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Responses of the circumpolar boreal forest to 20th century climate variability

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Abstract

We examined relationships between tree ring-width and climate at 232 sites around the circumpolar boreal forest to explore variability in two types of response to temperature: a browning response characterized by inverse correlations between growth and temperature, and a greening response characterized by positive correlations between growth and temperature. We used moving-window correlation analysis for eight 30-year time windows, lagged by 10 years, to characterize the climate response at each site from 1902 to 2002. Inverse growth responses to temperature were widespread, occurring in all species, all time periods, and in nearly all geographic areas. The frequency of the browning response increased after 1942, while the frequency of the greening response declined. Browning was concentrated in five species (*Picea abies*, *Picea glauca*, *Picea mariana*, *Picea obovata* and *Pinus banksiana)*, and occurred more frequently in the warmer parts of species' ranges, suggesting that direct temperature stress might be a factor. In some species, dry sites were also more likely to experience browning; moisture stress might thus be an additional explanation in some cases. As inverse responses to temperature are widespread, and occur in a broad array of species, there is unlikely to be any single explanation for their occurrence.

1. Introduction

1.1. Background

High northern latitudes have warmed at a rapid rate since the mid-1900s (Chapin *et al* 2005, Serreze *et al* 2000). The response of boreal forest ecosystems to this warming has significant implications for the arctic climate system as a result of vegetation/climate feedbacks that occur as the productivity and distribution of the boreal forest changes. These feedbacks arise from two processes: changes in C cycling (Beer *et al* 2006, D'Arrigo *et al* 1987, Dixon *et al* 1994, Keyser *et al* 2000, Kimball *et al* 2007, McGuire *et al* 1995, 2002) and changes in reflectance and energy exchange that result from the expansion or contraction of evergreen coniferous vegetation at high latitudes (Beringer *et al* 2005, Chapin III *et al* 2000,

Chapin *et al* 2000, 2005, McGuire *et al* 2002). Understanding of future climate-induced changes in boreal forest tree growth and distribution is crucial for estimating the direction and magnitude of vegetation feedbacks on climate (Bala *et al* 2007, Chapin *et al* 2005).

High-latitude forests are commonly believed to be limited by cold temperatures (e.g., Nemani *et al* 2003), in which case warming would be expected to result in increased productivity and range expansion of boreal species. This expectation is partially borne out by recent changes in the distribution of the boreal forest, as evergreen coniferous forests have begun to expand into adjacent tundra ecosystems in many, although not all, locations in the circumpolar boreal forest in recent decades (Kharuk *et al* 2005, Lloyd and Fastie 2003, Lloyd *et al* 2002, Lloyd 2005, MacDonald *et al* 2000, Szeicz and Macdonald 1995). The response of tree growth and forest productivity to rising temperatures, however, has been

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characterized by high spatial and temporal variability, and has in some cases contradicted the expectation that warmth will stimulate growth in boreal regions (Bunn *et al* 2005). While tundra ecosystems exhibited a significant positive trend in seasonal photosynthetic activity over the last few decades, some boreal forest ecosystems, particularly in continental interiors, exhibited no trend or a significant downward trend in seasonal photosynthetic activity, particularly after 1990 (Bunn and Goetz 2006, Goetz *et al* 2005).

Tree ring studies have identified similarly complex patterns of tree growth response to climate variability, although changes in tree response to temperature generally predate, often by decades or more, recent changes observed in satellite NDVI data. At many boreal sites the response of trees to temperature changed after the mid-20th century. Correlations with temperature weakened or, in some cases, changed direction (from positive to negative correlations) after that time (Briffa *et al* 1998a, Buntgen *et al* 2006, D'Arrigo *et al* 2007, Davi *et al* 2003, Driscoll *et al* 2005, Jacoby and D'Arrigo 1995, Jacoby *et al* 1999, 2000, Lloyd and Fastie 2002, Wilmking *et al* 2004, 2005, Wilson and Elling 2004). Similar large-scale changes in tree response to temperature have been identified in analyses of wood density data, which show a decline in wood density during the 20th century, concurrent with decreasing sensitivity to summer temperatures (Briffa *et al* 1998b). Together, tree-ring and satellite-based studies of tree growth response to climate suggest a change in the role of temperature as a limiting factor in boreal forest ecosystems.

A number of causes have been proposed for the divergence of tree growth and temperature, including direct temperature stress (D'Arrigo *et al* 2004), drought stress caused by higher evaporative demands in warmer temperatures (Barber *et al* 2000, Jacoby and D'Arrigo 1995, Lloyd and Fastie 2002), changes in the relative timing of key growth windows (Vaganov *et al* 1999), changes in the relationships among mean, maximum, and minimum temperatures (Wilson and Luckman 2003), pollution (Lopatin *et al* 2006, Wilson and Elling 2004), ozone depletion (Briffa *et al* 2004), and global dimming (D'Arrigo *et al* 2007). There is no consensus, however, on the relative importance of each. The full spatial extent of the growth declines also remains unknown. Although they have been documented in a large number of sites, patterns of prevalence among species and geographic regions have not been fully described. In this paper, we address these unknowns with an analysis of broad-scale patterns of variability in tree response to climate from a network of 232 tree-ring sites representing 10 important boreal forest species.

1.2. Hypotheses

We tested four hypotheses related to tree growth response to climate since the early 1900s. The hypotheses and associated predictions follow.

(1) Browning, which we define as an inverse relationship between tree growth and temperature (see section 2.3), is not a species-specific phenomenon, and occurs at similar frequencies in all species.

(2) Browning has become more common as it has warmed since 1900.

 (i) The frequency of browning exhibits a significant positive trend over time.
 (ii) The frequency of browning exhibits a significant positive relationship with northern hemisphere temperature.

(3) Browning is a direct response to temperature stress as ambient temperatures exceed species' optimum temperature range.

 (i) Within any given species' range, browning occurs more frequently in warm than in cool sites.
 (ii) Sites in which browning has occurred at least once are significantly warmer in the summers than those at which browning never occurs.

(4) Browning is a response to moisture stress associated with the increased evapotranspirative demands experienced at high temperatures.

 (i) Within any given species' range, browning is more common in dry than in wet sites.
 (ii) Sites that have never experienced browning have significantly higher precipitation than those that have experienced browning at least once.
 (iii) Because moisture stress is hypothesized to be induced by high temperatures, we expect to find an interaction between precipitation and temperature: browning should be most frequent in sites that are warm and dry.

