

Holocene records of *Dendroctonus* bark beetles in high elevation pine forests of Idaho and Montana, USA

Andrea Brunelle^{a,*}, Gerald E. Rehfeldt^b, Barbara Bentz^c, A. Steven Munson^d

^a University of Utah, Department of Geography, 260 S. Campus Dr. Room 270, Salt Lake City, UT 84112-9155, United States

^b USDA Forest Service, Rocky Mountain Research Station, 1221 S. Main, Moscow, ID 83843, United States

^c USDA Forest Service, Rocky Mountain Research Station, 860 N. 1200 E., Logan, UT 84321, United States

^d USDA Forest Service, Forest Health Protection, 4746 S. 1900 E., Ogden, UT 84403, United States

Received 15 December 2006; received in revised form 27 September 2007; accepted 2 October 2007

Abstract

Paleoecological reconstructions from two lakes in the U.S. northern Rocky Mountain region of Idaho and Montana revealed the presence of bark beetle elytra and head capsules (cf. *Dendroctonus* spp., most likely *D. ponderosae*, mountain pine beetle). Occurrence of these macrofossils during the period of time associated with the 1920/1930 A.D. mountain pine beetle outbreak at Baker Lake, Montana suggest that when beetle populations reach epidemic levels, beetle remains may be found in the lake sediments. In addition to the beetle remains found at Baker Lake during the 20th century, remains were also identified from ca. 8331, 8410, and 8529 cal yr BP. At Hoodoo Lake, Idaho remains were found at ca. 7954 and 8163 cal yr BP. These Holocene records suggest the infestations occurred during a period when climate changed rapidly to cooler and effectively wetter than present in forests dominated by whitebark pine. These two lake records provide the first preliminary data for understanding the long-term history of climatic influences on *Dendroctonus* bark beetle activity, which may be useful for predicting climate and stand conditions when mountain pine beetle activity occurs.

Published by Elsevier B.V.

Keywords: Bark beetles; *Dendroctonus*; Holocene; Macrofossils; 8200 year event; Pollen; Whitebark pine

1. Introduction

1.1. Background

Recent anthropogenically induced changes in climate have drawn attention to the influence of temperature and precipitation on disturbance regimes. Some disturbance agents such as fire are well studied with respect to linkages to climate dynamics (e.g. Swetnam, 1993; Sherriff et al., 2001; Brunelle et al., 2005; Westerling et al., 2006). The influence of climate change on development, survival, and distribution of insect herbivores is also a recent topic of investigation (Williams and Liebhold, 1997; Coley, 1998; Hill et al., 1999; Hansen et al., 2001; Watt and McFarlane, 2002; Berg et al., 2006). As poikilothermic organisms, insect body temperature is directly tied to the temperature of their environment, and because of this sensitivity, outbreak behavior of many pest species is closely

linked to climate variability (Logan et al., 2003). It is known that warmer temperatures can facilitate insect activity. For example during the late Palaeocene-early Eocene global warming period, insect-caused damage increased in both intensity and diversity (Wilf and Labandeira, 1999). However, the full range of climatic and environmental scenarios that might facilitate insect expansion is not well understood.

Bark beetles within the genus *Dendroctonus* (Coleoptera: Curculionidae, Scolytinae) are considered important drivers of ecological change in many western forest ecosystems (Schmid and Hinds, 1974; Amman, 1977; Veblen et al., 1994; Schmid and Mata, 1996; Dale et al., 2001). Outbreaks of many bark beetle species are currently occurring simultaneously across western North America, and a variety of factors are implicated including drought-induced changes in host susceptibility (Breshears et al., 2005), land management practices (Keane, 2001), current stand conditions (Amman et al., 1977; McCambridge et al., 1982; Negrón et al., 1999, 2000) and direct effects of warming temperatures on beetle reproductive capacity (Logan and Bentz, 1999; Logan and Powell, 2001; Berg et al., 2006). One species in particular, the mountain pine beetle (*D. ponderosae* Hopkins)

* Corresponding author. Tel.: +1 801 585 5729; fax: +1 801 521 8219.

E-mail address: andrea.brunelle@geog.utah.edu (A. Brunelle).

(MPB), is infesting lodgepole pine (*Pinus contorta* (Douglas)) at historically unprecedented rates in many areas of western North America, most notably in British Columbia and Alberta, Canada. This is in part due to a shift in the thermal suitability for sustaining MPB populations (Carroll et al., 2004) but also due to changes in forest age structure and susceptibility due to effective fire suppression (Taylor et al., 2006). Although MPB impacts have been affecting forest structure for millennia (Schmidt, 1988), climate change may disrupt the co-evolved associations resulting in devastating ecological consequences in high elevation forests and at latitudes where MPB impacts have historically remained at endemic levels (Ayres and Lombardero, 2000; Logan and Powell, 2001).

MPB egg galleries and horizontal larval mining in the phloem of host trees disrupts nutrient and water transport (Amman and Cole, 1983; Safranyik and Carroll, 2006), thereby killing the host tree. Infestations can be small in extent, affecting only a few individual trees- or large in spatial extent with high rates of mortality (e.g. Glacier National Park outbreaks in 1970s and 1980s) (Raffa, 1988; Amman and Logan, 1998). As a native disturbance agent, periodic MPB outbreaks are considered important for maintaining healthy structure and function of many western pine ecosystems such as those dominated by lodgepole pine (Romme et al., 1986). However, the role of MPB in other forest ecosystems including high elevation whitebark pine (*Pinus albicaulis* Engelman) and limber pine (*Pinus flexilis* James) is unclear. Cold temperatures in high elevation forests can result in long generation times (Amman, 1973), and increased insect mortality (Cole, 1981) thereby reducing the probability of a MPB outbreak (Safranyik, 1978). However, during the warm period of the 1930s and 1940s, outbreaks of MPB were observed in high elevation whitebark pine forests (Perkins and Swetnam, 1996a,b; Furniss and Renkin, 2003), with periodic outbreaks also observed in the 1970s (Arno, 1986; Keane and Arno, 1993). MPB-caused mortality of whitebark and limber pine has increased again in the recent past and warming temperatures are implicated (Logan and Powell, 2001; Gibson, 2006).

High elevation whitebark and limber pine forests throughout the West are in peril due to recent increases in MPB-caused tree mortality and an introduced pathogen, whitepine blister rust (*Cronartium ribicola*) (Tomback et al., 2001). Although it is known that MPB reproduces more effectively under warm climate conditions, there are few data points from high elevation forests regarding the significance of vegetative composition or the necessary persistence of reproductively suitable climate in facilitating outbreaks. A better understanding of the historical role of MPB in these sensitive ecosystems would significantly contribute to informed decisions concerning management and restoration of high elevation pine ecosystems. To date, published tree-ring and documentary records for MPB do not exceed the 20th century (Perkins and Swetnam, 1996a,b; Alfaro et al., 2004), and therefore our understanding of the complex relationships among climate, host plant, and disturbance events is limited. Sub-fossil insect remains in lake sediments, however, can extend baseline knowledge to earlier in the Holocene. This study documents two occurrences of *Dendroctonus* spp. infestations, which, along with records of fire (from sedimentary

charcoal), climate (as inferred from vegetation composition), and vegetation change (determined through pollen abundances) can be used to enhance our knowledge associated with historical disturbance related events in high elevation pine ecosystems.

1.2. Site descriptions

The study was conducted in the Bitterroot Range of the northern Rocky Mountains (NRM) in the United States (U.S.). The sites include Hoodoo Lake, Idaho (46°19'14"N, 114°39'01"W, elevation 1770 m) on the Clearwater National Forest, Lochsa Ranger District, and Baker Lake, Montana (45°53'31"N, 114°15'43"W, elevation 2300 m), on the Bitterroot National Forest, Darby Ranger District. Hoodoo Lake, on the west side of the Bitterroot Range, is located near the crest of the mountains (Fig. 1). Hoodoo Lake occupies a cutoff stream channel formed ca. 12,000 cal yr BP (Brunelle et al., 2005). The lake has a surface area of approximately 3.5 ha, a small inflowing and outflowing stream, and a maximum water depth of ca. 4 m. Spline climate surfaces of Rehfeldt (2006) predict a contemporary (1961–1990) average minimum January temperature for Hoodoo Lake of -12.4°C , a maximum July temperature of 24.0°C , and growing degree-days (base 5°C) of 960. Average January and July precipitation are estimated at 98 mm and 34 mm, respectively, while annual precipitation averages 770 mm. An annual dryness index (ratio of degree-days $>5^{\circ}\text{C}$ to annual precipitation) would be about 1.2.

