



The pollen record of a 20th century spruce beetle (*Dendroctonus rufipennis*) outbreak in a Colorado subalpine forest, USA

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ARTICLE INFO

Article history:

Received 26 January 2010

Received in revised form 22 April 2010

Accepted 2 May 2010

Keywords:

Spruce beetle outbreak

Dendroctonus rufipennis

Pollen analysis

Fire history

Colorado

ABSTRACT

The frequency and intensity of ecosystem disturbance, including outbreaks of forest insects and forest fires, is expected to increase in the future as a result of higher temperatures and prolonged drought. While many studies have concentrated on the future climatic impacts on fire, little is known about the impact of future climate on insect infestation. Paleocological techniques are important in this regard in identifying the potential relationships between climate and insect outbreaks in the past, as a predictive tool for the future. We examine a high-resolution 20th century record of spruce beetle (*Dendroctonus rufipennis*) infestation from a small, subalpine lake, comparing the paleocological record to the historical and tree-ring record of the event. An extensive spruce beetle outbreak occurred in northwestern Colorado during the 1940s and 1950s, causing widespread mortality of mature *Picea engelmannii*. Pollen analysis of this period documents the decline of *Picea* and its replacement locally by *Abies lasiocarpa*, paralleling age and composition studies of modern forest stands in the region. This study is a proof of concept that, when applied to longer sedimentary records, could produce a detailed record of infestation for the Late Holocene or older time periods. This information will be useful to forest managers in efforts to plan for the effects of *D. rufipennis* infestations, and subsequent succession within high elevation conifer forests.

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1. Introduction

The relationship between vegetation type, ecosystem disturbance and temporal response has fascinated ecologists, biogeographers and land managers for nearly a century (Clements, 1916). Investigators have long recognized that certain species and plant communities are adapted to fire (Veblen et al., 2003), and that certain forests pests, such as *Arceuthobium* sp. (dwarf mistletoe) and *Dendroctonus rufipennis* Kirby (spruce beetle) can have a significant impact on stand history and dynamics (Schmid and Frye, 1977; Baker and Veblen, 1990; Hawksworth and Wiens, 1996; Kipfmüller and Baker, 1998; Parker et al., 2006). Critical to our understanding of present forest structure is our knowledge of the processes that have created modern forest communities and species distributions. Paleocological research is crucial in this regard for providing a long-term perspective on ecosystem distur-

bance (Whitlock et al., 2003; MacDonald et al., 2008). Consequently, a large body of literature has accumulated on the long-term history of fire and climate using both fire scars from trees (for example, Swetnam and Baisan, 2003) and charcoal from sediments (e.g., Brunelle and Anderson, 2003; Toney and Anderson, 2006; Anderson et al., 2008), and rarely both (Allen et al., 2008).

However, considerably less is known about the long-term history of insect and pest infestation in coniferous forests. Outbreaks of *D. rufipennis* (Baker and Veblen, 1990; Veblen et al., 1991a, b; Zhang et al., 1999; Eisenhart and Veblen, 2000), *Choristoneura occidentalis* (western spruce budworm; Swetnam and Lynch, 1989; Ryerson et al., 2003), and *Coloradia pandora* (pandora moth; Speer et al., 2001) among others have been documented from tree-ring records. Sediment studies have been instrumental in tracking the chestnut blight, a 20th century decline in *Castanea dentata* (American chestnut) caused by a fungal pathogen (*Cryphonectria parasitica*; Anderson, 1974), and the mid-Holocene “hemlock decline”, a massive widespread die-off of *Tsuga canadensis* (eastern hemlock), beginning ca. 5400 calendar years ago (Allison et al., 1986; Anderson et al., 1986; Bhiry and Filion, 1996; Fuller, 1998; Bennett and Fuller, 2002).

Only recently have remains of *Dendroctonus* been recovered from lake sediments (Brunelle et al., 2008), suggesting preservation in sediments might be rare (Watt, 2008). A multiproxy methodol-

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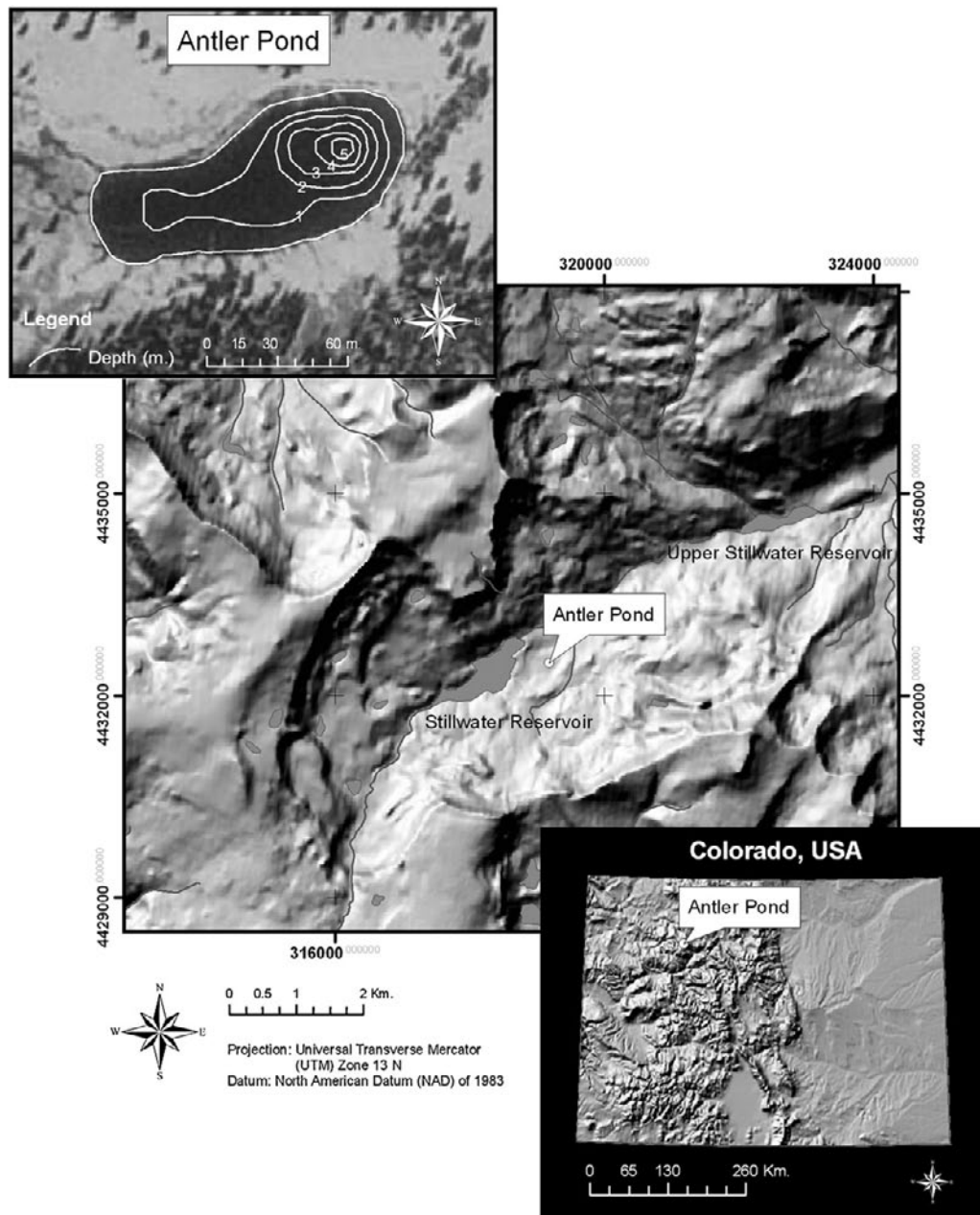


