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Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes

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Abstract

When spruce beetles (*Dendroctonus rufipennis*) thin a forest canopy, surviving trees grow more rapidly for decades until the canopy closes and growth is suppressed through competition. We used measurements of tree rings to detect such growth releases and reconstruct the history of spruce beetle outbreaks at 23 mature spruce (*Picea* spp.) forests on and near the Kenai Peninsula, Alaska and four mature white spruce (*Picea glauca*) forests in Kluane National Park and Reserve, Yukon Territory. On the Kenai Peninsula, all stands showed evidence of 1–5 thinning events with thinning occurring across several stands during the 1810s, 1850s, 1870–1880s, 1910s, and 1970–1980s, which we interpreted as regional spruce beetle outbreaks. However, in the Kluane region we only found evidence of substantial thinning in one stand from 1934 to 1942 and thinning was only detected across stands during this same time period. Over the last 250 years, spruce beetle outbreaks therefore occurred commonly among spruce forests on the Kenai Peninsula, at a mean return interval of 52 years, and rarely among spruce forests in the Kluane region where cold winter temperatures and fire appear to more strongly regulate spruce beetle population size. The massive 1990s outbreaks witnessed in both regions appeared to be related to extremely high summer temperatures. Recent outbreaks on the Kenai Peninsula (1971–1996) were positively associated with the 5-year backwards running average of summer temperature. We suggest that warm temperature influences spruce beetle population size through a combination of increased overwinter survival, a doubling of the maturation rate from 2 years to 1 year, and regional drought-induced stress of mature host trees. However, this relationship decoupled after 1996, presumably because spruce beetles had killed most of the susceptible mature spruce in the region. Thus sufficient numbers of mature spruce are needed in order for warm summer temperatures to trigger outbreaks on a regional scale. Following the sequential and large outbreaks of the 1850s, 1870–1880s, and 1910s, spruce beetle outbreaks did not occur widely again until the 1970s. This suggests that it may take decades before spruce forests on the Kenai Peninsula mature following the 1990s outbreak and again become susceptible to another large spruce beetle outbreak. However, if the recent warming trend continues, endemic levels of spruce beetles will likely be high enough to perennially thin the forests as soon as the trees reach susceptible size.

Keywords: Alaska; Climate warming; *Dendroctonus rufipennis*; Growth release; Forest disturbance; Spruce beetle; Yukon Territory

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1. Introduction

The 1990s witnessed massive outbreaks of bark beetles (*Dendroctonus* spp.) in conifer forests across western North America; ranging from Alaska and the Yukon Territory to the southwestern United States (Holsten et al., 1999; Nijhuis, 2004; Logan and Powell, 2005). The regional synchrony of these outbreaks led investigators to examine the relationship between their occurrence and the unusually warm worldwide temperatures of the 1990s. Models based on such examinations and climate warming scenarios predicted declines among conifer forests across North America as insect pests expand their ranges, the tree species they infest, and the aggressiveness of their attacks (Harrington et al., 2001; Logan et al., 2003; Juday et al., 2005; Logan and Powell, 2005).

Recent outbreaks of spruce beetles have caused extensive mortality of spruce across more than 1.2 million ha of forest in

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south-central Alaska from 1989 to 2004 (U.S. Forest Service, 2005) and more than 350,000 ha of forest in the southwestern Yukon Territory from 1990 to 2004 (R. Garbutt, Canadian Forest Service, unpublished data). Advance warning of these massive outbreaks would have helped forest managers in these regions respond more effectively to the rapid changes in forest condition (Ross et al., 2001). However, a poor understanding of the factors that contributed to these outbreaks has made forecasting such events difficult. Previously, spruce beetle populations erupted to outbreak levels when forests were mature and a triggering disturbance, such as windthrow, fire, or harvest, created sufficient numbers of injured and dying spruce which were favorable for beetle reproduction (Schmid and Frye, 1977; Werner et al., 1977; Holsten, 1990; Safranyik et al., 1990). However, the recent outbreaks were different from previous regional events in that they did not result from a clearly identifiable disturbance. Furthermore, it is unclear whether the recent outbreaks were within the normal historical range of outbreak sizes (Ross et al., 2001) because records of outbreaks in the region date back only to 1920 (Holsten, 1990); less than the mean interval of 116 years between outbreaks in Colorado (Veblen et al., 1994).

Evidence for past outbreaks of spruce beetles can be found in growth pulses of trees that survived previous outbreaks (Veblen et al., 1991a,b). Spruce beetles selectively attack mature spruce, because large, slow-growing spruce are less able to resist the establishment of adult spruce beetles in the inner bark or phloem layer (Hard et al., 1983; Hard, 1987). After the overstory spruce are killed by spruce beetles, the smaller surviving spruce have less competition for light, soil moisture, and nutrients, and often increase their growth abruptly (Veblen et al., 1991a,b). In this paper, we used the dendrochronology techniques developed by Veblen et al. (1991a,b) and reconstructed spruce beetle outbreak histories among mature spruce forests in the Kenai Peninsula and Cook Inlet region of south-central Alaska and the Kluane National Park and Reserve in the southwestern Yukon Territory. Specifically, we reconstructed outbreak histories back to the mid-1700s in these two regions using measurements of annual growth rings among mature white (*Picea glauca*), Sitka (*P. sitchensis*), and Lutz spruce (*P.* x *luztii*) in order to (1) estimate the timing, magnitude, and extent of previous spruce beetle outbreaks; (2) estimate the return interval of beetle outbreaks; (3) compare spruce beetle disturbance regimes between the more maritime forests of south-central Alaska and arid interior forests of the southwestern Yukon Territory. We then used data from aerial surveys of forest area infested by spruce beetles from the Kenai Peninsula from 1971 to 2003 to test the hypothesis that the occurrence of regional outbreaks of spruce beetles was related to warm summer temperatures.

2. Materials and methods

2.1. Study area

The Kenai Peninsula–Cook Inlet region (Kenai Peninsula hereinafter) lies in south-central Alaska west of Prince William Sound (Fig. 1). The topography of the area is variable with the Kenai Mountains forming a rugged spine of peaks, icefields, and glaciers along the eastern side of the Peninsula, with elevations rising to 2000 m. The Kenai Lowland forms a broad plateau 15–100 m in elevation, extending to Cook Inlet. On the

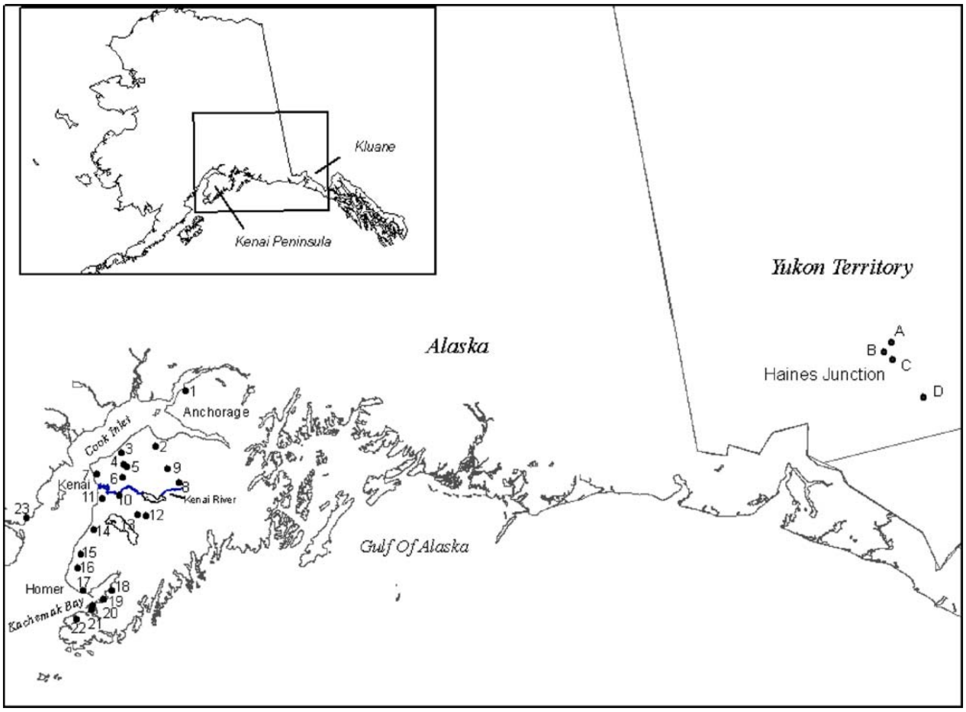

Fig. 1. Locations of mature spruce forests sampled in the Kenai Peninsula—Cook Inlet region, Alaska, USA, and Kluane National Park and Reserve, Yukon Territory, Canada. Site names are shown in Fig. 3.

coast, the climate was moderately maritime with a mean annual temperature of 1.1 °C and mean annual precipitation of 485 mm (WRCC, 2005). The climate graded to a more continental condition in the rainshadow of the mountains. The forests of the Kenai Lowland were transitional between coastal rainforests of Sitka spruce and boreal forests of white spruce and resin birch (*Betula neoalaskana*) that are more typical of interior Alaska. A hybrid zone of Lutz spruce extended north from Kachemak Bay to the Kenai River. We separated the Kenai Peninsula into two geographic areas divided by Tustumena Lake in our analyses, Northern and Southern Kenai Peninsula. The area north of Tustumena Lake contained a diverse mix of forest types and stand ages, due in part to an active fire regime (De Volder, 1999). The area south of Tustumena Lake was primarily continuous mature white/Lutz spruce forest where most stands have not burned for hundreds of years (Berg et al., this issue).