2. Methods

2.1. Tree-ring data processing

We obtained tree-ring data from the International Tree-Ring Data Bank (http://www.ncdc.noaa.gov/paleo/treering.html). Our initial data set consisted of all tree-ring chronologies from sites north of 55°N that pre-dated 1900 and extended at least to 1990. In order to maintain relatively constant sample depth, we set a limit on the number of young trees (establishing after 1902) permitted within each set: sites with more than 10% young trees were subsampled to remove those establishing after 1902. We ran the remaining samples through the quality control program Cofecha (Holmes 2000) and eliminated three sites in which average interseries correlations were not significant ($P > 0.05$). Our analyses are based on the remaining 272 sites (appendix 1, available from stacks.iop.org/ERL/2/045013). We assessed the signal uniformity of tree-ring series within each site using the expressed population signal (EPS), using a threshold EPS value of 0.85 (Wigley *et al* 1984). Ring-width measurements were unavailable for three sites, so this analysis was conducted on 269 of the 272 chronologies. The EPS value exceeded the threshold of 0.85 for 226 of 269 (84%) of these chronologies, and the majority of chronologies in which the EPS value failed to exceed the threshold had EPS values greater than 0.8. Only 20 of the 269 (8%) chronologies had an EPS value less than 0.8. We opted to include these sites in the analysis despite
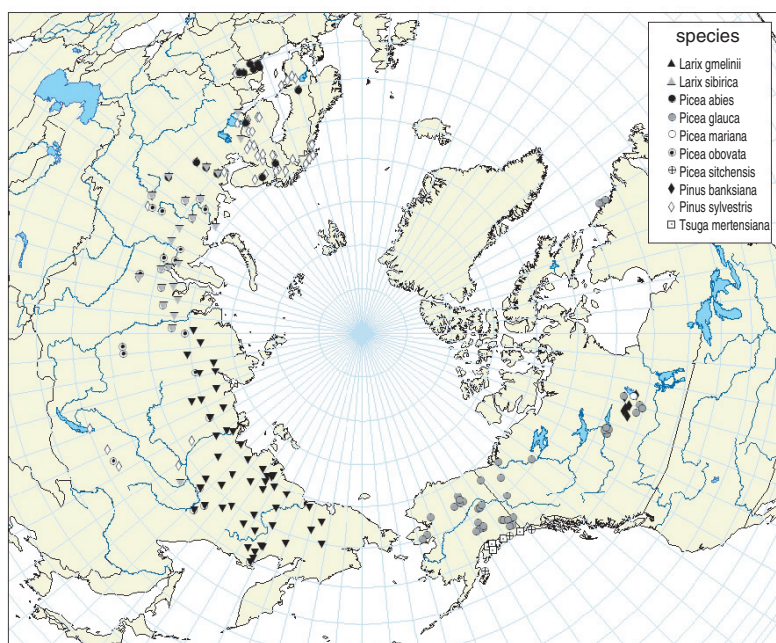
Figure 1. Map of tree-ring locations used in this study. Full details are provided in appendix 1 (available from stacks.iop.org/ERL/2/045013).

Table 1. Summary of chronologies included in the analysis. A full list of sites and authors is included in appendix 1 (available from stacks.iop.org/ERL/2/045013).

Region	Species	Range of end years	Range of latitudes (°N)	Number of chronologies
Eurasia	*Larix gmelinii*	1990–1998	59.78°–72.50°	52
Eurasia	*Larix sibirica*	1990–1994	60.27°–69.12°	24
Eurasia	*Picea abies*	1990–2005	55.07°–68.77°	14
North America	*Picea glauca*	1991–2005	55.12°–68.27°	41
North America	*Picea mariana*	2001–2005	56.65°–67.53°	3
Eurasia	*Picea obovata*	1990–1996	56.50°–70.27°	27
North America	*Picea sitchensis*	1992–1996	58.05°–60.25°	3
North America	*Pinus banksiana*	2002	56.50°–57.85°	6
Eurasia	*Pinus sylvestris*	1990–2004	55.25°–69.53°	56
North America	*Tsuga mertensiana*	1990–1995	60.00°–60.83°	6

their relatively poor uniformity. This decision likely results in a greater number of sites with no significant climate response, but given the very small number of sites involved it does not substantially affect our analyses.

Ring-width measurements were detrended using a negative exponential curve, line of negative slope, or horizontal line, and standardized by division to produce ring-width indices for each tree; using a uniform standardization method eliminates one potential source of variability in tree ring patterns. A ring-width chronology was produced for each site as the mean of the standardized, detrended ring-width series. Because our interest is specifically in decadal-scale trends in tree growth, we performed all analyses on the standard, rather than residual, chronology. In 23 cases where more than one site from a single species was located within a single 0.5° × 0.5° grid cell (the scale of our climate data, see section 2.2), we created composite chronologies by averaging the component site chronologies. Composite chronologies were created only if the multiple sites were significantly correlated ($P < 0.05$)

with one another. Our final data set after creating composites thus consisted of 232 chronologies representing ten species (table 1, figure 1). A full list of sites and authors is provided in appendix 1 (available from stacks.iop.org/ERL/2/045013).

2.2. Climate data

Climate variables were derived from the CRU interpolated spatial data set for the years 1901–2002 (Climate Research Unit; CRU TS 2.10, http://www.cru.uea.ac.uk). The data set has a resolution of 0.5° × 0.5° latitude and longitude. Although these data are probably of lower quality than the best station data, they are of better quality than the station data available to the majority of our sites. Nonetheless, CRU data may be biased during the early part of our analysis period by the paucity of climate stations, which might produce an excessively smoothed climate record (i.e. one with low variance among years). To test for this bias, we compared CRU data to station data for a subset of our sites at which both high quality station data and CRU data were available. We confined

Table 2. Comparison of HCN station data and CRU data for eight study sites. The site name is the name of the ITRDB tree-ring site within the $0.5° \times 0.5°$ grid cell. The years included within the early and late periods varied depending on the characteristics of the station data. In some cases (e.g. CA125) station data were sufficiently incomplete during the early part of the record that we used a shorter time period for the early period. For two sites (AK034 and AK040), the station data were near, but not within, the grid cell.

