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Effects of Manipulated Precipitation and Shading on *Cassiope tetragona* Growth and Carbon Isotope Discrimination: a High Arctic Field Study

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Abstract

The reliability of *Cassiope tetragona* as temperature proxy might be restricted by influence on growth of precipitation and amount of Photosynthetically Active Radiation (PAR). Carbon-13 discrimination (Δ) in C_3 -plants is generally influenced by temperature and precipitation and can therefore potentially record important additional climatic information.

We doubled precipitation and reduced PAR (-43%), during four and two growing seasons, respectively, at a high arctic site in Svalbard. Differences in discrimination in leaves from separate light, and thus temperature, regimes (sun-facing and soil-facing leaves) were also assessed. A Δ -chronology (1975–2008) in annual shoot length increments was developed.

C. tetragona growth did not respond to enhanced precipitation and only slightly to PAR-reduction. Discrimination against carbon-13 was stronger in leaves and shoots receiving extra precipitation and weaker in sun-exposed leaves compared to soil-facing leaves. The annual climate signal in the Δ -chronology was strongly smoothed by secondary radial growth.

Our results show that the temperature signal in *C. tetragona* is hardly disturbed by changes in summer precipitation or PAR, which confirms its suitability as temperature proxy. The experimental evidence for the sensitivity of carbon-13 discrimination in *C. tetragona* to precipitation and temperature changes shows its potential as proxy for hydrological changes in the polar semi-desert.

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Introduction

Although it is known that temperatures in the Arctic have very probably risen over the 20th century and total annual precipitation has probably increased, the scarcity of instrumental and proxy climate records restricts extensive analysis of the complex arctic climate system and the reliability of climate projections (ACIA, 2005; Anisimov et al., 2007). This emphasizes the need for proxy climate data to fill in spatial and temporal gaps in the arctic climate record. Previous studies have shown that annual growth parameters of the circumpolar dwarf shrub *Cassiope tetragona* can serve as a temperature proxy, providing a database of past and ongoing climate change throughout the Arctic, well beyond the instrumental record (Rayback and Henry, 2005, 2006; Weijers et al., 2010, 2012). Both experimental (Rozema et al., 2009; Weijers et al., 2012) and correlative evidence (Johnstone and Henry, 1997; Rayback and Henry, 2006; Weijers et al., 2010, 2012) suggest that *C. tetragona* growth is strongly limited by growing season temperatures, resulting in a strong temperature-growth relationship allowing for temperature reconstructions (Johnstone and Henry, 1997; Rayback and Henry, 2006; Weijers et al., 2010). In the High Arctic, mostly growing season temperatures have been pinpointed as the strongest driver of *C. tetragona* growth (Havström et al., 1993, 1995; Rayback and Henry, 2005, 2006; Weijers et al., 2010, 2012), but some correlative evidence exists for a positive impact of May precipitation and a negative impact of summer precipitation (Callaghan et al., 1989; Johnstone and Henry, 1997). Callaghan et al. (1989) identified

precipitation as the most important driver of growth in Svalbard through multiple regression analyses between *C. tetragona* leaf performance variables and monthly climate data. Such influence of precipitation could potentially interfere with the temperature signal in *C. tetragona* growth parameters and result in less reliable temperature reconstructions. As accurate measurement of snowfall and rainfall in cold environments is problematic (Goodison et al., 1998), it is important to assess the influence of precipitation on growth in experimental settings, besides correlative analyses.

Changing amounts of Photosynthetically Active Radiation (PAR) due to fluctuations in cloudiness could similarly impact the reliability of temperature reconstructions based on *C. tetragona* growth, as reduction of PAR might affect its growth rate (Havström et al., 1993). The general short and scarce character of existing instrumental cloudiness records (Young et al., 2012), limits the reliability of correlative analyses. This illustrates the importance of assessment of the influence of cloudiness on annual growth parameters in an experimental setting.

Carbon isotope ratios in annual fragments of plants using the C_3 -photosynthetic pathway can potentially capture strong precipitation signals (e.g. Fichtler et al., 2010). This is a direct result of the fact that the reaction of the lighter $^{12}\text{CO}_2$ with the enzyme Rubisco during photosynthesis is faster than with $^{13}\text{CO}_2$, which causes these plants to be more depleted in ^{13}C than source air (Farquhar et al., 1982, 1989). This discrimination against the heavier isotope by Rubisco is, however, largely prevented when plants close their stomata to prevent water loss. Dry periods will thus generally result in plant tissue enriched in ^{13}C , compared to plant tissue formed in

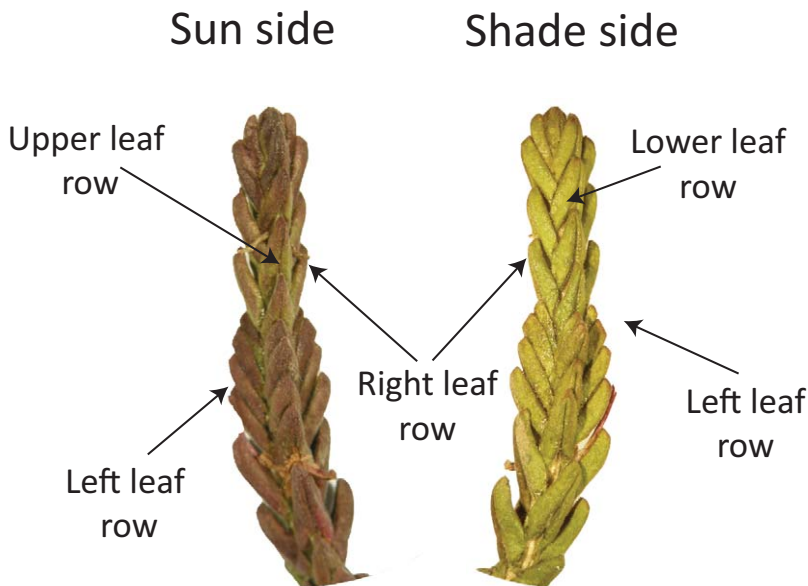


FIGURE 1. Photographs of two sides of a single *Casiope tetragona* shoot. Leaves and parts of leaves facing the sun have a dark red-green color, whereas leaves and parts of leaves pointed towards the soil are bright green.

wetter periods. Consequently, a climatic fingerprint is left behind. Beside stomatal conductance, discrimination against $^{13}\text{CO}_2$ is also controlled by photosynthetic rate, with higher rates resulting in reduced discrimination (Farquhar et al., 1982; Welker et al., 2005). Photosynthetic rate is influenced by amount of PAR and temperature, which are generally positively correlated during the growing season. Thus, when temperature and PAR increase, discrimination against ^{13}C is likely to decrease. An increase in precipitation will have the opposite effect.

