

Pollen and macrofossil evidence of Late Pleistocene and Holocene treeline fluctuations from an alpine lake in Colorado, USA

The Holocene
23(1) 68–77
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DOI: 10.1177/0959683612450199
hol.sagepub.com


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Abstract

High-resolution pollen, plant macrofossil and magnetic susceptibility (MS) data are presented from an alpine lake sediment core from west-central Colorado, recording changes in vegetation and sedimentation for the latest Pleistocene and Holocene (c. the last 12.5 ka; 1 ka = 1000 cal. yr BP). During the Younger Dryas chron (c. 12.9–11.5 ka), *Artemisia* steppe or tundra grew around the lake, but by the earliest Holocene (10.7–9.5 ka) a subalpine *Picea* and *Abies* parkland was established there. *Picea* remained important through the early Holocene, but also bristlecone and lodgepole pines (*Pinus aristata* and *P. contorta*) grew around the lake. Warming conditions are indicated from 9.5 ka, lasting until c. 4.5–3.5 ka, which may have been the warmest period, with greatest development of monsoonal conditions. Trees subsequently retreated downslope from Kite Lake c. 150–200 m during the last 3.5 ka, establishing their present treeline position. A decrease in total *Pinus* and increases in *Artemisia* and piñon (*P. edulis*) indicate a trend toward progressive climate cooling and enhanced winter precipitation. These long-term climatic trends correlate with Holocene changes in summer insolation.

Keywords

climate, Colorado, macrofossil analysis, *Picea engelmannii*, *Pinus aristata*, pollen analysis, treeline fluctuations

Received 22 November 2011; revised manuscript accepted 22 April 2012

Introduction

Analyses of sedimentary sequences from high-elevation alpine lakes and bogs have been important in documenting the effects of climate change on the distribution of high elevation forests during the Holocene. This is particularly true for the subalpine *Picea engelmannii* (Englemann spruce)–*Abies lasiocarpa* (subalpine fir) forests of the southern Rocky Mountains (Anderson et al., 2008; Fall, 1997; Jiménez-Moreno et al., 2008, 2011; Reasoner and Jodry, 2000; Toney and Anderson, 2006), which presently cover large areas between c. 2700 and 3650 m elevation (Komarek, 1994). Within this same area other high-elevation species occur with more limited distribution, such as *Pinus aristata* (Rocky Mountain bristlecone pine). In Colorado, *P. aristata* occurs in at least 65 stands, primarily on the eastern slope of the continental divide, by itself as well as a part of the *Picea*–*Abies* subalpine forest (Baker, 1992; Krebs, 1972).

The impact of climate change on treeline position worldwide is well documented (Cairns and Malanson, 1998; Grace et al., 2002). Subalpine treeline movements during the Holocene have been recognized palynologically from changing pollen percentages. For instance, modern pollen percentages within the subalpine forest of the southern Rockies up to the treeline are dominated by frequencies of *Picea*, *Abies* and *Pinus* pollen that together average 60–70% or more (Fall, 1997; Feiler et al., 1997). Above treeline in the krummholz zone, the abundance of *Picea* and *Abies* pollen drops below 15%, values virtually indistinguishable from those for *Picea* and *Abies* in alpine tundra (Fall, 1997). The lower montane vegetation belt is often characterized in this area by higher percentages of *Pinus* with little *Picea* or *Abies* pollen (Fall, 1997; Feiler et al., 1997). In rare instances, the presence of plant

macrofossils (Benedict et al., 2008; Carrara et al., 1984, 1991; Fall, 1997) or even beetle assemblages (Elias et al., 1991), have demonstrated higher treelines during the Holocene.

Climatic fluctuations during the Holocene have been demonstrated to have millennial- or even centennial-scale influence on long-term vegetation change (Jiménez-Moreno et al., 2007, 2008, 2011). More recently, climate models strongly suggest that anthropogenic climate change is likely to cause treelines to rise here as elsewhere worldwide (e.g. Holtmeier and Broll, 2005). However, little research has focused on the vegetation trends at the subalpine forest–alpine tundra ecotone within the southern Rockies, and studies in locations dominated by treelines composed of the three species – i.e. *Picea engelmannii*, *Abies lasiocarpa* and *Pinus aristata* – are novel.

If widespread changes are in store for high elevation forests in the future, it is desirable to understand the role of climate and ecosystem processes in shaping the vegetation of the subalpine forests of the Rocky Mountain corridor in the past, as a way of understanding the natural range of variability of forest composition in planning for the future. In this paper we use high-resolution

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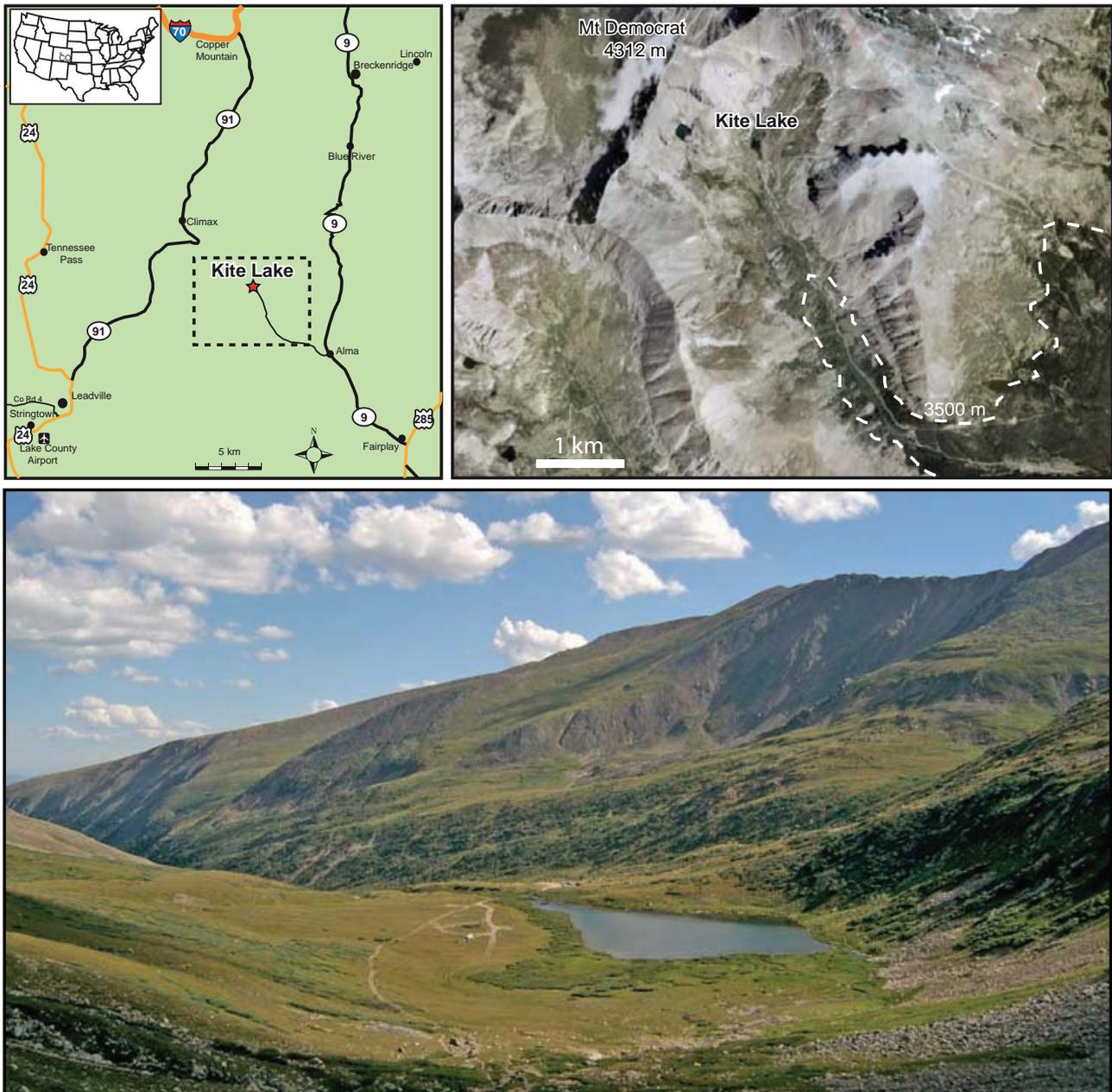