Site	Time period	Variance HCN data	Variance CRU data	F-test	Correlation
FI046	Early (1910–1929)	379 184.2	293 395.5	$F = 1.292$ $df = 19$ $P = 0.2908$	$r = 0.979$ $P < 0.001$
	Late (1974–1993)	1273 750.3	850 933.3	$F = 1.496$ $df = 19$ $P = 0.1935$	$r = 0.758$ $P < 0.001$
FI054	Early (1908–1927)	673 362.9	314 265.5	$F = 2.143$ $df = 19$ $P = 0.053$	$r = 0.974$ $P < 0.001$
	Late (1983–2002)	835 605.0	399 038.7	$F = 2.094$ $df = 19$ $P = 0.057$	$r = 0.947$ $P < 0.001$
NO007	Early (1902–1921)	380 352.6	532 802.9	$F = 0.714$ $df = 19$ $P = 0.235$	$r = 0.982$ $P < 0.001$
	Late (1971–1990)	413 513.9	754 922.2	$F = 0.548$ $df = 19$ $P = 0.099$	$r = 0.950$ $P < 0.001$
CA207	Early (1938–1957)	996 794.8	865 840.3	$F = 1.151$ $df = 19$ $P = 0.381$	$r = 0.996$ $P < 0.001$
	Late (1971–1990)	1112 106.1	1019 224.9	$F = 1.091$ $df = 19$ $P = 0.426$	$r = 0.990$ $P < 0.001$
CA125	Early (1919–1928)	203 743.8	139 777.8	$F = 1.457$ $df = 9$ $P = 0.292$	$r = 0.630$ $P = 0.051$
	Late (1971–1988)	1489 974.9	172 589.4	$F = 8.633$ $df = 17$ $P < 0.001$	$r = 0.561$ $P = 0.015$
CA173	Early (1908–1927)	551 466.1	640 954.3	$F = 0.860$ $df = 19$ $P = 0.373$	$r = 0.895$ $P < 0.001$
	Late (1971–1990)	158 702.7	640 954.3	$F = 0.680$ $df = 19$ $P = 0.204$	$r = 0.782$ $P < 0.001$
AK034	Early (1907–1926)	4 258.3	3 351.6	$F = 2.013$ $df = 19$ $P = 0.067$	$r = 0.904$ $P < 0.001$
	Late (1980–1999)	1031 488.6	600 798.2	$F = 1.717$ $df = 19$ $P = 0.124$	$r = 0.923$ $P < 0.001$
AK040	Early (1931–1950)	493 572.6	192 340.9	$F = 2.566$ $df = 19$ $P = 0.023$	$r = 0.596$ $P = 0.006$
	Late (1980–1999)	409 849.7	203 632.5	$F = 2.013$ $df = 19$ $P = 0.068$	$r = 0.812$ $P < 0.001$

our comparisons to annual precipitation, as precipitation is more highly spatially and temporally variable than temperature and thus more likely to suffer the smoothing effects of spatial interpolation. We identified eight locations in which station data (from the Historical Climatology Network) were available within (or, in two cases, near) the $0.5° \times 0.5°$ grid cell in which our site was located: three in Scandinavia, three in Canada, and two in Alaska. For each location, we used an F-test to test the null hypothesis that variances did not differ between HCN and CRU data, and a Pearson's correlation coefficient to compare the year to year variability in precipitation. The two analyses were conducted for an early period (the first 10–20 years for which station data were available) and a late period (the last 20 years for which station data were available). The data from HCN and CRU were significantly and positively correlated for both time periods (table 2). Variance was significantly
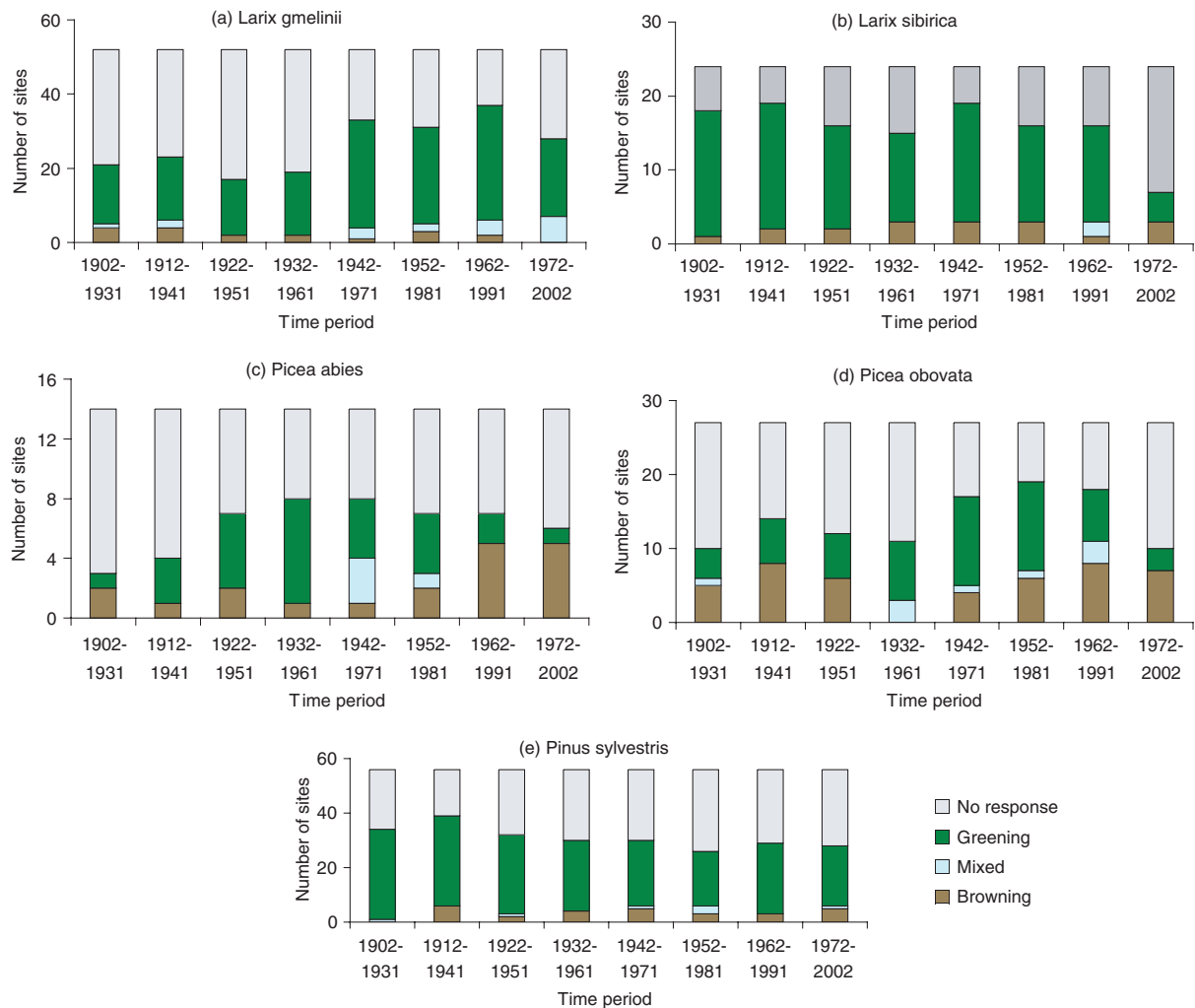
Figure 2. Number of sites exhibiting the four temperature response types for each Eurasian species.

