Received: 1 March 2022 | Accepted: 9 March 2022

DOI: 10.1002/ecs2.4106

ARTICLE

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Retrogressive thaw slumps in the Alaskan Low Arctic may influence tundra shrub growth more strongly than climate

Diane C. Huebner[1] | **Agata Buchwal**[2] | **M. Syndonia Bret-Harte**[3]

[1]Institute of Arctic Biology/Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, Alaska, USA

[2]Institute of Geoecology and Geoinformation, Adam Mickiewicz University, Poznań, Poland

[3]Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska, USA

Correspondence
Diane C. Huebner
Email: dchuebner@alaska.edu

Present address
Diane C. Huebner, NASA Ames Research Center, NASA Postdoctoral Program, Oak Ridge Associated Universities, Oak Ridge, Tennessee, USA

Funding information
University of Alaska Fairbanks; UAF Institute of Arctic Biology Graduate Research Fellowship; Arctic Institute of North America; Polish-U.S. Fulbright Commission; National Science Foundation, Grant/Award Numbers: PLR 1623461, DEB 1637459, DEB 1556481

Handling Editor: Debra P. C. Peters

Abstract

Thermokarst disturbance in permafrost landscapes is likely to increase across the tundra biome with climate warming, resulting in changes to topography, vegetation, and biogeochemical cycling. Tundra shrubs grow on permafrost, but shrub–thermokarst relationships are rarely studied in detail. Since the 1980s, Alaska's North Slope has experienced increased thermokarst activity, including retrogressive thaw slumps (RTSs) on hillslopes. Within decades, RTSs near Toolik Lake, Alaska, were colonized by tall (≥0.5 m) deciduous shrubs. We used dendrochronology methods on 66 shrubs (182 stem cross sections) representing dominant deciduous species: willows (*Salix pulchra* and *S. glauca*) and dwarf birch (*Betula nana*) at two RTS chronosequences on Alaska's North Slope comprising seven sites, to quantify thermokarst and climate effects (25 years of temperature and precipitation records) on shrub secondary growth (i.e., annual rings) in RTS-disturbed and undisturbed moist acidic tussock (MAT) tundra. Across species, average growth ring widths were two times wider for shrubs in RTSs than in MAT, and ring widths decreased with RTS age. A 1°C June temperature increase was associated with 2% wider rings across species and sites, but shrubs showed marginal growth in warmer summers, supporting tundra-wide shrub climate sensitivity studies. A 4.5% average ring width increase per 1 mm of previous year's September precipitation was seen in shrubs in mid-successional RTSs, suggesting protective effects of early snowfall in RTSs versus open tundra. Retrogressive thaw slump age category explained 47% and 30% of average ring width variance of willows and dwarf birch, respectively, in linear mixed-effects models. Climate variables explained 2% average ring width variance across species. Our results suggest that RTS exerts strong successional effects on tundra shrub growth. Climate effects appear to show weaker synoptic patterns across the study area. Retrogressive thaw slumps will likely contribute to tundra greening where RTS activity is increasing.

KEYWORDS
climate sensitivity, microsite, retrogressive thaw slump, secondary growth, shrubs, tundra

INTRODUCTION

Approximately 20% of northern permafrost landscapes are vulnerable to thermokarst, that is, land subsidence caused by thaw of ice-rich permafrost soils, which are estimated to contain half of the region's soil organic carbon (Olefeldt et al., 2016). Retrogressive thaw slumps (RTSs) are a form of thermokarst characterized by active layer detachment resulting in large (≥1 ha) bare soil depressions on hillslopes (Lantz & Kokelj, 2008; Swanson, 2021) whose initiation is associated with warm summers and increased precipitation (Abbott et al., 2014; Balser et al., 2014; Gooseff et al., 2009; Kokelj & Jorgenson, 2013; Lacelle et al., 2010; Luo et al., 2019; Osterkamp et al., 2007; Swanson, 2021). On Alaska's North Slope, RTS formation increased twofold between the 1980s and 2006 (Balser et al., 2009; Bowden et al., 2008). Stabilized RTSs often provide sheltered nutrient-rich microsites that support fast-growing tundra species, including woody shrubs (Huebner & Bret-Harte, 2019; Lantz et al., 2009; Schuur et al., 2007). Within a few decades, RTSs in Western Canada and Alaska support dense colonies of tall (≥0.5 m) deciduous shrubs that are structurally and functionally different from surrounding dwarf tundra communities (Huebner & Bret-Harte, 2019; Lantz et al., 2009; Pizano et al., 2014).

Interannual variation in shrub growth in RTS has not been measured previously, although vegetation and soil changes in RTSs have been documented since the 1970s (Lambert, 1972). Deciduous shrubs are among the largest form of tundra plant life, and they exert strong controls on ecosystem processes where they are dominant. Deciduous shrubs might offset large nutrient losses from RTS (Abbott & Jones, 2015) because they can accumulate larger biomass than dwarf tundra species (Pizano et al., 2014). Increased vertical and lateral growth of shrubs can also drive changes to ecosystem feedback and food webs (Euskirchen et al., 2009; Myers-Smith & Hik, 2013; Tape et al., 2018). Retrogressive thaw slump activity is likely to increase in vulnerable areas with warming (Kokelj et al., 2015; Kokelj et al., 2021; Luo et al., 2019; Nitze et al., 2018) and may lead to tall shrub communities that can persist for many decades (Lantz et al., 2009). Quantifying shrub growth response to interannual climate variation in RTS versus undisturbed tundra is therefore important to understand the greening of the Arctic that is currently underway (Myers-Smith et al., 2020).

Secondary growth, that is, annual growth ring formation in woody plant stems, provides a natural record of interannual climate variation (d'Arrigo et al., 2001; Fritts, 1966, 1976; George St & Ault, 2014; Schweingruber et al., 1990; Schweingruber & Poschlod, 2005). It is used to track seedling recruitment and stand development (age) of woody species following disturbance (Oliver, 1980) and is a sensitive indicator of environmental alterations brought about by fire (Bergeron et al., 2002), geomorphic processes (Gärtner-Roer et al., 2013; Owczarek et al., 2013; Siekacz & Rachlewicz, 2014), and changes in seasonal conditions such as increased snow depth (Addis & Bret-Harte, 2019). Recent Pan-Arctic evidence suggests that shrubs are sensitive to soil moisture, and in areas experiencing moisture limitation, shrubs may show reduced radial growth under a warming climate (Ackerman et al., 2017; Myers-Smith et al., 2015). Shrub dendrochronology is thus a useful tool for understanding tundra response to climate and environmental change across a biome scale.

We compared shrub climate sensitivity, that is, the comparison of interannual variation in shrub growth rings with interannual climate variation across a time series (Myers-Smith et al., 2015) in RTS-disturbed tundra and undisturbed tundra on Alaska's North Slope. We investigated direct versus indirect climate effects on secondary growth of dominant deciduous tundra shrubs, willows (*Salix* spp.) and dwarf birch (*Betula nana*), at two RTS-disturbed lake shores on Alaska's North Slope. We define the RTS microsite as an indirect effect of climate warming, and changes in temperature and precipitation over time as direct effects. The goal of the study was to compare shrub ages with minimum time since RTS disturbance, and to compare growth ring widths in RTS-disturbed and undisturbed tundra across a climate record, to test whether variation in secondary growth is primarily caused by interannual climate variation or RTS microsites. Woody plant growth in northern environments is especially sensitive to changes in growing season temperature (Buchwal et al., 2019; Forbes et al., 2010), largely as a function of nutrient availability (Bret-Harte et al., 2002; Chapin III et al., 1995). Improved microsite conditions in RTS (available space, light, nutrients, and warmer soils) may therefore enhance shrub growth and may increase climate sensitivity in the secondary growth of tundra shrubs due to the positive interaction between climate and microsite (Figure 1a,b). We hypothesized that shrub ring widths will be positively associated with climate warming directly, regardless of disturbance, and indirectly, due to enhanced microsite conditions for shrub growth in RTS as compared to undisturbed tundra.

Based on this conceptual model, the following hypotheses were tested in this study:

> **H1:** Shrub ages reflect shrub stand development following RTS disturbance; therefore, shrub age derived from growth ring counts performed on shrub stems (ramets) will reflect a minimum time since RTS disturbance, with

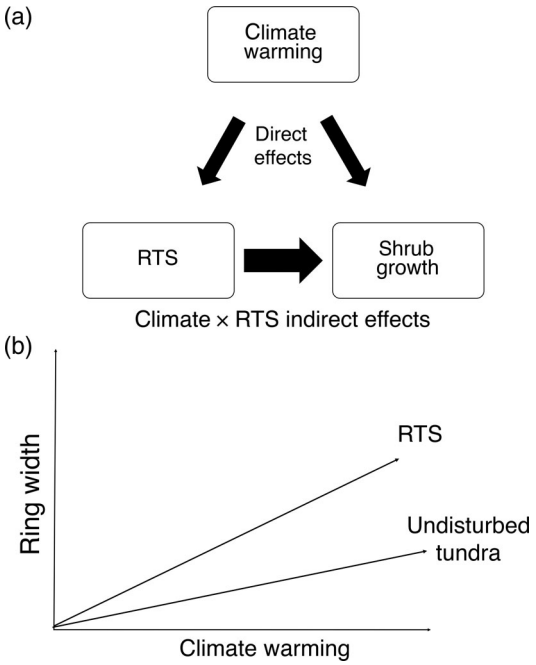

FIGURE 1 Conceptual diagram of hypothesized direct and indirect climate warming effects on secondary growth of deciduous shrubs on Alaska's North Slope. (a) Increasing retrogressive thaw slump (RTS) disturbances in the study area are associated with climate warming. Shrub growth may be positively associated with climate warming directly, and indirectly, due to enhanced microsite conditions (space, light, and nutrients) in RTS than in undisturbed tundra. Indirect effects may have a stronger positive effect on shrub growth than climate alone. If the latter is true, shrub ring widths in a warming climate will show (b) the same direction of slope, but the RTS slope will be higher due to the production of wider rings in shrubs growing within the RTSs than shrubs in undisturbed tundra.

the oldest shrubs found in the oldest RTSs and in moist acidic tussock (MAT) tundra undisturbed by RTS (control condition).

H2: Growth rings are wider in shrubs growing in RTS than in shrubs from undisturbed tundra, due to post-disturbance conditions being more optimal for plant growth. Growth will slow as sites age and conditions become less optimal, due to increased competition for space, light, and nutrients. Thus, the widest rings will be found in shrubs in recently disturbed tundra, that is, the youngest RTSs, and the narrowest rings will be found in the oldest RTSs and undisturbed MAT.

H3: Shrubs are sensitive to climate in RTS and undisturbed MAT, but climate sensitivity (expressed by the slope coefficient of linear regression) is enhanced in RTS due to the positive interaction between climate warming and RTS microsites on secondary growth. Climate sensitivity will be highest in shrubs in the youngest RTSs and will decrease with site age.

METHODS

Study site

The study area is located near Toolik Field Station (68°37′39″ N, 149°35′51″ W, elevation 720 m above sea level) in the Alaskan Low Arctic (Figure 2). The climate is characterized by a mean annual temperature of −8°C and mean annual precipitation of 320 mm, at least half of which falls as snow (1988–2016; Toolik Environmental Data Center Team, 2020). Soils form thin peaty organic layers above mineral substrate over Itkillik phase II glacial till deposits (approximately 11.5 ka BP; Hamilton, 2003) underlain by >200 m (average depth) of continuous permafrost that thaws to approximately 0.5-m active layer depth in summer (Romanovsky et al., 2002). Moist acidic tussock is the dominant tundra type, characterized by sedges (*Eriophorum vaginatum* and *Carex* spp.), a mix of dwarf deciduous and evergreen shrubs, herbaceous forbs, mosses, and lichens (Bliss & Matveyeva, 1992).

