A Warming-Induced Biome Shift Detected in Tree Growth of Mountain Hemlock [Tsuga mertensiana (Bong.) Carrière] Along the Gulf of Alaska

Authors: Jarvis, Stephanie K., Wiles, Gregory C., Appleton, Sarah N., D'Arrigo, Rosanne D., and Lawson, Daniel E.

A Warming-Induced Biome Shift Detected in Tree Growth of Mountain Hemlock [*Tsuga mertensiana* (Bong.) Carrière] along the Gulf of Alaska

Stephanie K. Jarvis*§
Gregory C. Wiles*
Sarah N. Appleton*
Rosanne D. D'Arrigo† and
Daniel E. Lawson‡

*Department of Geology, The College of Wooster, 1189 Beall Avenue, Wooster, Ohio 44691, U.S.A.
†Tree Ring Lab, Lamont-Doherty Earth Observatory, Columbia University, Palisades, New York 10964, U.S.A.
‡Cold Regions Research and Engineering Lab, 72 Lyme Road, Hanover, New Hampshire 03755, U.S.A.
§Corresponding author. Present address: Department of Geology, Southern Illinois University, 1259 Lincoln Drive, Carbondale, Illinois 62901, U.S.A.
sjarvis@siu.edu

Abstract

Recent observations of divergence between tree growth at high-latitude sites and temperature, as well as the decline of yellow cedar [*Callitropsis nootkatensis* (D. Don) Oerst. ex D.P. Little] in southeast Alaska due to warming, emphasize a need to investigate nonstationary climate response of Alaskan coastal forests to warming in other tree species. Comparison of annual tree growth in mountain hemlock [*Tsuga mertensiana* (Bong.) Carrière] to mean monthly temperature and precipitation data from Sitka, Alaska, from A.D. 1830s to 1990s along an elevational transect reveals nonstationarity in tree growth response to climate that suggests an ongoing biome shift. We observe a marked weakening in the positive relationship between annual growth and warmer growth season temperatures at low-elevation hemlock sites, and a concurrent increase in growth and sensitivity at higher elevations coupled with increased correlation between growth and April precipitation at all sites along our transects. As previously observed with yellow cedar, the mechanism of the hemlock biome shift may be due to an increased susceptibility of roots to damage from late frosts resulting from earlier seasonal loss of protective snowpack.

Introduction

Tree rings are an important paleoclimatic proxy record that has been used to increase our understanding of climatic variability and to reconstruct past climate (Jansen et al., 2007). Dendroclimatology depends on the stationarity of the climate response of trees over time in order to confidently reconstruct past climate. In recent decades divergence, the dissociation between trends in tree growth parameters (e.g. ring width) and climate (Esper and Frank, 2009), has been observed in northern sites that were previously tracking temperature (D'Arrigo et al., 2008). This loss of sensitivity to temperature results in the underestimation of recent warming in reconstructions and presents the possibility of underestimation of similarly warm periods prior to meteorological observation (D'Arrigo et al., 2008; Esper and Frank, 2009).

In addition to divergence, increased temperature and drought conditions have contributed to increased tree mortality in the past decade around the world (Adams et al., 2010). Understanding the response of forests to climatic and environmental changes, especially the possibility of widespread tree mortality, is important for predicting changes in ecosystem functioning, global carbon cycling, regional hydrology, and regional climatology (Adams et al., 2010). One example of contemporary widespread tree mortality in coastal northeast Pacific is the recently observed decline in yellow cedar [*Callitropsis nootkatensis* (D. Don) Oerst. ex D.P. Little], which has been attributed to warming (Hennon et al., 2005; Beier et al., 2008). Using long-term temperature and precipitation data from the Sitka Magnetic Observatory in Sitka, Alaska, Wiles et al. (2012) demonstrated that this decline can be detected as a decreased correlation between ring widths and temperature, beginning with the period of warming marking the end of the Little Ice Age (LIA).

Mountain hemlock [*Tsuga mertensiana* (Bong.) Carrière] is an important late-successional species that provides wildlife habitat and watershed protection in subalpine environments and is under increasing harvest pressure (Ally et al., 2000; Edwards et al., 1993). It is commonly used in tree ring reconstructions due to its temperature sensitivity (e.g., Wilson et al., 2007; Wiles et al., 1998; Peterson and Peterson, 2001; Laroque and Smith, 2005). The northernmost extent of the range of this species is south-central, coastal Alaska, where it occurs from sea level to treeline in pure stands or associated with Sitka spruce [*Picea sitchensis* (Bong.) Carrière] (Gedalof and Smith, 2001).

Although inhabiting different elevations in southeast Alaska, mountain hemlock and yellow cedar share certain physiological characteristics, particularly low root hardiness, that have been implicated in the yellow-cedar decline (Coleman et al., 1992; Schaberg et al., 2008). By comparing growth to summer temperature and winter snowpack, Smith and Laroque (1998) determined that high growth in mountain hemlock is associated with either cool summers and shallow winter snowpack or warm summers and deeper (<4 m) snowpack. This is consistent with what would be expected if trees relied on snowpack for protection against late frosts, as has been suggested for yellow cedar (Beier et al., 2008). A combination of low temperatures and shallow snowpack results in snowpack remaining until the growing season begins, as typically does the combination of high temperatures with a deep snowpack. High temperatures, however, can cause a shallow snowpack to melt before frosts end, resulting in root damage (Schaberg et al., 2008),

while low temperatures and high snowpack delays the growing season (Graumlich and Brubaker, 1986). Here, long-term climate data from Sitka, Alaska, is used to investigate climate-response patterns of mountain hemlock in southeast Alaska at multiple elevations during the duration of the Sitka climate data, from the latter part of the LIA to the 1990s, to determine if the beginning of a yellow-cedar–like shift in climate response can be detected.