Figure 1. Left: The star marks the approximate location of Kite Lake in the Pike National Forest, Colorado. Right: Aerial photo of the Kite lake area. The dashed line at 3500 m marks the elevation of upper treeline. Below is a photo of Kite Lake looking to the north.

pollen, plant macrofossil and magnetic susceptibility (MS) data from a Late Pleistocene and Holocene sedimentary record from Kite Lake, central Colorado (Figure 1), to document the occurrence of subalpine conifer forest composed of *Picea engelmannii*, *Abies lasiocarpa* and *Pinus aristata* at a site presently within the alpine zone above treeline.

Study site

Kite Lake (39°19' 47.18"N, 106°07' 47.38"W; 3665 m above sea level) is located ~10 km northwest of Alma, Colorado, in the Pike National Forest (Figure 1). The lake occurs in a Late Pleistocene cirque basin surrounded by four high-elevation peaks (Mts Democrat, 4312 m, Cameron, 4340 m, Lincoln, 4354 m and Bross, 4320 m). The Kite Lake outlet stream feeds into Buckskin Creek, a tributary of the South Platte River. When cored in July of 2007, the maximum depth of the lake was c. 5.3 m.

Climate of north-central Colorado is influenced both by winter storms originating from the Pacific, and summer convective

storms influenced by subtropical air masses (Colorado Climate Center: <http://ccc.atmos.colostate.edu/climateofcolorado.php>). The closest weather station to Kite Lake is at Climax, Colorado (3460 m elevation), which has been in operation since AD 1893, and is 6 km NW of Kite Lake. Average annual high and low temperature there is c. 6.1°C and -7.3°C, respectively, with average summer (JJA) high temperature of 16.6°C and average winter (DJF) low of -16.3°C. Annual precipitation averages 62.8 cm, with 713 cm of snow. Winter precipitation peaks in April, and is followed by a minimum in June. A second peak occurs in July and August, with a second minimum in September and October (Western Regional Climate Center (WRCC), data accessed October 2011).

Modern vegetation in the southern Rocky Mountains of central Colorado is characterized by alpine and upland herb communities above c. 3500 m (11,500 feet), high-elevation conifer forest with *Populus tremuloides* (quaking aspen) above c. 2900 m (9500 ft), and *Artemisia* (sagebrush) steppe below this (Langenheim, 1962). Krummholz of *Picea engelmannii* (Engelmann spruce)

commonly occurs in the lowest part of the alpine zone. In the alpine community, generally above 3800 m (c. 12,500 feet), are typically found *Hymenoxys (Tetranneuris) grandiflora* (graylocks four-nerve daisy), *Poa alpine* (alpine bluegrass), *Artemisia scopulorum* (alpine sagebrush), *Oxytropis deflexa* (nodding locoweed), *Erigeron pinnatisectus* (featherleaf fleabane), *Trisetum spicatum* (spike trisetum), *Silene acaulis* (moss campion), *Geum rossii* (Ross' avens), and many others. In central Colorado, the upland herb community generally occupies non-forested elevations from c. 3500 to 3800 m (11,500 to 12,500 feet). This community, today surrounding Kite Lake, commonly includes sparse *Picea engelmannii* krummholz, with numerous species of *Salix* (willow). Common herbs include *Senecio crassulus* (thickleaf ragwort), *Ligusticum porteri* (Porter's licorice-root), *Lupinus parviflorus* (lodgepole lupine), *Phleum alpinum* (alpine timothy), *Potentilla (Argentina) spp.* (cinquefoil), *Castilleja spp.* (Indian paintbrush), *Achillea lanulosa* (yarrow), *Delphinium barbeyi* (subalpine larkspur), and *Poa alpina*, among many others.

The *Picea engelmannii*–*Abies lasiocarpa* (subalpine fir) community can occur as low as c. 2590 m (c. 8500 feet) and as high as c. 3800 m (c. 12,500 feet) as patches of krummholz, but is best developed locally between 3200 and 3500 m (c. 10,500–11,500 feet) (Langenheim, 1962; personal observations). Dominant trees are *Picea engelmannii* and *Abies lasiocarpa*, but *Populus tremuloides* and *Pinus contorta* (lodgepole pine) can be locally common, while *Pinus aristata* (bristlecone pine) is common at the highest elevations of the community near Kite Lake. Common shrubs in this community include *Ribes montigenum* (gooseberry currant) and *R. wolfii* (Wolf's currant), *Vaccinium myrtillus* (whortleberry) and/or *V. cespitosum* (dwarf bilberry), with numerous herbs including *Arnica cordifolia* (heartleaf arnica), *Fragaria (ovalis) virginiana* (strawberry), *Pedicularis spp.* (lousewort),

Polemonium spp. (Jacob's-ladder), *Geranium richardsonii* (Richardson's geranium) and many others.

The sagebrush steppe community, which occurs primarily to the SW in South Park, is dominated by *Artemisia tridentata* (big sagebrush) and *Chrysothamnus spp.* (rabbitbrush), with *Achillea (millifolium) lanulosa* (common yarrow), *Eriogonum spp.* (buckwheat), *Erigeron speciosus* (aspen fleabane), *Vicia americana* (American vetch), *Arenaria congesta* (sandwort), and various grasses including *Festuca thurberi* (Thurber's fescue), *Agropyron (Elymus) trachycaulum* (wheatgrass), *Bromus frondosus* (weeping brome), *Stipa (Achnatherum) lettermanii* (Letterman's needlegrass) and others (terminology follows USDA Plants Database nomenclature). Isolated stands of *Pinus edulis* (piñon) occur within 50 km southeast and northwest of Kite Lake (Charles Truettner, personal communication, 2012; <http://swbiodiversity.org/seinet/taxa>).