The two chronosequence sites we selected, Lake I-minus 1 and Lake NE14, have been characterized as analogous in vegetation, soil characteristics, and minimum estimated time since disturbance (Huebner et al., 2019; Huebner & Bret-Harte, 2019; Pizano et al., 2014). Aerial photographs of Lake I-minus 1 from 1949 showed a developed RTS headwall on the southern shore (U.S. Geological Survey, 2022), but shrub ring counts and radiocarbon dating of moss macrofossils at the organic–mineral soil interface suggest that these sites have formed discrete RTS lobes varying in age from one to several decades since disturbance (Huebner et al., 2019; Huebner & Bret-Harte, 2019; Pizano et al., 2014). Therefore, we used minimum age estimates. We classified the RTS chronosequences into minimum age categories as young (≤1 decade since disturbance, one site), middle-aged (>1 to <3 decades since disturbance, two sites), old (≥3 decades since disturbance, two sites), and undisturbed MAT (two sites) (Figure 2a,b). The two undisturbed MAT sites, representing the control condition, have not been aged, but are assumed to be undisturbed by RTS for at least a century.

Shrub sampling and processing

In late July and early August 2012 and 2013, we collected 141 ramets (rooted branches), each ramet representing an individual dwarf birch (*B. nana*) or willow shrub

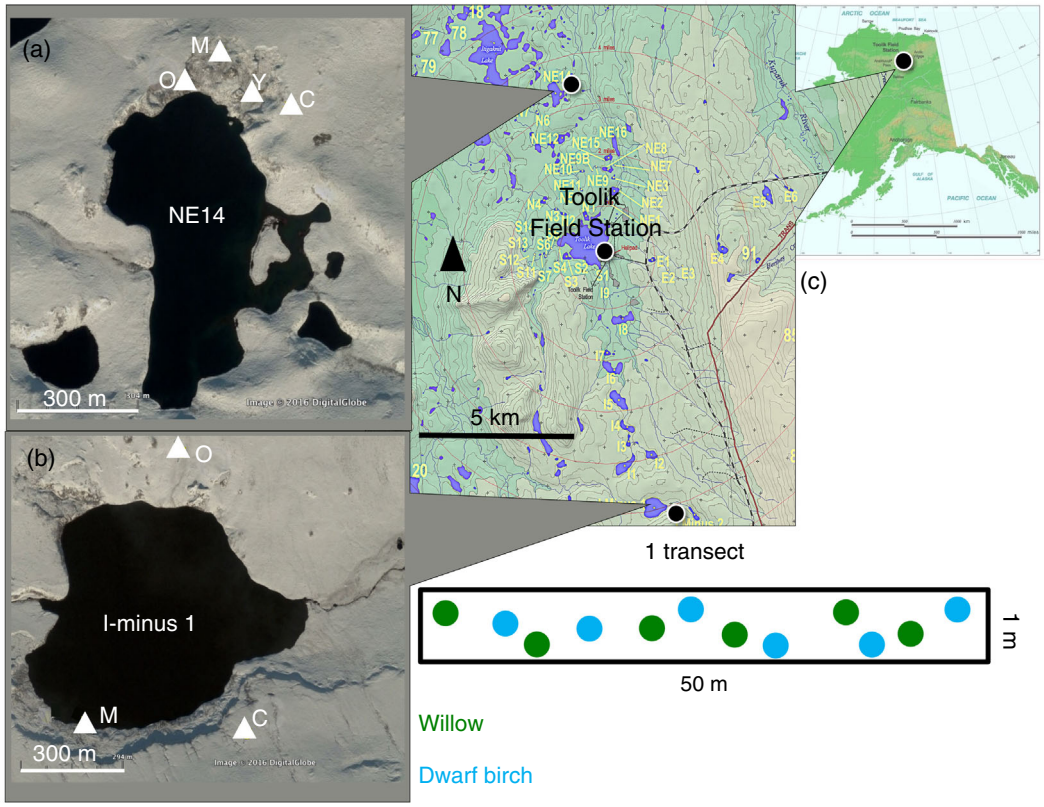

FIGURE 2 Study sites and shrub sampling scheme. Location of two retrogressive thaw slump (RTS) chronosequences on Alaska's North Slope at two lakes: (a) NE14 and (b) I-minus 1 (Sources a and b: Google Earth, 2020; insets: Toolik Field Station GIS). RTS time since disturbance categories: Y = young (≤1 decade), M = middle-aged (>1 to <3 decades), O = old (≥3 decades), and C = undisturbed control in moist acidic tussock (MAT) tundra. (c) Scheme of shrub sampling design: Willow (*Salix pulchra* and *S. glauca*) and dwarf birch (*Betula nana*) shrub ramets (i.e., rooted branches) were randomly sampled along seven 1 × 50 m transects on slopes. Dwarf birch ramets were found only at NE14 "O" and "C," and I-minus 1 "M" and "C" plots.

(*Salix pulchra* and *S. glauca*). Shrub sampling was done in seven RTS sites: four sites at Lake NE14 consisting of one young, middle-aged, and old RTS, plus one undisturbed MAT site (Figure 2a), and three sites at Lake I-minus 1 consisting of one middle-aged and one old RTS, and one undisturbed MAT site (Figure 2b). We collected 6–23 ramets per species per site (83 willows and 57 dwarf birches), along 1 × 50 m transects (1 transect per site and 7 transects in total) (Figure 2c).

Transects were run upslope at all RTS and control sites to capture variation in vegetation and soil characteristics along slope gradients formed by RTS, with transect origins at the slope bottom (Huebner & Bret-Harte, 2019). Because shrub species can spread laterally by resprouting of underground stems, ramets were sampled at intervals of ≥2 m along transects to avoid resampling the same individual. To determine time since seedling recruitment, ramets were excavated to remove aboveground and belowground material with clippers at the point just below the root collar (the root–shoot interface of the seedling). Where possible, the entire shrub was harvested. Willows were found at all seven sampling sites. Dwarf birches were found at four sites: the old RTS and undisturbed control at NE14, and the middle-aged RTS and undisturbed control at I-minus 1. We did not sample shrubs at the young RTS at Lake I-minus 1 due to ongoing studies inside the RTS that precluded destructive sampling.

Shrub age estimates were performed using two methods. Initially, we determined the age of a shrub by counting growth rings along a minimum of two radii per cross section (Method 1), using two to three cross sections per individual shrub. Cross sections were cut by hand with a razor blade and stained with 1% phloroglucinol in 20% HCl (Bret-Harte et al., 2002), and growth rings were counted under a compound microscope. Due to low resolution in determining time since recruitment of individuals, we later used a thin-sectioning method (Schweingruber & Poschlod, 2005) to verify estimates of shrub age and quantify secondary growth rings on a subset of the putatively oldest individuals (Method 2). For this analysis, archival slides were

made from cross-sectional cuts (15–20 μm thickness) prepared from shrub stems using a GSL1 sledge microtome (Schenkung Dapples, Zürich; Gärtner et al., 2014). In total, there were 182 cross sections analyzed from 42 willows (6 shrubs per 7 sites) and 24 dwarf birch (6 shrubs per 4 sites). Stems were serially sectioned 10 cm apart along the main ramet (i.e., 2–4 cross sections per ramet) to account for potential differences in aboveground and belowground growth as a function of resource allocation, including discontinuous or missing rings (Buchwal et al., 2013). Cross sections were mounted on glass slides, stained with 1% aqueous Astra Blue–Safranin dye (Astra Blue 6GLL: Marker Gene Technologies, Inc., Eugene, OR, USA; Safranin: Ward's Natural Science, Ltd, St. Catharines, ON, Canada), washed with 95% ethanol, and fixed in Canada Balsam (Alfa Aesar, Heysham, UK) by curing slides for 48 h at 60°C. High-resolution images were made from slides with a Leica microscope camera at 40–100× magnification, and composite images were stitched together in Adobe Photoshop (Adobe Systems, USA) (Figure 3).

Ring widths were measured along three radii per cross section (i.e., nine radii per individual) at 0.001-μm resolution using the ImageJ software (Abràmoff et al., 2004) (Method 2). Growth ring measurements were first cross-dated visually between all cross sections from an individual shrub, and later between all shrubs per site. Because secondary growth of arctic shrubs can be irregular due to harsh environmental conditions, we used positive pointer year rings (i.e., conspicuously wide, complete rings common to all radii; Schweingruber et al., 1990) to detect missing or discontinuous rings in each cross section. We first compared ring counts between positive pointer years on different radii for each cross section to detect where incomplete rings occurred, then verified the position of discontinuous rings by following narrow rings completely around the circumference of the cross section. Where we detected discontinuous rings, a value of 1 μm was assigned as a value of minimum growth for that radius for that year, in order to calculate average ring widths for each cross section. Where missing rings were detected as a variation in growth allocation between different cross sections along a ramet, a value of 1 μm was assigned for all radii in that cross section for that year. In total, missing or discontinuous rings occurred in less than 11% of all cross sections.

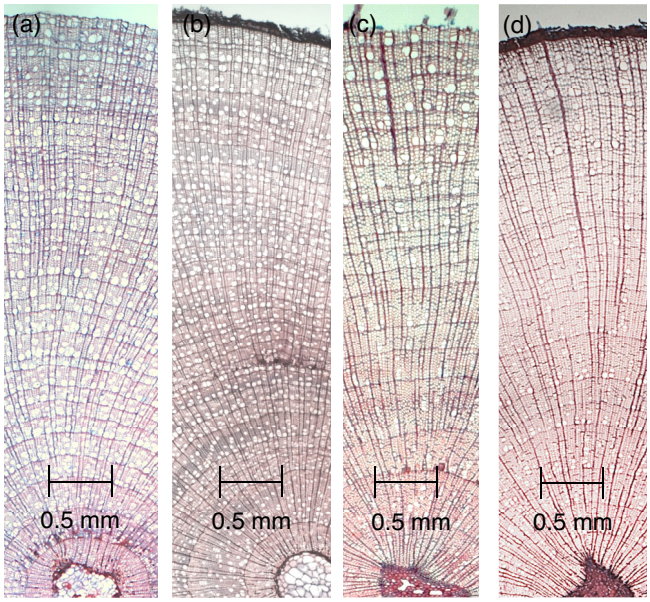

FIGURE 3 Cross-sectional view on a single radius of shrub growth rings: (a) willow (*Salix pulchra* or *S. glauca*) from undisturbed moist acidic tussock (MAT); (b) willow from a middle-aged retrogressive thaw slump (RTS) (>1 to <3 decades since disturbance); (c) dwarf birch (*Betula nana*) from undisturbed MAT; and (d) dwarf birch from an old RTS (≥3 decades since disturbance). For each example, the pith is presented on the bottom of the image.

Visual cross-dating results were then verified using the COFECHA software (Grissino-Mayer, 2001). Verification per individual was done by comparing time series intercorrelations ($\bar{r}$) for each species at each site to detect growth patterns common to all individuals. Growth patterns of site chronologies were compared with *S. pulchra* chronologies from nearby sites in the Toolik Lake research corridor (Ackerman et al., 2017, 2018). Two types of chronologies of our samples were built for each species at each site: (1) a raw chronology calculated from the arithmetic mean of raw ring widths per individual shrub and (2) a standardized chronology using detrended ring width indices (RWIs). In order to test detrending robustness, two detrending methods were compared: (1) a cubic smoothing spline with a default frequency response value of 0.5n years and a default spline length of two thirds of each series; and (2) basal area increment (BAI), where BAI is the surface area of each year's growth, assuming the stem cross section is circular. Detrending and chronology building procedures were performed in the dplR package (Bunn, 2008) in R (R Core Team, 2020). Chronology statistics including $\bar{r}$, mean sensitivity, expressed population signal (EPS), first-order autocorrelation, and signal-to-noise ratio (Wigley et al., 1984) were obtained using COFECHA and the dplR package.

Statistical analysis

To test the hypothesis that shrub age reflects estimated minimum RTS age (H1), we first compared the accuracy

of our two ring counting methods (Method 1 and Method 2) performed on a subset of the oldest shrubs selected for dendrochronological analysis ($n = 66$ shrubs). This step was completed using linear regression analysis. All linear models in this study were created using the JMP Pro 16.1.0 software (SAS Institute, 2021). We used two-way ANOVA, with the number of years assessed for each shrub as the response variable, and the method (Method 1 and Method 2) and species (dwarf birch and willow) as explanatory variables, plus an interaction term for method and species to account for differences in identifying ring boundaries for dwarf birch and willow. Next, we used one-way ANOVA to determine whether shrub age can predict RTS age categories, with estimated shrub age in years (derived from our most accurate ramet aging method) as the response variable and RTS age category (four levels: young, middle-aged, old, and undisturbed control MAT, derived from independent sources cited above) as the explanatory variable. Because we only had one young RTS site (at lake NE14; Figure 2a) at which we found only willows, and because dwarf birch was found in only four sites, we performed separate analyses for each species averaged across each analogous RTS category. We used Tukey's post hoc test for comparison of statistically significant mean values across each category.