The subalpine forest around Hoodoo Lake is dominated by Engelmann spruce (*Picea engelmannii*) with subalpine fir (*Abies bifolia*) on the moist, north facing slopes, and some lodgepole pine on the dry, south facing slopes. Only a few young whitebark pine were found in the Hoodoo Lake watershed. Willow (*Salix*) and sedges (*Scirpus*) are in seeps and wetter areas. Dominant understory species include whortleberry (*Vaccinium scoparium*), beargrass (*Xerophyllum tenax*), and mountain

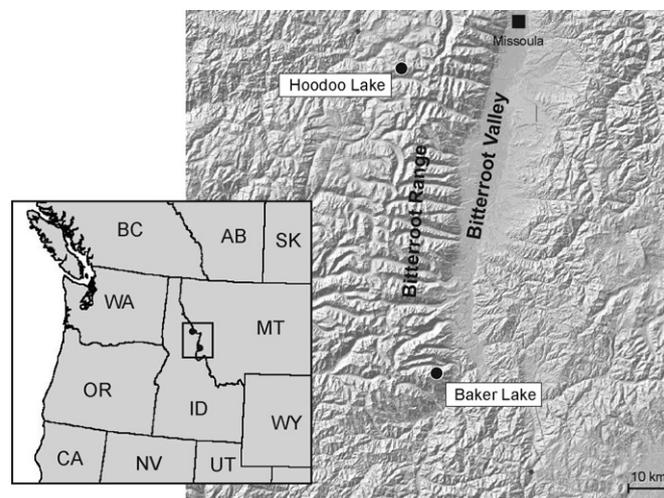


Fig. 1. Site map of the study area. Smaller inset map identifies the region while the larger map identifies lake locations on a 30 m digital elevation model (DEM). Hoodoo Lake, Idaho is located in the northern part of the Bitterroot Range, and Baker Lake, Montana is located in the southern part of the range on the eastern slope.

heather (*Phyllodoce empetriformis*). Various members of the grass family (Poaceae) and sunflower family (Asteraceae) are also present in the watershed.

Baker Lake is on the east side of the Bitterroot Range in a late-Pleistocene cirque basin (Fig. 1) in subalpine forest. The lake has a surface area of approximately 2 ha, a small inflowing and outflowing stream, and a maximum water depth of nearly 17 m. Climate estimate for the minimum January temperature is $-5.7\text{ }^{\circ}\text{C}$ while the July maximum temperature is about $21\text{ }^{\circ}\text{C}$; degree-days $>5\text{ }^{\circ}\text{C}$ average 530; the average January and July precipitation is 75 mm and 37 mm, respectively; annual precipitation is about 700 mm; the annual dryness index averages 0.9 (see Rehfeldt, 2006).

The forest around Baker Lake is dominated by whitebark pine and subalpine larch (*Larix lyallii*) on dry slopes and subalpine fir on moist slopes. Lodgepole pine and Engelmann spruce also grow in the watershed. Dominant understory species include whortleberry, huckleberry (*Vaccinium membranaceum*), beargrass, and mountain heather.

2. Data collection

2.1. Field methods

Both lakes were cored from an anchored platform. Hoodoo Lake was cored in the deepest part of the lake in approximately 3.8 m of water. Baker Lake was cored in 15.9 m of water. The

deepest area was not cored (ca. 17 m of water) because of the limitations of the coring equipment. The uppermost-unconsolidated sediments (i.e. short cores) were collected with a plastic tube outfitted with a piston and sampled in the field in 1 cm increments. Long cores were obtained using a modified Livingstone corer. Each drive was extruded and wrapped in plastic wrap and aluminum foil in the field. All core samples are stored under refrigeration.

2.2. Fire history

Five cm^3 samples were taken from the long and short cores at contiguous 1 cm intervals for charcoal and macrofossil analyses. The samples were soaked in sodium hexametaphosphate to disaggregate the sediment which was then washed through 125 and 250 μm mesh sieves. These size fractions were chosen to reconstruct the watershed-scale fire history because modern studies have shown that large charcoal particles do not travel far from their source (Clark, 1988; Whitlock and Millspaugh, 1996; Gardner and Whitlock, 2001). The sieved material was counted under a dissecting microscope at 20–32 \times magnifications. The charcoal analysis follows methods described in Long et al. (1998). A fire episode (defined in Brunelle and Whitlock, 2003) is identified when charcoal accumulation rates (CHAR; particles/ cm^2/year) exceed background charcoal influx (running mean of the CHAR) by a prescribed threshold ratio. The fire return interval varies at both

