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Warmer temperatures promote shrub radial growth but not cover in the central Canadian Arctic

Robert W. Buchkowski[a,b], Douglas W. Morris[a], William D. Halliday[a,c], Angélique Dupuch[a,d], Clara Morrissette-Boileau[e], and Stéphane Boudreau[e]

[a]Department of Biology, Lakehead University, Thunder Bay, Ontario, Canada; [b]Department of Biology, University of Western Ontario, London, Ontario, Canada; [c]Wildlife Conservation Society Canada, Department of Biology, University of Victoria, Victoria, , Canada; [d]Département des Sciences Naturelles, Université du Québec en Outaouais Institut des Sciences de la Forêt Tempérée, Québec City, Québec, Canada; [e]Département de Biologie, Centre d'études Nordiques Université Laval 1045 Avenue de la Médecine Québec, Laval, Québec, Canada

ABSTRACT

We assessed the response of *Salix richardsonii*, a deciduous shrub, to climate change by determining the combination of climatic factors that regulated its growth over the past half-century. We tested whether increasing arctic temperatures promote shrub growth and increased cover. We analyzed fifty-four stems (out of seventy sampled) from *S. richardsonii* shrubs near the Walker Bay research station in Nunavut, Canada (68°21′ N, 108°05′ W) and surveyed shrub cover in 1996 and 2010. We measured annual growth rings, removed the age-related pattern, and used a response function analysis to explore the climate–growth relationship. The standardized chronology was positively associated with mean July temperature, corroborating other evidence that summer temperature is an important driver of shrub radial growth. Basal area increment revealed a long-term increase in radial growth, although it has stabilized this century. Surveys showed no significant increase in shrub cover at Walker Bay from 1996 to 2010. Our results support a growing body of evidence that increased shrub growth does not necessarily translate into a prolonged increase in shrub cover. Instead, we conclude that the heterogeneity of the arctic shrub response to climate change may be associated with variation in the proximate factors limiting recruitment such as water table saturation and herbivory.

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Climate change; dendrochronology; response function; *Salix richardsonii*; Walker Bay

Introduction

Global climate change is altering ecosystem dynamics and function, especially in the Arctic region (ACIA 2005; Macias-Fauria et al. 2012; Intergovernmental Panel on Climate Change 2013; Van der Kolk et al. 2016). Compared to other ecosystems, tundra is experiencing a substantial air temperature increase and more extreme precipitation events (e.g., Hinzman et al. 2005). Concurrent with this climate change, most of the Arctic is "greening," as evidenced by increases in the Normalized Difference Vegetation Index (NDVI; Raynolds et al. 2008; Verbyla 2008; Ju and Masek 2016; Bonney, Danby, and Treitz 2018). Field surveys indicate that shrub cover increase is a major driver of the greening across the Arctic (Tape, Sturm, and Racine 2006; Forbes, Fauria, and Zetterbergs 2010; Blok, Schaepman-Strub et al. 2011; Myers-Smith et al. 2011; Ropars and Boudreau 2012). However, in other regions of the Arctic, disturbances such as extreme climatic events, defoliating insects, and fire can lead to a decrease of the primary productivity, a phenomenon better known as the "browning" of the Arctic (Jepsen et al. 2013; Bjerke et al. 2014; Phoenix and Bjerke 2016). Determining where and why the Arctic is greening or browning is foundational to our understanding of global change.

Pan-Arctic estimates of shrub expansion are based on overall correlations with temperature, precipitation, and NDVI (Walker 1987; Sturm et al. 2005; Blok, Schaepman-Strub et al. 2011; Loranty, Goetz, and Beck 2011; Bonney, Danby, and Treitz 2018). Shrub expansion is, however, heterogeneous at the circumpolar scale (Raynolds et al. 2008; Myers-Smith et al. 2011; Tape et al. 2012; Bonney, Danby, and Treitz 2018), so that these large-scale correlations can be poor predictors of site-specific dynamics when they are not causal relationships (e.g., Bradford et al. 2014). Consequently, estimates of pan-Arctic shrub expansion require thorough field data to identify why shrub expansion

CONTACT Robert W. Buchkowski robert.buchkowski@gmail.com Department of Biology, Lakehead University, 955 Oliver Road, Ontario G1V 0A6, Canada.
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is heterogeneous. For example, an increase in radial growth might not lead to an increase in shrub cover if recruitment is inhibited by local factors (Sturm et al. 2005). An imperfect relationship at small scales is possible even if data from ground surveys across large spatial scales suggest that increases in shrub cover are correlated with higher radial growth (Sturm et al. 2005; Forbes, Fauria, and Zetterbergs 2010; Hallinger, Manthey, and Wilmking 2010; Boelman et al. 2011; Büntgen et al. 2015). It is therefore important to further document temporal patterns in shrub cover as well as spatial variation in the combination of climate factors influencing growth and recruitment (Myers-Smith et al. 2011; Myers-Smith, Elmendorf et al. 2015).

Site-specific relationships between climate and shrub radial growth can be assessed by using dendrochronological techniques that allow the study of growth ring formation in woody species. Previous dendrochronological studies on shrub species in the Arctic revealed that summer temperature and/or precipitation are important drivers of shrub growth (Myers-Smith, Elmendorf et al. 2015; Ropars et al. 2015; Young et al. 2016; Weijers et al. 2018; Ackerman et al. 2018). Warmer summer temperature can lead to higher photosynthetic rate, lengthen the growing season, and indirectly increase nutrient availability through a positive impact on nutrient mineralization (Chapin 1983; Chapin, Matson, and Vitousek 2011). On the other hand, warmer summer temperatures can lead to hydric stresses triggered by greater evapotranspiration rates (Fritts 1976; Chapin 1983). Empirical data suggest that the relationship between a shrub's radial growth and climate variables was stronger at sites with higher satellite-derived estimates of soil moisture (Myers-Smith, Elmendorf et al. 2015), although Ropars et al. (2017) argued that such observations might result from differences in the sampling protocol (stems vs. root collars). Hydric stress can halt cell expansion and division and reduce the rates of photosynthesis, thereby limiting radial growth (Fritts 1976; Słupianek, Wojtuń, and Myśkow 2019). Given the aridity of many Arctic regions, a warmer climate regime could exacerbate this hydric stress and decouple the relationship between temperature and radial growth (Zalatan and Gajewski 2006; Verbyla 2008; McKenney et al. 2011; Bjorkman et al. 2018). We address this theme by evaluating the causal factors influencing *Salix richardsonii* growth and its correlation with shrub cover in Canada's central Arctic.

