Temperature-induced water stress in high-latitude forests in response to natural and anthropogenic warming

MATTHEW W. TRAHAN and BRIAN A. SCHUBERT

School of Geosciences, University of Louisiana at Lafayette, 611 McKinley St, Box 43705, Lafayette, LA 70504, USA

Abstract

The Arctic is particularly sensitive to climate change, but the independent effects of increasing atmospheric CO_2 concentration (pCO_2) and temperature on high-latitude forests are poorly understood. Here, we present a new, annually resolved record of stable carbon isotope ($\delta^{13}C$) data determined from *Larix cajanderi* tree cores collected from far northeastern Siberia in order to investigate the physiological response of these trees to regional warming. The tree-ring record, which extends from 1912 through 1961 (50 years), targets early twentieth-century warming (ETCW), a natural warming event in the 1920s to 1940s that was limited to Northern hemisphere high latitudes. Our data show that net carbon isotope fractionation ($\Delta^{13}C$), decreased by 1.7‰ across the ETCW, which is consistent with increased water stress in response to climate warming and dryer soils. To investigate whether this signal is present across the northern boreal forest, we compiled published carbon isotope data from 14 high-latitude sites within Europe, Asia, and North America. The resulting dataset covered the entire twentieth century and spanned both natural ETCW and anthropogenic Late Twentieth-Century Warming (~0.7 °C per decade). After correcting for a ~1‰ increase in $\Delta^{13}C$ in response to twentieth century pCO_2 rise, a significant negative relationship ($r = -0.53$, $P < 0.0001$) between the average, annual $\Delta^{13}C$ values and regional annual temperature anomalies is observed, suggesting a strong control of temperature on the $\Delta^{13}C$ value of trees growing at high latitudes. We calculate a 17% increase in intrinsic water-use efficiency within these forests across the twentieth century, of which approximately half is attributed to a decrease in stomatal conductance in order to conserve water in response to drying conditions, with the other half being attributed to increasing pCO_2. We conclude that annual tree-ring records from northern high-latitude forests record the effects of climate warming and pCO_2 rise across the twentieth century.

Keywords: boreal forest, carbon dioxide, carbon isotopes, climate change, drought stress, global warming, tree-rings, water-use efficiency

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Introduction

The taiga (i.e., boreal forest) biome extends across much of the northern portions of North America, Europe, and Asia and includes forests of *Pinus*, *Picea*, and *Larix* that span ~1 billion hectares, and represents ~30% of all forested land (FAO, 2000). This region, like much of the northern high latitudes, is likely to be especially sensitive to warming due to climate change (IPCC, 2007). The classic description of carbon isotope fractionation between plant tissue and the atmosphere (Farquhar *et al.*, 1982, 1989) has been widely used to investigate the physiological response of trees growing within the taiga to climate change (e.g., Robertson *et al.*, 1997; Waterhouse *et al.*, 2000; Buhay *et al.*, 2008; Gagen *et al.*, 2008; Hilasvuori, 2011; Holzkämper *et al.*, 2012; Sidorova *et al.*, 2013). Researchers have shown that the $\delta^{13}C$ value measured from successive annual tree-rings reflects changes in the $\delta^{13}C$ value of atmospheric CO_2 ($\delta^{13}C_{CO_2}$) and atmospheric CO_2 concentration (pCO_2)

(McCarroll & Loader, 2004; McCarroll *et al.*, 2009; Schubert & Jahren, 2012) and is modified by changes in stomatal conductance (Warren *et al.*, 2001; Arneth *et al.*, 2002; Leavitt, 2002; McCarroll *et al.*, 2003). Factors that directly (i.e., precipitation, relative humidity, vapor pressure deficit) or indirectly (i.e., temperature, sunshine) influence moisture status therefore correlate well with tree-ring $\delta^{13}C$ values. As a result, annual or subannual changes in tree-ring $\delta^{13}C$ values have been interpreted in terms of changes in local climate or environmental conditions at these sites, including precipitation (Holzkämper *et al.*, 2008; Knorre *et al.*, 2010; Schubert & Jahren, 2011), relative humidity (Edwards *et al.*, 2000), vapor pressure deficit (Berninger *et al.*, 2000; Sidorova *et al.*, 2008), temperature (Gagen *et al.*, 2007; Kirdyanov *et al.*, 2008; Tardif *et al.*, 2008; Porter *et al.*, 2009; Sidorova *et al.*, 2009; Loader *et al.*, 2010; Seftigen *et al.*, 2011), river flow depth (Waterhouse *et al.*, 2000), and sunshine/cloudiness (Hilasvuori & Berninger, 2010; Young *et al.*, 2010, 2012; Loader *et al.*, 2013).

