Spatial Variability of the Dominant Climate Signal in *Cassiope tetragona* from Sites in Arctic Canada

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ABSTRACT. Our study investigates the nature of the climate signal in three populations of the Arctic dwarf-shrub *Cassiope tetragona* using dendrochronological and stable isotope analysis techniques. We present 15 new *C. tetragona* chronologies from three sites (Axel Heiberg, Bathurst, and Devon islands) in the eastern Canadian Arctic, of which three are the first continuous stable carbon isotope ratio ($\delta^{13}C$) time series developed for Arctic shrubs. Correlation and multivariate regression analyses revealed that multiple and different climate factors influenced the chronologies within and between the three sites. At the Axel Heiberg Island site, the dominant climatic influences over annual stem elongation were previous year (t-1) and current year (t) summer precipitation, while annual production of flower buds was influenced by (t) winter precipitation and spring temperature. At Bathurst Island, annual production of flower buds responded to (t-1) growing season sunshine hours and winter precipitation and to (t) late growing season temperature and moisture availability. Our analysis of the Axel Heiberg and Bathurst Island models revealed the positive influence on $\delta^{13}C$ values of (t-1) winter temperature—and on Bathurst Island only, of (t-1) spring sunshine hours. The combined influence of these parameters on spring moisture availability suggests that the $\delta^{13}C$ ratios varied in response to stomatal conductance. At Devon Island, the $\delta^{13}C$ values varied in response to (t) and (t-1) spring and summer temperature and spring and fall solar radiation, which in turn influence the rate of photosynthesis. Our study supports the emerging hypothesis that Arctic shrubs are sensitive to climate. However, strong spatial variation in plant-climate response characterized our sampling sites. This variation may be linked to site sensitivity, or regional climate variability due to geographic and topographic differences, or both.

Key words: *Cassiope tetragona*, dendrochronology, stable isotope analysis, carbon-13, shrubs, Arctic

RÉSUMÉ. Notre étude prend la forme d'une enquête sur la nature du signal d'effet de serre au sein de trois populations arctiques d'arbustes nains *Cassiope tetragona* à l'aide de techniques d'analyse dendrochronologique et d'isotopes stables. Nous présentons 15 nouvelles chronologies de *C. tetragona* provenant de trois emplacements (îles Axel Heiberg, Bathurst et Devon) dans la partie est de l'Arctique canadien, dont trois de ces chronologies représentent la première série chronologique de rapport isotopique de carbone stable continu ($\delta^{13}C$) à avoir été établie pour des arbustes de l'Arctique. Des analyses de corrélation et de régression à plusieurs variables ont permis de révéler que des facteurs climatiques différents et variables ont exercé une influence sur les chronologies au sein des trois emplacements et entre ceux-ci. À l'emplacement de l'île Axel Heiberg, les influences climatiques dominantes par rapport à la montaison annuelle étaient les précipitations d'été de l'année précédente (t-1) et de l'année en cours (t), tandis que la production annuelle des boutons à fleur était influencée par les précipitations d'hiver (t) et les températures du printemps. À l'île Bathurst, la production annuelle de boutons à fleur réagissait à (t-1), soit le nombre d'heures d'ensoleillement pendant la saison de croissance et les précipitations d'hiver et à (t), soit les températures en fin de saison de croissance et l'humidité disponible. Notre analyse des modèles des îles Axel Heiberg and Bathurst a révélé l'influence positive des températures d'hiver (t-1) sur les valeurs de $\delta^{13}C$ — et à l'île Bathurst seulement, des heures d'ensoleillement du printemps (t-1). L'influence conjointe de ces paramètres sur l'humidité disponible au printemps laisse entendre que les rapports de $\delta^{13}C$ varient en fonction de la conductance stomatique. À l'île Devon, les valeurs de $\delta^{13}C$ varient en fonction de (t) et de (t-1), soit les températures du printemps et de l'été ainsi que le rayonnement solaire du printemps et de l'automne, qui exercent, à leur tour, une influence sur le taux de photosynthèse. Notre étude vient appuyer la nouvelle hypothèse selon laquelle les arbustes de l'Arctique sont sensibles au climat. Cependant, nos lieux d'échantillonnage étaient caractérisés par une importante variation spatiale en matière de réponse climatique des végétaux. Cette variation pourrait se rattacher à la sensibilité de l'emplacement, ou à la variabilité climatique attribuable aux différences géographiques et topographiques, ou encore, à ces deux éléments.

Mots clés : *Cassiope tetragona*, dendrochronologie, analyse d'isotopes stables, carbone 13, arbustes, Arctique

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INTRODUCTION

Large-scale changes in Arctic climate and their cascading effects on multiple physical and biotic systems are documented in numerous studies and compilations based on direct observations, experiments, and computer models (Serreze et al., 2000; ACIA, 2004; Hinzman et al., 2005; Serreze and Francis, 2006). For the North American Arctic, the average annual air temperature increased by +1.06 ± 0.22°C per decade between 1980 and 2000 (Comiso, 2003), a rate five times that of the global average for the same period (Hansen et al., 2006). While the overall trend in the Arctic is one of increasing temperatures (Chapman and Walsh, 1993; Serreze et al., 2000), there is still considerable climatic heterogeneity among and within regions (Hinzman et al., 2005; Richter-Menge et al., 2006). In addition to regional variability related to atmospheric circulation patterns, geographic location—including latitude, proximity to mountains, glaciers, open water bodies, and pack ice— also significantly affects site-level climate conditions and in turn, plant populations and communities.

Recent evidence indicates that Arctic shrub and tundra ecosystems are sensitive to climate change (e.g., Forbes et al., 2009). Studies of shrub response to past environmental change provide evidence of long-term dynamics in Arctic plant ecosystems and their relationship to climate at different spatio-temporal scales (Callaghan et al., 1993; Aas and Faarlund, 1995; Cramer, 1997). Since the late 1980s, dendrochronological techniques have been adapted to shrubs at high-latitude sites to investigate the effects of climate on growth and reproduction (e.g., Callaghan et al., 1989; Havström et al., 1993; Woodcock and Bradley, 1994; Johnstone and Henry, 1997; Rayback and Henry, 2006; Schmidt et al., 2006; Zalatan and Gajewski, 2006; Au and Tardiff, 2007; Bär et al., 2008; Levanĭc and Eggertsson, 2008; Forbes et al., 2009; Rozema et al., 2009). Dendroecological evaluation of Arctic shrub productivity in response to long-term changing environmental conditions may identify unique plant population or functional group responses within the greater shrub or tundra plant community and raise important questions about the spatio-temporal consistency of plant response across smaller regions.

In addition to biologically based measures used to investigate the long-term response of plants to changing environmental conditions and to reconstruct past climate, dendrochronologists now include stable isotope analysis in their suite of techniques. Stable isotopes, such as hydrogen, oxygen, and carbon, are fixed permanently into the physical structure of the plant stem; they are sensitive to and record directly environmental factors such as relative humidity, soil moisture, temperature, and irradiance (Farquhar et al., 1989; McCarroll and Loader, 2004). Through the leaf stomata, plants take in CO_2 and lose water via transpiration. When the internal concentration of CO_2 drops in the stomatal chamber because of stomatal closure or a high photosynthetic assimilation rate, the internal partial pressure of CO_2 drops, and a greater proportion of ^{13}C is stored permanently in the annual growth as carbohydrate (McCarroll and Loader, 2004). Thus, stable carbon isotope ratios ($^{13}C/^{12}C$) record changes in isotopic composition and internal CO_2 concentration that vary in direct response to the influence of climate on the rate of photosynthesis and stomatal control of moisture (Farquhar et al., 1989). The stable carbon isotope ratios of a sample are expressed as $\delta^{13}C$ values, representing the $^{13}C/^{12}C$ deviation of a sample relative to the Vienna Pee Dee Belemnite (V-PDB) standard in per mil (‰) units.

At sites where and during years when plants may be moisture-stressed, $\delta^{13}C$ values are influenced primarily by stomatal conductance. Relative humidity and moisture availability influence stomatal pore conductance and the leaf boundary layer under xeric conditions (Saurer et al., 1995; Robertson et al., 1997; Barber et al., 2004; Gagen et al., 2004, 2006). In years or at sites that are cool and moist, factors that influence carbon assimilation, such as sunlight and temperature, will be more important. In this case, assimilation rate, and therefore photosynthesis, will dominate (Schleser et al., 1999; McCarroll and Pawellek, 2001; McCarroll et al., 2003; Gagen et al., 2007; Loader et al., 2007, 2008). Thus, an investigation of $\delta^{13}C$ time series together with growth and reproduction chronologies may provide a clearer understanding of the effect of climate on Arctic shrub populations at different sites.

In this study, we use dendrochronological and stable isotope analysis techniques to develop five chronologies (two growth, two reproduction, $\delta^{13}C$) from each of three populations of the Arctic dwarf-shrub *Cassiope tetragona* (Arctic white heather). Sampling sites are located in Arctic Canada on Axel Heiberg, Bathurst, and Devon islands, Nunavut, in three distinct climatic and biogeographic zones (Maxwell, 1981; Elvebakk et al., 1999). Our goal is to investigate the nature of the climate-plant relationships and to understand the spatio-temporal characteristics of the responses across the region of the eastern Canadian High Arctic. To this end, we present five terrestrial-based chronologies from each of the three study sites, including the first-ever, long duration, continuous stable carbon isotope ratio chronologies developed from terrestrial plants for the Canadian Arctic. We address the following questions: 1) What is the nature of the common climate signal in each chronology? 2) Which climate variable(s) control each chronology? and 3) Do annual plant growth, reproduction, and stable carbon isotope ratios respond consistently to climate variables across space?