Methods

STUDY SITE

Tree-ring sites are located in Glacier Bay National Park and Preserve, Alaska, and in the Tongass National Forest of the Coast Mountain Range near Juneau (Fig. 1). Climate patterns in the area are dominated by the Pacific Decadal Oscillation (PDO), the interdecadally fluctuating first principle component of North Pacific sea surface temperature described by Mantua et al. (1997) and Shulski and Wendler (2007). The mountainous terrain, combined with high precipitation from the Gulf of Alaska, has contributed to extensive glaciation (Tuttle, 1990). The most recent glacial advance in the region occurred during the broadly defined cold period known as the Little Ice Age (LIA) and ended in the late 1800s (Motyka et al., 2007; Mann et al., 1998). Since the LIA, glacial retreat has been prevalent across the Gulf of Alaska region (Conner et al., 2009; Larson et al., 2005; Barclay et al., 2009). In the glaciated areas during the LIA, patches of forest were left on mountains above the glaciers, called glacial refugia (Cooper, 1923). Other areas in the Tongass National Forest were located below the LIA ice limit and are several-hundred-year-old continuous forests.

DATA AND ANALYSIS

We developed six mountain hemlock ring-width chronologies from sites 200 to 800 m above sea level (Fig. 1). Cores were prepared using standard dendrochronological techniques (Stokes and Smiley, 1968; Cook and Kairiukstis, 1990). Each core was sanded with progressively finer sandpaper, and rings were measured to the nearest 0.001 mm using a Velmex measuring system and the program MeasureJ2X. Dating and quality control was confirmed using COFECHA (Holmes, 1983). Visual and graphical comparisons of cores were used to locate locally absent rings in the series. Descriptive statistics for each chronology (Table 1) are reported from the COFECHA chronologies.

To meaningfully compare and average individual series, exactly dated ring-width series were standardized in ARSTAN (Cook, 1985) using the interactive detrending option. A negative exponential curve, which follows the expected growth function of a radially expanding tree, was used to detrend individual series where appropriate. Where an age-related decrease in ring widths with time was not detected, a horizontal mean line was used to avoid adding or removing long-term growth trends. Standardization results in a series of ring width indices that are then averaged to develop a mean site chronology. A Mann-Whitney test was performed to determine significant changes in ring width between the four time periods. As part of this statistical analysis, Levene's Test for Equality of Variances was also performed to detect changes in variability of yearly growth (Levene, 1960).

Monthly temperature and precipitation records from Sitka, Alaska, were obtained from the Global Historical Climatology Network (GHCN) (Peterson and Vose, 1997; Jones and Bradley, 1992). These records cover the years 1832–1993 for temperature and 1842–1990 for precipitation, with incomplete data from 1876 to 1900. Monthly series were divided into four time periods for analysis: LIA: 1832/1842–1876; post-LIA: 1900–1993/1990; first half of the 20th century: 1900–1950; and second half of the 20th century: 1951–1993/1990.

Standardized tree ring chronologies were correlated to temperature and precipitation data from Sitka for the different time periods. For temperature comparisons, the 20-month dendroclimatic year was used (Fritts, 1976), comparing annual ring growth to each month's temperature from the previous March to the current October. The hydrologic year of the previous January to the current August was used for precipitation analysis.

Results

Average mountain hemlock ring-width indices (Fig. 2) increased significantly ($p \leq 0.05$) from the LIA (pre-1876) to the post-LIA (20th century) at the Beartrack (BT) and Juneau Mountain (JM) sites. A significant decrease in growth from the first to the second half of the 20th century was observed at BT, Son of Repeater (SR), Lemon Creek (LC), and McGinnis Trail (MT), while an increase in ring width during this time was observed at JM. The mid-elevation site Repeater Station (RS) experienced no significant change in growth over either time step. Average ring indices increased in variability from the LIA to the post-LIA at high-elevation sites SR and JM (Levene's Test for Equality of Variances: $p \leq 0.05$) (Table 2).

The significant positive correlation to temperature at low-elevation mountain hemlock sites during the LIA is present at high elevation sites during the second half of the 20th century (Fig. 3). This trend is especially visible for the Glacier Bay sites, where the high-elevation site SR shifts from no significant correlation with February–August temperature during the LIA to a strong positive correlation during the post-LIA interval. In contrast, the lower elevation site BT shows the opposite, while the mid-elevation site RS is significantly correlated to temperature throughout all time periods.

We also examined the responses of tree growth to monthly and seasonal precipitation. A significant trend in growth response to seasonal precipitation through the record was not observed. However, an increasing positive response to April precipitation over time is evident at all sites (Fig. 4).