Unfortunately, within remote regions of the planet, high-quality climate data for comparison with tree-ring

Correspondence: Brian A. Schubert, tel. +1 337 482 6967, fax +1 337 482 5395, e-mail: schubert@louisiana.edu

$\delta^{13}C$ records are often lacking in spatial and/or temporal resolution. Climate information, including basic temperature data, is particularly poor in high-latitude sites, with little to no coverage across large land areas (Cowtan & Way, 2014). As a result, regional temperature trends must be determined by interpolating widely spaced temperature data within gridded areas (e.g., Jones *et al.*, 1999; Polyakov *et al.*, 2003). Using these gridded datasets, two broad intervals of warming have been identified within northern high-latitude sites during the twentieth century (see review by Yamanouchi, 2011). These include (i) the early twentieth-century warming (ETCW), a natural warming event in the 1920s to 1940s that was limited to high-latitude Northern hemisphere sites and (ii) the anthropogenic late twentieth-century warming (LTCW), which began slowly ('slow LTCW', 1966–1985), but has been especially rapid in the Arctic since 1985 ('rapid LTCW'). To investigate how regional warming impacts the northern taiga forest, we first present a new, annually resolved $\delta^{13}C$ dataset across a 50-year interval (1912–1961) spanning the ETCW from *Larix cajanderi* trees growing in far northeastern Siberia. We then combine these data with published tree-ring data spanning the entire twentieth century from trees growing across 14 northern high-latitude sites to identify any region-wide trends in carbon isotope discrimination across both warming events. We used these data to test two hypotheses regarding the boreal forest biome: (i) warming temperatures induce a decline in stomatal conductance characteristic of increasing water stress, and (ii) intrinsic water-use efficiency (iWUE) increases as a result of the independent effects of decreasing stomatal conductance in response to climate warming and increasing pCO_2.

Materials and methods

Study area

Three *L. cajanderi* trees (Larix01, Larix02, and Larix03) were cored at breast height on the eastern side of their trunk in August 2013. The trees were growing within 1 km of each other at a single, open-forested site near the Northeast Science Station in Cherskiy, Sakha Republic, Russia (68° 44′ N, 161° 23′ E; Fig. 1). The instrumental climate record of Cherskiy is limited, but characterizes a cold Köppen–Geiger climate type with cold and dry summers (Dsc) (Peel *et al.*, 2007). Mean annual temperature and mean annual precipitation across the instrumental record are −11.3 °C (1955–2013) and 190 mm (1940–2013), respectively (NOAA Climate Services, 2013).

Wood-core sampling

Each core was sanded by hand using 100-grit, then 600-grit sandpaper in order to produce a flat surface for sampling and to better identify tree-ring boundaries. Each core contained well-defined annual rings, and calendar years were assigned by counting the annual growth bands under an optical stereomicroscope (Fisher S90017 Stereo Student Microscope; Thermo Fisher, Bremen, Germany). Visual inspection of the ring widths was used to cross-check the dating across the three cores. Latewood was sampled by hand from each core using a razor blade from annual rings across a 50-year interval (1912–1961) to bracket the entire ETCW event. The latewood, rather than the earlywood, was targeted because latewood forms entirely from recent sugars obtained during the current growing season, and therefore, its isotopic composition contains the climate signal of the corresponding growth year (Lipp *et al.*, 1991); earlywood formation in some species has been shown to incorporate stored carbon from previous years' growth (Jäggi *et al.*, 2002; Helle & Schleser, 2004).
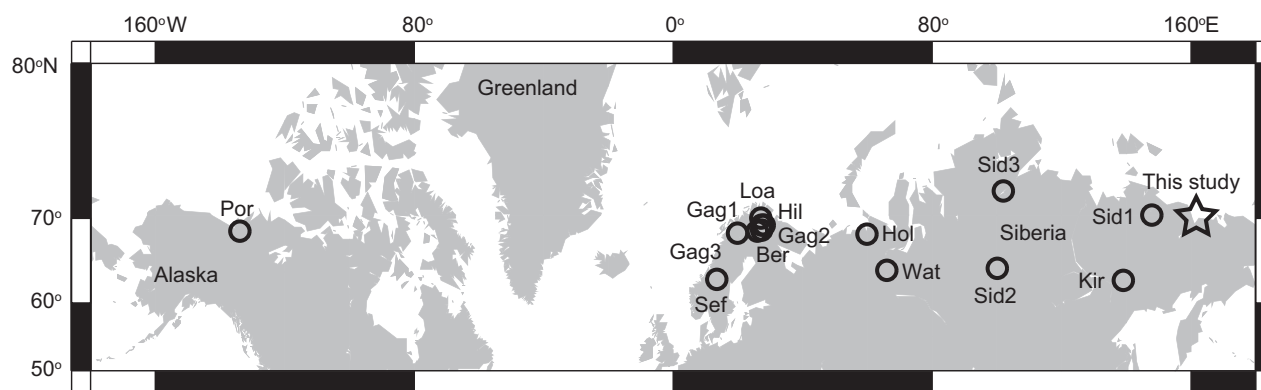
Fig. 1 Distribution of the 15 sites (including the new site reported here from near Cherskiy, Russia in far northeastern Siberia; star) from which annual $\delta^{13}C$ tree-ring data were compiled for analysis. Sites are labeled according to the abbreviated site names listed in Table 2.

Carbon isotope analysis

Latewood subsamples of between 75 and 200 μg were weighed into tin capsules for isotope analysis. $\delta^{13}C$ values were determined on whole wood using a Delta V Advantage Isotope Ratio Mass Spectrometer (Thermo Fisher) joined with a Thermo Finnigan Elemental Analyzer (Flash EA1112 Series, Bremen, Germany) at the University of Louisiana at Lafayette. Multiple studies have demonstrated a constant linear offset between whole wood and cellulose $\delta^{13}C$ values (Leavitt & Long, 1982; Borella & Leuenberger, 1998; Berninger et al., 2000; Sidorova et al., 2008; Tei et al., 2013; Edvardsson et al., 2014). The resulting tree-ring isotope values were expressed in δ-notation in units of per mil (‰) and normalized to the Vienna Pee Dee Belemnite scale using three internal laboratory reference materials (JGLY = −43.51‰; JHIST = −8.13‰; JRICE = −27.37‰). At least one quality assurance sample (JGLUC = −10.52‰) was analyzed within each batch of tree-ring subsamples and analyzed as an unknown. Over the course of all analyses, the JGLUC quality assurance sample averaged −10.46 ± 0.26‰ (±1σ, n = 9), which is in agreement with the calibrated value.