($P < 0.05$) lower in CRU than in HCN data during the early period at one site, and during the late period at a second site, suggesting that although the CRU data might in some cases suffer from reduced variance this effect is unlikely to be reflected as a systematic bias in time (table 2). Our analyses did not, therefore, indicate any widespread systematic bias in the CRU data that might have resulted from interpolation effects.

We defined a 19-month climate window, extending from April of the year prior to the growth year to October of the growth year. Because our climate window begins in the year prior to the growth year, 1902 was the first year of analysis. We used one precipitation variable (total precipitation) and three temperature variables (average minimum, mean, and average maximum temperature) for each month.

2.3. Statistical analyses

We used a moving window correlation approach to describe changes in growth–climate response over time. We defined eight 30-year time periods, lagged by 10 years: 1902–1931, 1912–1941, 1922–1951, 1932–1961, 1942–1971, 1952–1981, 1962–1991, and 1972–2002. Because the end date of each

chronology varied, the actual length of the final analysis period ranged from 23 to 31 years. Our use of a 30-year time window represented a compromise between the need to have a sufficient number of distinct time windows in the analysis period and the need to maintain a sufficient length of each time window that robust correlations could be detected. For each site and time period, we calculated correlation coefficients between tree growth and the 76 climate variables (19 months × 4 variables). As this approach involves multiple tests on the same data, we used a more conservative significance level of $P < 0.01$ as our criterion for rejecting the null hypothesis. The climate response function of each site during each time period was categorized into one of four response types: no response (no significant correlation with temperature variables), greening (more than two-thirds of all significant correlations with temperature were positive), browning (less than one-third of all significant correlations with temperature were positive), and mixed (between one-third and two-thirds of significant correlations with temperature were positive). Our primary response variable is thus frequency of each response type.
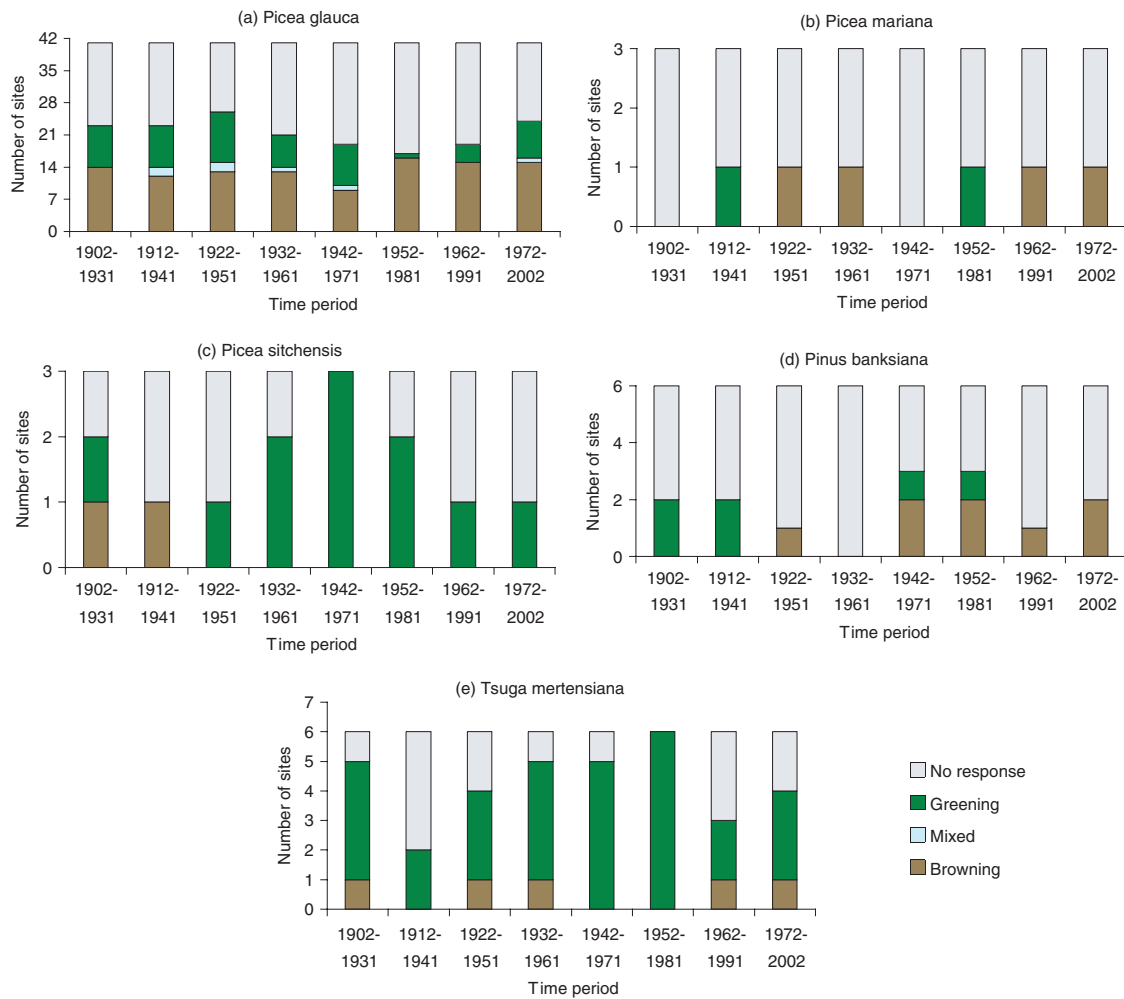
Figure 3. Number of sites exhibiting the four temperature response types for each North American species.

The distribution of climate responses among species (hypothesis 1) was tested for each time period using a χ^2 contingency table. Expected values were determined under the null hypothesis that each response type occurred with an equal relative frequency in each species.

The temporal stability of climate responses (hypothesis 2) was assessed using linear regression. Because replication varied widely among species (table 1), we calculated the proportion of sites browning and greening during each time period for each species, and averaged these values across all species to produce an overall mean proportion of sites browning and greening during each time period. These were the dependent variables in the analysis. The independent variables were either time (prediction 1; start year of the 30-year time period) or temperature (prediction 2). For a temperature variable in this analysis, we calculated growing-year (October–September) temperature anomalies (relative to the 1902–2002 growing-year mean temperature) from the CRU data.

