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Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska

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Abstract. We examined direct and indirect impacts of millennial-scale climate change on fire regimes in the south-central Brooks Range, Alaska, USA, using four lake sediment records and existing paleoclimate interpretations. New techniques were introduced to identify charcoal peaks semi-objectively and to detect statistical differences between fire regimes. Peaks in charcoal accumulation rates provided estimates of fire return intervals (FRIs), which were compared among vegetation zones identified by fossil pollen and stomata. Climatic warming between ca. 15 000–9000 yr BP (calendar years before Common Era [CE] 1950) coincided with shifts in vegetation from herb tundra to shrub tundra to deciduous woodlands, all novel species assemblages relative to modern vegetation. Two sites cover this period and show decreased FRIs with the transition from herb to *Betula*-dominated shrub tundra ca. 13 300–14 300 yr BP ($FRI_{mean} = 144$ yr; 95% CI = 120–169 yr), when climate warmed but remained cooler than present. Although warming would have favored shorter FRIs in the shrub tundra, the shift to more continuous, flammable fuels relative to herb tundra was probably a more important cause of increased burning. Similarly, a vegetation shift to *Populus*-dominated deciduous woodlands overrode the influence of warmer- and drier-than-present summers, resulting in lower fire activity from ca. 10 300–8250 yr BP ($FRI_{mean} = 251$ yr; 95% CI = 156–347 yr). Three sites record the mid-to-late Holocene, when climatic cooling and moistening allowed *Picea glauca* forest–tundra and *P. mariana* boreal forests to establish ca. 8000 and 5500 yr BP, respectively. FRIs in forest–tundra were either similar to or shorter than those in the deciduous woodlands (FRI_{mean} range = 131–238 yr). The addition of *P. mariana* ca. 5500 yr BP increased landscape flammability, overrode the effects of climatic cooling and moistening and resulted in lower FRIs ($FRI_{mean} = 145$ yr; 95% CI = 130–163). Overall, shifts in fire regimes were strongly linked to changes in vegetation, which were responding to millennial-scale climate change. We conclude that shifts in vegetation can amplify or override the direct influence of climate change on fire regimes, when vegetation shifts significantly modify landscape flammability. Our findings emphasize the importance of biophysical feedbacks between climate, fire, and vegetation in determining the response of ecosystems to past, and by inference, future climate change.

Key words: Alaska (USA); arctic; boreal forest; charcoal analysis; climate change; deciduous woodland; fire history; landscape flammability; pollen analysis; shrub tundra; tundra.

Introduction

Recent warming in northern high latitudes (Overpeck et al. 1997, Serreze et al. 2000, ACIA 2004) has initiated a variety of changes in vegetation and fire regimes, including population expansion and increased growth of trees and shrubs (Lloyd 2005, Tape et al. 2006) and increased area burned across boreal forests (Kasischke and Turetsky 2006, Soja et al. 2007). Although the response of fire regimes to climate change is complex and will vary regionally (Flannigan et al. 1998, Bergeron et al. 2004), there is general agreement that area burned across arctic and boreal regions will increase over the next century as climate change lengthens the fire season, decreases effective moisture, and increases ignition rates (Stocks et al. 1998, ACIA 2004, Calef et al. 2005, Flannigan et al. 2005, Girardin and Mudelsee 2008). These predictions are based primarily on short-term fire–climate relationships established in recent decades (Johnson 1992, Kasischke et al. 2002, Duffy et al. 2005, Girardin and Sauchyn 2008), but paleoecological studies also suggest that changes in relative moisture have influenced fire regimes throughout the Holocene (Carcaillet and Richard 2000, Millspaugh et al. 2000,

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Carcaillet et al. 2001, Lynch et al. 2002, 2004*b*). Nevertheless, the response of fire regimes to climate change will also depend strongly upon feedbacks between climate, fire, and vegetation (Rupp et al. 2000, ACIA 2004, Chapin et al. 2004, McGuire et al. 2006), complicating predictions of fire based on direct climate–fire relationships.

Vegetation can alter the direct link between climate and fire by influencing the abundance, structure, and moisture content of fuels across space and time. In ecosystems with low and/or discontinuous fuels, fire is limited primarily by the lack of burnable materials, even though weather and climate may be favorable for burning (e.g., the Mojave Desert in the southwestern U.S.; Brooks and Matchett 2006). In ecosystems supporting dense, continuous vegetation, fires are limited primarily by weather and climate conditions that promote fuel drying and ignitions over daily to weekly time scales (e.g., North American boreal forest; Johnson 1992, Bessie and Johnson 1995). However, even in these ecosystems, vegetation can have a subtle, secondary influence on fires regimes. For example, in areas of Alaska where black spruce (*Picea mariana* Mill. BSP.) boreal forests provide abundant flammable fuels (south of the Brooks Range and north of the Alaska Range; Fig. 1), area burned was positively correlated with tree density (Kasischke et al. 2002). In these forests, the probability of fire also increases with stand age because fuel accumulation at decadal time scales increases the probability of fire occurrence and spread (Yarie 1981, Schimmel and Granstrom 1997, Lynch et al. 2002). Given the complex interactions between fuels and climate, vegetation change can have profound impacts on fire regimes, resulting in fire regimes shifts that are opposite or independent of climate's direct influence on fire (Rupp et al. 2002, Hu et al. 2006, Tinner et al. 2008).

We used a paleoecological approach to examine the relationships between climate, vegetation, and fire regimes in the foothills of the south-central Brooks Range, Alaska (Fig. 1), where millennial-scale climate and vegetation histories have been investigated for several decades (Anderson et al. 2004). Specifically, our goal was to examine alternative hypothesis of climatic vs. vegetational controls over fire regimes by documenting fire history and vegetation assemblages that covered the study region from late glaciation and through the Holocene (ca. 15 000 yr BP to present). We used macroscopic charcoal from lake sediments to reconstruct fire occurrence and statistically compare fire return intervals (FRIs, years between consecutive fires) among vegetation zones inferred from fossil pollen, stomata stratigraphy, and modern analog analysis. If climatic variations were the dominant control of fire regimes, changes in fire occurrence between vegetation zones should be consistent with direct climate–fire relationships and relatively independent of vegetation characteristics (e.g., Carcaillet et al. 2001). However, if vegetation was the dominant control of fire regimes, changes in fire occurrence between vegetation zones should be consistent with the role that fuel type plays in determining landscape flammability (e.g., Lynch et al. 2002) and possibly unexpected given the direct effects of climate change on fire regimes. In addition, our study provides examples of how direct and indirect impacts of climate change may shape future fire regimes in arctic and boreal ecosystems.

STUDY LAKES AND REGIONAL SETTING

We examined sediment cores from four lakes along a 120-km east–west transect in the foothills of the south-central Brooks Range, Alaska, USA (Table 1, Fig. 1). Modern climate in the study region is continental. January and July mean maximum temperatures in Bettles (Fig. 1) are −20.1°C (SD = 5.6) and 20.8°C (SD = 1.8), respectively; mean annual precipitation is 360 mm (SD = 94), with 55% falling between June and September (Western Regional Climate Center, 1951–2007 observations; *available online*).[6] Forests and woodlands dominate lowlands and hill slopes in the study region, with *Picea mariana* in wet muskegs, *P. glauca* (Moench) Voss. and *Populus balsamifera* Mill. along riparian areas, and *P. glauca*, *Betula papyrifera* Marsh. and *Populus tremuloides* Michx. on uplands and warm, south-facing slopes (Nowacki et al. 2000). *Salix* spp., *Betula glandulosa* Michx., and *Alnus* spp. form shrub communities in non-forested areas (Nowacki et al. 2000). Fire is the primary disturbance agent in the region, with an estimated fire rotation period of 175 years (based on observations from 1950 to 2001 from the Kobuk Ridges and Valleys Ecoregion; Kasischke et al. 2002).

We cored lakes 2–15 ha in size and 7.0–11.6 m deep (Table 1), which are currently surrounded by discontinuous *P. mariana*-dominated forest. Recent fires burned to the edge of Ruppert Lake (RP) in Common Era (CE) 1991 (15 357 ha), to 1 km and 3 km east of Code Lake (CO) in CE 1959 (788 ha) and 1949 (2456 ha), and to 5 km west and 1 km southwest of Wild Tussock Lake (WK) in CE 1997 (9750 ha) and 1991 (6390 ha; Fig. 1; Alaska Fire Service 2004).

METHODS

Lake sediments

Sediments were collected from the center of each lake with two parallel, overlapping 8-cm diameter cores in summer 2001 (CO), 2002 (RP), or 2003 (XI, WK), using a modified Livingstone piston corer (Wright et al. 1984). Surface sediments (roughly <50 cm) were collected with a polycarbonate tube and the top 10–20 cm sliced at 0.5–1.0 cm in the field. All cores had intermittent laminae, which were used to match records from overlapping segments of adjacent cores. Sediments >10–20 cm depth

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[6] ⟨http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ak0761⟩