Materials and methods

In July 2007, we collected two cores from Kite Lake – an 830 cm long sediment Livingstone core (KL-07-01), and a shorter record (KL-07-02) using a plexiglass tube, which included the unconsolidated upper 20 cm of sediments. The two cores were within 1 m of each other in the deepest part of the lake.

The Kite Lake chronology was developed from a combination of $^{239+240}\text{Pu}$ activity profile of the upper sediments, and 12 calibrated AMS radiocarbon dates (Table 1; Figure 2). No $^{239+240}\text{Pu}$ was detected below 5.5 cm, suggesting below this depth shows 'pre-bomb' conditions, and dates prior to AD 1952. Maximum $^{239+240}\text{Pu}$ activity (i.e. AD 1963–1964) occurred at 3–3.5 cm depth (ME Ketterer, personal communication, 2010). Material for AMS dates consisted of terrestrial plant remains and bulk sediment

Table 1. Age data for Kite Lake, Colorado.

Lab number ^a	Core	Depth (cm)	Material dated	$\delta^{13}\text{C}$ (‰)	Dating method	Age (^{14}C yr BP $\pm 1\sigma$, $^{239+240}\text{Pu}$)	Calibrated age (cal. BP) 2σ ranges	Median
NAU Chemistry	#07-02	0	Bulk sediment	N/A	Present	AD 2007	–57	–57
NAU Chemistry	#07-02	3.5	Bulk sediment	N/A	$^{239+240}\text{Pu}$	AD 1963	–13	–13
NAU Chemistry	#07-02	5.5	Bulk sediment	N/A	$^{239+240}\text{Pu}$	AD 1952	–2	–2
UCIAMS 41396	#07-01	46	Bulk sediment, 0.18 mg C	–26.5	^{14}C	740 ± 15	667–689	678
UCIAMS 41397	#07-01	106	Bulk sediment, 0.13 mg C	N/A	^{14}C	1950 ± 15	1867–1945	1898
UCIAMS 71779	#07-01	170–174	Microcrustaceans	–26.6	^{14}C	4120 ± 25	4529–4813	4647
UCIAMS 41398	#07-01	238–239	Wood, leaf fragments	–26.1	^{14}C	4535 ± 15	5062–5309	5149
UCIAMS 71780	#07-01	265–267	Microcrustaceans	–25.4	^{14}C	6335 ± 25	7173–7319	7267
UCIAMS 46095	#07-01	295	Bulk sediment	N/A	^{14}C	8230 ± 25	9091–9294	9199
UCIAMS 71770	#07-01	319–322	<i>Picea engelmannii</i> , <i>Abies</i> needles, twig	–21.6	^{14}C	8330 ± 25	9282–9436	9359
UCIAMS 46096	#07-01	340	Bulk sediment	N/A	^{14}C	$11,460 \pm 35$	13,222–13,432	13,308
UCIAMS 41399	#07-01	361–362	Bulk sediment, 0.050 mg C	N/A	^{14}C	$11,820 \pm 180$	13,301–14,034	13,669
UCIAMS 51259	#07-01	438	Bulk sediment, 0.14 mg C	N/A	^{14}C	$10,330 \pm 60$	11,843–12,412	12,173
UCIAMS 41400	#07-01	443	Leaf fragments	–25.2	^{14}C	$10,360 \pm 20$	12,084–12,382	12,214
UCIAMS 51260	#07-01	680	Bulk sediment, 0.15 mg C	N/A	^{14}C	$13,980 \pm 100$	16,805–17,419	17,112

Note: All ages were calibrated using CALIB 5.0.2 (Stuiver and Reimer, 1993).

^aSample number assigned at radiocarbon laboratory; UCIAMS: University of California at Irvine W.M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory. NAU Chemistry: Northern Arizona University Department of Chemistry.

$\delta^{13}\text{C}$ values shown were measured to a precision of better than 0.1‰ on CO_2 aliquots, using a Finnigan Delta Plus IRMS with Gas Bench input. Some radiocarbon samples were too small to provide sufficient extra CO_2 for the $\delta^{13}\text{C}$ measurements.

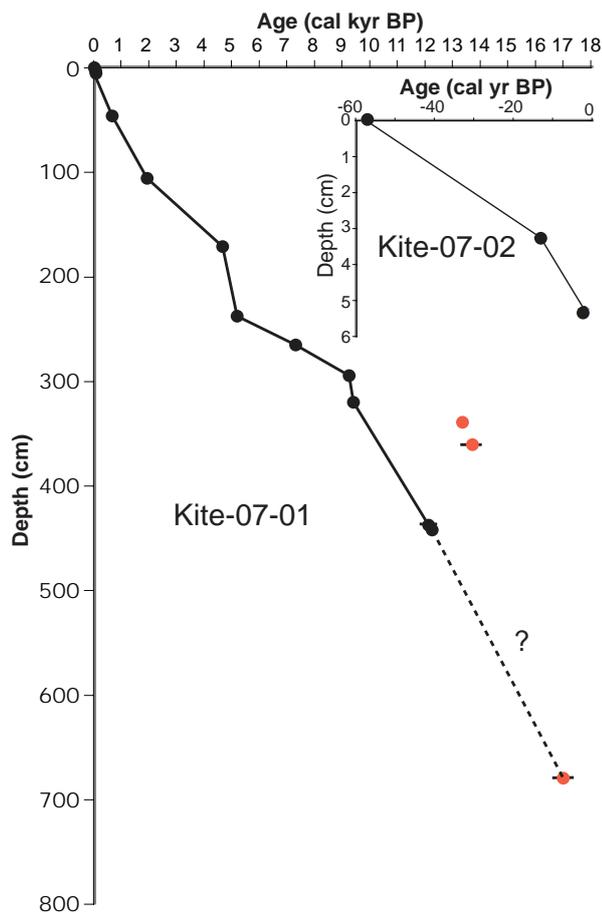


Figure 2. Age–depth diagram for the Kite Lake record. The red dots are dates that were not used in the age model. Kite-07-02 represents the short core and Kite-07-01 the long ‘Livingstone retrieved’ core (colour figures available online).

samples (Table 1). Samples for AMS dating were initially dried and weighed before submission. Radiocarbon ages were calibrated to calendar ages using CALIB version 5.0.2 (Stuiver et al., 1998). Our chronology for the dated part of the core consists of linear interpolation between adjacent ages, using the median value of the calibrated age of the date.

Lithology and wet Munsell color were described from split core segments (Figure 2) in the lab. Magnetic susceptibility (MS), a measure of the tendency of sediment to carry a magnetic charge (Snowball and Sandgren, 2001), was measured with a Bartington MS2E meter in dimensionless cgsu units (cgsu; Figure 3). Measurements were taken directly from the core surface every 0.5 cm for the entire length of the Kite Lake 07-01 core.