Discussion

The low-elevation mountain hemlock sites (LC and BT; Fig. 3) that were positively correlated with temperature during the LIA show a steadily weakening response to temperature over the past 100 years. While trees at low elevations are becoming less sensitive to temperature, trees at mid-elevation sites RS and MT remained consistently positively correlated with temperature for each time period. Those at the highest elevation site, SR, have transitioned from no significant correlation during the LIA to strong positive correlations toward the end of the 20th century (Fig. 3).
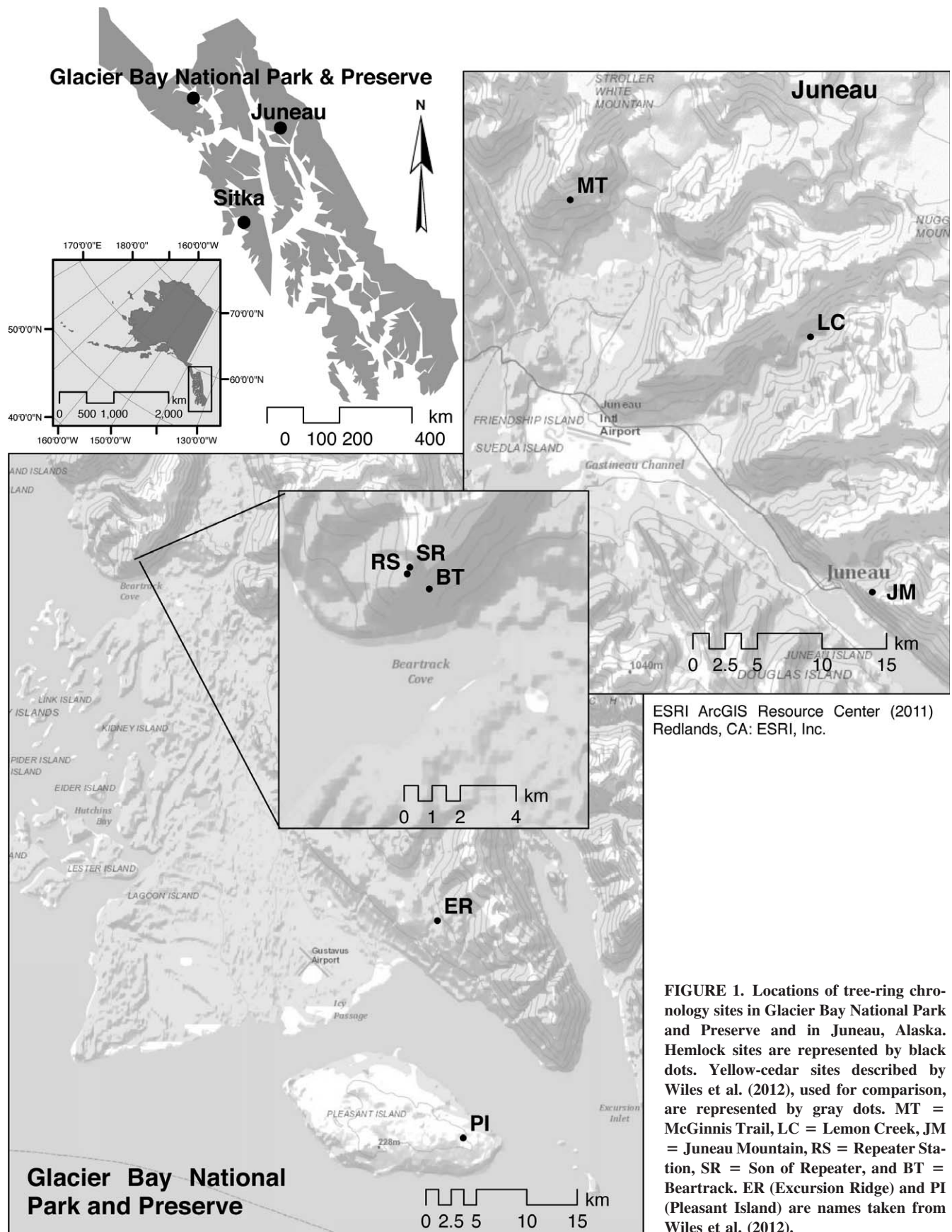
FIGURE 1. Locations of tree-ring chronology sites in Glacier Bay National Park and Preserve and in Juneau, Alaska. Hemlock sites are represented by black dots. Yellow-cedar sites described by Wiles et al. (2012), used for comparison, are represented by gray dots. MT = McGinnis Trail, LC = Lemon Creek, JM = Juneau Mountain, RS = Repeater Station, SR = Son of Repeater, and BT = Beartrack. ER (Excursion Ridge) and PI (Pleasant Island) are names taken from Wiles et al. (2012).

TABLE 1

Chronology descriptions.

