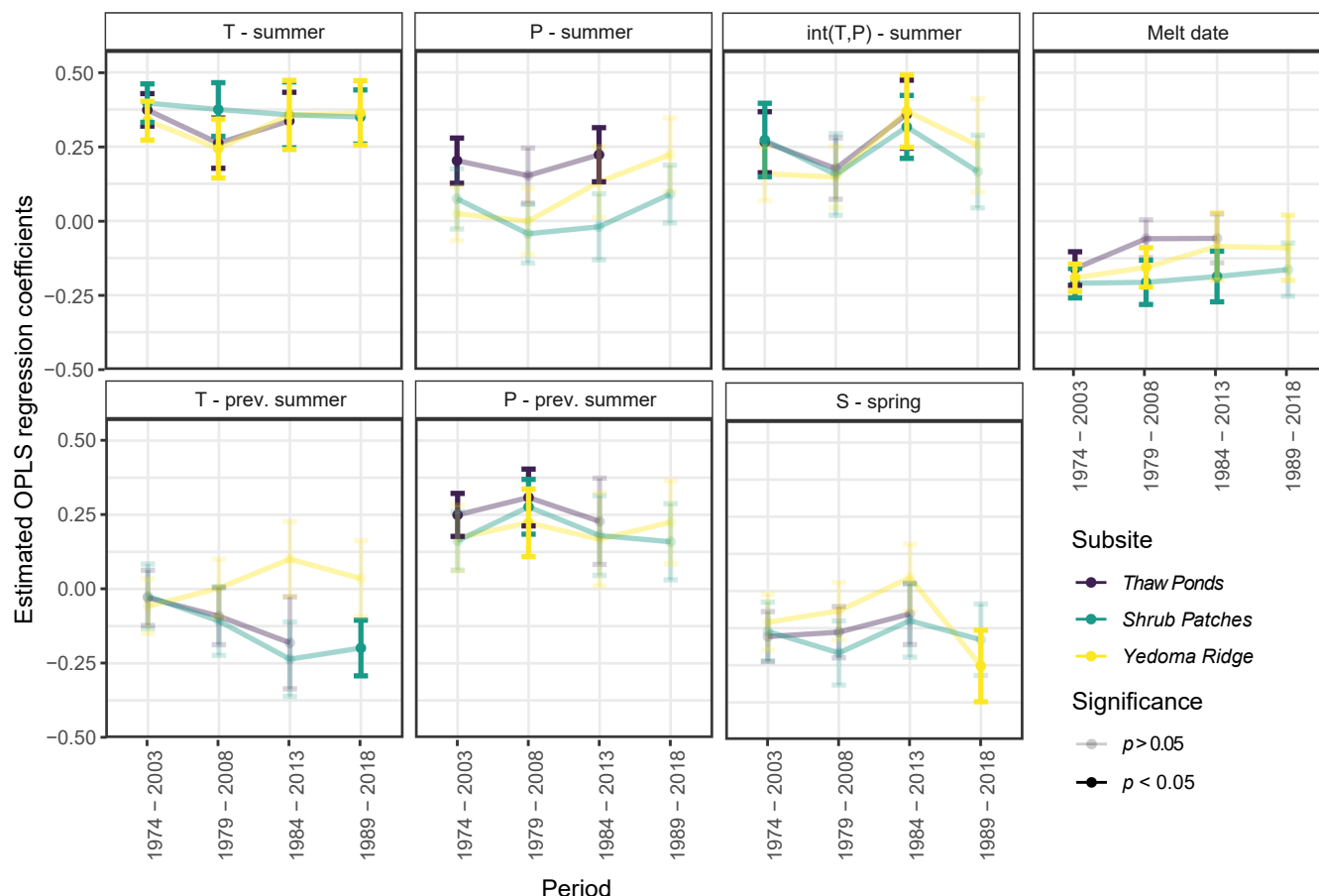


FIGURE 7 Stability of estimated OPLS regression coefficients over time for each climate variable. Only those variables that showed significant associations with any of the subsite chronologies during any of the time periods were included. Variables included in Figure 6 that are not shown here (SPEI12, spring frost, previous spring snow height, winter temperature) showed no significant correlation with any of the chronologies in any of the 30-year periods. Note that the period 1989–2018 is omitted for the *Thaw Ponds* chronology, as too few observations were available to extend the chronology after 2013.