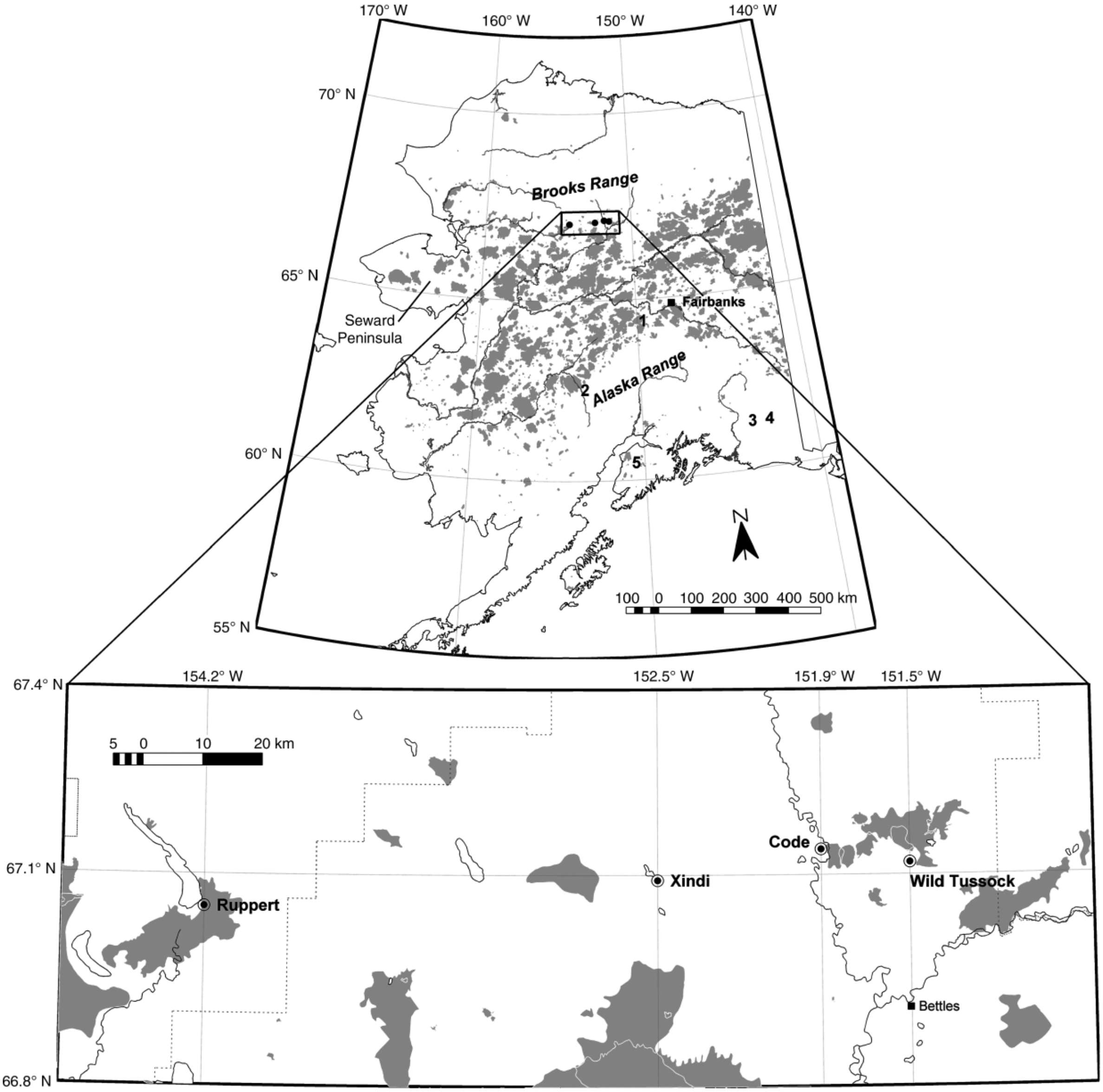

FIG. 1. Location of lakes in this study and others discussed in the text (1, Dune Lake; 2, Low Lake; 3, Moose Lake; 4, Chokosna Lake; 5, Paradox Lake). Gray polygons are areas that have burned between Common Era (CE) 1950 and 2003 (Alaska Fire Service 2004), and the dashed line on the lower map is the southern border of Gates of the Arctic National Park. The black dots and larger circles identifying each lake on the bottom map have 1- and 2-km diameters, representing the approximate spatial scale of each fire-history record.

were sliced at 0.25 cm to 0.50 cm intervals, and 1-cm^3 subsamples were prepared at varying intervals for pollen and stomata analysis according to PALE protocols (PALE members 1994), except that samples were not subjected to a coarse sieve so as not to remove any stomata (Carlson 2003, Pisaric et al. 2003). Pollen was counted at 400–1000× magnification to a terrestrial pollen sum > 300 (mean $= 398$, SD $= 107$) and displayed as percentages of total terrestrial pollen. In samples bracketing the *Picea* pollen rise ca. 5500 yr BP at selected sites (Brubaker et al. 1983), (1) pollen slides were scanned for *Picea* stomata, identified based on comparison with an Alaskan reference collection and Hansen (1994), while counting *Lycopodium* spores to an equivalent pollen sum of 2000 grains (Carlson 2003), and (2) *Picea* pollen grains were classified as *P. mariana* or *P. glauca* based on morphological measurements on ~30 *Picea* pollen grains per sample (Appendix A). For charcoal identification, 3–5-cm^3 subsamples were taken from contiguous core slices and prepared following Higuera et al. (2005). Charcoal was identified at 10–40× magnification based on color, morphology, and texture.

TABLE 1. Lake locations, characteristics, and record quality.

Lake name (unofficial)	Latitude (N)	Longitude (W)	Elevation (m above sea level)	Surface area (ha)	Age of record (ka)	Sedimentation rate (cm/yr; mean ± SD)	Resolution (yr/sample; mean ± SD)	Median signal-to-noise index
Ruppert	67°04′16″	154°14′45″	230	3	14.0	0.040 ± 0.023	13 ± 6	0.88
Xindi	67°06′42″	152°29′30″	240	7	15.5	0.025 ± 0.016	32 ± 24†	0.71†
Code	67°09′29″	151°51′40″	250	2	7.5	0.017 ± 0.003	16 ± 3	0.83
Wild Tussock	67°07′40″	151°22′55″	290	15	8.0	0.019 ± 0.001	14 ± 5	0.84

† Mean (±SD) sample resolution and the signal-to-noise index for the section of core used for charcoal peak identification were 23 (±13) years and 0.83, respectively.

Charcoal concentrations (pieces per cubic centimeter) were multiplied by the estimated sedimentation rate (centimeters per year) to obtain the charcoal accumulation rate (CHAR; number of pieces per square centimeter per year) of each sample. Quantifying charcoal pieces instead of area was supported by empirical and theoretical studies linking fires with high charcoal counts (Whitlock and Millspaugh 1996, Gardner and Whitlock 2001, Gavin et al. 2003, Higuera et al. 2005, Peters and Higuera 2007) and by strong correlations between charcoal area and charcoal counts within individual records (Hallett and Walker 2000, Hallett et al. 2003). By using charcoal counts, we implicitly assumed that fragmentation of charcoal pieces was constant through time.

Chronologies

Sediment chronologies for each site were based on ^{210}Pb dates for the upper 10–20 cm (using the CRS model; Binford 1990) and/or on AMS ^{14}C ages of concentrated charcoal from charcoal peaks, concentrated *Picea* pollen, or terrestrial macrofossils for deeper sediments. Age models were developed individually for the ^{210}Pb and ^{14}C portions of each core using a weighted cubic smoothing spline in Matlab (MathWorks 2005) taking into account the number and uncertainty of age estimates. The number of age estimates in a chronology determined the smoothing parameter for each spline, such that a larger number of ages for a given time interval resulted in a more flexible spline. The uncertainty of each age estimate (i.e., two standard deviations) was used to weight the influence of each age in the age–depth model (cf. Telford et al. 2004). Finally, confidence intervals for each age–depth model, reflecting the combined uncertainty of all age estimates in a model, were derived from 1000 bootstrapped chronologies. For each bootstrapped chronology, each age used to develop the chronology was selected randomly based on the probably distribution of the ^{210}Pb or calibrated ^{14}C date. The final chronology represents the median age at each depth from the 1000 bootstrapped chronologies.

Analysis of pollen and stomata data

Pollen zones were delineated primarily by visual inspection of pollen percentages of major tree, shrub, and herb taxa (i.e., Cyperaceae, *Betula*, *Populus*, *Picea*, *Alnus*) using the midpoint of the pollen increase or decrease of a taxon to establish a zone boundary. In addition, we used a modern analog analysis based on squared-chord distances (SCD) and receiver operating characteristic curves to quantify the probability that fossil pollen assemblages resembled modern pollen assemblages from North American Arctic Tundra, Boreal Forest, and Forest–tundra biomes (Appendix A). The arrival of *P. mariana* and development of the modern boreal forest was estimated via (1) *Picea* stomata presence/absence (RP and WK), (2) discriminant analysis (RP and WK) of *Picea* pollen grains, and (3) modern analog analysis (Appendix A). This approach yielded pollen zones and vegetation interpretations similar to those previously recognized in the region (Anderson and Brubaker 1994).

Statistical treatment of charcoal records

To assess whether CHAR differed between past biomes, we compared CHAR distributions between pollen zones in each lake using a two-sample Kolmogorov-Smirnov (K-S) test (e.g., Clark 1990, Lynch et al. 2002). Prior to subsequent analyses, we interpolated CHARs to 15-yr time steps (C_{int}), approximating the mean sampling resolution at all sites (Table 1). This procedure combines samples based on their proportional contribution to each time step. In instances where sample resolution was >15 yr, the nature of the record is not altered, but when sample resolution is <15 yr, some variations are lost (Long et al. 1998, Carcaillet et al. 2001, Gavin et al. 2006). This step was necessary to reduce biases in the ability to detect fires due to variable sample resolution within and between records.

We inferred the timing of "local" fires by decomposing charcoal records (e.g., Clark et al. 1996) to identify distinct charcoal peaks based on a standard set of threshold criteria applied to all records. Consistent with empirical and theoretical studies (Lynch et al. 2004*a*, Higuera et al. 2007), we use the term "local" to refer to distances within ~500–1000 m of each lake, corresponding to an area of ~100–300 ha (1–3 km^2). We assumed that low-frequency variations in CHAR (background), C_{back}, reflect changes in the rate of total charcoal production, secondary charcoal transport, and sediment mixing (Clark et al. 1996, Long et al. 1998, Higuera et al. 2007). We estimated C_{back} by calculating a 500-yr moving median (XI, CO, WK) or mode (RP, because this yielded a higher signal-to-noise index; see end of this