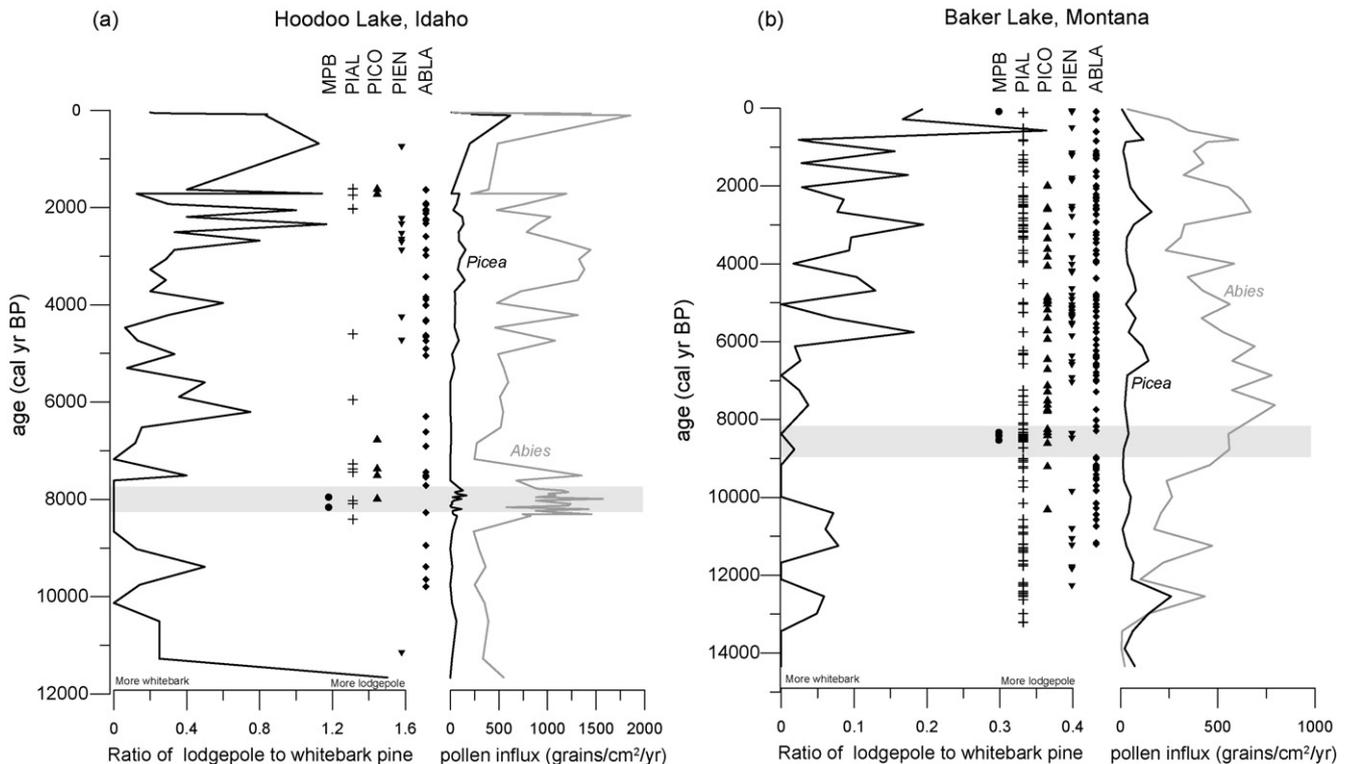


Fig. 2. (a and b) The y-axis represents time (cal yr BP) and the x-axis of these graphs reflect the relative abundance of whitebark (*Pinus albicaulis*) versus lodgepole (*Pinus contorta*) pollen. When the curve is far to the left of the diagram the forest was likely dominated by whitebark pine, when it is to the right, lodgepole pine. Macrofossils are indicated by symbols and labeled at the top of the diagram. PIAL = *Pinus albicaulis*, PICO = *Pinus contorta*, PIEN = *Pinus engelmannii*, ABLA = *Abies bifolia*. Influx of subalpine fir (*Abies*) and Engelmann spruce (*Picea*) are also plotted on time to demonstrate the increase in fir prior to the 8200 year event and the peak in fir after the MPB outbreak. Gray shading indicates the 2 sigma range of ages for the MPB remains.

sites over the Holocene, controlled mainly by variations in large scale climate controls such as insolation and dominant climate regime as delineated by topography (Brunelle et al., 2005). For a complete discussion of the fire reconstructions from the two lakes see Brunelle et al. (2005).

2.3. Vegetation history

Needle and male cone remains in the core were identified from the sieved residues using the modern reference collection at the University of Oregon and reference material from the Oregon State University Herbarium. The presence of needle and male cone macrofossils of lodgepole pine and whitebark pine are noted in Fig. 2.

Pollen samples were taken every 10 cm (at ca. 100–400 year intervals) in both long and short cores and processed following the methods of Faegri et al. (1989). *Lycopodium* was added to each sample as an exotic tracer. Pollen grains were identified at 500× magnification to the lowest possible taxonomic level using the University of Oregon pollen reference collection and published atlases (e.g. Kapp, 1969; Moore et al., 1991). Pollen ratios (Fig. 2) are based on influx data (grains/cm²/year).

Diploxyton- and haploxyton-type *Pinus* grains were assigned to whitebark pine and lodgepole pine based on the presence or absence of verrucae on the distal membrane,

respectively (Moore et al., 1991). Both species grow in the region and the presence of needle fragments in the cores confirmed the assignments. The possibility that ponderosa pine (*Pinus ponderosa* Lawson) contributed to the diploxyton-type *Pinus* pollen, and that western white pine (*Pinus monticola* Douglas) and limber pine (*Pinus flexilis* James) pollen were components of the haploxyton-type *Pinus* cannot be completely dismissed, because these conifers also grow in the NRM. However, it should be noted their macrofossils have not been identified in any of the core samples.

A ratio of diploxyton (lodgepole type) to haploxyton (whitebark type) pollen accumulation rates (influx) (Fig. 2) were used to assess forest composition during the periods for which *Dendroctonus* remains were found. Accumulation rates refer to the deposition of a given pollen type per unit area over time (e.g. grains/cm²/year) and represent changes in the abundance of a particular taxon. When the ratio is far to the left of the diagram it reflects high accumulation rates of whitebark pine pollen which is interpreted as more whitebark pine in the watershed. When the ratio is far to the right, it indicates high accumulation rates of lodgepole pine pollen, or more lodgepole pine in the watershed. Increases in haploxyton pine pollen indicate an increase in the local population of whitebark pine as the influx of haploxyton pine pollen is faithful to its relative abundance in the watershed (Minckley, 2003). Macrofossils are

Table 1
Uncalibrated and calibrated age determinations for study sites with age model regression equations

Depth (cm)	Lab number ^a	Material/Source	Age (¹⁴ C yr B.P.)	Age (cal yr B.P.) ^b
Hoodoo Lake (0–50 cm: $y = 0.0235x^2 + 3.27x - 47$, $R^2 = 0.9825$; 50–400 cm: $y = -5E - 05x^3 + 0.0786x^2 - 1.0051x + 1418.7$, $R^2 = 0.9984$)				
0				–47
16		1934 Fire		16
30		1889 Fire		61
34		1851 Fire		99
49.5	AA-34825	Charcoal	1620 ± 40	1574–1411 (1525)
64.5	AA-34826	Charcoal/wood	1825 ± 40	1839–1690 (1731)
113.5	AA-35509	Needle/male cone	2245 ± 35	2274–2154 (2265)
313.5	AA-35510	Conifer needle	6595 ± 85	7614–7320 (7477)
322		Mazama ash		7627 ± 150 (7627) ^c
400	AA-35511	Male cone/charcoal	8270 ± 160	9544–8927 (9273)
Baker Lake ($y = 0.0226x^2 + 28.31x$, $R^2 = 0.9977$)				
0				–47
12		1896 Fire		54
20		1748 Fire		202
28		1204 Fire		746
55	AA-34823	Conifer needles	1600 ± 40	1568–1405 (1520)
75	AA-38087	Male cone	2209 ± 49	2341–2111 (2262)
120	AA-38088	Conifer needles	3306 ± 67	3644–3385 (3512)
169	AA-38089	Wood	4617 ± 51	5472–5262 (5316)
207	AA-38090	Needles/seeds/wood	6302 ± 55	7325–7154 (7249)
222		Mazama ash		7627 ± 150 (7627) ^c
246	AA-38091	Needles/wood	7164 ± 74	8113–7834 (7965)
289	AA-38092	Male cone/seeds	8870 ± 120	10217–9625 (10083)
330	AA-38093	Male cone/needles/wood	10239 ± 79	12375–11553 (11782)
362	AA-36943	Needles	11100 ± 130	13441–12855 (13132)
375		Glacier Peak tephra	11200 ^d	13425–12997 (13155)

^a Lab numbers refer to University of Arizona AMS Laboratory (AA-).

^b CALIB 4.1 (Stuiver et al., 1998).

^c Zdanowicz et al. (1999).

^d Carrara and Trimble (1992).

also plotted in Fig. 2 indicating when different conifers were locally present in the watershed. This diagram suggests that during the early Holocene, both sites had more whitebark than either before or after the ca. 8200 year period, and the occurrences of *Dendroctonus* remains recovered in the core samples occur during this period.

2.4. Chronology

Age models were developed from accelerator mass spectrometry (AMS) ^{14}C age determinations and correlations between known fires in the watershed and ^{210}Pb dated peaks in sedimentary charcoal (Table 1) (Brunelle et al., 2005). ^{210}Pb is an unstable isotope of lead that has a short half-life and allows for the precise dating of materials less than 200 years old. The accepted ages for the Mazama (7627 cal yr BP, Zdanowicz et al., 1999) and Glacier Peak tephras (13,155 cal yr BP, Carrara and Trimble, 1992), were also used in the age models. Radiocarbon dates were converted to calendar years before present (cal yr BP) using CALIB 4.1 and most likely ages were determined by examining the calibration curve (Stuiver et al., 1998). Age versus depth relations were described by a series of polynomial regressions (Table 1). Bark beetle occurrences are described in the text by the most likely age (based on CALIB 4.1 calibrations) followed by the 2 sigma range of dates in parentheses.