Samples for pollen analysis (1 cm³) were taken every 2 cm throughout the upper 474 cm of the cores (Figure 4). Pollen extraction followed a modified Fægri and Iversen (1989) methodology. Counting was performed at 400× magnification to a minimum pollen sum of 300 terrestrial pollen grains. Fossil pollen was identified using published keys and the modern pollen reference collection at Northern Arizona University. *Pinus* pollen was divided into four categories: (1) diploxylon (verrucae absent; locally, *P. contorta* but perhaps *P. ponderosa* from long distances), (2) haploxylon > 65 µm (verrucae present; bristlecone, *P. aristata* or limber, *P. flexilis*), (3) haploxylon < 65 µm (*P. edulis* (piñon)) and (4) indeterminate (Jacobs, 1985). A summary of important pollen type percentages are plotted in Figure 4. The pollen zonation was accomplished by cluster analysis of the pollen percentages using CONISS (Grimm, 1987).

Macrofossil analysis consisted of taking 5 cm³ every 5 cm, except for the section between 150 and 310 cm, being sampled

every 2.5 cm (Figure 5). Each sample was deflocculated in a solution of 10% Na(PO₃)₃ (sodium hexametaphosphate) for 2 to 5 days, then wet-sieved (250 and 125 µm screens). The residue containing the macrofossils was analyzed under a dissecting microscope at 25–50×. Conifer needles and bryophytes were recorded (Figure 5).

Because the upper elevation boundary of forest species is primarily sensitive to temperature (Cairns and Malanson, 1998), we interpret pollen changes in the abundance in subalpine species (mainly *Picea engelmannii* and *Abies lasiocarpa*) as temperature-induced elevational shifts of the subalpine zone (Figure 6). Also, declines in subalpine species and relative increases in lower elevation species (i.e. below lower treeline) such as *Artemisia*, are interpreted as a warming- and drying-induced upslope elevational displacement of the steppe. We follow several studies from the southern Rocky Mountains (e.g. Carrara et al., 1984; Fall, 1997; Jiménez-Moreno et al., 2008, 2011; Markgraf and Scott, 1981; Reasoner and Jodry, 2000; Toney and Anderson, 2006) who have used this relationship to document treeline fluctuations during the Holocene.

Results

Chronology and sedimentary rates

The age–depth model suggests that the Kite Lake record covers at least the last *c.* 13 ka (Table 1; Figure 2). There were two age reversals. Samples UCIAMS – 460996 and 41399 were considered too old and were not used in the age-model construction (Figure 2). A seemingly old date (17,112 cal. yr BP at 680 cm) on bulk sediment was also rejected, as there is little evidence of deglaciation before *c.* 16 ka (Benson et al., 2005; Young et al., 2011) at high elevations in Colorado.

Sediment accumulation rates (SAR) are based on linear interpolation between the radiocarbon and ²³⁹⁺²⁴⁰Pu dates. The SAR vary from 1.59 to 0.15 mm/yr during the Late Pleistocene and postglacial from 12,214 to 9199 cal. yr BP. SAR during most of the Holocene are characterized by values between 0.05 and 1.32 mm/yr. SAR increased considerably during the last few decades, with values between 1.8 and 1.35 mm/yr. This rapid sedimentation rate is consistent with the flocculent, non-compacted nature of sediments at the top of lake sediment cores.

Lithology and magnetic susceptibility

Kite Lake sediments are primarily inorganic in the lower portion of the core, progressively becoming more organic towards the top (Figure 3). Many sediment sections throughout the core are laminated indicating little if any bioturbation. The core bottoms at *c.* 8.30 m with 75 cm of light greenish-brown, glacial clayey sand resting on bedrock. Alternating greenish brown clays, grey clays and silts layers occur upcore from *c.* 7.50 m to *c.* 4.90 m depth. More massive and lighter greenish-brown clays occurred from 4.90 to 4.50 m. Laminated lighter grayish clays overlie this until 3.60 m. From 3.60 to 2.30 m laminated dark brown gyttja occurred. Above this to the core top the lithology is characterized by alternations of grayish, brown and greenish laminated gyttja (Figure 3).

High-variability is observed in the Kite Lake MS record (Figure 3). MS variations coincide with lithologic changes throughout the core and lighter and organic depleted clays seem to correspond to higher MS. High MS values characterize the bottom of the core, from 8.30 to 4.90 m (latest Pleistocene), with values around 200 cgsu. MS decreased to around 85 cgsu between 4.90 and 4.50 m. Later on, MS increased with values around 125 cgsu between 4.50 and 3.60 m (latest Pleistocene – *c.* 10.3 ka). The darkest and most organic-rich portion of the core, between 3.60 and 2.40 m (*c.* 10.3–5.3 ka), is characterized by the lowest

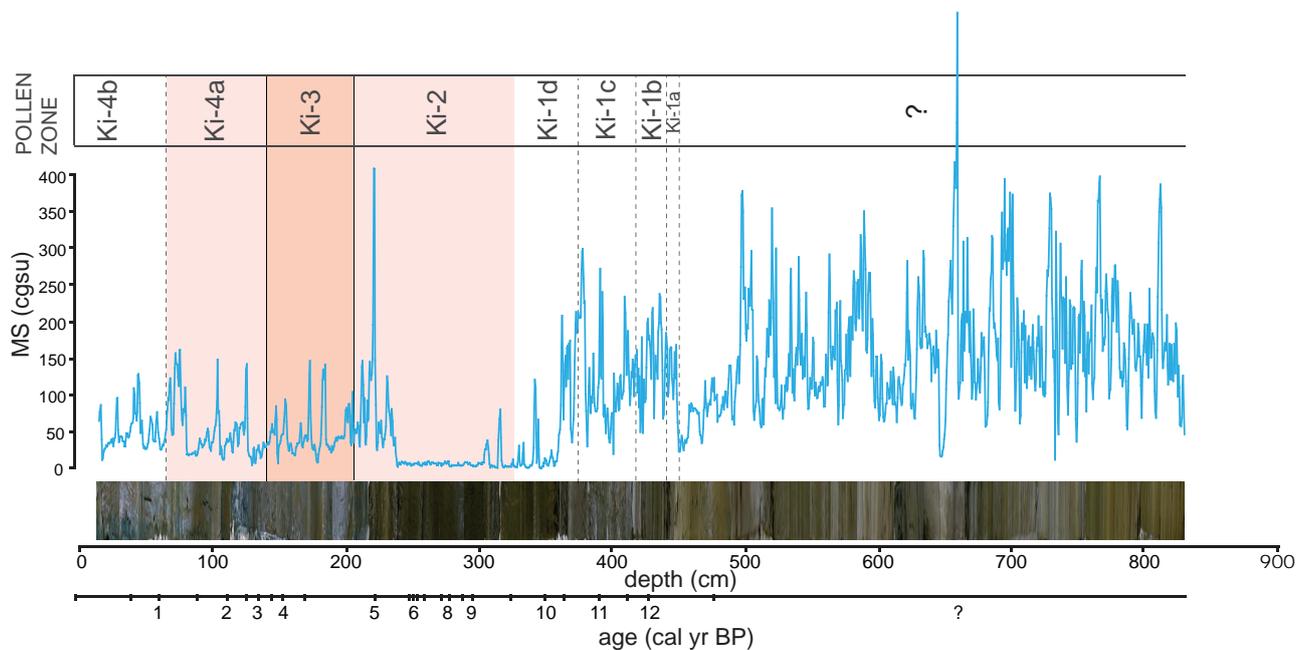


Figure 3. Core composite photo and magnetic susceptibility (MS) profile of Ki-07-01 core. Pollen zones deduced from the pollen data are shown (see Figure 4).