Atmospheric corrections of tree-ring $\delta^{13}C$ values

Because the $\delta^{13}C$ value of atmospheric CO_2 ($\delta^{13}C_{CO_2}$) changes across the study interval, here we analyzed the data in terms of net carbon isotope fractionation ($\Delta^{13}C$), after Farquhar et al. (1989):

$$\Delta^{13}C = a + (b - a)(c_i/c_a) \qquad (1)$$

where

$$\Delta^{13}C = (\delta^{13}C_{CO_2} - \delta^{13}C)/(1 + \delta^{13}C/1000) \qquad (2)$$

Within the above, a and b are constants relating to gaseous diffusion through leaf stomata (a = 4.4‰) and enzymatic carbon fixation (b = 28.3‰, Schubert & Jahren (2012)), respectively, and c_i and c_a represent the intercellular and atmospheric concentration of CO_2, respectively. Correction of $\delta^{13}C$ records for changes in $\delta^{13}C_{CO_2}$ via Eqn (2) has long been a standard procedure when interpreting tree-ring records (see review by McCarroll & Loader, 2004). More recently, workers have also been adjusting tree-ring records for changes in pCO_2 concentration (Treydte et al., 2001, 2009; Gagen et al., 2007; Kirdyanov et al., 2008; McCarroll et al., 2009; Seftigen et al., 2011; Wang et al., 2011; Kern et al., 2012; Szymczak et al., 2012; Schollaen et al., 2013; Tei et al., 2013, 2014; Konter et al., 2014; Xu et al., 2014; Bégin et al., 2015), but the corrections used are wide-ranging (reviewed within Schubert & Jahren, 2012). Here, we applied the hyperbolic relationship developed within Schubert & Jahren (2012) to adjust the raw $\Delta^{13}C$ values (from here out called '$\Delta^{13}C_{raw}$') for the increase in pCO_2 observed across the study period. This correction, which has also been applied to fossil organic matter (Schubert & Jahren, 2013, 2015), reconciles the wide range of previous corrections that have been applied, and can be described by the following equation:

$$
\begin{aligned}
\Delta^{13}C_{corr} = \Delta^{13}C_{raw} &- [(A)(B)(pCO_{2(t)} + C)]/[A + (B)(pCO_{2(t)} \\
&+ C)] - [(A)(B)(pCO_{2(t=0)} + C)]/[A + (B)(pCO_{2(t=0)} \\
&+ C)]
\end{aligned}
$$
$$(3)$$

where A = 28.26, B = 0.22, and C = 23.9 (after Schubert & Jahren, 2015), $pCO_{2(t=0)}$ is the pre-industrial pCO_2 level (i.e., 285 ppm), and $pCO_{2(t)}$ is the pCO_2 level at each year t (Table 1).

Results

Relative changes in the $\delta^{13}C$ value of the three tree cores showed good agreement with each other (Fig. 2a). An overall decreasing trend of 0.20‰ per decade is observed in the averaged $\delta^{13}C$ record, which is attributed in part to the 0.39‰ decline in $\delta^{13}C_{CO_2}$ across the 50-year study interval (0.08‰ per decade). $\Delta^{13}C_{raw}$ values (Eqn (2)) showed an overall increasing trend of 0.13‰ per decade (Fig. 2b) that is consistent with the observed positive relationship between $\Delta^{13}C$ and pCO_2 (Feng & Epstein, 1995; Treydte et al., 2009; Schubert & Jahren, 2012). However, within this long-term increasing trend, $\Delta^{13}C_{raw}$ values show a notable 1.7‰ decrease from 1931 to 1940, which then increases back to background values by 1951 (Fig. 2b). The pCO_2 corrected record ($\Delta^{13}C_{corr}$, Eqn (3)) yielded an insignificant (P = 0.22) positive trend of only 0.06‰ per decade and maintained the relatively low $\Delta^{13}C$ values in the 1930s and 1940s (Fig. 2c).

The period of decreased $\Delta^{13}C$ values from the 1930s through the 1940s can be interpreted in terms of a decrease in c_i/c_a in response to a decrease in stomatal conductance or increase in photosynthetic rate (Eqn (1)). Support for this is provided by the regional surface air temperature (SAT) data, which shows clear Arctic warming associated with the ETCW event across the period of decreased $\Delta^{13}C_{corr}$ values (Fig. 4d). Notably, we see greatest correlations between the SAT and $\Delta^{13}C_{corr}$ records for the latitudinal band that includes our study site (65–70° N, r = −0.55) and the band immediately to the north (70–75° N, r = −0.54), while correlation strength decreases with increasing distance toward the south (Fig. 2d). The inverse relationship between the regional SAT data and $\Delta^{13}C_{corr}$ suggests that increased temperatures during the ETCW contributed to a decrease in water availability (e.g., soil drying, Natali et al. (2015)) and an increase in water stress at the site. To compensate, the trees likely decreased stomatal conductance (decrease of c_i/c_a), which resulted in a decrease in $\Delta^{13}C$ (Eqn (1)). Correlations between $\Delta^{13}C$ and temperature (e.g., Loader et al., 2010; Liu et al., 2014) or sunshine (e.g., Young et al., 2010; Gagen et al., 2011b; Loader et al., 2013) may also suggest an increase in photosynthetic rate, but declines in stomatal conductance in response to drying cannot

