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SCIENCE DIRECT

Quaternary Research 62 (2004) 126-133

QUATERNARY RESEARCH

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Tree-ring growth curves as sources of climatic information

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Received 1 October 2002

Abstract

Regional growth curves (RGCs) have been recently used to provide a new basis for removing nonclimatic trend from tree-ring data. Here we propose a different use for RGCs and explore their properties along two transects, one meridional and the other elevational. RGCs consisting of mean ring width plotted against cambial age were developed for larch samples from 34 sites along a meridional transect (55-72°N) in central Siberia, and for 24 sites on an elevational gradient (1120 and 2350 m a.s.l.) in Tuva and neighboring Mongolia at approximately 51°N. There are systematic gradients of the parameters of the RGCs, such as I_0-maximum tree-ring width near pith, and $I_{\min}$, the asymptotic value of tree-ring width in old trees. They are smaller at higher latitude and elevation. Annual mean temperature and mean May-September temperature are highly correlated with latitude here, and hence RGC parameters are correlated with these climatic variables. Correlations with precipitation are more complex, and contradictory between meridional and elevational transects. The presence of a similar gradient in the elevational transect is consistent with temperature being the causal factor for both gradients, rather than, for example, latitude-dependent patterns of seasonal photoperiod change. Taking ring measurements from collections of relict and subfossil wood, the RGC-latitude and RGC-temperature relationships are used to estimate paleo-temperatures on centennial time scales. These estimates are consistent with earlier "traditional" dendroclimatic approaches, and with independent information on the northern extent of forest growth in the early mid-Holocene. It may be possible to use this same approach to make estimates of century-scale paleo-temperatures in other regions where abundant relict wood is present.

Keywords: Tree rings; Larch; Regional curve standardization (RCS); Centennial-scale temperature estimates; Siberia; Meridional transect; Elevational transect

Introduction

Regional growth curves (RGCs) have been recently used to provide a new basis for removing nonclimatic trend from tree-ring data. Here we propose a different use for RGCs, and explore their properties along two transects, one meridional, the other elevational. To remove age- and size-related trend from tree-ring measurements while retaining low-frequency climate information, Briffa et al. (1992, 1995) proposed the use of regional curve standardization (RCS) in which a common regional growth curve (RGC) is used to detrend all individual series measured in a given region. The RGC is an empirically defined age/ring width or age/maximum late wood density curve. In RCS, it is used in place of, for example, the modified negative exponential curve to detrend each of measurement series before they are averaged to produce a site chronology. Unlike the fitted curves used in "traditional" standardization (Cook and Kairiukstis, 1989; Fritts, 1976; Hughes et al., 1982), a single detrending curve (the RGC) is applied to all the measurement series in that region. As Cook et al. (1990) state, "The premise behind RCS is that there is a single, common age and size-related biological growth curve for a given species and site that can be applied to all series regardless of when the trees were growing." This technique has been used in the reconstruction of summer temperatures at high-latitude sites or regions using conifer ring widths (TRW) or densities (MXD) (e.g., Briffa et al., 1992, 1995,

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doi: 10.1016/j .yqres.2004.06.005

1996; Naurzbaev and Vaganov, 2000), and on much larger spatial scales (Esper et al., 2002). It characteristically results in both more marked century-scale fluctuations, and weaker correlation between individual samples after treatment, leading to greater statistical uncertainty than with "traditional" methods (Briffa et al., 1992).

Here we examine parameters of RGCs along a latitudinal transect in Siberia, and argue that they can be linked to temperature on century time scales. We test this interpretation by a similar analysis of RGC parameters along an elevation gradient. We then describe a novel application of RGCs in which we use their parameters in the evaluation of climate change on time scales of centuries and millennia. We do not use these RGCs in regional curve standardization (RCS) here.