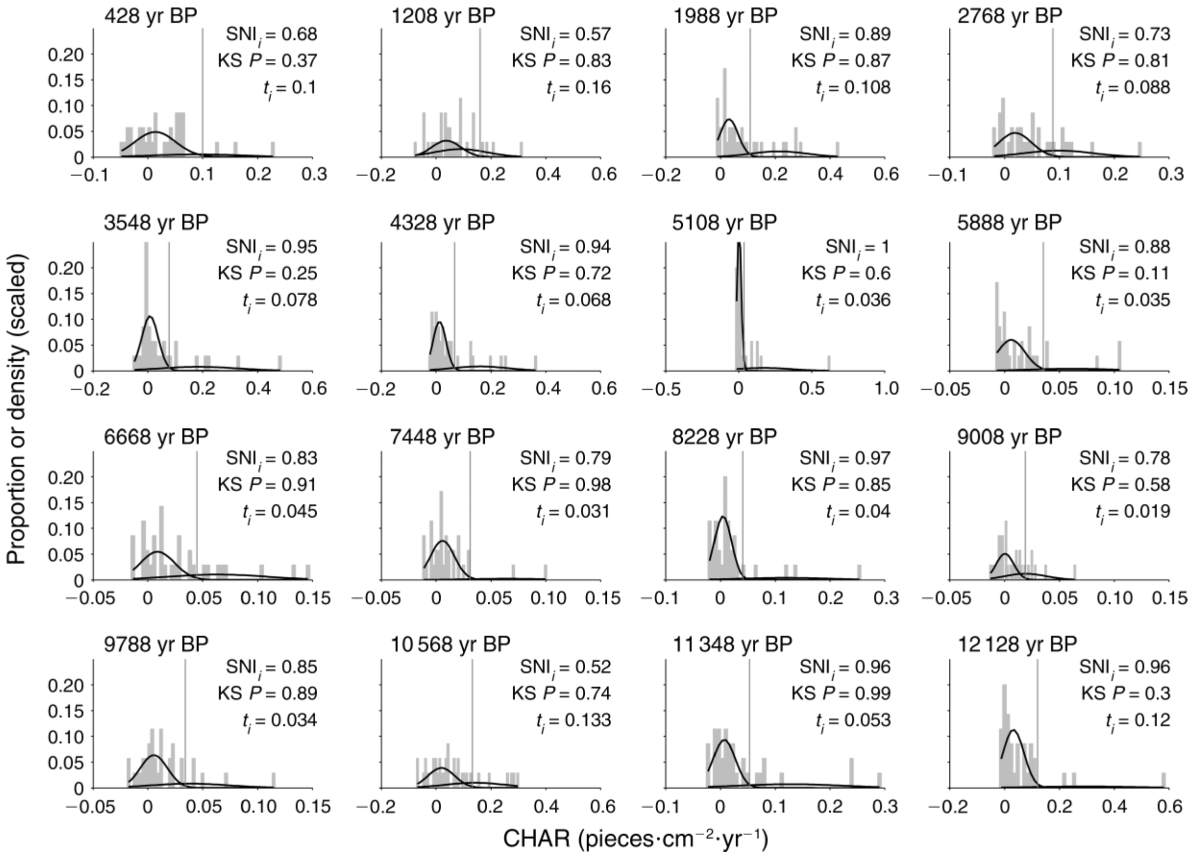

FIG. 2. Selected local distributions of the peak charcoal series, C_{peak}, from Ruppert Lake (gray bars). Each panel represents a 500-year, nonoverlapping section of the record and includes the two modeled Gaussian distributions (and is thus analogous to panels c and d in Fig. 6 of Gavin et al. 2006, but for distinct portions of the Ruppert Lake record). All samples above the threshold value, t_i (vertical line), represent charcoal from local fires, C_{fire}. The threshold cuts off 99% of the samples assumed to represent natural and analytical noise, C_{noise} distribution (black line with lower mean). This procedure is repeated for every sample in the record, resulting in a unique threshold value reflecting the variability in C_{noise} around each sample. Note that the distribution of C_{noise} varies throughout the record, and thus, t_i and the signal-to-noise index (SNI, see *Methods*) also vary. "KS *P*" is the *P* value resulting from a two-sample Kolmogorov-Smirnoff goodness-of-fit test between the empirical C_{noise} values and the modeled C_{noise} distribution, thus providing an index of how well the C_{noise} model fits the empirical data.

section) across each record, and then smoothing this series with a locally weighted regression using a 500-yr window. C_{back} was subtracted from C_{int} to obtain a residual series, C_{peak} (i.e., $C_{\text{peak}} = C_{\text{int}} - C_{\text{back}}$), which contains high-frequency variability around the long-term trend described by C_{back} (e.g., Clark et al. 1996). Previous decomposition methods have assumed a constant relationship between C_{peak} and C_{back} and applied a globally defined threshold value to C_{peak} series to identify charcoal peaks. Because the variability of C_{peak} around C_{back} changes through time in our records (Fig. 2), we developed a novel approach to identify peaks using a locally defined threshold based on variability around each sample. Specifically, we used a Gaussian mixture model to separate C_{peak} values within each overlapping 500-yr portion of a record into two components: (1) C_{noise}, variations around C_{back} that reflect natural and analytical effects (e.g., sediment mixing, sediment sampling), and (2) C_{fire}, variations exceeding variability in the C_{noise} distribution, assumed to reflect the occurrence of one or more local fires ("fire events"; Clark et al. 1996, Gavin et al. 2006). Because the threshold separating C_{fire} from C_{noise} should occur in the upper range of the C_{noise} population, we considered three possible threshold values corresponding to the 95th, 99th, and 99.9th percentile of the C_{noise} population for every 500-yr portion of the record. We present results from all three criteria but discuss only those using the 99th percentile criterion. Finally, all peaks identified were screened to test whether variations between a "peak" and the smallest "non-peak" sample within the previous five samples (i.e., 75 yr) differed statistically based on the original charcoal counts and sample volume (Gavin et al. 2006; Appendix A). This screening eliminates "peaks" when variations in CHAR are based on small differences in charcoal counts. Our methods are described in detail in Appendix A and in the publicly available program CharAnalysis (written by P. E. Higuera; *available online*).[7]

In addition, as an indication of the suitability of charcoal records for peak identification, we calculated a signal-to-noise index (SNI) for each sample, *i*, which describes the variance within the C_{fire} distribution (i.e., signal) relative to the total variance in C_{peak} in the 500 years surrounding that sample:

$$\mathrm{SNI}_i = \frac{\mathrm{var}(C_{\mathrm{fire},i})}{\mathrm{var}(C_{\mathrm{noise},i}) + \mathrm{var}(C_{\mathrm{fire},i})}.$$

The SNI varies from 0 to 1, with high values representing large separation between charcoal peaks and non-peaks, and values near zero represent little separation between peaks and non-peaks.

Quantifying and detecting differences in fire regimes

We inferred aspects of past fire regimes based on the magnitude and temporal pattern of identified charcoal peaks. Peak magnitude, the number of charcoal pieces from all samples defining a given peak (i.e., all samples above the threshold value; number of pieces per square centimeter per peak), is a measure of total charcoal deposition per fire event (Whitlock et al. 2006). Systematic changes in peak magnitude at millennial time scales were used as a qualitative proxy for average fuel consumption per fire, which should reflect fire size and/or fuel consumption for a given area burned. Interpretations rest on theoretical relationships between fire and charcoal deposition at a lake (Higuera et al. 2007), although links between fuel consumption and peak magnitude have yet to be tested empirically. For a given fire, charcoal deposition at a lake varies based on location, size, and charcoal production (i.e., fuel consumption). When a large number of fires are recorded, variations in peak magnitude due to fire location contribute little to the long-term pattern, which should thus reflect relative changes in charcoal production.

We used the distribution of fire return intervals (years per fire; FRIs) within each pollen zone to characterize the temporal characteristics of fire regimes for each vegetation zone. FRI distributions were described by the mean FRI ($\mathrm{FRI}_{\mathrm{mean}}$), although the median FRI ($\mathrm{FRI}_{\mathrm{median}}$) is also reported in tabular form. If a pollen zone had >5 FRIs (>6 fires), a two-parameter Weibull model was fit to FRIs using maximum-likelihood techniques (in Matlab; Clark 1989, Johnson and Gutsell 1994, MathWorks 2005). Goodness of fit for each Weibull model was tested with a one-sample K-S test (Zar 1999); Weibull models are not reported unless $P > 0.10$ (i.e., there was >10% chance that the empirical distribution was not different from the Weibull model; Johnson and Gutsell 1994). Confidence intervals (95%) for Weibull parameters, $\mathrm{FRI}_{\mathrm{mean}}$, and $\mathrm{FRI}_{\mathrm{median}}$ were estimated based on 1000 bootstrapped samples from each distribution.

We tested two null hypotheses using a likelihood-ratio test (LRT) based on estimates of the Weibull *b* and *c* parameters (Appendix A): (1) FRIs did not differ between pollen zones within a given site, and (2) FRIs did not differ between sites within a given pollen zone. By utilizing both parameters of the Weibull distribution, the LRT provides a more powerful method for detecting difference in FRI distributions than possible by interpreting confidence intervals around the mean or median FRI and estimated Weibull statistics (e.g., Clark 1990, Lynch et al. 2002) or by using the nonparametric K-S test (Lynch et al. 2002, Anderson et al. 2006, Gavin et al. 2006). We rejected the null hypothesis if $P \leq 0.05$. If FRI distributions within a single vegetation zone were statistically similar across sites (i.e., null hypothesis 2 was not rejected), we pooled FRIs to form a composite record representing FRIs from across the study area (i.e., two to three sites). With the pooled FRIs we performed the same between-zone comparisons as with individual records. Due to the increased sample size in the composite records, this procedure yields greater statistical power for detecting differences between fire regimes in different vegetation zones. Because, in most cases, comparisons between zones at individual sites were similar to results for the pooled data (although not always significant), we focus our discussion on results from the pooled data.

RESULTS AND PALEOVEGETATION INTERPRETATIONS

Chronologies and sedimentation rates

The Ruppert (RP) and Xindi (XI) records are older (starting ca. 14 000 and 15 500 yr BP) than the Code (CO) and Wild Tussock (WK) records (starting ca. 7500 and 7800 yr BP; Fig. 3). At all lakes, age models since 8000 yr BP were well constrained and generally pass through the 95% confidence interval of ^{14}C or ^{210}Pb dates (Fig. 3). At RP, we did not use two ^{14}C dates on concentrated pollen (19.02 and 29.50 cm) because they were ~500–1000 years older than ages defined by five other ^{14}C dates on charcoal in sediments spanning these core depths (10–60 cm; Fig. 3, Appendix B). At RP and XI, age models >8000 yr BP were less well constrained, and predicted ages do not always intersect the uncertainty of ^{14}C dates (e.g., RP; Fig. 3). Given these results and the sensitivity of CHAR to sedimentation rate, we evaluated whether different choices of age–depth relationships altered the general features of the CHAR series at these sites. We developed five to seven alternative age–depth relationships by excluding individual dates and changing the age–depth model criteria. In no case did the overall nature of the CHAR records change.

Sedimentation rates ranged from 0.017 to 0.040 cm/yr (Table 1, Fig. 3) and varied little in the CO and WK records, but were higher prior to ca. 8000 and 11 000 yr BP at RP and XI, respectively (Fig. 3). The mean sample resolution at each site was ~15 yr/sample (Table 1) and

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[7] ⟨http://CharAnalysis.googlepages.com⟩

varied from <5 to ~50 yr/sample (Fig. 3). Slow sedimentation resulted in low sample resolution at XI from 8000–0 yr BP (>50 yr/sample).

Peak identification in charcoal records

The median signal-to-noise index (SNI) for all records where peak analysis was interpreted exceeded 0.80 (Table 1; e.g., Ruppert Lake, Fig. 2). This is well above the median SNI expected from records without a peak signal (e.g., 0.15 for red noise; Appendix A) and indicates good separation between peak and non-peak values. We did not interpret peak analysis results at XI from 8000–0 yr BP because the SNI in this period was consistently <0.5 (data not shown). The sensitivity of charcoal peak identification to different threshold criteria varied between pollen zones and between sites (Fig. 4), but characterizations of FRI distributions were generally insensitive to all three threshold criteria (data not shown).

Comparisons between known fire events and the most recent charcoal peaks at RP, CO, and WK support the assumption that identified charcoal peaks detect fires within (and not beyond) 1 km of these lakes. The CE 1991 (–41 yr BP) fire that burned to the edge of RP was represented by an identified peak centered at –39 yr BP, while the most recent peaks identified at CO (69 yr BP) and WK (38 yr BP) both occur before the start of fire observation in CE 1950 (0 yr BP); thus, the post-1950 fires that burned to ~1, 3, and 5 km from these lakes were not detected by the charcoal record.