We tested the first prediction of hypothesis 3, that the frequency of browning would be greater at the warm than

at the cool end of a species' range, by classifying each site as 'warm' or 'cool' based on its normalized summer (June–August) temperature. Summer temperatures were normalized relative to the mean summer temperature of all sites occupied by a species, and sites were classified as cool (normalized temperature < 0) or warm (normalized temperature > 0). Tree-ring samples are not taken from across a species' entire thermal niche, so our designations of 'warm' and 'cool' are relative terms and do not define in any absolute sense the warmest or coolest half of a species' range. We used a Mann–Whitney U-test to test the null hypothesis that the frequency of browning would not differ between warm and cool sites. We tested the second prediction of hypothesis 3 using a t-test to compare the normalized summer temperature at sites that never experienced browning and those in which browning occurred at least once.

Predictions 1 and 2 of hypothesis 4 were tested using the same methodology, except that annual precipitation was the climate variable; sites were categorized as 'wet' or 'dry' based on normalized annual precipitation. To test prediction 3, we classified each site into one of four climate regimes
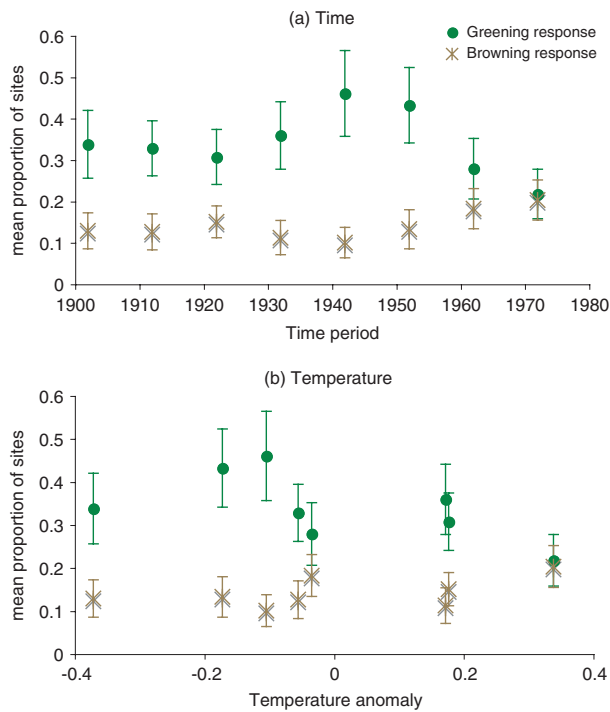
Figure 4. Mean (±1 standard error, $n = 10$ species) proportion of sites browning or greening and (a) time or (b) temperature anomaly. Temperature anomaly is the average temperature anomaly for each 30-year time period (see section 2.3).

(cool/wet, cool/dry, warm/wet, warm/dry) based on normalized temperature and precipitation, and used a Kruskal–Wallis test to assess the null hypothesis that the frequency of browning did not differ among those categories.

3. Results

3.1. Hypothesis 1: climate response types are evenly distributed across species

The frequency of the four types of temperature response varied significantly among species during all time periods (figures 2 and 3, table 3). Although our categories of temperature responses do not distinguish between responses to minimum, mean, and maximum temperature, we found that within a species patterns of response were highly correlated among the three variables (e.g., sites with a positive response to minimum temperature in a given time period tended to also respond positively to maximum and mean temperature; data not shown). Five species had a higher-than-expected frequency of browning and/or a lower-than-expected frequency of greening: *Picea abies* (figure 2(c)), *Picea glauca* (figure 3(a)), *Picea mariana* (figure 3(b)), *Picea obovata* (figure 2(d)), and *Pinus banksiana* (figure 3(d)). Five species had a higher-than-expected frequency of greening or a lower-than-expected frequency of browning: *Larix gmelinii* (figure 2(a)), *Larix sibirica* (figure 2(b)), *Picea sitchensis* (figure 3(c)), *Pinus sylvestris* (figure 2(e)), and *Tsuga mertensiana* (figure 3(e)).

Table 3. Results of χ^2 goodness-of-fit tests testing the null hypothesis that the four climate responses occurred with equal frequency in all species.

Time period	χ^2	df	P
1902–1931	70.59	27	<0.001
1912–1941	53.91	27	0.002
1922–1951	50.46	27	0.004
1932–1961	63.79	27	<0.001
1942–1971	53.27	27	0.002
1952–1981	64.93	27	<0.001
1962–1991	74.28	27	<0.001
1972–2002	64.25	27	<0.001

3.2. Hypothesis 2: browning has become more common as it has warmed since 1900

There was no significant trend in the overall frequency of greening and browning across all eight time periods, but the highest frequency of browning and lowest frequency of greening occurred during the most recent (and warmest) time period (figure 4(a); greening, $R^2 = 0.052$, $F = 0.327$, $df = 1$, $P = 0.588$; browning, $R^2 = 0.375$, $F = 3.607$, $df = 1$, $P = 0.106$). From 1942 onwards, there was a significant negative trend in the frequency of greening ($R^2 = 0.937$, $F = 29.612$, $df = 1$, $P = 0.032$, $\beta = -0.968$), and a significant positive trend in the frequency of browning ($R^2 = 0.979$, $F = 93.874$, $df = 1$, $P = 0.010$, $\beta = 0.990$). Neither browning (figure 4(b); $R^2 = 0.248$, $F = 1.973$, $df = 1$, $P = 0.210$) nor greening (figure 4(b); $R^2 = 0.306$, $F = 2.643$, $df = 1$, $P = 0.155$) was significantly related to northern hemisphere temperature anomalies.

3.3. Hypothesis 3: browning is a direct response to temperature stress

The hypothesis that browning is a response to direct temperature stress was supported for at least some of the species. The median frequency of browning was significantly greater in warm than cool sites when tallied over all species (figure 5(a); $U = 5331$, $n = 232$, $P = 0.004$), and for *Picea glauca* (figure 5(b), $U = 91.5$, $P = 0.002$, $n = 27$), *Picea obovata* (figure 5(c), $U = 40.5$, $P = 0.012$, $n = 27$), and *Pinus sylvestris* (figure 5(d), $U = 231.5$, $P = 0.003$, $n = 56$). The median frequency of browning did not differ between warm and cool sites for the remaining species.

The mean normalized summer temperature of sites that never experienced a browning response (-0.346 ± 0.1588, $n = 111$) was significantly lower than that of sites that experienced browning during at least one time period (0.317 ± 0.2036, $n = 121$; $t = 2.573$, $df = 221.269$, $P = 0.011$). This pattern also held for *Larix sibirica*, *Picea glauca*, and *Pinus sylvestris* (table 4). The mean normalized summer temperature did not differ between browning and non-browning sites for the remaining species.