Materials and methods

Wood samples were collected from larch trees at 34 sites located from 72°30' N to 56°05' N in Central Siberia (Fig. 1). In cases where the pith ring was not present (approximately 40% of samples), pith offset was estimated using the curvature of the rings. The sites are distributed from north to south in the forest-tundra, northern, middle, and southern taiga subzones. At each site, samples were taken at approximately 1 m above ground from 15 to 25 larch trees. The numbers of trees, their age distribution, and site locations, are given in Table 1a. Similarly, samples were collected and RGCs developed at 23 sites along an elevational transect in the region of Tuva, and one site from Mongolia developed by G.C. Jacoby (pers. comm., 2003) (Fig. 1, Table 1b). Elevations on the Tuva transect ranged between 1120 and 2350 m above sea level (m.a.s.l.). All samples were cross-dated and tree-ring width measured with the help of a semiautomatic device (Rinn, 1996). To get the RGC for each site, the tree-ring widths of all samples were averaged according to their cambial age (number of rings from pith).

Climatic data from nine meteorological stations located along the meridional transect were used for comparison with the tree-ring width data. They are the annual mean and mean of May-September temperature for the period A.D. 1951-1990 (Anonymous, 1970, 1989). The validity of this comparison depends on the meridional gradient of these temperatures having been consistent for several centuries, the period during which the analyzed RGCs were formed. That this has been so is supported by the consistency of the geographical distribution of tree species along this meridian in recent centuries (Pleshikov, 2002).

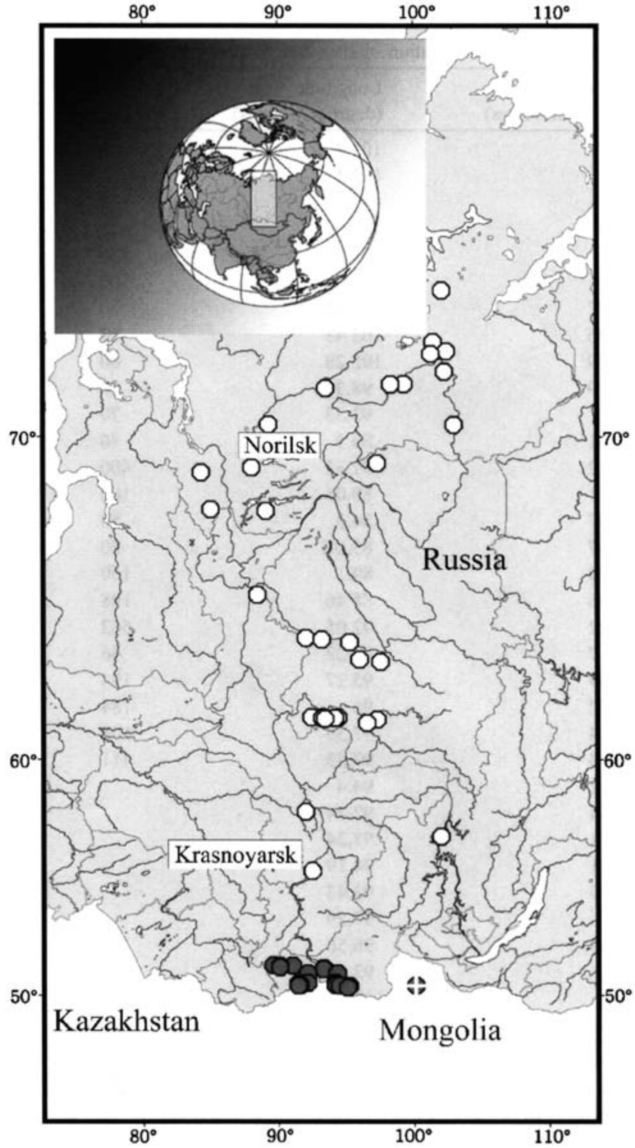

Figure 1. Locations of tree-ring sites. Open circles, meridional transect; closed circles, elevational transect; closed circle with open cross, site in elevation transect by G.C. Jacoby (pers. comm., 2003). See Tables 1a and 1b for details of sites.

Why temperature?