2.5. *Dendroctonus* record

Beetle remains (head capsules and elytra) were tallied and plotted from the contiguous 5 cm³ samples that were analyzed for charcoal and plant macrofossils (Table 2). Assignment of beetle remains to the genus *Dendroctonus* were confirmed by Dr. Steven Wood, a leading authority on scolytinae beetle taxonomy (see Wood, 1993). Dr. Wood indicated that the beetle remains compared most favorably to the species *D. ponderosae*. Currently, MPB is the only recorded *Dendroctonus* species that colonizes whitebark pine (Furniss and Carolin, 1977). Locating Holocene *Dendroctonus* remains is significant because long-term records of bark beetle occurrence provide information on conditions that are conducive to outbreaks over longer periods of time compared to historical and dendrochronological

Table 2
Ages of mountain pine beetle occurrence with minimum number of individuals (MNI)

Age (cal yr BP)	Depth (cm)	Age (cal yr BP-2 sigma range)	MNI
Baker Lake, MT			
85	3		2
8331	246	8331–8726	2
8410	248	8392–8801	1
8529	251	8483–8914	3
Hoodoo Lake, ID			
7954	333	7782–7954	1
8163	339	7850–8213	1

An individual was determined by the presence of one head capsule, thorax, or two elytra (wing covers).

records. At Baker Lake, Montana, *Dendroctonus* remains were found at ca. 85, 8331 (8331–8726), 8410 (8392–8801), and 8529 (8483–8914) cal yr BP. At Hoodoo Lake, Idaho, remains were found at ca. 7954 (7782–7954) and 8163 (7850–8213) cal yr BP (Table 2). The occurrence of *Dendroctonus* at Baker Lake at ca. 85 cal yr BP corresponds with a region-wide MPB outbreak during the 1920s and 1930s (Kipfmüller et al., 2002). There is no evidence of MPB activity surrounding Hoodoo Lake in the 1920s and 1930s, likely because the forest was almost completely burned over in 1896 (Kipfmüller, 2003), and modern forest is dominated by spruce and fir rather than pine. Early Holocene sediment samples collected from Hoodoo Lake and Baker Lake indicate the presence of bark beetles when fire frequency was relatively low compared to the rest of the record (Fig. 3) and show no distinct relationship to individual fire events (Fig. 4).

2.6. Climate relationships

To assist in interpreting historical changes in climate associated with shifts in vegetative composition (Fig. 2), recent records of the presence, absence, and co-occurrence of lodgepole and whitebark pines were collated from the database maintained by Forest Inventory and Analysis (Alerich et al., 2004; Bechtold and Patterson, 2005). This database was augmented with 719 field plots of Cooper et al. (1991) from the Inland Northwest forests to provide records from approximately 119,000 locations in western U.S. Of the 7941 plots containing lodgepole pine, 9.6% also contained whitebark pine, and of the 1589 plots containing whitebark pine, 47.3% also

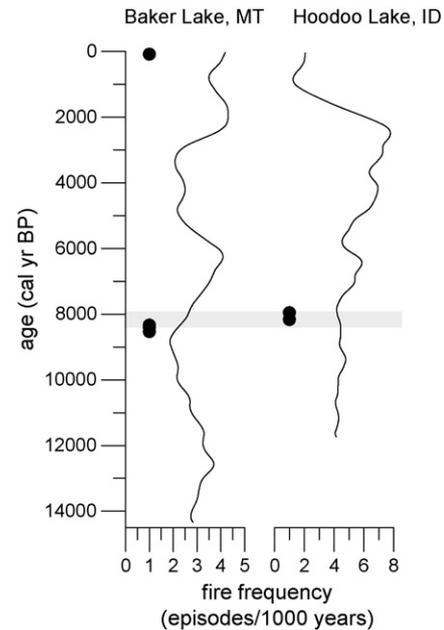


Fig. 3. Fire frequency and the occurrence of mountain pine beetle macrofossils (●), for Baker and Hoodoo Lakes. Fire frequency is calculated using the methods described in Long et al. (1998). Dots indicate the most likely timing of MPB occurrence based on the age model. Shaded area indicates the overlap in beetle occurrences and therefore the possible period of widespread beetle infestation.

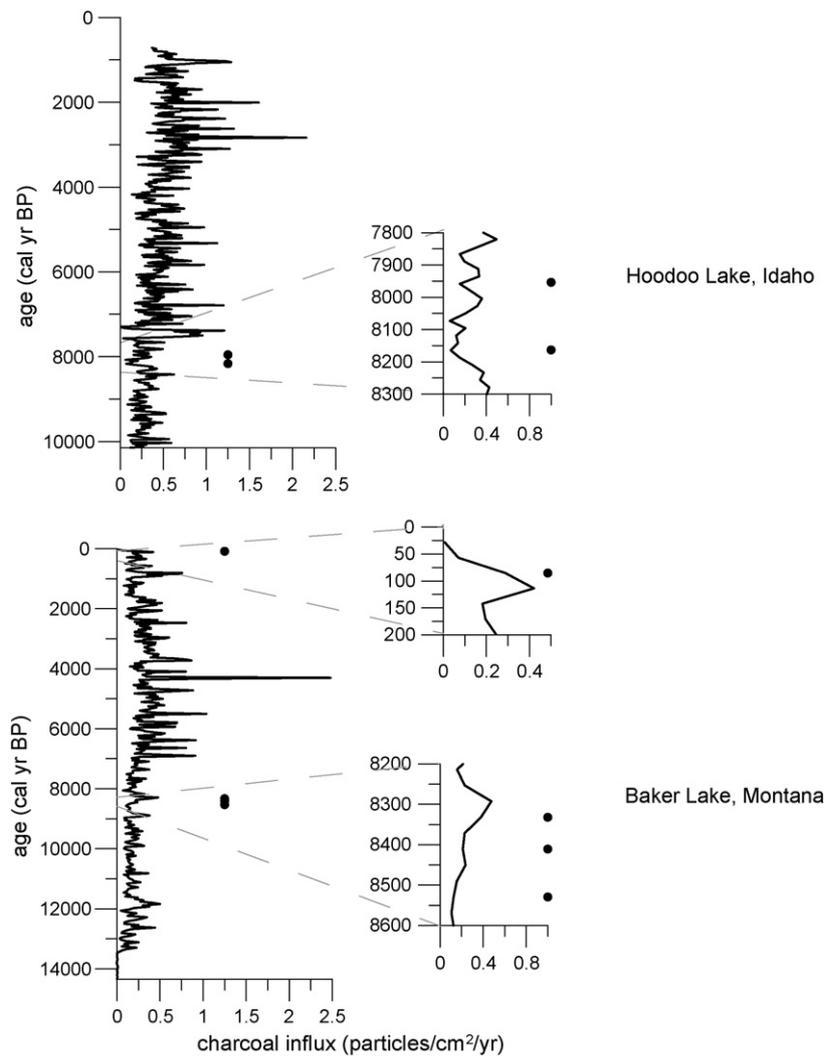


Fig. 4. Examination of the amount of charcoal entering each lake (influx: particles/cm²/year) and MPB remains for both Hoodoo and Baker lakes.

contained lodgepole pine. The current climate of each plot was estimated for 35 derived climate variables (see Rehfeldt et al., *in press*) from the surfaces of Rehfeldt (2006).

The Random Forests classification tree of Breiman (2001) was used to determine which of the climate variables were important in separating the occurrence of the two species. This algorithm, available in R (R Development Core Team, 2004), builds a set of independent trees, called a forest. The process begins with the drawing of a boot-strap sample consisting of about two-thirds of the total number of observations. This sample is used to build a tree while those omitted are used to compute classification errors. For each node of a tree, a random sample of the predictor variables is selected. The number ordinarily equals the square root of the number of predictors. Of these, the variable that minimizes the classification error is identified. For classification trees, the algorithm in R produces two measures for evaluating the importance of independent variables, the mean decrease in accuracy and the mean decrease in the Gini index of class purity.

Our analyses began by using a full complement of the 35 predictors for building the trees in each of 100 forests. Importance values calculated from either the Gini index or the

mean decrease in accuracy then were used to remove the least important variables in a stepwise iterative process. Although separate analyses were made using the alternative measures of variable importance, models using the Gini index to select relevant variables consistently provided the least error and are used herein.