Fig. 1. Location of Antler Pond, Northwestern Colorado, USA.

ogy may be critical to reconstructing such outbreaks. In this study we use high-resolution pollen analysis to investigate a record of *D. rufipennis* Kirby infestation around a small pond in the *Picea engelmannii* [Parry] Engelm. (Engelmann spruce)–*Abies lasiocarpa* [Hook.] Nutt (subalpine fir) forest, White River Plateau, northwestern Colorado. We then compare the paleoecological record to historical and tree-ring records. Much of the high elevation forests of the Plateau were heavily impacted by a *D. rufipennis* outbreak that lasted from ca. 1939 to 1951 AD, when beetles killed nearly six billion board feet of standing *Picea*, nearly 90% by volume of several 100,000 ha within the region (Hinds et al., 1965; Schmid and Frye, 1977; Alexander and Sheppard, 1990; Baker and Veblen, 1990).

D. rufipennis is the most common outbreak beetle of *P. engelmannii* (Schmid and Frye, 1977). Endemic *D. rufipennis* populations are found in scattered live and fallen trees. During outbreaks, beetles can kill most canopy *Picea* over wide areas (Schmid and Frye, 1977; Holsten et al., 1999; Berg et al., 2006; Werner et al., 2006)

by mining through the cambium under the tree's bark, disrupting moisture and nutrient flow (Packee, 1997). *D. rufipennis* is restricted mostly to mature and overmature *Picea*, and epidemics have been periodically recorded. For instance, a serious outbreak was documented in northwestern Colorado during the 1880s (Sudworth, 1900; Schmid and Frye, 1977), which was followed by the outbreak of the mid-20th century.

Our goal is to demonstrate the potential for using high-resolution pollen analysis to determine the occurrence, progress, and aftermath of insect outbreaks in the sedimentary record. Sedimentary documentation of a known recent *D. rufipennis* infestation provides a unique opportunity to investigate the history and effect of large outbreaks in the past, important in determining strategies for management of insect populations. GIS techniques (Bebi et al., 2003), stand structure (Veblen et al., 1994) and tree-ring (Eisenhart and Veblen, 2000) evidence are critical to understanding the ecological effects and spatial extent of large outbreaks over the last few

hundreds of years. However, by using a paleoecological approach the record could be extended by centuries to millennia. For sites with laminated sediments, high-resolution, decadal-scale changes in forest composition can also be deduced.

Anticipated future climate changes are expected to have a considerable influence on forest disturbance regimes (Dale et al., 2001; Allen et al., 2010), including outbreaks of forest insect pests (Ayres and Lombardero, 2000; Logan et al., 2003; Raffa et al., 2008) and fire (Flannigan et al., 1998, 2000; Miller, 2003; Westerling et al., 2006). It is highly likely that the distribution of forest defoliators will change (Williams and Liebhold, 1995, 1997, 2002; Ungerer et al., 1999; Carroll et al., 2003), as will the intensity and frequency of outbreaks (Fleming, 1996; Bylund, 1999), the rates of herbivory in general (Coley, 1998) and the rate of carbon sequestration (Kurz et al., 2008). Climate variations may also serve to provide synchrony in outbreaks of different species (Myers, 1998). Because substantial outbreaks can cause tree mortality over vast forest areas, changes to outbreak patterns have considerable management implications, including long-term planning of pest control, hazard rating models, depletion forecasts, ecosystem resilience and nutrient cycling (Fleming and Volney, 1995; Gunderson and Holling, 2002), as well as recreational potential.

2. Study area

The Flattops Wilderness Area forms a portion of the White River Plateau in northwestern Colorado (Fig. 1). The area is named for its gently sloping alpine summits, many exceeding 3660 m elevation. Bedrock is early and middle Tertiary alluvial and aeolian deposits, capped by late Tertiary basalt flows (Reider, 1971). Quaternary sediments in the Bear River valley consist of glacial moraines, landslide and alluvial deposits (Kucera, 1962).

Vegetation zones generally follow elevation and precipitation gradients (Marr, 1967; Feiler et al., 1997). Although elevations vary with aspect, alpine tundra is generally found above 3400 m, with a montane zone (dominants *Pinus contorta* var. *latifolia* Dougl. ex. Loud (lodgepole pine) and *Pseudotsuga menziesii* (Mirb.) Franco [Douglas-fir]) occurring below ca. 2700–2900 m elevation. Between is the subalpine zone, which is dominated mostly by *P. engelmannii* and *A. lasiocarpa*. *P. contorta* var. *latifolia* and *Populus tremuloides* Michx. (quaking aspen) also occurs in this zone, but only rarely in pure stands.

Antler Pond (40°02' N, 107°04' W) is a small (ca. 1 ha) kettle lake located at 3128 m (10,260 ft) elevation on a large lateral moraine adjacent to the Bear River (Figs. 1 and 2). Maximum depth of the pond is 6 m. Though sediment deposition began at Antler Pond by at least 11,390 ± 120 year BP (ca. 13,250 cal BP), we report on only the last ca. 200 years here. Antler Pond occurs within the subalpine zone, and presently is surrounded by old-growth, dead *P. engelmannii*, with an understory of *P. engelmannii* and some *A. lasiocarpa* (Fig. 2). The pond is fringed by sedges (Cyperaceae), grasses (Poaceae) and willows (*Salix* sp.). Additional species near the pond include *Ribes coloradense* (Colorado currant),



Fig. 2. The Antler Pond site, located in the subalpine zone. The photo shows dead, standing *Picea engelmannii* trees killed during the 1940s spruce beetle infestation. Photo was taken in 1997, looking east, with Flattop Mountain in right background, but ghost spruce trees were still standing in 2008.