C. tetragona is a species with an initial upright, but later prostrate growth habit. Leaves are formed in opposite pairs, alternating at 90° angles, forming four rows of leaves along its branches. Leaves remain attached to the stems for up to 40 years. Prostrate branches generally have one row of leaves facing the sun, and one row facing the soil. The other leaves are partly facing the sun and partly facing the soil. Sun-facing leaves of *C. tetragona* commonly have a dark red-green color and can often be distinguished from soil-facing leaves, which have a bright green color (Fig. 1). This allows the assessment of the effect of different light regimes, and thus temperature, on carbon isotope discrimination in leaves of *C. tetragona*, by comparing the carbon isotope composition of different leaf rows. Carbon isotope discrimination in the warmer, sun-facing (upper) leaf row is expected to be stronger compared to that in the shaded soil-facing (lower) leaf row. The right and left leaf rows likely have values in between those of the upper and lower rows.

Correlative evidence suggests that $\delta^{13}\text{C}$ ratios in *C. tetragona* are sensitive to changes in hydrology. Welker et al. (1995) reported a significant relationship between spring (April and May) precipitation and a cellulose $\delta^{13}\text{C}$ chronology of annual *C. tetragona* shoot fragments from Ny-Ålesund, in high arctic Svalbard. In a later study, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements were successfully linked to Arctic and North Atlantic oscillation phase changes in high arctic Canada (Welker et al., 2005). Rayback et al. (2011) found a variety of climate signals in $\delta^{13}\text{C}$ chronologies, which differed between three sites in the Canadian High Arctic. Thus, as carbon isotope discrimination is influenced by hydrology, $\delta^{13}\text{C}$ values of annual

C. tetragona fragments could potentially reveal past climate changes other than just temperature.

The aims of this study were to further validate the use of annual growth parameters of *C. tetragona* as an arctic temperature proxy and to test the potential of stable carbon isotope ratio discrimination values in annual *C. tetragona* fragments as a climate proxy. At a site in the high arctic Svalbard archipelago, separate field experiments were carried out in which precipitation was doubled and PAR was halved. The effects of summer precipitation and shading on annual growth parameters of *C. tetragona* were assessed. Furthermore, it was tested whether the carbon isotope discrimination was affected by the enhanced precipitation regime and whether the carbon isotope signature differed between leaves from different leaf rows, and thus light regimes. Finally an annually resolved Δ -shoot chronology (1975–2008) was developed and relationships with the local climate were examined.

Material and Methods

SITE DESCRIPTION

Our research location was at Isdammen, approximately 1.5 km southeast of Longyearbyen, Svalbard ($78^\circ 12' \text{N}$; $15^\circ 44' \text{E}$; Fig. 2). At this site, located on a gentle east-northeast-facing slope about 30 m above sea level (a.s.l.), the tundra vegetation is dominated by *C. tetragona* with a cover between 40 and 50% (Rozema et al., 2006, 2009). Between 2005 and 2008, 10 randomly chosen hexagonal plots (diameter 2.2 m) received double the amount of the 30-year average monthly precipitation from mid-June until late August, by manually adding water several times a week. Water was collected from the nearby local artificial drinking water lake. Ten other hexagonal plots were randomly selected as controls. At an adjacent site, just below the other (about 25 m a.s.l.), 40 smaller plots (50×50 cm) were randomly chosen. During the summers of 2007 and 2008 PAR-reduction cubes were installed over 20 of those plots. The cubes ($50 \times 50 \times 50$ cm) were constructed by placing 4 iron poles at each corner and spanning gauze (maze width

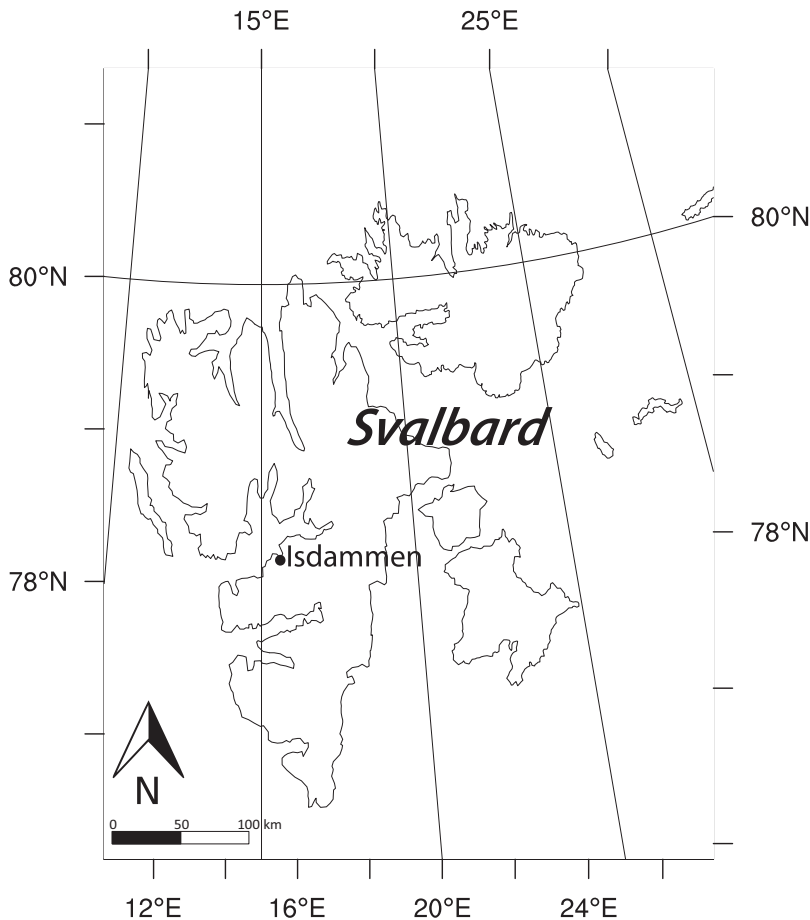


FIGURE 2. Map of the Svalbard archipelago, with the location of our research site at Isdammen.

1 mm) between and over these poles to form a tent. During the summer of 2008, PAR was measured at hourly intervals by placing PAR sensors connected to loggers underneath one of these tents and in one control plot. At the end of August 2008, 3 to 4 shoots were harvested from each plot, stored in paper bags, and transported for analysis to Amsterdam. Two other shoots were harvested outside the plots for the comparison of $\delta^{13}\text{C}$ values between the different leaf rows. Growth parameters were measured for one shoot per plot for each of the 20 control and PAR-reduction plots. For the doubled precipitation experiment, growth parameters and $\delta^{13}\text{C}$ values in leaves and annual shoot fragments were measured for 17 control (one or two per plot) and 10 water-addition shoots (one per plot).