	Site	Lat/Long	Elevation (m)	Period of Record	Trees/ Cores	Series Intercorrelation	Average Mean Sensitivity	Auto-correlation	Standard Deviation (filtered)
Glacier Bay	Beartrack (BT)	58°36′39.52″N 135°51′32.05″W	449	1535–2005	26/38	0.548	0.249	0.789	0.327
	Repeater Station (RS)	58°36′48.41″N 135°51′57.54″W	721	1562–2009	44*/78	0.672	0.308	0.679	0.378
	Son of Repeater (SR)	58°36′52.54″N 135°51′54.58″W	766	1618–2009	17/31	0.650	0.404	0.681	0.473
Juneau	Lemon Creek (LC)	58°23′23.56″N 134°25′41.69″W	222	1450–2009	34*/87	0.489	0.265	0.779	0.343
	McGinnis Trail (MT)	58°26′22.65″N 134°35′43.46″W	526	1380–1999	29/45	0.632	0.288	0.729	0.358
	Juneau Mountain (JM)	58°17′49.10″N 134°23′6.86″W	538	1557–1999	11/18	0.624	0.275	0.778	0.346

*Duplicated sampling may have occurred because of multiple sampling trips resulting in fewer individuals than stated.

This trend is more apparent in Glacier Bay than Juneau, a difference that may be attributed to local climatic conditions and is perhaps associated with the ongoing 120-km retreat of ice from the bay (Larson et al., 2005). The increase in annual growth variation at SR and JM (both treeline sites), coupled with a strengthening relationship with warmer temperatures and an increase in growth at JM, suggest that trees at these sites have been released from growth-stunting stresses (i.e. low temperature) and are now tracking the rising air temperature (Fritts, 1976; Holtmeier and Broll, 2007).

Wiles et al. (2012) found a shift in the relationship between yellow-cedar growth and January–July temperature since the LIA. A slight negative correlation to temperature was present at the low-elevation site at the end of the LIA, while the higher-elevation site was significantly positively correlated to temperature. By the second half of the 20th century both sites had become strongly negatively correlated to temperature. This strong negative response to warming by the yellow cedar together with a positive relationship with total March and April precipitation suggested that the yellow-cedar sites may be susceptible to decline and is consistent with the hypothesis that the yellow-cedar decline is linked to decreased snowpack (Wiles et al, 2012).

While no mountain hemlock sites have become negatively correlated to temperature as the yellow cedars have, the patterns in growth response to climate observed over the 20th century at the low-elevation mountain hemlock sites resemble those observed by Wiles et al. (2012) from the LIA to the first half of the 20th century in the higher elevation cedar site in Glacier Bay. This suggests that the change in growth response of both species is related and elevationally determined, the effects traveling upslope with time and warming. The yellow-cedar decline has been linked to decreased snowpack since the LIA, which exposes roots to damaging spring frosts (Beier et al., 2008; Schaberg et al., 2008). As mountain hemlocks also have low root hardiness (Coleman et al., 1992), it is likely that they are also being affected by a decrease in snowpack with warming. This mechanism is supported by the patterns in growth response to temperature and also by the change

in growth response to precipitation (Fig. 4). April precipitation has become more important for annual growth at all six sites since the end of the LIA, suggesting an increased reliance on late spring snowfall.

It is expected that treeline would be advancing with warming. Although a release in growth was found at the high elevation sites, no regeneration data were collected. If mountain hemlocks are in the beginning of a cedar-like decline at the lower extent of their range, as suggested by our findings, and not advancing at the upper extent, then the range of this species will diminish and the species as a whole may begin to decline. If, however, regeneration is occurring and treeline is advancing at a rate equal to or greater than the rate of decline at low elevations, then a biome shift will occur in response to climatic warming. If this is the case, the habitat range of hemlocks will move up in elevation, potentially resulting in habitat fragmentation as the lower extent of the range moves out of valleys and up mountain sides and in habitat loss as the upper habitat range extends beyond the elevation of the mountains.

This study provides data that are consistent with the modeled findings of Laroque and Smith (2003). Using forecasted temperatures and a biologically based deterministic tree growth model, Laroque and Smith (2003) modeled future growth of multiple tree species in British Columbia (mountain hemlock, yellow cedar, western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), and western hemlock (*Tsuga heterophylla*). Their predictive model indicates that, of these species, mountain hemlock will be most negatively affected by predicted warming, beginning a sharp decline in growth around 2030. They attributed this decline mainly to the projected decrease in future spring precipitation, to which growth in mountain hemlocks is positively correlated at higher temperatures (Smith and Laroque, 1998).