Pollen, stomata, and charcoal records

Herb Tundra Zone, 14 000–13 300 (RP), 15 500–14 300 (XI) yr BP.—This zone was characterized by Cyperaceae (>25%), *Salix* (~25%), Poaceae (~15%), and *Artemisia* (~10%) pollen, with relatively high percentages of *Pediastrum* algal cell nets (>25%; Fig. 5, Appendix B). Although SCD was lowest for comparisons with Arctic Tundra (~0.2), the probability of analog (<20%) indicates little similarity with modern tundra (Fig. 2, Appendix B). Our pollen results are consistent with previous studies in the region (Anderson et al. 1989, Anderson and Brubaker 1994) and suggest the presence of a discontinuous prostrate shrub tundra and grass–forb tundra (see Anderson et al. 2004). CHARs were low at both sites (medians = 0.00–0.01 pieces·cm^{-2}·yr^{-1}; Appendix B). The presence of only one identified charcoal peak (at RP; Fig. 4) precludes the analysis of fire regimes but suggests long FRIs in this zone.

Shrub Tundra Zone, 13 300–10 300 (RP), 14 300–10 300 (XI) yr BP.—Increased *Betula* pollen, interpreted as *B. glandulosa* and/or *B. nana* (Anderson and Brubaker 1994), to >60% marks the transition from herb to shrub tundra (Fig. 5, Appendix B). SCD (~0.2) continues to indicate a low similarity of fossil to modern pollen assemblages from all modern biomes (probability of analog <20%; Fig. 5, Appendix B). *Betula* pollen percentages higher than in modern tundra communities suggest that the landscape was covered by relatively dense thickets of tall (>1 m) birch shrubs (Brubaker et al. 1983, Anderson and Brubaker 1993). CHARs increase at the onset of this zone (medians = 0.02–0.05 pieces·cm^{-2}·yr^{-1}), and CHAR distributions were distinct from those in the Herb Tundra Zone ($P < 0.01$; Appendix B). Maximum peak magnitudes exceed 5 pieces·cm^{-2}·peak^{-1} (Fig. 4). Fire regimes at RP and XI were characterized by a FRI$_{\text{mean}}$ (95% CI) of 137 (107–171) and 150 (115–186) yr, respectively (Table 2, Fig. 6), with no difference in FRI distributions between sites (Table 3, Fig. 6). The FRI$_{\text{mean}}$ (95% CI) of the pooled record was 144 (120–169) yr (Fig. 7).

Deciduous Woodland Zone, 10 300–8500 (RP), 10 300–8000 (XI) yr BP.—This zone was characterized by increased *Populus* pollen percentages (10%–20%; Fig. 5, Appendix B) and was inferred to represent woodland of *P. balsamifera* and *P. tremuloides* (Anderson et al. 2004, Edwards et al. 2005). Limited macrofossil evidence (Edwards et al. 2005) also suggests the possibility of tree-size *Betula* within this period. SCD was the highest for the entire record (>0.3), and no analogs exist with modern North America pollen spectra (probability of analog <0.2; Fig. 5, Appendix B). CHARs decrease (medians = 0.01–0.02 pieces·cm^{-2}·yr^{-1}) and distributions were distinct from those in the Shrub Tundra Zone ($P <$ 0.01; Appendix B). Peak magnitudes decrease to <5 pieces·cm^{-2}·peak^{-1} (Fig. 4). The FRI$_{\text{mean}}$ (95% CI) at RP and XI was 223 (90–390) yr and 293 (225–360) yr, respectively (Table 2, Fig. 6). Because XI recorded only four FRIs (Table 3, Fig. 6), we deemed the FRI$_{\text{mean}}$ between RP and XI sufficiently close to pool data from within this zone. The FRI$_{\text{mean}}$ (95% CI) of the composite record was 251 (156–347) yr, significantly different from the composite record of the Shrub Tundra Zone ($P =$ 0.03; Fig. 7, Appendix B).

Forest–tundra Zone, 8500–5500 (RP), 8000–5500 (XI), 7500–5500 (CO), 7800–5500 (WK) yr BP.—Decreased *Populus* (<10%) and increased in *Picea* (≥1%, <10%) pollen percentages mark the onset of the Forest–tundra Zone. Discriminant analysis of *Picea* pollen at RP and WK (Appendix B) and previous research (Brubaker et al. 1983), indicate the nearly exclusive presence of *P. glauca* in this zone. *Alnus* pollen percentages increased from trace amounts to >50% starting around 7250–7500 yr BP, coinciding with the start of the CO and WK records (Fig. 5, Appendix B). With the rise in *Alnus* pollen, SCD decreases for comparisons to modern Boreal Forest and Forest Tundra (<0.1), and probability-of-analog for these biomes increase to >30%–40% (Fig. 5, Appendix B). Together, pollen and stomata data suggest that the vegetation resembled modern treeline, with *P. glauca* trees or stands dispersed within a landscape of *Betula* or *Betula* and *Alnus* shrubs (Fig. 5, Appendix B).

CHARs at XI (median = 0.03 pieces·cm^{-2}·yr^{-1}) were higher than in all previous zones ($P < 0.01$), while CHARs at RP were intermediate between the Herb

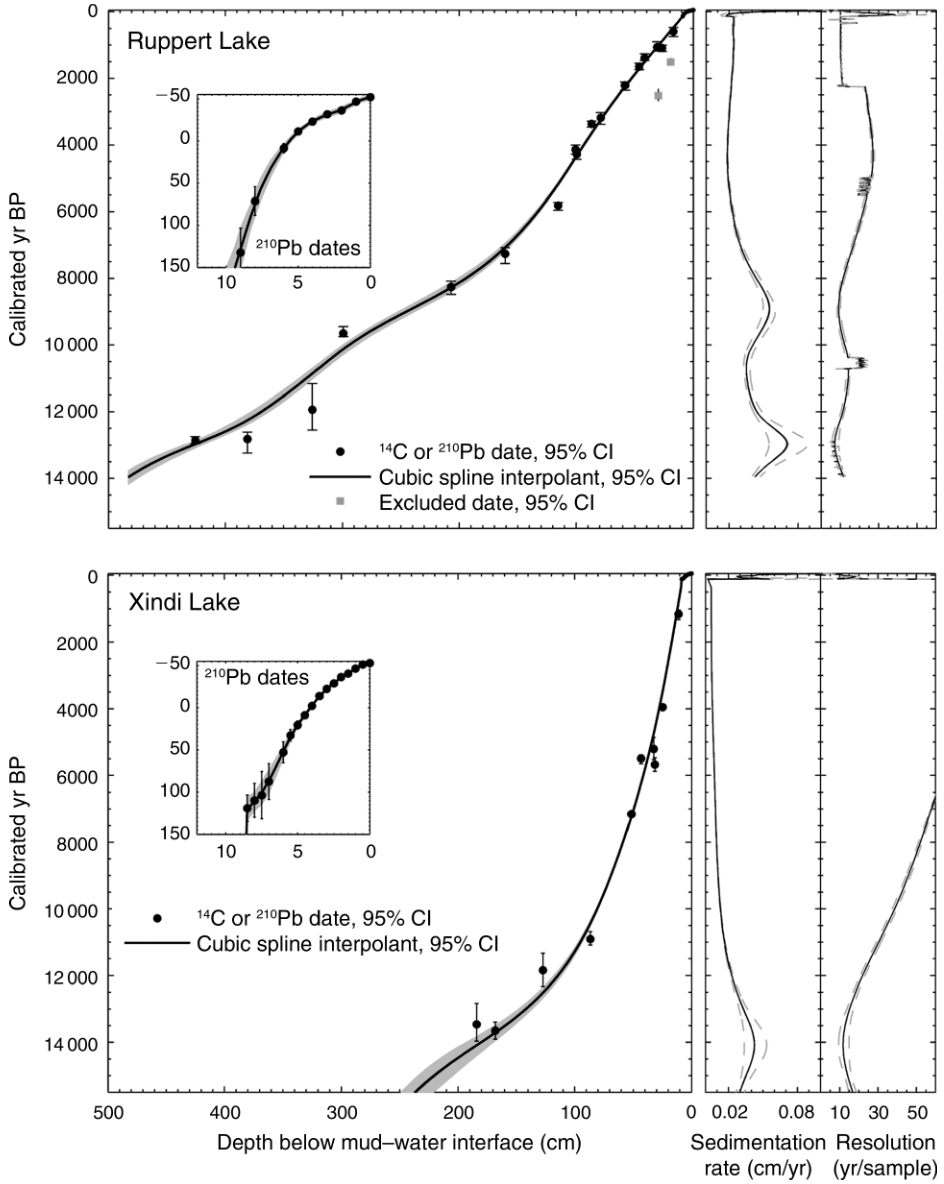


FIG. 3. Age–depth models for each site with the resulting sedimentation rates and sample resolution, with 95% confidence intervals. At Ruppert Lake, temporal resolution changes from ~25–10 yr/sample at 2200 BP because sampling intervals change from 0.5 cm to 0.25 cm. See *Results* for explanation of the excluded dates for Ruppert Lake.

Tundra ($P < 0.01$) and Shrub Tundra Zones ($P < 0.01$; medians = 0.02–0.03 pieces·cm^{-2}·yr^{-1}; Appendix B). Charcoal peak magnitudes were similar to the previous zone at RP and generally remain below 5 pieces·cm^{-2}·peak^{-1} at all sites (Fig. 4). FRI$_{\text{mean}}$ (95% CI) for RP, CO, and WK were 238 (158–324), 210 (145–277), and 131 (95–172) yr, respectively. Except for RP vs. WK ($P = 0.04$), FRI distributions did not differ among sites (Table 3, Fig. 6). Given the statistical difference between RP and WK, the composite FRI distribution only includes FRIs from RP and CO. The composite record had a FRI$_{\text{mean}}$ (95% CI) of 227 (170–287) yr, similar to the composite record from the Deciduous Woodland Zone, but significantly longer than the composite records from the Shrub Tundra Zone ($P = 0.02$; Fig. 7, Appendix B).