size (11 *Yedoma Ridge* shrubs, 13 *Thaw Pond* shrubs and 15 *Shrub Patch* shrubs) for individual shrub OPLS was limited. We found little association between OPLS estimated regression coefficients for climate variables at the individual shrub level, individual shrub growth characteristics (average BAI per year, average BAI during the first 10 years of growth, shrub age) and remote sensing-based terrain characteristics of the shrub's location (mean WorldView-2 NDWI, ArcticDEM elevation; Figure S7). We identified several significant correlations between climate response coefficients and shrub age: Within the common time period, older shrub individuals showed a more negative response to warm winters with higher snow accumulation, while younger shrubs tended to show a moderately positive response (Figure S7). Older shrubs also showed a tendency ($p < 0.1$) for less positive response to summer precipitation.

3.6 | Pointer year analysis

Analysis of pointer years showed that patterns of RWI extremes differ among subsites, consistent with the outcomes of moving window

OPLS regression. We identified 1974, 1975, 1978, 1994 and 2011 as pointer years (Table S3). Negative pointer years in the *Thaw Ponds* and *Shrub Patches* chronology were mostly associated with cold conditions, while the positive pointer years generally occurred in summers with both high temperature and rainfall. Only the *Thaw Ponds* chronology showed a positive pointer year in 2010, which showed high summer temperature but lower than average summer precipitation. The *Yedoma Ridge* chronology showed only one positive pointer year in 2011, which showed warm summer and winter conditions and high rainfall.

Similarly, analysis of shrub radial stem growth in years with extreme weather conditions (identified here as the 3 years with highest or lowest values for a particular climate variable; Table S4), shows relatively high RWI in summers that are both warm and rainy. High RWI in summers with high temperatures or high summer precipitation alone are less common. Of the three warmest years observed from 1974 to 2018 (1991, 2005, 2010), only the year that also showed high summer rainfall (1991) showed higher than average RWI. Negative responses to dry summers were less evident (Table S4). *Yedoma Ridge* shrubs show relatively low RWI in years with high snow depth but relatively average RWI in years with cold

winter temperatures compared to other shrubs. Due to shrub mortality upon waterlogging in recent years (Figure S9), insufficient samples from Pond shrubs were available to assess the effects of recent extreme snow accumulation on growth of Thaw Pond shrubs.

4 | DISCUSSION

Our study identifies considerable variability in precipitation-growth associations of *Betula nana* across topographical gradients and time periods, implying that such associations scale poorly across a heterogeneous tundra landscape and in a rapidly changing climate. Specifically, increased year-to-year variability of rainfall and recent snow height extremes were accompanied by differential development of precipitation-growth associations across subsites representing a topographical gradient (higher elevation, lower elevation and thermokarst-affected terrain; Figure 7). Such responses would not be predicted based on seemingly linear or lacking associations inferred under the absence of such extremes (Figures S6 and S8).

4.1 | Climate-growth associations of *Betula nana* in the Siberian lowland tundra

Our findings largely match those of earlier dendrochronological studies conducted in the study site (Blok et al., 2011; Li et al., 2016). Previous work over the period of 1948–2006 has found *Betula nana* to be sensitive to summer temperatures in an approximately 1-month period between mid-June and mid-July and found a positive association between shrub radial stem growth and precipitation during the previous summer season (Blok et al., 2011). We identified similar positive associations with summer precipitation in the previous year prior to 2008. In addition, positive associations with same-year rainfall were found over the period 1962–2011, but only in relatively warm years (Li et al., 2016), similar to the interactive effect identified in this study. However, contrary to earlier studies (Buchwal et al., 2020; Gamm et al., 2018; Myers-Smith, Elmendorf, et al., 2015), we did not find poor shrub growth in any of our subsites during very dry summers, nor significant associations with SPEI. This suggests that while high precipitation enables better than average growth, low moisture availability does not necessarily lead to compromised growth in this ecosystem. *Betula nana* has been found to be relatively tolerant to low-precipitation climates and drought (De Groot et al., 1997; Fujinami et al., 2016; Scharn et al., 2021), suggesting that recent drought in the study region may have been more detrimental for shrub genera associated with wetter conditions such as *Salix* (Blok et al., 2011; Scharn et al., 2021). The period between 2000 and 2010 with low rainfall (Figure 2b) does, however, show relatively undifferentiated growth dynamics in *Betula nana*. Afterwards, high summer rainfall in 2011 shows a distinct and sudden peak in RWI across subsites (Figure 5). This further suggests a general pattern of reduced temperature response under decreases in moisture availability.