Our results also bear importantly on the application of tree rings as a proxy record of paleoclimate and its application to understanding the projected future changes in climate (Jansen et al., 2007). The basic assumption of dendroclimatology is that trees are stationary in their climatic response and are responding to climatic
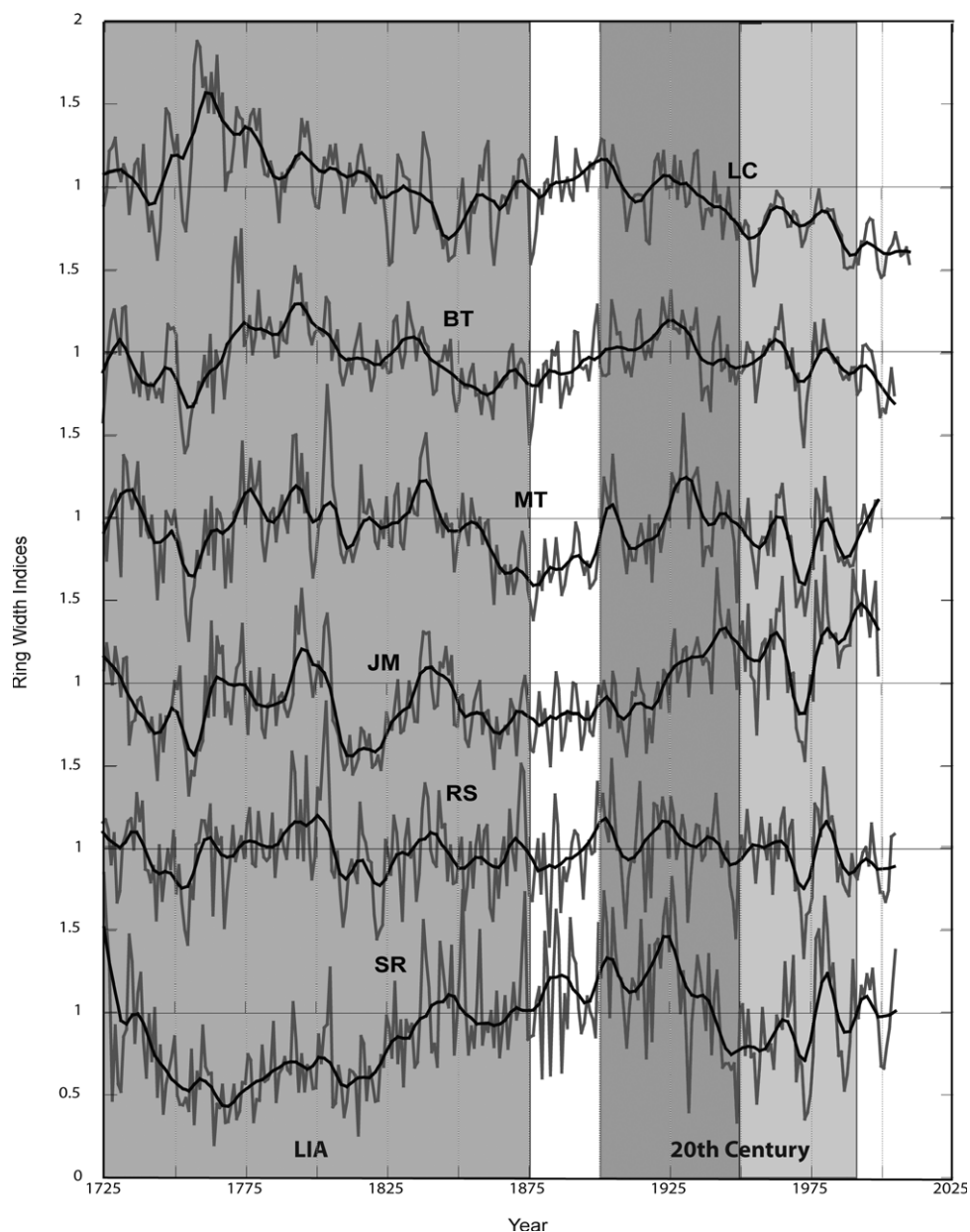
FIGURE 2. Chronologies beginning in 1725. Chronologies are smoothed with a 5% weighted curve and arranged in increasing elevation from the top to the bottom. Shading denotes the time periods compared.

TABLE 2

Mean ring-width indices, rounded to the nearest 0.001 mm, for each time period, and Mann-Whitney test results (_p_ value) for Little Ice Age (LIA)/Post-LIA and 1st/2nd half of 20th century annual growth comparisons. Shaded rows indicate a significant (_p_ < 0.05) change in ring width.

	Site	LIA (1832–1876)	Post-LIA (1900–1993)	_p_	1st half 20th C (1900–1950)	2nd half 20th C (1900–1993)	_p_
Glacier Bay	BT	0.882	0.993	0.001	1.041	0.936	0.006
	RS	0.984	0.997	0.500	1.028	0.961	0.161
	SR	1.023	1.033	0.841*	1.132	0.916	0.002
Juneau	LC	0.890	0.865	0.554	0.969	0.740	0.000
	MT	0.907	0.922	0.736	0.990	0.841	0.002
	JM	0.870	1.102	0.000*	1.031	1.187	0.004