Boreal Forest Zone, 5500 yr BP–present (RP, XI, CO, WK).—Picea pollen percentages increased to >10% at all sites between 6000 and 4000 BP (Fig. 5, Appendix B) and indicate the development of the modern boreal forest (Anderson and Brubaker 1994). With the rise in *Picea* pollen, all sites show an increase in the probability-of-analog with the modern Boreal Forest biome (>75%) and lower probabilities for modern Forest–tundra (roughly <70%; Fig. 5, Appendix B). The first presence of *Picea* stomata ca. 5000 yr BP (RP; Fig. 5)

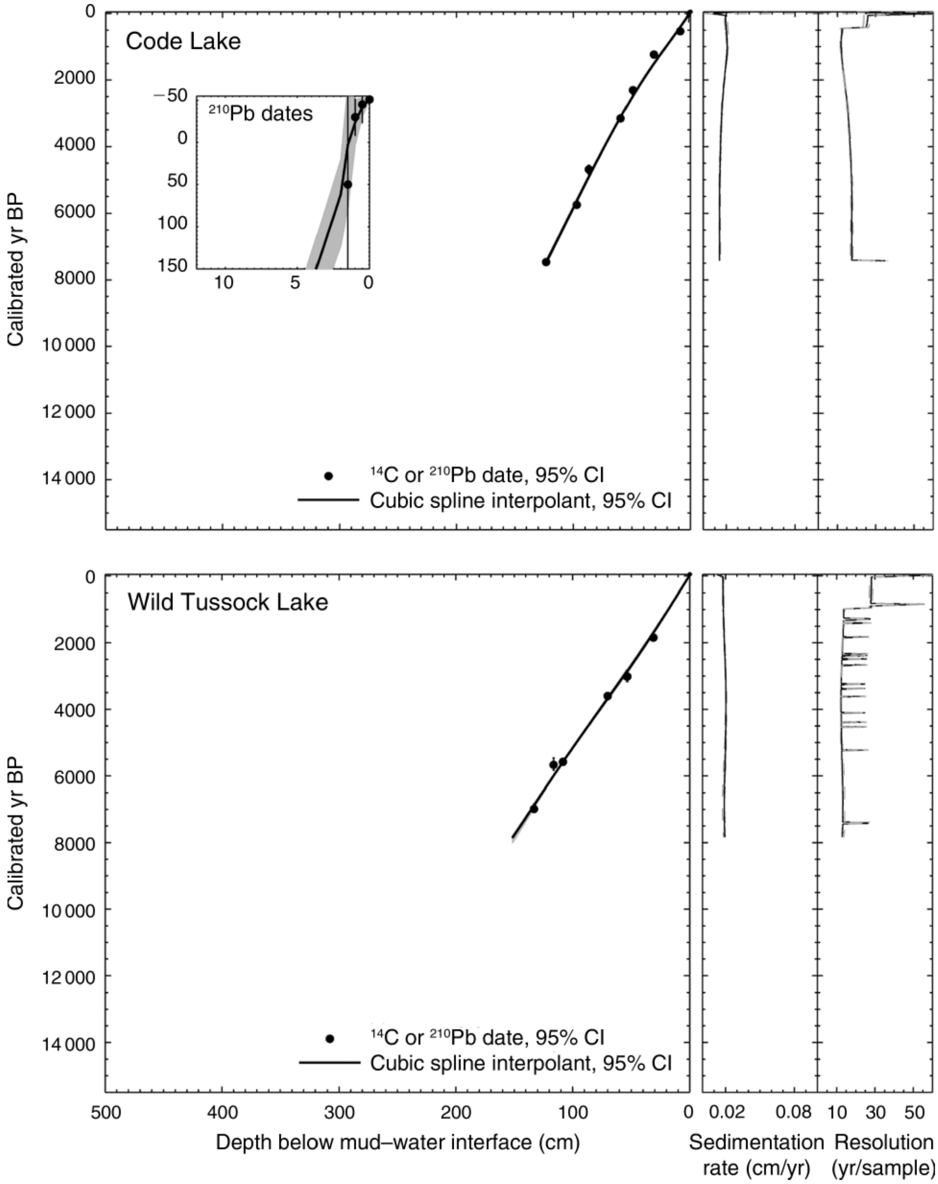


FIG. 3. Continued.

and 5400 yr BP (WK; Appendix B) coincides with the transition from Forest–tundra to Boreal Forest inferred from the modern analog analysis (Fig. 5, Appendix B), *Picea* pollen morphology from RP and WK (Appendix B), and previous research (Brubaker et al. 1983), indicating an increase of *P. mariana* at this time (Appendix B). While the beginning age of this zone differed across sites (e.g., RP vs. CO and WK; Fig. 5, Appendix B), our statistical comparisons of FRI distributions were insensitive to starting date of 5000 vs. 5500 yr BP (data not shown). We used 5500 yr BP at all sites for simplicity.

CHARs increased to their highest level in most records (median CHAR = 0.05–0.11 pieces$\cdot$cm$^{-2}\cdot$yr^{-1}; Fig. 4, Appendix B). FRI$_{\text{mean}}$ (95% CI) at RP, CO, and WK were 171 (135–216), 135 (113–160), and 135 (113–157) yr, respectively (Table 2, Fig. 6), and FRI distributions did not differ between sites (Table 3, Fig. 6). The FRI$_{\text{mean}}$ (95% CI) of the composite record was 145 (130–163) yr; significantly shorter than the FRI$_{\text{mean}}$ in the composite record from the Forest–tundra and Deciduous Woodland Zones, but similar to the composite record from the Shrub Tundra Zone (Fig. 7, Appendix B). To test the sensitivity of our results to FRIs from WK, we constructed a pooled record for the Boreal Forest Zone that excluded WK. Significant differences remained when comparing the pooled Forest–tundra and Boreal Forest Zones ($P = 0.05$), but not when comparing pooled Deciduous Woodland and Boreal Forest Zones ($P = 0.07$).

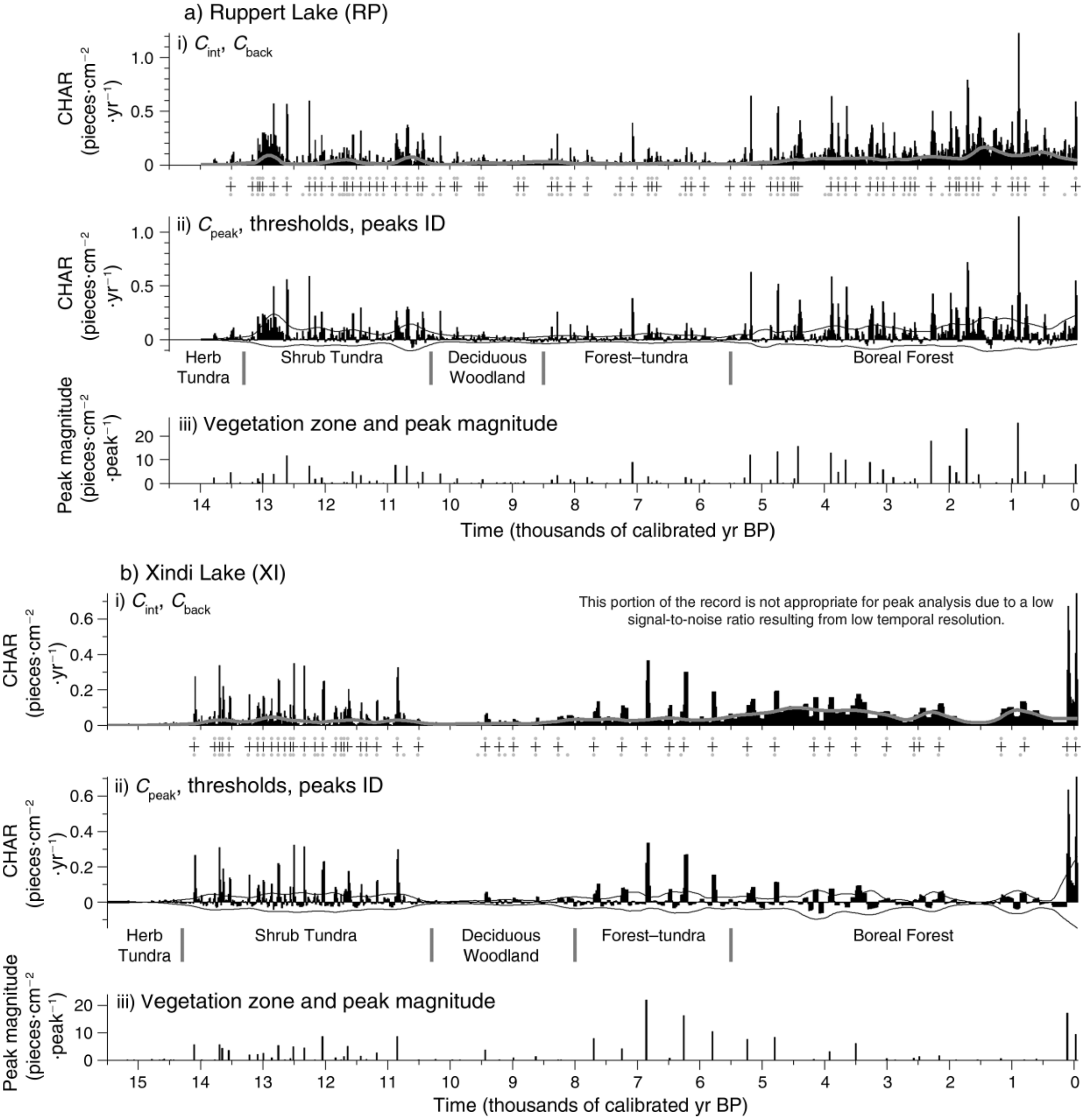
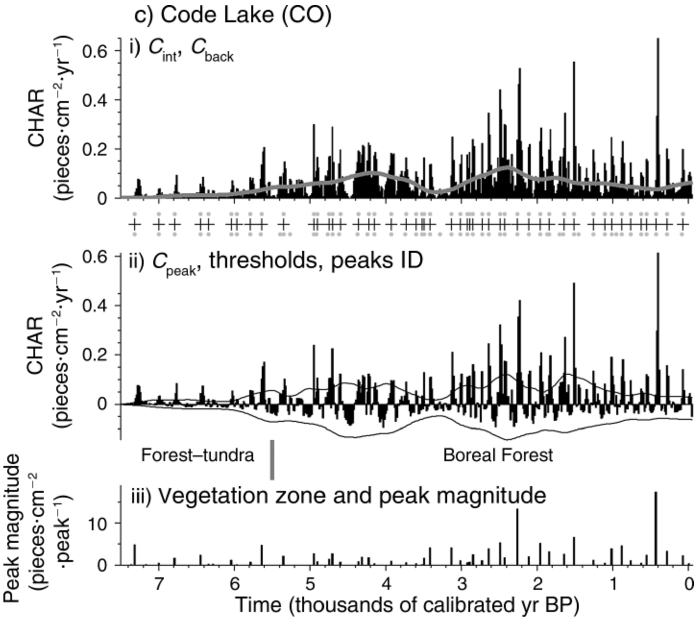


FIG. 4. Charcoal records for (a) Ruppert, (b) Xindi, (c) Code, and (d) Wild Tussock lakes. (i) Interpolated charcoal accumulation rates (CHAR), C_{int} (black), and background CHAR, C_{back} (gray); (ii) Peak CHAR, C_{peak}, with the values identifying noise-related variability (positive and negative gray lines) and peaks identified with each threshold criterion. The 99th percentile criterion used for interpretation is represented with +, and the 95th and 99.9th percentile results are represented with gray dots. (iii) Pollen-inferred vegetation zone and peak magnitude for all charcoal accumulation rate (CHAR) values exceeding the positive threshold value in panels ii. Note peak magnitude values not corresponding to + symbols in panels ii are those that did not pass the minimum-count screening (see *Methods* for details), and + symbols in panels ii with no apparent peak magnitude value correspond to very small peak magnitudes.