Salix shrub species are widely distributed throughout the Arctic (Bret-Harte, Shaver, and Chapin 2002; Walker et al. 2006; Elmendorf et al. 2012; Büntgen et al. 2015), which make them suitable indicators to assess the effects of global warming on terrestrial ecosystems. The dendrochronological potential of *Salix* species has already been demonstrated by studies on *S. richardsonii* (Walker 1987), *S. lanata* (Forbes, Fauria, and Zetterbergs 2010), *S. pulchra* (Blok, Sass-Klaassen et al. 2011; Weijers et al. 2018), *S. glauca* (Young et al. 2016; Gamm et al. 2018), *S. herbacea* (Büntgen et al. 2015), *S. polaris* (Buchwal et al. 2019), and *S. arctica* (Woodcock and Bradley 1994; Schmidt, Baittinger, and Forchhammer 2006; Schmidt et al. 2010; Buchwal et al. 2019). Their growth chronologies exhibit a strong climate signal (temperature or precipitation), but only Forbes, Fauria, and Zetterbergs (2010) reported a long-term positive trend in *S. lanata* growth. Moreover, because *Salix* shrubs are dioecious, males and females may display differential climate sensitivity because females are thought to allocate more resources to reproduction (Sakai, Sasa, and Sakai 2006) and may have fewer resources left over for radial growth (Nissinen et al. 2016; Gouker et al. 2020; but see Schmidt et al. 2010).

In this study, we sampled *S. richardsonii* stems in order to explore trends in the annual radial growth of this poorly studied species (most recent study: Walker 1987) near Walker Bay (Nunavut, Canada), which is an understudied region (Myers-Smith, Elmendorf et al. 2015). We also conducted two field surveys to evaluate shrub cover changes over the last two decades. Our main objectives were to answer the following research questions: (1) What are the drivers of *S. richardsonii* radial growth? (2) Does radial growth differ between males and females? (3) Can we detect a long-term trend in *S. richardsonii* radial growth? and (4) Has shrub cover changed at our study site? Based on the current literature (Liang and Eckstein 2009; Forbes, Fauria, and Zetterbergs 2010; Hallinger, Manthey, and Wilmking 2010; Hantemirov et al. 2011; Boudreau and Villeneuve-Simard 2012; Myers-Smith, Elmendorf et al. 2015; Ropars et al. 2015, 2017; Young et al. 2016), we predict that radial growth of *S. richardsonii* will be positively associated with summer temperature. We expect that radial growth of male shrubs will be higher than for female shrubs because of differences in the resources allocated to reproduction. We also expect to observe a long-term increase in *S. richardsonii* radial growth in response to warmer summer temperatures since the 1950s. Finally, we predict that shrub cover will have increased over the last two decades in response to warmer temperatures.

Methods

Study species, study site, and climate data

Salix richardsonii is a widely distributed North American shrub species. From Alaska, it extends eastward across northern Canada to Baffin Island. It grows in a variety of habitats such as floodplains, river terraces, and wet meadows, as well as on drumlin fields and gravel ridges (Argus

2004), and displays notable phenotypic variation associated with local climate conditions (Walker 1987; Argus 2004).

We conducted field surveys and collected stems of *S. richardsonii* near Walker Bay on the Kent Peninsula in Nunavut, Canada (68°21′ N, 108°05′ W; Figures 1a and 1b). This species is unevenly distributed across the landscape in patches that can be up to 0.2 km^2. The relatively flat landscape at Walker Bay is characterized by a mosaic of xeric upland hummocks covered with *Dryas integrifolia, S. arctica, S. richardsonii*, and other shrub species that grade into mesic sedge-dominated (*Carex* spp.) meadows. At Walker Bay, *S. richardsonii* is the dominant erect shrub species, growing approximately 0.5 to 1.25 m high with significant horizontal spread (Figure 1c).

We acquired climatic data (mean monthly temperature and total monthly precipitation) from an Environment Canada weather station located at Cambridge Bay, approximately 150 km northeast of the field site (http://climate.weather.gc.ca/historical_data/search_historic_data_ e.html). This climatic station was chosen because temperature and precipitation data were only available from 1998 to 2004 at our study site. Cambridge Bay, like Walker Bay, is in bioclimate subzone D (Walker et al. 2005) with mean annual temperature of −14.4°C (8.4°C in July) and mean annual precipitation of 141.6 mm for the period from 1949 to 2014. Grouping these data into pre-1980 and post-1980 intervals demonstrates a clear mean annual temperature shift in the region, from −15.1°C ± 1.0°C for the 1949–1979 period to −13.8°C ± 1.3°C afterward. Mean total precipitation has not changed (1949–1979: 138 ± 27 mm; 1980–2014: 145 ± 28 mm).

Sample collection and preparation

A total of seventy stems, each from an individual *S. richardsonii* shrub, were sampled in June of 2010 (n = 17), 2011 (n = 41), and 2015 (n = 12; Supporting Information Table 1). In June 2010, we randomly sampled one shrub in each of twelve 0.35 ha lemming sampling grids that were also used to survey shrub cover (Figure 1b). We collected four additional shrubs in separate quadrats of a 7.3 ha former predator field exclosure (description in Dupuch