The model using the full complement of independent variables produced an out-of-bag error of 18.15%. The error rate fluctuated between 19.34% and 18.03% until only three predictor variables remained. Decay in the error rate began with the two-variable model (20.89%) and reached a maximum of 28.1 with a single predictor variable. The three-variable model (error = 19.23%) thus emerged as being reasonably parsimonious. The three independent variables, listed in order of importance, were: (1) an annual dryness index calculated from the ratio of degree-days >5 °C to mean annual precipitation, (2) the coldness of the winter as measured by degree-days <0 °C, and (3) the product of degree-days >5 °C with the ratio of summer to annual precipitation.

The out-of-bag error can be subdivided into errors of omission and errors of commission for each of the species. These errors averaged 11.7% for lodgepole pine and 42.1% for

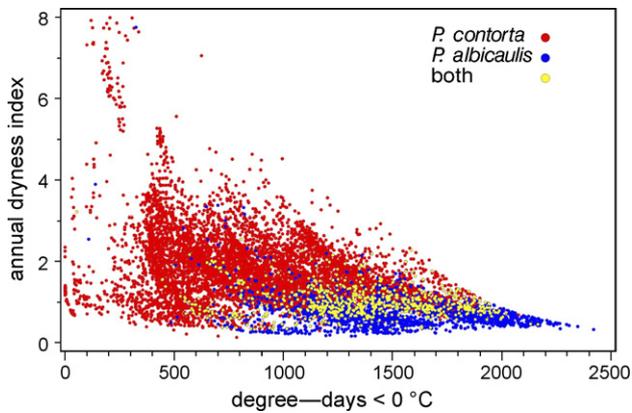


Fig. 5. Two-dimensional ordination of the occurrence of lodgepole and whitebark pines according to two climate variables. Increasing values on the y-axis indicate greater potential drought stress; increasing numbers on the x-axis are indicative of climates with colder winters. Note that the array of whitebark pine (*Pinus albicaulis*) is associated with conditions not conducive to moisture stress.

whitebark pine. The errors are consistent with the co-occurrence of these species as documented in the Forest Inventory database and thereby illustrate the effectiveness of a climatically driven model to represent the natural distribution of these species.

Ordination of data points (Fig. 5) according to the dryness index and negative degree-days, the two variables of greatest importance, shows in general that cold winters, low dryness index values, and cool summers tend to favor whitebark pine. Low dryness index values would correspond to a climate in which moisture ordinarily would not be a limiting factor. A dryness index value of 1 indicates that 1mm of precipitation would be available for each growing degree-day. By contrast, a dryness index value of 4 indicates that 1 mm of precipitation would be rationed across 4 degree-days, producing an environment more conducive to the development of moisture stresses. As shown in Fig. 5, a value of 1 tends to be associated with whitebark pine while a value of 4 would be more typical of sites inhabited by lodgepole pine. Whitebark pine tends to occur in climates with a more equitable balance between moisture and temperature than lodgepole pine; the latter species tends to inhabit dryer sites.

It is important to note the position of the Hoodoo and Baker Lake sites within the scatter of Fig. 5. Climate surfaces (Rehfeldt, 2006) suggest that Hoodoo Lake has an annual dryness index of 1.2 and negative degree-days of 978; comparable estimates for Baker Lake are 0.9 and 1396. Therefore, the Hoodoo Lake site should be more amenable to lodgepole pine while Baker Lake would be more typical of whitebark pine sites. These predictions correspond suitably with the contemporary vegetation described previously.

3. Discussion: bark beetles, climate, and whitebark pine

The average duration of MPB outbreaks in the U.S. NRM is 10 years, and tree mortality is typically concentrated in the larger tree diameter size classes (Amman and Cole, 1983;

Perkins and Swetnam, 1996a,b; Safranyik and Carroll, 2006). Outbreak initiation is believed to result from a decline in host tree resistance, combined with conditions favorable for beetle survival and reproduction (Raffa, 1988; Safranyik and Carroll, 2006). Although endemic populations are often maintained by the presence of stressed trees within a landscape, outbreak MPB populations require a sufficient number of healthy host trees and weather conditions favorable for beetle establishment and survival (Amman, 1972; Raffa, 1988; Safranyik and Carroll, 2006). Because MPB development is dependent on a series of life-stage specific temperature thresholds, below which development does not proceed, climatic conditions suitable for sustaining an outbreak are limited (Safranyik, 1978; Logan and Bentz, 1999). In particular, temperatures in high elevation whitebark pine forests have not always been conducive to MPB outbreaks, often resulting in life-cycles requiring 3 years to complete (Amman, 1973). The recent warming trend, similar to that observed from 1920 to 1940, has enabled MPB to maintain outbreak-level populations in high elevation forests, resulting in widespread whitebark pine mortality (Logan and Powell, 2001; Gibson, 2006).

The *Dendroctonus* macrofossils from Baker Lake at 85 cal yr BP are contemporaneous with the 1920s/1930s MPB watershed outbreak identified from dendrochronological records (Kipfmüller et al., 2002). The 1920s/1930s Baker Lake outbreak was of longer temporal duration across the region, continuing up to 30 years in parts of Montana (Evensen, 1944). The fossil evidence of this outbreak is a calibration point for this study because it demonstrates a link between abundant beetles in the forest and associated beetle remains in sediment cores. The evidence from a 20th century outbreak also provides climate data for a historic outbreak. No outbreak occurred during the 1930s at Hoodoo Lake (Kipfmüller, 2003), which correlates with the absence of *Dendroctonus* remains in the sediment core. Although the climate conditions during the 1920s/1930s outbreak were variable (NCDC, 2006), there were many years that were warmer and drier than those observed just prior to this period. Perkins and Swetnam (1996a,b) suggested that a MPB outbreak from 1920 to 1940 in central ID may have resulted from prolonged drought which effectively reduced tree growth. Above average departures in summer temperatures during this period (Finklin, 1988) would have directly benefited MPB population survival due to a shift in life-cycle timing (Logan and Bentz, 1999).

Dendroctonus macrofossils were also found during the early Holocene at Baker and Hoodoo lakes (Fig. 3). The two periods are not exactly synchronous, although they do overlap temporally at ca. 8250 cal yr BP (Fig. 3). This timing corresponds well with an early Holocene climate event called the 8200 year event (8200 cal yr BP).

The 8200 year event is identified as one of the most abrupt climate changes of the Holocene epoch (Morrill and Jacobsen, 2005). Paleoclimate records indicate that this period was colder-than-previous and colder-than-present at many sites in the northern hemisphere, triggered by the final drainage of Lake Agassiz into the North Atlantic (Morrill and Jacobsen, 2005). While it was originally suggested that this event was only 100–

200 years long; many sites demonstrate a prolonged response to the 8200 year event (Rohling and Palicke, 2005).

Sites in North America that record evidence of a cooling event include Elk Lake in Minnesota (Dean et al., 2002), BC2 in British Columbia (Pisaric et al., 2003), and Bear Lake, ID and UT (Dean et al., 2006). Sediment samples collected from Deep Lake, Minnesota also indicate a period of cooling around the 8200 year event (8900–8300 cal yr BP), and support the hypothesis that the cooling event lasted more than one or two centuries in areas distant from the North Atlantic (Hu et al., 1999). The periods over which *Dendroctonus* remains were found at the Idaho and Montana lakes also span time periods greater than a century. Beetle remains at Baker Lake represent the window of ~8914–8331 cal yr BP (Table 2) and the three intervals with beetle remains only span 6 cm of the core, suggesting that it was a temporally cohesive event. The beetle remains at Hoodoo Lake represent the period of 8213–7782 cal yr BP (Table 2). The seven total samples from the two sites that contain beetle remains cover approximately 200 years of time, again suggesting temporal cohesion.

Analysis of forest composition associated with the pollen influx data suggest that the *Dendroctonus* remains recovered during the early Holocene occurred when forests were dominated by whitebark pine (Fig. 2). Whitebark pine and lodgepole pine have distinct climatic niches that overlap (Fig. 5). However, the ability of the Random Forests classification tree to separate these species using climate variables demonstrates that the domination of one taxon over another in the pollen record is indicative of the climate. Whitebark pine occurs when degree-days <0 are more than 1000 and the annual dryness index is low (degree-days >5 °C/annual precipitation less than 2) (Fig. 5). This combination of measurements represents climates that are cold and effectively wet, a climate scenario that is often associated with western North America during the 8200 year event (Dean et al., 2002, 2006; Pisaric et al., 2003). Whitebark pine reaches its greatest dominance during the time period surrounding the 8200 year event, suggesting that the climate at that time not only was cold, but possibly the coldest of the Holocene period (Fig. 2).