3.4. Hypothesis 4: browning is associated with moisture stress

The median frequency of browning did not differ between wet and dry sites overall ($U = 6313$, $P = 0.713$, $n = 232$), nor
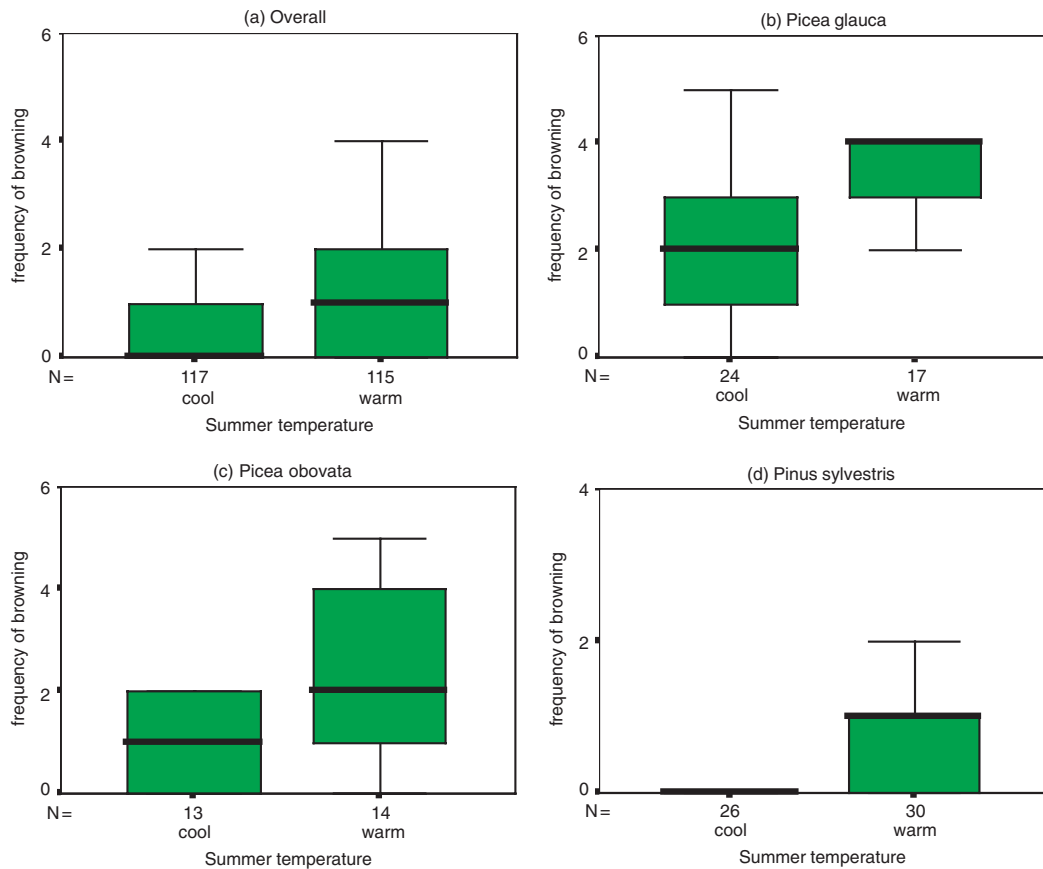
Figure 5. Frequency of browning events at cool and warm sites (see section 2.3). The bold line indicates the median value. The lower and upper limits of the box represent the first and third quartiles. The whiskers indicate the 10th and 90th percentiles. Sample sizes (number of sites) are indicated under the x-axis.

Table 4. Mean summer temperature of sites that have never experienced browning, and those in which browning has occurred in at least one time period. Values are mean ± 1 standard error.

	Mean summer temperature (°C) of sites in which:		
Species	Frequency of browning = 0	Frequency of browning > 0	t-test results
Larix gmelinii	9.48 ± 0.248	9.44 ± 0.494	$t = 0.067, df = 50, P = 0.947$
Larix sibirica	11.66 ± 0.423	13.62 ± 0.717	$t = 2.499, df = 22, P = 0.020$
Picea abies	15.35 ± 1.140	14.58 ± 0.562	$t = 0.685, df = 12, P = 0.506$
Picea glauca	9.23 ± 0.374	10.53 ± 0.528	$t = 2.019, df = 24.335, P = 0.055$
Picea mariana	(All sites have experienced browning at least once)		
Picea obovata	10.92 ± 0.624	11.83 ± 0.352	$t = 1.234, df = 25, P = 0.229$
Picea sitchensis	11.49 ± 0.731	10.67	No test possible
Pinus banksiana	13.88 ± 0.305	14.07 ± 0.157	$t = 0.552, df = 4, P = 0.610$
Pinus sylvestris	12.62 ± 0.334	14.08 ± 0.36	$t = 2.882, df = 54, P = 0.006$
Tsuga mertensiana	9.58 ± 0.904	10.49 ± 0.736	$t = 0.778, df = 4, P = 0.480$

for any individual species (all $P > 0.05$). The normalized annual precipitation did not differ significantly between sites at which browning had occurred at least once and those at which browning never occurred, either overall ($t = 0.636, df = 230, P = 0.525$) or for any individual species (all $P > 0.05$).

The median frequency of browning differed significantly among the climate regimes (cool/wet, cool/dry, warm/wet, warm/dry) overall, and for three species. In two of these cases, the significant result was driven by the effect of temperature alone: the median frequency of browning was greatest in warm sites, regardless of precipitation, both overall (figure 6(a); $H = 9.435, df = 3, P = 0.024$) and for *Picea glauca* (figure 6(b); $H = 11.057, df = 3, P = 0.011$). In the remaining two species, however, an interaction between temperature and precipitation consistent with hypothesis 4 was indicated. In *Picea obovata*, browning occurred most frequently in warm
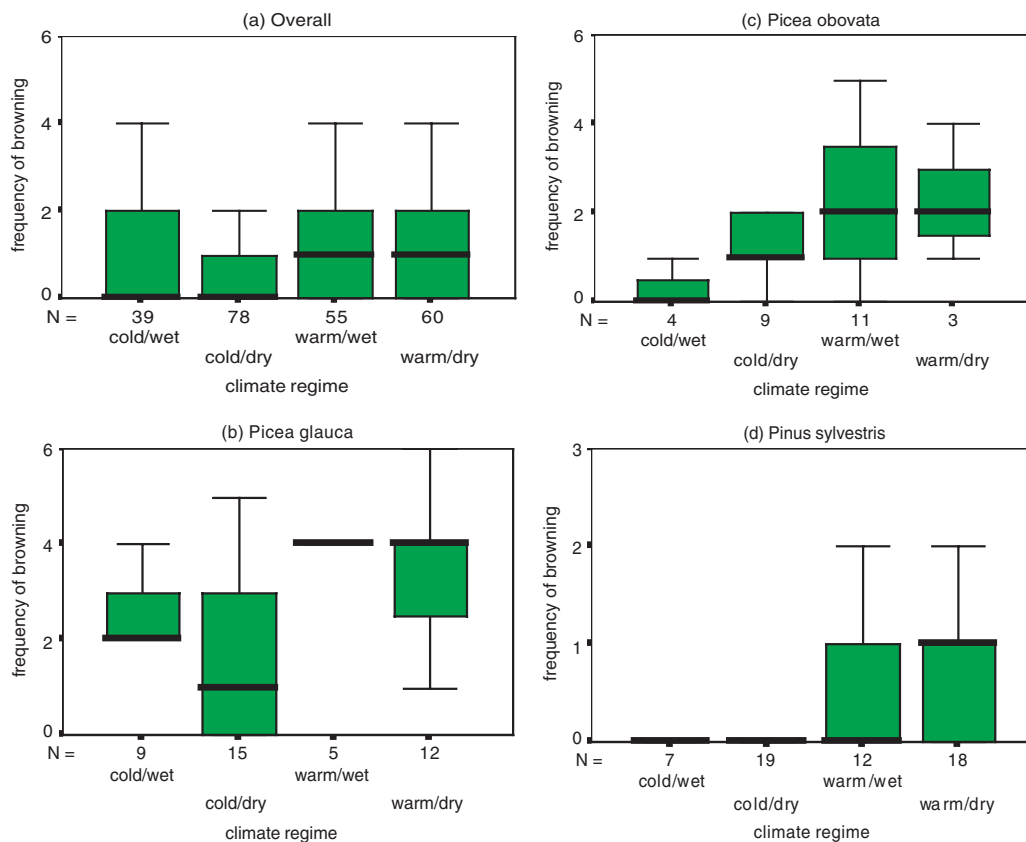
Figure 6. Frequency of browning events at sites in four climate regimes (section 2.3); boxes and whiskers are as defined in figure 5.