Table 1 $\delta^{13}C$ data for the three *Larix* tree cores (Larix01, Larix01, and Larix03) sampled in this study. pCO_2 and $\delta^{13}C_{CO_2}$ data are from McCarroll & Loader (2004)

Year	pCO_2 (ppmv)	$\delta^{13}C_{CO_2}$ (‰)	$\delta^{13}C$ Larix01 (‰)	$\delta^{13}C$ Larix02 (‰)	$\delta^{13}C$ Larix03 (‰)
1912	298.4	−6.69	−26.23	−25.71	−25.17
1913	299.4	−6.69	−25.64	−26.37	−25.98
1914	300.4	−6.70	−26.72	−24.04	−26.01
1915	301.0	−6.70	−25.81	−24.31	−26.76
1916	301.6	−6.70	−26.34	−25.35	−25.47
1917	302.2	−6.71	−24.46	−22.73	−25.48
1918	302.8	−6.71	−26.89	−25.96	−26.12
1919	303.5	−6.72	−25.87	−25.35	−25.63
1920	303.4	−6.72	−26.47	−25.70	−27.11
1921	303.3	−6.73	−26.18	−24.23	−26.83
1922	303.3	−6.73	−26.17	−24.37	−26.38
1923	303.2	−6.74	−25.95	−26.22	−25.33
1924	305.2	−6.74	−25.90	−24.78	−25.76
1925	305.5	−6.74	−26.62	−26.35	−26.83
1926	305.8	−6.75	−26.42	−24.94	−25.83
1927	306.1	−6.75	−26.80	−25.18	−26.94
1928	306.4	−6.76	−26.35	−25.29	−25.71
1929	306.8	−6.76	−26.37	−24.94	−26.15
1930	306.9	−6.77	−26.01	−25.85	−26.67
1931	307.0	−6.77	−26.51	−26.45	−27.23
1932	307.1	−6.78	−26.37	−25.59	−26.49
1933	307.2	−6.78	−26.79	−26.38	−26.77
1934	307.5	−6.78	−26.16	−26.78	−25.84
1935	307.8	−6.79	−26.84	−25.23	−26.84
1936	308.4	−6.79	−26.60	−25.24	−26.39
1937	309.0	−6.80	−26.15	−24.97	−25.97
1938	309.6	−6.80	−25.99	−24.02	−25.69
1939	310.9	−6.81	−25.60	−24.37	−25.90
1940	311.9	−6.81	−25.54	−24.78	−24.87
1941	310.7	−6.82	−25.63	−24.81	−26.05
1942	311.3	−6.82	−25.52	−24.55	−25.68
1943	310.8	−6.82	−25.83	−24.22	−25.95
1944	311.6	−6.83	−26.64	−26.21	−25.81
1945	309.7	−6.83	−26.96	−25.60	−26.26
1946	311.5	−6.84	−26.83	−25.39	−25.24
1947	311.0	−6.84	−26.65	−25.31	−26.54
1948	310.5	−6.85	−26.78	−25.08	−26.48
1949	311.2	−6.85	−26.48	−25.59	−26.45
1950	312.6	−6.86	−26.78	−25.15	−27.52
1951	312.4	−6.86	−27.79	−25.92	−26.59
1952	312.3	−6.86	−27.25	−26.12	−26.36
1953	312.1	−6.87	−27.71	−25.84	−26.23
1954	311.7	−6.87	−27.01	−24.16	−27.01
1955	313.7	−6.88	−27.67	−25.53	−26.93
1956	316.3	−6.88	−27.13	−24.75	−27.36
1957	314.0	−6.89	−27.60	−25.45	−26.54
1958	314.3	−6.89	−27.79	−25.18	−25.83
1959	315.4	−6.90	−28.08	−26.58	−26.59
1960	316.3	−6.90	−27.85	−26.83	−26.59
1961	317.8	−6.90	−27.49	−26.60	−26.19

be discounted and likely dominate in similar dry climates (e.g., Gagen *et al.*, 2007). Separation of the effect of stomatal conductance and photosynthetic rate on $\Delta^{13}C$ is difficult (McCarroll & Pawellek, 2001), but may be able to be achieved through conceptual models requiring a multi-isotopic approach and determination of relative humidity from $\delta^{18}O$ (Scheidegger *et al.*, 2000).

Discussion

Is twentieth-century warming evident within annual $\delta^{13}C$ tree-ring records from across the northern high latitudes?