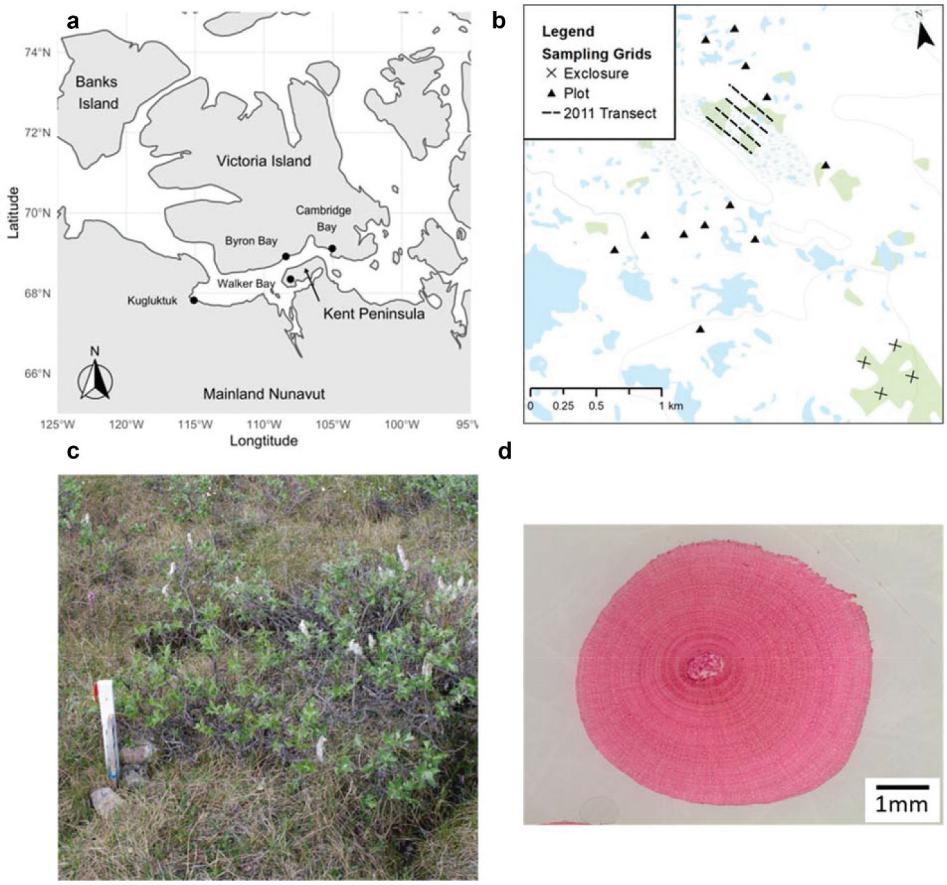

Figure 1. (a) The location of Walker Bay and potential sources of climate data in the central Canadian Arctic, (b) the location of our sampling plots at Walker Bay, (c) an image of a *Salix richadsonii* shrub at Walker Bay, and (d) an example of a stained cross section. There was one shrub sampled in 2010 from a snap-trap transect hidden by the legend in (b). Photo credit: Angélique Dupuch and Clara Morrissette-Boileau.

et al. 2014), plus one additional shrub on an abandoned snap-trap transect used by Krebs et al. (2002) in their assessment of synchronous rodent dynamics. In June 2011, we randomly sampled forty-one shrubs from four 500-m-long transects spaced 100 m apart in a large patch of shrubs parallel to a low rocky ridge. We selected the shrub nearest to each of ten randomly generated distances along each 500-m transect (Figure 1b). We completed our sampling in June 2015 by collecting one additional shrub growing adjacent to each of the twelve lemming sampling grids sampled in 2010 (the closest shrub to a randomly assigned corner of the grid). The 2010 and 2015 shrubs yielded a more representative geographical sample across our 20 km^2 study area as well as potential for a longer dendrochronological series. Whereas our sampling in 2010 and 2015 was designed to capture variation in shrub growth at long-term research plots spread across the landscape, our 2011 sampling was designed to study an extensive patch of *S. richardsonii* located outside the long-term plots. Upon collating the data, we merged the data sets because there was not enough statistical power to analyze differences among them.

We sampled only undamaged shrubs with at least three stems because herbivory or disturbance from muskoxen (*Ovibos moschatus*; Blok, Schaepman-Strub et al. 2011) can depress shrub growth. We harvested the base of the largest stem of each shrub, excluding any shrubs for which the base was frozen in ice. We placed the labeled stems and representative catkins for sex determination in labeled and sealed plastic bags.

In the laboratory, we determined the sex of each sampled individual, when possible, by examining catkins under a dissecting microscope. We were only able to identify the sex of twenty-two shrubs, all sampled in 2011, because many plants did not have catkins that were developed enough to identify sex. Our analysis of differences between male and female shrubs is restricted to these individuals. Samples from the base of each stem were boiled for at least 4 hours before 20-μm sections were sliced using a sledge microtome (WSL-Core-Microtome, Zürich, Switzerland). We stained one section per shrub using safranin (1 percent solution, Safranin O; Fisher Science Education, Hanover Park, IL) and mounted them on glass slides using a 66 percent toluene solution (SHUR/mountTM liquid cover glass; Triangle Biomedical Sciences, Cincinnati, OH).

Tree-ring measurement, cross-dating, and chronology development

We digitized individual slides with a binocular-mounted camera at 0.67× magnification, unless a higher magnification was necessary to visualize the rings (Figure 1d; Olympus SZ61 with a SC100 camera, Richmond Hill, ON, Canada). We uploaded images to LIGNOVISION (v1.36; Rinntech, Heidelberg, Germany), a dendrochronological software, and we measured two radii for each cross section (Hallinger, Manthey, and Wilmking 2010). We identified discontinuous rings by comparing the number of rings counted on each radius and then searched sections manually when we encountered discrepancies (Stokes and Smiley 1968). We assigned a width of 1 μm (i.e., the lower limit of precision) to growth rings that were partially missing or too narrow to be measured ($N = 2$), in order to obtain accurate chronologies in relation to age (Stokes and Smiley 1968). We accounted for eccentric growth by averaging the yearly ring width from each radius. Individual chronologies were visually and statistically verified with COFECHA by inspecting the dating quality of the series and calculating the correlations between chronologies (Center for Northern Studies, Québec, QC, Canada; COFECHA, Tree Ring Lab, Palisades, NY). We used the cross-dating information from COFECHA to add missing rings into growth series with significant negative correlations to the chronology and excluded sixteen shrubs that did not cross-date with the remaining fifty-four. Considering the heterogeneity of the sampling method, this number is acceptable (e.g., Zalatan and Gajewski 2006). The selected shrubs had an expressed population signal of 0.87 (Wigley, Briffa, and Jones 1984; Buras 2017) and a mean series intercorrelation of 0.43 ± 0.23, and the first-order autocorrelation of the chronology was 0.43 ± 0.21. The individual cross-dated ring width curves were standardized using a cubic spline with a knot every nine years to eliminate age related growth trends. We averaged these standardized chronologies to produce a standardized ring width chronology.

One serious limitation in many assessments of shrub growth over time is that standardization will remove temporal trends from the data (Ropars et al. 2015). A significant correlation between average shrub age and year in our data set ($r = 0.77$, $p < .001$, $df = 91$) suggests that a relatively large amount of variation associated with time was removed by age standardization. We therefore used the standardized chronology only to identify the climatic drivers of *S. richardsonii* radial growth (response function; see Statistical analysis section). To infer the long-term growth trend, we estimated radial growth by calculating the basal area increment (or ring area) of the fifty-four individuals used to build the standardized ring width chronology, assuming circular cross sections after averaging the two radii for each shrub. This procedure eliminates the geometrical decrease of ring widths with increasing stem diameter (LeBlanc 1996), thus emphasizing the ecological or climatic signal. The regional curve standardization technique used by others (e.g., Forbes, Fauria, and Zetterbergs

2010) to standardize age-related growth was not appropriate for our data because our shrubs had a variable age–growth trend (Supporting Information Figure 7). Finally, we used the raw ring width data to search for a difference in growth between males and females.

Shrub cover surveys

We collected data on the cover of tall (>25 cm) and short shrubs (<25 cm) in twelve permanent 60 m × 60 m lemming sampling grids located at least 100 m apart and separated by ridges, ponds, or mud flats (see Morris, Davidson, and Krebs [2000] for a complete plot description). Tall shrubs were mostly *S. richardsonii*, whereas short shrubs were mostly *S. arctica*. To determine tall and short shrub cover, we recorded their presence at 3,000 systematically distributed points along 300 10-m transects located within the twelve sampling grids (Morris, Davidson, and Krebs 2000). These surveys were conducted in 1996 and 2010.