sites (regardless of precipitation), but within cool sites the median frequency of browning was greater in dry than in wet locations (figure 6(c); $H = 8.655, df = 3, P = 0.034$). The frequency of browning in *Pinus sylvestris* was greatest in warm/dry sites relative to sites in all other climate regimes (figure 6(d); $H = 10.739, df = 3, P = 0.013$).

4. Discussion

4.1. Climate responses differ among species

Although all response types occurred in all species, inverse responses to temperature were concentrated in five species (all members of the genus *Picea* except for *Picea sitchensis*, plus *Pinus banksiana*). The prevalence of browning among the boreal species of the genus *Picea* is striking: the only *Picea* species in which browning did not occur more frequently than expected is *Picea sitchensis*, which is found only in coastal areas of southern Alaska at the northern edge of the coastal temperate rain forest. Despite this taxonomic distinction, there is substantial overlap in ecological traits between those species with higher-than-expected frequencies of browning and those with lower-than-expected frequencies of browning. Both groups contain species tolerant of permafrost-affected soils (e.g. *Picea glauca*, *Picea mariana*, *Larix gmelinii*), and species intolerant of such soils (*Pinus sylvestris* and *Picea abies*). Drought tolerance does not differ between the two groups

(Niinemets and Valladares 2006; data not shown). Both include Eurasian and North American species, and both include species that occupy locations prone to pollution (e.g. *Picea abies* and *Pinus sylvestris*) and those that occupy more pristine locations (e.g. *Picea glauca* and *Larix gmelinii*).

The only clear distinction between the two groups of species is a geographical one, and this might provide some insight into potential causes of inverse temperature responses. In North America, species with higher-than-expected frequencies of browning occur in dry continental interiors, and are absent from wet coastal locations, suggesting moisture stress might contribute to the browning response. In Eurasia, species with higher-than-expected frequencies of browning are found in more pollution-affected areas of western Siberia and north-eastern Europe, while species with a lower-than-expected frequency of browning tend to be more common in the more pristine regions of central and eastern Siberia. Although the mechanistic explanation for greater browning in some species (particularly members of the genus *Picea*) than others remains unknown, the distinct distribution of these taxa suggests that an understanding of these patterns would be a fruitful area of future research.

A final factor that might influence the frequency with which different climate responses were detected is the difference among species in chronology end dates. The *Larix* chronologies in particular suffer from a reduced sample size after the early 1990s: 21 of the 24 *Larix sibirica* chronologies

and 34 of the 52 *Larix gmelinii* chronologies had an end year earlier than 1992. It is thus possible that browning rates in these species during the most recent time period could be substantially underestimated; this analysis of species differences in climate response should thus be updated as updated chronologies become available.

4.2. Prevalence of browning has increased over time

The frequency of inverse responses to temperature varied significantly among species. Our results indicate that the frequency of these responses also varied significantly over time. Since the 1940s, boreal forest trees at an increasing proportion of sites responded negatively to warmer temperatures. This finding is consistent with both the wealth of tree-ring studies that have demonstrated a weakening or changing relationship with temperature in recent decades (e.g. Briffa *et al* 1998a, 1998b, D'Arrigo *et al* 2004, 2007, Jacoby and D'Arrigo 1997, Jacoby *et al* 1999, 2000, Lloyd and Fastie 2002, Wilmking *et al* 2004, 2005), and with the downward trend in satellite–NDVI data observed for some boreal areas, particularly after 1990 (Bunn *et al* 2005, Goetz *et al* 2005, Bunn and Goetz 2006). Our results thus indicate that inverse, temporally unstable responses to temperature are a widespread phenomenon, occurring in all species and in virtually all geographic locations in the boreal forest during the 20th century. The finding of widespread temporal instability in climate response clearly poses a significant challenge to attempts to use tree rings to reconstruct climate back in time, as it suggests that the response of many—if not most—boreal trees to climate is quite plastic through time, and statistical models developed for one time period may not adequately describe the response of tree growth to climate during another time period. To some extent, the effects of this temporal instability can be dealt with through careful selection of chronologies (see, e.g., Wilson *et al* 2007); indeed, climate response at some of our sites was relatively stable through time, and historical climate inferences based on these sites are likely to be comparatively robust. However, if, as our data indicate, plasticity in the face of climate variation is a characteristic of most boreal species, the possibility remains that varying climate responses may have occurred during previous time periods, even at sites at which climate response is stable during the 20th century. This possibility increases the importance of basing climate reconstructions on large networks of sites representing multiple species (which may increase the likelihood of detecting past episodes of temporal instability from unexpectedly divergent growth trends), on multiple proxy data sources, and statistical models that incorporate interacting and non-linear variables on tree growth.

Two categories of potential explanations for changing patterns of tree response to temperature exist: non-climatic causes, in which some factor independent of temperature has changed tree growth, and climatic factors, in which the changing climate has, itself, caused a change in growth/climate relationships. This study was designed specifically to address two climatic causes: temperature-mediated drought stress and direct temperature stress.