METHODS

Cassiope tetragona

Cassiope tetragona (L.) D. Don (Ericaceae), an evergreen dwarf-shrub, is found in multiple heath communities throughout the circum-Arctic area (Bliss and Matveyeva, 1992). Individual plants display monopodal, upright growth that may develop into a loose prostrate mat of stems
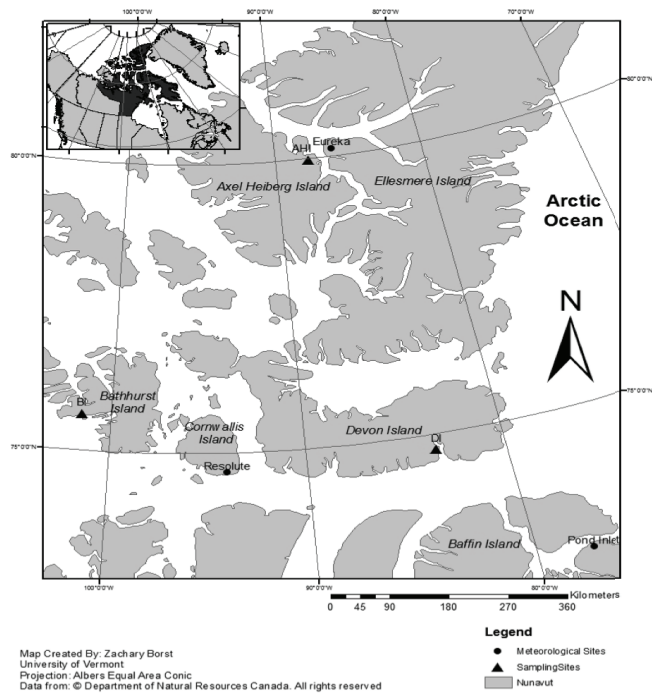
FIG. 1. The eastern Canadian High Arctic. Triangles (▲) indicate the locations of the three sampling sites on Axel Heiberg Island (AHI), Bathurst Island (BI), and Devon Island (DI). Circles (●) indicate the three corresponding meteorological stations at Eureka on Ellesmere Island, Resolute on Cornwallis Island, and Pond Inlet on Baffin Island.

(Havström et al., 1993). Individual stems have two alternating sets of opposite, xeromorphic leaves that form four distinct rows. The stems are further characterized by wave-like patterns in leaf lengths (Warming, 1908; Callaghan et al., 1989; Havström et al., 1993, 1995) and in the positioning of leaf node scars along adjacent leaf rows (Johnstone and Henry, 1997). The wavelike patterns have been used to identify and date individual annual growth increments and to develop growth and reproduction chronologies (Callaghan et al., 1989; Havström et al., 1995; Johnstone and Henry, 1997; Rayback and Henry, 2005, 2006). More recently, Rozema et al. (2009) have used wintermarksepta to identify annual growth increments. The species is also characterized by solitary white, bell-like flowers that are produced from auxiliary buds one to two years after bud formation (Molau, 2001). Fruit maturation may occur at the end of the growing season, with local seed dispersal taking place in winter or spring (Molau, 1997, 2001). Reproduction chronologies, based on the count of flower buds and flower peduncles present within individual annual growth increments, have also been developed for this species (Havström et al., 1995; Johnstone and Henry, 1997; Rayback and Henry, 2006).

Study Sites

We collected plants from three sites in the Canadian High Arctic, on Axel Heiberg Island (AHI), Bathurst Island (BI), and Devon Island (DI) (Fig. 1, Table 1). The Panarctic Flora

Project (Elvebakk et al., 1999; Elven, 2008) indicates that the AHI and DI sites fall into bioclimatic zone C (middle Arctic tundra), which is dominated by open to often closed vegetation of dwarf and prostrate shrubs, graminoids, and forbs (Elven, 2008). AHI is situated in climatic Region Vb (Nansen Sound and Adjacent Lowlands) (Maxwell, 1981), which is characterized by the largest range (covering 50 °C) of mean annual temperature in Arctic Canada and influenced by a rain shadow effect caused by adjacent mountains, which block cyclonic circulation from Baffin Bay and Parry Channel. DI falls into climatic zone IVa (Northern Baffin Bay–Lancaster Sound), and is characterized by a high degree of cyclonic activity off Baffin Bay, high precipitation totals with orographic uplift, the presence of the North Water Polynya, and a smaller temperature range (covering only 33 to 36°C) (Maxwell, 1981). The BI site is located within bioclimatic zone B (northern Arctic tundra), a region with discontinuous, polar-desert vegetation cover dominated by prostrate shrubs, forbs, graminoids, and luxuriant moss and lichen vegetation (Elven, 2008). Bathurst Island is situated in climatic zone Ic (Bathurst-Prince of Wales Islands), where the annual temperature range is wide (covering 37–39°C), and anticyclonic activity and low-to-moderate precipitation are prevalent (Maxwell, 1981).

Instrumental Climate Data

We obtained instrumental climate data from three meteorological stations operated by the Meteorological Service of Canada (MSC) selected for their proximity to the sampling sites and the length of their record (Fig. 1, Table 1). We used homogenized and rehabilitated records from the MSC Adjusted Historical Canadian Climate Data (AHCCD), including monthly maximum, minimum, and mean air temperatures (0.1°C) and monthly total rainfall (0.1 mm), snowfall (0.1 cm), and precipitation (0.1 mm) (Vincent et al., 2002; Environment Canada, 2010a). The rehabilitated climate data have been adjusted for instrument relocation, trace observations, and changes in observing procedures (Vincent et al., 2002). We also used non-homogenized climate data, including mean monthly dewpoint temperature (0.1°C), relative humidity (%), sunshine hours (0.1 hrs), and solar radiation (0.001 MJ/m²) (Environment Canada, 2010b). For individual months during which 10% to 12% of the daily data were missing (~3.5 days per month), that monthly value was eliminated from further analysis. Because of extensive data gaps and the shorter record of climate data from the Pond Inlet meteorological station, we used only the temperature data from that station in our analysis.

Chronology Development

We collected individual stems from 15 *C. tetragona* plants at BI in July 1998, and from 10 plants at AHI and 20 plants at DI in August 1999. Variation in the number of plants collected depended on the number of individuals present in the *C. tetragona* population sampled at each site. Individual

TABLE 1. Sampling site details and meteorological station information.

Sampling Sites:	Axel Heiberg Island	Bathurst Island	Devon Island
Latitude	80° 10′ N	75° 35′ N	74° 33′ N
Longitude	87° 30′ W	100° 08′ W	82° 48′ W
Elevation (m)	55 m	45 m	50 m
Slope	2–3°	2°	4–5°
Aspect (N, S, E, W)	S	W	S
Meteorological Stations[1]:	Eureka-A, Ellesmere Island	Resolute Cars, Cornwallis Island	Pond Inlet-A, Baffin Island
Latitude	79° 58′ N	74° 43′ N	72° 40′ N
Longitude	85° 55′ W	94° 59′ W	77° 58′ W
Elevation (m)	10.4	65.5	4.0
Mean annual temperature (°C)[2]	-19.7	-16.4	-15.1
Mean July temperature (°C)[2]	5.7	4.3	6.0
Total annual precipitation (mm)[2]	75.5	150.0	190.8

[1] Meteorological Service of Canada.

[2] 1971–2000 mean.

plants were selected for the longest stems and live, green tips. To ensure that the individual plants sampled were independent genets, we maintained a minimum distance of 5 m between sampled plants. The spatial area covered by each of the *C. tetragona* populations was approximately 250 m^2 for AHI, 150 m^2 for BI, and 400 m^2 for DI.

In the laboratory, we measured five to eight stems per plant. First, we removed two adjacent rows of leaves, and then, under a binocular microscope, we measured the internode distance between leaf scars from the base of the stem to its tip using a Velmex unislide traversing table, an Accurite encoder (0.01 mm), and a Quick-Chek digital readout system. We identified the annual growth increments (AGIs) by the wavelike patterns in internode lengths (Johnstone and Henry, 1997). The terminus of each AGI was delimited by the shortest internode length at the end of each wave series (Johnstone and Henry, 1997; Rayback and Henry, 2006). Graphic illustrations of the measuring technique are available in Johnstone and Henry (1997) and Rayback and Henry (2006). The annual production of leaves (Leaf), flower buds (Bud) and flower peduncles (Flo) were calculated by counting the total number of each variable found within each AGI (Rayback and Henry, 2006). Annual growth increment measurements were visually cross-dated using a pattern-matching technique (skeleton plots) (Stokes and Smiley, 1996) and then statistically verified by comparing individually measured stems with the full chronology (COFECHA; Holmes et al., 1983). When an individual stem was flagged in COFECHA and the correlation calculated between the individual series and the master dating series was low, we attempted to resolve the conflict. In some cases, we eliminated stems or entire plants from the analyses because of irresolvable dating errors. Thus, we included between seven and 16 plants to develop the growth and reproduction chronologies for each site (Table 2).