MEASUREMENT OF GROWTH PARAMETERS

To measure the potential effect on growth of the environmental perturbations, for each shoot 4 different annual growth parameters were assessed: shoot length, total leaf length, number of leaves, and average leaf length. Annual leaf cohorts can be distinguished on *C. tetragona* shoots as smaller leaves are formed at the start and end of each growing season, resulting in wave-like patterns (Warming, 1908). Usually, the shortest leaf pair is the boundary of each cohort (last-formed pair). To verify the absolute year boundaries, we measured shoot length both as the distances between wintermarksepta (WMS), which clearly demark annual shoot length increments (Weijers et al., 2010), and as annually summed leaf scar distances. Similar to leaf lengths, leaf scar distances are

much shorter at the beginning and end of each growing season (Johnstone and Henry, 1997; Rayback and Henry, 2005, 2006). By using WMS distances as a reference for absolute annual shoot length growth, annual leaf cohorts were precisely distinguished. Leaves were removed from the tip to the base of the shoots, and leaf lengths were consequently measured under $30\times$ magnification to 0.1 mm precision. To reveal the WMS within the pith of the stems, a top layer was laterally removed with a scalpel. Thereafter, annual shoot length growth was measured under $30\times$ magnification to 0.1 mm precision. Total leaf lengths were calculated by summing the leaf lengths of each cohort, and the number of leaves was derived from these measurements. Average leaf length was calculated by dividing total annual leaf length by the number of leaves. Exact calendar years could easily be assigned to each of the annual growth parameters due to the relative young age of the shoots analyzed and the known date of harvest. For the construction of longer *C. tetragona* growth chronologies, cross-dating is required as older (side) branches often cannot be directly dated (see Weijers et al., 2010, 2012).

CARBON ISOTOPES

The collection of individual leaves and annual shoot fragments of *C. tetragona* for $\delta^{13}\text{C}$ analysis was completed for 17 control shoots (1 or 2 per plot) and for 10 shoots of the extra water treatment (1 per plot), directly after measurement of growth parameters on the same shoots. Annual shoot fragments were separated from each

other with a scalpel. In addition, 2 extra shoots were analyzed in detail. For the latter, leaf samples were divided into four different sequences (upper, lower, right, and left) to determine the impact of different light/temperature regimes on $\delta^{13}\text{C}$ (Fig. 1). We looked at differences between average carbon isotope discrimination values between the separate rows of these two individual branches. This way, intra- and interannual differences, as well as differences between individuals, were disregarded. *C. tetragona* leaves retain their color for at least 2 years after harvest, when stored under dry conditions, and remain attached to the stems. Identification of the different rows was based on color, with the upper row being dark red-green, the lower row bright green, and the leaves of the right and left row both partly dark red-green and bright green (Fig. 1). For this type of analysis, *C. tetragona* shoots were selected which showed a clear color distinction between the different rows and which showed little signs of spiral growth.

Prior to the $\delta^{13}\text{C}$ measurement, leaves and annual shoot length fragments for each plant were oven dried at 60 °C for a minimum of 48 h. Afterwards, leaves with weights above 1 mg were ground and ± 1 mg was placed into a 4 × 6 mm tin capsule. The rest of the leaf was used as duplicate. Leaves with weights below 1 mg were directly placed into tin capsules, without grinding. We assumed a homogeneous distribution of ^{13}C over the entire length of each annual shoot fragment. Vertical thin sections were taken from each shoot length fragment, ground, and weighed to ± 1 mg. Duplicates were taken from each shoot length fragment, when possible. Annual shoot length fragments with weights below 1 mg were used entirely for $\delta^{13}\text{C}$ measurement. The minimum weight used of bulk shrub material was 0.1 mg. The maximum weight was 1.2 mg. Carbon isotope composition was determined by an elemental analyzer (NC2500, ThermoQuest Italia, Rodano, Italy) coupled online to a stable isotope ratio mass spectrometer (Deltaplus; ThermoFinnigan, Bremen, Germany). For calibration the following standards were used: IAEA-601 benzoic acid (−28.81‰), USGS24 graphite (−16.05‰), and IAEA CH-7 polyethylene (−32.15‰). A plant sample (−28.50‰; 45.2% C) was used as a quality control sample and measured in triplicate in each run. The amount of carbon in the standards was adjusted relative to amount of carbon in the samples. The analytical precision of the measurement is better than 0.1‰ based on three replicate measurements of the plant sample; in other words: the standard deviation of the three quality control sample measurements in one run of 96 samples was better than 0.1‰. Stable isotope abundance was expressed using the δ notation:

$$\delta^{13}\text{C}_p(\text{‰}) = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000 \quad (1)$$

where $\delta^{13}\text{C}_p$ represents the ^{13}C content and R_{sample} and R_{standard} denote the $^{13}\text{C}/^{12}\text{C}$ ratios of the sample and the standard (Vienna Pee Dee Belemnite [VPDB]), respectively.

Afterwards, $\delta^{13}\text{C}$ values were averaged per individual leaf or shoot length fragment, if duplicates were present. The $\delta^{13}\text{C}$ values from the leaves of each individual shoot were then averaged per year, except for the $\delta^{13}\text{C}$ comparison between separate leaf rows. This resulted in individual annually resolved leaf and shoot $\delta^{13}\text{C}$ chronologies for each analyzed shoot from control and water-addition plots.

Carbon isotope discrimination (Δ) values were then calculated using the average annual $\delta^{13}\text{C}$ -values of leaves and shoots and the $\delta^{13}\text{C}$ -values of air (Farquhar et al., 1982; Evans et al., 1986), using the following formula:

$$\Delta \approx \frac{\delta^{13}\text{C}_a - \delta^{13}\text{C}_p}{1 + \frac{\delta^{13}\text{C}_p}{1000}} \quad (2)$$

where $\delta^{13}\text{C}_a$ is the atmospheric stable carbon isotope ratio of CO_2 relative to the VPDB ratio. The $\delta^{13}\text{C}_a$ decreases over time as a result of the combustion of fossil fuel (Francey et al., 1999) and fluctuates seasonally due to the discrimination of plants against $^{13}\text{CO}_2$. We used the average June through September atmospheric $\delta^{13}\text{C}$ as measured at Alert, Nunavut, Canada (82°30'N, 62°20'W) for $\delta^{13}\text{C}_a$ over the period 1985–2008 (Keeling et al., 2010). We extrapolated the average change in this data set to estimate $\delta^{13}\text{C}_a$ prior to 1985. Δ was not calculated for the comparison of $\delta^{13}\text{C}$ in leaves from different rows, as the month in which individual leaves are formed during the growing season is unknown, and $\delta^{13}\text{C}_a$ fluctuates during the growing season. Hereafter, 4 Δ chronologies were created, 2 for annual shoot length and 2 for annual leaf cohorts by averaging the individual series per year and per treatment (control or water addition).

METEOROLOGICAL DATA AND STATISTICS

The average difference in PAR between control and PAR reduction plots was assessed with a paired samples *t*-test. Differences between annual growth and Δ in control and water-addition plots and differences between annual growth in control and PAR-reduction plots were tested for significance with one-way ANOVAs with treatment as between-subject factor. Differences between average $\delta^{13}\text{C}$ in leaves from different rows were assessed with one-way ANOVAs with row as between-subject factor.

We used monthly climate data from the nearby Svalbard Airport weather station (78°25'N, 15°47'E; 8 m a.s.l.) to calculate Pearson correlation coefficients (*r*) between local monthly climate parameters and the Δ -shoot chronology. Monthly temperature (August 1975–2008) and monthly precipitation data (1976–2008) were obtained from the eKlima database of the Norwegian Meteorological Institute (DNMI, 2011). For earlier monthly climate data prior to August 1975 the homogenized Svalbard Airport series was used, as published by NORDKLIM. All statistics were carried out in PASW Statistics 17.0.