DISCUSSION

Interpreting sediment charcoal records and detecting changes in fire regimes

We introduce three general tools that facilitate the interpretation of fire history from sediment-charcoal records. First, the signal-to-noise index provides a semi-objective way to judge if a record is appropriate for peak analysis. For example, while >0.8 in most records, SNI values were consistently <0.5 for the 8000–0 yr BP in the Xindi Lake record (data not shown), indicating that this section was not suitable for peak identification. Second, our use of a Gaussian mixture model to determine threshold values for peak identification allowed us to treat all charcoal records with one set of semi-objective criteria. These criteria are consistent with a mechanistic



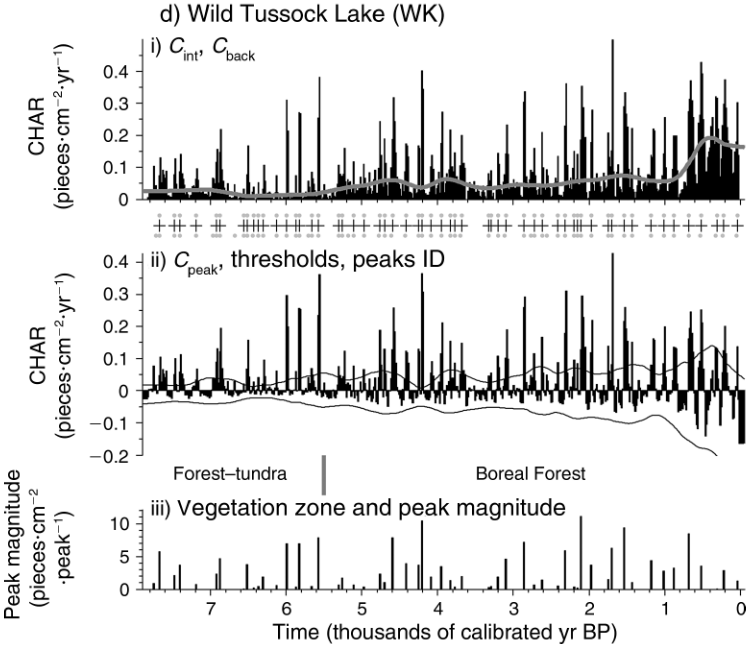


FIG. 4. Continued.

model of the origin of charcoal records (Higuera et al. 2007) and have the advantage of being established a priori. Further, because thresholds are defined locally, this approach is appropriate for records with changing variability in charcoal accumulation and is insensitive to variety of analytical choices (e.g., transforming charcoal data, defining C_{peak} via ratios vs. residuals; P. E. Higuera, *unpublished data*). Although a robust calibration requires a large data set of known fires, our approach appears successful, as the 99th-precentile criterion accurately identified known fires within one km of each lake. Third, using the likelihood-ratio test and pooling FRIs from multiple records greatly improved the ability to detect changes in fire regimes with long return intervals. In stand-replacing fire regimes with long and variable FRIs, individual records can detect only large or long-lasting changes in FRI_{mean} (e.g., >30%–50% change over millennial time scales). Pooling data from several sites increased the sample size of FRIs in this study and allowed the detection of statistical differences between pollen zones that were not possible using single records (e.g., Ruppert Lake record; Fig. 6). This approach assumes that fire regimes are homogenous across sites and within time periods. We used

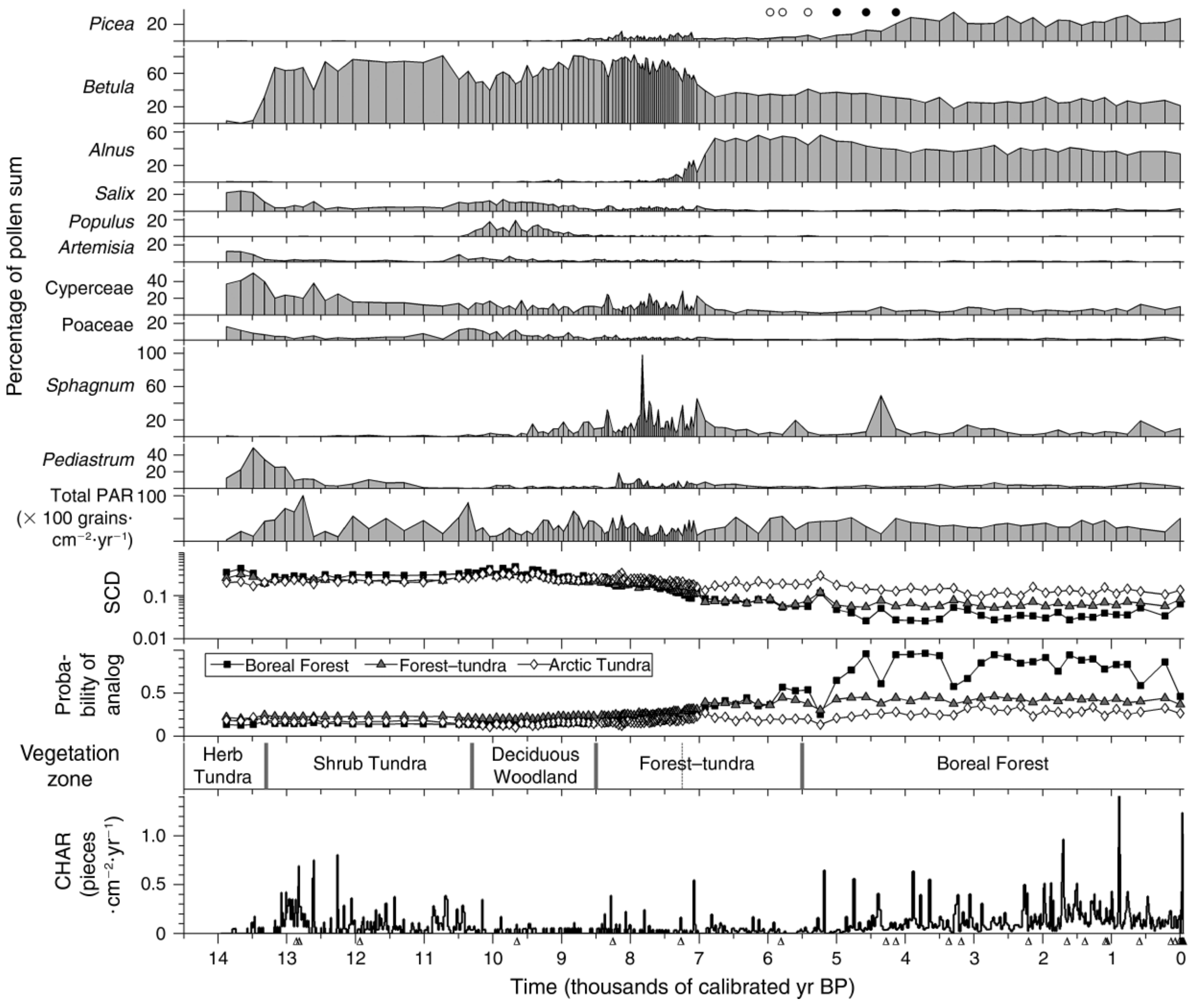


FIG. 5. Paleovegetation and charcoal data from Ruppert Lake. From top to bottom: pollen and spore percentages of selected taxa; total pollen accumulation rate (PAR); squared chord distance (SCD) and probability of analog values for comparisons between fossil samples and those from modern Boreal Forest, Forest–tundra, and Arctic Tundra vegetation zones; and charcoal accumulation rate (CHAR). Solid and open circles on *Picea* panel represent *Picea* stomata presence and absence, respectively. Triangles below lower horizontal axis represent the location of ^{14}C or ^{210}Pb dates. See Appendix B for the same figures for Xindi, Code, and Wild Tussock Lakes.

between-site comparisons to evaluate the assumption of homogenous fire regimes, leading to the elimination of sites with statistically different records from the pooled data set (e.g., WK within the Forest–tundra Zone).

Late-glacial and Holocene fire regimes: patterns and inferred controls

Herb Tundra Zone.—Though our records span a brief portion of this zone, the charcoal series suggest that fire was rare in the late-glacial herb tundra. Both climate and vegetation change likely reduced the probability of fire. Summers were cooler and drier than present (Anderson and Brubaker 1994, Edwards et al. 2001, Anderson et al. 2004), with cold temperatures implying limited fuel drying and limited convection necessary for lightning ignition. While species composition differed from modern tundra, the structure of vegetation in this zone may have been similar to present high-arctic tundra, where a cold and dry climate results in discontinuous vascular plant cover (Walker et al. 2005) that supports few fires (Kasischke et al. 2002).

Shrub Tundra Zone.—Fire activity increased markedly with the transition from herb to shrub tundra ca. 13 300–14 300 yr BP, resulting in a $\mathrm{FRI}_{\mathrm{mean}}$ (144 yr [120–169]; Fig. 7) statistically similar to those of modern Alaskan boreal forests (Figs. 6 and 7; Kasischke et al. 2002, Lynch et al. 2002). These short FRIs contrast sharply with those of modern Alaskan tundra, as only ~3% of arctic tundra burned between CE 1950 and 2004 (Alaska Fire Service 2004, Walker et al. 2005) and even the most flammable tundra region, the Seward Peninsula (Fig. 1), has an estimated fire rotation period (analogous to a $\mathrm{FRI}_{\mathrm{mean}}$) of 270 yr (Kasischke et al. 2002). Lower overall CHARs and peak magnitudes (Fig. 4, Appendix

TABLE 2. Fire regime statistics for each site, stratified by pollen-defined vegetation zone.