On the basis of signal-to-noise ratio (SNR) and a priori information regarding the plant's growth and reproduction characteristics, we standardized the two growth chronologies using a low-pass digital filter (67% *n* criterion) based on dendrochronological methods (ARSTAN; Cook, 1985). We did not standardize the two reproduction chronologies because we have incomplete information regarding when a *C. tetragona* plant first reproduces. In addition, we don't know whether our flower bud and flower counts underestimated the actual total either because some flowers or buds were lost or because identifiable scars were lacking in the early part of the chronology. Following standardization, the growth chronology indices were averaged using a biweight robust mean (Cook and Briffa, 1990). Reproduction chronologies were averaged using an arithmetic mean. Standardized growth chronologies were used in subsequent analyses.

Stable Isotope Analysis

After constructing standardized master chronologies, we selected three of the longest, continuously overlapping individual stems (1 stem per plant, n = 3) per site for stable isotope analysis (Table 3). Under a microscope, we removed the remaining leaves and severed the stems with a razor into individual AGIs, which were frozen with liquid nitrogen (LN$_2$) and ground into a fine powder. As financial resources were limited and we needed sufficient matter for isotopic analysis, we pooled AGIs from the three plants per site before analysis. Samples were prepared using an offline combustion and cryogenic distillation system, followed by analysis on a V.G. SIRA II stable isotope ratio mass spectrometer (IRMS). Results are reported using a delta (δ) notation in per mil (‰) units relative to the carbonate V-PDB standard. Sample precision is ± 0.05‰ offline (based on replicate standards). Individual values were corrected for the anthropogenically driven decline of δ^{13}C in the atmosphere (Saurer et al., 1997) using a procedure proposed by McCarroll and Loader (2004).

Theoretically, in woody plants, a small amount of wood is laid down beneath the cambium as secondary growth

TABLE 2. Standardized (AGI, LEAF) and non-standardized (BUD, FLO) chronology summary statistics by site.[1]

	Axel Heiberg Island				Bathurst Island				Devon Island			
	AGI	LEAF	BUD	FLO	AGI	LEAF	BUD	FLO	AGI	LEAF	BUD	FLO
Time Period	1959–99	1959–99	1959–99	1959–99	1924–98	1924–98	1924–98	1924–98	1895–99	1895–99	1895–99	1895–99
Number of years	41	41	41	41	75	75	75	75	105	105	105	105
Number of plants	7	7	7	7	12	12	12	12	16	16	16	16
Index mean	0.96	0.98	0.14	0.40	0.97	0.98	0.34	0.15	0.99	0.99	0.20	0.26
Standard deviation	0.17	0.11	0.15	0.32	0.19	0.15	0.29	0.58	0.18	0.14	0.29	0.21
Mean sensitivity	0.17	0.13	0.90	0.57	0.23	0.17	0.45	0.81	0.16	0.15	0.90	0.65
AC-1	0.23	0.02	0.17	0.33	-0.11	-0.01	0.77	0.00	0.15	-0.08	-0.14	0.26
Common Period	1975–98	1975–98	1975–98	1975–98	1968–95	1968–95	1968–95	1968–95	1936–95	1936–95	1936–95	1936–95
SNR	1.18	1.40	1.70	0.98	1.72	1.59	3.12	0.44	3.99	3.49	0.05	0.60
EPS (# of plants)	0.54 (8)	0.58 (8)	0.63 (9)	0.50 (13)	0.63 (17)	0.61 (17)	0.76 (17)	0.31 (15)	0.81 (13)	0.78 (13)	0.05 (8)	0.37 (15)
SSS (# of plants)	0.87 (6)	0.88 (6)	0.85 (6)	0.87 (10)	0.87 (12)	0.86 (12)	0.86 (10)	0.91 (10)	0.85 (7)	0.88 (8)	0.88 (7)	0.91 (13)

[1] AGI = annual growth increment; LEAF = annual production of leaves; BUD = annual production of flower buds; FLO = annual production of flowers; AC-1 = first order auto-correlation coefficient; SNR = signal-to-noise ratio (Wigley et al., 1984); EPS = Expressed Population Signal (Wigley et al., 1984), and SSS = Sub-sample Signal Strength (Wigley et al., 1984).

TABLE 3. Summary statistics for stable carbon isotope ratio ($\delta^{13}C$) chronologies by site.

	Axel Heiberg Island	Bathurst Island	Devon Island
Time period	1963–99	1941–98	1923–99
Total number of years	37	58	77
Mean $\delta^{13}C$ (‰)	-28.36	-27.41	-27.46
Minimum $\delta^{13}C$ (‰)	-29.65	-28.47	-28.29
Maximum $\delta^{13}C$ (‰)	-26.40	-23.16	-24.95
Range $\delta^{13}C$ (‰)	3.25	5.31	3.34

each year. To examine *C. tetragona* for secondary growth, a cross-section of a 20-year-old stem stained with 1% solutions of safranin and astrablue was prepared, and digital photos were taken under a microscope at a camera focal magnification of 20×. The photo was examined for evidence of secondary growth and clearly identifiable annual rings.

Correlations and Response Function Model Calibrations

We correlated each of the five chronologies (AGI, Leaf, Bud, Flo, $\delta^{13}C$) from the three sampling sites with climate variables from the nearest meteorological station. Correlations (Spearman's Rank) were run over a 22-month period including the previous year (t-1) and the current year (t), beginning in January of the previous year and ending in October of the current year. In addition, we examined seasonal periods including winter (December to February), spring (March to May), summer (June to August) and fall (September to November) of the previous year, and September-October of the current year, as well as the annual period for the previous year. We included the current-year months of September and October in the analysis to account for more recent changes in the length of the growing season and within-plant translocation of nutrients and winter hardening. The five chronologies were also correlated within and between sites.

We developed response function models that regress the proxy (*y*) on some combination of climate variables (*x*) revealed via the correlation analysis. The significantly correlated climate variables ($p < 0.05–0.01$) for each chronology per site were further investigated through factor analysis using PASW, v. 17 (SPSS, Inc., 2009). We investigated only those variables for which a reasonable biological relationship could be hypothesized. Factor analysis simplifies complex and diverse relationships that exist among a set of variables by identifying common factors that link the variables together and provide insight into the underlying structure of the data (Dillon and Goldstein, 1984). The factors that result from the orthogonal rotation (Varimax) of principal components are statistically uncorrelated (Kaiser, 1958; Dillon and Goldstein, 1984). Factor scores were used in a multivariate regression analysis for each of the five proxies at each site. All parameters were significant ($p < 0.05$) in the models selected. To demonstrate the temporal stability of the empirically derived models linking the chronology with climate, a jackknife was used for model validation. The reduction of error (RE) statistic was also calculated to test model stability (Briffa et al., 1988). In most instances, tests of the residuals met the requirements of parametric statistics (Neter et al., 1996).

RESULTS AND DISCUSSION

Chronology Characteristics and Signal Strength

Fifteen high-resolution chronologies are presented for three Canadian High Arctic sites for which no other paleo-
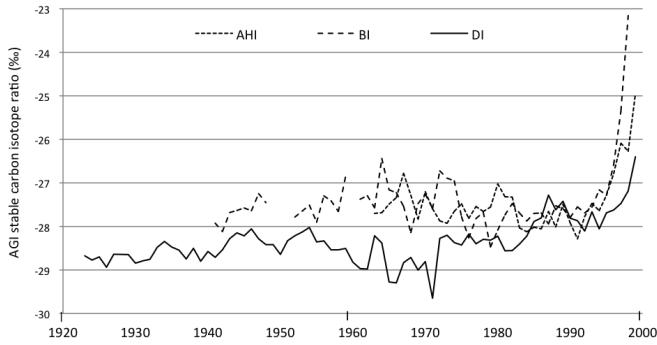
FIG. 2. Time series of stable carbon isotope ratios from *C. tetragona* annual growth increments for each of the three study sites, Axel Heiberg Island (AHI), Bathurst Island (BI), and Devon Island (DI). n = 3 plants per site.
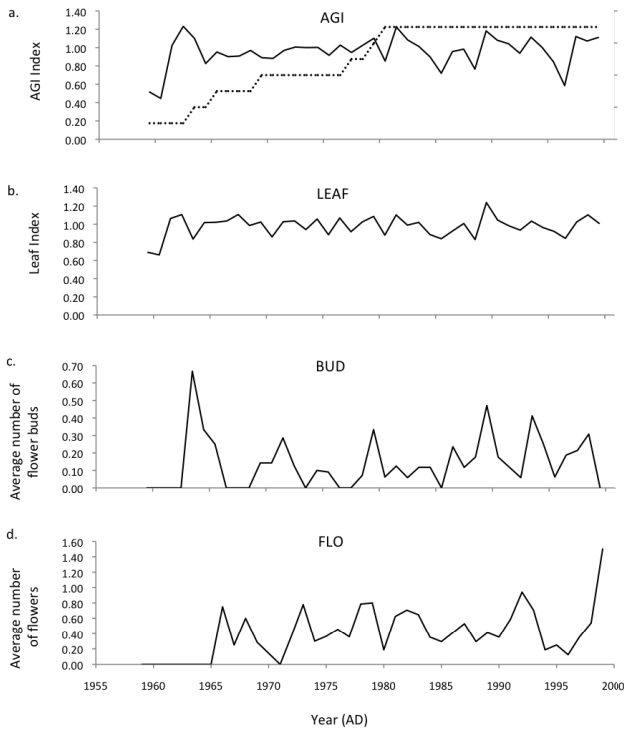

FIG. 3. Chronologies for the Axel Heiberg Island site (AHI), 1959–99. Standardized growth chronologies include (a) annual growth increments (AGI) and (b) annual production of leaves (LEAF). Unstandardized reproduction chronologies include annual production of (c) flower buds (BUD) and (d) flowers (FLO). The dotted line in section (a) represents sample depths (number of plants) for growth and reproduction chronologies at this site.

records exist, and the three δ¹³C site chronologies are the first continuous, stable carbon isotope ratio time series published for *C. tetragona* (Figs. 2–5, Table 3). The DI growth and reproduction chronologies are currently the second-longest set of chronologies (1895–99; 105 years) developed from *C. tetragona* for a site in Arctic Canada (Rayback and Henry, 2006).