Kluane National Park and Reserve (Kluane hereinafter) lies in the southwestern corner of the Yukon Territory, an area dominated by mountains and glaciers. Approximately 18% of the area was vegetated, largely along the Shakwak Trench, Duke Depression, and the flanks of the Kluane Range (Environment Canada, Parks, 1987). The area is continental in climate with a mean annual temperature of −2.5 °C and mean precipitation of 305 mm (W. Miller, Environment Canada, personal communication). The Kluane forests were primarily composed of white spruce and quaking aspen (*Populus tremuloides*).

2.2. Dendrochronology and spruce beetle outbreaks

We used measurements of spruce growth rings to detect past outbreaks of spruce beetles following the methods of Veblen et al. (1991a,b). This assumes that growth releases of understory spruce, as evidenced by larger growth rings, are best explained by past attacks by spruce beetles and not by some other source of spruce mortality. This assumption is reasonable among spruce forests in south-central Alaska and southwestern Yukon Territory as (1) no other forest insect or tree disease is known to preferentially kill mature spruce and create accelerated growth among understory trees (Holsten et al., 2001); (2) fires among spruce stands in the region are typically stand-replacing events with few surviving spruce (Rowe and Scotter, 1983); (3) windstorms in the region only blow down mature spruce on a sporadic or localized basis; (4) few stands in the region show evidence of stumps from historic selective logging (E.E. Berg, U.S. Fish and Wildlife Service, unpublished data).

We sampled growth rings from mature white, Sitka, and Lutz spruce at 23 sites on and near the Kenai Peninsula from 1994 to 2002 and from mature white spruce at four sites in Kluane in 2001 (Fig. 1). On the Kenai Peninsula, our selection of sites was conditioned by access of stands by road, boat, or trail; limited availability of a helicopter; and permissions to enter private and public lands. We chose most sites to represent typical mature spruce forests with no visible signs of fire, windthrow, past cutting, or other human disturbance. However, we chose three sites because of known historical disturbances: Polly Creek for an 1899 report of a dead forest, Moraine Lake for evidence of an 1860s fire, and Humpy Creek for a report of a 1970s blowdown. Similarly we chose the four Kluane sites to represent typical mature spruce forests in road accessible areas. The Papineau Road site was selected because of reports of spruce beetle outbreak in the 1940s (Furniss, 1950; Downing, 1957). Mature forest stands in the Kluane area usually exhibited evidence of previous fire activity (Francis, 1996; Hawkes, 1983) so we also sampled growth rings from well-preserved burn poles to date previous fires.

At most sites, we extracted cores from 37 to 258 mature white, Lutz, or Sitka spruce with increment borers. We preferentially sampled larger trees to get the longest possible time record and extracted cores at 70–130 cm above the root crown to avoid buttress swell. To avoid growth effects unrelated to competition, we did not sample trees with scars, broken tops, severe lean, or multiple or deformed trunks. Cored trees were located at least 10 m apart, and sampled stands ranged from 2 to 100 ha. We collected cross-sections from stumps at four Kenai sites following recent logging (Juneau Creek, Falls Creek, Anchor River, and Homer) and at one site following forest clearing for a new road (Bufflehead Road). At Homer we collected approximately 550 cross-sections in a complete census of a 1.75 ha logged stand, and measured ring-widths on a randomly selected subsample of 49 cross-sections. At Bufflehead Road we collected cross-sections from all mature spruce cut along a 1.1-km × 7-m right-of-way along a new road.

We processed all cores and cross-sections using standard dendrochronological methods (Stokes and Smiley, 1968). We measured ring-widths from cores and cross-sections with a Velmex® sliding bench micrometer, visually cross-dated ring-width series with marker rings when possible, and confirmed dates with program COFECHA (Holmes et al., 1986). We used program JOLTS (R.L. Holmes, University of Arizona, unpublished data), to detect growth releases for individual trees by calculating for each year a ratio of the forward 10-year mean of growth-ring widths to the backward 10-year mean of growth-ring widths. If this ratio exceeded 2.0, we scored a release for that year (Fig. 2). Using the 1950–1990 record as a calibration period, we found the 10-year mean window for

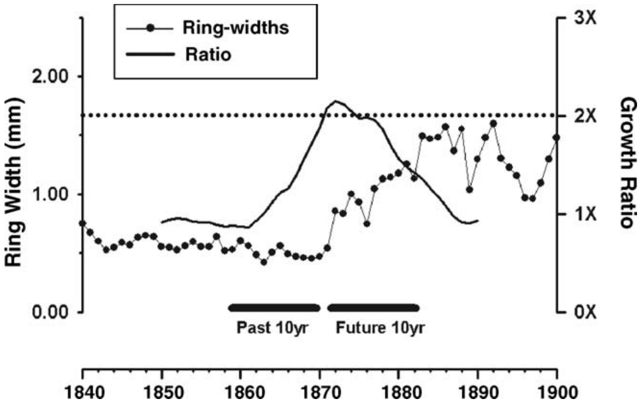

Fig. 2. A growth release was defined as a doubling (2×) of the ratio of the forward 10-year mean to the past 10-year mean of annual ring-widths (growth ratio) in a spruce tree. In this example, a growth release was detected in 1871.

evaluating releases to be (1) long enough to smooth the 5- to 8-year periodicity in ring-widths associated with the El Niño–La Niña cycle and (2) short enough to detect short duration releases that only lasted 4–10 years following low-intensity outbreaks. Our choice of 2.0 as the release factor was conservative, however, and may have missed detecting some small-scale, short-lived canopy thinning events. Using this method the first and last 10 years of the ring-width series for an individual tree were not available for detecting releases because of insufficient number of years to calculate the release factor. To control for lack of independence among releases within an individual tree, we only counted the first year of release and omitted any of the releases in the ensuing 10 years. After this 10-year censuring of data, the tree was again available for detecting releases.

We estimated the probability of encountering the observed number of first-year releases in a given 5-year period and stand using a binomial model described by Ross (1988). We used a minimum sample size of 10 trees for each year for each stand and chose the 5-year interval to smooth temporal variation among first-year releases. Specifically, we first estimated for each stand the overall probability of a tree releasing across all years of sampling. This was calculated by taking the ratio of the total number of first-year releases observed among all trees sampled to the total number of available tree-years; the latter omitting for each tree the first and last 10 years of the tree-ring series and the decades following first-year releases. Next, we tallied separately for each 5-year period both the number of trees releasing and the number of trees available for release in the stand and then used the binomial model to compare these to the overall probability of a tree releasing in the same stand across all years of sampling. For example, given an overall probability of 1% that a tree in a stand will express a first-year release, the binomial formula calculated that the probability of 12 out of 80 trees exhibiting a first-year release during a 5-year period (80 trees × 5 years = 400 tree-years) was 0.0006, a highly significant event compared to the expected value of 4 releases over 5 years for the 80 trees (0.01 year × 400 tree-years).

2.3. Models of spruce beetle outbreaks relative to summer temperature

We used autoregressive logistic regressions (Allison, 1999) to model the probability that a large spruce beetle outbreak (>15,000 ha) would occur relative to temperature, geographic area, and their interaction. We constructed the binary response variable using data on forest area infested from 1971 to 1996 as estimated from aerial surveys of recently killed spruce with red needles conducted by the U.S. Forest Service and Alaska Division of Forestry (U.S. Forest Service, 2004). We chose the large outbreak size so as to include equal numbers of observations of outbreaks and non-outbreaks. We also excluded data after 1996 because the depletion of spruce available after the peak year of the recent outbreak would decouple potential relationships between outbreaks and temperature. We restricted analyses to data from the Kenai Peninsula because we only had a short time series of data (1994–2004) available from similar surveys in the Kluane region by the Canadian Forest Service (Garbutt, 2005).

We included as a categorical explanatory variable, geographic area (area), by separating the Kenai Peninsula into two areas, Northern and Southern Kenai Peninsula. We computed annual estimates of mean summer temperature from May to August (°C) using meteorological data collected at the city airports of Kenai (Northern Kenai Peninsula) and Homer (Southern Kenai Peninsula; WRCC, 2005). We chose the period from May to August because it covered the phase of the spruce beetle life cycle when warm ambient temperature can cause spruce beetle maturation to accelerate from 2 years to 1 year (Werner and Holsten, 1985a,b). We examined seven explanatory variables of annual summer temperature; the current year and backwards running averages of 2–7 years.

For each of the seven temperature explanatory variables we developed autoregressive logistic regression models with (1) temperature alone, (2) temperature and area, and (3) temperature, area, and their interaction. This resulted in a total of 21 candidate models whose relative fit we compared using Akaike's information criterion adjusted for small samples size (AIC_c), standardized by subtracting the AIC_c value from the model with lowest AIC_c (Δ_i), and expressed as a relative likelihood that the model was the best among the set of candidate models (Akaike weight, w_i). We considered models with $\Delta_i \leq 2.0$ to be best supported by the data. We also summed Akaike weights ($\sum w_i$) to summarize the overall support for models that shared a common effect (Burnham and Anderson, 2002). Finally we used a two-tailed, paired *t*-test to compare between the Northern and Southern Kenai Peninsula (1) annual summer temperature from 1971 to 1996 and (2) annual area infested by spruce beetles from 1971 to 2003.