Results

GROWTH RESPONSE TO MANIPULATIONS

Four years of doubling of mean monthly summer precipitation did not affect any of the *C. tetragona* growth parameters. Growth in control plots did not significantly differ from that in manipulated plots, neither in the years before, nor in the years after the onset of the experiment ($p > 0.05$; Fig. 3).

On average, installation of PAR cubes over the vegetation reduced daily PAR by 43% during the growing season of 2008 (199 instead of 348 $\mu\text{E m}^{-2} \text{s}^{-1}$; $p < 0.0001$). This reduction in PAR had generally little impact on the 4 measured growth parameters (Fig. 4). After the first year of the experiment (2007) annual

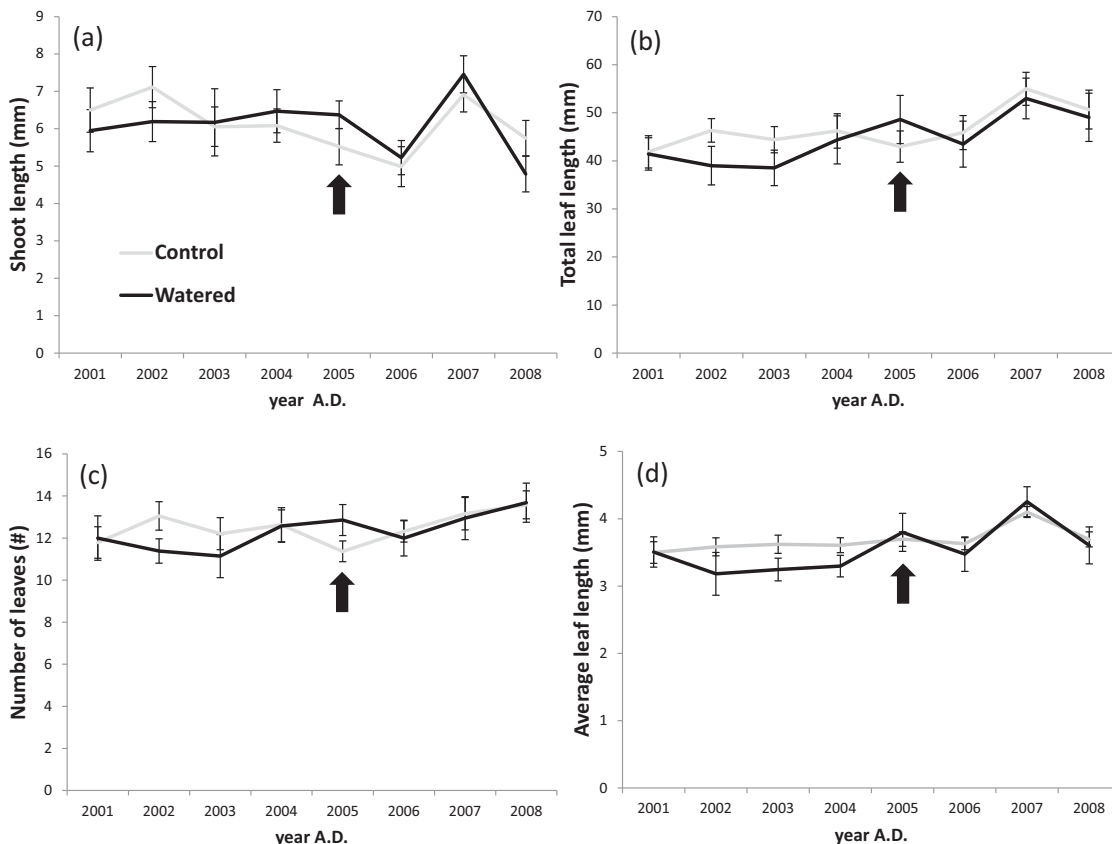


FIGURE 3. Average annual growth of *C. tetragona* measured as (a) shoot length, (b) total leaf length, (c) number of leaves, and (d) average leaf length both in control (gray lines) and water-addition plots (black lines). Error bars show the standard error of the mean. Black arrows indicate the start of the experiment. There was no difference in growth, neither before the start of the experiment (2001–2004) nor after (2005–2008).

shoot length and average leaf length per year of plants growing under reduced PAR conditions were significantly larger than in plants from controls (8.5 vs. 7.0 mm or 19.3% increase; $p = 0.047$ and 4.4 vs. 4.0 mm or 9.5% increase; $p = 0.024$, respectively). However, in the year before the onset of the experiment (2006), average shoot length was 6.1 mm in PAR-reduction plots and 5.1 mm in control plots (17.9% difference; $p = 0.13$). Average leaf length in 2006 was 3.7 mm in control plots and 4.0 mm in PAR-reduction plots (7.8% difference; $p = 0.059$). There was no difference in growth after the second year of PAR reduction, in 2008 ($p > 0.05$). All growth parameters were equal in controls and PAR reduction plots before the experiment started, except for total leaf length, which was significantly greater in PAR-reduction plots in 2002 (54.2 vs. 46.6 mm or 15.1%; $p = 0.047$).

CARBON ISOTOPE DISCRIMINATION

Leaves from the upper row of the first *C. tetragona* branch (Fig. 5, part a) were on average less depleted in ^{13}C than leaves from the lower row (-28.9 vs. -30.1‰ ; $p < 0.0001$). Average $\delta^{13}\text{C}$ in leaves from the right row (-29.3‰) was higher than in the lower row ($p < 0.0001$) and lower than in the upper row ($p = 0.006$). Leaves from the left row were on average more depleted in ^{13}C than upper row leaves (-29.7‰ vs. -28.9‰ ; $p < 0.0001$), but their $\delta^{13}\text{C}$ values did not significantly differ from the right and lower row leaves (Fig. 5; $p > 0.05$). Measurements

of ^{13}C in the four distinct leaf rows of the second branch (Fig. 5, part b) confirmed these findings, with the upper leaf row less depleted in ^{13}C than the lower leaf row and $\delta^{13}\text{C}$ values in-between those for both the right and left leaf row.

Discrimination against carbon-13 (Δ) was significantly ($p < 0.05$) greater in annual shoot fragments and leaf cohorts from water-addition plots in comparison with controls from the onset of the experiment in 2005 and onward (1.24 and 0.95‰ greater on average, respectively; Fig. 6, parts a and b). However, Δ in annual leaf cohorts and shoot length increments, initially formed before the onset of the experiment (before 2005), was sometimes already higher on average in water-addition plots compared to that in leaves and shoots from control plots. Average discrimination against carbon-13 was significantly ($p < 0.05$) greater in leaves formed from 2002 onwards and in shoots from 2004 onwards.

Δ CHRONOLOGY

Averaging Δ values in annual shoot length fragments from control plots resulted in a Δ chronology spanning the period 1975–2008 (Fig. 7). Discrimination values are generally stable between 1975 and 2004, with values between 22 and 23‰. After 2004, values decrease, from 22.2‰ in 2005 to 20.1‰ in 2008. Furthermore, we found a positive and linear relationship ($r = 0.67$, $p < 0.0001$) between annual shoot length growth and annual shoot length Δ values over the period 1975–2004 (Fig. 8).