In terms of winter conditions, we found that *Betula nana* radial stem growth was negatively associated with snowmelt date and spring snow height, indicating better growth under earlier snow-free conditions (Figure 6a). No effects of winter conditions were evident from earlier dendrochronological studies in this ecosystem (Blok et al., 2011; Li et al., 2016). Here, we find a positive association between *Betula nana* growth and timing of snowmelt, and no indication of negative response to spring frost events under early snowmelt. This is consistent with studies in other ecosystems (Dobbert et al., 2021b; Hallinger et al., 2010; Hollesen et al., 2015; Krab et al., 2018) and with *Betula nana*'s relative frost-tolerance compared to more frost-sensitive (generally evergreen) shrub genera (Dobbert et al., 2021b; Krab et al., 2018). Additionally, climatic conditions in spring determine to what extent frost damage can occur (Krab et al., 2018). Our highly continental study site shows sharp transitions from extremely cold (average January temperature 1945–2019: -34.1°C) to fairly warm (average July temperature 1945–2019: 10.6°C) summer conditions. Winter thaw episodes or rain on snow events were not evident from the climate record. Occasional spring frost after snowmelt was moderate and not significantly related to shrub growth (Figure 6, Figure S6). These findings suggest that positive effects of earlier snowmelt predominate for *Betula nana* in this continental setting, but it is unclear whether this finding translates to other shrub species in the study area (e.g. *Salix pulchra*).

4.2 | Spatiotemporal contrasts in association of radial growth and summer climate

Shrubs on the elevated (± 10 – 25 m higher) Yedoma ridge showed only marginally lower temperature sensitivity compared to the two lakebed sites (Figure 6b). *Salix* and *Alnus* shrubs growing on elevated sites have previously been found to show lower temperature response or productivity due to drier conditions (Ackerman et al., 2017; Black et al., 2021). However, drier conditions on the Yedoma ridge are not evident from available field measurements (Table 1) and WorldView-2 based NDWI values (Figure 4e). Additionally, Yedoma ridge shrubs show no significant positive response to summer precipitation or interactive effect between summer precipitation and summer temperature over the study period as a whole (Figure 6b). Only after a series of summers with low precipitation (2000–2010) (Figure 2c), Yedoma ridge shrubs showed very pronounced radial stem growth in the wet summers of 2011 and 2015 (Figures 2c,i and 5a) and relatively pronounced increases in the degree of association with summer precipitation compared to the other subsites (Figure 7). This likely reflects *Betula nana*'s relative drought-tolerance compared to other deciduous shrubs (e.g. *Alnus* and *Salix*; Ackerman et al., 2017; Black et al., 2021; Scharn et al., 2021), but further suggests that radial growth of *Betula nana* may become locally moisture limited under prolonged drought.

Thaw Pond shrubs showed the strongest positive association with summer precipitation and a significant, positive

interactive effect of summer temperature and summer precipitation (Figure 6b). This seems counterintuitive, given earlier observations of shrub mortality in thaw ponds due to waterlogging (Magnússon et al., 2020; Nauta et al., 2015). Thaw Pond shrubs were sampled from small, isolated thaw ponds surrounded by shrub-dominated vegetation in which they likely formed (Magnússon et al., 2020). Such small depressions in the landscape show active layer deepening and may become focal points for lateral flow of water and accumulation of snow, triggering a positive feedback of enhanced permafrost thaw and further soil subsidence (Nauta et al., 2015). The positive association of radial growth with summer precipitation could indicate an initially positive response to accumulation of soil moisture in small depressions in otherwise dry soils (Table 1), or could reflect shallow rooting patterns in response to generally higher water tables. Many thaw pond shrubs died during the extremely rainy summer of 2011 (Figure S9), possibly due to *Betula nana*'s intolerance to permanently saturated soils (De Groot et al., 1997). This pattern of enhanced response to summer precipitation, followed by pond formation and shrub mortality, suggests a highly localised and nonlinear response of *Betula nana* to moisture in poorly drained ice-rich permafrost landscapes.