3. Results

3.1. Dendrochronology and spruce beetle outbreaks

All 23 stands of white, Sitka, and Lutz spruce that we examined on the Kenai Peninsula exhibited growth releases during the last 200–250 years with many showing evidence of repeated thinning. However, we only detected evidence of fire in one stand (Fig. 3). We detected statistically significant thinning events in several stands on the northern (6 of 13 stands) and southern (5 of 10 stands) Kenai Peninsula in the 1810–1820s (Figs. 3 and 4), with moderate percentages of trees released (up to 50% of trees released per 5 years). Thinning events were detected across most sites (17 of 23 sites) during the 1870–1880s with southern sites showing the strongest evidence of major thinning (up to 60% of trees released per 5 years), including the Polly Creek site on the west side of Cook Inlet. Following this large and intensive outbreak many spruce in effected stands experienced accelerated growth (≥2 times the historical average growth in the stand) for 60–80 years, into the 1950s after which growth slowed and became suppressed (Fig. 5). Most northern Kenai Peninsula sites showed moderate releases in the 1910–1920s (8 of 13 sites) and more intense

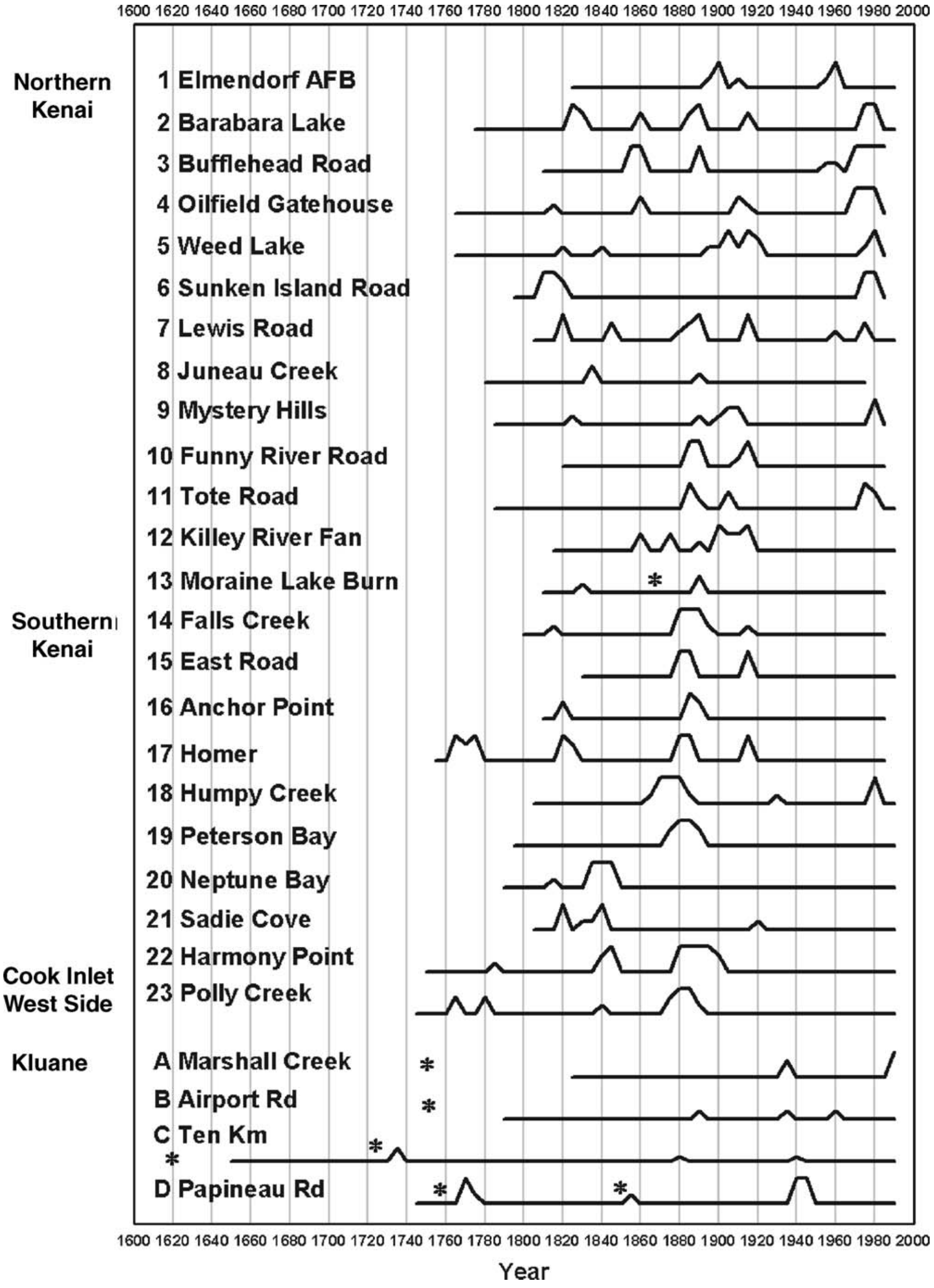

Fig. 3. Growth release patterns among mature spruce at 23 sites in Kenai Peninsula—Cook Inlet, Alaska and four sites in Kluane National Park and Reserve, Yukon Territory, as detected by program JOLTS. Peaks show significance of releases among spruce trees in a given stand during discrete 5-year intervals: small peaks ($0.01 < P \leq 0.05$), medium peaks ($0.001 < P \leq 0.01$), large peaks ($P \leq 0.001$). Dates of fires (*) were determined by cross-dating burned poles against live trees.

releases during the 1970s (7 of 13 sites) (Fig. 5). Although few statistically significant outbreaks were detected in the early 1960s, most sites (20 of 23 sites) exhibited short-lived growth pulses of 3–5 years that were suggestive of light thinning events (Fig. 5). During the 1990s all 23 sites sustained major infestations and spruce mortality. The mean and median return interval between statistically significant release events, which we interpret as either local or regional spruce beetle outbreaks, was 52 and 45 years, respectively (Fig. 6).

Of the four Kluane stands, only Papineau Road showed a substantial growth release, confirming an outbreak reported from the 1940s (Furniss, 1950; Downing, 1957). The other three Kluane stands showed small but statistically significant releases in the 1930 and 1940s, as well as other releases not correlated among stands. These 1930–1940s outbreaks were further verified by cores extracted from both standing and downed spruce with beetle scars on the Papineau Road site which had estimated death dates ranging from 1934 to 1942, 6–8 years before construction of the Haines Road began in the 1940s. Surviving trees on the Papineau Road site exhibited strong releases with many still growing today at more than twice the historical average growth rate for the stand (Fig. 5).

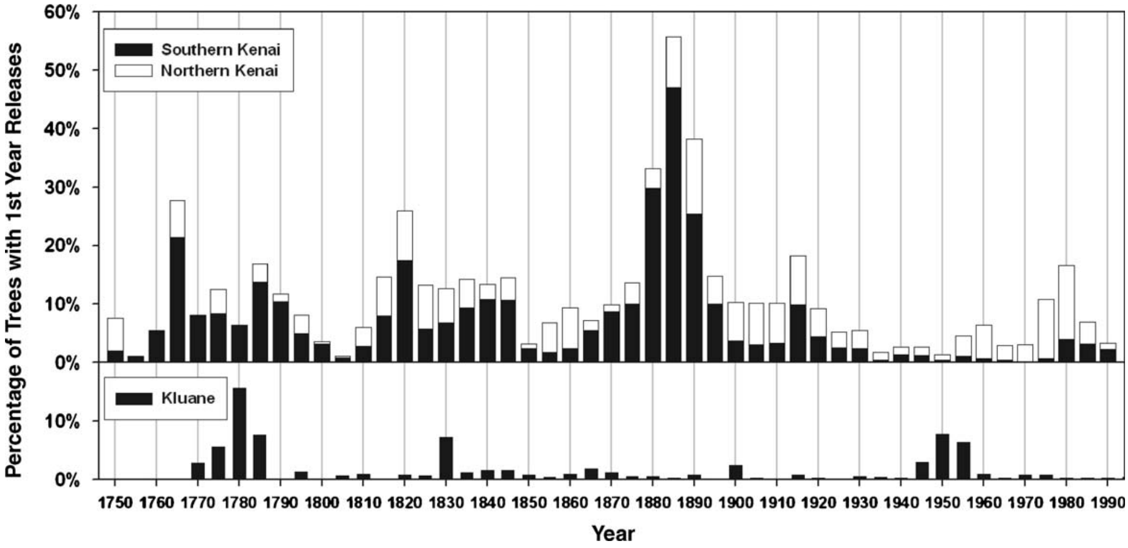

Fig. 4. Average percentage of trees in a stand showing a growth release during a 5-year period; southern Kenai (10 stands), northern Kenai (13 stands), and Kluane (4 stands).

Burn poles on this site provided evidence for fires in 1758 and 1850. With the exception of the periods of 1934–1942 and 1994–2004, the white spruce forests examined in the Kluane region had not experienced a major spruce beetle outbreak within the last three centuries. Fires, however, were detected on all four Kluane sites and limited the early parts of our chronologies. At all four sites at least moderate infestations were observed in the 1990s and early 2000s.