We focus on temperature because numerous observational and modeling studies have established that summer temperature is the prime determinant of radial growth in conifers in these regions on interannual and multidecadal time scales (Briffa et al., 1995, 2001; Earle et al., 1994; Furyaev et al., 2001; Graybill and Shiyatov, 1992; Hughes et al., 1999; Johansen, 1995; Kirdyanov et al., 2003; Panyushkina et al., 1996; Shiyatov et al., 1996; Vaganov et al., 1996, 1999). In fact, not only has temperature been established as the main factor affecting ring width and maximum late wood density, but there is sufficiently detailed knowledge of the mechanisms involved to permit the development of effective process-based models (Vaganov et al., 1999). This applies across the wide range of hydrological conditions seen in the 20th century from the Polar Urals to Northern Yakutia. Comparisons with ground-temperature histories derived from geophysical inversion of borehole temperature logs have demonstrated that tree-ring

Table 1a
Meridional transect: location of sites and details of tree-ring samples

Latitude (degrees.minutes)	Longitude (degrees.minutes)	Elevation (m.a.s.l.)	Number of trees	Mean age (yr)	Minimum age (yr)	Maximum age (yr)
72	101.3	6	31	276	47	548
73.4	102.1	6	32	100	21	350
71.3	99.3	6	9	270	133	636
70.3	103	300	17	231	90	535
70.3	103	300	19	313	141	631
70.3	103	300	29	183	57	369
72.27	101.45	20	15	276	131	493
72.06	102.43	10	18	328	122	464
71.59	102.28	60	10	299	144	498
71.29	98.31	60	17	110	55	284
71.2	93.53	70	24	304	131	451
70.31	89.3	70	18	231	114	376
69.32	97.32	400	16	287	64	474
69.21	88.06	100	11	96	14	162
69.07	84.3	50	29	248	150	327
68.07	85.03	50	23	290	163	438
68.03	89.1	150	31	334	128	474
65.58	88.46	108	10	370	250	487
64.22	92.05	562	11	244	168	323
64.17	93.22	46	15	336	255	381
64.09	95.27	194	12	284	183	376
63.52	96	184	12	236	65	304
63.44	97.55	108	13	270	92	382
63.44	97.55	111	11	180	91	245
61.52	94.4		12	235	143	366
61.54	92.44		12	203	149	248
61.51	93.24		20	140	64	213
61.51	94.19		22	146	54	200
61.49	93.43		21	157	113	284
61.46	97.29		11	267	237	287
61.33	96.56		11	206	162	269
58	92		15	171	85	288
57	102		12	324	205	403
55.59	92.5	455	22	138	88	215

chronologies are also temperature-controlled on century time scales in this (Pollack et al., 2003) and similar regions (Beltrami et al., 1995; Majorowicz and Skinner, 2001). Our confidence in the appropriateness of treating temperature as the controlling factor is further strengthened by evidence that "during the early Holocene... conditions in the lower Yenisey River region were moist compared to the present" (Wolfe et al., 2000). As temperature has been amply demonstrated to be the relevant factor under present conditions, it is hardly likely to have been supplanted in a wetter regime.

Results

Meridional transect

In this region, mean annual temperature decreases almost linearly with increasing latitude, while the northward decrease of mean May-September average temperature accelerates at the highest latitudes (Fig. 2). To compare growth data with temperatures along the meridional gradient, the nine station temperature records were interpolated to the latitudes of the tree sampling sites by least-squares fitting.

For each tree-ring sampling site, all of the measured ring-width series were aligned, not by the calendar year in which the ring was formed, but by the cambial age of the ring. The mean of the widths for all rings of each cambial age (the RGC) shows a common pattern that is fitted quite well by a modified negative-exponential curve (Fig. 3):

$$I_A = I_0 \exp(- c * A) + I_{\min}, \qquad (1)$$

where I_A is tree-ring width (mm) at age A (yr), I_0 is maximum tree-ring width in rings near pith, c is a constant related to site, and $I_{\min}$ is the asymptotic value of tree-ring width. This pattern has been extensively used in the removal of age- and size-related trend from tree-ring width series (Cook and Kairiukstis, 1989; Fritts, 1963; Hughes et al., 1982). We chose three parameters extracted from the RGCs for further comparison: I_0, the average tree-ring width for cambial ages 50-100 yr ($I_{50\text{-}100}$), and the asymptotic value of tree-ring width ($I_{\min}$).