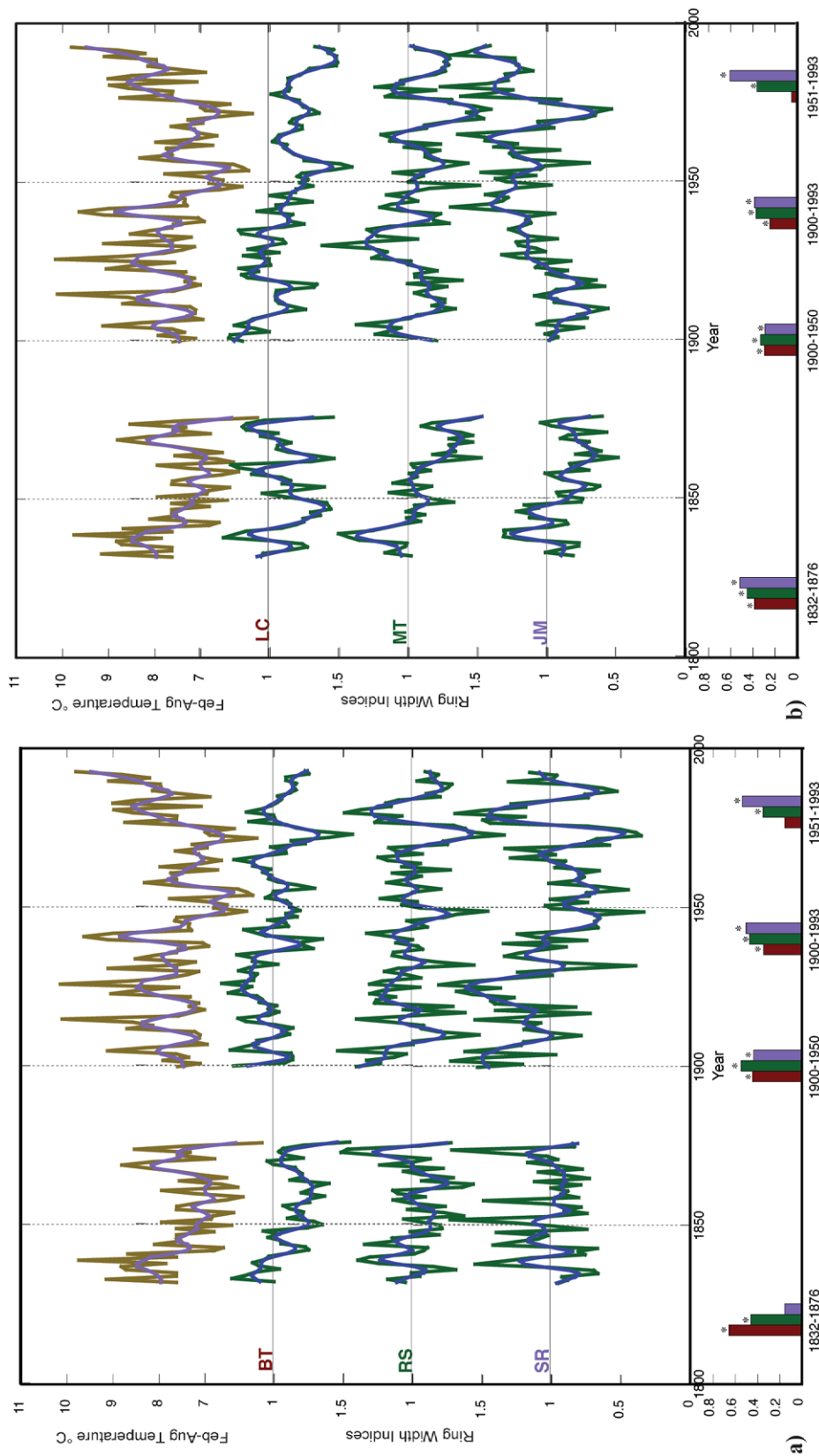*Failed Levene's Test for Equality of Variances. See Table 1 for site names.

FIGURE 3. Average February–August temperature (°C, top) and mountain hemlock ring width indices at (a) Beartrack Mountain transect and (b) Juneau sites, ordered from top to bottom by increasing elevation. Bottom bar graph shows correlation coefficients for the Little Ice Age (LIA) (1832–1876), post-LIA (1900–1993), and first and second halves of the 20th century. Colors of bars correlate to colors of chronology labels. All correlations are significant at $p < 0.05$, indicated with asterisks, except SR during the LIA and BT and LC during 1951–1993.
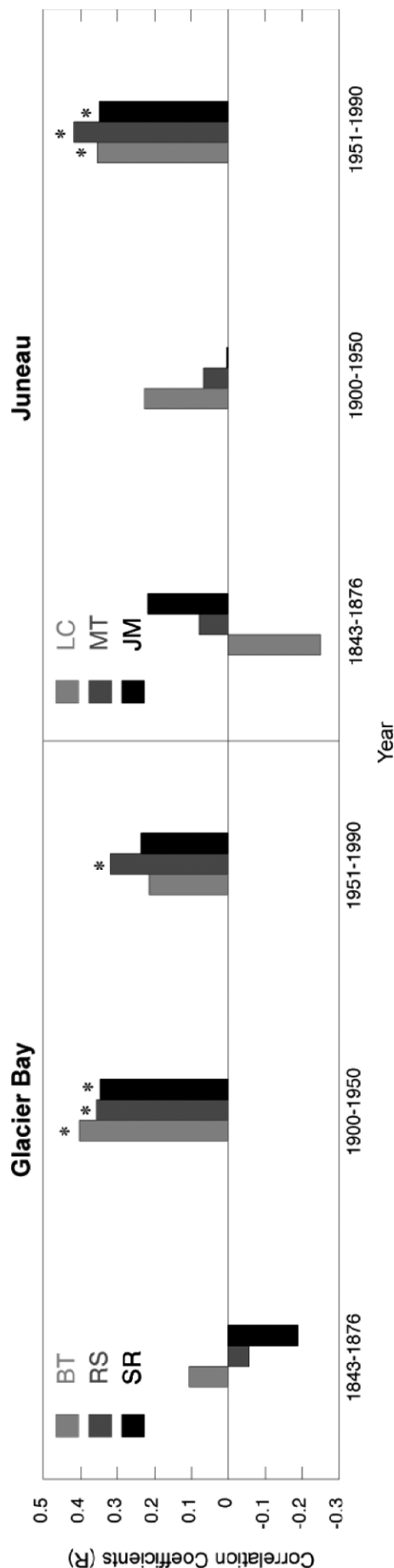
FIGURE 4. Growth correlation to April precipitation at mountain hemlock sites. Asterisks indicate significance at $p < 0.05$.