3.2. Models of spruce beetle outbreaks relative to summer temperature

When we examined the record of annual red needle area relative to summer temperature, regional spruce beetle outbreaks appeared to be associated with periods of warm summers (Fig. 7). The first major outbreak of the post-1950 period occurred in the early 1970s, following the extremely warm and dry period of 1968–1969 on the Northern Kenai Peninsula. Red-needle area dropped to nearly zero by 1975, following three cool summers from 1973 to 1975. On the Southern Kenai Peninsula, the sustained onset of warm summers beginning in 1987 was followed by substantial increase in red-needle mortality beginning in 1990 and climaxing in 1996. Notably, the relationship between spruce beetle outbreaks and temperature was not observed during the warm summers of 1997 and 2001–2004. In the Kluane region, higher than average temperatures beginning in 1989 were associated with the outbreak that continued through 2005.

The logistic regression model that best fit these data from the Kenai Peninsula was one that included a positive relationship with the backwards 5-year running average of summer temperature (Model 1, $\Delta_i = 0.0$, $w_i = 0.59$; Tables 1 and 2). A nearly equivalent model included a positive relationship with the backwards 6-year running average of temperature (Model 2, $\Delta_i = 1.21$, $w_i = 0.32$; Table 1). The best model predicted that the odds of a large outbreak occurring increased by 17.8 times (95% CI = 12.6–25.2) with each 1 °C increase in average temperature and that the probability of a large outbreak occurring equaled 0.5 at an average temperature of 10.3 °C (Table 2 and Fig. 8). Using the predicted probability of 0.5 as a cutoff, this model correctly classified 81% of the observed data, with classification better on the Southern (85%) than on the Northern Kenai Peninsula (76%). Using this model and temperature data from Kenai (1944–2003) and Homer (1932–2003), we predicted that outbreaks occurred with a probability ≥ 0.5 on the Northern Kenai Peninsula on 1960–1961, 1969–1973, 1980–1985, and 1990–2003 and Southern Kenai Peninsula on 1944, 1984, 1990–2001, and 2003. Model fit was poor for data from 1997 to 2003 with only 1 of 7 years and

Table 1
Comparisons of fit[a] among the 10 best autoregressive logistic regression models of the probability of a large spruce beetle outbreak (>15,000 ha) occurring relative to covariates for May–August average temperature (°C) and geographic areas (north vs. south) 1971–1996, Kenai Peninsula, Alaska

Model[b]	K	-2LL	AIC$_c$	Δ_i	w_i
1. temp(5 y)	3	54.5	61.0	0.0	0.42
2. temp(6 y)	3	55.7	62.2	1.2	0.23
3. temp(5 y), area	4	54.5	63.3	2.3	0.13
4. temp(6 y), area	4	55.7	64.6	3.6	0.07
5. temp(7 y)	3	59.0	65.5	4.5	0.04
6. temp(5 y), area, interaction	5	54.4	65.7	4.7	0.04
7. temp(6 y), area, interaction	5	55.7	67.0	6.0	0.02
8. temp(4 y)	3	60.8	67.3	6.3	0.02
9. temp(7 y), area	4	59.0	67.8	6.8	0.01
10. temp(4 y), area	4	60.4	69.2	8.3	0.01

[a] Model fit was compared using Akaike's information criterion adjusted for small sample size (AIC$_c$), rescaled by subtracting the lowest AIC$_c$ value (Δ_i), and expressed as a relative likelihood of the model given the data (w_i). AIC$_c$ was calculated based on the number of parameters (K), including the error term, and the -2 log likelihood (-2LL) of the model.

[b] Covariates considered for logistic regression models included geographic area (area), temperature of the current year (temp), backwards running averages of temperature of 2–7 years [temp(2 y)–temp(7 y)], and interactions between temperature covariates and area (interaction). Models not included in the table all had $w_i < 0.01$.

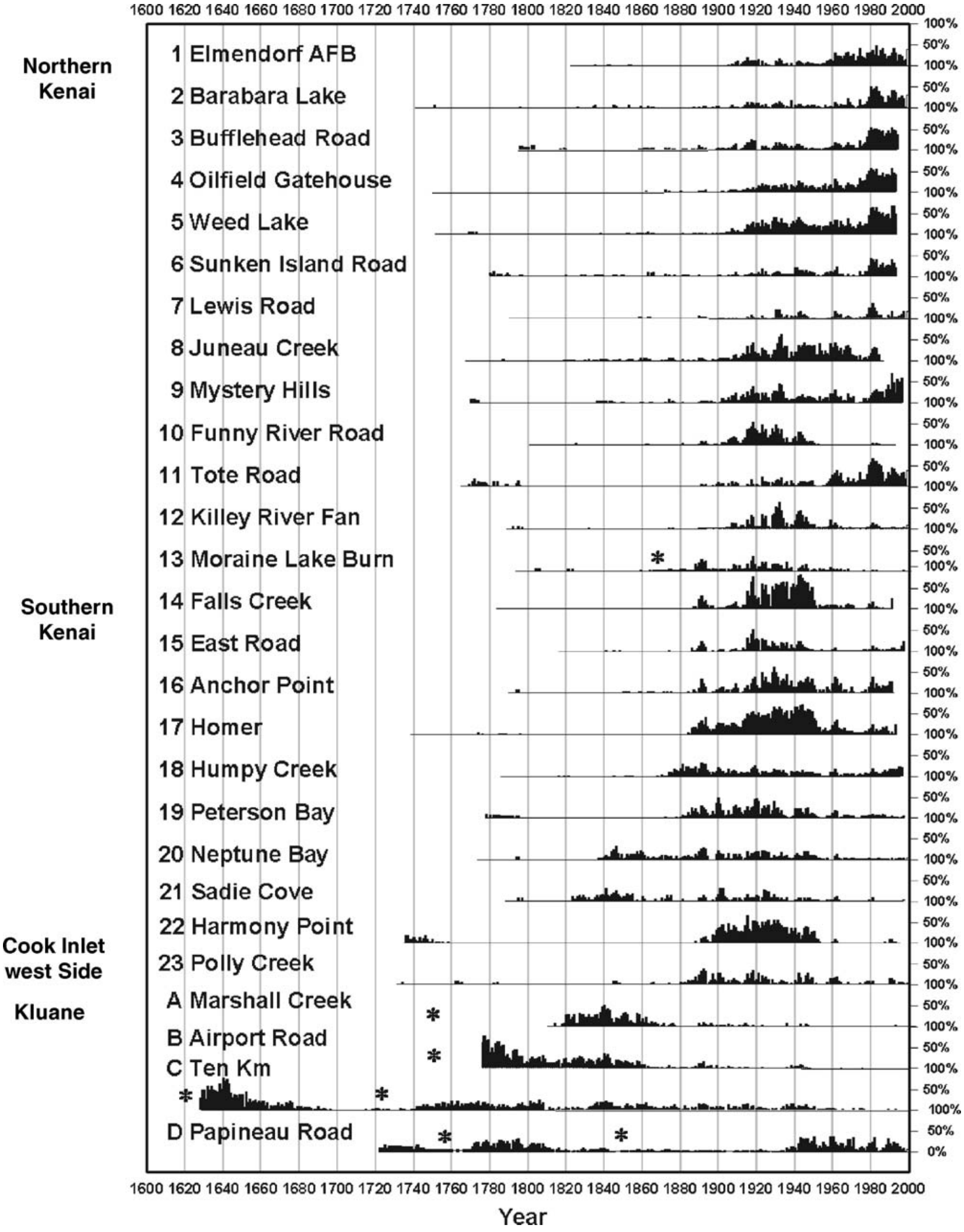

Fig. 5. Percentage of trees growing at least twice the stand average growth rate. All stands were mature or old growth white, Lutz, or Sitka spruce with up to 50% hardwoods. Dates of fires (*) were determined by cross-dating burned poles against live trees.

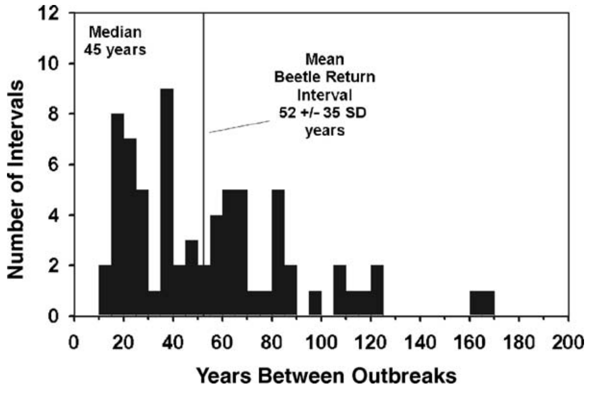

Fig. 6. Return intervals (years) between statistically significant ($P \leq 0.05$) growth releases at 23 mature spruce forests (71 total intervals), Kenai Peninsula—Cook Inlet, Alaska.

3 of 7 years classified correctly for the Northern and Southern Kenai Peninsula, respectively.