Pine was not the only taxa that responded to the 8200 year climate event (Fig. 2). At both sites there is an increase in fir pollen, beginning at ~8500 cal yr BP at Hoodoo Lake, and ~9000 cal yr BP at Baker Lake (Fig. 2). The onset of the increase in fir is likely due to the cool and moist conditions that favor both whitebark pine and fir which tolerate cold and wet climates (see Daubenmire, 1966). It should be noted that at both sites the maximum fir influx occurs shortly after the occurrence of *Dendroctonus*. We propose that this “release” in fir is a result of a bark beetle outbreak causing whitebark pine mortality. Release of understory spruce and fir has previously been used as an indicator of *Dendroctonus*-caused mortality in several western ecosystems (Schmid and Hinds, 1974; Veblen et al., 1990; Alfaro et al., 2004).

The outbreak scenario from the early Holocene is not an exact analog for the early 1900s and recent MPB infestations in the western United States. During the early Holocene outbreak,

the climate was cooler and effectively wetter than present, which is not necessarily a favorable climatic condition for increased MPB reproductive success. However, cool and wet conditions will favor healthy whitebark pine forests, thereby providing improved host conditions for MPB population expansion once established. Healthy host trees and favorable weather are important for sustaining outbreak level MPB populations (Amman, 1972; Raffa, 1988; Safranyik and Carroll, 2006). Moreover, evidence suggests that MPB reproductive capacity is increased in phloem from 5-needle pines when compared to 2 and 3-needle pine species (Amman, 1982; Langor et al., 1990).

One feature recent outbreaks have in common with those of the early Holocene is the abruptness of the climate change. The speed of the current climate shift is well documented (Mann et al., 1998), and the 8200 year event is commonly referred to as the most abrupt climate change of the Holocene (Alley et al., 1997; Renssen et al., 2001; Morrill and Jacobsen, 2005; and others). Considering the stress that rapid climate change can impose on vegetation, MPB outbreaks during the 8200 year event, and recent widespread outbreaks, may have been influenced by abrupt climate shifts.

We found no relationship in the sediment core data between beetle remains and fire in either the 20th century recordings or those from the Holocene. Kulakowski et al. (2003) found that stands affected by a 1940s spruce beetle outbreak in Colorado were less affected by a low severity fire in 1950 than stands without signs of outbreak. However, a large scale MPB outbreak from 1972 to 1975 in the Yellowstone area did significantly influence fire risk and the burn pattern associated with the 1988 Yellowstone fires, although no significant correlations were found associated with the 1980–1983 MPB beetle outbreak (Lynch et al., 2006). The important effect of beetle activity on fire risk may occur through a change in stand structure and composition, which is a delayed second order effect, rather than a direct and immediate increase in fuels (Lynch et al., 2006). The complex temporal and spatial relationships between these two important disturbance agents require further investigation.

Within the several hundred years that whitebark pine was climatically favored at the two sites, short periods of warm and dry conditions that were suitable for bark beetle development may have allowed beetle populations to proliferate. Because the climatic response of long-lived conifer species is much slower compared to forest insects, forest composition would not reflect short-term variability in climate. In fact, many records of the 8200 year event indicate a “two-pronged” structure with a rapid onset of cooling, followed by a brief return to pre-event conditions, a return to cold, and then an abrupt termination of the event (Baldini et al., 2002). In addition to the extensive evidence for a short warming during the 8200 year event, several highly resolved studies (e.g. Sarmaja-Korjonen and Seppä, 2007 (supradecadal); and Baldini et al., 2002 (seasonal)) record significant variability throughout the event. Moreover, recent evidence suggests that MPB outbreak populations in high elevation forests can develop during periods when relatively warm years are interspersed with relatively cold

years (B. Bentz unpublished). Therefore, in the case of these early Holocene occurrences of MPB remains, it was likely the effect of climate on vegetative composition combined with a healthy susceptible host type (the dominantly whitebark pine forest) and favorable weather for insect reproduction allowed the beetles to become abundant enough on the landscape to be recorded in lake sediments.

This research provides initial data points for understanding long-term relationships of MPB in high elevation forests during the Holocene. Multiple scenarios are presented for the interpretation of the results, with the caveat that more sites need to be sampled in order to work out the history and relationships among climate, vegetation and beetles over long time scales. This work and its continuation is relevant because understanding climate conditions, forest composition, and bark beetle response over prolonged periods of time is important to develop an increased knowledge regarding how these components affect western forest stand dynamics now and in the future.

4. Conclusions

Remains of *Dendroctonus* bark beetles, most likely *D. ponderosae*, in two lake cores provide evidence that bark beetles have been associated with whitebark pine forests since the early Holocene if not earlier, indicating the antiquity of the relationship between whitebark pine and MPB. At Baker Lake, *Dendroctonus* remains were found at ca. 85,8331 (8331–8726), 8410 (8392–8801), and 8529 (8483–8914) cal yr BP. At Hoodoo Lake, Idaho remains were found at ca. 7954 (7782–7954) and 8163 (7850–8213) cal yr BP. These Holocene records suggest that prehistoric outbreaks occurred during a period that was cooler and effectively wetter than present. In addition, the early Holocene infestation also occurred when fire frequency was relatively low and susceptible host types predominated.

While this study provides new information regarding the long-term history of bark beetles in subalpine forests, additional research in this area most certainly needs to be conducted. Selecting additional sites that may have experienced historic outbreaks are necessary to evaluate the correlation between *Dendroctonus* remains in the sedimentary record and bark beetle activity in the watershed. Specific attention needs to be directed to the role of bark beetle outbreaks affecting fire probability and pattern, which can be achieved through the analysis of additional sites using high-resolution sedimentary and dendrochronological records of fire. In the face of changing climate and fire regimes, the conditions that give rise to bark beetle outbreaks deserve further study. Whitebark pine is a keystone species in many high elevation forests, and bark beetle/climate/forest dynamics require a better understanding of these unique relationships to manage this species. Analysis of additional long-term records in high elevation forests throughout western North America will increase our understanding of how climate affects bark beetle activity at local and regional scales by extending the spatial scale of the analysis.

Acknowledgements

The authors would like to express gratitude to the following people for their contributions to this paper. Thanks to Tom Swetnam for pointing out A.B.'s first beetle infested tree; Cathy Whitlock and Patrick Bartlein for reviewing early ideas regarding paleo-insect infestations in the NRM; Scott Anderson for his time and energy reviewing and improving the manuscript, Allan Carroll and an anonymous reviewer for their insightful and constructive reviews; Kurt Kipfmüller for many long discussions about mountain pine beetles and whitebark pine; and Dr. Steven Wood for his confirmation of beetle identifications. This work was partially supported by NSF Grant SBR-9616951 and is RED Lab Contribution #1.