Site and zone	N_{FRI}	Fire history parameter (95% CI) Mean fire return interval (yr)	Median fire return interval (yr)	Weibull b parameter (yr)	Weibull c parameter (unitless)
Ruppert					
Shrub Tundra	20	137 (107–171)	128 (90–180)	151 (116–191)	1.84 (1.43–3.35)
Deciduous Woodland	6	223 (90–390)	158 (53–458)	229 (94–429)	1.16 (0.90–3.11)
Forest–tundra	12	238 (158–324)	210 (90–383)	262 (172–360)	1.63 (1.30–2.75)
Boreal Forest	31	171 (135–216)	120 (98–173)	188 (147–239)	1.53 (1.31–2.06)
Xindi					
Shrub Tundra	24	150 (115–186)	113 (90–173)	164 (122–207)	1.68 (1.45–2.25)
Deciduous Woodland	4	293 (225–360)	292 (225–360)	Weibull model not fit (<5 FRI)	
Code					
Forest–tundra	8	210 (145–277)	195 (105–315)	235 (162–302)	2.39 (1.78–5.20)
Boreal Forest	39	135 (113–160)	135 (105–150)	150 (123–178)	1.85 (1.52–2.60)
Wild Tussock					
Forest–tundra	16	131 (95–172)	105 (60–180)	145 (104–191)	1.66 (1.38–2.50)
Boreal Forest	39	135 (113–157)	135 (105–165)	149 (123–174)	1.96 (1.61–2.75)

Notes: Parentheses enclose 95% confidence intervals estimated by 1000 bootstrapped samples of the fire return interval (FRI) distributions. N_{FRI} is the number of fire return intervals in each zone (the total number of fires in a zone, minus 1).

B) in the Shrub Tundra Zone also suggest that fuel consumption (i.e., biomass burned per fire) was lower than in modern boreal forests.

We suggest elsewhere (Higuera et al. 2008) that a change in tundra fuel characteristics was the primary driver of increased fire activity in the Shrub Tundra Zone. Although summer temperatures increased between the Herb and Shrub Tundra zones, temperatures remained cooler than present (Anderson and Brubaker 1994, Edwards et al. 2001, Anderson et al. 2004), making it unlikely that temperature alone caused fire frequencies to be similar to modern boreal forests (Table 3, Fig. 4). Similarly, changes in moisture were unimportant, as moisture remained similar to or increased slightly from

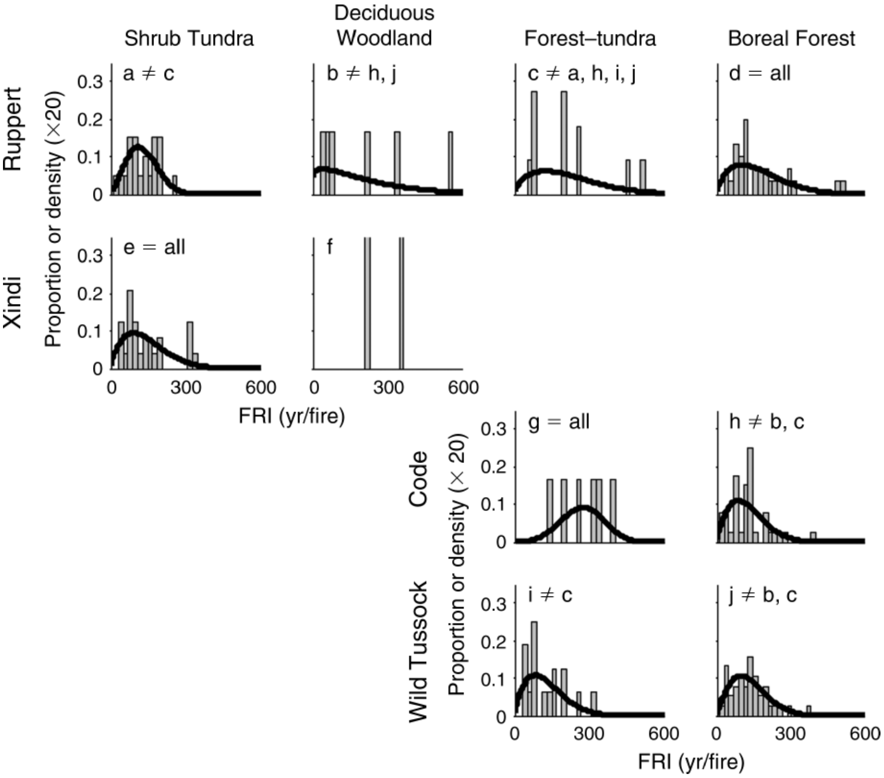


FIG. 6. Distribution of fire return intervals (FRIs) and fitted Weibull models for each vegetation zone (columns) at each site (rows). Results from statistical comparisons are summarized by =, similar ($P > 0.05$), or ≠, not similar ($P \leq 0.05$). Table 3 contains P values for all comparisons. Panel (f) has too few intervals (<5 FRIs) to compare to the other populations.

TABLE 3. Probability of Type I error for within-site, between-zone (italic), between-sites, within-zone (boldface), and between-site, between-zone (non-boldface type) comparisons of fire-return-interval distributions based on the likelihood-ratio test.

Zone and site	ST, XI	DW, RP	FT, RP	FT, CO	FT, WK	BF, RP	BF, CO	BF, WK
ST, RP (20)	**0.60**	*0.10*	0.05*	0.15	0.89	0.29	0.99	0.96
ST, XI (24)		0.18	0.10	0.18	0.73	0.59	0.58	0.33
DW, RP (6)			*0.65*	0.23	0.15	0.44	0.05*	0.02*
FT, RP (12)				**0.46**	**0.04***	*0.28*	0.02*	0.00*
FT, CO (8)					**0.09**	0.40	*0.15*	0.07
FT, WK (16)						0.41	0.92	*0.75*
BF, RP (31)							**0.17**	**0.11**
BF, CO (39)								**0.92**
BF, WK (39)								

Notes: There were no fire return intervals (FRIs) in the Herb Tundra Zone and only four FRIs in the Deciduous Woodland Zone at Xindi Lake; thus, these zones were not compared. Zone abbreviations are: Shrub Tundra (ST), Deciduous Woodland (DW), Forest–tundra (FT), and Boreal Forest (BF). Site abbreviations are: Ruppert (RP), Xindi (XI), Code (CO), Wild Tussock (WK). Numbers in parentheses are the sample sizes for each zone.

* $P \leq 0.05$.

the Herb Tundra Zone (Anderson et al. 2004). In contrast, vegetation flammability changed dramatically with the expansion of *B. glandulosa*, which has highly resinous stems (Dugle 1966), burns readily (de Groot and Wein 2004), and resprouts well after fires (de Groot and Wein 1999). We propose, therefore, that increased landscape flammability was the primary driver of increased burning during the Shrub Tundra Zone. This inference is also compatible with the hypothesis that the extinction of grazing megafauna (e.g., *Equus*, *Mammuthus*) and the arrival of humans was the primary driver of increased shrub cover (Guthrie 2006). The co-occurring changes in climate, vegetation, megafauna, and human populations makes this period unusually complex ecologically.

Deciduous Woodland Zone.—With the development of deciduous woodlands ca. 10 500 yr BP, fires became less common ($\mathrm{FRI}_{\mathrm{mean}}$ 251 yr [156–347]; Fig. 7) and produced little charcoal (Fig. 4, Appendix B). Given regional evidence that summers that were 1°–2°C warmer and 25%–40% drier than present (Edwards et al. 2001, Anderson et al. 2004, Kaufman et al. 2004), one would predict an increase, rather than decrease, in fire activity during this period. Though inconsistent with direction of climate change, the decline in fire during this period is consistent with the lower flammability of deciduous trees and their tendency to act as fire breaks in modern boreal forests (Johnson 1992, Cumming 2001, Hely et al. 2001). Thus, one scenario for the decrease in fire occurrence in this zone is that deciduous trees reduced fire spread across the landscape. The association of *Populus* pollen and decreased fire occurrence in our records differs from studies from southern Alaska (Anderson et al. 2006) and eastern Canada (Richard et al. 1992, Carcaillet and Richard 2000), which inferred high fire occurrence during early Holocene periods with a presence of *Populus*. For example, at Paradox Lake (Fig. 1) on the Kenai Peninsula, Alaska, Anderson et al. (2006) infer that fires were common ($\mathrm{FRI}_{\mathrm{mean}}$ of 77 yr, ±49 SD) when *Populus* pollen was abundant (8500–10 700 BP). Though it is difficult to reconcile the short FRIs at Paradox Lake with the low CHAR in the Paradox record, this finding suggests that *Populus* itself does not preclude frequent burning. Climatic difference between the Kenai Peninsula and Brooks Range may have resulted in different ignition rates and moisture levels during this period. The differences in studies, plus an alternative climatic interpretation of increased moisture during the Deciduous Woodland Zone (Anderson and Brubaker 1993), suggest the possibility that both climate (via increased moisture) and vegetation lower the probability of fire.

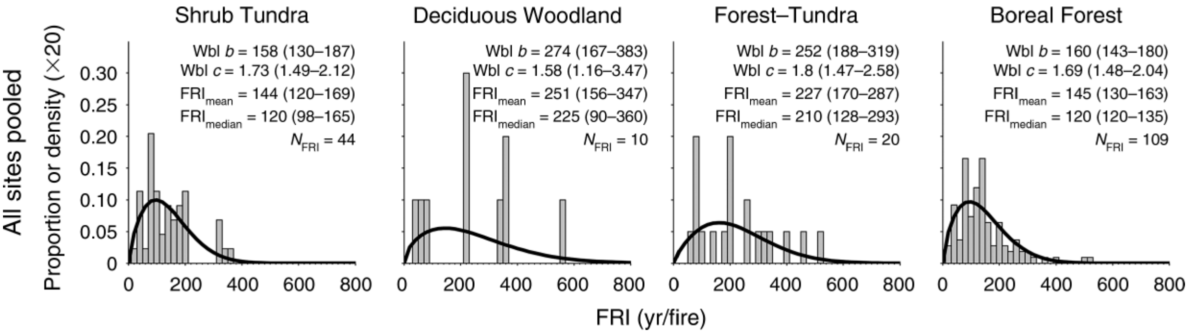


FIG. 7. Results from the analysis of pooled fire return intervals (FRIs). For each vegetation zone, we show distributions of FRIs, fitted Weibull models, Weibull *b* and *c* parameters (95% CI), median and mean fire return intervals ($\mathrm{FRI}_{\mathrm{median}}$, $\mathrm{FRI}_{\mathrm{mean}}$; 95% CI), and number of FRIs in each vegetation zone. Results from statistical comparisons are summarized as in Table 3 and Fig. 6. Note that Wild Tussock Lake (WK) is not included in the pooled record for the Forest–tundra Zone because of statistical differences between WK and Ruppert Lake (RP) during this period (Table 3, Fig. 6).

Untangling the interactions between climate, vegetation, and fire in the Deciduous Woodland Zone remains an important goal of future research and requires more precise paleoclimate records from this region.