Statistical analysis

Response functions (equivalent to partial regression coefficients from a multiple regression on the principal components of temperature and precipitation data) during the period 1949–2013 (i.e., when we had data for both shrub growth and monthly climatic data) were performed with the bootRes package (dcc function; Zang and Biondi 2013) of the R software (v3.0.2; R Development Core Team, Vienna, Austria) to assess the influence of mean monthly temperatures and total monthly precipitation on standardized ring width chronology. We examined the climate–growth relationship between June of the previous growing season to September of the current growing season. The default functions in the bootRes package use 1,000 iterations, a setting that is hard-coded into the functions. We recoded these functions to allow us to run 10,000 iterations, because some of our response function confidence intervals were close to zero. We also examined the climate–growth relationship on a restricted time frame corresponding to the period where shrub cover was assessed (1996–2010). Due to the restricted number of years during this time frame ($N = 15$), we assessed only the influence of mean monthly temperature and total monthly precipitation from March to September (seven months) of the current growing year.

We tested whether there was a significant difference in growth between male and female shrubs using a linear mixed effects model with individual shrub as a random effect and a correction of autocorrelated values within raw data using a first-order autoregressive covariance structure. Models were run in the R Package nlme with the function lme maximizing the restricted maximum likelihood (Pinheiro et al. 2010).

We used Fisher's exact test to determine whether there was a significant change in the cover of tall and short shrubs between 1996 and 2010. We evaluated the possible impact of comparing shrub growth and shrub cover over different periods of time using a moving correlation analysis. We measured shrub cover change over a fourteen-year period (1996–2010), and so we calculated the trend in radial growth and the relationship between growth and climate variables for every fourteen-year window in the data set to plot changes over time. This analysis helped us identify whether the fourteen-year period for which we had shrub cover data (1996–2010) was typical of the entire chronology.

Results

Mean annual temperature at Cambridge Bay between 1949 and 2014 increased significantly (mean annual temperature = 0.04(year) − 93.1, $r = 0.57$, $p < .001$; Figure 2a). There was no significant trend in total annual precipitation ($r = 0.17$, $p = .174$). Overall, the regional climate records suggest a general increase in temperatures with no associated changes in precipitation. There was no significant increase in mean annual temperature during the 1996–2010 period ($r = 0$, $p = .65$; Figure 2a).

The shrubs used to build the standardized chronology (Figure 3) had a mean age of thirty-one years (minimum = eight, maximum = eighty-eight). The response coefficient for July temperature was significantly correlated with shrub growth between 1949 and 2013 (Figure 4a; $r = 0.34$; 95 percent confidence interval [CI], 0.11–0.54). July temperature increased significantly between 1949 and 2014 (mean July temperature = 0.03(year) − 57.6, $r = 0.40$, $p < .001$; Figure 2b). For the restricted chronology (1996–2010), the response function coefficient for July temperature was not significantly correlated with shrub growth ($r = 0.09$; 95 percent CI, −0.07 to 0.28) even though the univariate relationship was still significant (Figure 5b). Across the entire chronology, the relationship between July temperature and shrub growth strengthened in the 1970s (before 1970s, r≈0 and after 1970s, r≈0.5; Figure 6b).

Mean monthly precipitation was not a significant driver of *S. richardsonii* radial growth for the full chronology (Figure 4b; Question 1). However, precipitation became important in the restricted chronology. Total monthly precipitation response function coefficients for May ($r = −0.26$; 95 percent CI, −0.51 to −0.03), July ($r = −0.38$; 95 percent CI, −0.60 to −0.17), and August ($r = −0.29$; 95 percent CI, −0.11 to −0.17) were significant for the restricted chronology, although only July precipitation

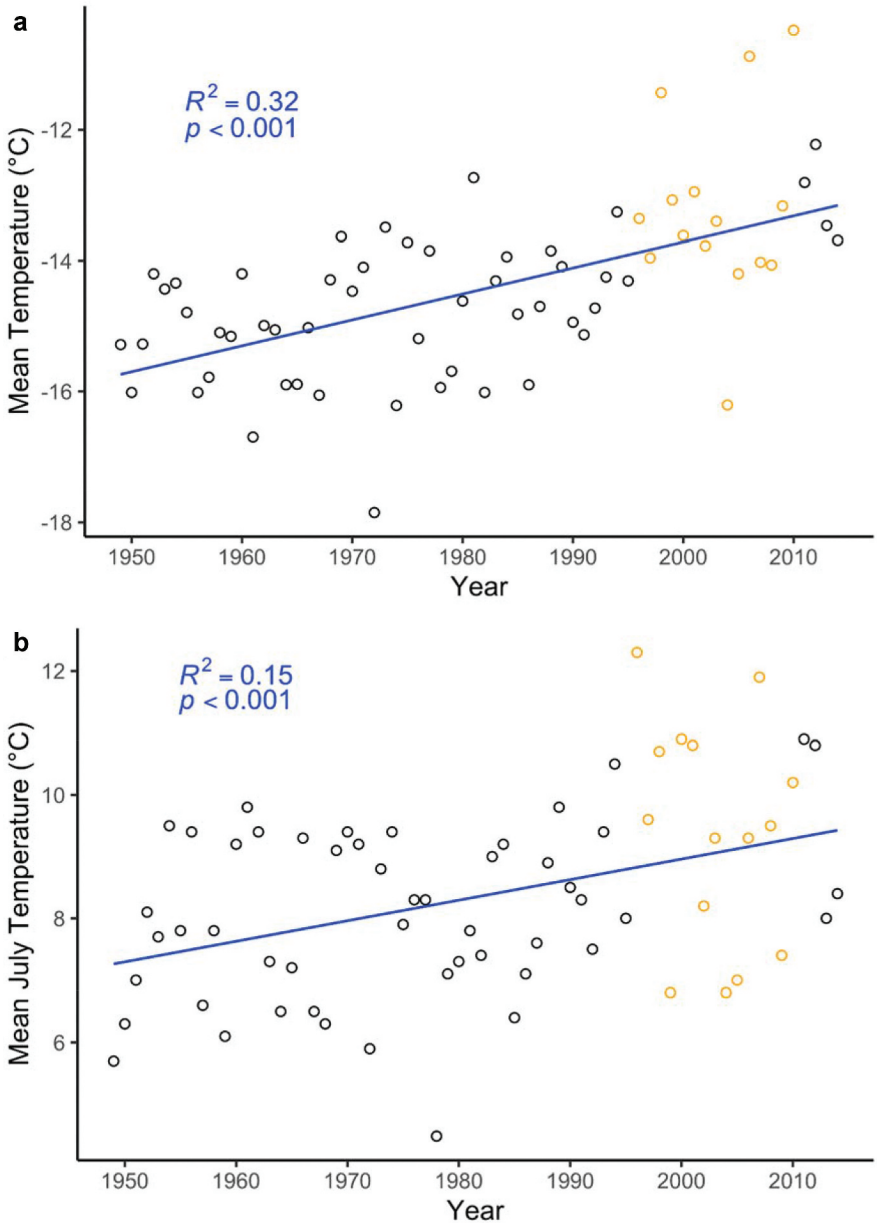

Figure 2. The trend in mean (a) annual temperature and (b) July temperature at the Cambridge Bay Airport since 1949 (data from Environment Canada's weather station at Cambridge Bay, approximately 150 km northeast of the field site); Blue lines are predicted from linear models using the full data set, and orange data points represent the data from 1996 to 2010 (no significant regressions: [a] $p = .65$; [b] $p = .39$) when we have shrub cover estimates.

showed a strong univariate correlation (Supporting Information Figure 9).