Table 1b
Elevational transect: location of sites and details of tree-ring samples

Latitude (degrees.minutes)	Longitude (degrees.minutes)	Elevation (m.a.s.l.)	Number of trees	Mean age (yr)	Minimum age (yr)	Maximum age (yr)
51.41	89.58	1950	25	169	41	302
51.4	91	1800	10	239	85	388
51.4	91	1800	18	188	93	250
51.4	91	1800	6	246	210	287
51.38	90.06	1670	26	151	71	279
51.34	90.07	1460	24	177	78	265
51.32	90.08	1260	28	186	94	227
51.03	92.13	1320	29	191	38	375
51.03	94.33	1140	31	107	46	234
50.57	94.18	1860	16	275	77	397
50.56	94.18	1720	29	275	161	375
50.56	94.2	1720	24	248	101	377
50.55	91.41	1490	12	164	112	201
50.54	94.18	1740	25	291	131	422
50.52	94.18	2085	13	103	42	238
50.51	91.54	2100	11	148	76	232
50.5	94.18	1800	20	126	39	221
50.48	94.18	1610	24	208	31	306
50.48	91.46	1710	7	208	141	330
50.46	100.12	2300[a]	13	192	86	373
50.45	91.44	1590	20	214	46	455
50.45	94.48	1710	24	95	34	177
50.37	95.1	1480	21	156	41	267

[a] Site at 2300 m elevation from G.C. Jacoby (pers. comm., 2003).

I_0, $I_{50\text{-}100}$, and $I_{\min}$ all decrease exponentially with increasing latitude (R = -0.74, -0.67 and -0.77, $P < 0.001$, respectively) although standard deviations are rather high (Fig. 4). The standard deviations of the growth curve parameters are I_0, 0.71; $I_{50\text{-}100}$, 0.63; and $I_{\min}$, 0.49. Not surprisingly, the three indices increase exponentially with increasing mean annual (R = 0.83, 0.72, and 0.80, $P < 0.0001$) and summer (R = 0.80, 0.69, and 0.79, $P < 0.0001$) temperatures. These high correlations of the indices with latitude and temperature indicate that there is a systematic gradient of RGC parameters along the meridional transect, each increasing with lower latitude and the associated higher temperature.

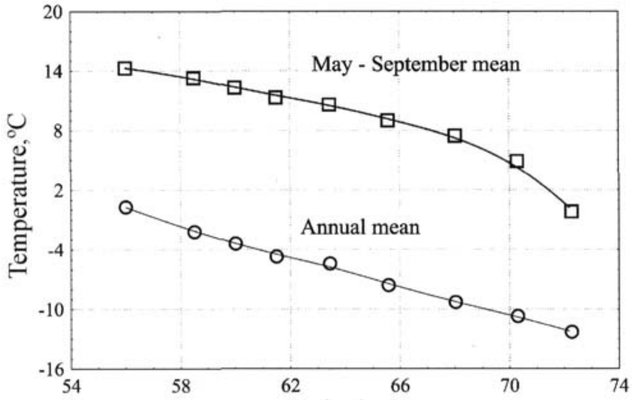

Figure 2. Annual mean temperature and mean May-October temperature at nine meteorological stations along the meridional gradient, A.D. 1951-1990.

The relationship between precipitation and the growth parameters is less simple, both in winter and summer. For instance, annual precipitation has a significant positive correlation (0.76, n = 29, $P < 0.001$) with $I_{50\text{-}100}$ when calculated for the entire latitude range. Focusing only on the high latitudes (72-64°), the correlation is positive and even higher (0.81, n = 16, $P < 0.001$). For the rest of the meridian (64-52°), the correlation is negative (-0.62, n = 13, $P < 0.05$). These results contrast with the monotonic decrease in growth parameters with increasing latitude shown in Figure 4.