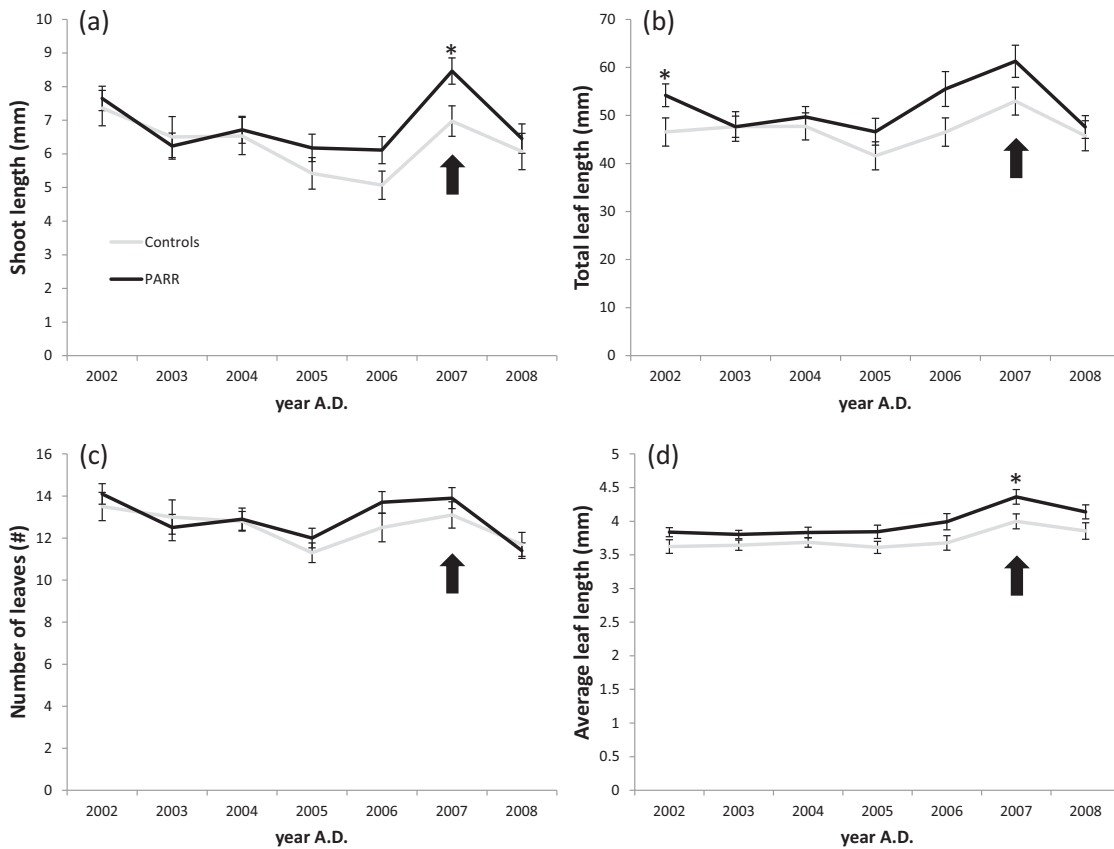


FIGURE 4. Annual growth parameters of *Cassiope tetragona* in control plots and in PAR-reduction (PARR) plots: (a) shoot length, (b) total leaf length, (c) number of leaves, and (d) average leaf length. Error bars show the standard error of the mean and the black arrows indicate the onset of the experiment in 2007. Significant differences in growth ($p < 0.05$) are indicated with an asterisk (*).

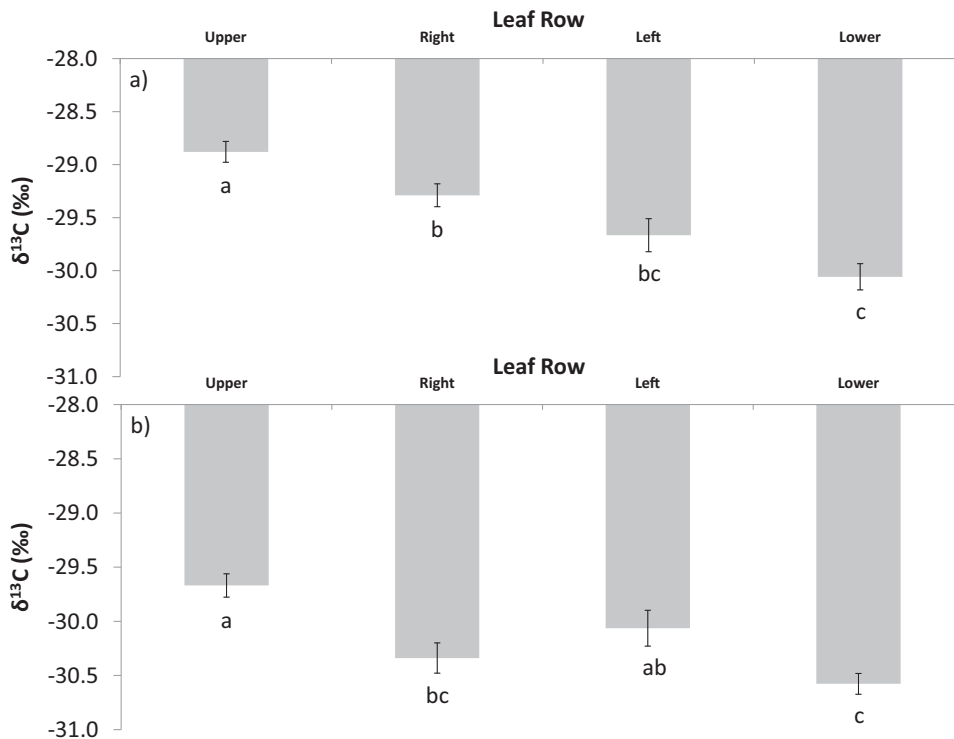


FIGURE 5. Average $\delta^{13}\text{C}$ values for each of the four leaf rows for two *C. tetragona* branches. Different letters under each bar (a, b, and c) indicate, separately for each branch, significant differences ($p < 0.01$) between $\delta^{13}\text{C}$ values averaged per row. The error bars represent the standard error of the mean. Leaves from the upper leaf rows were pointed towards the sky, receiving direct sunlight. The lower leaf rows were pointed towards the soil.