Female ($n = 15$) and male ($n = 7$) shrubs did not differ significantly in their annual growth (mean male ring width = 82.1 ± 64.8 µm; mean female ring width = 79.5 ± 54.7 µm; df = 20, $t = 0.03$, $p = .975$; Question 2).

Basal area increment (or ring area) increased over time, suggesting an increase of S. *richardsonii* radial growth ($F_{1,91} = 269$, $p < .001$; Figure 5a; Question 3). Such a result accords with the fact that radial growth is positively influenced by July mean temperature which increased from 1949 to 2013. As expected, we observed a significant relationship between basal area increment and mean July temperature ($F_{1,64} = 25.56$, $p < .001$; Figure 5b). For the restricted chronology (1996–2010), there was no significant trend in shrub growth ($r = 0$, $p = .74$; Figure 5a) but there was still a significant univariate relationship between growth and July temperature ($F_{1,13} = 4.98$, $p = .04$; Figure 5b) even though the response function coefficient was no longer significant (Figure 4a).

Point count data on the cover of both tall—mostly *S. richardsonii*—and short shrubs at Walker Bay indicate no change in mean cover from 1996 to 2010 (Fisher's

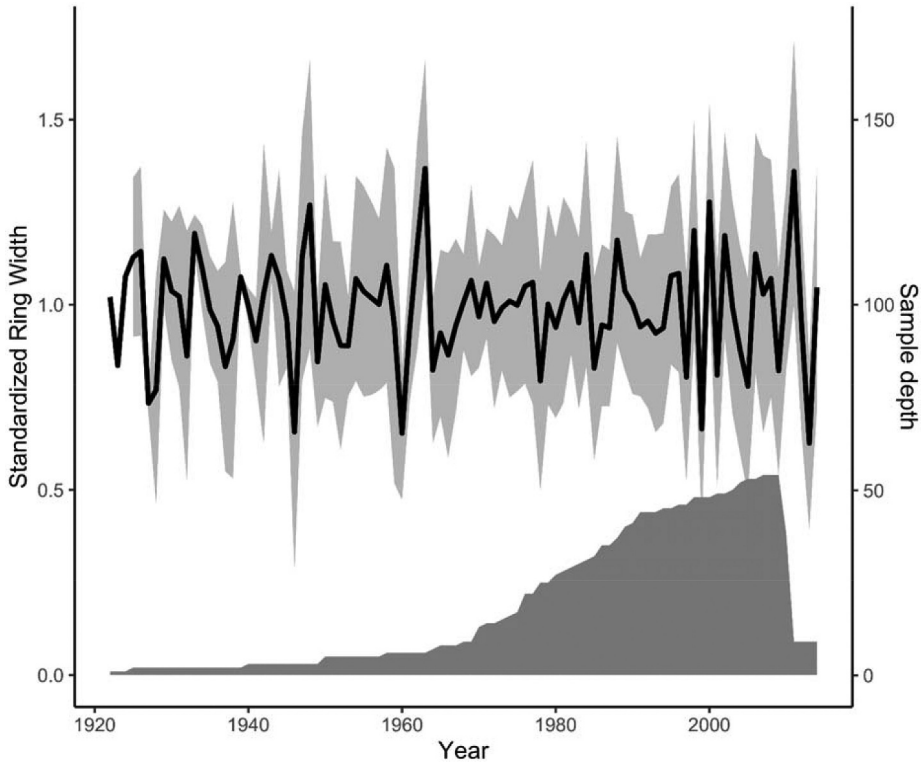

Figure 3. Standardized ring width chronology built from fifty-four *Salix richardsonii* shrubs from Walker Bay, Nunavut, Canada. The number of individual shrubs (sample depth) that contribute to each point in the chronology is indicated by the filled polygon (minimum = one shrub from 1922 to 1924).

exact test $p > .1$; Supporting Information). Twenty percent of transects had tall shrubs in 1996 compared to 15 percent in 2010. Short shrubs were more common, being found on 72 percent and 61 percent of transects in 1996 and 2010, respectively. Fewer transects in 2010 had short shrubs than in 1996 ($p < .01$; Supporting Information), but there was no significant change in the proportion of transects with tall shrubs ($p = .14$; Supporting Information). These results suggest that shrub cover did not change at Walker Bay between 1996 and 2010 (Question 4).

We found serveal fourteen-year periods in the 1930s, 1950s, and 1980s with a positive growth trend over time (Figure 6a). These windows correspond to times where shrub growth was less variable between years (Figure 3). There was no significant increase in growth during the fourteen-year period from 1996 to 2010, as already shown (Figure 5a: orange points; Figure 6a: arrow). In summary, the correlation between growth and July temperature was positive in recent decades even though the trend in shrub growth (Figure 6a) and response function coefficients (Figure 4) no longer predicts a significant relationship.

Discussion

Our results indicate that *S. richardsonii* and the other common shrub species (*S. arctica*) did not expand from 1996 to 2010 at our study site near Walker Bay. Therefore, Walker Bay does not appear to be contributing to the recent shrub greening or browning trends observed elsewhere in the Arctic (Tape, Sturm, and Racine 2006; Forbes, Fauria, and Zetterbergs 2010; Myers-Smith et al. 2011; Ropars and Boudreau 2012; Phoenix and Bjerke 2016; Bonney, Danby, and Treitz 2018; Andruko, Danby, and Grogan 2020). Paradoxically, our long-term dendrochronological analysis revealed that radial growth has significantly increased with July temperatures since the 1950s (Figure 5). We resolve this conflict by arguing that July temperature may still be one of the drivers of radial growth (Figures 5b and 6b) but that summer precipitation and other variables flattened the positive growth trend in the early 2000s (Figures 4b and 5a). Overall, our data from Walker Bay support a more complex relationship between shrub cover dynamics and climatic trends that is likely to be modified by site- and species-specific recruitment limitation (Myers-Smith, Elmendorf et al. 2015; Young et al. 2016).