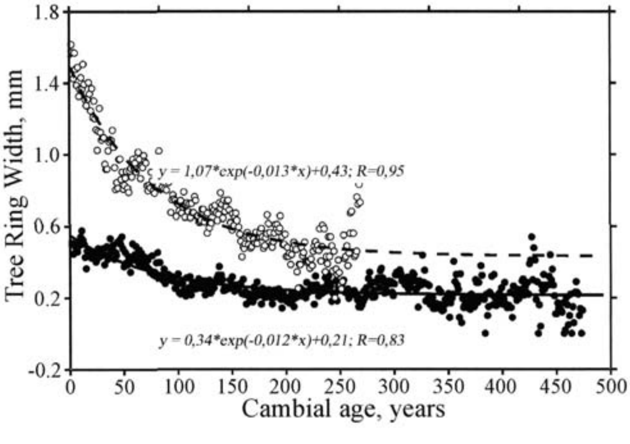

Figure 3. Estimation of regional growth curves for two sites. Points - mean ring width of all samples at that site for a particular cambial age. Open circles - the site at 61.33°N; closed circles - the site at 69.32°N. Fitted lines - modified negative exponential (see text).

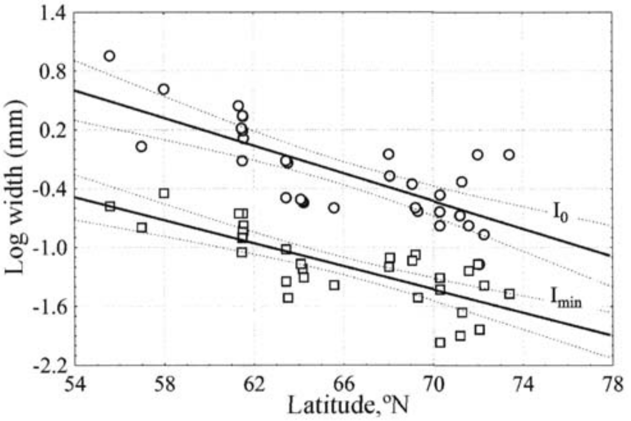

Figure 4. Parameters I_0 and $I_{\min}$ for the chronologies of the meridional transect against latitude. Heavy lines are the fitted linear regression lines, with 95% confidence limits shown as broken lines.

The ratios among the parameters (I_0:$I_{50\text{-}100}$:$I_{\min}$) show slight gradients against latitude, but these are not statistically significant. This indicates that the form of the RGC is almost constant throughout the gradient. Note that maximum age (from Table 1) has a positive weak, but significant, correlation with latitude (R = 0.53, $P < 0.05$) and negative correlation with annual (-0.53) and summer (-0.50) temperatures. Here, as elsewhere, slowly growing trees achieve greater ages than fast growing (Schulman, 1954). This is also associated with a weak negative correlation between maximum age and, for example, $I_{50\text{-}100}$ (R = -0.45, $P < 0.05$).

Elevational transect

Although we show strong correlations between latitude and both annual and mean May-September temperatures, and larch RGC parameters along the meridional transect, temperature is not the only environmental variable that may affect tree-ring growth. In particular, there is a dramatic difference in seasonality and especially the diurnal cycle at 72°N compared to the southern end of the meridional transect at 55°N. Within a single region at approximately the same latitude, however, temperature will vary with elevation, and so will the length of the growing season, but photoperiod will not. The 1230-m Tuva elevational gradient would represent a 7.4°C temperature range if a lapse rate of 6°C/km were assumed. This may be compared with a range of approximately 12°C (9°C) temperature range for summer (whole year) over the meridional transect. As might be expected, the parameters of the RGCs along the Tuva elevational gradient do indeed decline with increasing elevation (Fig. 5). The inferred temperature dependence of the growth-curve parameters is somewhat stronger than on the meridional transect. For example, $I_{50\text{-}100}$ changes by 0.09 mm/°C on the elevational transect and 0.05 mm/°C on the meridional transect.

Discussion

The application of RGC parameters to the estimation of temperatures on centennial time scales

The similarities between the meridional and elevational patterns of RGC parameter change, and the scales of their association with temperature suggest that, in these environments, the levels of the RGC parameters reflect temperature. The association between RGC parameters and both annual and summer temperature is of the same sign and broadly similar size in both meridional and elevational transects. The relationship with precipitation is complex along the meridional gradient. Furthermore, there is a negative relationship between radial growth and elevation in the elevational transect, where temperature decreases with elevation as precipitation increases. Thus, we treat the growth curve parameters as being independent of hydrological variables. As a result, it is possible to estimate annual and summer temperature on century time scales from wood samples collected in this region, if the cambial age of each ring is known, and if sufficient samples are available to determine the RGC accurately for the periods of interest. The time scale is centennial, because the parameters represent the response of the tree to environment over its life span.