Prior to 1989, the average area infested was greater on the Northern (15,250 ± 2326 ha) than the Southern Kenai Peninsula (6703 ± 1997 ha; $t = 4.2$, d.f. = 17, $P = 0.001$; Fig. 7). From 1989 to 2003 the area infested conversely was higher on the Southern (58,919 ± 15,795 ha) than the Northern Kenai Peninsula (15,422 ± 3600 ha; $t = 2.9$, d.f. = 14, $P = 0.011$; Fig. 7). However, we did not find strong support for regional differences in the relationship between the probability of outbreaks occurring and temperature despite these differences in area infested, a slightly higher frequency of large outbreaks on the Northern (16 of 26 years) compared to the Southern Kenai Peninsula (10 of 26 years), and higher summer temperatures on the Northern (10.50 ± 0.18 °C) versus South-

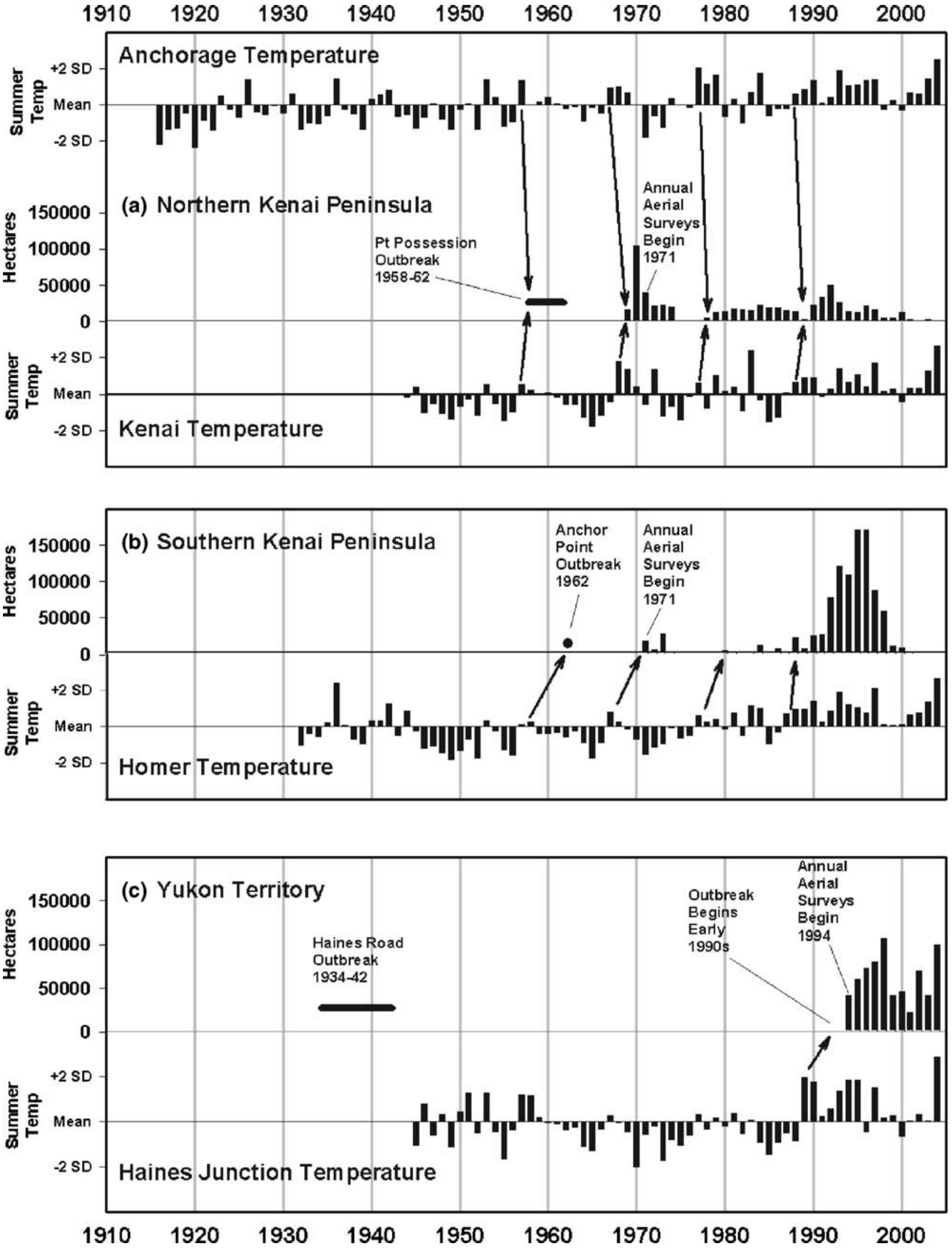

Fig. 7. Annual summer temperatures and estimates of forest area (ha) infested by spruce beetles for (a) Northern Kenai Peninsula, (b) Southern Kenai Peninsula, and (c) southwestern Yukon Territory. May–August temperatures are shown as departures from the mean, in units of standard deviations. Forest area infested by spruce beetles was estimated from aerial surveys of spruce with red-needles that are characteristic or mortality by spruce beetles starting in 1971 and 1994 for the Kenai Peninsula and Yukon Territory, respectively. Kenai forest insect monitoring began in 1950 with ground-based field reports and estimates of spruce beetle affected area.

ern Kenai Peninsula (10.16 ± 0.15 °C; $t = 2.36$, d.f. = 25, $P = 0.026$; Fig. 8). Overall the seven models with single temperature variables were better supported by the data ($\sum w_i = 0.71$) than the 7 models that included temperature and region ($\sum w_i = 0.22$) or the 7 full-factorial models ($\sum w_i = 0.06$; Table 1). All models including region suggested that the probability of outbreaks was higher on the Northern compared to the Southern Kenai Peninsula.

Table 2

Autoregressive model of the relationship between the probability of a large outbreak (>15,000 ha) occurring relative to the 5-year backwards running average of summer temperatures, Kenai Peninsula, Alaska 1971–1996

Parameter	Estimate	S.E.	Lower 95% CL	Upper 95% CL	Z	P
Intercept	−29.70	1.78	−33.20	−26.20	−16.64	<0.0001
Temp (5 y)	2.88	0.18	2.54	3.23	−16.35	<0.0001

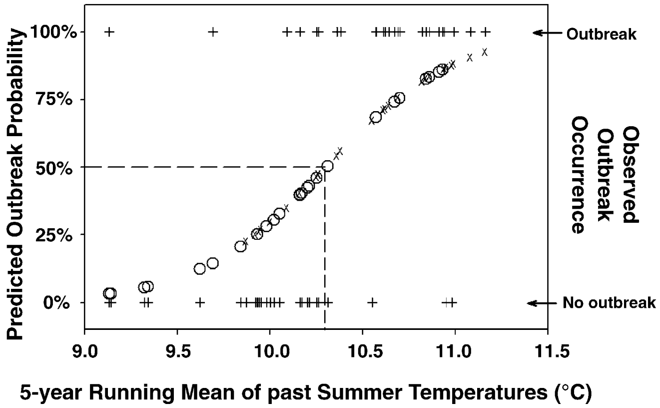

Fig. 8. Predicted probabilities of the occurrence of spruce beetle outbreaks (>15,000 ha forest area infested) in relation to mean summer temperatures (May–August) on the northern (○) and southern (×) Kenai Peninsula, Alaska, 1971–1996. Predicted probabilities were based on an autoregressive logistic regression model (Table 2).

4. Discussion

Our findings show that spruce beetle outbreaks have occurred frequently on the Kenai Peninsula, rarely in the Kluane region, and have been initiated and sustained by periods of 5–6 years of warm summer temperature. Our measurements of growth releases combined with historical documents suggest that prior to the 1990s outbreaks, the last massive outbreak of spruce beetles on the Kenai Peninsula occurred in 1870–1880s. Our tree growth chronologies further suggest that spruce among Kenai forests grew vigorously for decades following this outbreak until the 1950s when forest canopies began to close and competitively suppress annual growth of trees. When an unprecedented run of warm summers began in 1987, many trees were growing slowly in closed-canopy stands and were highly susceptible to an exhaustive outbreak.

4.1. Regional differences in disturbance regimes

We found that spruce beetle disturbance regimes on the Kenai Peninsula were dramatically different from those of the Kluane region. Most of the 23 Kenai Peninsula forests had repeatedly experienced spruce beetle outbreaks over the past 250 years with a mean return interval of 52 years and evidence of thinnings across multiple stands in 1810s, 1850s, 1870–1880s, 1910s, and 1970–1980s, which we interpret as regional spruce beetle outbreaks. Among the four Kluane stands we found strong evidence of a 1930–1940s outbreak in one stand, including still standing beetle-scarred snags, and weak evidence of this outbreak in the other three stands. In contrast to Kenai Peninsula forests, we found no evidence of regional spruce beetle outbreaks in the 18th or 19th century, suggesting that regional outbreaks were largely a 20th century phenomenon among the Kluane forests we sampled. This regional difference in disturbance regimes is probably attributable to regional differences in climate. In the Kluane region, the minimum daily temperature from December to February averaged −23.7 ± 0.5 °C (Haines Junction, 1949–2000; AHCCD, 2003), which is close to the ambient temperature threshold of −24 °C when survival of adult and larval spruce beetles in Alaska is unlikely unless protected by snow (Miller and Werner, 1987) and much lower than the average minimum daily temperature on the Kenai Peninsula over the same time period (Kenai = −14.6 ± 0.6 °C, Homer = −8.3 ± 0.6 °C; WRCC, 2005). Garbutt (2003) noted that recent winters in Kluane, although not significantly warmer overall, have not experienced prolonged periods of extreme cold.