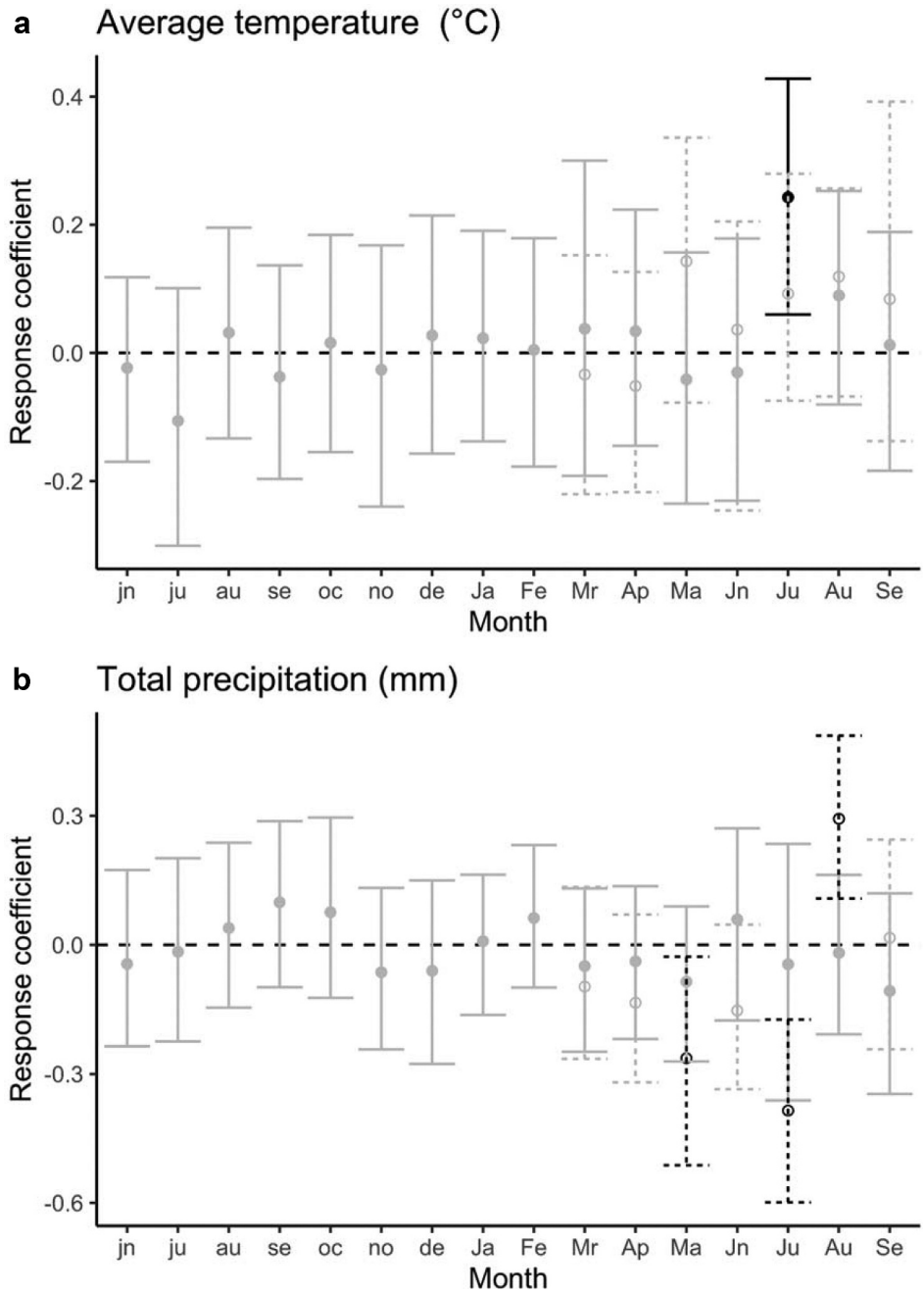

Figure 4. The response function coefficients for the annual growth (estimated as the standardized ring width) of *Salix richardsonii* and (a) mean monthly temperature and (b) total monthly precipitation from 1949 until 2013. Lowercase letters on the horizontal axis denote the months in the year before growth; uppercase letters refer to months in the year of growth. Black points represent statistically significant response function coefficients. Dashed lines and open symbols represent an analysis using the data from 1996 to 2010, which is the same period for which we have shrub cover data. We could only conduct the 1996 to 2010 analysis from March to September of the growth year because there were only fourteen available degrees of freedom for seven months each with two climate variables.

Radial growth: Climatic drivers, long-term pattern, and sex

Our work corroborates many studies that concluded that summer temperature is one of the major drivers of arctic shrub's radial growth (Liang and Eckstein 2009; Forbes, Fauria, and Zetterbergs 2010; Hallinger, Manthey, and Wilmking 2010; Hantemirov et al. 2011; Boudreau and Villeneuve-Simard 2012; Myers-Smith, Elmendorf et al. 2015; Ropars et al. 2015, 2017; Young et al. 2016). In high-latitude regions, the positive impact of warmer temperatures on radial growth can be driven by direct (physiological activity) and indirect (increase soil microbial activity and