variables in the same way today as they have in the past. While many of the studies describing diverging chronologies discussed in D'Arrigo et al. (2008) point to drought stress as a probable cause, the timing of divergence in those studies (mid-20th century) is consistent with the decreased correlation between temperature and growth response described in this study. Since few climatic records begin before the 20th century, our understanding of the relationship between climate and tree growth is limited to the relatively warm 20th century, making it difficult to accurately predict past or future climate without more understanding of the growth dynamics of the species being used. For climatic reconstruction, growth response should be relatively stable to decrease the potential for inaccuracy of reconstruction due to changes in the climate-growth response. While high elevation sites are desired for their climatic sensitivity, they are more likely to have experienced a change in dominant stress over the extent of the chronology than sites at a lower elevation. In this study, the mid-elevation sites RS and MT appear to be the most consistently correlated to growth season temperature and would thus be the most appropriate for growth-season temperature reconstruction (Fig. 3).

Conclusion

Mountain hemlocks in southeast Alaska have been shown to be non-stationary in their growth response to climate over the past 200 years. Stands at elevational treeline are becoming more variable in annual growth and positively correlated to temperature, suggesting a growth release at these previously stunted sites, whereas at low-elevation sites the positive correlation of the past between temperature and growth is declining. This negative trend in correlation between temperature and growth at low-elevation mountain hemlock sites during the 20th century is similar to that observed in the declining Alaskan yellow cedar from the LIA through the 20th century. Correlation of mountain hemlock growth to April precipitation at all sites is becoming more positive, suggesting an increased importance of spring snowpack to tree growth. These observations are consistent with the hypothesis that spring snowpack is a critical insulating layer for root protection needed to maintain healthy tree growth in mountain hemlock.

Acknowledgments

References Cited

Adams, H. D., Macalady, A. K., Breshears, D. D., Allen, C. D., Stephenson, N. L., Saleska, S. R., Huxman, T. E., and McDowell, N.

G., 2010: Climate-induced tree mortality: Earth system consequences. *Eos (Transactions, American Geophysical Union)*, 91: 153–154.

Ally, D., El-Kassaby, Y., and Ritland, K., 2000: Genetic diversity, differentiation and mating systems in mountain hemlock (*Tsuga mertensiana*) across British Columbia. *Forest Genetics*, 7: 97–108.

Barclay, D. J., Wiles, G. C., and Calkin, P. E., 2009: Holocene glacier fluctuations in Alaska. *Quaternary Science Reviews*, 71: 22–26.

Beier, C. M., Sink, S. E., Hennon P. E., D'Amore, D. V., and Juday, G. P., 2008: Twentieth-century warming and the dendroclimatology of declining yellow-cedar forests in southeastern Alaska. *Canadian Journal of Forest Research*, 38: 1319–1334.

Coleman, M. D., Hinckley, T. M., McNaughton, G., and Smit, B. A., 1992: Root cold hardiness and native distribution of subalpine conifers. *Canadian Journal of Forest Research*, 22: 932–938.

Conner, C., Streveler, G., Post, A., Monteith, D., and Howell, W., 2009: The neoglacial landscape and human history of Glacier Bay, Glacier Bay National Park and Preserve, southeast Alaska, USA. *The Holocene*, 19: 381–393.

Cook, E. R., 1985: A time series analysis approach to tree-ring standardization. Ph.D. thesis, University of Arizona, Tucson, 171 pp.

Cook, E. R., and Kairiukstis, L. A. eds., 1990: *Methods of Dendrochronology*. Dordrecht: Kluwer Academic Publications, 394 pp.

Cooper, W. S., 1923: The recent ecological history of Glacier Bay, Alaska: the interglacial forests of Glacier Bay. *Ecology*, 4: 93–128.

D'Arrigo, R., Wilson, R., Liepert, B., and Cherubini, P., 2008: On the 'Divergence Problem' in northern forests: a review of the tree-ring evidence and possible causes. *Global and Planetary Change*, 60: 289–305.

Edwards, D. G. W., Meagher, M. D., and El-Kassaby, Y. A., 1993: Genetic diversity in mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.). *In* Marshall, V. G. (compiler), *Proceedings Forest Ecosystem Dynamics Workshop*. Canada-British Columbia Partnership Agreement on Forest Resource Development, FRDA II, FRDA Report 210, 68–71.

Esper, J., and Frank, D., 2009: Divergence pitfalls in tree-ring research. *Climate Change*, 94: 261–266.

Fritts, H. C., 1976: *Tree Rings and Climate*. London, New York: Academic Press, 567 pp.

Gedalof, Z., and Smith, D., 2001: Dendroclimatic response of mountain hemlock (*Tsuga mertensiana*) in Pacific North America: *Canadian Journal of Forest Research*, 31: 322–332.