Rosa woodsii (wild rose), *Castilleja* cf. *miniata* (paintbrush), *Achillea lanulosa* (yarrow), *Penstemon whippleanus* (beard-tongue), *Aconitum columbianum* (monkshood), *Lupinus* sp. (lupine), *Pedicularis groenlandica* (elephantella), *Plantago* sp. (plantain), and *Fragaria virginiana* (strawberry).

3. Data collection

A short frozen core (75 cm long) was obtained from a small floating platform, using a modified hollow box corer (Wright, 1991), filled with ethyl alcohol and dry ice. The corer was lowered into the sediments, remaining there until a thick (ca. 1–2 cm) crust of undisturbed lake sediment froze onto the outside of the box. At the lake surface, the slabs of sediment were chipped off the box corer, wrapped in plastic and foil, and stored in coolers filled with dry ice.

In the laboratory, cross-sections of the frozen cores were cut with a bandsaw in a cold room to expose a clean face. Sediment “ribbons” were cut from the main frozen section, measuring 0.75 cm thick, 2.5 cm deep, and 5.5 cm long each. Pollen subsamples (0.5 cm³) were taken at contiguous (mostly 0.5 cm intervals) over the length of the core. *Lycopodium* tracers were added to each sample to calculate pollen concentration. Sediments were processed after Fægri and Iversen (1989) (10% KOH, 10% HCl, HF, and acetolysis solution), with dehydration in alcohol, staining with safranin “O”, and suspension in silicone oil. Pollen assemblages were identified at 400×, with comparison to species in the Laboratory of Paleoecology reference collection and published keys. The pollen sum of non-aquatic grains averaged over 300 grains. In order to track changes in dominant pollen types, we calculated a *Picea/Abies* ratio.

Table 1
Radiocarbon dates and calendar age ranges for Antler Pond, Colorado, Core 9b.

Core	Laboratory number	Depth (cm)	13C/12C ratio	14C year BP	Calibrated median probability used in age model ^a	Max & min of 2s calibrated age ranges	AD/BC Age	Max & min of 2s AD/BC Age	Date type	Material dated
9b	USC Geology	4.5					1964		¹³⁷ Cs	Lake sediment
9b	USC Geology	14.0					1910		²¹⁰ Pb	Lake sediment
9b	Beta-178749	43.5–44.0	–28.7	950 ± 40	855	771–934	1095	1016–1179	AMS	Lake sediment
9b	Beta-158259	55.0–55.5	–29.4	1530 ± 40	1419	1342–1523	531	427–608	AMS	Lake sediment

^a Using CALIB 5.0 Stuiver et al. (1998), after Telford et al. (2004).

Charcoal subsamples (1 cm^3) for each 0.5 cm depth of the core were disaggregated in water, and sieved through standard soil sieves ($250 \mu\text{m}$ and $125 \mu\text{m}$ openings). Charcoal particle numbers were counted using a dissecting microscope and reported as numbers/ cm^3 .

To independently date the uppermost sediments of Antler Pond we used small subsamples (1.875 cm^3) for ^{210}Pb and ^{137}Cs analyses (Table 1). ^{210}Pb is suitable for dating the most recent 150 years, since its half-life is 22.26 ± 0.22 years (Blais et al., 1995; Appleby, 2001). ^{137}Cs has a half-life of ca. 30 years, and was produced in great abundance during nuclear atmospheric testing beginning in 1945 (Olsson, 1986; Beck and Bennett, 2002). The first pronounced increase of ^{137}Cs in sediment dates to 1954 AD, with a maximum occurring 1963–1964 AD, and a decline by 1965 AD.

4. Results

4.1. Sediment chronology

The sediments are indistinctly laminated above ca. 20 cm depth, but retain remnant banding (Fig. 3); sediments below are more distinctly laminated. Although we are presently unsure of the nature of the lamina in this core, we suggest they consist of annual couplets. We measured couplets (light and dark laminae) for two intervals lower in the core, calculating a sediment accumulation rate (SAR) of 0.36 mm/yr between 14.0 cm and a calibrated ^{14}C AMS date of 855 cal year BP at 43.75 cm (Table 1). Twenty-two laminae were identified between 21.24 and 22.02 cm depth, with 14 laminae occurring between 26.53 and 27.23 cm. Using the SAR of 0.36 mm/yr for this

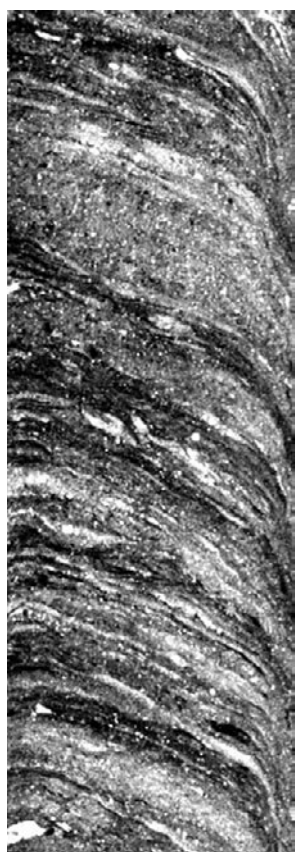


Fig. 3. Antler Pond Core 9b sediments (468–505 mm depth), showing semi-laminated nature of levels. Deformation to right of photo was caused during the coring process.