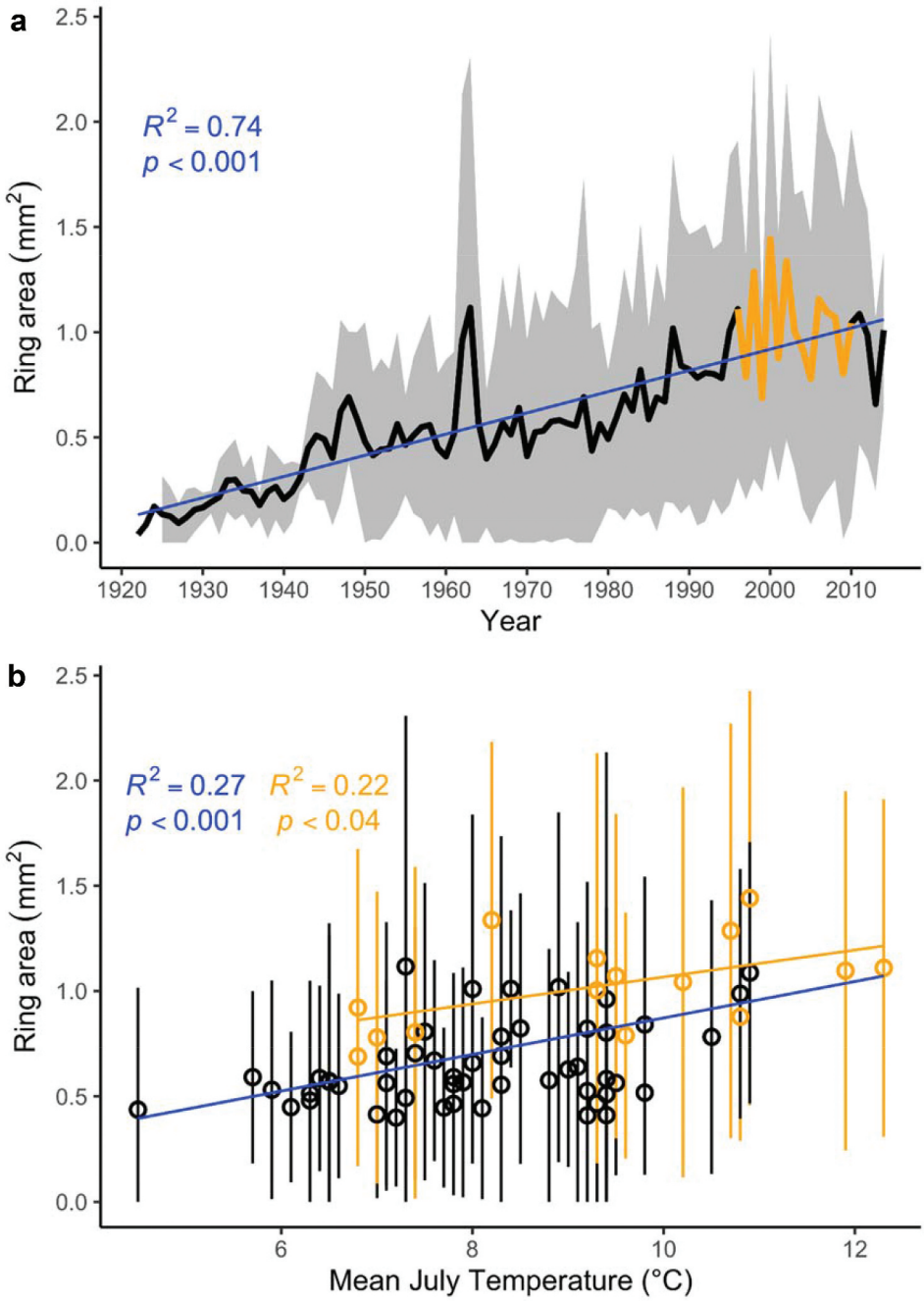

Figure 5. (a) The trend in average ring area over time and its (b) relationship with July temperature. Ring area significantly increased over time and was significantly correlated with July temperature. Blue lines are predicted from linear models using the full data set, and orange points and lines use the data from 1996 to 2010 when we have shrub cover estimates (there was no significant relationship between ring area and year in the restricted data set; $p = .74$). The range in (a) and error bars in (b) show ±1 standard deviation in ring area truncated at zero. The sample depth for the ring area chronology (a) is the same as the ring width chronology (Figure 2).

decomposition rates) effects (see Myers-Smith et al. 2011). Unfortunately, we cannot discriminate the relative contributions of these effects on the positive relationship between warmer summer temperatures and *S. richardsonii* growth. Experiments testing the relative effect of higher soil nutrient availability and temperature on growth would provide estimates of these direct and indirect effects and improve our ability to predict the response of *S. richardsonii* to higher temperatures at other sites.

The relationship between *S. richardsonii* radial growth and precipitation was not significant at Walker Bay when we used the entire dendrochronological data set. However, an analysis from 1996 to 2010 produced three significant response function coefficients that suggest

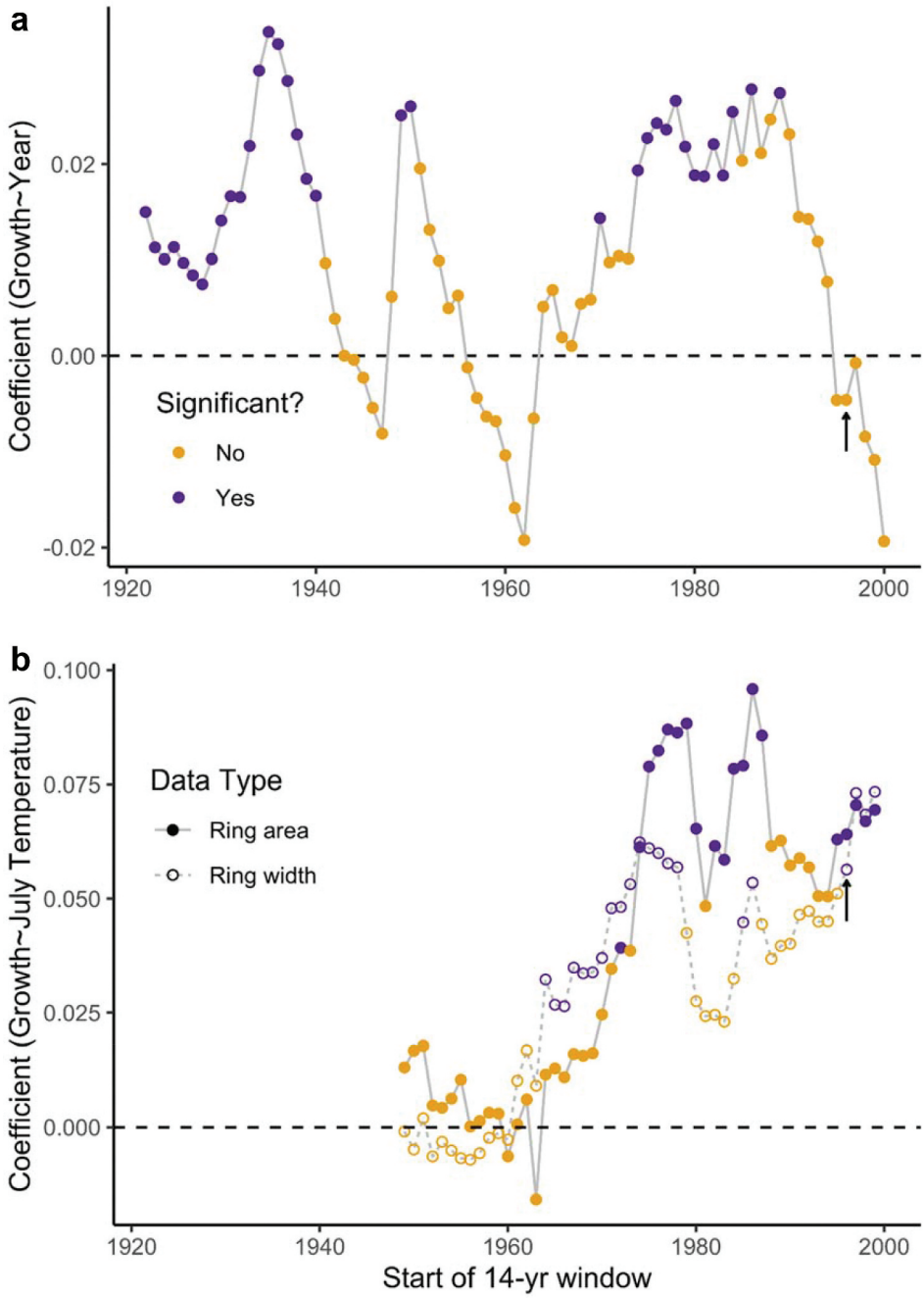

Figure 6. (a) The changes in growth trends and the (b) relationship with July temperature over time. (a) Each point represents the linear model coefficient relating growth and year for the fourteen-year window starting from the year on the *x*-axis. This linear model was significant if the point is purple. (b) The linear model coefficient for July temperature with ring width or ring area, for the same fourteen-year windows. The results that use data from the same years as our shrub cover analysis correspond to black arrows in each plot.