Visual inspection of cross-sections of *C. tetragona* stems showed some possible evidence of secondary growth (Fig. 6). Unfortunately, without further information on the growth characteristics of *C. tetragona*, at this time we do not
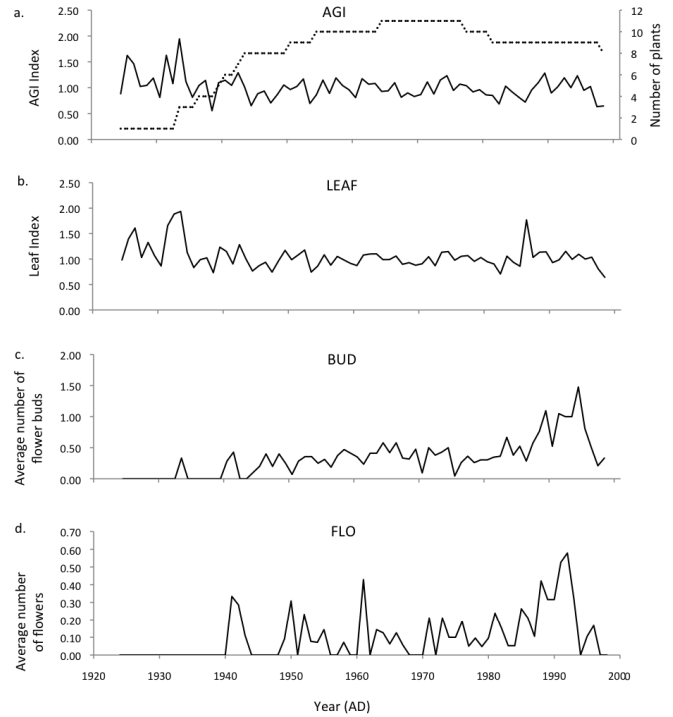

FIG. 4. Standardized growth and unstandardized reproduction chronologies for the Bathurst Island site (BI), 1924–98. Arrangement and details as in Figure 3.
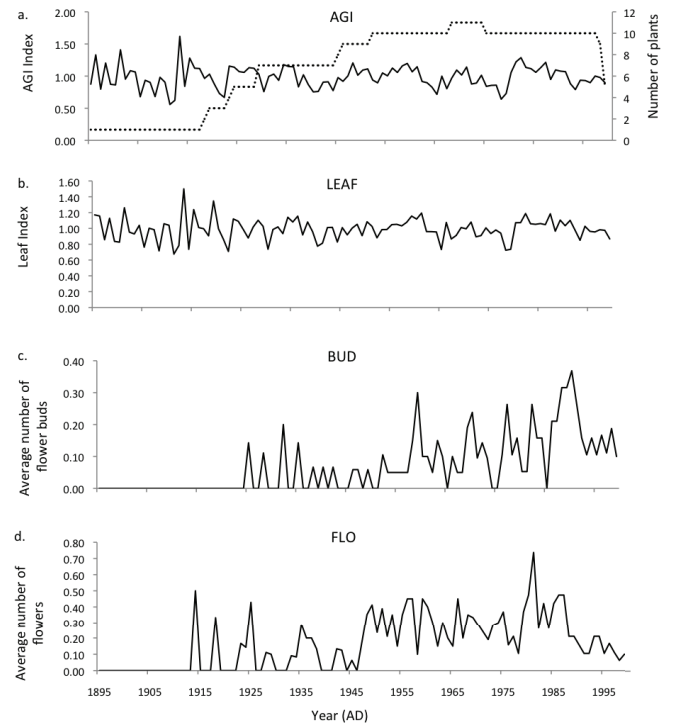

FIG. 5. Standardized growth and unstandardized reproduction chronologies for the Devon Island site (DI), 1895–1999. Arrangement and details as in Figure 3.

know 1) where and how to identify the end of each period of growth, 2) whether the secondary growth is annual, or 3) whether missing rings are common (P.M. Lintilhac, pers.
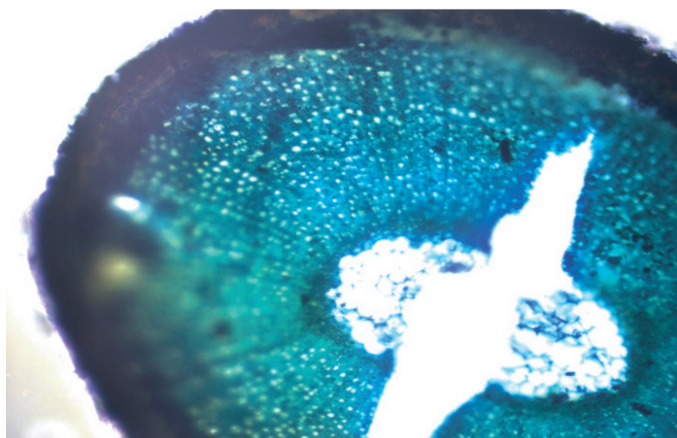
FIG. 6. Cross section of a 20-year-old *Cassiope tetragona* stem, magnified twenty times. (Photo courtesy of P.M. Lintilhac, November 2009).

comm. 2009). As the diameter of a plant stem ranges from 2 to 3 mm, it would be difficult to isolate individual rings and process them independently. Given these unknowns, we acknowledge that the secondary growth may smooth the annual climate signal, and that each $\delta^{13}C$ value may not represent a single year (Rayback et al., 2010). However, we hypothesize that the signal contained within the primary growth laid down along the length of the stem will override any signal in the secondary growth over the years (Rayback et al., 2010). Our hypothesis is based on results using *C. tetragona* $\delta^{18}O$ and Δ-carbon isotope discrimination time series to identify shifts in atmospheric circulation on Ellesmere Island, Canada (Welker et al., 2005).

As we pooled samples across stems at each site before performing the stable carbon isotope analysis, we cannot define inter-plant variability or the error associated with annual values, which precludes detection of trends in the individual isotopic series that are unrelated to climate (McCarroll and Loader, 2004). However, the pooling of samples is not uncommon in dendro-isotopic analysis, particularly in light of the high cost of analysis (e.g., Leavitt and Long, 1988; Leavitt et al., 2002; Treydte et al., 2006; Leavitt, 2008).

The growth chronologies for each of the three sites were characterized by low mean sensitivity and first-order autocorrelation coefficients, indicating minimal persistence and a lower sensitivity to year-to-year variability in climate (Table 2). Greater variability around the mean in the early portion of the two growth chronologies from each site is due to lower sample depth (Figs. 3–5). However, lower fluctuations along the more recent portion of the chronologies may be a product of the species' conservative growth strategy within resource-poor communities (Sørensen, 1941; Shaver and Kummerow, 1992).

The reproduction chronologies, on the other hand, revealed high mean sensitivity values, suggesting a greater sensitivity to annual changes in climate. Examination of the two reproduction chronologies from each of the three sites shows high interannual variability along the length of the chronologies (Figs. 3–5). The BI flower bud chronology

was also characterized by a high first-order autocorrelation value, indicating that previous-year climate is a strong determinant of flower bud formation in the current year. Similar values for *C. tetragona* growth and reproduction chronologies have been reported for other populations on Ellesmere Island, Canada (Johnstone and Henry, 1997; Rayback and Henry, 2006). The sensitivity of *C. tetragona* reproduction to warmer growing-season conditions and to experimental warming has been shown for sites on Ellesmere Island and northern Sweden (e.g., Nams and Freedman, 1987; Johnstone, 1995; Johnstone and Henry, 1997; Molau, 1997, 2001).

The growth and reproduction chronologies from each of the three sites showed low to moderate signal-to-noise (SNR) ratios, yet these values were higher than those published in a previous study (Table 2) (Rayback and Henry, 2006). The Expressed Population Signal (EPS) values across all chronologies were low, indicating that individual plant-level noise is interfering with the expression of the stand-level signal (Wigley et al., 1984). The subsample-signal-strength (SSS), a measure of the variance in common between a subset of samples and the master chronology, was strong for both the growth and reproduction chronologies at each of the three sites (Wigley et al., 1984). Increased sample size would reduce the size of the confidence limits and lengthen the useable portion of the chronology for which the reconstruction uncertainty is reduced (Cook and Briffa, 1990). At this time, no other study of *C. tetragona* has published SNR, EPS, or SSS values for comparison with our populations.

We hypothesize that the common climate signal at each site may be obscured by a high level of noise present in the chronologies (Rayback and Henry, 2006). We believe that the high degree of inter-plant variability is caused by individual plant architecture (multiple branching stems), variable microenvironmental conditions (e.g., temperature, insolation, soil moisture, soil nutrients), within-plant resource partitioning (among multiple dominant stems), and Arctic plant community dynamics, all of which may be responsible for complex plant-climate relationships. Despite the high noise level present in *C. tetragona* chronologies, Rayback and Henry (2005, 2006) developed models of past summer temperature for two sites on Ellesmere Island that explained between 45% and 51% of the variance (R^2adj).