To test the hypothesis that growth rings are wider in RTS than in undisturbed MAT (H2), we used one-way ANOVA of RTS age categories (four levels: young, middle-aged, old, and undisturbed control MAT) on ring widths for each species in linear models, using separate models for willows and for dwarf birch. We initially compared models using raw ring widths and BAI-detrended rings as the response variable, rather than the unitless RWI, which has a mean value of 1. Because BAI detrending may not entirely remove developmental effects, including juvenile growth, which can produce irregular ring widths (Speer, 2010; Sullivan et al., 2016; Weijers et al., 2018), we controlled for developmental effects by excluding the five innermost rings (i.e., juvenile rings) from the raw ring data to reduce error in ring width estimates. The latter method has been applied to shrub-specific time series, including tundra willows (Myers-Smith et al., 2015; Weijers et al., 2018). We used Tukey's post hoc test for comparison of statistically significant mean values by category.

To test the hypothesis that climate sensitivity is greater in shrubs growing in RTS relative to shrubs in undisturbed MAT (H3), we first determined the climate variables most likely affecting growth of each species (willow and dwarf birch) at our sites using the R package treeclim, which quantifies relationships between RWI and climate data (Zang & Biondi, 2015). We computed bootstrapped (1000 iterations) correlation coefficients between standardized growth ring data (comparing results for cubic spline and BAI-detrended data) using mean monthly temperature (average of minimum and maximum values) and monthly total precipitation (computed from 24-h averages) from 1988 to 2013 recorded continuously at Toolik Field Station, which is within 10 km of both study sites (Toolik Environmental Data Center Team, 2020). Monthly climate variables producing significant ($p < 0.05$) correlations across populations were selected for further analyses. These were June mean temperature in the current year of growth and September precipitation in the previous year of growth. For dwarf birch models, we included July mean monthly temperature because it was a significant explanatory variable ($p < 0.05$) of raw and log-transformed ring widths in linear regression.

We used linear regression to test goodness of fit of ring widths to the monthly temperature and precipitation variables selected in a first stage of climate–growth relationship analyses performed in treeclim for each species. Because climate sensitivity of shrubs is expected to vary where there are other limiting factors, we included a polynomial (i.e., quadratic) temperature term for June to account for variation in shrub growth, after Ackerman et al. (2017). This term accounts for ring width variation in warmer years, as previous studies suggest that soil moisture can affect the climate sensitivity of tundra shrubs (Myers-Smith et al., 2015).

To control for variation in secondary growth explained by climate and nonclimate variables, we used linear mixed-effects (LME) models, running separate analyses for willows and for dwarf birch. Fixed effects included RTS age category and the selected climate variables listed above (including the quadratic term for June mean temperature), plus the interaction between RTS age category and each fixed continuous variable; site was a random effect (Lake NE14, Lake I-minus 1). To account for changes in growth rate associated with shrub age and increasing stem diameter, we included ramet age as a fixed effect in LME models, using the same age estimates derived from shrub ramets used for H1 (minus juvenile growth rings to control for developmental effects on ring width as above). We compared models using log-transformed raw ring widths (with juvenile rings excluded), and BAI-detrended ring widths, which included all growth rings. Cubic spline-detrended data were not used in models because it produced a mean of 1 for each population, precluding comparisons across RTS age categories.

Linear mixed-effects models selection was based on comparison of corrected Akaike information criterion (AIC_c) and Bayesian information criterion (BIC) values of the full model to a reduced model to determine overall goodness of fit. AIC_c was used due to small subsample sizes (Burnham & Anderson, 1998). For each model, the reduced

model was derived from the full model by removing parameters that had nonsignificant interactions across all the factor levels. Because we were interested in the interaction of RTS with continuous variables, if at least one significant interaction was found in one of the RTS levels, then all significant and nonsignificant results were retained in the final (best) model where AIC and BIC values were lower. The strength of climate effects in H3 was determined comparing the slope coefficient (with associated 95% confidence intervals) of climate variables between RTS categories. To understand the strength of RTS effects versus undisturbed tundra, we ran separate analysis by each RTS age category (young, middle-aged, and old) and across all RTS averaged together, versus undisturbed MAT, for each shrub species. To compare model strength of LME best models using juvenile-detrended rings versus BAI-detrended rings as the response variable, we computed conditional R^2 and marginal R^2 for full and reduced models, after Nakagawa et al. (2017), using the R package "MuMIn" (Bartoń, 2020). Conditional R^2 reports variability contributed by all explanatory variables, and marginal R^2 reports variability contributed by fixed variables only. To assess each fixed and random variable's contribution to LME best model variance, we reported the proportion of variance over all parameters used in the fitted model, after Saltelli (2002). LME models and proportional variance analyses were run using R packages lme and lmer (R Core Team, 2020) and JMP Pro 16.1.0 software (SAS Institute, 2021).

RESULTS

Comparison of shrub rings dating methods to test H1

Method 2 found an average of 4.4 more rings per individual shrub than the original Method 1 used to date the same individuals ($F_{3,128} = 4.005$, $p = 0.009$). There was no significant interaction between method and species. Because Method 2 fit shrub rings to a specific chronology based on common growth patterns, we chose Method 2 for its greater accuracy to compare shrub minimum age estimates in H1.

H1: Shrub age derived from shrub ramets will reflect minimum time since RTS disturbance

Overall, H1 was not supported across species, with the exception of the willow ramets in the youngest RTS, which were 18–26 years younger than willow ramets elsewhere (Figure 4a). Although RTS age category explained over two thirds of the variance in willow ramet age ($F_{3,38} = 29.1953$, $p < 0.0001$, adjusted R^2: 0.675), against expectations, willow ramets from the middle-aged RTSs were 5–8 years older than willow ramets from the oldest RTSs and the undisturbed MAT, which were not different from each other (Figure 4a). For dwarf birch, the difference in average ramet age between RTS age categories was not statistically significant at $p < 0.05$ ($F_{2,21} = 3.1765$, $p < 0.0623$, adjusted R^2: 0.159; Figure 4b).

H2: Growth rings are wider in RTS than in undisturbed tundra, with the widest rings in the youngest RTS

Results showed strong support for H2 across species (Figure 5). Willow ramets from the youngest RTS had average growth ring widths over three times the width of those growing in undisturbed MAT sites, and those from the middle-aged and old RTSs were 2 times and 1.5 times the width, respectively, of growth rings of willow ramets

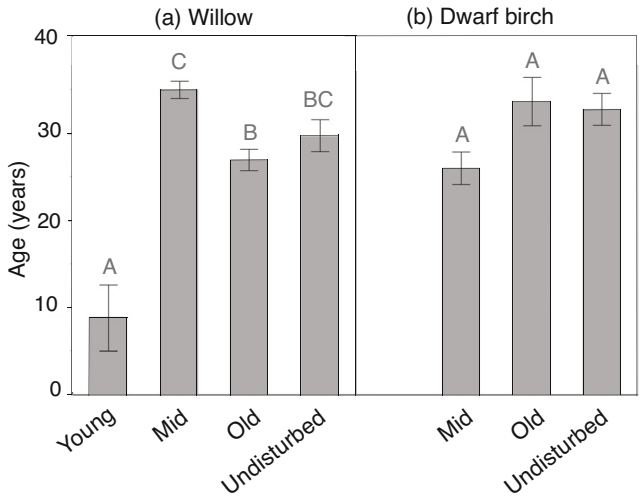

FIGURE 4 Mean shrub age estimates by retrogressive thaw slump (RTS) age category for (a) willow (*Salix pulchra* and *S. glauca*) and (b) dwarf birch (*Betula nana*) at two North Slope, Alaska, lake shores disturbed by RTSs of different ages as in Figure 2. No dwarf birches were found in the Young RTS in (b). Shrub age estimates from ramets were determined by dendrochronological methods (Schweingruber & Poschlod, 2005). Error bars show standard error of the mean. Levels connected by different letters indicate the mean is statistically significant at $p < 0.05$ in Tukey's honestly significant difference post hoc test of one-way ANOVA. For (a) willows: young RTS versus undisturbed: $t_{2.69,38} = -7.36$, $p = <0.0001$; mid versus undisturbed: $t_{2.69,38} = 2.26$, $p = 0.125$; old versus undisturbed: $t_{2.69,38} = -1.22$, $p = 0.618$. For (b) dwarf birch: mid versus undisturbed: $t_{2.52,21} = -2.26$, $p = 0.085$; old versus undisturbed: $t_{2.52,21} = 0.31$, $p = 0.9497$

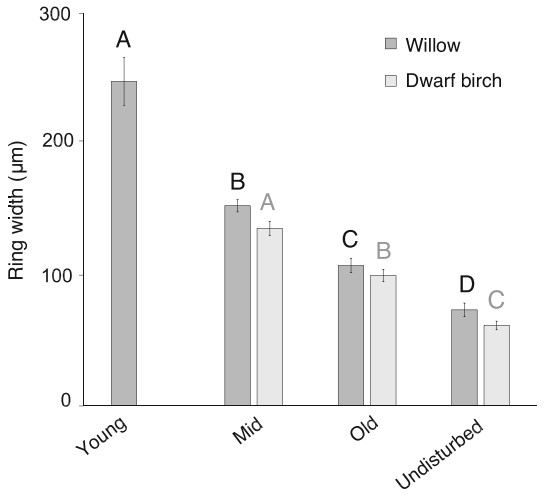

FIGURE 5 Mean shrub growth ring widths (raw ring widths, with five innermost rings removed) in separate analysis for willow (*Salix pulchra* and *S. glauca*) (dark bars) and dwarf birch (*Betula nana*) (light bars) averaged from two retrogressive thaw slump (RTS) chronosequence sites, North Slope, Alaska. Retrogressive thaw slump age categories are classified as in Figure 2 (no dwarf birches were found at the young RTS). Error bars show standard error of the mean. Levels not connected by the same letter indicate the mean is statistically significant ($p < 0.05$) in Tukey's post hoc test of one-way ANOVA.

from undisturbed MAT sites (Figure 5). Growth rings of dwarf birch ramets from the middle-aged and old RTSs were twice the width and 1.6 times the width, respectively, of dwarf birch growth rings from the undisturbed MAT (Figure 5). Compared with lake site, which explained less than 1% of the variance of growth ring widths of willow and birch ramets and was not significant ($p > 0.1$) for both species, RTS age category explained 16% of willow growth ring variance (ANOVA for willows: $F_{3,934} = 61.2248$, $p < 0.0001$; adjusted R^2: 0.162) and 18% of dwarf birch growth ring variance (ANOVA for dwarf birch: $F_{2,646} = 72.0954$, $p < 0.0001$; adjusted R^2: 0.180).

H3: Climate sensitivity of shrubs in RTS versus undisturbed tundra

Shrub chronology and climate–growth statistics

Shrub chronology statistics showed mean series intercorrelation values ($\bar{r}$) ranging from 0.419 to 0.712 across species and sites (Table 1); mean $\bar{r}$ values were 0.500 and 0.502 for dwarf birch and willow, respectively. Of the 11 populations across species, 7 populations had EPS threshold values ≥0.85; the other 4 populations ranged from 0.81 to 0.83 (Table 1), with mean values of 0.86 for both dwarf birch and willow. Climate–growth analysis performed on cubic spline-detrended series (period 1989–2013) found stronger correlations between RWI and climate variables across populations than on the BAI-detrended or raw chronologies (Appendix S1: Tables S1 and S2). The strongest correlations were obtained for June mean temperature and previous September precipitation across populations (Appendix S1: Tables S1 and S2). Except for the youngest RTS (found only at NE14), which shows low growth prior to 2005, growth patterns showed consistent increases in warmer, wetter years and decreases in cooler, drier years across species (Figure 6).