To determine whether the decrease in $\Delta^{13}C$ observed in far northeastern Siberia is in fact a result of ETCW, and not a local change in precipitation, for example, we compare our dataset to annual tree-ring $\delta^{13}C$ records produced from other northern high-latitude sites (Fig. 1; Table S1). We limit this comparison to sites north of 62° N (in order to match the spatial range of the SAT dataset provided within Fig. 3 of Yamanouchi, 2011) and include all records that span at least the entirety of the Cherskiy record reported here (1912–1961) (in order to produce a common reference period). Although several of the records extend older than the year 1900 (Berninger *et al.*, 2000; Gagen *et al.*, 2007, 2008; Kirdyanov *et al.*, 2008; Loader *et al.*, 2013), we limit our analysis to data from the twentieth century. The resulting dataset spans 99 years and includes five different species of *Pinus*, *Picea*, and *Larix* growing across sites in northern Asia ($n = 7$), Europe ($n = 7$), and North America ($n = 1$; Fig. 1; Table 2). The wide range of $\delta^{13}C$ values within this dataset (−21.7 to −28.2‰, Fig. 3a) is consistent with the wide range of species and environments sampled (Leavitt, 2010). A compilation of annual tree-ring $\delta^{13}C$ data from across this broad area should reflect regional climate trends (such as the ETCW), while averaging out differences attributable to local site conditions (Gagen *et al.*, 2011a). Studies have shown that combining $\delta^{13}C$ chronologies of disparate species collected from widely spaced sites into a single average record removes species-specific physiological influences and typically leads to stronger correlations with large-scale temperature trends than $\delta^{13}C$ chronologies sourced from a single site (Treydte *et al.*, 2007; Saurer *et al.*, 2008). We note that several individual tree-ring chronologies from the taiga do suggest the presence of the ETCW (as low $\Delta^{13}C$ values or high $\delta^{13}C$ values) (Gagen *et al.*, 2007, 2008; Sidorova *et al.*, 2008; Loader *et al.*, 2013), but changes in $\delta^{13}C$ or $\Delta^{13}C$ have not been specifically attributed to the ETCW in these, or any other study. Because the compiled tree-
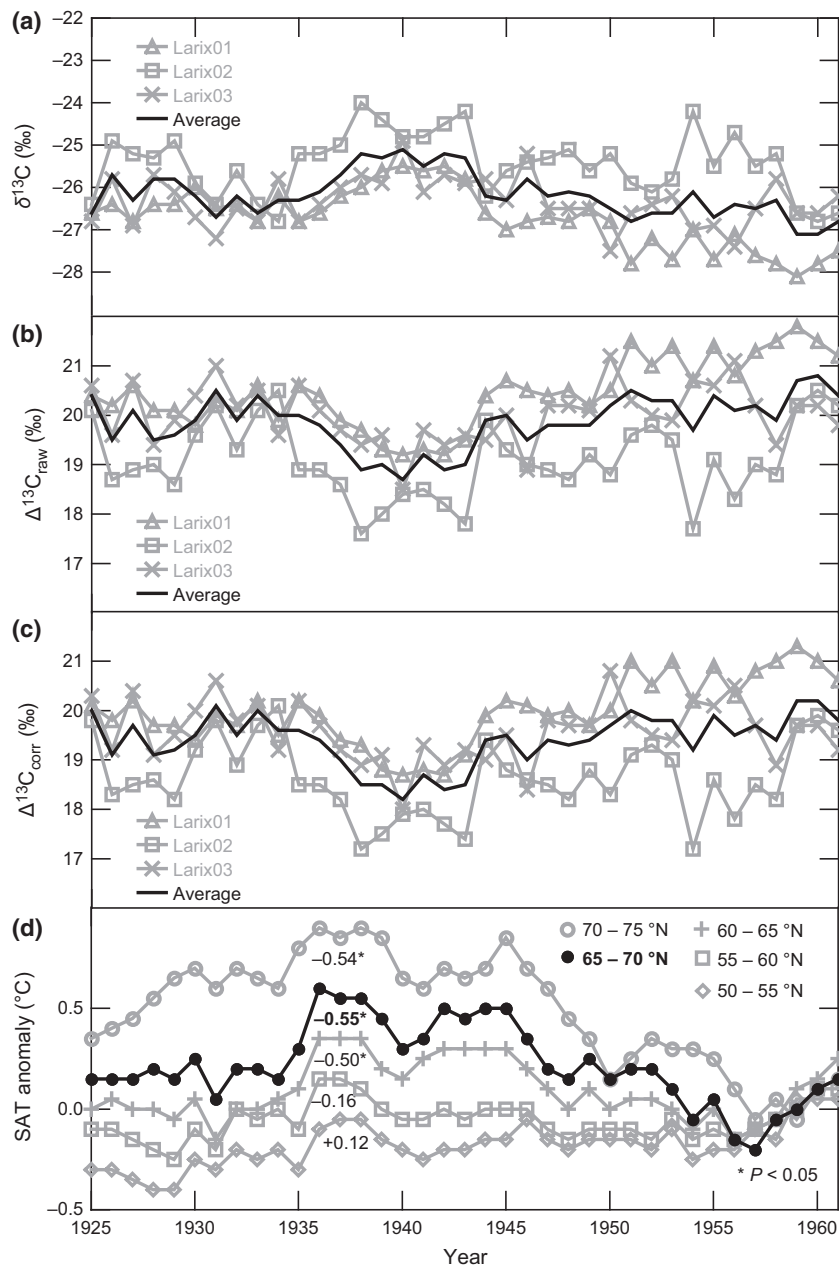
Fig. 2 Annual $\delta^{13}C$ (a), $\Delta^{13}C_{raw}$ (b), and $\Delta^{13}C_{corr}$ (c) values across the ETCW from three tree cores sampled from near Cherskiy, Russia, in far northeastern Siberia. The measured $\delta^{13}C$ data are available in Table 1. (d) Mean annual SAT anomalies determined over land for five latitudinal bands (50–55, 55–60, 60–65, 65–70, and 70–75° N) from Figure 5 within Yamanouchi (2011). Correlation coefficients are reported between $\Delta^{13}C_{corr}$ and SAT for each latitudinal band. Note that lower $\Delta^{13}C$ values from the late 1930s through the 1940s correspond with the period of increased temperatures at high latitudes (i.e., the ETCW).

ring dataset extends throughout the 20th century, here we also discuss whether the anthropogenic warming of the latter part of the 20th century can be observed in these high-latitude tree-ring records.