Intra- and Inter-Site Chronology Relationships

An analysis of the intra-site correlations among the growth, reproduction, and $\delta^{13}C$ chronologies revealed 5, 11, and 17 significant ($p < 0.05$) correlations at the AHI, BI, and DI sites, respectively (excluding matching correlations of the same pair of chronologies for the previous year) (Table 4). However, only four correlations were common to all three sites. The first was a positive correlation between the AGI and the annual production of leaves (AHI, $r = 0.80$, $p < 0.0001$; BI, $r = 0.53$, $p < 0.0001$; DI, $r = 0.88$, $p < 0.0001$). The second was a similar correlation between the AGI and

TABLE 4. Intra-site Spearman's rank correlation (r) coefficients between chronologies for previous year (t-1) and current year.[1]

Axel Heiberg Island:

	AGI	AGI (t-1)	LEAF	LEAF (t-1)	BUD	BUD (t-1)	FLO	FLO (t-1)	$\delta^{13}C$
AGI									
AGI (t-1)	0.25								
LEAF	**<u>0.80</u>**	0.05							
LEAF (t-1)	0.27	**0.80**	0.02						
BUD	0.30	0.16	0.19	-0.02					
BUD (t-1)	0.00	0.30	0.11	0.19	0.17				
FLO	**<u>0.41</u>**	0.28	0.30	0.29	-0.18	-0.03			
FLO (t-1)	0.10	**<u>0.41</u>**	0.07	0.30	-0.04	-0.18	**<u>0.41</u>**		
$\delta^{13}C$	0.15	-0.13	0.17	0.09	-0.08	0.12	**0.32**	-0.01	
$\delta^{13}C$ (t-1)	0.27	0.15	0.29	0.17	-0.02	-0.08	0.25	**0.32**	**<u>0.74</u>**

Bathurst Island:

	AGI	AGI (t-1)	LEAF	LEAF (t-1)	BUD	BUD (t-1)	FLO	FLO (t-1)	$\delta^{13}C$
AGI									
AGI (t-1)	0.15								
LEAF	**<u>0.53</u>**	-0.01							
LEAF (t-1)	0.08	**<u>0.53</u>**	0.01						
BUD	**<u>0.45</u>**	0.14	0.20	0.12					
BUD (t-1)	0.10	**<u>0.45</u>**	0.09	0.20	**<u>0.60</u>**				
FLO	**<u>0.37</u>**	0.06	**0.32**	0.08	**<u>0.40</u>**	0.31			
FLO (t-1)	0.15	**<u>0.37</u>**	0.19	**0.32**	**<u>0.55</u>**	**<u>0.40</u>**	**<u>0.36</u>**		
$\delta^{13}C$	-0.05	0.05	-0.15	-0.08	0.13	0.26	**-0.30**	-0.03	
$\delta^{13}C$ (t-1)	0.18	-0.05	0.14	-0.15	0.03	0.13	-0.21	**-0.30**	**<u>0.49</u>**

Devon Island:

	AGI	AGI (t-1)	LEAF	LEAF (t-1)	BUD	BUD (t-1)	FLO	FLO (t-1)	$\delta^{13}C$
AGI									
AGI (t-1)	**<u>0.53</u>**								
LEAF	**<u>0.88</u>**	**<u>0.44</u>**							
LEAF (t-1)	0.33	**<u>0.88</u>**	0.28						
BUD	0.18	0.23	0.24	0.21					
BUD (t-1)	0.01	0.18	0.11	0.24	**<u>0.48</u>**				
FLO	**<u>0.46</u>**	0.14	**0.37**	-0.03	-0.21	**-0.29**			
FLO (t-1)	**<u>0.50</u>**	**<u>0.46</u>**	**<u>0.42</u>**	**0.37**	-0.03	-0.21	**0.30**		
$\delta^{13}C$	-0.07	0.01	-0.07	0.04	**0.30**	0.27	**-0.28**	**-0.28**	
$\delta^{13}C$ (t-1)	0.01	-0.07	0.02	-0.07	**0.33**	**0.30**	-0.24	**-0.28**	**<u>0.77</u>**

[1] AGI: annual growth increment; LEAF: annual production of leaves; BUD: annual production of flower buds; FLO: annual production of flowers; $\delta^{13}C$: stable carbon isotope ratio. Bold numbers indicate $p < 0.05$. Bold and underlined numbers indicate $p < 0.01$.

annual flower production (AHI, $r = 0.41$, $p = 0.008$; BI, $r = 0.37$, $p = 0.008$; DI, $r = 0.46$, $p = 0.001$). The third common correlation was between the annual production of flowers in the previous and current years (AHI, $r = 0.41$, $p = 0.009$; BI, $r = 0.36$, $p = 0.01$; DI, $r = 0.30$, $p = 0.03$). The fourth was between previous-year and current-year $\delta^{13}C$ values (AHI, $r = 0.74$, $p < 0.0001$; BI, $r = 0.49$, $p < 0.001$; DI, $r = 0.77$, $p < 0.0001$). Three additional correlations characterized both the BI and DI sites: the annual production of leaves and that of flowers (BI, $r = 0.32$, $p = 0.02$; DI, $r = 0.37$, $p = 0.007$), the annual production of flower buds in the previous and current years (BI, $r = 0.60$, $p < 0.0001$; DI, $r = 0.48$, $p < 0.0001$), and the annual production of flowers and $\delta^{13}C$ chronologies (BI, $r = -0.30$, $p = 0.05$; DI, $r = -0.28$, $p = 0.05$). A further six and seven significant correlations were either unique to the BI or the DI site or of opposite sign at the two sites, or both. The remaining correlations were not significant ($p > 0.05$) and were not considered further.

The significant correlations within each site suggest that the chronologies may not be completely independent of one another and may respond similarly to the same climatic or other environmental variables. For example, a comparison of the annual growth and leaf production chronologies at each of the three sites revealed synchronous fluctuations over time (Fig. 7). The similar growth responses may reflect the conservative growth strategy of the species, which serves to stabilize annual variability in productivity over time (Sørensen, 1941; Shaver and Kummerow, 1992). However, intra-site responses held in common across the three sites were rare. Instead, the general lack of a strong common pattern of intra-site and inter-site (not shown) correlations suggests different controlling variables at each of the sites. While some of these factors may be associated with large-scale climate, others may be linked to geographically specific local conditions, such as elevation or proximity to open water or mountains. These unique sets of influential factors may also result in fundamentally different strategies of plant allocation within this species, even within a relatively small geographic region.

Chronology-Climate Relationships

Investigation of the chronology-climate relationships revealed a limited number of cases in which a single climate
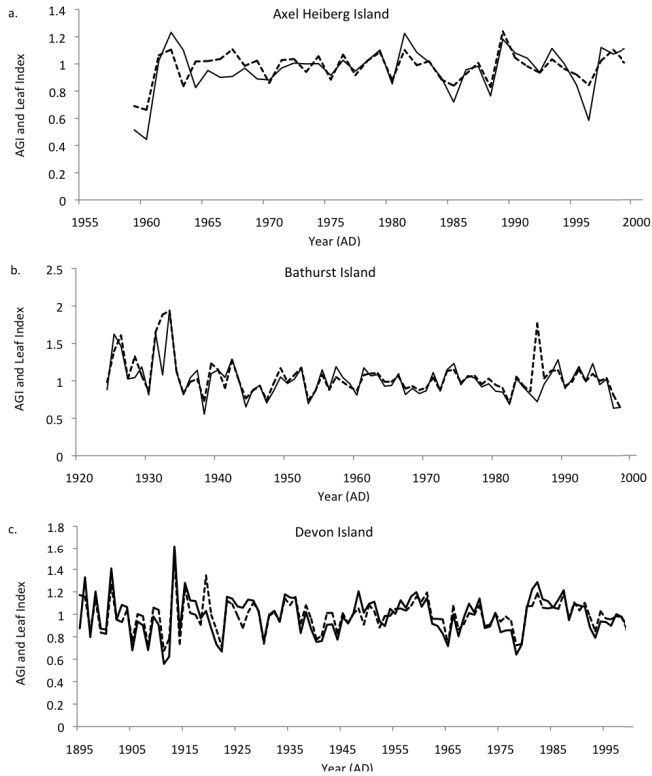
FIG. 7. Comparison of standardized annual growth increment (AGI, solid line) and annual leaf production (LEAF, dashed line) chronologies over time at (a) Axel Heiberg Island (r = 0.80, *p* < 0.0001), (b) Bathurst Island (r = 0.53, *p* < 0.0001), and (c) Devon Island (r = 0.88, *p* < 0.0001).
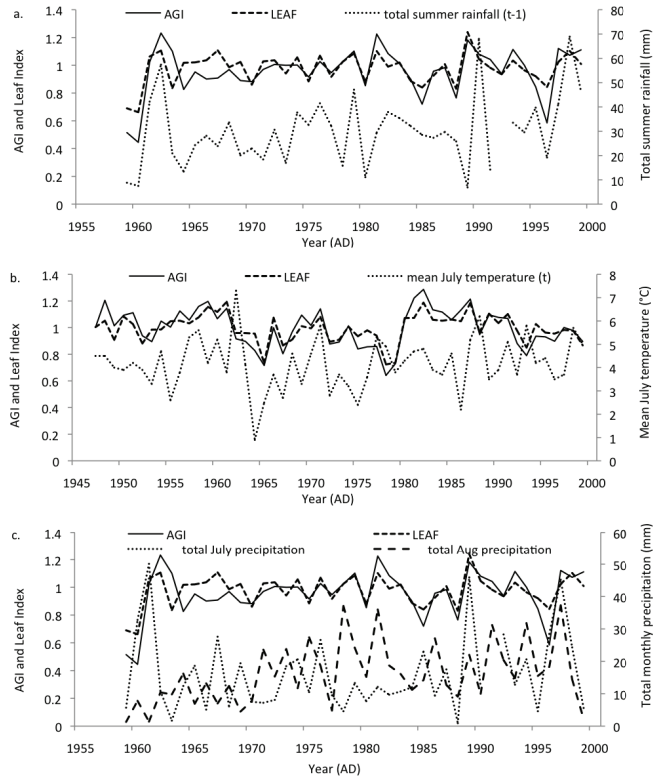