Variability in growth ring widths in LME full and best models, explained by the contribution of all effects versus fixed effects alone and reported as conditional and marginal R^2, respectively, was higher in models using log-transformed ring widths with juvenile rings excluded rather than BAI-detrended rings as the response variable (Appendix S1: Table S3). Based on these model selection results, we present here the results of LME best models using log-transformed ring widths that excluded juvenile growth rings from the response variable.

H3: Willow growth response to climate variables

Greater climate sensitivity of all RTS willows to June mean temperature in H3 was not supported. LME best models showed that all willow growth rings were on average 2.5% wider per 1°C linear increase in June mean temperature with no significant interactions between temperature and RTS age category (Figure 7a, Table 2). As a single explanatory variable, June mean temperature was associated with a uniformly linear increase in ring widths for willows in the middle-aged RTSs and the undisturbed MAT sites (Figure 7b). Quadratic relationships between willow secondary growth and June mean temperature were significant without RTS age category interactions (Table 2); average willow secondary growth at most sites decreased when June mean temperatures exceeded 10°C (Figure 7a,b).

Growth sensitivity of willows to previous September precipitation in H3 was not supported across all RTSs (Figure 7c), but there were significant interactions between RTSs by age category, lending support for greater climate sensitivity of willows in some RTSs but not in others (Table 2, Figure 7d). Average ring widths of willows in the middle-aged RTSs were 5% larger per 1 mm increase in previous September precipitation

TABLE 1 Chronology statistics of willow and dwarf birch (six shrubs per species) at two retrogressive thaw slump (RTS) chronosequence lake sites on Alaska's North Slope (I-minus 1 and NE14)

Site/RTS/Species	Age (years)	Ring width (μm)	EPS	$\bar{r}$	MS	1*r*	snr
I-minus 1							
RTS mid							
Dwarf birch	26.00 (2.67)	0.136 (0.006)	0.85	0.492	0.524	0.031	5.811
Willow	35.67 (2.11)	0.171 (0.006)	0.85	0.481	0.418	0.003	5.561
RTS old							
Willow	26.50 (2.10)	0.095 (0.007)	0.82	0.439	0.457	−0.015	4.695
Undisturbed MAT							
Dwarf birch	33.83 (2.67)	0.051 (0.005)	0.83	0.451	0.574	0.010	4.929
Willow	32.67 (2.11)	0.062 (0.006)	0.83	0.444	0.461	0.024	4.791
NE14							
RTS young							
Willow	8.83 (2.45)	0.353 (0.020)	0.94	0.712	0.464	−0.273	14.833
RTS mid							
Willow	34.33 (2.45)	0.135 (0.009)	0.87	0.485	0.464	0.008	5.650
RTS old							
Dwarf birch	33.67 (2.28)	0.100 (0.004)	0.87	0.518	0.424	−0.024	6.448
Willow	27.33 (2.45)	0.120 (0.010)	0.81	0.419	0.401	0.022	4.327
Undisturbed MAT							
Dwarf birch	31.67 (2.28)	0.075 (0.004)	0.88	0.540	0.457	0.015	7.043
Willow	26.83 (2.45)	0.089 (0.010)	0.87	0.533	0.344	−00.15	6.848

Notes: RTS categories (time since disturbance): young (≤1 decade), mid (>1 to <3 decades), old (≥3 decades), and undisturbed moist acidic tussock (MAT) tundra (control condition). Values for age and ring width are means with SE in parentheses.
Abbreviations: 1*r*, first-order autocorrelation; EPS, expressed population signal; MS, mean sensitivity; $\bar{r}$, mean series intercorrelation; snr, signal-to-noise ratio.

(Table 2, Figure 7d). Ring widths of willows were 3% larger in the undisturbed MAT sites but were not statistically significant for willows in the youngest or oldest RTSs in LME best models (Table 2). Due to these contrasting growth responses across disturbance categories, previous September precipitation was not a statistically significant fixed effect on willow secondary growth in LME best models (Table 2).

H3: Dwarf birch growth response to climate variables

Retrogressive thaw slump interactions with temperature on dwarf birch secondary growth response were mixed, and H3 was largely not supported (Figure 7e,f, Table 2). In LME best models, the quadratic relationship of June mean temperature to dwarf birch ring width was significant without RTS interactions showing a 1% average decrease in ring width across sites when June mean temperatures exceeded 10°C (Table 2). June and July mean temperatures were significant predictors of secondary growth of dwarf birch in LME best models, showing a 2% and 1% linear increase, respectively, in ring width per 1°C increase in temperature across sites (Table 2). However, June mean temperature showed significant RTS interactions that were not seen with July mean temperature (Table 2). Average secondary growth of dwarf birch ramets from the middle-aged RTS increased by 2% per 1°C increase in June mean temperature but decreased by 2% in the oldest RTS (Table 2). As a single variable, June mean temperature had low significance in explaining variance in dwarf birch secondary growth across all RTSs and undisturbed MAT sites (Figure 7e,f).

Support of H3 was seen in the middle-aged RTS where average dwarf birch ring widths showed a trend ($p < 0.1$) of increasing by 4% and a significant 5% decrease in the oldest RTS per unit increase in previous September precipitation in Table 2. Previous September precipitation showed significant RTS interactions in LME best models predicting average growth response of

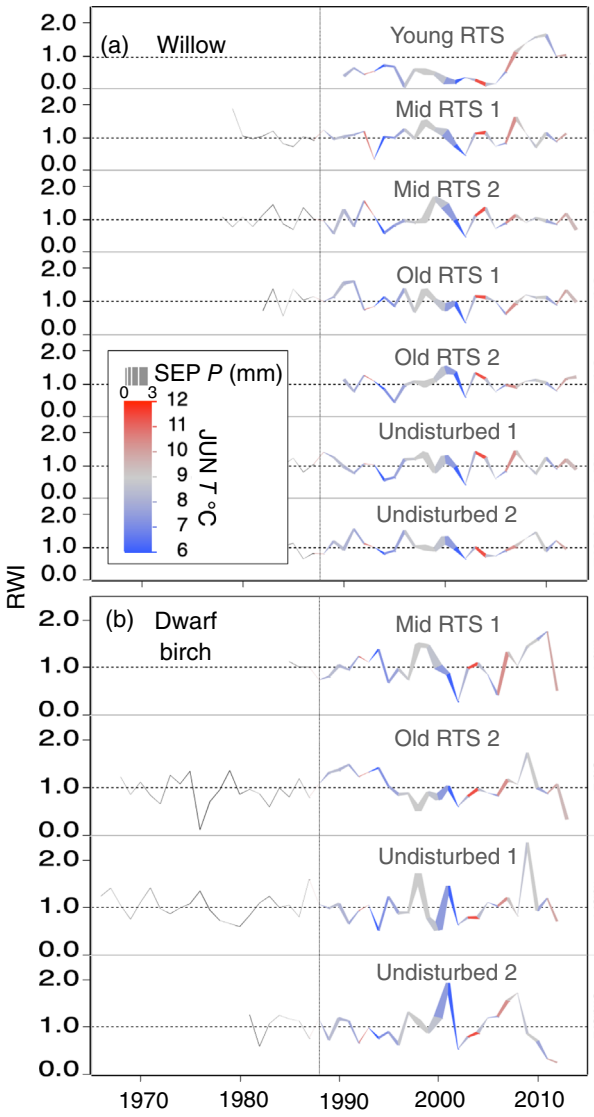

FIGURE 6 Standardized shrub chronologies of ring width indices (RWIs; values are cubic spline-detrended and averaged from six individuals per population) for (a) seven willow (*Salix pulchra* and *S. glauca*) and (b) four dwarf birch (*Betula nana*) populations located in retrogressive thaw slump (RTS) and undisturbed control sites in North Slope, Alaska. Retrogressive thaw slump categories are as in Figure 2. "1" and "2" refer to sites I-minus 1 and NE14, respectively. Line color and line thickness on each chronology indicate growth relationships to June mean temperature (JUN *T*) and previous year's September mean cumulative precipitation (SEP *P*) for the period 1989–2013 (area right of vertical line)

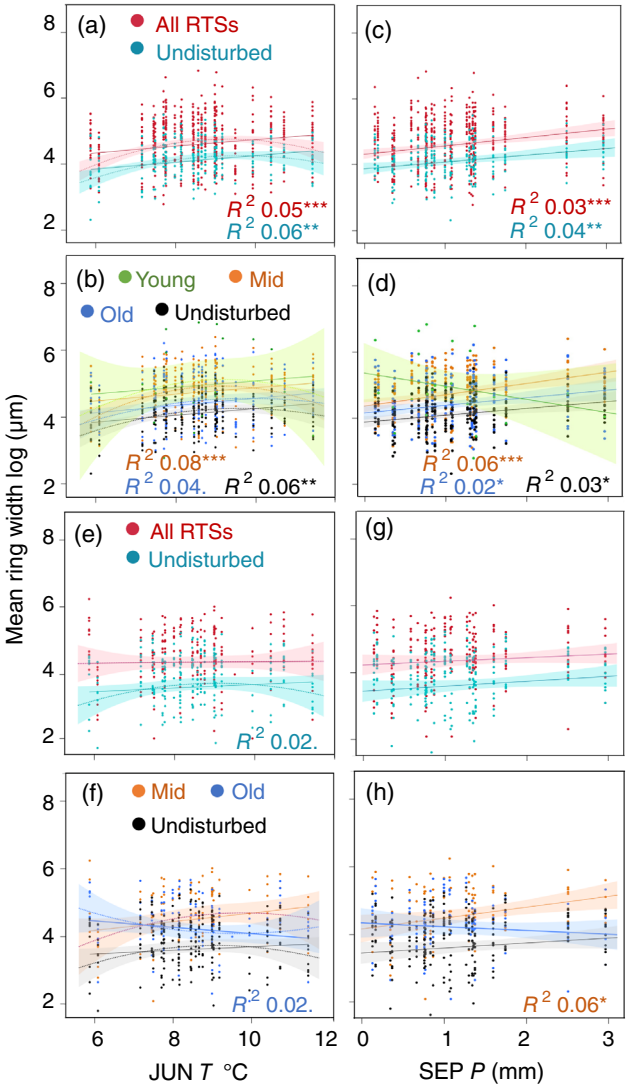

FIGURE 7 Linear regression of ring width (raw widths, log-transformed, and juvenile rings removed) as a function of current year's June mean temperature (JUN *T*, left column) and previous year September precipitation (SEP *P*, right column) for willow (*Salix pulchra* and *S. glauca*: a–d) and dwarf birch (*Betula nana*: e–h) averaged by all retrogressive thaw slump sites (RTSs) versus all undisturbed sites (a, c, e, and g); and averaged by RTS age category (b, d, f, and h), classified as in Figure 2, at two North Slope, Alaska, lake sites (for f and h, there is no young RTS category). Solid lines show linear goodness of fit, and dotted lines show polynomial (quadratic) goodness of fit for June mean temperature. Shaded areas show confidence intervals ($\alpha = 0.05$). R^2 values show proportion of variance explained by each model (color coded by RTS category). Statistical significance indicated for regression: ***$p < 0.0001$, **$p < 0.01$, *$p < 0.05$, and .$p < 0.1$.

dwarf birch (Table 2), but it was a variable of low explanatory power when averaged across RTSs and undisturbed MAT sites (Figure 7g, Table 2). As a single explanatory variable, previous September precipitation was statistically significant at $p < 0.05$ in explaining increased ring widths of dwarf birches in the middle-aged RTS (Figure 7h).