For this comparison, all $\delta^{13}C$ records were corrected for changes in $\delta^{13}C_{CO_2}$ and pCO_2 following the same methods used for our dataset from far north-

eastern Siberia (Eqns (2) and (3)). The resulting $\Delta^{13}C_{raw}$ and $\Delta^{13}C_{corr}$ records were normalized relative to the reference period represented by the Cherskiy record (1912–1961) to allow comparison across the wide range of absolute values measured (Fig. 3b, c). The average, normalized $\Delta^{13}C_{corr}$ record yielded decreasing values across the periods spanning the

Table 2 List of tree-ring sites north of 62° N that were used in this study. Site names correspond with the labels in Fig. 1

Site name	Location	Species	No. of trees	Reference
This study	68.73° N, 161.38° E	*Larix cajanderi*	3	This study
Ber	68.4° N, 26.17° E	*Pinus sylvestris*	4	Berninger *et al.* (2000) (Fig. 1a)
Gag1	69.67° N, 27.08° E	*Pinus sylvestris*	2	Gagen *et al.* (2007) (Fig. 2a, solid black line)
Gag2	68.5° N, 27.5° E	*Pinus sylvestris*	10	Gagen *et al.* (2007) (Fig. 2a, solid gray line)
Gag3	68.89° N, 27.5° E	*Pinus sylvestris*	10	Gagen *et al.* (2008) (Fig. 2a, avg of black and gray lines)
Hil	69° N, 28.2° E	*Pinus sylvestris*	4	Hilasvuori (2011) (Fig. 4)
Hol	68.1° N, 60° E	*Picea abies*	2	Holzkämper *et al.* (2008) (Fig. 9, avg of T2, T5)
Kir	63.1° N, 139.08° E	*Larix cajanderi*	10	Kirdyanov *et al.* (2008) (Fig. 2, bottom panel, δ^{13}C corr1)
Loa	68.2° N, 20° E	*Pinus sylvestris*	5	Loader *et al.* (2013) (Fig. 4, black line)
Por	68.4° N, 133.81° W	*Picea glauca*	3	Porter *et al.* (2009) (Fig. 4, thin black line)
Sef	63.17° N, 13.5° E	*Pinus sylvestris*	7	Seftigen *et al.* (2011) (Fig. 2a)
Sid1	70° N, 148° E	*Larix cajanderi*	4	Sidorova *et al.* (2008) (Fig. 3 dashed line)
Sid2	64.53° N, 100.23° E	*Larix gmelinii*	8	Sidorova *et al.* (2009) (Fig. 3a, thin line)
Sid3	72° N, 102° E	*Larix gmelinii*	4	Sidorova *et al.* (2013) (Fig. 2b, thin line)
Wat	64.27° N, 66.05° E	*Pinus sylvestris*	9	Waterhouse *et al.* (2000) (Fig. 2a)

ETCW and the LTCW (Fig. 3c). These declines in Δ^{13}C are consistent with a decrease in c_i/c_a (Eqn (1)) *via* a decrease in stomatal conductance or increase in photosynthetic rate.

In order to investigate whether the trends in Δ^{13}C$_{corr}$ can be attributed to temperature-induced water stress, we compared the Arctic-wide Δ^{13}C$_{corr}$ chronology with SAT anomalies reported for 62–90° N (Fig. 3d). Across the entire record (1900–1998), there was a significant negative relationship ($r = -0.53$, $P < 0.0001$) between the Arctic-wide Δ^{13}C$_{corr}$ chronology and the SAT record, suggesting that the natural and anthropogenic region-wide warming events are recorded in tree-ring tissue. The negative correlation is particularly strong across the periods of greatest warming (ETCW, $r = -0.84$, $P < 0.0001$; rapid LTCW, $r = -0.55$, $P = 0.04$), suggesting that rapid warming had a significant effect on Δ^{13}C$_{corr}$. An increase in Δ^{13}C$_{corr}$ is observed during the 1940s, which corresponds with middle twentieth-century cooling (MTCC), but Δ^{13}C$_{corr}$ values decrease during the latter part of the MTCC, while temperatures continued to cool (Fig. 3c, d). The small decline in Δ^{13}C$_{corr}$ across the slow LTCW (1966–1985) is consistent with gradual warming during this period (Fig. 3c, d). The negative correlations observed here between Δ^{13}C$_{corr}$ and SAT across the twentieth century are consistent with drying conditions in permafrost environments in response to climate warming (Bryukhanova *et al.*, 2015; Natali *et al.*, 2015).