We have used this approach to make exploratory estimates of century-scale annual and May-September temperatures, and paleolatitudes for various wood samples from this region (Table 2). It is clear from Figure 6 that although there is a notable relationship between, for example, $I_{\min}$ and annual temperature, there are other sources of variability that we have not yet identified. We plan to investigate these, particularly elevation and aspect, but in the meantime have made these illustrative calculations to demonstrate the potential for estimating century-scale temperatures from RGC parameters. The equation fitted to the data from the meridional transect was $T = a + b$

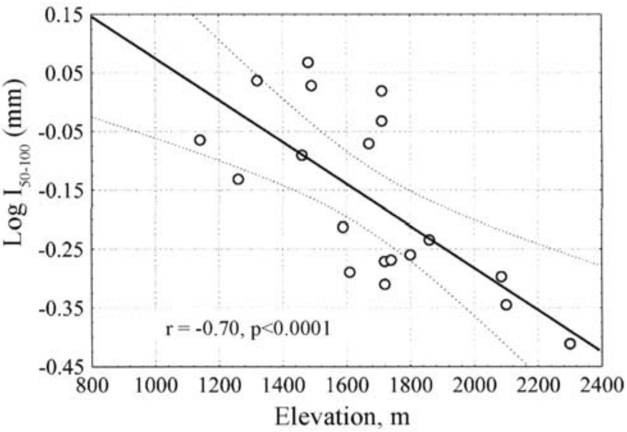

Figure 5. $I_{50\text{-}100}$ for the chronologies of the elevational transect against elevation. Heavy line is the fitted linear regression line, with 95% confidence limits shown as broken lines.

Table 2
Evaluation of annual and summer temperatures from age curves in north-central Siberia

Latitude	Wood source	Date	Estimated temperature (°C)		Latitude equivalent
			Annual[a] (±1.53)	Summer[a] (±2.15)	
72°27	Living trees, northern tree line	AD 1600-1900[b]	-10.8 (+1.3)[c]	4.3 (+3.6)[c]	71°15'
71°00'	Dead wood north taiga edge	AD 900-1200[b]	-9.9 (+1.5)[c]	5.1 (+2.3)[c]	69°42'
72°00'	Subfossil wood	4140-2700 cal yr BC[d]	-6.6 (+5.6)[c]	9.2 (+7.6)[c]	64°48'
73°30'	Subfossil wood	6700-7100 ^{14}C yr B.P.[e]	-7.8 (+5.5)[c]	7.7 (+8.2)[c]	66°50'

[a] Calculations based on three parameters (I_0, $I_{50\text{-}100}$, I_{MIN}) and averaged.

[b] Tree-ring dates.

[c] Difference with modern temperature at same latitude.

[d] Calibrated radiocarbon and floating tree-ring chronology (see Naurzbaev et al., 2001 and text).

[e] Uncalibrated radiocarbon dates-three timbers: BB-38, 200 rings, 6710 ± 110 ^{14}C yr B.P., COAH-4745; BB-20, 257 rings, 6750 ± 60 ^{14}C yr B.P., COAH-4744; BB-85, 98 rings, 7090 ± 100 ^{14}C yr B.P., COAH-4746; all dated at the Institute of Geology, Geophysics, and Mineralogy, Novosibirsk, Russia.

($\log_e I$) + e, where T is temperature (either annual or summer), I is the specific RGC parameter (I_0, $I_{50\text{-}100}$, or $I_{\min}$), a and b are constants, and e is an error term. For summer temperature for the three RGC parameters, respectively, the terms a and b are 10.09, 6.937; 13.884, 7.576; and 19.008, 9.15. For annual temperature, they are -5.789, 6.035; -2.553, 6.498; and 1.775, 7.79.