MS values around 0 cgsu. High-variability and average values around 75 cgsu characterize the top of the core, from 2.40 m up (c. 5.3 ka–present).

Pollen and macrofossil analyses

Pollen data come only from the top 460 cm of the Kite Lake sediment record – the lower 3.7 m were barren. The CONISS zonation – using *Pinus* total, *Juniperus*, *Abies*, *Picea*, *Artemisia* and Poaceae – suggests four pollen zones that are described using the pollen and plant macrofossils (Figures 4 and 5). Preservational irregularities probably accounted for the variability in *Pinus* species (Figure 4) and so individual changes in those types were not used in the CONISS analysis.

Zone Ki-1 (c. 12.5–9.5 ka (460–320 cm depth)). Ki-1 encompasses the latest Pleistocene and early Holocene. This zone is dominated by pollen of *Artemisia*, *Picea* and *Pinus* haploxylyon-type (either *P. aristata*, bristlecone pine, or *P. flexilis*, limber pine). This zone is subdivided into four subzones (1a–1d); subzones 1a and 1c are characterized by the highest percentages in *Artemisia* (above 40%) and subzones 1b and 1d by relatively lower *Artemisia* and higher *Picea* (with values sometimes higher than 15%), *Abies* and *Pinus* haploxylyon-type. No conifer macrofossils were recovered from these sediments except for zone 1d (c. 10.7–9.5 ka) where spruce needles were found (Figure 5). Poaceae, Cyperaceae and other Asteraceae are prominent in Ki-1, and *Juniperus* and Amaranthaceae pollen, as well as the aquatic algae *Pediastrum*, increase at the upper part of the zone.

Zone Ki-2 (c. 9.5–4.9 ka (320–200 cm depth)). Zone 2 is characterized by a significant decrease in *Artemisia* (reaching values around 20%) and *Picea* (now around 5%, but with needle fragments present as well (Figure 5)) and an increase in *Pinus* (c. 40%, mostly indeterminate, but late in the zone an increase in the *Pinus* haploxylyon-type). *Juniperus* (probably *J. communis*) is important in this zone, averaging about 4%. Other pollen types that increase by the beginning of Ki-2 include *Populus* (quaking aspen), *Quercus* (oak), and *Sarcobatus* (greasewood), as well as types tied to wetlands around the lake (i.e. *Salix* (willow) and

Ranunculus (buttercup)). *Pediastrum* percentages are highest in this zone, especially at the beginning with values up to 3300% (calculated with respect to the total pollen sum).

Zone Ki-3 (c. 4.9–3.4 ka (200–140 cm depth)). In this zone *Pinus* total reaches its highest percentage (sometimes higher than 60%), with *P. diploxylyon* type (probably *P. contorta*) dominating. *Picea* also has sustained high percentages. *Artemisia* shows its lowest percentages in the record averaging about 10% (see Figures 4 and 6). *Juniperus* declines, but Poaceae and Cyperaceae continue to be important herbs in the record. *Pediastrum* decreases progressively in this zone. A single needle fragment of *Picea* was found at c. 4.5 ka, with a needle fragment of *Pinus* cf. *aristata* recovered at c. 3.5 ka.

Zone Ki-4 (c. 3.4 ka–AD 2007 (140–0 cm depth)). Pollen spectra of Ki-4 show a gradual increase in *Pinus edulis* (which began with sporadic occurrence in Ki-3), and especially in *Artemisia* in two steps (zones 4a and 4b; Figures 4 and 6). A two-step (4a–4b) decrease in the total percentage of *Pinus* and *Picea*, as well as in *Pediastrum*, is also observed in this zone. However, pollen of *Pinus* diploxylyon-type (probably *P. contorta*) dominates the identified pine pollen in Ki-4a, while pollen of *Pinus* haploxylyon-type (probably *P. aristata*) is more abundant in Ki-4b. Conifer needle fragments were not recovered from sediments of Ki-4 (Figure 5).

Discussion

Kite Lake, at 3665 m above sea level, is today located above the upper treeline, within the upper limit of krummholz *Picea engelmannii* and *Abies lasiocarpa* (Figure 1), and several 100 m above the nearest *Pinus aristata* stand. The elevational position of Kite Lake makes it an important site in understanding the movement of treeline during the Holocene.

Late Pleistocene environments

Like other alpine lakes in the southern Rockies Kite Lake formed on the floor of a cirque basin subsequent to deglaciation during the Late Pleistocene. Our bottom age for this core suggests a