We evaluated changes in iWUE within the northern taiga in response to increasing pCO_2 and changing climate using the following relationship presented in Farquhar & Richards (1984):

$$iWUE = (c_a - c_i)/1.6 \qquad (4)$$

where c_i is calculated using Δ^{13}C$_{raw}$ and Eqn (1). Although c_a and c_i both increased in our dataset, $c_a - c_i$ also increased, yielding a ~17% increase in iWUE across the 20th century (Fig. 4a). The net increase in iWUE observed here for the northern taiga is consistent with results from trees growing across Europe (Andreu-Hayles *et al.*, 2011; Gagen *et al.*, 2011a; Frank *et al.*, 2015), southeastern Asia (Loader *et al.*, 2011), eastern Siberia (Tei *et al.*, 2014), and high-altitude sites in Mexico, Italy, and Chile (Gómez-Guerrero *et al.*, 2013; Tognetti *et al.*, 2014). Although increased water stress and increased pCO_2 have opposite effects on Δ^{13}C (and c_i/c_a *via* Eqn (1)) (i.e., increased water stress = decreased Δ^{13}C; increased pCO_2 = increased Δ^{13}C), both cause an increase in $c_a - c_i$ (and iWUE) (Schubert & Jahren, 2012). To isolate the effects of climate change on iWUE, we removed the effects of changing pCO_2 by calculating iWUE using the pCO_2-corrected record (i.e., Δ^{13}C$_{corr}$) and holding c_a constant at the year 1900 level (Fig. 4b). From this calculation, we find that the increase in iWUE attributed to changing climate is 0.8% per decade across the twentieth century (Fig. 4b), compared with the calculated 1.7% per decade increase in iWUE when evaluating the combined effects of pCO_2 and climate (Fig. 4a). Therefore, approximately half of the 17% total increase in iWUE observed across the twentieth century can be attributed to a change in c_i/c_a in response to changing climate (i.e., 8%) with the other half (i.e., 9% increase in iWUE) resulted directly from increases in pCO_2.

Our compilation of annual tree-ring data suggests that a common region-wide temperature signal exists within tree-ring chronologies across the northern high
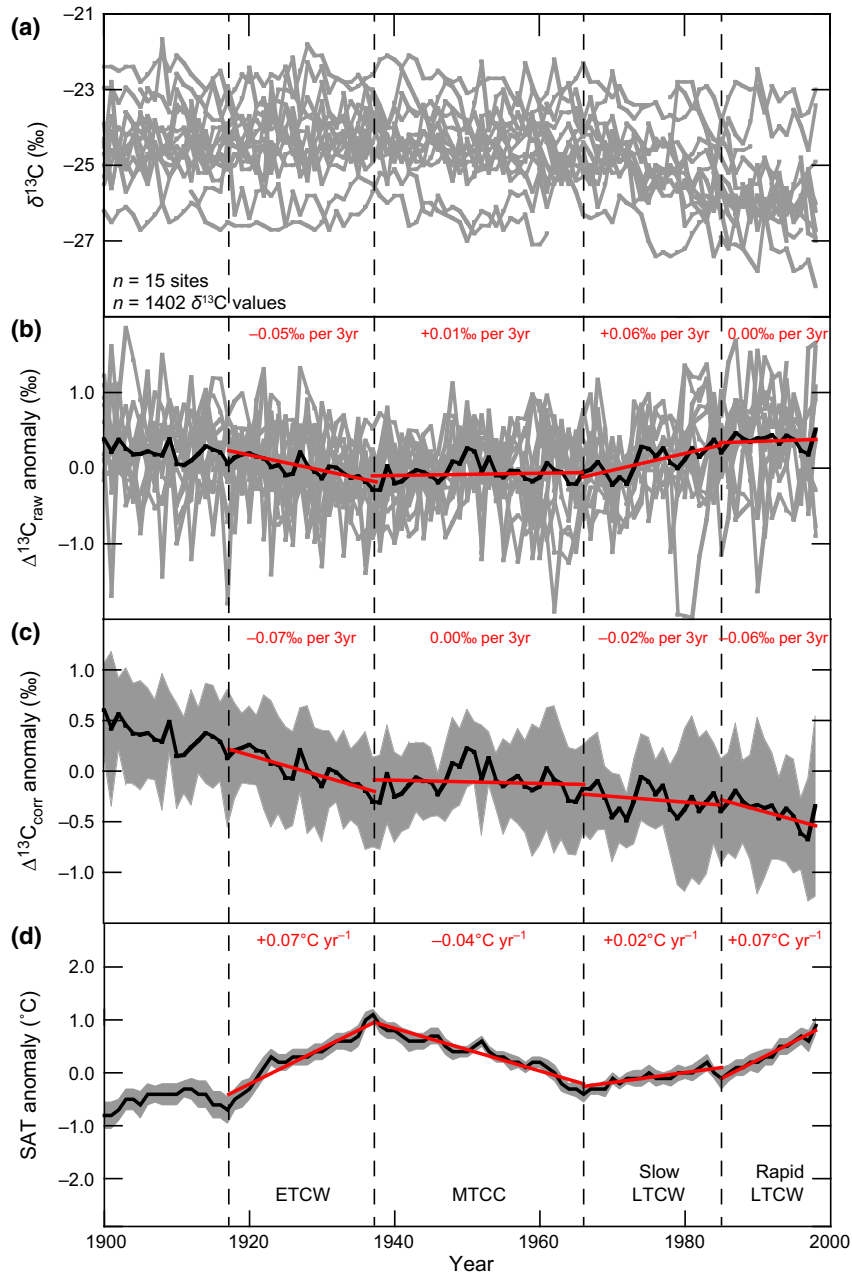
Fig. 3 Annual tree-ring data and SAT anomalies for sites >62° N across the twentieth century. (a) $\delta^{13}C$ data reported here from near Cherskiy, Russia, combined with $\delta^{13}C$ data compiled from 14 published records (Fig. 1, Table 2). The $\delta^{13}C$ data are available in Table S1. (b) $\Delta^{13}C_{raw}$ and (c) $\Delta^{13}C_{corr}$ anomalies calculated using 1912–1961 as the reference period. (d) Average annual SAT (°C) anomalies for the region poleward of 62° N (data from Fig. 3 within Yamanouchi, 2011). Shaded region in (c) and (d) represents the 68% confidence interval ($\pm 1\sigma$). Red numbers at the top of (b), (c), and (d) represent the slope values (in units of °C yr^{-1} or ‰ per 3 yr) for the best-fit red lines drawn through each subperiod (ETCW, MTCC, slow LTCW, rapid LTCW). Note the opposite signs when comparing the slope values for $\Delta^{13}C_{corr}$ (c) and SAT (d), consistent with an inverse relationship between temperature and $\Delta^{13}C$.