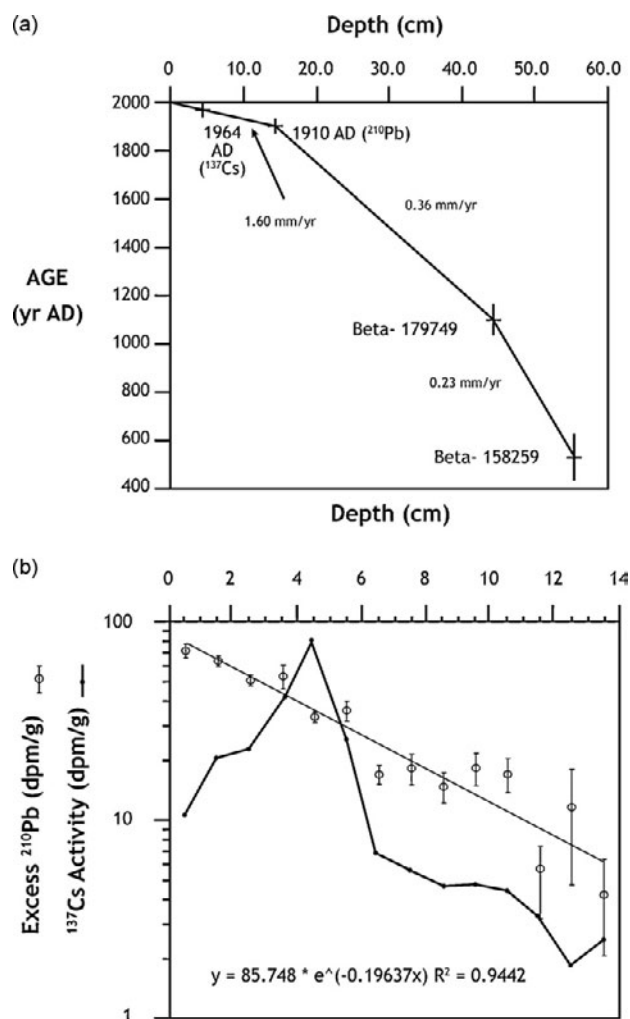


Fig. 4. (a) Sediment accumulation rate curve for Antler Pond Core 9b, based on ^{210}Pb , ^{137}Cs and ^{14}C AMS dates. Only the upper 19 cm of the core was analysed for this study. (b) ^{210}Pb and ^{137}Cs activity curves for the Antler Pond Core 9b. Note the peak in ^{137}Cs activity (ca. 1964 AD) lies at 4.5 cm depth. See text for sediment accumulation rate details.

section of the core there are 22 laminae in 22 years of sediment accumulation for the first section, and 14 laminae in 19.4 years for the second section. These data indicate a high probability that the laminae are varves.

However, due to the semi-banded nature of the sediments we could not rely completely on lamina counts for our core chronology. Instead, we relied on the ^{210}Pb and ^{137}Cs profiles. The SAR for the top 14 cm of the core as derived from the slope of the ^{210}Pb curve is 1.6 mm/yr (Fig. 4a). The ^{137}Cs fallout peaks at 4.5 cm depth, corresponding to 1964 AD, and demonstrating that the SAR for the top 4.5 cm is comparable to the ^{210}Pb rate (Fig. 4b).

4.2. Pollen stratigraphy

Twenty-nine pollen samples cover the 20th century portion of the record, providing an average of 3.5 years between pollen samples. The sampling interval from 100 to 200 years ago (essentially the 19th century) is 13.8 years (Fig. 5), and provides a context for late 20th century change. Though the 19th century sampling interval is greater, pollen evidence shows little change in forest composition, which is dominated by *Picea* (spruce), *Pinus* (pine) and *Artemisia* (sagebrush) (Fig. 5). Similarly, little change occurs in the aquatic and wetland environment, with consistent occurrence of

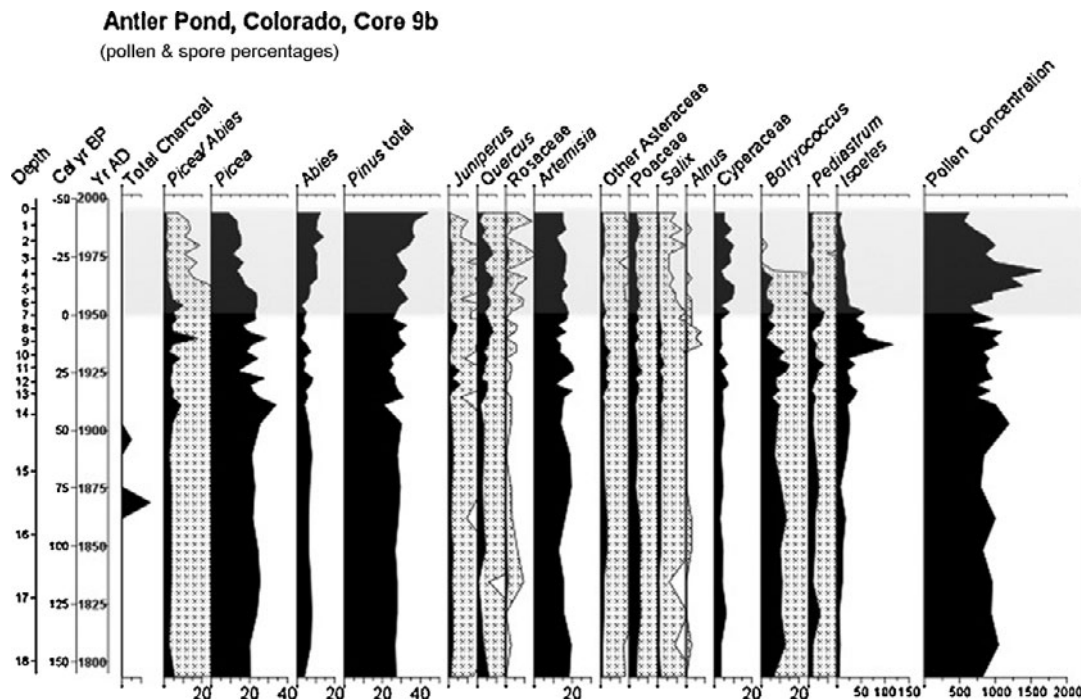


Fig. 5. Summary pollen diagram for Antler Pond Core 9b, for the 19th and 20th centuries. Note the near absence of charcoal in this core. Two age scales are shown, in calendar years BP and also in years AD. Silhouette is 10× actual value.

the algae *Pediastrum*, *Botryococcus*, with *Potamogeton* (pondweed), and *Salix* (willow) and *Cyperaceae* (sedge). *Isoetes* (quillwort) is the lone increasing taxon.

The pollen record from the period ca. 1900–1955 AD (Figs. 5 and 6) is dominated by fluctuating percentages of *Picea* (16–34%), but generally consistent percentages of *Pinus* (24–33%) and *Artemisia* (14–20%). Smaller amounts of *Abies* (fir; 2–8%), *Juniperus* (juniper; 1–6%), *Poaceae* (grass; 3–7%) and other *Asteraceae* (sunflower family; 1–5%) occur, with generally increasing amounts of *Quercus* (probably *Q. gambellii*; Gambel's oak; 2–9%). The occurrence of prominent wetland and aquatic plants occurs as before, with increasing *Isoetes* (quillwort).

Changes in the upper portion of the record, since ca. 1955 AD (~6.0 cm), show long-term shifts in pollen percentages. Initially, *Picea* remains consistent at ca. 20% from ca. 1950 to 1955 AD, but *Abies* percentages begin to increase. After ca. 1955 AD, to the top of the core (1996 AD), *Picea* percentages decline to 9%, but *Abies* percentages increase to 13%. This is shown most conclusively by a severely decreased *Picea/Abies* ratio (Fig. 6). During this period also pollen concentration nearly doubles for about 15 years. An increase in *Pinus* occurs at ca. 2.3 cm (1980 AD). These changes are accompanied by an increase in *Rosaceae* pollen, and a decline in other *Asteraceae* (Fig. 5). Significant changes also occur in wetland and aquatic pollen and spores, including declines in *Salix* pollen, in *Isoetes* spores, and in colonies of *Botryococcus* and *Pediastrum*, with an increase in *Cyperaceae* (Figs. 5 and 6).