Conversely, the dry and warm summer climate and high incidence of lightning in the Kluane region appears to create a more active fire regime among white spruce forests compared to the relatively wet and cool summer climate of the Kenai Peninsula where lightning is rare (Gabriel and Tande, 1983). We found evidence of burned wood in all four of the mature white spruce stands we sampled in the Kluane region. This was unlike the Kenai Peninsula where only 1 of 23 sites showed signs of past fires and mature upland white spruce forests have typically not burned for more than 600 years (Berg and Anderson, 2006). Fire likely reduces the proportion of spruce available to spruce beetles by keeping forests in earlier successional stages. Such forests contain a higher proportion of younger and more vigorously growing spruce which are less susceptible to attack by spruce beetles (Hard, 1985). On the Kenai Peninsula, forests that burned in 1947 and 1969 experienced few outbreaks during the 1990s (E.E. Berg, U.S. Fish and Wildlife Service, unpublished data). In the continental climate of northwest Colorado, Bebi et al. (2003) and Kulakowski et al. (2003) similarly reported that stands of Engelmann spruce (*Picea engelmanni*) that burned in 1879 were far less susceptible to spruce beetle attack during a large 1940s outbreak than were unburned stands, which were well-stocked with large-diameter trees. Thus two factors – low winter temperatures and a disturbance regime dominated by frequent fire – appear to have limited spruce beetle populations at low levels in the Kluane region until the dramatic warming of summers through the 1990s.

4.2. A massive outbreak on the Kenai Peninsula in the 1870–1880s

Based on our analysis of tree rings, only the 1870–1880s outbreak approaches the 1990s outbreak in magnitude and size, with 17 of 23 sites showing signs of canopy thinning. Similar to the recent outbreak, tree mortality appeared to be most extensive among southern Kenai Peninsula forests. However, this outbreak did not appear to be as large as the 1990s outbreak which caused extensive spruce mortality across all 23 Kenai Peninsula sites. Reports from foresters and naturalists around the turn of the century provide evidence that a massive forest disturbance occurred in the region prior to 1900, although the cause of the disturbance was not recognized at the time. In 1904, forester William A. Langille (1868–1956) evaluated the forest resources on the Kenai Peninsula for a possible national forest reserve (Rakestraw, 1981). He found the forests of the Kenai Peninsula to be in very poor condition, especially the area north of the Kenai

River for which he noted, ‘‘there is every evidence, indicated by old logs and decayed stumps of large size, that a prehistoric forest of greater proportions once existed, probably destroyed by fire before the Russian occupancy of the region’’ (Langille, 1904).

Langille’s (1904) observations along the north shore of Kachemak Bay in Homer (Coal Bay) also suggest a previous large-scale spruce beetle outbreak in the area, ‘‘Along both shores of Coal Bay and on the elevated plateau between it and Cook Inlet, the forest condition is poor. While there is a fair stand of trees for the region they are practically all gone. Along the bay shore 40–60% of the older standing trees are dead, and on the high plateau 80–100% are dead but still standing, having all died about the same time. They are being succeeded by a new growth seemingly not as thrifty as their predecessors; those of today are very limby, short-bodied, and have a rapid taper. This growth has not yet grown to lumber size, the largest being only 12–14 in. in diameter, and without care their future is destruction by fire.’’

Extensive dead forests around Kachemak Bay, as well as on the west side of Cook Inlet, were also mentioned briefly in accounts of the Harriman Alaska Expedition of 1899 by naturalist John Muir and forester Bernard Fernow who separately speculated that the mortality was due to ‘‘showers of ashes and cinders’’ from Iliamna volcano (Muir, 1938; Burroughs and Muir, 1986). However, we suggested that Langille, Muir, and Fernow had unknowingly observed the effects of the earlier widespread spruce beetle outbreak that we detected through growth releases of trees that survived the disturbance. We did not detect evidence of fire among mature spruce forests in the areas described by Langille (1904)—fires are rare in upland white spruce in the region (Berg and Anderson, 2006) and largely concentrated in lowland stands of black spruce, which have a mean fire return interval of approximately 80 years (De Volder, 1999). Also, Kachemak Bay lies approximately 100 km across Cook Inlet from Iliamna volcano, thus the inundation of forests by ‘‘ashes and cinders’’ seem unlikely. Although spruce beetles were not mentioned in these historical reports, we confirmed their presence near the Homer site described by Langille by a weathered snag with abundant spruce beetle egg galleries that we dated as dying in 1884. Furthermore, trees that we sampled with cross sections in the Homer area that survived the 1870–1880s outbreak were estimated to have averaged 9 ± 5 cm (S.D.) ($n = 393$ trees) in diameter at the time of the outbreak, a size similar to the spruce that survived the 1990s outbreak in the same area.

4.3. Spruce beetle outbreaks and summer temperature

In this study, spruce beetles populations on the Kenai Peninsula grew from endemic to outbreak levels when summer temperatures over the previous 5–6 years were unusually warm; specifically, when the 5-year average summer temperature reached 10.3 °C, the outbreak probability reached 50%. Spruce beetle outbreaks in the Kluane region also appeared to be initiated and maintained by periods of warm summer temperature, as evidenced by the 1994–2005 outbreaks following the unusually high summer temperatures from 1989 to 2004. Similarly the 1934–1942 outbreak in the Kluane region occurred during the extremely warm summers of the 1930s (Szeicz and MacDonald, 1995; Wilson and Luckman, 2003). Outbreaks of spruce beetles have also been attributed to localized forest disturbance such as windthrow, fire, logging, and construction (Werner et al., 1977). For example, spruce beetle actively increased on the Kenai Peninsula following a large fire on the central Kenai Peninsula in 1947 and powerline and road construction near Soldotna and Homer in the early 1950s. However, these infestations remained localized to the immediate areas initially disturbed and did not expand into adjacent expanses of mature white spruce forest (Furniss, 1950; Holsten, 1990). Thus runs of warm summers as demonstrated in this paper appear to be necessary for such local outbreaks of spruce beetles to become regionalized.

Periods of 5–6 years with warm summer temperatures likely resulted in spruce beetle outbreaks through a combination of increases in the rate of spruce beetle reproduction and drought-induced stress of trees. The life histories of spruce beetles have been found to be tightly governed by summer temperature. First, warm temperatures above 14.5 °C from late May to early June on the Kenai Peninsula lead to early adult emergence, attack, and breeding (Werner and Holsten, 1985a) which in turn provides spruce beetle larvae with a longer growing season to mature. Secondly, when phloem temperatures reach 16.5 °C during the first and second larval instar stages (mid-June to mid-July), spruce beetle larvae on the Kenai Peninsula develop into adults in one rather than 2 years; a doubling of the maturation rate (Werner and Holsten, 1985a,b). Similarly the cumulative number of hours with ambient temperature above 17 °C, 40–80 days after the peak flight of adults also predicted this increase in development rate (Hansen et al., 2001) which had no apparent effect on spruce beetle fecundity or brood survival (Hansen and Bentz, 2003). Direct solar radiation influences phloem temperature such that the number of summer days with cloud cover limits this maturation rate (Werner and Holsten, 1985a,b). Thirdly, warm weather may synchronize larval development and subsequent adult emergence, thereby increasing the number of spruce beetles simultaneously available to attack and overwhelm tree defenses, as has been found in mountain pine beetles (*Dendroctonus ponderosae*; Powell and Logan, 2005).

Spruce beetles concentrate their attack on mature spruce in the late spring when trees experience seasonal drought stress because cold or partially frozen soils retard water uptake and precipitation is normally low (Hard, 1987). Spruce on south-facing slopes are typically less prone to infestations by spruce beetles than spruce growing on north-facing slopes because of warmer soil temperatures (Hard, 1987). However, during warm summers, excessive heat causes drought stress of white spruce on south-facing slopes and can cause radial growth to slow (Barber et al., 2000, 2004). Such slow growing trees are highly susceptible to mortality by spruce beetles (Hard et al., 1983;

Hard, 1985; Doak, 2004) because their moisture uptake is too low to produce oleoresin flows to overcome spruce beetle attacks (R.A. Werner, U.S. Forest Service, unpublished data). Both warm temperatures and drought have been pervasive among boreal forests in Alaska since the late 1960s (Klein et al., 2005; Juday et al., 2005) and have been associated with the widespread drying of ponds, falling water levels in closed basin lakes, and a proliferation of shrubs among wetlands on the Kenai Peninsula and interior Alaska (Klein et al., 2005; Riordan, 2005). Such conditions may have led to widespread stress among mature white, Sitka, and Lutz spruce in the region and may well have played a substantial role in fueling the 1990s outbreak (Juday et al., 2005).

Because summer temperatures are on average warmer in Kluane than the Kenai Peninsula, we suspect that temperature-induced drought stress of host trees played a more important role in causing spruce beetle outbreaks in the Kluane region than did accelerated larval growth rates. However, not all spruce in Alaska responded to warming by decreasing radial growth, particularly at elevational treeline (Wilmking et al., 2004). Thus we suggest that the effects of warming on moisture availability and host susceptibility to spruce beetle attack should be examined either through the direct monitoring of moisture in live trees or through indirect assessment of drought stress using the $^{13}C/^{12}C$ stable isotope ratio in tree rings (Barber et al., 2000, 2004).

Although a relationship between spruce beetle outbreaks and temperature has been suggested (Juday et al., 2005), our results indicate that outbreaks are initiated and sustained by relatively long periods of high summer temperature which facilitate both exponential population growth of beetles and widespread drought stress of host trees. Indeed, the 5–6-year period of summer temperature that best predicted outbreaks in our models corresponds with the 5-year increment of radial growth that best predicted which individual trees would be attacked and killed by spruce beetles (Hard et al., 1983; Hard, 1985; Doak, 2004). The past outbreaks that we detected using dendrochronology also appeared to be associated with periods of warm summer temperature on the Kenai Peninsula. Barber et al. (2004) reconstructed the annual May–August temperature using tree rings from interior and south-central Alaska and found that the extremely warm summers from 1990s were potentially equaled in temperature only by the warm summers of 1834–1851 and 1862–1879. Thus long-term changes in spruce beetle populations as evidenced in this study by the large outbreaks of the 1850s, 1870–1880s, 1970s, and 1990s may have been driven in part by regional changes in temperature regimes over the past 200 years (Barber et al., 2004).