4.3 | Spatiotemporal contrasts in association of radial growth and winter climate

Associations of shrub growth with winter climate variables are mostly reflected in a negative association of growth with date of snowmelt (Figure 6). This association becomes insignificant in later decades (Figure 7), against a trend of earlier snow-free conditions in recent decades (Figure 2h). This could indicate that growth limitations related to onset of snow-free conditions become increasingly lifted. In recent years (2016–2018) with high snow accumulation (Figure 2c) and late snowmelt (Figure 2h), *Betula nana* radial growth showed a distinct decline at Yedoma ridge site (Figures 6b and 7, Table S3). Yedoma ridge shrubs also seemed relatively insensitive to winters with low snow cover and cold temperatures (Table S3). Sentinel-2 images (2016–2020) suggest overall earlier snowmelt and onset of vegetation growth at the Yedoma ridge sites (Figure 5). A possible explanation could be that shrubs growing at exposed ridges are adjusted to earlier snow-free conditions and may start growing at lower temperatures. This would match the observed earlier onset of greening on the ridge (Figure 4). Additionally, field observations suggest that *Betula nana* individuals on exposed ridge sites show relatively low stature and more decumbent growth (Blok et al., 2010), potentially making them less sensitive to low snow cover and exposure to cold winter temperatures, but more dependent on complete snowmelt. An earlier study found higher tolerance of *Betula nana* in exposed microsites to cold winter temperatures (Dobbert et al., 2021b), further suggesting local adaptations in growth strategy across topographical gradients and resulting divergence in climate response. Recent studies indicate that such adaptive strategies may be highly species specific (Dobbert et al., 2021a, 2021b; Krab

et al., 2018). More detailed studies are needed to understand the mechanisms behind this spatially heterogeneous response to extreme snowfall.

4.4 | Potential remaining drivers of spatiotemporal heterogeneity in climate–growth associations

Several other mechanisms may have influenced variability in climate sensitivity among subsites. Due to lack of in situ measurements, the influence of potential contrasts in soil properties and nutrient dynamics (Table 1; Bartholomeus et al., 2012; Siewert et al., 2015) could not be accounted for. The presence of other tundra plant species such as other dwarf shrubs and tussock sedges may differ among subsites (Table 1), which could potentially affect the relative importance of competition for resources and climate in determining the growth of *Betula nana* across the landscape. Lastly, the subsite chronologies showed some variability in autoregressive dynamics (Table 3, Figure S10). This could indicate variable degrees of intrinsic (e.g. density dependence, resource allocation) or trophic controls on growth relative to climatic influence (Forchhammer, 2017). Spatial and temporal contrasts in herbivory for instance may modulate local climate–growth relationships in Arctic shrubs. However, a recent analysis of panarctic shrub ring width and ungulate density data indicated no significant interactive effect between herbivore density and climate variables on shrub radial growth at temperature ranges such as those observed at our site (Vuorinen et al., 2022).

Changes in climate sensitivity over time in tree ring records (nonstationarity) (D'Arrigo et al., 2008; Francon et al., 2020; Hollesen et al., 2015; Wilmking et al., 2005) can also result from changes in the age distribution of sampled shrub datasets over the dataset period (Gamm et al., 2018; Voelker, 2011). By comparing individual shrubs' association with weather variables and their mean age over a common time period (Figure S7), we found that older shrub individuals tend to show a more negative association with snow depth in winter, but less positive association with summer precipitation compared to younger individuals. This suggests that increasing shrub age over the timespan of our chronologies may have contributed to the distinctly negative association of Yedoma ridge shrubs with recent extreme snow heights. However, the association of shrub growth with snowmelt date generally decreased (Figure 7), which makes it unlikely that this is an artefact of increasing shrub age. Similarly, association of growth with summer precipitation (Figure 7) and rainfall extremes (Tables S3 and S4) seems to increase rather than decrease. We therefore do not expect changes in shrub age distribution to have had a substantial confounding effect on the observed nonstationarity of climate–growth associations.