5. Discussion

Although Antler Pond sediments are mostly semi-laminated, several indicators suggest that an annual or, at least, a sub-decadal record is preserved. First, photographs of the sediments (Fig. 3) show dark and light laminae, which are varved for at least portions of the record (see above). Second, a distinct peak in ^{137}Cs occurs at ca. 4.5 cm in the record (Fig. 4b; the height of atmospheric nuclear testing in 1963–1964; Beck and Bennett, 2002). Significant biological or physical mixing of the sediments would blur the isotopic

signature of the record. Third, many of the microfossil types in the pollen record exhibit distinct boundaries between levels (e.g., the increase in *Isoetes* between 10.25 and 9.75 cm; the disappearance of *Botryococcus* between 4.25 and 3.75 cm). For these reasons, we feel confident in interpreting the record as one with at least sub-decadal resolution.

5.1. The 20th century event

Initial research from nearby basins suggested that widespread episodic outbreaks of *Dendroctonus* infestation could be detected in the 20th century sedimentary record (Feiler et al., 1997; Anderson, unpublished). After an extensive blowdown on the White River Plateau (Hinds et al., 1965; Schmid and Frye, 1977) in 1939, populations of *D. rufipennis* reached outbreak levels. The infestation raged throughout the 1940s, and into the early 1950s, killing primarily mature *Picea* in ca. 290,000 ha (Hinds et al., 1965; Cahill, 1977; Veblen et al., 1991a) surrounding Antler Pond, and subsided by about 1952 (Massey and Wygant, 1954; Veblen et al., 1991a). The record from Antler Pond has provided an opportunity to examine potential successional changes in the subalpine forest, and other effects around the pond, in detail.

The pollen percentage diagram shows clear evidence of 20th century *Dendroctonus* impact on subalpine forests near Antler Pond. In the upper ca. 5.0 cm declines in *Picea* pollen percentages are accompanied by an increase in *Abies* (Figs. 5 and 6). We calculated a *Picea/Abies* ratio to track the relative changes in the two taxa. For the period 1955–1996, the *Picea/Abies* ratio averages 0.45, as old-growth *Picea* trees died locally, pollen concentrations of *Picea* declined, and *Abies* increased locally. This compares to a series (200-yr) average ratio of 1.36.

The relationship between *Picea* and *Abies* pollen follows the same pattern as determined from stand composition analyses on the White River Plateau, within the area impacted by the same 20th century outbreak, but ca. 10 km to the southwest of Antler Pond (Veblen et al., 1991b). In each stand there, near Trappers Lake, tree composition had shifted from dominance by *P. engel-*

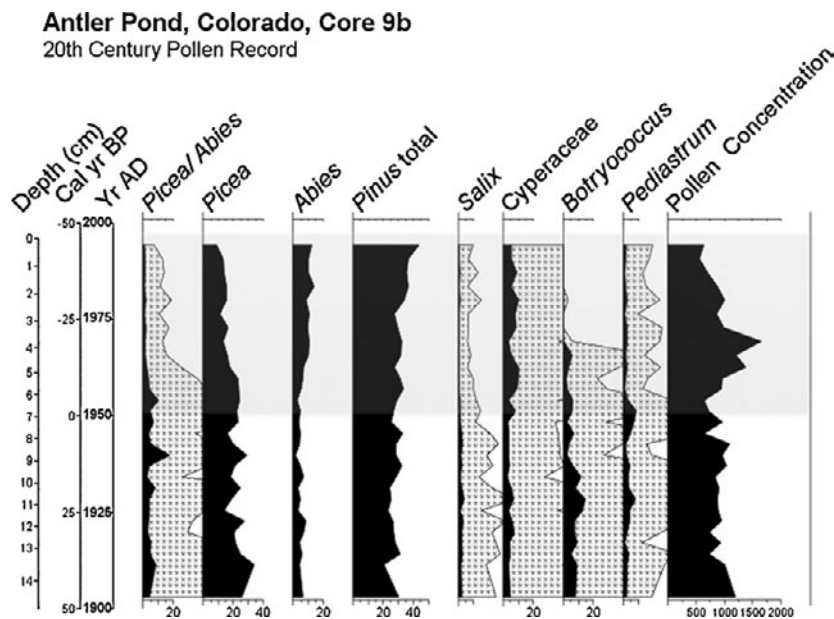


Fig. 6. Summary of major pollen and spore types, along with a *Picea/Abies* ratio, for the 20th century data only. Note two age scales, in calendar years BP and also in years AD. Silhouette is 10× actual value.

mannii prior to the outbreak, to *A. lasiocarpa* subsequent to the outbreak. Post-outbreak basal areas of live *A. lasiocarpa*, *P. engelmannii* and *P. contorta* ranged from 13.5 to 30.3, 2.5 to 11.6, and 0 to 3.9 m²/ha, respectively, and contrasted with standing dead basal areas of 2.0–6.4, 8.0–15.3 and 0–14.1 m²/ha (Table 2 of Veblen et al., 1991a). By the time their study concluded in 1986, reproduction by *A. lasiocarpa* far outpaced reproduction by *P. engelmannii* or *P. contorta*.

At Antler Pond the decline in *Picea* pollen was not immediate, however. Death of the canopy trees in plots (primarily *P. engelmannii*) did not lead to a major recruitment event for *P. engelmannii* (Veblen et al., 1991a). For survivors, growth-ring thickness increased substantially throughout the 1950s and into the 1960s, demonstrating a pattern of growth release of trees not impacted by the infestation (Fig. 5 of Veblen et al., 1991a). Control sites did not show the same release pattern during the 1950s, indicating that the release pattern was a direct result of the beetle-kill. We interpret the short-term increase in *Picea* pollen subsequent to the beetle outbreak as the result of release of sub-dominant and sub-canopy *Picea* trees. Similarly, the long-term increase in *Abies* pollen to the sediments reflects the shift to dominance of that species in the local forest composition. We conclude that the pollen record is consistent with the forest composition model developed by Veblen et al. (1991a) for areas on the White River Plateau that were severely impacted by *Dendroctonus* infestation during the 1940s, most specifically for *Picea* and *Abies*.

The trend for *Pinus* is somewhat different. The Veblen et al. (1991a) model predicts that *P. contorta* trees continue to decline, but the pollen record shows a recent increase. This could be explained by the differences in pollen production. *Picea* and *Abies* produce large grains that do not travel far from their source, but *Pinus* produces copious amounts of pollen that is widely dispersed. We suggest that the increase in *Pinus* does not reflect the local population, but instead reflects deposition of *P. contorta* pollen from large, mature stands region wide, established after fires during the late 19th century (Sibold and Veblen, 2006).