H3: Proportional variance of fixed and random effects

Overall, RTS age and ramet age had higher explanatory power than climate variables for all shrubs in LME

TABLE 2 Linear mixed-effects models fixed and random-effects parameter estimates for the best full and reduced models for raw growth ring widths (in micrometers; log-transformed and juvenile rings excluded) of willows (*Salix pulchra* and *S. glauca*; upper panel) and dwarf birch (*Betula nana*; lower panel) sampled at two retrogressive thaw slump (RTS) chronosequence sites, Lake NE14 and Lake I-minus 1, North Slope, Alaska

	Reduced model			Full model		
Parameter	**Estimate**	**SE**	***p***	**Estimate**	**SE**	***p***
Willow (*S. pulchra* and *S. glauca*)						
Intercept	4.187	0.177	**<0.0001**	4.180	0.237	**<0.0001**
RTS Mid	0.297	0.141	0.1163	0.302	0.142	0.1146
RTS Old	−0.290	0.142	0.1266	−0.280	0.143	0.1306
Undisturbed MAT	−0.430	0.141	**0.0472**	−0.430	0.142	**0.0484**
June T	0.102	0.016	**<0.0001**	0.107	0.026	**<0.0001**
June T × RTS Mid	–	–	–	0.020	0.033	0.5390
June T × RTS Old	–	–	–	−0.010	0.033	0.8192
June T × Undisturbed MAT	–	–	–	−0.030	0.033	0.3014
Prev Sept precipitation	−0.050	0.049	0.3299	−0.060	0.050	0.2534
Prev Sept precip × RTS Mid	0.195	0.061	**0.0014**	0.198	0.062	**0.0015**
Prev Sept precip × RTS Old	0.070	0.061	0.2547	0.083	0.063	0.1870
Prev Sept precip × Undisturbed MAT	0.114	0.061	0.0630*	0.131	0.063	**0.0380**
June T^2	−0.040	0.008	**<0.0001**	−0.050	0.014	**0.0003**
June T^2 × RTS Mid	–	–	–	0.017	0.017	0.3274
June T^2 × RTS Old	–	–	–	0.022	0.017	0.2161
June T^2 × Undisturbed MAT	–	–	–	0.012	0.017	0.4966
Ramet age	−0.020	0.005	**0.0007**	−0.020	0.005	**0.0006**
Ramet age × RTS Mid	−0.010	0.006	**0.0095**	−0.020	0.006	**0.0076**
Ramet age × RTS Old	−0.030	0.006	**<0.0001**	−0.030	0.006	**<0.0001**
Ramet age × Undisturbed MAT	0.005	0.006	0.3539	0.007	0.006	0.2477
Random effect: Site	0.044	0.038	0.2464	0.045	0.039	0.2461
Dwarf birch (*B. nana*)						
Intercept	4.063	0.323	**<0.0001**	4.039	0.302	**<0.0001**
RTS Mid	0.211	0.278	0.5854	−0.790	0.384	**0.0395**
RTS Old	0.184	0.277	0.6276	0.960	0.374	**0.0106**
June T	0.071	0.026	**0.0073**	0.067	0.031	**0.0381**
June T × RTS Mid	0.077	0.037	**0.0368**	0.098	0.049	**0.0457**
June T × RTS Old	−0.080	0.035	**0.0254**	−0.110	0.047	**0.0252**
July T	0.050	0.021	**0.0186**	0.060	0.019	**0.0020**
July T × RTS Mid	–	–	–	0.015	0.041	0.7215
July T × RTS Old	–	–	–	0.015	0.041	0.7308
Prev Sept precip	0.003	0.047	0.9517	0.001	0.096	0.9944
Prev Sept precip × RTS Mid	0.132	0.068	0.0542*	0.194	0.117	0.1036
Prev Sept precip × RTS Old	−0.160	0.068	**0.0157**	−0.220	0.114	0.0561*
June T^2	−0.050	0.013	**0.0006**	−0.040	0.035	0.4713
June T^2 × RTS Mid	–	–	–	0.020	0.032	0.5222
June T^2 × RTS Old	–	–	–	0.001	0.030	0.9683
Ramet age	−0.040	0.004	**<0.0001**	−0.040	0.005	**<0.0001**

(Continues)

TABLE 2 (Continued)

Parameter	Reduced model			Full model		
	Estimate	SE	*p*	Estimate	SE	*p*
Ramet age × RTS Mid	–	–	–	0.001	0.007	0.8949
Ramet age × RTS Old	–	–	–	−0.010	0.006	0.0966
Random effect: Site	0.122	0.178	0.4925	0.147	0.213	0.4909

Notes: Effects of climate parameters and ramet ages on growth ring widths were compared across four RTS age categories: young (≤1 decade since disturbance), mid (>1 to <3 decades), old (≥3 decades), and undisturbed moist acidic tussock (MAT) tundra (control condition). Fixed effects include RTS age category, air temperature (T) in degrees Celsius, total monthly precipitation (24-h average; in millimeters), ramet age in years, and two-way interactions between fixed effects and RTS age categories. June T^2 is second-order June temperature. Site (NE14, I-minus 1) is the random effect. AIC_c and BIC values indicate goodness of fit of best models. The p values in bold are statistically significant at $p < 0.05$. The p values with an asterisk (*) are marginally significant at $p < 0.1$. Willow, reduced model: $AIC_c = 1399$, BIC = 1474; full model, $AIC_c = 1408$, BIC = 1510. Dwarf birch, reduced model, $AIC_c = 1008$, BIC = 1066; full model, $AIC_c = 1009$, BIC = 1091.

models and H3 was not supported. Retrogressive thaw slump age category was the most important fixed main effect in willow LME best models, accounting for nearly half of the variance in willow growth ring widths and a third of the variance for dwarf birch (Appendix S1: Figures S1 and S2). Ramet age, used as a fixed main effect in LME models for changes in ring width as a function of increasing stem diameter, was the next most important fixed variable, explaining 21% of the average variance of willow and 40% of dwarf birch ring widths (Appendix S1: Figures S1 and S2), and ring widths decreased by 1% per year with increasing ramet age for dwarf birches versus 0.4% per year for willows (Figure 8a,b). June mean temperature (linear relationship) accounted for 6% of the variance in LME best models for willow and 2% of the variance in dwarf birch models (Appendix S1: Figures S1 and S2). July mean temperature explained 1.5% of the variance in the dwarf birch LME best models (Appendix S1: Figure S2) but was not a significant predictor for willow growth and therefore was not used in the final LME models for willows. The quadratic term for June mean temperature explained 2% and 3% of the average variance in LME best models for willow and dwarf birch, respectively (Appendix S1: Figures S1 and S2). Previous September precipitation had the lowest explanatory power as a fixed variable for all LME best models, explaining 1.4% of the variance in willow ring widths but less than 1% as a main effect on dwarf birch ring width (Appendix S1: Figures S1 and S2). Site as a random main effect explained 2% of the variance of willow growth rings on average in LME best models and 6% in dwarf birch models (Appendix S1: Figures S1 and S2).

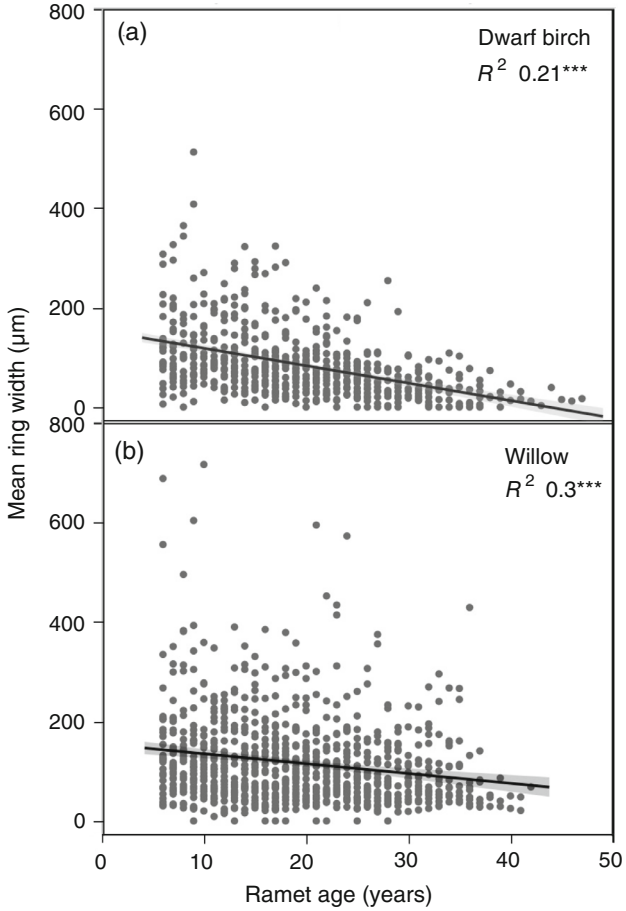

FIGURE 8 Relationships between mean ring widths (raw, with five innermost juvenile rings removed) and shrub ramet age for (a) dwarf birch (*Betula nana*) and (b) willows (*Salix pulchra* and *S. glauca*) sampled in two retrogressive thaw slump (RTS) chronosequences, North Slope, Alaska. R^2 values show proportion of variance explained by each model. Shaded areas show confidence intervals ($\alpha = 0.05$). Statistical significance indicated for regression: ***$p < 0.0001$, **$p < 0.01$, and *$p < 0.05$.

DISCUSSION

Our study revealed that RTS age category had the strongest effect on the secondary growth of dominant deciduous shrubs across the studied sites in the Alaskan Low Arctic. Average shrub ring widths were larger in younger RTSs and smaller in old RTSs and tundra

undisturbed by RTSs. This suggests conditions in RTS influence shrub productivity over time and may have a stronger influence on tundra shrub growth than climate alone. Lower climate sensitivity of tundra shrubs has been found in other regions of the Low Arctic and subarctic where microsite heterogeneity following thermokarst and herbivore interactions appear to be stronger drivers of shrub response (Andruko et al., 2020; Schuur et al., 2007). In agreement with classical forest successional theory (Clements, 1916), which states that plant growth proceeds in stages from denuded sites to specific developed communities, our results suggest that RTSs support the development of tall shrub communities whose growth declines over time. These tall shrub communities may represent a mid-successional stage of Low Arctic tundra. Moreover, our results agree with other studies of tundra plant response following permafrost thaw (Becker et al., 2016; Lantz et al., 2009; Lantz & Kokelj, 2008; Pizano et al., 2014) in that RTSs appear to feature microsites that support enhanced shrub growth.

Climate sensitivity of tundra shrubs at our sites explained far less variance in our models than RTS effects on shrub growth, and without long-term measurements of meteorological and soil conditions at the RTS sites, we must approach the question of shrub climate sensitivity in RTS with some caution. Of the significant climate effects we found, declining shrub secondary growth in warmer years (quadratic relationship to June mean temperature) agreed with previous studies from the Toolik Lake area (Ackerman et al., 2017, 2018). Climate sensitivity of tundra shrubs may be additionally driven by changes in available soil moisture at our sites, in agreement with biome-wide studies (Myers-Smith et al., 2015). Support for H3, that is, amplified climate sensitivity of shrubs growing in RTS, was limited to shrubs growing in mid-successional RTSs in response to increased previous September precipitation. Below we discuss some likely mechanisms behind our findings.

Retrogressive thaw slump effects on shrub growth and shrub age

Plant successional trajectories in disturbed permafrost landscapes depend upon many factors including the nature and severity of the disturbance (Bret-Harte et al., 2013; Vavrek et al., 1999), the natural variation in microsite conditions following disturbance (Becker et al., 2016), and the viability of available sexual and vegetative propagules (Alsos et al., 2007; Ebersole, 1989). Tundra willows, dwarf birch, and alder have been observed as the dominant shrub species in RTSs in the Low Arctic of Canada and Alaska in the mid-successional stage, that is, within the first few decades after disturbance (Cray & Pollard, 2015; Lambert, 1972; Lantz et al., 2009; Pizano et al., 2014), suggesting that they are colonizers that can maintain dominance decades after severe permafrost thaw. In our area, canopy heights of willow and dwarf birch shrubs growing in mid-successional RTSs often exceeded the height of MAT vegetation many times over (Huebner & Bret-Harte, 2019). Dominant deciduous shrub species in this area have repeatedly demonstrated a superior competitive advantage over other tundra vegetation types by rapidly gaining biomass when exposed to experimental warming and fertilization treatments (e.g., Bret-Harte et al., 2008; Chapin III et al., 1995; Mack et al., 2004). The enhanced shrub growth we found in the RTSs suggests that growth conditions in RTS are similar to plots experimentally altered by fertilization because RTSs are known to release large amounts of labile nutrients (Abbott & Jones, 2015).