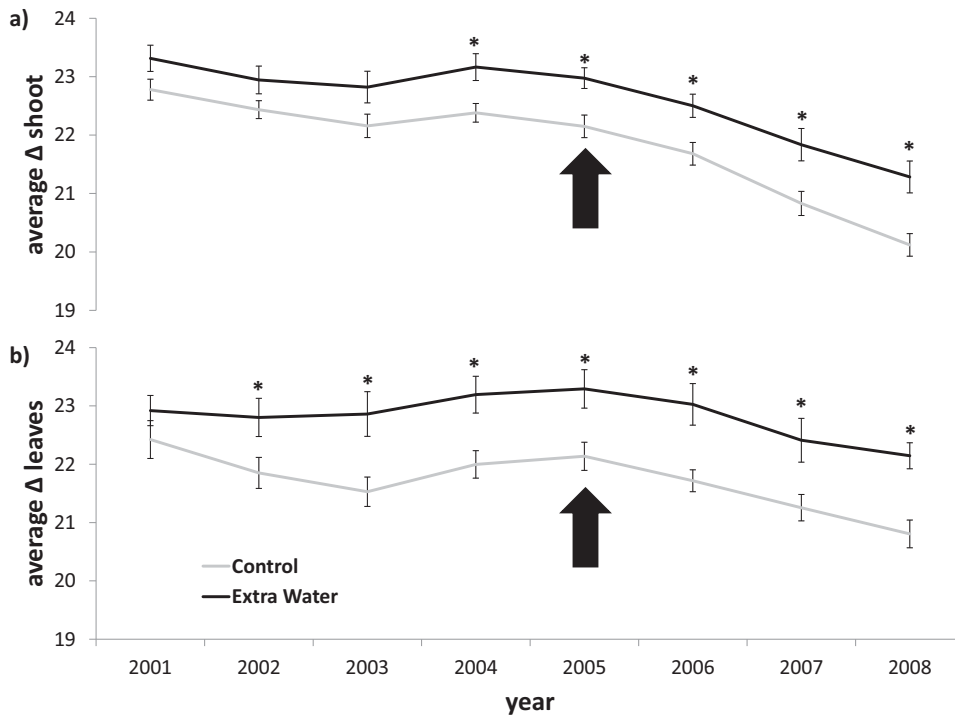


FIGURE 6. Differences in average carbon isotope discrimination (Δ) in (a) annual shoot fragments and (b) annual leaf cohorts between plants from control (gray lines) and water addition plots (black lines). The arrows indicate the onset of the experiment in 2005. Significant differences in Δ ($p < 0.05$) are indicated with an asterisk (*).

The Δ shoot length chronology was neither significantly correlated with mean monthly temperatures nor with monthly precipitation sums during the current growing season (Fig. 9). In Svalbard, the growing season starts after snowmelt in June (Cooper et al., 2011). Instead, we found significant ($p < 0.05$) negative correlations between mean temperatures from previous May and June and current May and Δ . We also found a significant ($p < 0.05$) positive correlation between previous September precipitation sums and current Δ .

Discussion

We have shown that, in high arctic Svalbard, disturbance of the strong temperature signal previously found in annually resolved

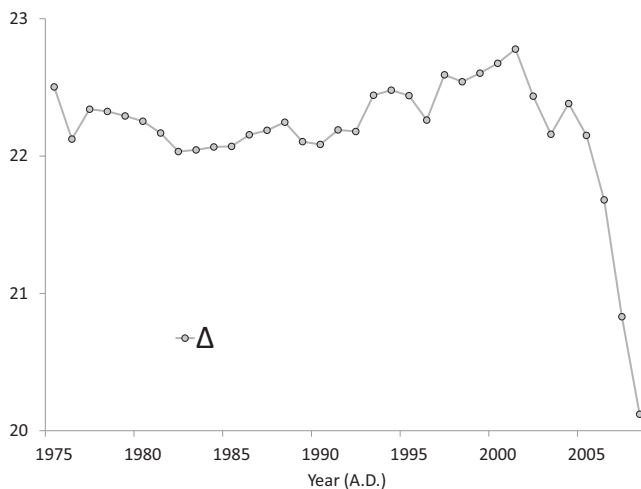


FIGURE 7. Average annual Δ in *C. tetragona* shoots from control plots between 1975 and 2008.

growth chronologies of *C. tetragona* by natural fluctuations in summer precipitation and PAR is probably limited. This confirms the suitability of annual growth parameters of *C. tetragona* as proxy for past arctic summer temperature. The increase in *C. tetragona* shoot and leaf Δ to enhanced precipitation and the different $\delta^{13}\text{C}$ values in leaves from diverse light regimes in this study provide, to our knowledge, the first experimental evidence of sensitivity of discrimination against ^{13}C in *C. tetragona* in response to summer precipitation and temperature. Carbon isotope ratios in annual fragments of *C. tetragona* are thus likely to capture and preserve past changes in hydrological conditions during the high arctic growing season.

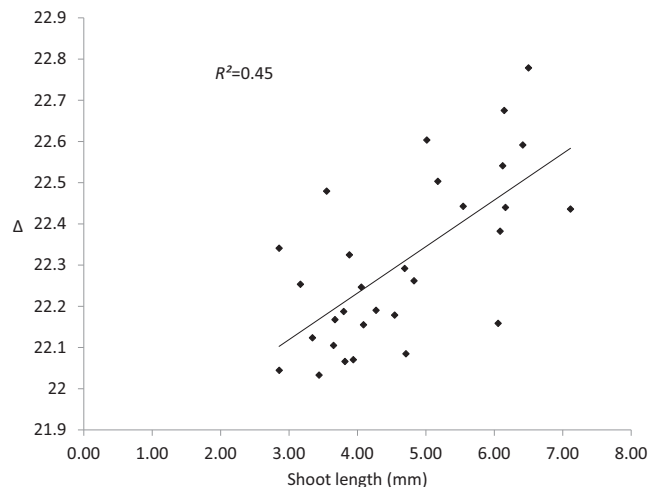


FIGURE 8. Relationship between annual shoot length growth and Δ values in shoots of *C. tetragona* between 1975 and 2004. The greater the annual increase in shoot length, the greater the discrimination against ^{13}C . * $p < 0.0001$.

