



High-elevation paleoenvironmental change during MIS 6–4 in the central Rockies of Colorado as determined from pollen analysis



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ABSTRACT

Paleoecological studies from Rocky Mountain (USA) high elevations encompassing the previous interglacial (MIS 5e) are rare. The ~10-m composite profile from the Ziegler Reservoir fossil site (2705 m asl) of central Colorado allows us to determine paleoenvironments from Marine Oxygen Isotope Stages (MIS) 6–4 using pollen zones that are approximately equivalent to marine oxygen isotope stages. During Pollen Zone (PZ) 6 time, pollen assemblages dominated by *Artemisia* (sagebrush) suggest that alpine tundra or steppe occurred nearby. The transition to PZ 5e was characterized by a rapid increase in tree pollen, initially *Picea* (spruce) and *Pinus* (pine) but also *Quercus* (oak) and *Pseudotsuga menziesii* (Douglas-fir). Non-arboreal pollen (NAP) types increased during PZ 5d, while *Abies* (fir) and *Juniperus* (juniper) increased during PZ 5c. Pollen evidence suggests that temperatures during PZ 5b were as cold as during PZ 6, with the site again surrounded by alpine tundra. *Picea* dominated during PZ 5a before the onset of cooler conditions during PZ 4. The MIS 6–MIS 5e transition here was similar to the MIS 2–MIS 1 transition at other Rocky Mountain sites. However, the Ziegler Reservoir pollen record contains evidence suggesting unexpected climatic trends at this site, including a warmer-than-expected MIS 5d and cooler-than-expected MIS 5b.

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Introduction

Our ability to determine the long-term record of vegetation and climate change in western North America has been enhanced vastly by analysis of long pollen records from long-lived basins. Several records have used low-resolution techniques to provide the broadscale outline of vegetation change over long time scales, including from Owens Lake, California (Litwin et al., 1997; ca. 800 ka) and from the Great Salt Lake, Utah (Davis, 1998; Davis and Moutoux, 1998; >1.5 Ma). On the other hand, numerous high-resolution records of vegetation and climate change from continuous sedimentary sequences have also been published that encompass multiple glacial–interglacial time scales. To date, these records have been spatially dispersed in western North America, with most being located along or near the Pacific margin (Fig. 1). For example, the Humptulips (Heusser and Heusser, 1990) and Carp Lake (Whitlock et al., 2000; Marine Oxygen Isotope Stages (MIS) 1–5) sites are located in Washington state, while Clear Lake

(Adam and West, 1983; MIS 1–5), the Santa Barbara Basin (Heusser, 1995, 1998, 2000; MIS 1–6+) and a recent Owens Lake record (Woolfenden, 2003; MIS 1–5) are from California. More recently Jiménez-Moreno et al. (2007) documented multiple glacial–interglacial cycles (MIS 2–7) from Bear Lake, in the northern Great Basin along the Utah–Idaho border. Only a single site has been studied from the Rocky Mountain region. This is the record from the Valles Caldera of northern New Mexico (Sears and Clisby, 1952; Fawcett et al., 2011), which encompasses MIS 10–14. These studies have become critical to our understanding of millennial-scale coupling of climate and vegetation change and the long-term history of drought. However, with the exception of the Valles Caldera study, previously compiled records have been from low-elevation sites or have characterized the pollen record from very large drainage basins.

Within the high altitudes of the central Rockies, paleoecological sites extending backward in time beyond the Last Glacial Maximum (LGM) are extremely rare, due largely to widespread ice that covered the region during the Pinedale Glaciation (Pierce, 2004). A short list of sites includes a sequence of buried lake sediments from Yellowstone National Park, Wyoming (Baker and Richmond, 1978; Baker, 1986); Devlins Park, Colorado (Legg and Baker, 1980); and the Mary Jane site