Additionally, wood anatomy may affect climate–growth associations. Earlier studies suggest adaptations in xylem anatomy and vessel size in *Betula nana* upon exposure to cold extremes (Dobbert et al., 2021a, 2021b) and under climatic variability (Nielsen et al., 2017),

attributed to trade-offs between water transport capability and sensitivity to frost and drought events (cavitation; Fonti et al., 2010; Hacke et al., 2001). Hence, local adaptation in wood anatomical traits, or variable occurrence of cambial inactivity under climatic extremes (Wilmking et al., 2012) may further regulate spatiotemporal variability in climate–growth associations of *Betula nana*. Analysis of vessel properties may provide further insight into such mechanisms.

Lastly, apart from annual growth, recruitment and mortality dynamics likely shape the temporal dynamics of shrub abundance and biomass. In our study site, recruitment of *Betula nana* is positively associated with summer precipitation (Li et al., 2016). This may imply that with recent conditions of generally dry and few very wet summers (Figure 2c), shrub recruitment may show stronger pulse dynamics. It is currently unclear how combined dynamics of recruitment, mortality and annual growth of *Betula nana* shrubs affect future carbon balances, vegetation communities and surface energy balance in this ecosystem.

4.5 | Implications for growth of *Betula nana* in the future Arctic

Our results show a temporally consistent positive association of radial growth of keystone Arctic shrub species *Betula nana* and summer temperature. However, associations between growth and precipitation showed substantial spatiotemporal variability. Hence, future increases in precipitation variability in the Siberian lowland tundra may impact growth of *Betula nana* differently across landscape gradients. In combination with the highly dynamic, ice-rich permafrost landscape (Magnússon et al., 2021), this complicates efforts to extrapolate climate–growth associations over larger areas and over future climate scenarios. We make several inferences about future growth of *Betula nana* in this ecosystem and implications for the use of climate–growth associations under climatic change:

1. Recent decades have shown peaks in radial growth of *Betula nana* during summers that were both warm and wet, rather than only warm. Hence, increasing year-to-year variability in rainfall might result in pulse dynamics in growth of *Betula nana*, based on (a)synchronicity in summer temperature and rainfall peaks. The role of such dynamics may vary over small-scale landscape gradients. Upland sites in particular may show strong growth pulses in warm and rainy summers following dry periods.
2. *Betula nana* shrubs sampled from thaw ponds initially showed a positive association with rainfall, but eventually died as a result of waterlogging. This suggests that changes in microtopography due to thermokarst may induce highly local nonlinear precipitation–growth responses. This introduces additional spatiotemporal variability in climate–growth associations in dynamic ice-rich permafrost environments.
3. We found that responses to precipitation extremes varied across landscape positions and were not evident from climate–growth associations inferred under the absence of such extreme conditions. This suggests that the potential for upscaling of present-day

climate–growth responses of *Betula nana*, and possibly other Arctic shrubs, may be limited in a more extreme future Arctic.

4.6 | Recommendations for future studies of Arctic shrub climate–growth associations

Currently, our understanding of the exact mechanisms that underlie the observed spatial and temporal variability in climate–growth associations of *Betula nana* in the Siberian Lowland tundra is limited. This complicates estimates of potential future growth trajectories. Similar spatiotemporal heterogeneity in climate response is being observed in other regions for other Arctic shrub genera, with species-specific dynamics suggesting regulating roles of growth strategy and plasticity thereof. Hence, under increasing variability and extremes in Arctic precipitation (AMAP, 2021; Bintanja et al., 2020; IPCC, 2021; Wang et al., 2021), the type of nonlinear and localised effects identified in this study may become increasingly evident. This begs caution in the extrapolation of associations between Arctic shrub growth and precipitation beyond current and past climatic ranges. Informed experimental manipulation of rainfall, snow or soil moisture across landscape gradients would be necessary to make informed projections. Particular attention should be dedicated to combined effects of multiple or consecutive weather extremes (Tables S3 and S4) and the role of moderate changes versus extreme events.