The pollen and spore record also suggests that impacts of the *Dendroctonus* infestation were not limited to the forest. Declines in both *Pediastrum* and *Botryococcus* suggest that aquatic productivity was impacted. Perhaps more importantly, the decline in *Salix* and

increase in *Cyperaceae* suggests local paludification occurred subsequent to the event. We suggest that, for this latter occurrence, this could have been caused by a decline in shallow groundwater uptake and transpiration as mature trees died, allowing greater runoff to Antler Pond.

6. Conclusions

Recent studies have demonstrated the importance of *Dendroctonus* infestations as a factor of disturbance in the *Picea–Abies* forests of the Rocky Mountains during the most recent centuries. Our ability to recognize successional sequences in the pollen record from the most recent *Dendroctonus* outbreak in the 1940s and 1950s, when compared to tree-ring and stand-age studies, is an important proof of concept. High-resolution analyses are critical to illuminating these relationships. Presently, our research at Antler Pond has been limited to the most recent outbreak in the 20th century, but we expect that outbreaks of greater antiquity could be determined from lake sediment when high-resolution pollen analytical techniques are used. For instance, it may be possible to confirm other events identified from tree-ring studies, such as the 1716–1750 AD, 1827–1845 AD, and 1860–1870 AD events documented from other areas of the White River Plateau (Miller, 1970; Baker and Veblen, 1990; Veblen et al., 1991a, 1994; Eisenhart and Veblen, 2000). However, such events may be obscured in the pollen record, because other factors might be important locally, such as available seed sources (e.g., Turner et al., 2003), or the complexity of successional pathways in subalpine forests (e.g., Kipfmüller and Kupfer, 2005). The size of the infestation could also be important in our ability to recognize outbreaks in the sedimentary record, with larger outbreaks being more easily recognized than smaller ones. Since each small pond primarily records the events nearby the site, a network of detailed, high-resolution pollen-based reconstructions may be necessary to determine the spatial distribution of infestation through time. High-resolution studies may also be important in distinguishing between successional changes in the pollen and flora after infestation, and potentially spurious changes in ratios due to short-term depositional irregularities.

Several studies have suggested that forest fires often occur within the beetle-affected area with time lags of several years, as

coarse woody debris increases across the landscape (Wein, 1990; Fleming, 1996). However, the relationship between insect infestation and forest fire may be more complex (Parker et al., 2006). Forests that burned on the White River Plateau in 1879 were less affected by the 1940s outbreak than were older stands (Bebi et al., 2003). But areas affected by the 1940s outbreak were no more susceptible to fire than stands that were unaffected by *Dendroctonus* outbreaks. For certain *Picea*-dominated forests, *Dendroctonus* is more important than fire as a disturbance agent. Estimates of fire and *Dendroctonus* return intervals on the Kenai Peninsula, Alaska, imply that spruce beetle outbreaks exceed fires in those forests by at least a factor of three (Berg and Anderson, 2006). Although we searched extensively, charcoal was not recovered from the post-infestation sediments (Fig. 5), and the drainage area around Antler Pond has yet to burn, after nearly 70 years since initiation of the beetle outbreaks. This has occurred in spite of the fact that considerable coarse woody debris still occurs near the pond. This may be due to the 20th century fire suppression policy, or simply due to the long fire rotations in high elevation subalpine forests of the region (Buechling and Baker, 2004). Our understanding of these relationships in the past needs further study, and analysis of high-resolution fire histories should accompany future insect infestation studies in order both to exclude the potential for ascribing pollen changes to fire disturbance, and analyzing the role of fire in the total picture of forest disturbance in the past.

A combination of factors is undoubtedly responsible for initiation, and perpetuation, of *Dendroctonus* outbreaks. Blowdowns often trigger outbreaks, but not always (Kulakowski and Veblen, 2003). Warm temperatures and droughty conditions appear to be prominent factors. If present trends in increasing global temperature continue into the future (IPCC, 2007) it is likely that insect defoliator outbreaks (Mattson and Haack, 1987; Williams and Liebhold, 1995, 1997, 2002; Coley, 1998; Ayres and Lombardero, 2000; Logan et al., 2003; Carroll et al., 2004) and forest fires (Flannigan et al., 1998, 2000; Neilson and Drapek, 1998; Dale et al., 2001) will occur with greater frequency and intensity. Additional paleoecological and retrospective studies will be helpful in identifying potential analog conditions that have occurred in the past. This information will be useful to forest managers in efforts to plan for the effects of *Dendroctonus* beetle infestations, and subsequent succession within high elevation conifer forests.

Acknowledgements

We are grateful to Chris Black, John Wiley, Eric Feiler and Mike Timpson for assistance in sediment coring; Teh-Lung (Richard) Ku for analyzing the ^{210}Pb and ^{137}Cs profiles; Dan Boone for help in photographing the sediments; Kirsten Ironside for Fig. 1, and Tony DeLuz for Fig. 4; and Andrea Brunelle and one anonymous reviewer for their insightful comments. We also thank Jeff Overturf, Jerry Schmidt, Liz Mauch, and Robin Inhelder (US Forest Service) for their assistance. This research was funded, in part by cooperative agreements (USDA 28-JV7-949 and USDA 04-JV-11221615-317). Laboratory of Paleoecology Contribution # 127.