Annual and summer temperatures, and latitudes, derived from the RGC of trees living at the northern tree line coincide with those from instrumental records and dendroclimatic reconstructions (Naurzbaev and Vaganov, 2000). Note that annual temperature, for example, changes by 0.75°C for 1° in latitude. Trees that lived at the upper (elevational) tree limit during the so-called Medieval Warm Epoch (from A.D. 900 to 1200) show annual and summer temperature warmer by 1.5° and 2.3°C, respectively, approximately one standard deviation of modern temperature. Note that these trees grew 150-200 m higher (1-1.2°C cooler) than those at low elevation but the same latitude, implying that this may be an underestimate of the actual temperature difference. Notable results are derived from the analysis of age/growth curves of radiocarbon-dated subfossil trees from locations at 72°N close to the modern northern tree line and from a site located 170 km north of the modern tree line at 73°30' N. There are more than 25 radiocarbon dates for the first site (Naurzbaev et al., 2001), and a floating tree-ring width chronology covering 1443 yr based on 27 cross-dated samples, with individual ages of between 134 and 546 yr, most having more than 250 rings. The time period was from 4140 to 2700 cal yr B.C. Moist conditions at about 7000 ^{14}C yr B.R were inferred for a site in the lower Yenisey River region by Wolfe et al. (2000), followed by decreasing wetness from 7000 to 1500 yr ago. Consequently, our floating chronology covers much of the wettest inferred period for this region within the Holocene. As indicated earlier, it is thus extremely unlikely that moisture would be limiting to the trees forming the floating chronology, because it is not the controlling factor in the recent, drier period. The RGC corresponds to a mean annual temperature of -6.6°C and a mean May-September temperature of 9.2°C, and also to modern conditions at approximately 65°N. The estimated latitudinal difference is about 7°N. This implies that at the time these trees grew, growth conditions in this area were equal to those in the modern north taiga region. Average differences between modern and ancient annual temperature were estimated as 6.7°C (minimum difference is about 2.3°C if the standard deviation is taken into account), with the same magnitude of difference for May-September temperature. This value is close to our evaluation obtained from analysis of the "floating" chronology by the traditional dendroclimatic technique (Naurzbaev and Vaganov, 2000). Analysis of RGCs from another site with subfossil wood gives estimated annual and summer temperature of -7.8° and 7.7°C respectively, and corresponding to modern conditions at 66°50' N. The latitudinal difference is 6°40' , similar to the previous site. The latest date for this material, which consisted of three timbers, was about 700-800 yr earlier than the beginning of the floating chronology.

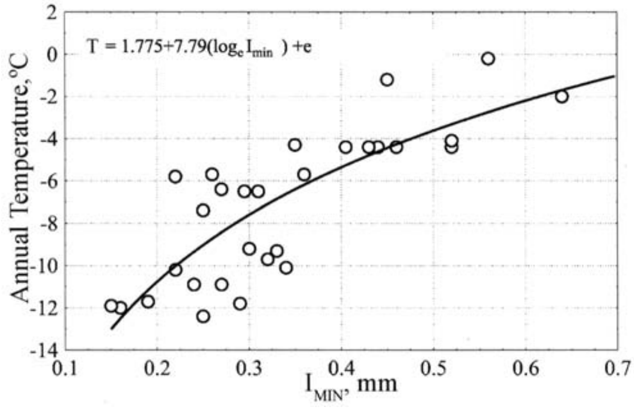

Figure 6. Annual temperature against $I_{\min}$ for chronologies of the meridional transect. A semilogarithmic fit is shown, with the equation given in the diagram.

Summarizing the results from subfossil wood, taking into account the change of annual temperature with latitude, we calculate that during the Holocene Climatic Optimum on the Taimyr Peninsula, the northern tree line was located about 450 km (minimally 250 km) further north than at present. This is consistent with other observations on ancient tree lines in northern Eurasia, some parts of North America and the north of Scandinavia (Huntley and Prentice, 1988; Kullman and Kjallgren, 2000; MacDonald et al., 1993, 2000). For example, Kullman and Kjallgren (2000) reported that the greatest elevational extension of forest in Scandinavian mountains at the beginning of the Holocene was about 500 m above the modern upper tree line, which means temperatures were warmer by at least 3°C (assuming 0.6°C temperature decrease for every 100 m increase in elevation). There are several other regions in Northern Eurasia and northern North America where RGC parameters may be subject to relatively simple control by temperature, and where abundant relict wood exists covering several periods in the Holocene. Thus, the possibility exists of adding a new kind of record for such times and regions, even if it is not possible to develop well-replicated tree-ring chronologies known to conserve century-scale climate information for the whole period.