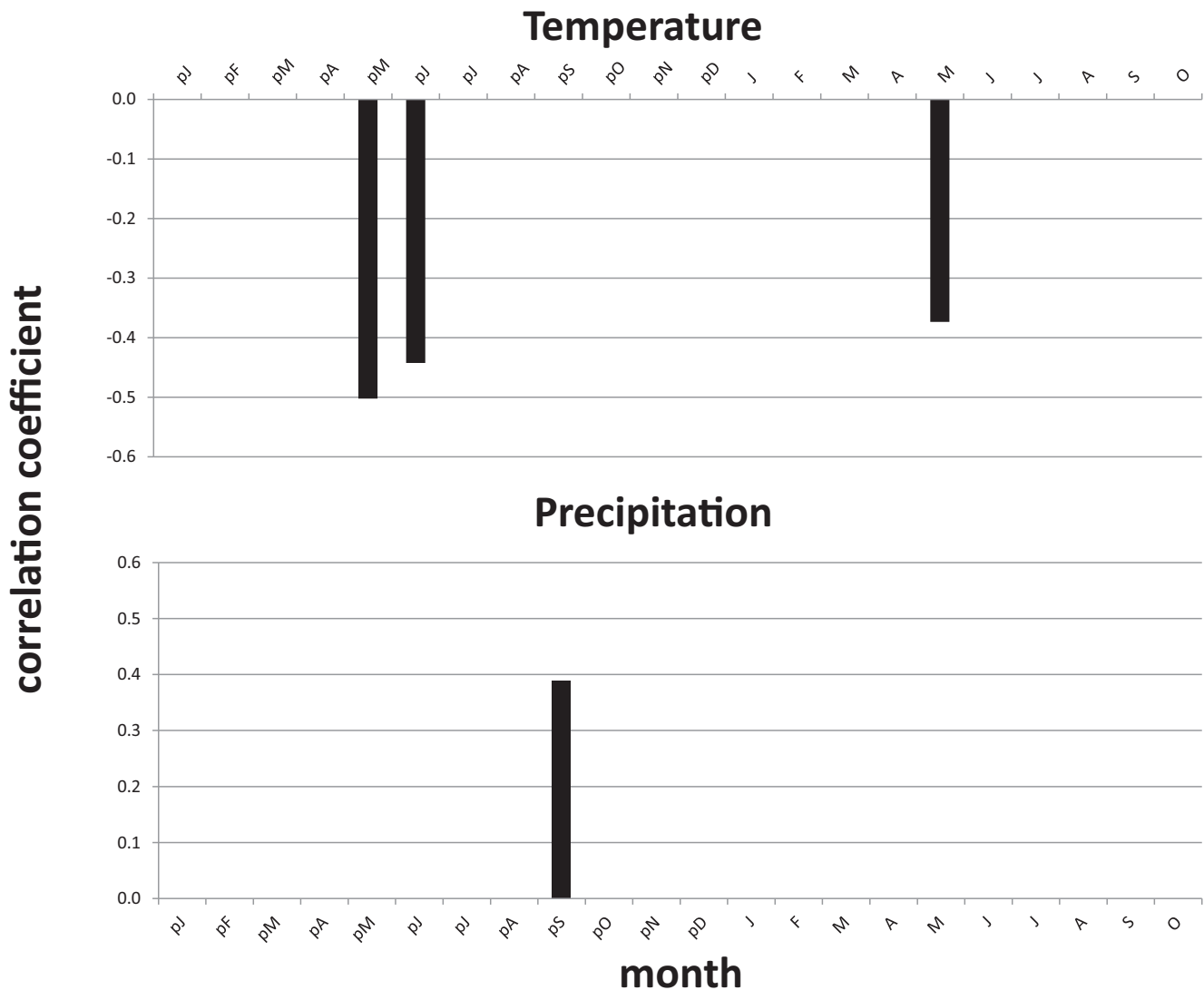


FIGURE 9. Significant correlation coefficients ($p < 0.05$) between monthly climate parameters from January of the previous year through October of the current year and the Δ shoot chronology.

CARBON ISOTOPE DISCRIMINATION

In theory, the weak correlations found between monthly climate parameters and the Δ chronology in this study might partly have a biologically meaningful explanation, with a negative impact of previous year late spring/early summer temperature and a positive impact of late growing season precipitation in the previous year. However, snow-covered conditions in May make a negative influence of May temperature on carbon isotope discrimination unlikely. Welker et al. (1995) also found no influence of summer climate on carbon isotope discrimination in annual stem length fragments of *C. tetragona*, and only a weak correlation between April and May precipitation sums and $\delta^{13}\text{C}$ ($r = -0.38$, $p < 0.02$). The relationships between individual climate parameters and $\delta^{13}\text{C}$ values, reported by Rayback et al. (2011) are, likewise, apparently weak: in a factor analysis, 4 factor scores, derived from 22 climate variables, explained 44% of the observed variation in $\delta^{13}\text{C}$ at 1 site. At the 2 other sites in that study, variations in $\delta^{13}\text{C}$ could only be explained with factor scores derived from climate variables outside the growing season (mainly previous winter temperatures).

In another study on climate and carbon isotope discrimination in *C. tetragona* (Welker et al., 2005), no correlation coefficients are mentioned.

Rayback et al. (2011) hypothesized that the annual climate signal of $\delta^{13}\text{C}$ in the primary growth laid down along the length of the shoot would overrule any influence of secondary growth over the years. Although radial growth is not necessarily continuous in this species, distinct rings are visible in radial cross sections of *C. tetragona* stems (Schweingruber and Landolt, 2005; Rayback et al., 2011). We believe that the annual climate signal in the shoot length increment Δ chronology in this study, and that in previous studies (Welker et al., 1995, 2005; Rayback et al., 2011), was strongly smoothed as a result of secondary radial growth. Firstly, we found rather stable discrimination values between 1975 and 2004. Secondly, we observed a linear and, unexpectedly, positive relationship between annual shoot length growth and carbon discrimination (Fig. 8), when the most recent years (2005–2008) are excluded. This relationship would have been expected to be negative, as higher rates of photosynthesis (and thus growth) result in

reduced discrimination against ^{13}C (Farquhar et al., 1989; Welker et al., 2005). Also, shoot length growth in *C. tetragona* has been shown to be mainly temperature driven (Rayback and Henry, 2006; Weijers et al., 2010, 2012), and higher temperatures result in lower stomatal conductance or higher photosynthetic rate, and thus reduced discrimination against ^{13}C (Farquhar et al., 1989). Notably, Welker et al. (2005) also reported a positive relation between growth and carbon isotope discrimination.

Only when temperature is decoupled from sunshine hours, a positive relationship between growth and carbon isotope discrimination may be expected, as photosynthetic rate is directly controlled by photon flux. During summer, temperature is commonly positively correlated to sunshine hours. A decoupling of temperature and sunshine hours has recently been demonstrated by comparing cloud cover and sunshine hour reconstructions based on $\delta^{13}\text{C}$ ratios from trees in northern Scandinavia to temperature reconstructions (Gagen et al., 2011; Young et al., 2012). In Svalbard, however, over the period 1976–2008, daily July mean cloudiness (ranked measurements 1–8) was negatively correlated to daily mean temperature ($r = -0.45$, $p < 0.0001$).

Changes in stomatal conductance or photosynthetic rate are thus unable to explain the observed positive relationship between shoot length and Δ . Instead, we believe that this relationship represents an age-related trend caused by changes in relative lignin, cellulose, and lipid content in each shoot length fragment caused by secondary radial growth. Lignin, cellulose, and lipid differ in $\delta^{13}\text{C}$ composition. Lignin, for example, is more depleted in ^{13}C than cellulose (Loader et al., 2003; Hobbie and Werner, 2004). Relative cellulose content might increase with age (more secondary radial growth) and result in a gradual decrease in Δ . This combined with an age trend in the shoot length chronology, with older parts being shorter, results in the unexpected positive relationship between shoot length and Δ . In the most recent years (2005–2008), Δ increases with age. Remarkably, the three *C. tetragona* stable carbon isotope ratio time series in annual shoot length increments, as published in Rayback et al. (2011), all show a course over time, very similar to what we found in our chronology. The $\delta^{13}\text{C}$ values in these series are reasonably stable up unto the most recent 4 years, when there is a sudden strong decrease in discrimination against ^{13}C . We hypothesize that this is caused by a relative increase in lignin abundance during the first years of wood formation. Perhaps such age trends could be eliminated from Δ chronologies, similar to the detrending of tree-ring width time series. With detrending, undesired age-related growth trends are removed from ring-width series by dividing them with an estimation of these trends to get undistorted series for correlation with climatic variables (Cook, 1985). For future Δ -chronology constructions, it would, however, be better to separate the inner part from the rest of the annual shoot length increments (pith and first ring layer) for stable carbon isotope analysis, in order to preserve the annual climate signal in $\delta^{13}\text{C}$ of annual shoot length increments of *C. tetragona*. The separated annual inner parts can then be pooled between several plants or over multiple years, to overcome weight limitations.