FIG. 8. Comparison over time of standardized annual growth increment (AGI) and annual leaf production (LEAF) chronologies with (a) previous-year total summer rainfall at Axel Heiberg Island, (b) mean current-year July temperature at Devon Island, and (c) total current-year July and August precipitation at Axel Heiberg Island.

variable exerted a dominant influence over one or two chronologies from the same site. As an example, at the AHI and DI sites, the annual growth increment and leaf production chronologies were influenced primarily by one climate variable (AHI: (t-1) summer total rainfall; DI: (t) July mean temperature), as evidenced by synchronous high and low values over multiple (but not all) years (Fig. 8a, b). At AHI, both growth chronologies responded positively to higher (t-1) total summer rainfall in 1962, 1976, 1979, and 1998, and negatively to lower rainfall in 1960, 1964, 1970, 1973, 1975, 1980, 1985, and 1996. At the DI site, growth chronologies responded positively to higher (t) July mean temperature in 1966, 1971, 1982, 1987, and 1991, and negatively to lower temperatures in 1964, 1975, 1986, and 1996. Our analysis also suggests that during years in which the annual growth was out of sync with the dominant climate variable, other climate variables, alone or in combination with the dominant one, may have influenced the plant's response. For example, at the AHI site, both growth chronologies responded positively in 1989 and 1997 despite the very low amount of total summer precipitation that had fallen in the previous year (Fig. 8a). However, the high amounts of precipitation that fell in July and August of 1989 and 1997 may have supplied sufficient moisture for plant growth during those growing seasons (Fig. 8c).

Despite these common responses, our analysis revealed that overall, *C. tetragona* chronologies responded to

different and multiple climate variables within-site. For example, at the BI site, the five chronologies did not respond consistently to maximum monthly temperature, and most of the correlations were not significantly different from zero (*p* < 0.05) (Fig. 9). Our analysis also showed that the influence of dominant variables varied temporally within a site, and non–growing season variables (e.g., precipitation) were influential over growth, reproduction, and δ¹³C chronologies.

Few chronologies responded to the same climate variable across all sites, suggesting strong spatial variation in the dominant climate signal. For example, the response of the annual growth increment (Fig. 10a–c) and flower production (Fig. 11a–c) chronologies to total monthly precipitation (in both prior and current years) was inconsistent when compared across the three sites, as this variable exerted either a positive, or a negative, or inconclusive influence over growth and reproduction in different months. The lack of spatial continuity in chronology-climate relationships raises questions regarding the consistency of plant responses even within relatively small regions. We note, however, that some of the chronologies were strongly influenced by climate variables that are spatially unstable over small and large regions (e.g., precipitation, sunshine hours, solar radiation receipt) or are difficult to measure accurately (e.g., precipitation) (Doesken and Robinson, 2009). We also hypothesize that elevation differences and distances between the study
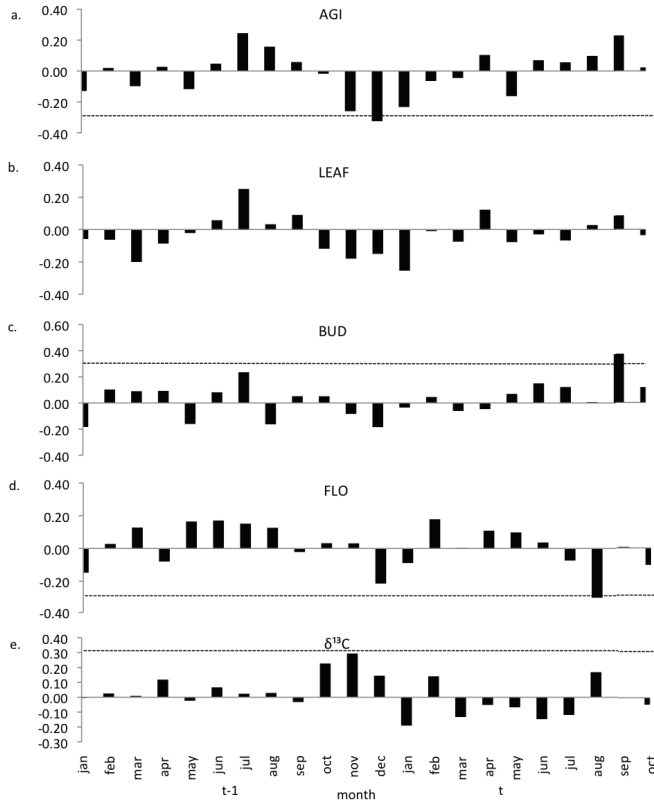
FIG. 9. An example from the Bathurst Island site showing correlation coefficients between maximum monthly temperature and the (a) annual growth increment, (b) annual production of leaves, (c) annual production of flower buds, (d) annual production of flowers, and (e) stable carbon isotope ratio chronologies. The horizontal axis indicates months in the previous year (t-1) and current year (t). The vertical axes represent the correlation coefficient. Dashed lines indicate significance at the $p < 0.05$ level.

FIG. 10. An example from the (a) Axel Heiberg, (b) Bathurst, and (c) Devon Island sites, showing the correlation coefficients between the annual growth increment (AGI) chronologies and total monthly precipitation for the previous year (t-1) and current year (t). Dashed lines indicate significance at the $p < 0.05$ level.

FIG. 11. An example from the (a) Axel Heiberg, (b) Bathurst, and (c) Devon Island sites, showing the correlation coefficients between the annual production of flowers (FLO) chronologies and total monthly precipitation for the previous year (t-1) and current year (t). Dashed lines indicate significance at the $p < 0.05$ level.

sites and the climate stations (AHI to Eureka: ~75 km; BI to Resolute: ~200 km; DI to Pond Inlet: ~275 km) and the associated differences in local precipitation accumulation or temperature may reduce the strength of the correlations. Several paleoclimatological studies in the Canadian Arctic have highlighted this problem (Hardy and Bradley, 1997; Rayback and Henry, 2006; Zalatan and Gajewski, 2006).

Multivariate Analysis

When different and multiple climatic variables influence growth, reproduction, and stable carbon isotope ratio chronologies at any one site, we may combine these variables to develop a stronger composite climate signal for each chronology (McCarroll and Pawellek, 2001). Through factor analysis and multiple linear regressions, we identified a suite of climatic factors that influence the individual chronologies at each site. Below, we discuss only those models with a multiple correlation coefficient (R) of ~0.60 or greater. In the case of the DI site, no growth or reproduction models meet this criterion, so only the $\delta^{13}C$ chronology is discussed.
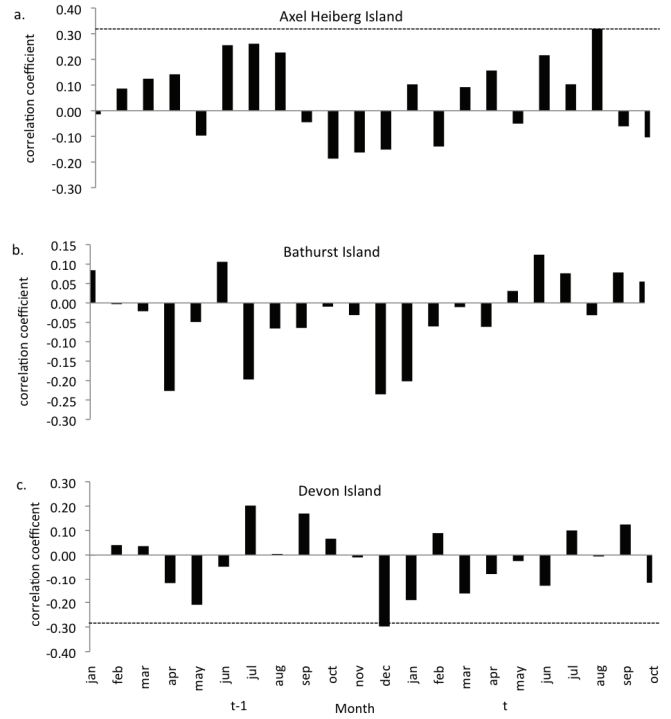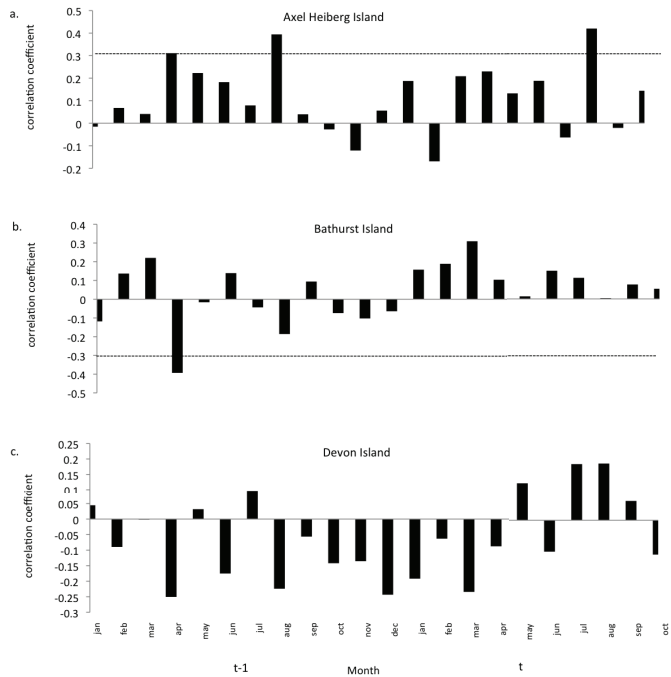
TABLE 5. Results from multivariate analysis (orthogonal regression after extraction of principal components) of chronology-climate relationships for Axel Heiberg Island, Bathurst Island, and Devon Island sites. Calibration and verification statistics were calculated using the period common to both chronology and climate data.[1]