In our previous study, we found that RTS microsites supported greater seedling abundance (including willow and dwarf birch seedlings), >50% deciduous shrub cover, and greater shrub height that were associated with several biologically important early-successional soil characteristics that were less apparent in late-successional tundra (Huebner & Bret-Harte, 2019). These soil characteristics included higher percent cover of exposed bare mineral soil and higher levels of plant-available NH_4^+ and NO_3^-. Available N levels were greater in RTSs on average than in undisturbed tundra at our sites (Huebner & Bret-Harte, 2019), in agreement with a previous study that found elevated nutrient levels in stabilized RTSs (Lantz et al., 2009). The lowest levels of NO_3^- that we observed in RTS plots were found in the mid-successional sites, whose shrub secondary growth was on average twice the width of shrubs found in undisturbed tundra, likely because plant demand for nutrients increased with plant biomass a few decades following disturbance (Huebner & Bret-Harte, 2019).

Variance in secondary growth of willows and dwarf birch in RTSs may also be explained in part by differential growth of species within genera as a function of changes in species richness over time, since it is more likely that younger RTSs feature bare microsites that support greater opportunities for seedling recruitment than late-successional sites (Eriksson & Fröborg, 1996). In our genotyping study of willows at these sites, we found that *S. pulchra* was the dominant willow species, but species richness of willows in the mid-successional RTS was twice that of willows in the undisturbed MAT site (Huebner et al., 2019). This diversity included a greater abundance of rare species, hybridized species, and pioneer species such as *S. glauca*, which is found in the Alaskan Arctic growing in a tree-like and a shrub-like habit (Viereck & Little, 1972).

Our shrub age distributions across the RTS chronosequences did not reflect time since disturbance at most sites, and did not support H1, except for young willows found at the youngest RTS site at Lake NE14. The age of willow ramets at this youngest RTS agreed with the year this RTS was discovered (Bowden et al., 2008; Pizano et al., 2014), suggesting the willows recruited around the same time. There was also a large increase in RWI of willows growing in the youngest RTS after year 2005, which corresponded to the estimated time since disturbance. Together, these observations suggest a post-disturbance recruitment pulse at the youngest RTS that we did not find in older RTSs. Most shrub ramets found in these sites were 25–35 years old (original ring counts not shown) and were similar in age to shrubs in the undisturbed MAT. Our results support other studies of boreal and Low Arctic tundra shrubs (Ackerman et al., 2017, 2018; Andreu-Hayles et al., 2020; Danby & Hik, 2007), and suggest that ramet turnover of dwarf birch and willow shrubs is occurring in mid- and late-successional sites where the average age of dwarf birch and willow ramets may peak at 30 years. Since these species are known to spread clonally by root layering, caused by partial burial of ramets and stimulation of their adventitious roots (Argus, 2006; Huebner et al., 2019), it was not always possible to identify the root crown, even for samples that were completely excavated. Growth ring counts in our study might therefore reflect ramet age rather than genet age. In light of our results, future studies should approach age estimations of clonal shrubs with caution and, where feasible, cross-date clonal woody species with nonclonal cohorts in order to assess shrub age with greater accuracy.

Climate effects on shrub growth

Climate sensitivity of shrubs was not consistently amplified across all RTSs and did not support H3. However, all shrubs sampled in mid-successional RTSs showed a positive growth relationship with previous September's precipitation. Precipitation in the form of early snowfall, which usually occurs in September at our study sites (Appendix S1: Figure S3), may exert stronger protective effects on shrub growth in RTSs than on shrubs growing in open tundra, because RTS depressions may trap deeper snow layers and provide a sheltered microenvironment at a critical time of the year. Snow depth is considered an important factor in the persistence and expansion of thaw slumps because of its ability to buffer ground temperatures (Kokelj et al., 2009, 2017; Lantz et al., 2009). We did not measure snow depth in the RTSs, but total September precipitation at Toolik Lake, which is within 10 km of our study sites, averaged 31.4 mm (SD ±20.3) from 1989 to 2013, and snowdrifts from high winds are common in this area. Shrub heights in RTSs were 0.3–0.9 m versus 0.2–0.3 m in our undisturbed MAT sites (Huebner & Bret-Harte, 2019). A combination of taller shrubs and windbreaks formed by RTS depressions might differentially trap early snow than open tundra (Sturm et al., 2001).

Climate sensitivity of shrubs in RTSs may be decoupled from local climate averages in the Toolik Lake area because temperature and moisture conditions at the RTS sites may be somewhat warmer and wetter than conditions recorded at the field station. For example, in the Canadian Low Arctic, winter ground temperatures measured 10°C warmer in RTSs than in control areas (Lantz et al., 2009), due to deeper snow cover. Furthermore, deeper snow trapped in RTSs in early winter could increase springtime N mineralization rates by buffering ground temperatures at a critical time of year (Sturm et al., 2005). The relationship of snow depth to nutrient mineralization remains poorly understood. Experimental winter snow additions have shown increased N mineralization in some tundra sites (Buckeridge & Grogan, 2008; DeMarco et al., 2011; Schimel et al., 2004) but not in others (Myers-Smith & Hik, 2013). However, increased radial growth in response to deeper snow has been seen in deciduous shrubs in snow fence experiments in the Toolik Lake area (Addis & Bret-Harte, 2019) and in evergreen shrubs in northern alpine tundra (Carrer et al., 2019; Hallinger et al., 2010). Early snowfall accumulations in some RTS microsites may provide protection and enhanced nutrient mineralization that positively affect shrub growth for decades after RTS disturbance (Pizano et al., 2014).

Climate sensitivity of shrubs across the tundra biome appears to be highest at the limits of their ranges and where shrubs have adequate soil moisture (Myers-Smith et al., 2015). Compared with other regions, tundra shrub growth response to warming in Alaska has been mixed, suggesting shrubs may be responding to other factors such as soil moisture extremes caused by drought or excessively wet conditions (Myers-Smith et al., 2015). The wide range in midsummer soil moisture levels we measured in a previous study of these sites (Huebner & Bret-Harte, 2019) appears to support this. Our results suggest that shrubs at all of our sites (RTS and undisturbed) may experience soil moisture stress in years when average June temperatures exceed 10°C, in agreement with shrub growth studies in the Toolik Lake area (Ackerman et al., 2017, 2018). Although this relationship was not as strong as RTS effects in our models, the lack of significant interactions between the quadratic term for June temperature and RTS suggests this relationship is not influenced by RTS.

Implications for tall shrub expansion

In the Canadian High Arctic, RTS activity from 1984 to 2015 increased from 63 to over 4500 observations and is predicted to increase to >10,000 RTSs per decade after year 2075 (Lewkowicz & Way, 2019). RTS activity in the Noatak Region of Alaska, in contrast, slowed in the 2000s, likely because revegetation has proceeded more rapidly than permafrost degradation (Swanson, 2021). Deciduous shrubs are likely to increase in areas vulnerable to RTS disturbance, which may contribute in an important way to increasing dominance of deciduous shrubs on the tundra landscape (Sturm et al., 2001). Further quantification of RTS frequency is needed to address knowledge gaps in the mechanisms of shrub expansion.

Tall shrub tundra appears to exert different seasonal effects whose influence on net ecosystem exchange is not well understood. Cooler soil temperatures and shallower active layer depths associated with tall shrub shade canopies (Blok et al., 2010; Huebner & Bret-Harte, 2019) may be offset by increased CO_2 emissions and atmospheric heating caused by increased carbon cycling during the growing season (Lafleur & Humphreys, 2018). Snow accumulation in shrub patches may result in no overall change in active layer thickness (ALT) in winter (Lawrence & Swenson, 2011), but in spring, decreased albedo caused by dark shrub branches protruding above the snowpack has been predicted to increase ALT by +10 cm with a 20% increase in shrub cover (Lawrence & Swenson, 2011).

Carbon loss through increased decomposition is expected to be substantial as soil nutrients are released from thawing permafrost (Mack et al., 2004), an effect that could be exacerbated by RTS (Abbott et al., 2014; Abbott & Jones, 2015). Alternatively, because shrubs can alter soil properties through shading and litter deposition (Chapin III et al., 2005; Huebner & Bret-Harte, 2019), they may play a key role in restabilization of permafrost soils (Blok et al., 2010).

Shrub tundra can have higher rates of carbon (C) turnover and respiration that might lead to net depletion of permafrost carbon stocks compared with heath and graminoid tundra (Parker et al., 2015; Sørensen et al., 2018). Deciduous tundra shrubs may initially act as a carbon sink in mid-successional RTSs due to increased growth following nutrient release, but these gains may be offset over time by increased decomposition of older carbon pools (Schuur et al., 2009). Considering the uncertainty of the role of arctic tundra as a carbon source versus sink under global warming, our results suggest successional shrub growth responses derived from RTS studies are important to add to climate models.

CONCLUSION

Our study revealed that RTS, which forms large areas of denuded tundra through permafrost thaw and mass soil wasting, enhances deciduous shrub growth in areas of Alaska's North Slope by creating microsites favored by shrubs. In our study area, shrub growth was more sensitive to RTS than to climate, and middle-aged RTS sites featured larger willow and dwarf birch shrubs with significantly wider growth rings than undisturbed sites. However, this enhanced growth decreased in older RTSs as succession proceeded. RTS activity is expected to increase as climate warms and may lead to larger areas of mid-successional RTS occupied by tall deciduous shrubs that persist for decades. The significant difference we found in shrub secondary growth in RTSs compared with undisturbed tundra suggests that RTS sites support large colonies of tall deciduous shrubs that may become hotspots of tundra greening. Future studies on shrub growth response to climate should not overlook the importance of disturbance such as thaw slumps and other forms of thermokarst activity, and call for greater inclusion of in situ climate data such as soil moisture and temperature in follow-up studies.

AUTHOR CONTRIBUTIONS

Diane C. Huebner, Agata Buchwal, and M. Syndonia Bret-Harte conceived of the ideas and designed the methodology. Diane C. Huebner conducted field sampling and laboratory work with laboratory methodology instruction from Agata Buchwal and assistance from M. Syndonia Bret-Harte. Diane C. Huebner analyzed the data, with assistance from Agata Buchwal, M. Syndonia Bret-Harte, Vladimir Douhovnikoff, Diane Wagner, and others. All authors contributed critically to the drafts with assistance from Vladimir Douhovnikoff, Diane Wagner, and others. All authors gave their final approval.

ACKNOWLEDGMENTS

The authors would like to thank the Indigenous communities of the Arctic for permission to access the locations we chose for our study. We acknowledge that the lands on which we did our work are the unceded ancestral lands of the Iñupiat people who stewarded these lands for thousands of years and continue to steward these lands. We thank you and respect your enduring relationship to your homelands. We thank the Institute of Arctic Biology, University of Alaska Fairbanks, and the staff of Toolik Field Station GIS for the use of digital map imagery and assistance with site selection. Thanks also to the Toolik Field Station Environmental Data Center for field assistance. Special thanks to D. Walsh for field assistance and to J. Drew for laboratory assistance. Thanks to the following for financial assistance: the National Science

Foundation (DEB 1556481, DEB 1637459, and PLR 1623461 to M. Syndonia Bret-Harte), the Polish-U.S. Fulbright Commission (to Agata Buchwal), the Arctic Institute of North America, the UAF Institute of Arctic Biology Graduate Research Fellowship, and the University of Alaska Fairbanks Dissertation Completion Grant (to Diane C. Huebner).

CONFLICT OF INTEREST

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Huebner, 2022) are available from the NSF Arctic Data Center: https://doi.org/10.18739/A2PV6B800.

ORCID

Diane C. Huebner https://orcid.org/0000-0003-2605-7534

REFERENCES

Abbott, B. W., and J. B. Jones. 2015. "Permafrost Collapse Alters Soil Carbon Stocks, Respiration, CH_4, and N_2O in Upland Tundra." *Global Change Biology* 21(12): 4570–87.

Abbott, B. W., J. R. Larouche, J. B. Jones Jr, W. B. Bowden, and A. W. Balser. 2014. "Elevated Dissolved Organic Carbon Biodegradability from Thawing and Collapsing Permafrost." *Journal of Geophysical Research: Biogeosciences* 119(10): 2049–63.