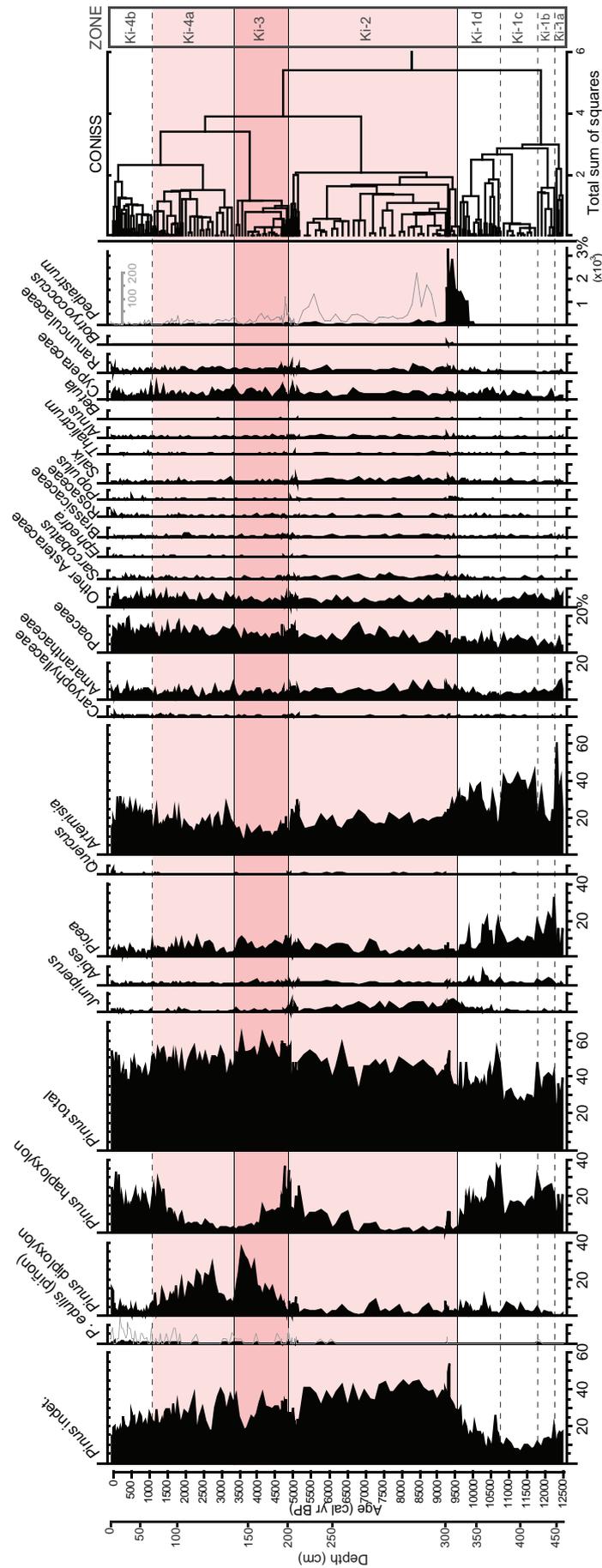


Figure 4. Pollen diagram of the Kite Lake record showing percentages of selected taxa. The aquatics (including *Alnus*, *Betula*, *Salix*, *Cyperaceae*, *Liliaceae*, *Ranunculaceae* and *Thalicttrum*) were excluded from the total pollen sum. Percentages of algae (*Pediastrum*) were calculated with respect to the terrestrial pollen sum. The zonation was made using cluster analysis provided by CONISS (Grimm, 1987).

potentially age for deglaciation ($13,980 \pm 100$; *c.* 16,805–17,419 cal. yr BP, Table 1), that is earlier than estimated at other equivalent high-elevation Colorado locations (Benson et al., 2005). However, the fact that we found no macroscopic organics to date in the bottom of the core, but obtained the above-mentioned age on bulk sediment, leaves open the question of an exact age of deglaciation and the beginning of sedimentation in this basin.

Deposition in this lake during the latest Pleistocene is characterized by high sediment accumulation rates and low organic content, as depicted by the relatively high MS values and the light clayey lithology in the lower part of the core (lower 3.4 m; Figure 3). Pollen data is lacking for most of the latest Pleistocene, however several pollen spectra, with the highest percentages in *Artemisia* (61.2%) and the lowest %AP (14.7%), indicate that during the early portion of the Younger Dryas (YD) (pollen zone Ki-1a) vegetation around the lake would have been characterized as a tundra or steppe with *Artemisia* as the most representative species (Figures 4 and 6). Therefore a relatively cold and dry climate is interpreted for this part of the record.

However, by *c.* 12,200 cal. yr BP a prominent change in the pollen is observed with an abrupt increase in the subalpine species *Picea* and *Abies*, essentially reaching their highest (*Picea*) or

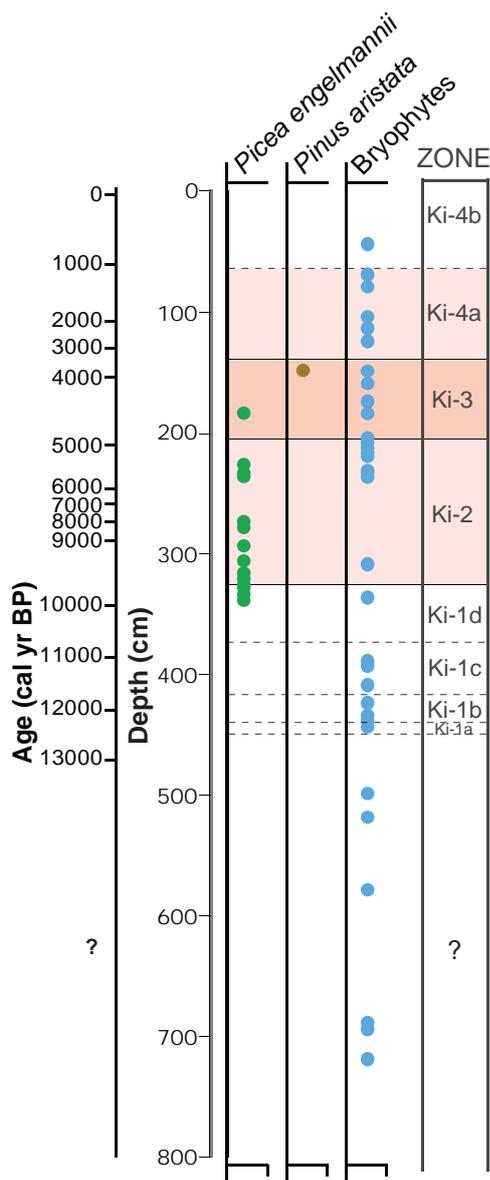


Figure 5. Macrofossil record from Kite Lake, Colorado. On the right, pollen zones as defined by the pollen record.

near-highest (*Abies*) percentages of the record, along with *Pinus aristata* (pollen zone Ki-1b; Figure 4). This is also shown by an abrupt increase in %AP and consequently, a decrease in *Artemisia* (Figure 6). Based upon the modern pollen samples from Feiler et al. (1997), pollen percentages of *Picea+Abies* at 15–35% with *Pinus* of *c.* 40% suggests that a subalpine forest with *Picea*, *Abies* and *P. aristata* probably grew around Kite Lake, and that treeline at that time would be at a higher elevation than today. However, conifer macrofossils were not recovered from sediments deposited during Ki-1b (Figure 5). Moreover, a higher treeline at this time would be in direct disagreement with other high-elevation studies from the southern Rockies, that show a downslope displacement of the subalpine vegetation of several hundred meters during the YD (Fall, 1997; Jiménez-Moreno et al., 2008, 2011; Markgraf and Scott, 1981; Reasoner and Jodry, 2000; Toney and Anderson, 2006). We suspect that the Kite Lake anomaly may be a function of the fact that the age control for this part of the core is inadequately constrained (Figure 2) and this pollen subzone could already belong to the early Holocene, showing a warming and thus the maximum elevational extent of the subalpine forest, recorded in the Southern Rocky Mountains at about 9 ka (Fall, 1997). However, we retain here the ages in our age model, which has not been adjusted to be consistent with this speculation.

Holocene environments

The earliest part of the Holocene is characterized in the Kite Lake pollen record by two rapid oscillations in the local vegetation. Abundant *Artemisia* with low conifer pollen suggests that alpine conditions probably prevailed at the site from *c.* 11.7 to 10.7 ka (subzone Ki-1c). Later, from *c.* 10.7–9.5 ka (subzone Ki-1d), a *Picea* and *Abies* parkland grew around the lake, probably with either *Pinus aristata* or *P. flexilis* and *Juniperus communis* in the understory. Definitive presence of *Picea engelmannii* is shown from the macrofossil record in sediments deposited after *c.* 10.0 ka (Figure 5). This may have been a time of relatively high lake levels at Kite Lake, as shown by the abundance of the planktonic alga *Pediastrum* (Figure 4).

A significant change in the vegetation is observed shortly after *c.* 9.5 ka (boundary between zones Ki-1 and Ki-2). A significant decline in *Artemisia* and *Picea* pollen occurs, and increases in *Pinus* suggest a pine forest, probably including bristlecone and lodgepole pines (*Pinus aristata* and *P. contorta*) expanded at middle to higher elevations in the area, indicating warming conditions. This was certainly the case regionally (Anderson et al., 1999; Fall, 1997; Jiménez-Moreno et al., 2008; Toney and Anderson, 2006; Weng and Jackson, 1999; and others). The presence of *Picea* needles in these sediments indicates that climate remained warm enough to support subalpine species around Kite Lake.