Meteorological station	Climate data series	Proxy	Calibration					Verification				Climate variables (Factor Scores) included ($p < 0.05$)
			R	R²	adjR²	SE	DW	R	R²	SE	RE	
Axel Heiberg Island:												
Eureka	1959–99	AGI	0.63	0.40	0.37	0.13	**1.67**	0.63	0.40	0.02	0.40	FS2 annual rain (t-1); summer R/P (t-1)
												FS4 August R/P (t)
Eureka	1959–99	LEAF	0.58	0.34	0.29	0.10	**1.81**	0.58	0.34	0.02	0.33	FS2 January min/mean T (t-1); July, summer P (t)
												FS3 February max/mean T (t-1)
												FS4 summer, annual R (t-1)
Eureka	1959–99	BUD	0.61	0.37	0.34	0.12	**2.12**	0.61	0.38	0.02	0.37	FS1 April, spring max/min/mean T (t)
												FS2 February, winter P (t)
Eureka	1959–99	FLO	0.47	0.22	0.18	0.29	1.38	0.47	0.22	0.03	0.21	FS1 August R/P (t)
												FS3 August R/P(t-1)
Eureka	1963–99	δ¹³C	0.60	0.36	0.32	0.52	1.04	0.60	0.36	0.03	0.36	FS1 November min/max/mean T (t-1)
												FS2 December min/mean T (t-1)
Bathurst Island:												
Resolute	1947–98	AGI	0.46	0.21	0.18	0.14	**1.56**	0.46	0.21	0.01	0.10	FS2 December max/mean T (t-1); December DP (t-1)
												FS4 November (t-1), May (t) DP
Resolute	1947–98	LEAF	0.44	0.19	0.16	0.15	**1.73**	0.44	0.19	0.01	0.30	FS1 April total/average SH (t-1); April P (t-1)
												FS2 June total/average SR (t-1); April average SR (t)
Resolute	1947–98	BUD	0.68	0.46	0.41	0.21	1.00	0.68	0.46	0.02	0.42	FS1 July, summer, annual total/average SH (t-1)
												FS2 September min/max/mean T (t); September, fall DP (t)
												FS3 March P (t-1); September, fall P (t)
												FS4 August RH (t)
Resolute	1947–98	FLO	0.57	0.33	0.27	0.12	1.31	0.57	0.33	0.01	0.45	FS2 March, April, spring RH (t)
												FS3 September, winter total/average SH (t)
												FS5 June, summer DP (t-1); September RH (t-1)
												FS7 winter total/average SH (t-1)
Resolute	1947–98	δ¹³C	0.65	0.42	0.38	0.63	1.08	0.65	0.42	0.04	0.10	FS3 April, Spring total/average SR (t-1); May average SR (t-1)
												FS5 November min/max/mean T (t-1)
Devon Island:												
Resolute/Pond Inlet	1947–98	AGI	0.48	0.23	0.20	0.13	1.16	0.48	0.23	0.01	0.12	FS1 July min/max/mean T (t)
												FS2 December P (t-1)
Resolute/Pond Inlet	1947–98	LEAF	0.44	0.19	0.16	0.10	**1.62**	0.44	0.19	0.02	0.19	FS1 July max/mean T (t)
												FS2 winter DP (t-1)
Resolute/Pond Inlet	1947–98	BUD	0.39	0.15	0.11	0.09	1.22	0.39	0.15	0.02	0.10	FS3 July total/average SH (t); July P (t-1)
												FS4 February S/P (t); winter S (t)
Resolute/Pond Inlet	1947–98	FLO	0.54	0.29	0.23	0.12	**1.71**	0.52	0.27	0.01	0.29	FS1 June min/max/mean, July max T (t-1); summer max/mean T (t-1); June DP (t-1)
												FS2 January min/max/mean T (t-1); January, winter DP (t-1)
												FS3 April, spring DP (t-1)
												FS5 spring DP (t); August RH (t-1)
Resolute/Pond Inlet	1947–98	δ¹³C	0.66	0.44	0.39	0.45	1.00	0.66	0.44	0.02	0.44	FS1 June, July, summer min/max/mean T (t-1)
												FS2 April, spring min/max/mean T (t-1)
												FS3 June min/mean, July max/mean T (t); fall total SR (t-1)
												FS8 May, spring total SR (t)

[1] T = temperature (˚C), P = precipitation (mm), R = rainfall (mm), S = snowfall (cm), DP = dewpoint temperature (˚C), SH = sunshine hours (hrs), SR = solar radiation (MJ/m²), RH = relative humidity (%), SE = Standard error of the prediction, DW = Durbin Watson statistic, RE = reduction of error (Briffa et al., 1988). Bold numbers indicate $p < 0.01$.

Growth and Reproduction Models

Axel Heiberg Island: At AHI, the annual growth increment (AGI, R = 0.63) and annual flower bud production (Bud, R = 0.61) models were characterized by moderate multiple calibration correlation coefficients (Table 5). No loss in explained model variance was confirmed by the jackknife (leave-one-out) procedure, and the models showed good predictive skill (AGI RE = 0.40; Bud RE = 0.37). Autocorrelation of the residuals was absent in the models. The climate parameters that characterized the AGI model included previous-year summer and annual total rainfall/precipitation and current-year August total rainfall/precipitation. The annual flower bud production model was influenced by April and spring maximum, minimum, and mean temperatures and February total precipitation in the current year.

In the Canadian High Arctic, AHI is one of the driest sites because the high mountains block cyclonic circulation from Baffin Bay and Parry Channel (Maxwell, 1981). The

importance of previous year annual and summer precipitation and February precipitation as predictors in the growth and reproduction models, respectively, supports the theory that Arctic plants, like *C. tetragona*, may be water-limited (Bliss, 1977; Wookey et al., 1993). Adequate soil moisture supply in the previous year may facilitate the production and winter storage of photosynthates in the leaves and stem of the plant (Chapin, 1980). During the first four to six weeks of the current growing season, *C. tetragona* draws upon these reserves for stem elongation during this period of intense plant growth (Shaver and Kummerow, 1992). In addition, winter precipitation acts to protect and insulate the plant's overwintering flower buds from extreme temperatures and wind (Callaghan et al., 1989; Johnstone and Henry, 1997).

Research suggests that the Arctic growing season is lengthening, driven by earlier and warmer spring temperatures (Zhang et al., 2000; Vincent et al., 2007), earlier snowmelt (Stone et al., 2002), and reduced area and depth of spring snow cover (Brown and Goodison, 1996; Brown and Braaten, 1998). Warmer (t) spring temperatures appear to positively influence annual flower bud production in *C. tetragona* on AHI by potentially increasing the length of the growing season. Experimental evidence supports the theory that *C. tetragona* reproduction may increase with a longer and warmer growing season by extending the period for development and resource allocation (Arft et al., 1999; Molau, 2001; Walker et al., 2006). However, earlier snowmelt may expose Arctic plants to frost damage through the earlier loss of frost hardiness or by the exposure of apical meristems and buds to low temperatures, as has been observed for alpine plant species at a site in the Swiss Alps (Wipf et al., 2009). It is also uncertain how changes in spring temperature will influence spring snowpack depth and moisture availability early in the growing season at this site. At a High Arctic site on Svalbard, Welker et al. (1995) found *C. tetragona* annual growth depended on spring snowmelt as its primary water source. On the other hand, evidence suggests that *C. tetragona* plants at a site on Ellesmere Island shifted from spring snowmelt to summer precipitation as the primary water source, in association with changes in predominant atmospheric circulation and precipitation supply (Welker et al., 2005). Understanding the potential interaction of earlier and warmer growing seasons and moisture supply on plant reproduction in xeric sites will be an important key to understanding future plant allocation and reproductive success.

Bathurst Island: Of the four BI growth and reproduction chronologies, only one model, annual production of flower buds, resulted in a moderately high-calibration multiple correlation coefficient (Bud, R = 0.68) and explained 46% of the variance (Table 5). There was also no loss in explained model variance as confirmed by the jackknife (leave-one-out) procedure, and the model showed good predictive skill (RE = 0.42). However, there was evidence of autocorrelation of the residuals in the model. Unlike the AHI model for annual production of flower buds, the BI model was characterized by a larger number of climatic parameters, including (t-1) annual, summer, and July total and average sunshine hours; (t) maximum, minimum, and mean September temperatures; (t) fall and September dewpoint temperature; (t-1) March and (t) fall and September total precipitation, and (t) August relative humidity.