Forest–tundra Zone.—Fire return intervals decreased slightly, but not significantly, with the establishment of *P. glauca* in the mid-Holocene (FRI_{mean} 227 yr [170–287]; Fig. 7). Summer temperatures cooled and relative moisture increased in this zone (but remained drier than present; Abbott et al. 2000, Anderson et al. 2001, Edwards et al. 2001). Although temperature and moisture trends would have reduced fire activity compared to the previous period, the unchanging FRI_{mean} values suggest that these climatic effects were balanced by the increase in landscape flammability resulting from the replacement of *Populus* by *P. glauca*. In addition, increased CHARs and peak magnitudes in this zone (Fig. 4, Appendix B) suggest greater biomass burning per fire due to increased fuel loads. Unlike other zones, fire regimes varied across the study region, with significantly higher fire activity in the east (WK) compared to the west (RP; Fig. 6). As pollen records do not indicate a gradient in vegetation that would account for this pattern (Appendix B), the shorter FRIs at WK suggest a gradient in climatic controls of fire during this period. Unfortunately, evaluating this possibility is difficult with existing paleoclimate records. Overall, FRI_{mean} values in this zone are at the lower end of estimated fire rotation periods in modern forest–tundra (180–1000+ yr; Payette et al. 1989, Kasischke et al. 2002), possibly reflecting the generally warmer, drier conditions during the Forest–tundra Zone compared to modern (Anderson et al. 2004).

Boreal Forest Zone.—A decrease in FRI_{mean} at two of the three study sites coincided with the development of *P. mariana*-dominated forests ca. 5500 yr BP (pooled FRI_{mean} of 145 yr [130–163]; Table 2, Figs. 6 and 7). The absence of a decrease in FRIs at WK is attributable to the significantly lower FRIs in the previous zone at this site (as described in the previous paragraph). Few studies provide detailed information on mid- and late-Holocene climate change in Alaska (e.g., Hu et al. 2003), making it impossible to pinpoint climatic factors causing the fire-regime shift at the transition to *P. mariana*-dominated forests. However, several lines of evidence indicate that effective moisture increased to near-modern levels by ca. 5000 yr BP and that temperatures continued to cool into the late Holocene (5000–0 BP; Ellis and Calkin 1984, Evison et al. 1998, Abbott et al. 2000, Anderson et al. 2001, 2004). Since these changes should have reduced fire ignition and spread, the increase in fire activity was likely due to increased landscape flammability associated with greater conifer density and the flammable fuels of *P. mariana* (Viereck et al. 1986, Johnson 1992). Increased fuel abundance and greater charcoal production per fire is also consistent with maximum peak magnitudes and/or CHARs reached at all sites within this zone (Fig. 4, Appendix B). Our interpretation that the shift to *P. mariana* dominance increased fire occurrence in this zone is consistent with several other Holocene fire-history studies from boreal Alaska (Dune, Low, Moose, and Chokosna Lakes, Fig. 1; Lynch et al. 2002, 2004*b*, Hu et al. 2006) and with modeling studies showing higher fire frequencies with increased *P. mariana* abundance (Rupp et al. 2002). However, these findings contrast with the Paradox Lake record (Anderson et al. 2006), which indicates that FRI_{mean} increased from 81 (±41 SD) to 130 (±66 SD) yr at the time of *P. mariana* arrival ca. 4600 yr BP. Thus, although the FRIs for the boreal forest period are similar to the central Brooks Range, the direction of change differed. It is possible that the low density of *P. mariana* at Parodox Lake (Anderson et al. 2006) did not cause a large enough increase in landscape flammability to override the effects of cooler, moister conditions on fire regimes.

Vegetation mediates the impacts of climate change on fire regimes

Vegetation influences fire regimes by affecting the size, abundance, and spatial patterns of fuels across a landscape, all of which potentially dampen or amplify the direct impact of climate change on fire regimes. A unique value of paleorecords is their ability to "observe" shifts in fire regimes as vegetation and climate change simultaneously. From this perspective, paleorecords from the south-central Brooks Range support inferences of modern studies that vegetation can substantially alter the direct effects of climate change on fire regimes.

Vegetation change amplifies the impact of climate on fire regimes when climate change directly promotes fire occurrence (e.g., via increased ignitions and fuel drying) and increases the abundance and continuity of fuels. For example, the shift from herb- to birch-dominated shrub tundra ca. 13 300–14 300 yr BP amplified the direct effects of climate warming by increasing the abundance and connectivity of woody fuels. Similarly, as climate warmed through the late-glacial and early Holocene periods across the northwestern United States, an increase in abundance of woody biomass appears to have amplified climate-driven increases in fire frequencies (Marlon et al. 2006). Modern studies demonstrate the impact of vegetation on fire regimes at shorter time scales. For example, interannual climate variability associated with the El Niño Southern Oscillation promotes fires in ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests of the southern Rocky Mountains (Veblen et al. 2000) and southwestern United States (Baisan and Swetnam 1990) by increasing herbaceous plant growth in wet springs and then facilitating fuel drying during summer droughts in following years.

A more unexpected outcome of vegetation change occurs when vegetation alters the probability of fire in the opposite direction of climate. Alaskan paleorecords include two examples of this effect. First, fire activity decreased during the early Holocene when deciduous woodlands expanded into shrub tundra, despite warmer-than-present summers (Fig. 7). In this case, the low flammability of deciduous trees reduced fire ignition and/or spread and overrode the impacts of increased temperatures on fire occurrence. Second, cooler and wetter climate in the mid-to-late Holocene would have reduced the probability of fire at the time climate-induced increases in *P. mariana* densities increased landscape flammability. The net result of these vegetation and climate shifts was greater fire occurrence, with the positive effect of increased fuel abundance overriding the negative effects of climate change (Figs. 6 and 7; Lynch et al. 2002, Hu et al. 2006). The potential for vegetation change to negate the direct impacts of climate on fire regimes is not unique to boreal regions. In grassland ecosystems of North America, the impact of drought on fire regimes has been mediated by vegetation change for thousands of years (Clark et al. 2002, Brown et al. 2005). By reducing grass cover, centennial-scale droughts limited this fuel source and reduced fire frequency. Periods of increased moisture promoted extensive grass cover, which in turn facilitated frequent fires.

Numerous modern examples illustrate that vegetation change can alter fire regimes independent of climate. For example, by reducing the abundance of fine fuels, livestock grazing can lower fire frequencies and fire intensity in ecosystems ranging from conifer forests (Swetnam et al. 1999) to savannas (Roques et al. 2001). Similarly, exotic grass introductions in a variety of ecosystems worldwide show that fire frequencies can increase rapidly when vegetation change adds fuels to a landscape (e.g., Dantonio and Vitousek 1992). If vegetation shifts represent a change to or from a fuels-limited system, their impacts on fire regimes can be dramatic. Thus, when vegetation shifts change the degree to which fuels limit fire in an ecosystem, the impacts of vegetation change can be more important than the direct cause of the vegetation change itself (e.g., land use, exotic species introduction, climate change).

A major conclusion of our study is that, over the past 15 000 years, vegetation shifts in the south-central Brooks Range strongly mediated the direct impacts of climate change on fire regimes by modifying the degree to which fire regimes were fuels limited. Combined with modern and paleostudies from other regions, these Alaskan examples lead to the general inference that future fire regimes will be determined by direct climate–fire relationships, in addition to the indirect impacts of climate on vegetation communities. In modern or future systems where fire occurrence is limited more by the abundance and continuity of fuels than by climate (i.e., ignition and short-term drought), vegetation shifts may play the more important role in shaping fire regimes than the direct impacts of climate change alone.

Implications for global change in arctic and subarctic ecosystems

Fire regimes in past herb tundra, shrub tundra, and deciduous woodlands reflect the effects of climates and vegetation biomes that do not have counterparts on the modern landscape (i.e., no analog climate and vegetation; Anderson et al. 1989, Bartlein et al. 1991, Williams and Jackson 2007; Appendix B). Given the potential for novel vegetation and climate in the future (Edwards et al. 2005, Williams and Jackson 2007), our results have important implications for anticipating future fire regimes in arctic and subarctic ecosystems.

Our finding that vegetation mediated the impacts of climate change emphasizes the importance of biological–physical feedbacks in past arctic and subarctic ecosystems. While direct climate–fire relationships may predict future fire regimes at annual to decadal time scales (Kasischke et al. 2002, Duffy et al. 2005), the paleorecord highlights that feedbacks between climate, vegetation, and fire can override the direct effects of climate change at longer time scales. For example, in boreal forests future warming is expected to increase the area burned in many regions, with a secondary effect of replacing coniferous with deciduous forest types (Rupp et al. 2000, Calef et al. 2005, Flannigan et al. 2005, Johnstone and Chapin 2006). Our finding of infrequent fires during the warmer-than-present Deciduous Woodland Zone implies that future increases in burning could lower the probability of subsequent fires by favoring succesional forests with less flammable fuels. If deciduous stands are maintained across the landscape via gap–phase replacement (Cumming et al. 2000, Johnstone and Chapin 2006), this negative feedback mechanism could result in fires being less frequent than would be predicted by climate's direct effect on area burned.

The importance of biological–physical feedbacks is also highlighted by high fire frequencies in past shrub tundra. Our records provide a clear precedence that shrub-dominated tundra can sustain higher fire frequencies than present-day tundra. Thus, the future expansion of tundra shrubs (Tape et al. 2006, Walker et al. 2006) coupled with decreased effective moisture (ACIA 2004) could enhance circumarctic burning and initiate important feedbacks with the climate system. Recent studies of modern tundra fires suggest the possibility for both short- and long-term impacts of increased tundra burning ranging from increased summer soil temperatures and moisture levels (Liljedahl et al. 2007) to the release ancient soil carbon from increased permafrost thawing and organic-layer consumption (Racine et al. 2006, Liljedahl et al. 2007). Given the concern over the fate of terrestrial carbon in tundra and other high-latitude ecosystems (Zimov et al. 1999, Chapin et al. 2000, Mack et al. 2004, Weintraub and Schimel 2005), the evidence of fires in early Holocene tundra should motivate research into the controls of tundra fire regimes and links between tundra burning and the climate system.

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APPENDIX A

Supplementary methods: (1) modern analog analysis; (2) *Picea* pollen grain classification via discriminant analysis; (3) charcoal analysis: locally defined thresholds, minimum-peak screening, and signal-to-noise index; and (4) likelihood-ratio test for comparing fire-return-interval distributions (*Ecological Archives* M079-007-A1).

APPENDIX B

Supplementary results: (1) radiocarbon dates; (2) pollen and charcoal records; (3) distribution of raw charcoal accumulation rates; (4) *Picea* pollen grain classification via discriminant analysis; and (5) likelihood-ratio test results for comparisons of pooled fire-return-interval distributions (*Ecological Archives* M079-007-A2).

SUPPLEMENT

Matlab source code for statistically comparing distributions of fire return intervals using maximum-likelihood estimates of Weibull models and a likelihood-ratio test (*Ecological Archives* M079-007-S1).