A priori knowledge of Arctic ecosystems and their dynamics in recent decades, for instance based on field measurements and satellite data, proved important for the selection of relevant spatial subunits for climate–growth studies (Table 1) and helped interpret results. However, field measurements suggest that microsite heterogeneity may play a role on smaller spatial scales (several metres to less than a metre, Figure 1c) than is evident even from relatively high-resolution data such as the ArcticDEM or WorldView (2 m resolution) and Sentinel-2 image material (10 m resolution; Table 1, Figure 3). Site conditions may also change over the studied time period due to for instance thermokarst processes. Microsite monitoring (e.g. of soil moisture and freeze–thaw cycles) at shrub sampling locations may provide better insight into links between growth and particular abiotic site conditions over time. In addition, detailed, plant-level physiological data of for instance sap flow (Black et al., 2021), high temporal resolution dendrometer data (Dobbert et al., 2021b), carbon isotope ratios (Gamm et al., 2018), vessel properties (Nielsen et al., 2017) or epidermal cell properties (Ercan et al., 2021) may help to link microsite variability to shrub radial stem growth dynamics and aid correct interpretation of typically complex and nonstationary results. Such additional data could potentially be embedded into an experimental context and linked to radial stem growth dynamics to provide new insights into future Arctic shrub growth.

AUTHOR CONTRIBUTIONS

Rúna I. Magnússon was involved in conceptualisation, methodology, investigation, formal analysis, visualisation and writing original draft. Ute Sass-Klaassen was involved in methodology, resources,

supervision and review and editing. Juul Limpens was involved in investigation, supervision and review and editing. Sergey V. Karsanaev was involved in investigation and resources. Susan Ras was involved in formal analysis and review and editing. Ko van Huissteden and Daan Blok were involved in resources and review and editing. Monique M. P. D. Heijmans was involved in funding acquisition, project administration and review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14165>.

DATA AVAILABILITY STATEMENT

Data and R code used for this study are available from the DANS EASY repository (<https://doi.org/10.17026/dans-xdm-p33t>; Magnússon, 2023). Sentinel images were obtained from Google Earth Engine (Gorelick et al., 2017). Weather data for the Chokurdakh weather station (WMO station code: 21946) are available from the All-Russia Research Institute of Hydrometeorological Information—World Data Centre (RIHMI-WDC, 2020). Soil moisture scatterometer data are available from EUMETSAT (HSAF, 2020, datasets H141, H142). The ArcticDEM digital elevation model is available from Porter et al. (2018). High-resolution WorldView-2 and GeoEye-1 satellite images used for this study were obtained from DigitalGlobe (2020) under a copyright licence for internal use.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Text S1. Ring width measurement.

Text S2. Sentinel data processing.

Figure S1. Comparison of chronologies of this study (Overall chronology and subsites) with earlier chronologies developed for *Betula nana* in this study site (Blok et al., 2011; Li et al., 2016) and a *Salix pulchra* chronology (Blok et al., 2011).

Figure S2. Visual summary of dendrochronological data analysis.

Figure S3. Results of moving window analysis of climate sensitive periods for growth of *Betula nana*.

Figure S4. Diameter–age plots for individual shrub's rings across the three types of subsites.

Figure S5. Growth properties of individual shrubs, coloured by subsite type.

Figure S6. Correlation matrices of Overall and Subsite RWI chronologies and standardised, preselected climate variables.

Figure S7. Correlation of individual shrub's estimated OPLS regression coefficients for climate factors, shrub characteristics and abiotic site conditions.

Figure S8. Moving window scatter plots for the three subsite chronologies and main climate factors.

Figure S9. Stacked bar graph of recruitment and mortality dynamics of selected shrubs.

Figure S10. Autoregressive dynamics of Overall and subsite chronologies.

Figure S11. Monthly Climate Variables from 1948 to 2020, derived from the Chokurdakh Meteorological Station (WMO code 29146).

Table S1. OPLS model fits.

Table S3. Climate extremes analysis.

Table S4. Climate extremes analysis.

Table S5. Temperature trends for the Chokurdakh Meteorological Station over the study period.

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