References

- Alexander, R.R., Sheppard, W.D., 1990. *Picea engelmannii* Parry ex Engelm. In: Burns, R.M., Honkala, B.H. (Coordinators), Silvics of North America, Volume 1, Conifers. USDA Forest Service, Agricultural Handbook 654. pp. 187–203.
- Allen, C.D., Anderson, R.S., Jass, R.B., Toney, J.L., Baisan, C.H., 2008. Paired charcoal and tree-ring records of high-frequency Holocene fire from two New Mexico bog sites. *Intern. J. Wild. Fire* 17, 115–130.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Venetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forest. *For. Ecol. Manage.* 259, 660–684.
- Allison, T.D., Moeller, R.E., Davis, M.B., 1986. Pollen in laminated sediments provides evidence of mid-Holocene forest pathogen outbreak. *Ecology* 67, 1101–1105.
- Anderson, T.W., 1974. The chestnut pollen decline as a time horizon in lake sediments in eastern North America. *Can. J. Earth Sci.* 11, 678–685.
- Anderson, R.S., Davis, R.B., Miller, N.G., Stuckenrath, R., 1986. History of late- and post-glacial vegetation and disturbance around Upper South Branch Pond, northern Maine. *Can. J. Bot.* 64, 1977–1986.
- Anderson, R.S., Allen, C.D., Toney, J.L., Jass, R.B., Bair, A.N., 2008. Holocene vegetation & forest fire regimes in subalpine & mixed conifer forests, southern Rocky Mountains, USA. *Intern. J. Wild. Fire* 17, 96–114.
- Appleby, P.G., 2001. Chronostratigraphic techniques in recent sediments. In: Last, W.M., Smol, J.P. (Eds.), *Tracking Environmental Change using Lake Sediments*, Vol. 1. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 171–203.
- 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.
- Baker, W.L., Veblen, T.T., 1990. Spruce beetles and fires in the 19th-century subalpine forests of western Colorado, USA. *Arct. Alp. Res.* 22, 65–80.
- 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.
- Beck, H.L., Bennett, B.G., 2002. Historical overview of atmospheric nuclear weapons testing and estimates of fallout in the continental United States. *Health Phys.* 82, 591–608.
- Bennett, K.D., Fuller, J.L., 2002. Determining the age of the mid-Holocene *Tsuga canadensis* (hemlock) decline, eastern North America. *The Holocene* 12, 421–429.
- 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.
- Berg, E.E., Henry, J.D., Fastie, C.L., De Volder, A.D., Matsuoka, S.M., 2006. 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. *For. Ecol. Manage.* 227, 219–232.
- Bhiry, N., Filion, L., 1996. Mid-Holocene hemlock decline in eastern North America linked with phytophagous insect activity. *Quat. Res.* 45, 312–320.
- Blais, J.M., Kalf, J., Cornett, R.J., Evans, R.D., 1995. Evaluation of ^{210}Pb dating in lake sediments using stable Pb, *Ambrosia* pollen and ^{137}Cs . *J. Paleolimn.* 13, 169–178.
- Brunelle, A., Anderson, R.S., 2003. Sedimentary charcoal as an indicator of late-Holocene drought in the Sierra Nevada, California, and its relevance to the future. *Holocene* 13, 21–28.
- Brunelle, A., Rehfeldt, G.E., Bentz, B., Munson, A.S., 2008. Holocene records of *Dendroctonus* bark beetles in high elevation pine forests of Idaho and Montana, USA. *For. Ecol. Manage.* 255, 836–846.
- Buechling, A., Baker, W.L., 2004. A fire history from tree rings in a high-elevation forest of Rocky Mountain National Park. *Can. J. For. Res.* 34, 1259–1273.
- Bylund, H., 1999. Climate change and outbreaks of geometrid moths in the north. *Växtskyddsnotiser* 63, 5–9.
- Cahill, D.B., 1977. Net impact of spruce beetle outbreak on White River National Forest, 1939–1951. Rocky Mountain Regional Report. USFS, Fort Collins, Colorado, USA.
- Carroll, A.L., Taylor, S.W., Regnière, J., Safranyik, L., 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. In: Shore, T.L., Brooks, J.E., Stone, J.E. (Eds.), *Mountain Pine Beetle Symposium: Challenges and Solutions*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria BC.
- Clements, F.E., 1916. *Plant Succession*. In: *An analysis of the Development of Vegetation*. Carnegie Inst. Washington Publication, 242 p.
- Coley, P.D., 1998. Possible effects of climate change on plant/herbivore interactions in moist tropical forests. *Climate Change* 39, 455–472.
- 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. Climatic change and forest disturbances. *Bioscience* 51, 723–734.
- Eisenhart, K.S., Veblen, T.T., 2000. Dendroecological detection of spruce bark beetle outbreaks in northwestern Colorado. *Can. J. For. Res.* 30, 1788–1798.
- Fægri, K., Iversen, J., 1989. *Textbook of Pollen Analysis*, 4th Edition. Wiley, Chichester.
- Feiler, E.J., Anderson, R.S., Koehler, P.A., 1997. Late Quaternary paleoenvironments of the White River Plateau, Colorado, USA. *Arct. Alp. Res.* 29, 53–62.
- Flannigan, M.D., Bergeron, Y., Engelmark, O., Wotton, B.M., 1998. Future wildfire in circumboreal forests in relation to global warming. *J. Veg. Sci.* 9, 469–476.
- Flannigan, M.D., Stocks, B.J., Wotton, B.M., 2000. Climate change and forest fires. *Sci. Total Environ.* 263, 221–229.
- Fleming, R.S., 1996. A mechanistic perspective of possible influences of climate change in defoliating insects in North America's boreal forests. *Silva Fennica* 30, 281–294.
- Fleming, R.A., Volney, W.J.A., 1995. Effects of climate change on insect defoliator population processes in Canada's boreal forest: some plausible scenarios. *Water Air Soil Pollut.* 82, 445–454.
- Fuller, J.L., 1998. Ecological impact of the mid-Holocene hemlock decline in southern Ontario, Canada. *Ecol.* 79, 2337–2351.
- Gunderson, L.H., Holling, C.S. (Eds.), 2002. *Panarchy, Understanding transformations in human and natural systems*. Island Press, Washington, DC, 507 p.