Given that *C. tetragona* flower buds are pre-formed one to two years prior to flowering (Sørensen, 1941), it is hypothesized that their development depends on plant reserves accumulated over the previous one to four years (Molau, 2001). A high number of sunshine hours during the previous growing season may facilitate the adequate production and storage of additional photosynthates, resulting in a greater number of flower buds produced in the current summer. In addition, the extension of warm temperatures into the fall may facilitate further bud maturation (Nams and Freedman, 1987). Comparing the BI and AHI models for annual flower bud production, it appears that late growing season temperature is more important to the successful production of flower buds at the BI site. Changes to the start, end, and overall length of the growing season due to future climate change may affect the two populations of *C. tetragona* differently, influencing their reproductive success and intra-plant resource allocation.

Like the annual flower bud production model for AHI, the BI model also depends upon multiple moisture-related climate parameters. Winter precipitation (snowpack) serves to insulate and protect overwintering leaf and flower buds, as well as providing antecedent moisture to photosynthesizing plants in the early growing season, when the active layer may still be partially frozen (Callaghan et al., 1989; Johnstone and Henry, 1997). In addition, our evidence suggests that at the BI site, higher August relative humidity and early fall moisture supply may cause the leaf stomata to remain open, leading to a subsequent carbon gain that may be directed toward late summer bud maturation (Kramer and Boyer, 1995). Vincent et al. (2007) provide evidence of recent (1953–2005) increases in spring and fall relative humidity in Arctic Canada that might have influenced reproductive success at the BI site.

Stable Carbon Isotope Models

Axel Heiberg and Bathurst Islands: At our study's two most northerly sites, the δ^{13}C models for AHI (R = 0.60) and BI (R = 0.65) were moderately strong, explaining 36% and 42% of the variance, respectively (Table 5). The jackknife (leave-one-out) procedure showed no loss of explained variance, and each model was characterized by good predictive skill (AHI: RE = 0.36; BI: RE = 0.10). However, autocorrelation of the residuals was identified in each model. The AHI model explained the δ^{13}C variations as a function of (t-1) November and December minimum, maximum, and mean temperatures, while the BI model explained the δ^{13}C variations as a function of (t-1) November minimum, maximum, and mean temperatures, as well as (t-1) spring, April, and May total and average solar radiation.

As the AHI and BI $\delta^{13}C$ models were both positively affected by warm winter temperatures in the previous year, we hypothesize that the $\delta^{13}C$ values from these high-latitude, cool-dry sites were influenced primarily by stomatal conductance, which, in turn, is dominated by moisture availability. As a possible driver for this physiological response, we propose that warmer conditions in early winter may facilitate an increase in winter precipitation, leading to a deeper snowpack. In Arctic Canada, Zhang et al. (2000) found that warmer winter, spring, and fall temperatures have made more moisture available to snowfall events, so that the ratio of snowfall to precipitation has increased significantly in this region. Deeper snowpack, in turn, may delay the start of the growing season by maintaining lower soil temperatures and delaying active layer melting at a time when increasing temperature may lead to increasing evapotranspiration. In fact, *C. tetragona* is often found in snowbed sites (Polunin, 1948), and its growth can begin when the ground is still covered with snow (Molau, 2001). Thus, in some years, plants may suffer from frost or physiological drought if deeper-than-normal snowpack hinders soil thawing in the early growing season (Tranquillini, 1979; Thomsen, 2001).

The effect of warmer early winter temperatures on BI $\delta^{13}C$ values is further compounded by the influence of higher (t-1) spring total and average solar radiation on moisture supply. Increased spring solar radiation may indicate a greater number of days with clear skies, which, in turn, may allow for greater heating and subsequent melting and sublimation of snowpack. Recent studies of Western Arctic climate provide evidence for a decrease in average cloudiness in spring and summer from 1953 to 2002 (Milewska, 2004). An increase in spring temperature (Rigor et al., 2000; Overland et al., 2002, 2004), the earlier disappearance of snow, and a greater number of snow-free days (Bamzai, 2003), also characterized Arctic climate in the late 20th century. Earlier spring melt may mean that less antecedent moisture is available for *C. tetragona* plants, as the meltwater cannot be absorbed by the still-frozen active layer and therefore runs off the ground surface. While the influences on BI $\delta^{13}C$ values of the two climate scenarios proposed above may appear to be mutually exclusive, they may, in fact, occur in different years and thus result in consistently high $\delta^{13}C$ values over time.

Here, we also note that the influence of previous year $\delta^{13}C$ values (Table 4) and climate conditions (e.g., solar radiation) on current-year $\delta^{13}C$ values may suggest some level of translocation of reserve carbohydrate from the previous summer. *Cassiope tetragona*, like other Arctic evergreen species, is thought to store reserves in current leaves and stems during the winter for use in the early portion of the following growing season (Chapin, 1980).

Devon Island: Of the five DI chronologies, only the $\delta^{13}C$ model resulted in a moderately high multiple correlation coefficient of R = 0.66, the second-highest R value calculated for this study (Table 5). The jackknife procedure confirmed no loss of explained model variance, and the model showed good predictive skill (RE = 0.44). Autocorrelation of the residuals was present in the model. The DI model explained the $\delta^{13}C$ variations as a function of previous-year spring, summer, April, June, and July maximum, minimum, and mean temperature; current-year June minimum and maximum temperature and July maximum and mean temperature; and previous-year fall and current-year spring and May total solar radiation.

For the DI site, we hypothesize that the $\delta^{13}C$ values are influenced by photosynthetic rate primarily during the growing season in the previous and current years. Photosynthetic rate is limited by temperature, which controls the rate at which the photosynthetic enzyme is produced, or by photon flux, which controls the rate at which the photosynthetic enzyme removes CO_2 from the stomatal chambers (Beerling, 1994). While warmer spring temperatures may cause an earlier snowmelt, depriving plants of antecedent moisture, we posit that the DI site's higher average precipitation totals (Table 1), which are due to high regional cyclonic activity, orographic uplift, and the contribution of the North Water Polynya to atmospheric moisture during the growing season, likely prevent moisture stress from being an important influence on $\delta^{13}C$ values in most years.

Spatial Variability in Plant Response

For the investigated models, our study suggests that variation in growth, reproduction, and $\delta^{13}C$ values is a function of multiple and different climate variables, resulting in strong spatial variation of plant response within a relatively small region of Arctic Canada. The geographic split in plant response to climate does not necessarily denote inconsistency. Instead, it may suggest that 1) the climate signals are simply different (Luckman, 1997), 2) the climatic sensitivity of the sites varies, or 3) strong regional climatic variability due to geographic differences accounts for differences in site or population responses (Treydte et al., 2007). In this study, we developed five chronologies from one single population at each site, so our understanding of local population-level response to climate is limited. However, at Alexandra Fiord, Ellesmere Island, growth and reproduction chronologies were developed from four populations along an elevation gradient and correlated with monthly average temperature and total precipitation values (Johnstone and Henry, 1997; Rayback, 2003; Rayback and Henry, 2006). Chronology comparison revealed similar growth-climate responses at the two low-elevation sites (30 m a.s.l.) (Johnstone and Henry, 1997; Rayback and Henry, 2006), suggesting that climate sensitivity may vary between sites while remaining consistent within any single site. However, when chronology-climate responses at two higher-elevation sites (150 m and 500 m a.s.l.) were compared with those at the two lowland ones, the responses differed markedly. These results indicate that local (and regional) climatic differences due to geographic location and topographic relief may account for differences in site or population responses. The responses of the three $\delta^{13}C$ models to climate illustrate

this point, as the DI site, characterized by high cyclonic activity, orographic precipitation, and the proximity of the North Water Polynya, receives enough moisture during the growing season so that photosynthetic rate, and hence temperature, more strongly influence the $\delta^{13}C$ chronologies. The AHI and BI sites, on the other hand, are more arid because of a rainshadow effect and greater anticyclonic activity, respectively; as a result, $\delta^{13}C$ chronologies are influenced primarily by stomatal conductance and moisture availability.

CONCLUSIONS

Our study concludes that multiple and different climate factors influence growth, reproduction, and stable carbon isotope ratio chronologies at three sites in the eastern Canadian Arctic. These differences underline a strong spatial variation in plant response that may be linked to the variable climate sensitivity of the sites and populations studied, or to regional climatic variability due to geographic and topographic differences within and between sites, or both. In general, precipitation and moisture availability, as mediated through temperature, influence annual stem elongation and production of flower buds at the AHI site and production of flower buds at the BI site. In addition, the importance of temperature in the early (AHI) and late (BI) growing season to annual flower bud production differs between the two sites, and raises questions around the future ability of the species to reproduce under changing growing season conditions. We also identified spatial variation in the response to climate of stable carbon isotope ratio time series. We hypothesize that the $\delta^{13}C$ values at AHI and BI vary in response to stomatal conductance, which is influenced by moisture availability, while the $\delta^{13}C$ values at DI vary in response to temperature, which influences photosynthetic rate. Results from our study underscore the hypothesis that Arctic shrubs are sensitive to climate. The dendroecological evaluation of annual growth, reproduction, and stable carbon isotope ratio chronologies provides important evidence of long-term population dynamics and differences among populations across various spatial scales, raising questions about the consistency of plant response even within small regions. Our results underline the need for a higher density of sampling sites in the Arctic to identify complex plant responses to climate and the need to pay closer attention to multiple climatic drivers that may influence one chronology more strongly than another, depending on site location.

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