both negative (May and July) and positive (August) effects of precipitation. By contrast, *S. alaxensis* radial growth on nearby Victoria Island was positively associated with spring precipitation, because spring snow accumulation builds up soil moisture reserves (Zalatan and Gajewski 2006). Such positive impacts of late snow precipitation are likely associated with dry landscapes where soil moisture could be limiting, although snow cover can also insulate shrubs and prevent late-frost damages (Sturm et al. 2005). At Walker Bay, moisture was probably not historically limiting, because the landscape is set on a broad snowmelt floodplain that is uncharacteristically wet and dotted with tundra ponds. Given this site-specific information and the short time series in the restricted analysis, we can only conclude that precipitation might play a role in shrub growth at Walker Bay now that summer temperatures are consistently higher (Myers-Smith, Elmendorf et al. 2015). Furthermore, our results suggest that shrubs at

Arctic sites with saturated water tables might not respond to precipitation as clearly as shrubs at dryer sites (Zalatan and Gajewski 2006; Myers-Smith, Elmendorf et al. 2015; Young et al. 2016).

The basal area increment data show that *S. richardsonii* radial growth at Walker Bay increased from the 1960s to the early 2000s but appears to have leveled off since then. A long-term increase in basal area increment was expected as July temperature, the only climatic driver of long-term radial growth identified in this study, increased significantly from 1949 to 2013. If we consider only the period when we have shrub cover data (1996 to 2010), there was no significant increase in basal area increment ($F_{1,13} = 0.11$, $p > .7$). There was also no significant change in annual temperature ($F_{1,13} = 0.21$, $p > .6$; Figure 2a), July temperature ($F_{1,13} = 0.79$, $p > .4$; Figure 2b), or annual precipitation ($F_{1,13} = 0.76$, $p > .4$) during this period. In fact, summer temperature was highly variable from 1996 to 2010 at our study site, which corresponded closely with variable interannual growth (Figures 3 and 5a). Instead of temperature, precipitation may have become a more important driver of radial growth in recent decades, although we can only confirm this result with a longer time series. The restricted dendrochronological analysis might itself be suspect. One reason to be skeptical is that the climate and growth data showed high variability over the entire time series (Figure 6). Some fourteen-year windows showed significant trends in growth or the relationship with July temperature, whereas others did not. Future dendrochronology work will be necessary to determine whether the increasing trend in shrub growth has plateaued or has been temporarily slowed by variable summer temperatures in the 2000s.

The similar radial growth between male and female shrubs suggests that female shrubs can maintain radial growth even while investing more in reproduction as seed development and maturation. A similar pattern was observed for *S. sachalinensis* in northern Japan (Ueno and Seiwa 2003) and *S. arctica* in Greenland (Schmidt et al. 2010). One hypothesis to explain this result is that males make their reproductive investment earlier in the year and so leaf out later than female shrubs. This hypothesis is consistent with data from *S. arctica*, which suggest that females can maintain higher stomatal conductance in the spring when they grow in environments with adequate resources (Dawson and Bliss 1989). Overall, it appears that there are enough interacting trade-offs between the resource allocation in male and female shrubs to nullify any long-term differences in radial growth at Walker Bay.

No evidence of increased shrub cover at Walker Bay

Our field surveys conducted fourteen years apart reveal that the shrub cover is relatively stable in the Walker Bay area. Our results are in accordance with Ju and Masek (2016), who showed that this region did not experience significant greening or browning from 1984 to 2012. Unfortunately, we do not have older estimates of shrub cover in this region and are therefore unable to determine whether shrub cover increased at Walker Bay during mid-twentieth century when *S. richardsonii* radial growth was clearly increasing. Data on local biotic or abiotic constraints, such as herbivory, nutrient limitation, or the depth of the water table, could explain why the shrub cover at Walker Bay has not tracked the average temperature increases over the last two decades (Martin et al. 2017). Interestingly, this period was also characterized by a relatively stable radial growth, suggesting that the overall shrub performance (growth and recruitment) did not increase significantly from 1996 to 2010. Although our data do not allow us to pinpoint the exact mechanism behind the apparent inertia in shrub cover, they fit a growing body of evidence that shrub recruitment and cover might be restricted by constraints, such as topography, herbivory, or nutrient supply, that vary at smaller spatial scales than temperature or precipitation (Post and Pedersen 2008; Ropars and Boudreau 2012; Young et al. 2016).

Conclusions

Our research reinforces an emerging perspective that considering factors beyond regional temperature and precipitation will add important mechanisms to our understanding of shrub growth and cover (Martin et al. 2017; Weijers et al. 2018). Likely features at Walker Bay include the saturated water table and damage from muskoxen trampling and browsing. Though pan-Arctic trends are useful for assessing change at global scales (Myers-Smith et al. 2015), our study suggests that understanding local change will require the consideration of biotic and abiotic variables measured at comparable scales. These site-specific factors are important for unraveling how climate change in the Arctic will alter individual species and their interactions (Rosenblatt and Schmitz 2016).

Finally, our study demonstrates a possible limitation of response function analysis pertinent to local managers and global modelers. Dendrochronology is a powerful tool for examining growth trends in the past when other proxies of shrub performance, such as shrub cover, are not available. However, patterns of growth and cover of *S. richardsonii* at Walker Bay demonstrate that historical relationships between shrub radial growth and climatic variables do not necessarily translate to contemporary change at the landscape level. Therefore, one must be careful about extrapolating the predictive power of historic relationships between climate and growth into climate models.

Our ability to predict the future state of arctic ecosystems will likely benefit from being cautious before equating changes in seasonal climates with changes in the growth of plant species.

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ORCID

Robert W. Buchkowski http://orcid.org/0000-0001-6381-8609
Douglas W. Morris http://orcid.org/0000-0003-4515-9261
William D. Halliday http://orcid.org/0000-0001-7135-076X
Clara Morrissette-Boileau http://orcid.org/0000-0001-5968-9568

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