References

- Alerich C.A., Klevgard, L., Liff, C., Miles, P.D., 2004. The forest inventory and analysis database: database description and users guide, version 1.7. http://www.ncrs2.fs.fed.us/4800/fiadb_documentation/FIADB_v17_122104.pdf.
- Alfaro, R., Campbell, R., Vera, P., Hawkes, B., Shore, T., 2004. Dendroecological reconstruction of mountain pine beetle outbreaks in the Chilcotin Plateau of British Columbia. In: Shore, T.L., Brooks, J.E., Stone, J.E. (Eds.), Mountain Pine Beetle Symposium: Challenges and Solutions, Natural Resources Canada, Information Report BC-X-399, pp. 245–256.
- Alley, R.B., Mayewski, P.A., Sowers, T., Stuiver, T., Taylor, K.C., Clark, P.U., 1997. Holocene climatic instability: A prominent, widespread event 8200 years ago. *Geology* 25 483–486.
- Amman, G.D., 1972. Some factors affecting oviposition behavior of the mountain pine beetle. *Environ. Entomol.* 1, 691–695.
- Amman, G.D., 1973. Population changes of the mountain pine beetle in relation to elevation. *Environ. Entomol.* 2, 541–547.
- Amman, G.D., 1977. The role of the mountain pine beetle in lodgepole pine ecosystems impact on succession. In: Mattson, W.J. (Ed.), The Role of Arthropods in Forest Ecosystems; Proceedings, 15th International Congress of Entomology, Washington DC, Springer-Verlag, New York, 1976 August 19–27, pp. 3–18.
- Amman, G.D., 1982. Characteristics of mountain pine beetles reared in four pine hosts. *Environ. Entomol.* 11, 590–593.
- Amman, G.D., Cole, W.E., 1983. Mountain pine beetle dynamics in lodgepole pine forests. Part II: population dynamics. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-145, 59 p.
- Amman, G.D., Logan, J.A., 1998. Silvicultural controls of the mountain pine beetle: prescriptions and the influence of microclimate. *Am. Entomol.* 44, 166–177.
- Amman, G.D., McGregor, M.D., Cahill, D.B., Klein, W.H., 1977. Guidelines for Reducing Losses of Lodgepole Pine to the Mountain Pine Beetle in Unmanaged Stands in the Rocky Mountains. GTR-INT-36. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT, p. 19.
- Arno, S.F., 1986. Whitebark pine cone crops—a diminishing source of wildlife food? *Western J. Appl. Forestry* 1 (3), 92–94.
- Ayres, M.P., Lombardero, M.J., 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci. Total Environ.* 262, 263–286.
- Bechtold, W.A., Patterson, P.L., 2005. The enhanced forest inventory and analysis program—national sampling design and estimation procedures. USDA Forest Service, Southern Research Station General Technical Report SRS-80, Asheville, North Carolina.
- Berg, E.E., Henry, J.D., Fastie, C.L., DeVolder, A.D., Matsuoka, S.M., 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Klauene National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecol. Manage.* 227 (3), 219–232.

- Breiman L., 2001. Random forests. *Machine Learn* 45:5–32. R Development Core Team 2004 R: A language and environment for statistical computing R Foundation for Statistical Computing, Vienna.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. *Proc. Natl. Acad. Sci. U.S.A.* 102, 15144–15148.
- Brunelle, A., Whitlock, C., 2003. Postglacial fire, vegetation, and climate history in the clearwater range, Northern Idaho, USA. *Quat. Res.* 60, 307–318.
- Brunelle, A., Whitlock, C., Bartlein, P.J., Kipfmüller, K., 2005. Holocene fire and vegetation along environmental gradients in the Northern Rocky Mountains. *Quat. Sci. Rev.* 24, 2281–2300.
- Carrara, P.E., Trimble, D.A., 1992. A Glacier Peak and Mount Saint Helens J volcanic ash couplet and the timing of deglaciation in the Colville Valley area, Washington. *Can. J. Earth Sci.* 29, 2397–2405.
- Carroll, A.L., Taylor, S.W., Régnière, J., Safranyik, L., 2004. Effects of Climate Change on Range Expansion by the Mountain Pine Beetle in British Columbia. Mountain Pine Beetle Symposium: Challenges and Solutions. October 30–31, 2003, Kelowna, British Columbia. In: Shore, T.L., Brooks, J.E., Stone, J.E. (Eds.). Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC, 298 p.
- Clark, J.S., 1988. Particle motion and the theory of stratigraphic charcoal analysis: source area, transportation, deposition, and sampling. *Quat. Res.* 30, 81–91.
- Cole, W.E., 1981. Some risks and causes of mortality in mountain pine beetle populations: a long-term analysis. *Res. Population Ecol.* 23, 116–144.
- Coley, P.D., 1998. Possible effects of climate change on plant/herbivore interactions in moist tropical forests. *Climatic Change* 39, 455–472.
- Cooper, S.V., Neiman, K.E., Roberts, D.W., 1991. Forest habitat types of northern Idaho: second approximation. General Technical Report INT-236. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate change and forest disturbances. *Bio. Sci.* 51, 723–734.
- Daubenmire, R., 1966. Vegetation: identification of typical communities. *Science* 151, 291–298.
- Dean, W.E., Forester, R.M., Bradbury, J.P., 2002. Early Holocene change in atmospheric circulation in the Northern Great Plains: an upstream view of the 8.2 ka cold event. *Quat. Sci. Rev.* 21, 1763–1775.
- Dean, W., Rosenbaum, J., Skipp, G., Colman, S., Forester, R., Liu, A., Simmons, K., Bischoff, J., 2006. Unusual Holocene and late Pleistocene carbonate sedimentation in Bear Lake, Utah and Idaho, 185. *Sedimentary Geol., USA*, pp. 93–112.
- Evenden, J.C., 1944. Montana's thirty-year mountain pine beetle infestation. United States Department of Agriculture Bureau of Entomology and Plant Quarantine. Forest Insect Laboratory, Couer d'Alene, ID.
- Faegri, K., Kaland, P.E., Kzywinski, K., 1989. *Textbook of Pollen Analysis*. Wiley, New York, 323 pp.
- Finklin, A.I., 1988. Climate of the Frank Church River of No Return wilderness, central Idaho. USDA Forest Service GTR INT-240, Ogden, UT, p. 221.
- Furniss, R.L., Carolin, V.M., 1977. *Western forest insects*. USDA, Forest Service, Miscellaneous Publication No. 1339.
- Furniss, M.M., Renkin, R., 2003. Forest entomology in Yellowstone National Park, 1923–1957: A time of discovery and learning to let live. *American Entomologist* 49 (4), 198–209.
- Gardner, J.J., Whitlock, C., 2001. Charcoal accumulation following a recent fire in the Cascade Range, northwestern USA, and its relevance for fire-history studies. *The Holocene* 5, 541–549.
- Gibson, K., 2006. Mountain pine beetle conditions in whitebark pine stands in the greater Yellowstone ecosystem, 2006. USDA For. Serv. FHP Rpt. 06-03.
- Hansen, E.M., Bentz, B.J., Turner, D.L., 2001. Physiological basis for flexible voltinism in the spruce beetle (Coleoptera: Scolytidae). *Can. Entomol.* 133, 805–817.
- Hill, J.K., Thomas, C.D., Huntley, B., 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proc. R. Soc. Ser. B. Biol.* 226, 1197–1206.
- Hu, F.S., Slawinski, D., Wright Jr., H.E., Ito, E., Johnson, R.G., Kelts, K.R., McEwan, R.F., Boedigheimer, A., 1999. Abrupt climate changes in North American climate during early Holocene times. *Nature* 400, 437–440.
- Kapp, R.O., 1969. *How to Know Pollen and Spores*. William C. Brown Publishing, Iowa.
- Keane, R.E., 2001. Successional dynamics: Modeling an anthropogenic threat. In: Tomback, D.F., Arno, S.F., Keane, R.E. (Eds.), *Whitebark Pine Communities*. Island Press, Washington, DC, pp. 159–192.
- Keane, R.E., Arno, S.F., 1993. Rapid decline of whitebark pine in western Montana: evidence from 20-year measurements. *West. J. Appl. Forest.* 8, 44–46.
- Kipfmüller, K.F., 2003. Fire-climate-vegetation interactions in subalpine forests of the Selway-Bitterroot Wilderness Area, Idaho and Montana, USA. Ph.D. Dissertation. The University of Arizona, 322 pp.
- Kipfmüller, K.F., Swetnam, T.W., Morgan, P., 2002. Climate and Mountain Pine Beetle-induced tree mortality in the Selway-Bitterroot Wilderness Area. USFS Final Report, Research Joint Venture Agreement RMRS-99611-RJVA.
- 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.
- Langor, D.W., Spence, J.R., Pohl, G.R., 1990. Host effects on fertility and reproductive success of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Evolution* 4, 609–618.
- Logan, J.A., Bentz, B.J., 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. *Environ. Entomol.* 28, 924–934.
- Logan, J.A., Powell, J.A., 2001. Ghost forests, global warming, and the mountain pine beetle. *Am. Entomol.* 47, 160–173.
- Logan, J.A., Regniere, J., Powell, J.A., 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers Ecol.* 1, 130–137.
- Long, C.J., Whitlock, C., Bartlein, P.J., Millsbaugh, S.H., 1998. A 9000-year fire history from the Oregon Coast Range, based on a high-resolution charcoal study. *Can. J. Forestry* 28, 774–787.
- Lynch, H.J., Renkin, R.A., Crabtree, R.L., Moorcroft, P.R., 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. *Ecosystems* 9, 1318–1327.
- Mann, M.E., Bradley, R.S., Hughes, M.K., 1998. Global-scale temperature patterns and climate forcing over the past six centuries. *Nature* 392, 779–787.
- McCambridge, W.F., Hawksworth, F.G., Edminster, C.B., Laut, J.G., 1982. *Ponderosa Pine Mortality Resulting from a Mountain Pine Beetle Outbreak*. RP-RM-235. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, 7 pp.
- Minkley, T.A., 2003. Holocene environmental history of the northwestern Great Basin and the analysis of modern pollen analogues in western North America. Ph.D. dissertation. University of Oregon, 310 p.
- Moore, P.D., Webb, J.A., Collinson, M.E., 1991. *Pollen Analysis*, second ed. Blackwell Scientific Publications, Oxford.
- Morrill, C., Jacobsen, R.M., 2005. How widespread were climate anomalies 8200 years ago? *Geophys. Res. Lett.* 32, 1–4.
- NCDC (National Climate Data Center), <http://www.ncdc.noaa.gov/oa/climate/climatedata.html>. Accessed January 2006.
- Negrón, J.F., Schaupp Jr., W.C., Gibson, K.E., Anhold, J., Hansen, D., Thier, R., Mocellini, P., 1999. Estimating extent of mortality associated with the Douglas fir beetle in the central and northern Rockies. *West. J. Appl. For.* 14, 121–127.
- Negrón, J.F., Wilson, J.L., Anhold, J.A., 2000. Stand conditions associated with roundheaded pine beetle (Coleoptera: Scolytidae) infestations in Arizona and Utah. *Environ. Entomol.* 29, 20–27.
- Perkins, D.L., Swetnam, T.W., 1996a. A dendroecological assessment of whitebark pine in the Sawtooth – Salmon river region, Idaho. *Can. J. For. Res.* 26, 2123–2133.
- Perkins, D.L., Swetnam, T.W., 1996b. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. *Can. J. Forest Res.* 26, 2123–2133.