Abràmoff, M. D., P. J. Magalhães, and S. J. Ram. 2004. "Image Processing with ImageJ." *Biophotonics International* 11(7): 36–42.

Ackerman, D., D. Griffin, S. E. Hobbie, and J. C. Finlay. 2017. "Arctic Shrub Growth Trajectories Differ across Soil Moisture Levels." *Global Change Biology* 23(10): 4294–302.

Ackerman, D. E., D. Griffin, S. E. Hobbie, K. Popham, E. Jones, and J. C. Finlay. 2018. "Uniform Shrub Growth Response to June Temperature across the North Slope of Alaska." *Environmental Research Letters* 13(4): 044013.

Addis, C. E., and M. S. Bret-Harte. 2019. "The Importance of Secondary Growth to Plant Responses to Snow in the Arctic." *Functional Ecology* 33(6): 1050–66.

Alsos, I. G., P. B. Eidesen, D. Ehrich, I. Skrede, K. Westergaard, G. H. Jacobsen, J. Y. Landvik, P. Taberlet, and C. Brochmann. 2007. "Frequent Long-Distance Plant Colonization in the Changing Arctic." *Science* 316(5831): 1606–9.

Andreu-Hayles, L., B. V. Gaglioti, L. T. Berner, M. Levesque, K. J. Anchukaitis, S. J. Goetz, and R. D'Arrigo. 2020. "A Narrow Window of Summer Temperatures Associated with Shrub Growth in Arctic Alaska." *Environmental Research Letters* 15(10): 105012.

Andruko, R., R. Danby, and P. Grogan. 2020. "Recent Growth and Expansion of Birch Shrubs across a Low Arctic Landscape in Continental Canada: Are These Responses More a Consequence of the Severely Declining Caribou Herd than of Climate Warming?" *Ecosystems* 23(7): 1362–79.

Argus, G. W. 2006. *Guide to Salix (Willow) in the Canadian Maritime Provinces (New Brunswick, Nova Scotia, and Prince Edward Island)*. Ottawa: Canadian Museum of Nature.

Balser, A. W., M. N. Gooseff, J. B. Jones, and W. B. Bowden. 2009. *Thermokarst Distribution and Relationships to Landscape Characteristics in the Feniak Lake Region, Noatak National Preserve, Alaska*. Fairbanks, AK: *Arctic Inventory and Monitoring Network*.

Balser, A. W., J. B. Jones, and R. Gens. 2014. "Timing of Retrogressive Thaw Slump Initiation in the Noatak Basin, Northwest Alaska, USA." *Journal of Geophysical Research: Earth Surface* 119(5): 1106–20.

Bartoń, K. 2020. "*Package 'MuMIn'—Tools for Performing Model Selection and Model Averaging. Automated Model Selection through Subsetting the Maximum Model, with Optional Constraints for Model Inclusion*." https://cran.r-project.org/web/packages/MuMIn/index.html.

Becker, M. S., T. Jonathan Davies, and W. H. Pollard. 2016. "Ground Ice Melt in the High Arctic Leads to Greater Ecological Heterogeneity." *Journal of Ecology* 104(1): 114–24.

Bergeron, Y., B. Denneler, D. Charron, and M.-P. Girardin. 2002. "Using Dendrochronology to Reconstruct Disturbance and Forest Dynamics around Lake Duparquet, Northwestern Quebec." *Dendrochronologia* 20(1–2): 175–89.

Bliss, L. C., and N. V. Matveyeva. 1992. "Circumpolar Arctic Vegetation." *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective* 59: 89.

Blok, D., M. M. P. D. Heijmans, S.-S. Gabriela, A. V. Kononov, T. C. Maximov, and F. Berendse. 2010. "Shrub Expansion May Reduce Summer Permafrost Thaw in Siberian Tundra." *Global Change Biology* 16(4): 1296–305.

Bowden, W. B., M. N. Gooseff, A. Balser, A. Green, B. J. Peterson, and J. Bradford. 2008. "Sediment and Nutrient Delivery from Thermokarst Features in the Foothills of the North Slope, Alaska: Potential Impacts on Headwater Stream Ecosystems." *Journal of Geophysical Research: Biogeosciences* 113(G2): 1–12.

Bret-Harte, M. S., M. C. Mack, G. R. Goldsmith, D. B. Sloan, J. DeMarco, G. R. Shaver, P. M. Ray, Z. Biesinger, and F. S. Chapin, III. 2008. "Plant Functional Types Do Not Predict Biomass Responses to Removal and Fertilization in Alaskan Tussock Tundra." *Journal of Ecology* 96(4): 713–26.

Bret-Harte, M. S., M. C. Mack, G. R. Shaver, D. C. Huebner, M. Johnston, C. A. Mojica, C. Pizano, and J. A. Reiskind. 2013. "The Response of Arctic Vegetation and Soils Following an Unusually Severe Tundra Fire." *Philosophical Transactions of the Royal Society B: Biological Sciences* 368(1624): 20120490.

Bret-Harte, M. S., G. R. Shaver, and F. S. Chapin, III. 2002. "Primary and Secondary Stem Growth in Arctic Shrubs: Implications for Community Response to Environmental Change." *Journal of Ecology* 90(2): 251–67.

Buchwal, A., G. Rachlewicz, P. Fonti, P. Cherubini, and H. Gärtner. 2013. "Temperature Modulates Intra-Plant Growth of *Salix polaris* from a High Arctic Site (Svalbard)." *Polar Biology* 36(9): 1305–18.

Buchwal, A., S. Weijers, D. Blok, and B. Elberling. 2019. "Temperature Sensitivity of Willow Dwarf Shrub Growth from Two Distinct High Arctic Sites." *International Journal of Biometeorology* 63(2): 167–81.

Buckeridge, K. M., and P. Grogan. 2008. "Deepened Snow Alters Soil Microbial Nutrient Limitations in Arctic Birch Hummock Tundra." *Applied Soil Ecology* 39(2): 210–22.

Bunn, A. G. 2008. "A Dendrochronology Program Library in R (DplR)." *Dendrochronologia* 26(2): 115–24.

Burnham, K. P., and D. R. Anderson. 1998. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York: Springer.

Carrer, M., E. Pellizzari, A. L. Prendin, M. Pividori, and M. Brunetti. 2019. "Winter Precipitation–Not Summer Temperature—Is Still the Main Driver for Alpine Shrub Growth." *Science of the Total Environment* 682: 171–9.

Chapin, F. S., III, M. Sturm, M. C. Serreze, J. P. McFadden, J. R. Key, A. H. Lloyd, A. D. McGuire, T. Scott Rupp, A. H. Lynch, and J. P. Schimel. 2005. "Role of Land-Surface Changes in Arctic Summer Warming." *Science* 310(5748): 657–60.

Chapin, F. S., III, G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. "Responses of Arctic Tundra to Experimental and Observed Changes in Climate." *Ecology* 76(3): 694–711.

Clements, F. E. 1916. *Plant Succession: An Analysis of the Development of Vegetation*, Vol 242. Washington, DC: Carnegie Institution of Washington.

Cray, H. A., and W. H. Pollard. 2015. "Vegetation Recovery Patterns Following Permafrost Disturbance in a Low Arctic Setting: Case Study of Herschel Island, Yukon, Canada." *Arctic, Antarctic, and Alpine Research* 47(1): 99–113.

Danby, R. K., and D. S. Hik. 2007. "Variability, Contingency and Rapid Change in Recent Subarctic Alpine Tree Line Dynamics." *Journal of Ecology* 95(2): 352–63.

d'Arrigo, R., R. Villalba, and G. Wiles. 2001. "Tree-Ring Estimates of Pacific Decadal Climate Variability." *Climate Dynamics* 18(3): 219–24.

DeMarco, J., M. C. Mack, and M. Syndonia Bret-Harte. 2011. "The Effects of Snow, Soil Microenvironment, and Soil Organic Matter Quality on N Availability in Three Alaskan Arctic Plant Communities." *Ecosystems* 14(5): 804–17.

Ebersole, J. J. 1989. "Role of the Seed Bank in Providing Colonizers on a Tundra Disturbance in Alaska." *Canadian Journal of Botany* 67(2): 466–71.

Eriksson, O., and H. Fröborg. 1996. "'Windows of Opportunity' for Recruitment in Long-Lived Clonal Plants: Experimental Studies of Seedling Establishment in Vaccinium Shrubs." *Canadian Journal of Botany* 74(9): 1369–74.

Euskirchen, E. S., A. D. McGuire, F. S. Chapin, III, S. Yi, and C. C. Thompson. 2009. "Changes in Vegetation in Northern Alaska under Scenarios of Climate Change, 2003–2100: Implications for Climate Feedbacks." *Ecological Applications* 19(4): 1022–43. https://doi.org/10.1890/08-0806.1.

Forbes, B. C., M. M. Fauria, and P. Zetterberg. 2010. "Russian Arctic Warming and 'Greening' Are Closely Tracked by Tundra Shrub Willows." *Global Change Biology* 16(5): 1542–54. https://doi.org/10.1111/j.1365-2486.2009.02047.x.

Fritts, H. C. 1966. "Growth-Rings of Trees: Their Correlation with Climate." *Science (New York, N.Y.)* 154(3752): 973–9. https://doi.org/10.1126/science.154.3752.973.

Fritts, H. C. 1976. *Tree Rings and Climate*. New York: Academic Press.

Gärtner, H., S. Lucchinetti, and F. H. Schweingruber. 2014. "New Perspectives for Wood Anatomical Analysis in Dendrosciences: The GSL1-Microtome." *Dendrochronologia* 32(1): 47–51.

Gärtner-Roer, I., I. Heinrich, and H. Gärtner. 2013. "Wood Anatomical Analysis of Swiss Willow (*Salix helvetica*) Shrubs Growing on Creeping Mountain Permafrost." *Dendrochronologia* 31(2): 97–104. https://doi.org/10.1016/j.dendro.2012.09.003.

George St, S., and T. R. Ault. 2014. "The Imprint of Climate within Northern Hemisphere Trees." *Quaternary Science Reviews* 89: 1–4.

Google Earth. 2020. "Map Showing Location of Lakes I Minus 1 and NE14." Google Earth. http://earthgoogle.com/web.

Gooseff, M. N., A. Balser, W. B. Bowden, and J. B. Jones. 2009. "Effects of Hillslope Thermokarst in Northern Alaska." *Eos, Transactions American Geophysical Union* 90(4): 29–30.

Grissino-Mayer, H. D. 2001. "Evaluating Crossdating Accuracy: A Manual and Tutorial for the Computer Program COFECHA." *Tree-Ring Research* 57(2): 205–21.

Hallinger, M., M. Manthey, and M. Wilmking. 2010. "Establishing a Missing Link: Warm Summers and Winter Snow Cover Promote Shrub Expansion into Alpine Tundra in Scandinavia." *New Phytologist* 186(4): 890–9. https://doi.org/10.1111/j.1469-8137.2010.03223.x.

Hamilton, T. D. 2003. *Glacial Geology of the Toolik Lake and Upper Kuparuk River Regions*. Fairbanks, AK: University of Alaska, Institute of Arctic Biology.

Huebner, D. 2022. "Tundra Shrub Ring Widths in Microns, North Slope Alaska 1965–2013." https://doi.org/10.18739/A2PV6B800.

Huebner, D. C., and M. S. Bret-Harte. 2019. "Microsite Conditions in Retrogressive Thaw Slumps May Facilitate Increased Seedling Recruitment in the Alaskan Low Arctic." *Ecology and Evolution* 9(4): 1880–97.

Huebner, D. C., V. Douhovnikoff, D. E. Wolf, and M. Syndonia Bret-Harte. 2019. "Recruitment Dynamics and Population Structure of Willows in Tundra Disturbed by Retrogressive Thaw Slump Thermokarst on Alaska's North Slope." *Perspectives in Plant Ecology, Evolution and Systematics* 41: 125494.

Kokelj, S. V., and M. T. Jorgenson. 2013. "Advances in Thermokarst Research." *Permafrost and Periglacial Processes* 24(2): 108–19.