Our short-term model of the relationship between spruce beetle outbreaks and temperature fit the Kenai Peninsula data well from 1971 to 1996. The beetle-temperature relationship was decoupled after the peak year of the 1990s outbreak in 1996, presumably because the supply of susceptible host trees was exhausted (Werner et al., 2006). Thus the availability of mature spruce likely governs whether warm temperature will elicit regional outbreaks of spruce beetles. The sequential outbreaks of the 1850s, 1870–1880s, and 1910s on the Kenai Peninsula may have similarly contributed to low beetle activity in ensuing decades by killing most mature spruce and leaving behind survivors that our data suggest experienced rapid growth well into the middle of the 20th century. This may have allowed forests in the region to escape outbreaks in the 1940s during a brief period of warming (Barber et al., 2004) that our model suggested would have been sufficient to cause outbreaks on the Southern Kenai Peninsula. By the 1950s, forest canopies had begun to close, as evidenced by growth rates slowing to the long-term within-stand means (Fig. 5). Outbreaks again occurred on the Northern Kenai Peninsula, as our model predicted, in response to a brief warming period in the late 1950s and early 1960s (Holsten, 1990; Barber et al., 2004). Although minor outbreaks were recorded around Anchor Point on the Southern Kenai Peninsula during this time (Holsten, 1990), our detection of small, short-lived growth pulses across our southern sites suggests that spruce had matured broadly across the Kenai Peninsula and were again becoming susceptible to widespread outbreaks. A more pronounced warming and especially dry period in the late 1960s (Holsten, 1990; Barber et al., 2004) again fueled outbreaks across approximately 120,000 ha of forest on the Kenai Peninsula (Holsten, 1990) but was apparently shut down in 1975 when the 5-year average of summer temperatures dropped to 9.9 °C and remained below the threshold of 10.3 °C through 1979. Thus the impoverished forests described by Langille in 1904 with small trees (“few trees suitable for 12 in. × 12 in. lumber”) and low timber volumes (“typically 1000 board-feet/acre”) had spent a full century recovering from the 1870–1880s outbreak. When an 11-year run of above average summer temperatures got underway in 1987, all the conditions were in place for the storm of spruce beetle outbreaks that inundated south-central Alaska forests through the 1990s. We note, however, that summer temperatures in south-central Alaska were generally low from at least 1916, when the Anchorage temperature record began, through the 1950s (Fig. 7). This suggests that climate as well as spruce immaturity contributed to low beetle activity in the early-to-mid-20th century.

Our examination of spruce beetle outbreaks relative to temperature on the Kenai Peninsula spanned only a few outbreaks (early 1970s, 1980s, 1990s) and a relatively brief period when annual summer temperatures were consistently above the 200-year average (Barber et al., 2004). Therefore, our parameter estimates of the relationship between summer temperature and the occurrence of outbreaks may not be robust and models based on a wider range of temperatures and greater number of outbreaks (spatially, temporally, or both) are needed. To this end, we are currently examining our long-term data on growth releases relative to long-term proxy records of summer temperature in the region. This was outside the scope of this paper because such analyses are complicated by lags between spruce beetle reproduction, tree mortality, and growth release of surviving trees and the attenuating effects of outbreaks on the subsequent availability of mature spruce for breeding. However, we feel that such models will be particularly useful in helping predict when the next large outbreak will likely occur in south-central Alaska and other parts of the state.

5. Conclusions

Recently, massive outbreaks of bark beetles have simultaneously infested conifer forests across western North America with the intensity, extent, and distribution of many of these events seemingly outside the normal range of historic variation (Logan and Powell, 2005). During the late 20th century summer temperatures warmed dramatically, particularly in northern forests (ACIA, 2004; Barber et al., 2004), and appear to explain the occurrence of the recent massive outbreaks of spruce beetles on the Kenai Peninsula and probably in the Yukon Territory as well. If this warming trend persists, spruce beetle outbreaks may continue to increase in their frequency and intensity and expand into areas and to tree species that have been uncommonly infested (Juday et al., 2005). Our study suggests that spruce beetle outbreaks have occurred on average every 52 years among mature spruce forests on the Kenai Peninsula, thus we should anticipate additional large-scale outbreaks in the future. However, regional outbreaks in the Kluane region to our estimation have been extremely rare over the past 250 years. Although we detected a massive regional outbreak in the 1870–1880s on the Kenai Peninsula, the massive 1990s outbreaks appeared to exceed even this outbreak in both magnitude and intensity with all sites thinned extensively. Thus the large outbreaks in both the Kenai Peninsula and the Kluane areas from 1994 to 2004 may be relatively anomalous events over the past 250 years and, with continued warming, a possible foreshadowing of future large-scale outbreaks in interior and southeast Alaska where the few recorded infestations have to date been small (Holsten, 1990).

More sophisticated models than we have provided in this paper would be useful to help predict the location, intensity, and spread of spruce beetle outbreaks given different warming scenarios. Models of population growth that incorporate relationships between climate and spruce beetle development rates (Werner and Holsten, 1985a,b; Hansen et al., 2001) and winter survival (Miller and Werner, 1987) may be particularly useful in predicting more precisely how outbreaks may spread in range with continued warming. For mountain pine beetles, Logan and Powell (2001) used such population models (Bentz et al., 1991; Logan and Bentz, 1999) in conjunction with spatial data on temperature and predicted that a warming of 2.5 °C associated with a doubling of atmospheric CO_2 would expand the range of outbreaks by 7° north in latitude and cause infestations in jack pines (*Pinus banksiana*) which are currently not a host of mountain pine beetles. Some of their predictions have come close to reality as the mountain pine beetle recently expanded its range northward to within 50 km of the nearest jack pines (Logan and Powell, 2005).

Applying an advanced understanding of the dynamic relationships between forest insects and their tree hosts in predictive models will therefore be important in forecasting future disturbances with sufficient warning so that appropriate responses can be implemented (Logan et al., 2003). However, considering the magnitude and intensity of recent forest insect outbreaks in North America, developing and implementing effective responses will be extremely challenging and may require innovative policies that address both the causes and effects of outbreaks. Such policies will need to be developed through an understanding of disturbance ecology of the forest system of interest (Schoennagel et al., 2004) and cooperation among scientists, policy makers, and the public if they are to reach a balance between protecting public property and safety, maintaining key ecological functions, and sustaining the socio-economic benefits of forests.

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References

ACIA [Arctic Climate Impact Assessment], 2004. Impacts of a warming Arctic: Arctic climate impact assessment. Cambridge University Press, Cambridge.

AHCCD [Adjusted Historical Canadian Climate Data], 2003. Rehabilitated precipitation and homogenized temperature data sets, version 2003. Climate Monitoring and Data Interpretation Division, Climate Research Branch, Meteorological Service of Canada. September 2005. Available at http://www.cccma.bc.ec.gc.ca/hccd/index.shtml.

Allison, P.D., 1999. Logistic Regression Using the SAS System: Theory and Application. SAS Institute Inc., Cary, North Carolina.

Barber, V.A., Juday, G.P., Finney, B.P., 2000. Reduced growth of Alaska white spruce in the twentieth century from temperature-induced drought stress. Nature 405, 668–673.

Barber, V.A., Juday, G.P., Finney, B.P., Wilmking, M., 2004. Reconstruction of summer temperatures in interior Alaska from tree-ring proxies: evidence for changing synoptic climate regimes. Clim. Change 63, 91–120.

Bebi, P., Kulakowski, D., Veblen, T.T., 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. Ecology 84, 362–371.

Berg, E.E., Anderson, R.S., 2006. Fire history of white and Lutz spruce forests on the Kenai Peninsula, Alaska over the last two millennia as determined from soil charcoal. For. Ecol. Manage. 227, 275–283.

Bentz, B.J., Logan, J.A., Amman, G.D., 1991. Temperature dependent development of the mountain pine beetle and simulation of its phenology. Can. Entomol. 5, 1083–1094.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach, 2nd ed. Springer-Verlag, New York.

Burroughs, J., Muir, J., 1986. Alaska: The Harriman Expedition, 1899. Dover, New York.

De Volder, A.D., 1999. Fire and climate history of lowland black spruce forests, Kenai National Wildlife Refuge, Alaska. Thesis, Northern Arizona University, Flagstaff.

Doak, P., 2004. The impact of tree and stand characteristics on spruce beetle (Coleoptera: Scolytidae) induced mortality of white spruce in the Copper River Basin, Alaska. Can. J. For. Res. 34, 810–816.

Downing, G.L., 1957. The recent history of destructive forest insect activity in Alaska. U.S. For. Ser., Alaska For. Res. Cent., For. Insect Sur. Rep. 1, Juneau, Alaska.

Environment Canada, Parks, 1987. Kluane National Park resource description and analysis. Natural Resource Conservation Section, Environment Canada, Parks, Prairie and Northern Region, Canada, 2 volumes.

Francis, S., 1996. Fire history of the Shakwak Trench. Thesis, University of British Columbia, Vancouver.

Furniss, R.L., 1950. Forest Insect Situation in Alaska. U.S. For. Ser., For. Insect Lab, Portland, Oregon.