- Pisarcic, F.J., Holt, C., Szeicz, J.M., Karst, T., Smol, J.P., 2003. Holocene treeline dynamics in the mountains of northeastern British Columbia, Canada, inferred from fossil pollen and stomata. *The Holocene* 13, 161–173.
- R Development Core Team, 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Raffa, K.F., 1988. The mountain pine beetle in western North America. In: Berryman, A.A. (Ed.), *Dynamics of Forest Insect Populations*. Plenum Press, pp. 506–525.
- Rehfeldt, G.E., 2006. A spline climate model for western United States. A spline climate model for western United States. General Technical Report 165. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, Colorado.
- Rehfeldt, G.E., Crookston, N.L., Warwell, M.V., Evans, J.S. Empirical analyses of plant-climate relationships for western United States. *Int. J. Plant Sci.*, in press.
- Renssen, H., Goosse, H., Fichefet, T., Campin, J.M., 2001. The 8.2 kyr BP event simulated by a global atmosphere-sea ice-ocean model. *Geophys. Res. Lett.* 28, 1567–1570.
- Rohling, E.J., Palicke, H., 2005. Centennial-scale climate cooling with a sudden cold event around 8,200 years ago. *Nature* 434, 975–979.
- Romme, W.H., Knight, D.H., Yavitt, J.B., 1986. Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? *Am. Nat.* 127, 484–494.
- Safranyik, L., 1978. Effects of climate and weather on mountain pine beetle populations. In: Kibbee, D.L., Berryman, A.A., Amman, G.D., Stark, R.W. (Eds.), *Theory and practice of mountain pine beetle management in lodgepole pine forests*. Symposium Proceedings, University of Idaho, Moscow, ID, pp. 77–84.
- Safranyik, L., Carroll, A.L., 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik, L., Wilson, W.R. (Eds.), *The Mountain Pine Beetle—A Synthesis of Biology, Management, and Impacts in Lodgepole Pine*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, p. 304.
- Sarmaja-Korjonen, K., Seppä, H., 2007. Abrupt and consistent responses of aquatic and terrestrial ecosystems to the 8200 cal yr BP cold event - a lacustrine record from Lake Arapisto, Finland. *The Holocene* 17, 455–464.
- Schmid, J.M., Hinds, T.E., 1974. Development of spruce-fir stands following spruce beetle outbreaks. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Paper RM-131, Ogden, UT, 16 p.
- Schmid, J.M., Mata, S.A., 1996. Natural variability of specific forest insect populations and their associated effects in Colorado. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-GTR-275, Ft. Collins, CO, 14 p.
- Schmidt, W.C., 1988. Lodgepole pine: an ecological opportunist. In: Amman, G.D. (compiler). *Proceedings, Symposium: The management of lodgepole pine to minimize the losses to the mountain pine beetle*, USDA Forest Service, Intermountain Research Station, General Technical Report, INT-GTR-262, Ogden, UT, pp. 14–20.
- Sherriff, R.L., Veblen, T.T., Sibold, J.S., 2001. Fire history in high elevation subalpine forests in the Colorado Front Range. *Ecoscience* 8, 369–380.
- Stuiver, M., Reimer, P.J., Braziunas, T.F., 1998. High-precision radiocarbon age calibration for terrestrial and marine samples. *Radiocarbon* 40, 1127–1151.
- Swetnam, T.W., 1993. Fire history and climate change in giant sequoia groves. *Science* 262, 885–889.
- Taylor, S.W., Carroll, A.L., Alfaro, R.I., Safranyik, L., 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. In: Safranyik, L., Wilson, W.R. (Eds.), *The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts on Lodgepole Pine*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, 304 (Chapter 2), pp. 67–94.
- Tomback, D.F., Arno, S.F., Keane, R.E. (Eds.), 2001. *Whitebark Pine Communities, Ecology and Restoration*. Island Press, Washington, DC, p. 440.
- Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1990. 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., Nel, E.M., Kitzberger, T., Reed, M., Villalba, R., 1994. disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *J. Ecol.* 82, 125–135.
- Watt, A.D., McFarlane, A.M., 2002. Will climate change have a different impact on different trophic levels? Phenological development of winter moth *Operophtera brumata* and its host plants. *Ecol. Entomol.* 27, 254–256.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western U.S. forest fire activity. *Science* 313, 940–943.
- Whitlock, C., Millspaugh, S.H., 1996. Testing the assumptions of fire-history studies: an examination of modern charcoal accumulation in Yellowstone National Park, USA. *The Holocene* 6, 7–15.
- Wilf, P., Labandeira, C.C., 1999. Response of plant-insect associations to paleocene-eocene warming. *Science* 285, 2153–2156.
- Williams, D.W., Liebhold, A.M., 1997. Latitudinal shifts in spruce budworm (Lepidoptera: Tortricidae) outbreaks and spruce-fir forest distributions with climate change. *Acta Phytopathol. Hun.* 32, 205–215.
- Wood, S., 1993. Great Basin Naturalist Memoirs No. 13 (Catalog of Scolytidae and Platypodidae (Coleoptera) Vols. A and B. Brigham Young University Press, p. 1553.
- Zdanowicz, C.M., Zielinski, G.A., Germani, M.S., 1999. Mount Mazama eruption: Calendrical age verified and atmospheric impact assessed. *Geology* 27, 621–624.