Secondary radial growth can similarly explain the effect of experimentally enhanced precipitation on shoot fragments before the start of the experiment in 2005 (Fig. 6, part a): increased discrimination against ^{13}C due to enhanced soil water availability has likely trickled down to older years through radial growth. The higher Δ in leaf cohorts from watered plots before the onset of the

experiment in 2005 are, in contrast, better explained by the leaf lifespan of *C. tetragona* leaves on Svalbard of 4 years (Weijers et al., 2010). In 2005, most leaves initially formed in 2002 were still green, and Δ in those leaves was therefore directly affected by the addition of water. The sensitivity of Δ in leaves to soil water availability is in line with an increase in carbon isotope discrimination in leaves of the arctic dwarf shrub *Dryas octopetala* found after water addition at Ny-Ålesund, Svalbard (Welker et al., 1993).

We consider the stronger discrimination against ^{13}C in the lower ‘shaded’ leaf row compared to the upper leaf row as possible indirect proof for the sensitivity of leaf carbon isotope discrimination in *C. tetragona* to temperature and related water stress. In accordance with Le Roux et al. (2001), we assume this observation to be predominantly caused by lower stomatal conductance in response to the overall higher temperatures in leaves receiving direct solar irradiance and to a lesser extent by reduced photosynthetic capacity due to lower PAR. The latter is supported by the small but positive growth response to strongly reduced PAR, which we found in this study. Similarly, Michelsen et al. (1996) attributed a reduction in discrimination against ^{13}C in *C. tetragona* leaves in response to artificial shading to an increase in stomatal conductance rather than to a reduction in assimilation, as biomass production was not affected by shading in their study. Still, higher discrimination against ^{13}C as a result of reduced photosynthetic rate under shaded conditions cannot definitively be excluded as explanation for the observed difference in $\delta^{13}\text{C}$. Different carbon isotope composition of leaves experiencing diverse light regimes (stronger discrimination in leaves near the soil compared to leaves from the upper canopy) might sometimes also be explained by the existence of a $\delta^{13}\text{C}$ gradient in CO_2 at different heights (Farquhar et al., 1989; Broadmeadow et al., 1992). In forests, CO_2 near soils is more depleted in ^{13}C , due to the respiration of soil organic matter. Here, such a gradient would, however, be a poor explanation for the observed difference, as both upper and lower leaves came from the same single branches growing at practically the same height.

GROWTH RESPONSE TO MANIPULATIONS

C. tetragona is mostly found on relatively dry localities on Svalbard (Rønning, 1996) and significant negative correlations between *C. tetragona* growth parameters and monthly summer precipitation sums (June and August) have been reported (Callaghan et al., 1989). This suggests a possible negative impact of relatively high amounts of summer precipitation on growth, perhaps as indirect result of the fact that in arctic semi-deserts soil water availability remains relatively high throughout large parts of the summer due to snowmelt and poor drainage of permafrost soils (Smith, 1956). However, our experimental findings suggest that growth is neither reliant on nor restricted by precipitation input during summer. Our findings confirm the lack of relationships between long-term shoot length growth and summer precipitation found in Svalbard (Weijers et al., 2010, 2012).

Callaghan et al. (1989) proposed poorer growth conditions due to increased cloud cover and lower light intensity as a possible explanation for the negative summer precipitation growth associations they found. This explanation seems unlikely, as the small growth response to reduced PAR, which we found, was positive. Still, if intensely overcast skies persist over many growing seasons,

growth could potentially be negatively impacted. Biomass of tussock tundra (including evergreen dwarf shrubs), e.g., has been shown to decrease after 9 years of intensive (–50% PAR) shading (Shaver and Jonasson, 1999). Enhanced shoot and leaf elongation is, however, a common reaction of plants to severe shading (Dormann and Woodin, 2002).

The differences in average leaf and shoot length between PAR reduction and control plots, which we found, are only small given the percentage differences in the year prior to the start of the experiment. Havström et al. (1993) reported a decline in leaf dry weight of *C. tetragona* after a 2-year experimental reduction of PAR (–64%) in the High Arctic. This, together with our findings, implies a possible trade-off between leaf biomass and shoot and leaf elongation in response to shading. Plant resources might thus have been insufficient to sustain increased shoot and leaf length growth in the second year of shading in our study.

The low photosynthetic rate in *C. tetragona* compared to other arctic dwarf shrub species under light saturation (Baddeley et al., 1994) and its potential to photosynthesize while still snow-covered in late spring (Starr and Oberbauer, 2003) could be indicative of a relatively low light saturation point. This would imply that relatively small reductions in PAR would not affect photosynthetic rate of this species. This, together with the small or absent response of growth parameters of *C. tetragona* in the High Arctic (this study and Havström et al., 1993) to PAR reductions likely exceeding natural reductions due to increased cloudiness (Dormann and Woodin, 2002), suggests that the impact of natural fluctuations in summer cloudiness on annual growth parameters of *C. tetragona* is probably small, if present at all.

Conclusions

We provide the first experimental evidence for the sensitivity of carbon isotope discrimination in *C. tetragona* to growing season precipitation and temperature. This shows the potential of $\delta^{13}\text{C}$ chronologies of this species as a proxy of past local hydrological changes throughout the vast polar semi-desert. However, we also demonstrated that the annual climate signal in $\delta^{13}\text{C}$ chronologies of *C. tetragona* is probably strongly smoothed over time due to secondary growth. This makes the method used in this and previous studies for the construction of such chronologies (Welker et al., 1995, 2005; Rayback et al., 2011) unsuitable for the purpose of climate reconstruction. Alternative methods are required to preserve the annual signal. We realize that the proposed new method of separating the pith and first ring layer from the rest of the annual shoot length fragments before $\delta^{13}\text{C}$ measurement is rather laborious and increases weight limitations. This will likely require pooling of samples before measurement. Annual growth of dwarf shrubs are increasingly used to reconstruct and monitor climatic changes in the Arctic (Zalatan and Gajewski, 2006; Forbes et al., 2010; Schmidt et al., 2010; Blok et al., 2011). In all these studies ring formation rather than length growth is used as a measure for annual growth. Therefore, if climate reconstruction in the Arctic based on stable carbon isotope analysis is to be pursued, *C. tetragona* remains an interesting species, as its annual shoot length increments are much larger than the rings of other dwarf shrub species. The results presented in our study of the experiments in which precipitation and PAR were manipulated, increase the empirical basis for

the use of annual growth parameters of *C. tetragona* as a temperature proxy. The low level and total lack of disturbance of the temperature signal present in annual growth parameters of *C. tetragona* by natural fluctuations in PAR and summer precipitation, respectively, confirm the suitability of these parameters to serve as an arctic-wide temperature proxy.

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