Gabriel, H.W., Tande, G.F., 1983. A regional approach to fire history in Alaska. Bur. Land Manage. Tech. Rep. 9, Anchorage, Alaska.

Garbutt, R., 2003. Yukon 2002 Forest Health Report. Can. For. Ser., Pac. For. Res. Cent., Victoria, British Columbia.

Garbutt, R., 2005. Yukon 2004 forest health report. Can. For. Ser., Pac. For. Res. Cent., Victoria, British Columbia.

Hansen, E.M., Bentz, B.J., 2003. Comparison of reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae). Can. Entomol. 135, 697–712.

Hansen, E.M., Bentz, B.J., Turner, D.L., 2001. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). Can. Entomol. 133, 827–841.

Hard, J.S., 1985. Spruce beetles attack slowly growing spruce. For. Sci. 31, 839–850.

Hard, J.S., 1987. Vulnerability of white spruce with slowly expanding lower boles on dry, cold sites to early seasonal attack by spruce beetles in south central Alaska. Can. J. For. Res. 17, 428–435.

Hard, J.S., Holsten, E.H., Werner, R.A., 1983. Susceptibility of white spruce to attack by spruce beetles during the early years of an outbreak in Alaska. Can. J. For. Res. 13, 678–684.

Harrington, R., Fleming, R.A., Wolword, I.P., 2001. Climate change impacts on insect management and conservation in temperate regions: can they be predicted? Agric. For. Entomol. 3, 233–240.

Hawkes, B.C., 1983. Fire history and management study of Kluane National Park. Can. For. Ser., Pac. For. Res. Cen., Victoria, British Columbia.

Holmes, R.L., Adams, R.K., Fritts, H.C., 1986. Quality control in crossdating, a users manual for program COFECHA. In: Holmes, R.L., Adams, R.K., Fritts, H.C. (Eds.), Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin. Chronology Series VI, Laboratory of Tree-Ring Research, University of Arizona, Tucson, pp. 41–49.

Holsten, E.H., 1990. Spruce beetle activity in Alaska 1920–1989. U.S. For. Ser. For. Pest Manage. Tech. Rep. R10-90-18, Anchorage, Alaska.

Holsten, E., Hennon, P., Trummer, L., Schultz, M., 2001. Insects and diseases of Alaskan forests. U.S. For. Ser. Alaska Reg. Tech. Rep. R10-TP-87, Anchorage, Alaska.

Holsten, E.H., Thier, R.W., Munson, A.S., Gibson, K.E., 1999. The Spruce Beetle. U.S. For. Ser. For. Insect and Disease Leaflet 127, Washington, DC.

Juday, G.P., Barber, V., Vaganov, E., Rupp, S., Sparrow, S., Yarie, J., Linderholm, H., Berg, E., D'Arrigo, R., Duffy, P., Eggertsson, O., Furyaev V.V., Hogg, E.H., Huttunen, S., Jacoby, G., Kaplunov, V.Ya., Kellomaki, S., Kirdyanov, A.V., Lewis, C.E., Linder, S., Naurzbaev, M.M., Pleshikov, F.I., Runesson, U.T., Savva, Yu.V., Sidorova, O.V., Stakanov, V.D., Tchebakova, N.M., Valendik, E.N., Vedrova, E.F., Wilmking, M., 2005. Forests, land management, agriculture. In: Arctic Climate Impact Assessment. Arctic Council. Cambridge University Press, pp. 781–862 (Chapter 14).

Klein, E., Berg, E.E., Dial, R., 2005. Wetland drying and succession across the Kenai Peninsula Lowlands, south-central Alaska. Can. J. For. Res. 35, 1931–1941.

Kulakowski, D., Veblen, T.T., Bebi, P., 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. J. Biogeogr. 30, 1445–1456.

Langille, W.A., 1904 The proposed forest reserve on the Kenai Peninsula, Alaska, October–December 1904. Chugach file, RG 95, National Archives, Washington, DC.

Logan, J.A., Bentz, B.J., 1999. Model analysis of mountain pine beetle seasonality. Environ. Entomol. 28, 924–934.

Logan, J.A., Powell, J.A., 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). Am. Entomol. 47, 160–173.

Logan, J.A., Powell, J.A., 2005. Ecological consequences of climate change altered forest insect disturbance regimes. Available on the Utah State University website at: http://www.usu.edu/beetle/publications_bark_beetle.htm.

Logan, J.A., Régnière, J., Powell, J.A., 2003. Assessing the impacts of global warming on forest pest dynamics. Front. Ecol. Environ. 1, 130–137.

Miller, K.L., Werner, R.A., 1987. Cold-hardiness of adult and larval spruce beetles *Dendroctonus rufipennis* (Kirby) in interior Alaska. Can. J. Zool. 65, 2927–2930.

Muir, J., 1938. John of the Mountains: the Unpublished Journals of John Muir. Houghton Mifflin, Boston, Massachusetts.

Nijhuis, M., 2004. Global warming's unlikely harbingers. High Country News 36, 8–12 14.

Powell, J.A., Logan, J.A., 2005. Insect seasonality: circle map analysis of temperature-driven life cycles. Theor. Popul. Biol. 67, 161–179.

Rakestraw, L.W., 1981. A history of the United States Forest Service in Alaska. The Alaska Historical Society for the Alaska Historical Commission and the Alaska Region. U.S. For. Ser, Anchorage, Alaska.

Riordan, B., 2005. Using remote sensing to examine changes of closed-basin surface water area in interior Alaska from 1950 to 2002. Thesis, University of Alaska, Fairbanks.

Ross, D.W., Daterman, G.E., Boughton, J.L., Quigley, T.M., 2001. Forest health restoration in south-central Alaska: a problem analysis. U.S. For. Ser. Gen. Tech. Rep. PNW-GTR-523, La Grande, Oregon.

Ross, S.M., 1988. A First Course in Probability, 3rd ed. Macmillan, New York.

Rowe, J.S., Scotter, G.W., 1983. Fire in the boreal forest. Quat. Res. 3, 444–464.

Safranyik, L., Simmons, C., Barclay, H.J., 1990. A conceptual model of spruce beetle population dynamics. Forestry Canada, Pac. For. Cent., Info. Rep. BC-X-316, Victoria, British Columbia.

Schmid, J.M., Frye, R.H., 1977. Spruce beetle in the Rockies. U.S. For. Ser. Gen. Tech. Rep. RM-49, Fort Collins, Colorado.

Schoennagel, T.L., Veblen, T.T., Romme, W.H., 2004. The interaction of fire, fuels and climate across Rocky Mountain forests. BioScience 54, 661–676.

Stokes, M.A., Smiley, T.L., 1968. An Introduction to Tree-ring Dating. University of Chicago Press. Reprinted 1996, University of Arizona Press, Tucson.

Szeicz, J.M., MacDonald, G., 1995. Dendroclimatic reconstruction of summer temperatures in northwestern Canada since A.D. 1638 based on age-dependent modeling. Quat. Res. 14, 257–266.

U.S. Forest Service, 2004. Forest health conditions in Alaska, 2003. U.S. For. Ser. Gen. Tech. Rep. R10-TP-123, Anchorage, Alaska.

U.S. Forest Service, 2005. Forest health conditions in Alaska, 2004. U.S. For. Ser. Protection Rep. R10-PR-3, Anchorage, Alaska.

Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1991a. Methods of detecting past spruce beetle outbreaks in Rocky Mountain subalpine forests. Can. J. For. Res. 21, 242–254.

Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1991b. The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology 72, 213–231.

Veblen, T.T., Hadley, K.S., Nel, E.M., Kitzberger, T., Reid, M., Villalba, R., 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. J. Ecol. 82, 125–135.

Werner, R.A., Holsten, E.H., 1985a. Factors influencing generation times of spruce beetles in Alaska. Can. J. For. Res. 15, 438–443.

Werner, R.A., Holsten, E.H., 1985b. Effect of phloem temperature on development of spruce beetles in Alaska. In: Safranyik, L. (Ed.), The role of the host in the population dynamics of forest insects. Proc. IUFRO Conf.

Can. For. Ser., Pac. For. Res. Cent., Victoria, British Columbia, pp. 155–163.

Werner, R.A., Baker, B.H., Rush, P.A., 1977. The spruce beetle in white spruce forests of Alaska. U.S. For. Ser. Tech. Pap. PNW-61, Portland, Oregon.

Werner, R.A., Raffa, K.F., Illman, B.L., 2006. Dynamics of phytophagous insects and their pathogens in Alaskan boreal forests, pp. 133–146. In: Chapin, F.S., Oswood III, M.W., van Cleve, K., Viereck, L.A., Verbyla, D.L. (Eds.), Alaska's Changing Boreal Forest. Oxford University Press, London, 354 pp.

Wilmking, M., Juday, G.P., Barber, V.A., Zald, H.S.J., 2004. Recent climate warming forces opposite growth responses of white spruce at treeline in Alaska through temperature thresholds. Glob. Change Biol. 10, 1724–1736.

Wilson, R.J.S., Luckman, B., 2003. Dendroclimatic reconstruction of maximum summer temperatures from upper treeline sites in Interior British Columbia, Canada. Holocene 13, 851–861.

WRCC [Western Regional Climate Center], 2005. Desert Research Institute, National Oceanographic and Atmospheric Administration, Reno, Nevada. September 2005. Available at http://www.wrcc.dri.edu.