Graumlich, L. J., and Brubaker, L. B., 1986: Reconstruction of annual temperature (1590–1979) for Longmire, Washington, derived from tree rings. *Quaternary Research*, 25: 223–234.

Hennon, P. E., D'Amore, D. V., Zeglen, S., and Grainger, M., 2005: Yellow-cedar decline in the north coast forest district of British Columbia. *U.S. Department of Agriculture Research Note PNW-RN-549*: 1–16.

Holmes, R. L., 1983: Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 43: 69–78.

Holtmeier, F. K., and Broll, G., 2007: Treeline advance—Driving processes and adverse factors. *Landscape Online*, 1: 1–33.

Jansen, E., Overpeck, J., Briffa, K. R., Duplessy, J. C., Joos, F., Masson-Delmotte, V., Olago, D., Otto-Bliesner, B., Peltier, W. R., Rahmstorf, S., Ramesh, R., Raynaud, D., Rind, D., Solomina, O., Villalba, R., and Zhang, D., 2007: Palaeoclimate. *In* Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. L. (eds.), *Climate Change 2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, U.K., and New York: Cambridge University Press, 435–497.

Jones, P. D., and Bradley, R. S., 1992: Climatic variations in the longest instrumental records. *In* Bradley, R. S., and Jones, P. D. (eds.), *Climate since A.D. 1500*. London: Routledge, 246–268.

Laroque, C. P., and Smith, D. J., 2003: Radial-growth forecasts for five high-elevation conifer species on Vancouver Island, British Columbia. *Forest Ecology and Management*, 183: 313–325.

Laroque, C. P., and Smith, D. J., 2005: Predicted short-term radial-growth changes of trees based on past climate on Vancouver Island, British Columbia. *Dendrochronologia*, 22: 163–168.

Larson, C. F., Motyka, R. J., Freymueller, J. T., Echelmeyer, K. A., and Ivins, E. R., 2005: Rapid viscoelastic uplift in southeast Alaska caused by post–Little Ice Age glacial retreat. *Earth and Planetary Science Letters*, 237: 548–560.

Levene, H., 1960: Robust tests for equality of variances. *In* Olkin, I., Ghurye, S. G., Hoeffding, W., Madow, W. G., and Mann, H. B. (eds.), *Contributions to Probability and Statistics: Essays in Honor of Harold Hotelling*. Stanford: Stanford University Press, 278–292.

Mann, D. H., Crowell, A. L., Hamilton, T. D., and Finney, B. P, 1998: Holocene geologic and climatic history around the Gulf of Alaska. *Arctic Anthropology*, 35: 112–131.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., and Francis, R. C., 1997: A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, 78: 1069–1079.

Motyka, R. J., Larsen, C. F., Freymueller, J. T., and Echelmeyer, K. A., 2007: Post Little Ice Age glacial rebound in Glacier Bay National Park and surrounding areas. *Alaska Park Science Journal*, 6: 36–41.

Peterson, D. W., and Peterson, D. L., 2001: Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology*, 82: 3330–3345.

Peterson, T. C., and Vose, R. S., 1997: An overview of the Global Historical Climatology Network temperature database. *Bulletin of the American Meteorological Society*, 78: 2837–2849.

Schaberg, P. G., Hennon, P. E., D'Amore, D. V., and Hawley, G. J., 2008: Influence of simulated snow cover on the cold tolerance and freezing injury of yellow-cedar seedlings. *Global Change Biology*, 14: 1–12.

Shulski, M., and Wendler, G., 2007: *The Climate of Alaska*. Fairbanks: University of Alaska Press, 216 pp.

Smith, D., and Laroque, C. P., 1998: High-elevation dendroclimatic records from Vancouver Island. *In* MacIver, D. C., and Meyer, R. E. (eds.), *Proceedings of the Workshop on Decoding Canada's Environmental Past: Climate Variations and Biodiversity Change during the Last Millennium*. Downsview, Ontario: Environment Canada, Atmospheric Environment Service, 33–44.

Stokes, M. A., and Smiley, T. L., 1968: *An Introduction to Tree-Ring Dating*: Tucson: University of Arizona Press, 73 pp.

Tuttle, S. D., 1990: Glacier Bay National Park and Preserve. *In* Harris, A. G., Tuttle, E., and Tuttle, S. D., (eds.), *Geology of National Parks*: Dubuque, Iowa: Kendall/Hunt Publ. Co., 348–360.

Wiles, G. C., D'Arrigo, R. D., and Jacoby, G. C., 1998: Gulf of Alaska atmospheric-ocean variability over recent centuries inferred from costal tree-ring records. *Climate Change*, 38: 289–306.

Wiles, G. C., Mennett, C. R., Jarvis, S. K., D'Arrigo, R. D., Wiesenberg, N., and Lawson, D. E., 2012: Tree-ring investigations into changing climatic responses of yellow-cedar, Glacier Bay, Alaska. *Canadian Journal of Forest Research*, 42: 814–819.

Wilson, R., Wiles, G., D'Arrigo, R., and Zweck, C., 2007: Cycles and shifts: 1,300 years of multi-decadal temperature variability in the Gulf of Alaska. *Climate Dynamics*, 28: 425–440.

MS accepted January 2013