Within the lake itself, lithologic changes from laminated lighter grayish clays below to laminated dark brown gyttja (Figure 3) indicate increasing productivity and thus more organic-rich deposition in the lake. *Pediastrum* maintains its highest abundance at *c.* 9.3 ka, suggesting both greater productivity as well as continued deep water levels. Elsewhere, this time witnessed the expansion of the summer monsoon (Anderson, 1989; Betancourt, 1990; Fall, 1997; Friedman et al., 1988) and high stands of some desert lakes (Castiglia and Fawcett, 2006). However, after *c.* 9.2 ka, *Pediastrum* declined, and many wetland plants including *Alnus*, *Salix*, *Thalictrum* and Ranunculaceae increased, all suggesting an opening of a marginal fringe around the lake, perhaps resulting from dropping lake levels or infilling of the basin.

Very similar changes in the pollen are observed in the records from northern New Mexico (Stewart Bog, Jiménez-Moreno et al., 2008; Chihuahueños Bog, Anderson et al., 2008) and Tiago Lake, northern Colorado at about the same age (Jiménez-Moreno et al., 2011). These trends – lowered lake levels but expansion of lower

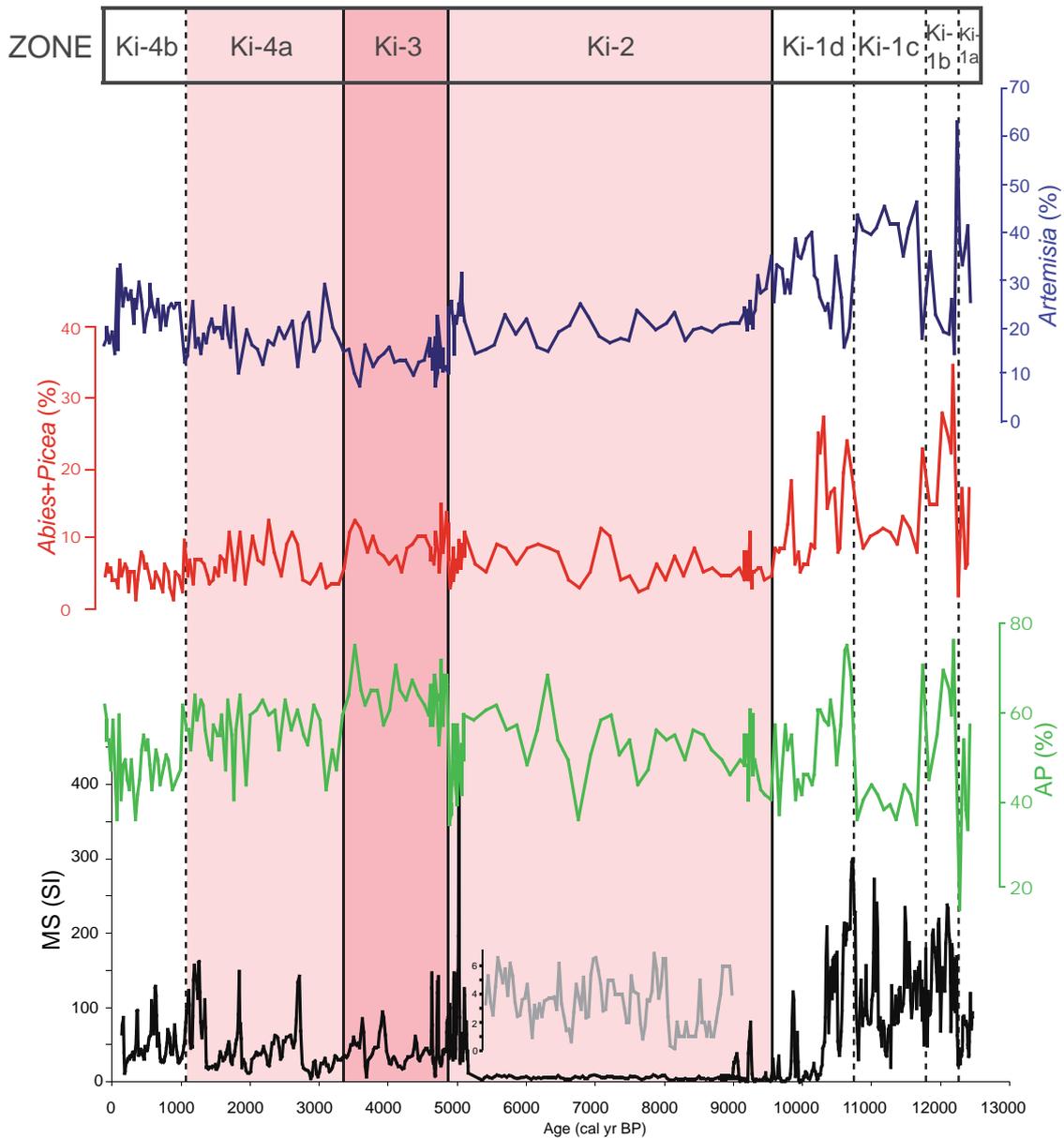


Figure 6. Comparison of magnetic susceptibility (MS; with an exaggeration of values between c. 9 and 5.4 ka), %AP (arboreal pollen), *Abies* and *Picea* percentages and *Artemisia* from Kite Lake. Pollen zones are represented.

elevation species' limits – seem to counter each other. Yet evidence for both trends is found in the region (Jiménez-Moreno et al., 2011; Shuman et al., 2009). In central (Fall, 1997; Markgraf and Scott, 1981) and northwest (Mayer et al., 2005) Colorado, montane forest expanded downslope into *Artemisia* steppe, suggesting summer monsoons continued to provide sufficient precipitation during the early and middle Holocene. Lake-level evidence from Hidden Lake (Shuman et al., 2009) in northern Colorado documented lowered lake levels throughout the same period. Further, Shuman et al. (2009) suggested that lowered lake levels were probably a result of reduced winter precipitation, while summer precipitation determined the location of the lower forest/steppe boundary.