Kokelj, S. V., J. Kokoszka, J. van der Sluijs, A. C. A. Rudy, J. Tunnicliffe, S. Shakil, S. E. Tank, and S. Zolkos. 2021. "Thaw-Driven Mass Wasting Couples Slopes with Downstream Systems, and Effects Propagate through Arctic Drainage Networks." *The Cryosphere* 15(7): 3059–81. https://doi.org/10.5194/tc-15-3059-2021.

Kokelj, S. V., T. C. Lantz, J. Kanigan, S. L. Smith, and R. Coutts. 2009. "Origin and Polycyclic Behaviour of Tundra Thaw Slumps, Mackenzie Delta Region, Northwest Territories, Canada." *Permafrost and Periglacial Processes* 20(2): 173–84.

Kokelj, S. V., M. J. Palmer, T. C. Lantz, and C. R. Burn. 2017. "Ground Temperatures and Permafrost Warming from Forest to Tundra, Tuktoyaktuk Coastlands and Anderson Plain, NWT, Canada." *Permafrost and Periglacial Processes* 28(3): 543–51.

Kokelj, S. V., J. Tunnicliffe, D. Lacelle, T. C. Lantz, K. S. Chin, and R. Fraser. 2015. "Increased Precipitation Drives Mega Slump Development and Destabilization of Ice-Rich Permafrost Terrain, Northwestern Canada." *Global and Planetary Change* 129: 56–68.

Lacelle, D., J. Bjornson, and B. Lauriol. 2010. "Climatic and Geomorphic Factors Affecting Contemporary (1950–2004) Activity of Retrogressive Thaw Slumps on the Aklavik Plateau, Richardson Mountains, NWT, Canada." *Permafrost and Periglacial Processes* 21(1): 1–15. https://doi.org/10.1002/ppp.666.

Lafleur, P. M., and E. R. Humphreys. 2018. "Tundra Shrub Effects on Growing Season Energy and Carbon Dioxide Exchange."

Environmental Research Letters 13(5): 055001. https://doi.org/10.1088/1748-9326/aab863.

Lambert, J. D. H. 1972. "Plant Succession on Tundra Mudflows: Preliminary Observations." *Arctic* 25(2): 99–106.

Lantz, T. C., and S. V. Kokelj. 2008. "Increasing Rates of Retrogressive Thaw Slump Activity in the Mackenzie Delta Region, NWT, Canada." *Geophysical Research Letters* 35(6): 1–5.

Lantz, T. C., S. V. Kokelj, S. E. Gergel, and G. H. R. Henry. 2009. "Relative Impacts of Disturbance and Temperature: Persistent Changes in Microenvironment and Vegetation in Retrogressive Thaw Slumps." *Global Change Biology* 15(7): 1664–75.

Lawrence, D. M., and S. C. Swenson. 2011. "Permafrost Response to Increasing Arctic Shrub Abundance Depends on the Relative Influence of Shrubs on Local Soil Cooling versus Large-Scale Climate Warming." *Environmental Research Letters* 6(4): 045504.

Lewkowicz, A. G., and R. G. Way. 2019. "Extremes of Summer Climate Trigger Thousands of Thermokarst Landslides in a High Arctic Environment." *Nature Communications* 10(1): 1–11.

Luo, J., F. Niu, Z. Lin, M. Liu, and G. Yin. 2019. "Recent Acceleration of Thaw Slumping in Permafrost Terrain of Qinghai-Tibet Plateau: An Example from the Beiluhe Region." *Geomorphology* 341: 79–85.

Mack, M. C., E. A. G. Schuur, M. Syndonia Bret-Harte, G. R. Shaver, and F. Stuart Chapin. 2004. "Ecosystem Carbon Storage in Arctic Tundra Reduced by Long-Term Nutrient Fertilization." *Nature* 431(7007): 440–3.

Myers-Smith, I. H., S. C. Elmendorf, P. S. A. Beck, M. Wilmking, M. Hallinger, D. Blok, K. D. Tape, S. A. Rayback, M. Macias-Fauria, and B. C. Forbes. 2015. "Climate Sensitivity of Shrub Growth across the Tundra Biome." *Nature Climate Change* 5(9): 887–91.

Myers-Smith, I. H., and D. S. Hik. 2013. "Shrub Canopies Influence Soil Temperatures but Not Nutrient Dynamics: An Experimental Test of Tundra Snow–Shrub Interactions." *Ecology and Evolution* 3(11): 3683–700.

Myers-Smith, I. H., J. T. Kerby, G. K. Phoenix, J. W. Bjerke, H. E. Epstein, J. J. Assmann, C. John, L. Andreu-Hayles, S. Angers-Blondin, and P. S. A. Beck. 2020. "Complexity Revealed in the Greening of the Arctic." *Nature Climate Change* 10(2): 106–17.

Nakagawa, S., P. C. D. Johnson, and H. Schielzeth. 2017. "The Coefficient of Determination R^2 and Intra-Class Correlation Coefficient from Generalized Linear Mixed-Effects Models Revisited and Expanded." *Journal of the Royal Society Interface* 14(134): 20170213.

Nitze, I., G. Grosse, B. M. Jones, V. E. Romanovsky, and J. Boike. 2018. "Remote Sensing Quantifies Widespread Abundance of Permafrost Region Disturbances across the Arctic and Subarctic." *Nature Communications* 9(1): 1–11.

Olefeldt, D., S. Goswami, D. Guido Grosse, G. H. Hayes, A. Peter Kuhry, V. E. David McGuire, A. B. Romanovsky, K. Sannel, and E. A. G. Schuur. 2016. "Circumpolar Distribution and Carbon Storage of Thermokarst Landscapes." *Nature Communications* 7(1): 1–11.

Oliver, C. D. 1980. "Forest Development in North America Following Major Disturbances." *Forest Ecology and Management* 3: 153–68.

Osterkamp, T. E., M. T. Jorgenson, E. A. G. Schuur, Y. L. Shur, M. Z. Kanevskiy, and J. G. Vogel. 2007. "Physical and Ecological Changes Associated with Warming Permafrost." *Climatic Change* 20: 235–56.

Owczarek, P., A. Latocha, M. Wistuba, and I. Malik. 2013. "Reconstruction of Modern Debris Flow Activity in the Arctic Environment with the Use of Dwarf Shrubs (South-Western Spitsbergen)—A New Dendrochronological Approach." *Zeitschrift für Geomorphologie* 57(3): 75–95.

Parker, T. C., J.-A. Subke, and P. A. Wookey. 2015. "Rapid Carbon Turnover beneath Shrub and Tree Vegetation Is Associated with Low Soil Carbon Stocks at a Subarctic Treeline." *Global Change Biology* 21(5): 2070–81.

Pizano, C., A. F. Barón, E. A. G. Schuur, K. G. Crummer, and M. C. Mack. 2014. "Effects of Thermo-Erosional Disturbance on Surface Soil Carbon and Nitrogen Dynamics in Upland Arctic Tundra." *Environmental Research Letters* 9(7): 075006.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Romanovsky, V., M. Burgess, S. Smith, K. Yoshikawa, and J. Brown. 2002. "Permafrost Temperature Records: Indicators of Climate Change." *Eos, Transactions American Geophysical Union* 83(50): 589–94.

Saltelli, A. 2002. "Making Best Use of Model Evaluations to Compute Sensitivity Indices." *Computer Physics Communications* 145(2): 280–97.

SAS Institute. 2021. *Release Notes for JMP 16.1.0*. Cary, NC: SAS Institute Inc.

Schimel, J. P., C. Bilbrough, and J. M. Welker. 2004. "Increased Snow Depth Affects Microbial Activity and Nitrogen Mineralization in Two Arctic Tundra Communities." *Soil Biology and Biochemistry* 36(2): 217–27.

Schuur, E. A. G., K. G. Crummer, J. G. Vogel, and M. C. Mack. 2007. "Plant Species Composition and Productivity Following Permafrost Thaw and Thermokarst in Alaskan Tundra." *Ecosystems* 10(2): 280–92.

Schuur, E. A. G., J. G. Vogel, K. G. Crummer, H. Lee, J. O. Sickman, and T. E. Osterkamp. 2009. "The Effect of Permafrost Thaw on Old Carbon Release and Net Carbon Exchange from Tundra." *Nature* 459(7246): 556–9.

Schweingruber, F. H., D. Eckstein, F. Serre-Bachet, and O. U. Bräker. 1990. "Identification, Presentation and Interpretation of Event Years and Pointer Years in Dendrochronology." *Dendrochronologia* 8: 9–38.

Schweingruber, F. H., and P. Poschlod. 2005. "Growth Rings in Herbs and Shrubs: Life Span, Age Determination and Stem Anatomy." *Forest Snow and Landscape Research* 79(3): 195–415.

Siekacz, L., and G. Rachlewicz. 2014. "Salix polaris *Growth Responses to Active Layer Detachment and Solifluction Processes in High Arctic*." Geophysical Research Abstracts, Vol. 17, EGU 2015-686, EGU General Assembly 2015.

Sørensen, M. V., R. Strimbeck, K. O. Nystuen, R. E. Kapas, B. J. Enquist, and B. J. Graae. 2018. "Draining the Pool? Carbon Storage and Fluxes in Three Alpine Plant Communities." *Ecosystems* 21(2): 316–30.

Speer, J. H. 2010. *Fundamentals of Tree-Ring Research*. Tucson, AZ: University of Arizona Press.

Sturm, M., T. Douglas, C. Racine, and G. E. Liston. 2005. "Changing Snow and Shrub Conditions Affect Albedo with Global Implications." *Journal of Geophysical Research: Biogeosciences* 110 (G1): 1–13.

Sturm, M., J. Holmgren, J. P. McFadden, G. E. Liston, F. S. Chapin, III, and C. H. Racine. 2001. "Snow–Shrub Interactions in Arctic Tundra: A Hypothesis with Climatic Implications." *Journal of Climate* 14(3): 336–44.

Sullivan, P. F., R. R. Pattison, A. H. Brownlee, S. M. P. Cahoon, and T. N. Hollingsworth. 2016. "Effect of Tree-Ring Detrending Method on Apparent Growth Trends of Black and White Spruce in Interior Alaska." *Environmental Research Letters* 11(11): 114007.

Swanson, D. K. 2021. "Permafrost Thaw-Related Slope Failures in Alaska's Arctic National Parks, c. 1980–2019." *Permafrost and Periglacial Processes* 32(3): 392–406.

Tape, K. D., B. M. Jones, C. D. Arp, I. Nitze, and G. Grosse. 2018. "Tundra Be Dammed: Beaver Colonization of the Arctic." *Global Change Biology* 24(10): 4478–88.

Toolik Environmental Data Center Team. 2020. *Meteorological Monitoring Program at Toolik, Alaska*. Fairbanks, AK: Toolik Field Station, Institute of Arctic Biology, University of Alaska Fairbanks.

U.S. Geological Survey. 2022. USGS EarthExplorer Website. https://earthexplorer.usgs.gov/.

Vavrek, M. C., N. Fetcher, J. B. McGraw, G. R. Shaver, F. S. Chapin, III, and B. Bovard. 1999. "Recovery of Productivity and Species Diversity in Tussock Tundra Following Disturbance." *Arctic, Antarctic, and Alpine Research* 31(3): 254–8.

Viereck, L. A., and E. L. Little. 1972. *Alaska Trees and Shrubs*. Washington, DC: US Forest Service.

Weijers, S., R. Pape, J. Löffler, and I. H. Myers-Smith. 2018. "Contrasting Shrub Species Respond to Early Summer Temperatures Leading to Correspondence of Shrub Growth Patterns." *Environmental Research Letters* 13(3): 034005.

Wigley, T. M. L., K. R. Briffa, and P. D. Jones. 1984. "On the Average Value of Correlated Time Series, with Applications in Dendroclimatology and Hydrometeorology." *Journal of Applied Meteorology and Climatology* 23(2): 201–13.

Zang, C., and F. Biondi. 2015. "Treeclim: An R Package for the Numerical Calibration of Proxy-Climate Relationships." *Ecography* 38(4): 431–6.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Huebner, Diane C., Agata Buchwal, M. Syndonia Bret-Harte. 2022. "Retrogressive Thaw Slumps in the Alaskan Low Arctic May Influence Tundra Shrub Growth More Strongly than Climate." *Ecosphere* 13(6): e4106. https://doi.org/10.1002/ecs2.4106