- Hawksworth, F.G., Wiens, D. (Geils, B.W., Nisley, R.G., Eds.), 1996. Dwarf mistletoes: biology, pathology, and systematics. USDA Forest Service, Agricultural Handbook 709.
- Hinds, T.E., Hawksworth, F.G., Davidson, R.W., 1965. Beetle-killed Engelmann spruce: its deterioration in Colorado. *J. For.* 63, 36–42.
- Holsten, E.H., Thier, R.W., Munson, A.S., Gibson, K.E., 1999. The Spruce Beetle. USDA Forest Service Forest Insect and Disease Leaflet 127., 11.
- Intergovernmental Panel on Climate Change, 2007. Climate Change 2007: The Physical Scientific Basis. Cambridge University Press, Cambridge, UK.
- Kipfmüller, K.F., Baker, W.L., 1998. Fires and dwarf mistletoe in a Rocky Mountain lodgepole pine ecosystem. *For. Ecol. Manage.* 108, 77–84.
- Kipfmüller, K.F., Kupfer, J.A., 2005. Complexity of successional pathways in subalpine forests of the Selway-Bitterroot Wilderness Area. *Ann. Am. Assoc. Geogr.* 95, 495–510.
- Kucera, R.E., 1962. Geology of the Yampa District, northwestern Colorado. Ph.D. Dissertation, University of Colorado, Boulder. 675 p.
- Kulakowski, D., Veblen, T.T., 2003. Subalpine forest development following a blowdown in the Mount Zirkel Wilderness Colorado. *J. Veg. Sci.* 14, 653–660.
- Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., Safranyik, L., 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452, 987–990.
- Logan, J.A., Regniere, J., Powell, J.A., 2003. Assessing the impacts of global warming on forest pest dynamics. *Front. Ecol. Environ.* 1, 130–137.
- MacDonald, G.M., Kremenetski, K.V., Hidalgo, H.G., 2008. Southern California and the perfect drought: simultaneous prolonged drought in southern California and the Sacramento and Colorado Rivers systems. *Quat. Intern.* 188, 11–23.
- Marr, J.W., 1967. Ecosystems of the east slope of the Front Range in Colorado. University of Colorado Studies, Series in Biology 8. University of Colorado Press, Boulder.
- Massey, C.L., Wygant, N.D., 1954. Biology and control of the Engelmann spruce beetle in Colorado. United States Forest Service Circular Number, 944.
- Mattson, W.J., Haack, R.A., 1987. The role of drought in outbreaks of plant-eating insects. *Bioscience* 37, 110–118.
- Miller, P.C., 1970. Age distributions of spruce and fir in beetle-killed forests on the White River Plateau Colorado. *Am. Midl. Nat.* 83, 206–212.
- Miller, C., 2003. Simulation of effects of climatic change in fire regimes. In: Veblen, T.T., Baker, W.L., Montenegro, G., Swetnam, T.S. (Eds.), *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*. Springer, NY, pp. 69–94.
- Myers, J.H., 1998. Synchrony in outbreaks of forest Lepidoptera: a possible example of the Moran Effect. *Ecology* 79, 1111–1117.
- Neilson, R.P., Drapek, R.J., 1998. Potentially complex biosphere responses to transient global warming. *Glob. Change Biol.* 4, 505–521.
- Olsson, I.U., 1986. Radiometric Dating. In: Berglund, B.E. (Ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*. John Wiley and Sons, Chichester, pp. 273–312.
- Packee, E.C., 1997. Restoring spruce beetle-impacted forests in Alaska. *Agroboreal* 29, 18–24.
- Parker, T.J., Clancy, K.M., Mathiasen, R.L., 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. *Agric. For. Entomol.* 8, 167–189.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* 58, 501–517.
- Reider, R.G., 1971. A geomorphological and pedological interpretation of the White River Plateau, Colorado. Ph.D. dissertation. University of Nebraska, Lincoln.
- Ryerson, D.E., Swetnam, T.W., Lynch, A.M., 2003. A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains Colorado USA. *Can. J. For. Res.* 33, 1010–1028.
- Schmid, J.M., Frye, R.H., 1977. Spruce beetle in the Rockies. USFS Forest Service, General Technical Report RM-49.
- Sibold, J.S., Veblen, T.T., 2006. Relationships of subalpine forest fires in the Colorado Front Range to interannual and multi-decadal scale climatic variation. *J. Biog.* 33, 833–842.
- Speer, J.H., Swetnam, T.W., Wickman, B.E., Youngblood, A., 2001. Changes in pandora moth outbreak dynamics during the past 622 years. *Ecology* 82, 679–697.
- Stuiver, M., Reimer, P.J., Bard, E., Beck, J.W., Burr, G.S., Hughen, K.A., Kromer, B., McCormac, F.G.v.d., Plicht, J., Spurk, M., 1998. INTCAL98 Radiocarbon age calibration 24,000–0 cal BP. *Radiocarbon* 40, 1041–1083.
- Sudworth, G.B., 1900. White River Plateau Timber Land Reserve. In: Twentieth annual report of the United States Geological Survey, Part V: Forest Reserves, U.S. Geological Survey, Washington, D.C, pp. 117–179.
- Swetnam, T.W., Baisan, C.H., 2003. Tree-ring reconstructions of fire and climate history in the Sierra Nevada and southwestern United States. In: Veblen, T.T., Baker, W.L., Montenegro, G., Swetnam, T.W. (Eds.), *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*. Springer, NY, pp. 158–195.
- Swetnam, T.W., Lynch, A.M., 1989. A tree-ring reconstruction of western spruce budworm history in the southern Rocky Mountains. *For. Sci.* 35, 962–986.
- Telford, R.J., Heegaard, E., Birks, H.J.B., 2004. The intercept is a poor estimate of a calibrated radiocarbon age. *Holocene* 14, 296–298.
- Toney, J.L., Anderson, R.S., 2006. A postglacial palaeoecological record from the San Juan Mountains of Colorado USA: fire, climate and vegetation history. *The Holocene* 16, 1–15.
- Turner, M.G., Romme, W.H., Tinker, D.B., 2003. Surprises and lessons from the 1988 Yellowstone fires. *Front. Ecol. Environ.* 1, 351–358.
- Ungerer, M.J., Ayres, M.P., Lombardero, M.J., 1999. Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *J. Biog.* 26, 1133–1145.
- 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 regimes and disturbance interactions in a Rocky Mountain subalpine forest. *J. Ecol.* 82, 125–135.
- Veblen, T.T., Baker, W.L., Montenegro, G., Swetnam, T.W., 2003. *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*. Ecological Studies 160. Springer, New York.
- Watt, J.H., 2008. A Late-Holocene reconstruction of spruce beetle (*Dendroctonus rufipennis*) disturbance from Antler Pond, Colorado, USA. MS Thesis, Northern Arizona University.
- Wein, R.W., 1990. The importance of wildfire to climate change-hypotheses for the taiga. In: Goldammer, J.G., Jenkins, M.J. (Eds.), *Fire in Ecosystem Dynamics*. Academic Press, The Hague, The Netherlands, pp. 185–190.
- Werner, R.A., Holsten, E.H., Matsuoka, S.M., Burnside, R.E., 2006. Spruce beetles and forest ecosystems in south-central Alaska: a review of 30 years of research. *For. Ecol. Manage.* 227, 195–206.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313, 940–943.
- Whitlock, C., Shafer, S.L., Marlon, J., 2003. The role of climate and vegetation change in shaping past and future fire regimes in the northwestern US and the implications for ecosystem management. *For. Ecol. Manage.* 178, 5–21.
- Williams, D.W., Liebhold, A.M., 1995. Herbivorous insects and global change: potential changes in the spatial distribution of forest defoliator outbreaks. *J. Biog.* 22, 665–671.
- Williams, D.W., Liebhold, A.M., 1997. Latitudinal shifts in spruce budworm (Lepidoptera: Tortricidae) outbreaks and spruce-fir forest distributions with climate change. *Acta Phytopathologica et Entomologica Hungarica* 32, 205–215.
- Williams, D.W., Liebhold, A.M., 2002. Climate change and the outbreak ranges of two North American bark beetles. *Agric. For. Entomol.* 4, 87–99.
- Wright Jr., H.E., 1991. Coring tips. *J. Paleolim.* 6, 37–49.
- Zhang, Q., Alfaro, R.I., Hebda, R.J., 1999. Dendroecological studies of tree growth, climate and spruce beetle outbreaks in Central British Columbia, Canada. *For. Ecol. Manage.* 121, 215–225.