Drought stress, associated with the higher evaporative demands experienced at warmer temperatures, has been frequently invoked as an explanation for inverse growth responses to temperature (Barber *et al* 2000, Lloyd and Fastie 2002). Our data provided only limited support for this hypothesis, however. The frequency of browning did not differ between wet and dry sites within each species' range, and there was no difference in annual precipitation between sites in which the browning response occurred frequently and those in which it did not. We found evidence in only two of seven species for higher rates of browning in dry sites. In sites occupied by *Picea obovata*, the frequency of browning was higher in cool/dry than in cool/wet sites, perhaps suggesting that moisture stress might be a factor towards the northern (cool) end of the species' range. In *Pinus sylvestris*, the median frequency of browning was zero in three of the four climate regimes: only in warm/dry sites did it rise above zero, suggesting that the direct effects of rising temperatures might be exacerbated by moisture stress in this species.

One other aspect of our analysis, however, argues for at least a limited role for moisture stress in explaining changing growth responses to climate. In North America, the species in which browning was particularly prevalent (*Picea glauca, Picea mariana*, and *Pinus banksiana*) are all distributed within the drier continental interior. The coastal species (*Tsuga mertensiana* and *Picea sitchensis*) both experienced higher-than-expected frequencies of greening. The near-absence of browning among species occupying the very wet climates along the Alaskan coastline, and its prevalence among species occupying the much drier continental interior, is consistent with the hypothesis that this response arises from moisture stress.

Our inferences with respect to moisture are limited by our choice of measures of site water balance, as annual precipitation has limits as a descriptor of actual moisture availability. Permafrost, for example, might strongly influence the water balance of a site by providing an alternative water source during dry summers; it has been established, for example, that *Larix* tolerates summer drought by virtue of its ability to use moisture from thawing permafrost (Sugimoto *et al* 2002). The failure to identify a strong association between precipitation and browning thus leaves open the possibility that browning might be related to some other measure of site water balance.

Direct temperature stress results as temperatures rise above the range of a species' physiological optima; this hypothesis predicts, therefore, that inverse growth responses to temperature should be more likely in the warmest sites, which are closest to a species' upper thermal limits. We find support for this prediction in our data: browning did occur more frequently in sites at the warmer end of a species' range. 56% of the sites that fell within the cool half of a species' sampled range *never* experienced browning, compared to only 39% of the sites that fell within the warm half. Evidence in support of the direct temperature stress hypothesis was strongest in four species: *Larix sibirica, Picea glauca, Picea obovata*, and *Pinus sylvestris*. In sites occupied by *Larix sibirica*, sites at which browning had occurred had a mean

summer temperature almost 2 °C higher than sites at which browning never occurred. In *Picea glauca*, *P. obovata*, and *Pinus sylvestris*, the frequency of browning in warm sites was almost twice that of cool sites. In sites occupied by *Picea glauca* and *Pinus sylvestris*, the summer temperature of sites at which browning occurred at least once was significantly greater than in those at which browning never occurred. Our results are thus consistent, both overall and for these four species, with the hypothesis that changing growth–climate relationships reflect the direct effects of temperature stress as temperatures exceed the upper limits of the optimal range.

Although our study was not designed to specifically test non-climatic explanations, three of these bear particular mention here. First, the possibility cannot be eliminated that some of the increased incidence of browning in recent decades is due to artifacts of standardization, which may distort growth trends at the end of tree-ring chronologies (Melvin 2004). The increased prevalence of browning substantially predates the end of the chronologies, however, so we assume that artifacts of standardization do not fully explain the increased prevalence of browning. In addition, because we used a uniform standardization procedure on all chronologies, these 'end effects' are unlikely to explain interspecific differences in the prevalence of browning. Second, air pollution has been invoked as an explanation for growth declines in parts of north-western Russia that are near pollution sources (large urban areas, smelters (e.g. Lawrence *et al* 2005, Lopatin *et al* 2005)) or affected by SO$_2$ deposition (Wilson and Elling 2004). We found that browning was prevalent both in areas likely to be affected by pollution (e.g. sites near heavily populated regions of north-western Russia and Fennoscandia) and in relatively pristine sites far from pollution sources (e.g. north-western and central Siberia, Alaska, north-western Canada), suggesting that air pollution is an unlikely explanation for the overall increase in the prevalence of browning. However, the higher-than-expected prevalence of browning in species dominating pollution-prone areas of eastern Europe and north-western Russia suggests that this explanation should not be disregarded as a contributor to browning at some sites.

A third non-climatic explanation for the divergence of tree growth and temperature was suggested by D'Arrigo *et al* (2007), who proposed that global dimming, the reduction in incident solar radiation resulting from increasing concentrations of dust and aerosols in the atmosphere, might explain declines in tree growth in recent decades. Although many of our sites are from open canopy forests where competition for light is not an important control of growth, according to this hypothesis, declines in light levels might affect tree growth by reducing growing season length in high-latitude forests, where a low sun angle already leads to relatively low irradiance. Reduced solar radiation should have the largest effect on the *least* shade-tolerant species, as these species typically have higher light compensation points and are most responsive to declines in irradiance. Our results contradict this hypothesis in one important respect. Four of the five species in which browning occurred at a relatively high frequency in our study (*Picea abies*, *P. glauca*, *P. mariana*, and *P. obovata*) are quite shade tolerant compared to the other

species in which browning occurs less frequently: together they constitute four of the five most shade-tolerant species included in this analysis (Niinemets and Valladares 2006). Only hemlock, *Tsuga mertensiana*, is more shade tolerant. The prevalence of browning among the *most* shade-tolerant species, and its rarity among the least shade tolerant, thus argues against this hypothesis.

In summary, our analysis of a circumpolar network of tree-ring chronologies indicates that tree growth at many boreal sites has declined since the mid-1900s, despite rising temperatures. This phenomenon has occurred in all ten of the species studied, although it has occurred with significantly greater-than-expected frequency in five species: all members of the genus *Picea* except *P. sitchensis*, and *Pinus banksiana*. Our results suggest three likely explanations for the increased prevalence of inverse responses to warming: direct temperature stress, temperature-mediated drought stress, and, in some locations, pollution. It is unlikely, given the large geographic area and broad array of species within the boreal forest, that any single explanation exists to explain declining tree growth. Furthermore, the large number of sites examined here precluded us from making detailed assessments of the role of site-specific factors in controlling climate response, rendering difficult the task of identifying the overarching cause of changing climate responses. Nonetheless, the widespread nature of the problem indicates that a concerted research effort into understanding the relative importance of and synergies among the various potential causal factors is warranted.

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