The early and middle Holocene (from c. 9.5 to 3.6 ka) witnessed the continued presence, and even expansion, of the pine forest near Kite Lake, while pollen suggests that *Artemisia* steppe probably remained confined to lower elevations away from the lake (Figures 4 and 6), patterns which continue until c. 3.6 ka

(zones Ki-2 and 3; Figure 4). *Pinus* trees probably populated the lake area at that time, as in zone Ki-3 percentages often reached values higher than 60–65%, typical of high-elevation forest (Anderson et al., 1999; Fall, 1997; Feiler et al., 1997). Unfortunately, poor preservation of *Pinus* grains in this interval (Figure 4) precludes assigning exact species occurrence, although the presence of one *Pinus aristata* needle supports our assertion (Figure 5). Even though low pollen percentages (c. 10% or less) of *Picea engelmannii* are characteristic of this period, needle fragments are common. If we assume that these fragments came from trees growing around Kite Lake at that time, an upward movement of treeline of 150–200 m by the early to middle Holocene is indicated. This is in strong agreement from other sites in Colorado and adjacent regions where conifer remains (Carrara et al., 1984, 1991; Fall, 1997), bark beetle assemblages (Elias et al., 1991), or pollen records (Anderson et al., 1999, 2008; Feiler et al., 1997; Jiménez-Moreno et al., 2008, 2011; Madsen and Currey, 1979; Munroe, 2003; Toney and Anderson, 2006) suggest higher

treelines and warmer temperatures. *Picea engelmannii* trees grew up to 150 m higher than today in north-central Colorado as late as 4.7–4.2 ka (Benedict et al., 2008).

These changes undoubtedly occurred in response to an increase in summer insolation and its influence on summer temperatures (Kutzbach et al., 1998). The delayed thermal maximum observed in this study, from the early-Holocene insolation maximum, may be related to the lingering effects of the Laurentide Ice Sheet (Kaufman et al., 2004; Renssen et al., 2009), continued relatively high summer insolation (Berger, 1978; Kutzbach et al., 1998), and/or positive September and October insolation anomalies (Shuman et al., 2009), which lasted through the middle Holocene, perhaps essentially ‘lengthening’ the summer and ‘shortening’ the winter precipitation seasons.

Subsequent to the warmest and wettest monsoonal conditions, the Kite Lake record shows a decrease in *Pinus* and increases in *Artemisia* and piñon (*P. edulis*; Zone Ki-4 in Figure 4). This vegetation change most likely resulted from the contraction of lower treeline upslope, accompanied by an upslope movement of *Artemisia* at lower elevations regionally (see also Allen et al., 2008; Anderson et al., 2008; Jiménez-Moreno et al., 2008; Markgraf and Scott, 1981). The downslope displacement of upper treeline is probably related to a progressive climate cooling. This is supported by the lack of fossil needles in the sediments, indicating that forest species were not present around the lake after c. 3.5 ka (Figure 5). These long-term climatic trends correlate to changes in summer insolation during the neoglacial period. The increase in winter precipitation in the last three millennia explains relatively higher lake levels in the Rocky Mountains (Shuman et al., 2009). The *P. edulis* increase since 1.7 ka at Kite Lake is part of a much broader geographic expansion across its range (Anderson and Feiler, 2009), likely due to several factors including changing insolation seasonality leading to cooler summers and warmer winters in the last millennia (Anderson and Feiler, 2009; Holmgren et al., 2007), multidecadal climate variability and periodic drought (Gray et al., 2006; Jackson et al., 2005) or chance establishment by jays or Native Americans (Betancourt et al., 1991).

Relationship of MS and Kite Lake vegetation

Magnetic Susceptibility (MS) has often been used as a proxy for clastic deposition (thus more ferromagnetic minerals) in lakes, and often varies with respect to organic deposition into the sediments (Dearing, 1999). For the Kite Lake record, MS is generally high, though variable, in zones Ki-1a, Ki-1b and Ki-1c (Figure 6), contemporaneous with the Younger Dryas, when our paleovegetation reconstructions suggest *Artemisia* tundra or steppe. Only when unequivocal evidence of trees growing directly around the lake first occurs in Ki-1d (and later on in zone Ki-2), in the early Holocene after c. 10 ka (Figure 5) do we see a decline in MS values (Figure 6). In reality, we do not know whether this change in MS resulted from (a) forest or woodland species stabilizing the steep slopes surrounding Kite Lake (allochthonous organic matter), or (b) an increase in lake productivity (autochthonous organic matter), such as shown by the profile of *Pediastrum*, or (c) both. This is because vegetation conversion and the *Pediastrum* increase were concurrent. We suspect that warming temperatures led to an elevated treeline in the early Holocene, which minimized erosion, and warmed the lake enough to increase productivity. This may be resolved with additional carbon isotope measurements on the lake sediments.

MS values increase once again at the end of Ki-2 (c. 5.2 ka; Figure 6), and remain high but fluctuate to the present. Plant macrofossil evidence suggests a period of waning forest occurrence around Kite Lake (Figure 5). But the late-Holocene pollen record suggests that the change in regime is associated with successive fluctuations in pollen of *Pinus aristata*-type (MS peaks 5.2–4.7 ka),

P. contorta-type (MS peaks 4.0–3.7 ka and 2.7 ka), and finally again *P. aristata*-type (MS peaks c. 1.7 ka to present) (Figure 4). We suggest that these data point to a series of environmental changes within the watershed and beyond, perhaps associated with landscape disturbance, such as fire or insect infestation. However, until additional charcoal or insect stratigraphies are determined, this explanation must remain a hypothesis.

Conclusions

Though more high-resolution pollen studies are appearing for forested sites in the southern Rockies (e.g. Jiménez-Moreno et al., 2008, 2011), the Kite Lake record is the first of its kind from a site presently above treeline. A rather old bottom age for these sediments suggests an early deglaciation of the Kite Lake basin, but only additional ages in similar basins will confirm deglaciation by c. 17 ka. The *Artemisia* steppe/tundra of the Younger Dryas gave way to establishment of a *Picea–Abies* woodland around the lake by the opening of the Holocene. Additional species of *Pinus*, probably *P. aristata*, became established shortly thereafter. This suggests that the ancestors of the present *P. aristata* at the nearby Windy Ridge Mount Bross stand (Baker, 1992; Langenheim, 1962) may have become established at this time. The occurrence of subalpine tree species above present treeline until c. 3.5 ka clearly suggests warmest Holocene temperatures then, while lake productivity was also enhanced during this time. The late-Holocene decline in treeline at Kite Lake is contemporaneous with ages of tree death at sites above treeline in the Mummy Range (Colorado), which Benedict et al. (2008) suggested to be a result of decreased summer temperatures that probably prevented regeneration at this high-elevation site. This is also evidenced by renewed glacial activity (i.e. Neoglaciation) in the southern Rockies, with widespread expansion of *Artemisia* steppe and of *Pinus edulis* at lower elevations, all suggesting climate cooling and increased winter precipitation. Additional analyses, such as carbon isotope and charcoal analyses, would be helpful in determining the exact role of climate and ecosystem disturbance in fostering vegetation change at this alpine site.

Acknowledgements

We thank Taylor Joyal and Amy Martin for their assistance in the field; Dena Skow for laboratory work on the plant macrofossils; Charles Truettner for assistance with species distribution models; and Michael E Ketterer for determining the $^{239+240}\text{Pu}$ ages of Core Ki-07-02. Two reviewers and the editor helped to improve the paper.

Funding

We gratefully acknowledge funding from the Spanish Ministry of Science (project number CGL2010-20857/BTE) to GJM and from US Geological Survey (Award numbers 1445-0009-94-1069, 99CRAG0019, and 04CRAG0033 (Western Mountain Initiative)) to RSA to help support this research. Laboratory of Paleocology Contribution 138.

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