Latitude- or elevation-specific RGCs

Secondly, knowing the latitude in this region of a new wood collection, or the elevation in Tuva, we can select the appropriate Regional Growth Curve for standardization of individual series, provided that ecological conditions resemble those in the sites discussed in this report. For instance, if we collect samples at a site located at 65 °N, the fitted equation for the RGC will be

$$I_A = 0.52\exp(-0.0117 * A) + 0.31. \qquad (2)$$

Alternatively, if the site is characterized by a mean annual temperature of, for example, -4°C, then the fitted equation for RGC will be

$$I_A = 0.72\exp(-0.0169 * A) + 0.42. \qquad (3)$$

This could be of value in building long chronologies from material found at differing latitudes or elevations during the chronology period, as caused, for example, by tree line movements.

Other sources of variability influencing RGC parameters

There are several sources of variability other than climate that may affect tree-ring RGCs and, as a result, any estimates of past temperature made using their parameters. There are many sources of variation between individual trees, including genetic variability, micro-site conditions, and stand structure and history. For example, it may be expected that the lower the density of the stand, the higher the value of I_0. At the same latitude, it would be higher in sites on sandy (light) soils than those on heavy (clay, loam) soils. I_{min} is likely to be lower in sites where permafrost is close to the surface, and in those with thick moss cover, or clay soils with lower thermal conductivity, and so on. It would also be lower in older stands with high tree density, and with strong competition from grasses and shrubs. The initial conditions determining I_0 will also influence I_{50-100}.

If the climatic influence on the age- and size-related trends is consistent, and if the other factors behave as Gaussian noise, this may be dealt with by increased replication. Stand-level disturbance, for example, fire and the ensuing growth release, may produce an RGC that is distorted, from a climatic point of view. Of course, careful examination of the primary samples should reveal evidence of major disturbance, for example, synchronous reaction wood, suppression, or growth releases, indicating that the samples, or indeed, the whole site collection, should be excluded. Basing RGCs, and if possible, collections for use in exploring past temperatures, on material from multiple sites, should also help reduce this effect.

Conclusions

(1) In two transects in central Siberia - one meridional, the other elevational - parameters of larch tree-ring width regional growth curves (RGCs) are smaller at higher latitude and elevation.

(2) Both annual mean and mean May-September temperature are highly correlated with latitude in this region, and therefore the RGC parameters are also correlated with these climatic variables. Unlike precipitation, they have a monotonic change with latitude.

(3) The existence of a similar gradient in the elevational transect is consistent with temperature being the causal factor for the gradients, rather than, for example, latitude-dependent patterns of seasonal photoperiod change. It is also inconsistent with precipitation being the primary limiting factor for the RGC parameters because their signs are opposite.

(4) Thus, in larch in central Siberia, latitude-specific RGCs may be calculated for use in tree-ring standardization according to the regional curve standardization (RCS) method. The same may be done on an elevational basis in Tuva.

(5) The RGC-latitude and RGC-temperature relationships are used to estimate paleo-temperatures on centennial time scales from the RGC parameters of collections of relict and subfossil wood, yielding estimates consistent with earlier "traditional" dendroclimatic approaches, and with independent information on the northern extent of forest growth in the early mid-Holocene.

(6) Considerable work remains to improve the reliability of these estimates. The approaches reported here are applicable to larch in the region from Tuva to the Taimyr Peninsula. Their applicability to other species and regions has yet to be tested, but there is reason to believe that this approach may work in much of the boreal zone.

Acknowledgments

This work was supported in part by grants RC1-29 and RB1-2020 from the Civilian Research and Development Foundation of the United States to EAV and MKH, and by grants ATM-0308525 from the Paleoclimate Program in the Division of Atmospheric Sciences at the U.S. National Science Foundation NSF and NA03OAR4310125 from the Climate Change Data and Detection Program of the U.S. National Oceanographic and Atmospheric Administration to MKH.

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