latitudes. Similar temperature trends may be visible in tree-ring records from other regions across the planet in response to global warming, with correlations between temperature and carbon isotope values being strongest in regions particularly sensitive to climate change. Dif-

ferences in the $\Delta^{13}C_{corr}$ chronologies among various sites also reflect local effects on carbon isotope fractionation, including site-specific changes in precipitation (e.g., Holzkämper *et al.*, 2008), humidity (e.g., Edwards *et al.*, 2000), soil moisture (e.g., Walker *et al.*, 2015),
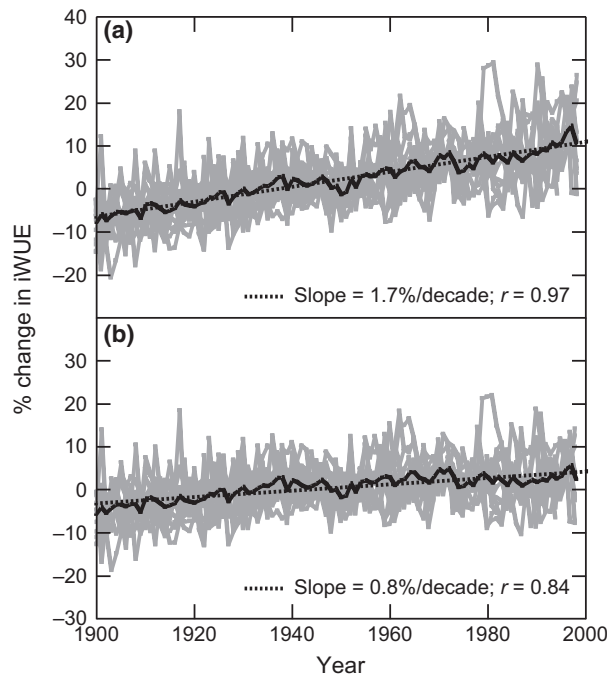
Fig. 4 Percent change in iWUE (relative to the 1912–1961 reference period) for each of the 15 tree-ring sites (gray lines). (a) Percent change in iWUE in response to increasing pCO_2 (i.e., c_a) and changes in stomatal conductance resulting from climate change. (b) Percent change in iWUE in response to only changes in stomatal conductance resulting from climate change (no pCO_2 effects). Average iWUE across the 15 sites (solid black line) increases linearly (dotted line) in both scenarios. iWUE was calculated for each tree-ring record using Eqn (4) with c_i calculated from Eqn (1) using either $\Delta^{13}C_{raw}$ (a) or $\Delta^{13}C_{corr}$ (b). Within Eqn (4), c_a was held constant at the year 1900 level for (b).

temperature (Gagen *et al.*, 2007), and cloud cover (e.g., Young *et al.*, 2010; Gagen *et al.*, 2011b). We therefore recognize that site-specific relationships between $\Delta^{13}C_{corr}$ and local climate records are likely to produce stronger correlations and perhaps indicate additional controls on the $\Delta^{13}C_{corr}$ signal than what can be gained from the regional context explored here. Averaging across these diverse sites, however, produces a region-wide record of warming, evident across high-latitude forests. The changes in carbon isotope fractionation observed here suggest decreasing stomatal conductance in response to natural and anthropogenic warming. This result is consistent with field experiments conducted using open-top chambers that demonstrated increased drying in permafrost soils in response to warming temperatures (Natali *et al.*, 2015), but we cannot rule out a change in photosynthetic rate caused by changes in summer sunshine, as has been measured at some sites (Gagen *et al.*, 2011b). The small change in $\Delta^{13}C_{corr}$ observed during the MTCC and slow LTCW

periods suggests that temperature changes were not sufficient to induce significant changes in soil moisture or a measureable stomatal response in the studied trees, or that other concomitant changes in climate canceled out the small decreases in $\Delta^{13}C_{corr}$ that may otherwise have been observed. Conversely, the significant warming associated with both the ETCW and rapid LTCW (0.7 °C per decade for each) did yield measureable decreases in $\Delta^{13}C_{corr}$, likely as a result of increasing water stress.

The $\Delta^{13}C$ data suggest increasing iWUE in northern taiga forests across the twentieth century that is driven in roughly equal proportions by reductions in c_i/c_a in response to changing climate and increasing pCO_2. Although rates of change in iWUE in response to climate change averaged 0.8% per decade across the entire record, rates of 2.1% per decade and 1.7% per decade were observed across the two intervals with the greatest rates of warming (ETCW and rapid LTCW, respectively). These results demonstrate that removal of the effect of pCO_2 on $\Delta^{13}C$ yields a clear signal of temperature-induced water stress within northern, high-latitude forests in response to climate warming.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Raw tree-ring δ^{13}C data compiled from the literature for trees growing north of 62° N.