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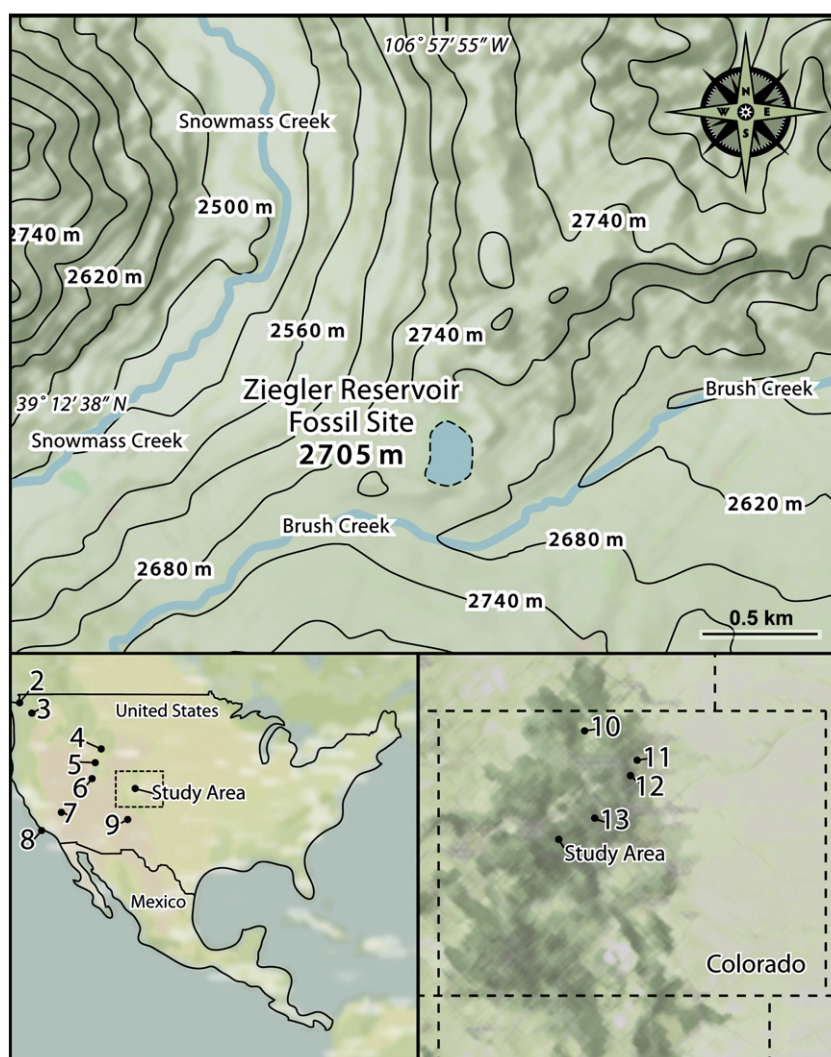


Figure 1. Location map of the Ziegler Reservoir fossil site in central Colorado. The site sits on a ridge between Snowmass and Brush Creeks. Other sites mentioned in the text include (2) Humptulips, WA (Heusser and Heusser, 1990); (3) Carp Lake, WA (Whitlock et al., 2000); (4) Yellowstone sections (Baker and Richmond, 1978; Baker, 1986); (5) Bear Lake, UT/ID (Jiménez-Moreno et al., 2007); (6) Great Salt Lake, UT (Davis, 1998; Davis and Moutoux, 1998); (7) Owens Lake (Litwin et al., 1997; Woolfenden, 2003); (8) Santa Barbara Basin, CA (Heusser, 1995, 1998, 2000); (9) Valles Caldera, NM (Fawcett et al., 2011); (10) Tiago Lake, CO (Jiménez-Moreno et al., 2011); (11) Devlins Park site, CO (Legg and Baker, 1980); (12) Mary Jane site, CO (Nelson et al., 1979); (13) Kite Lake, CO (Jiménez-Moreno and Anderson, 2012).

in Fraser Valley, Colorado (Nelson et al., 1979). However, the Mary Jane and Devlins Park sites are limited to records of short duration not covering more than a few thousand years.

In October, 2010, while excavating the small ca. 5 ha Ziegler Reservoir basin near Snowmass Village, Colorado, in order to provide additional water storage capacity, workmen uncovered rib bones, vertebrae and part of a tusk of a juvenile Columbian mammoth (Pigati et al., 2014–in this volume). Since that time, the Ziegler Reservoir fossil site (ZRFS) has become one of the most prolific sources of bones and other paleontologic materials from any high-elevation paleoecologic site in the Rocky Mountains (Johnson et al., 2014–in this volume). During the following field season, in May–June 2011, dozens of investigators converged on the site to collect samples for analysis of diverse proxies from the exposed sediments that could be used to reconstruct the paleoenvironments in the area when the small lake was in existence. Our high-resolution pollen analysis of the nearly 10-m section of the ZRFS exposed during the excavations is unique in that it collectively spans a time range that we regard as equivalent to MIS 6 through MIS 4 in the mountainous terrain of central Colorado. In this publication we describe the pollen assemblages and provide paleoenvironmental and paleoclimatic interpretations.

Site setting – geology and chronology

The ZRFS is a small basin ca. 300 m in diameter, located at ca. 2705 m elevation within the Elk Mountains of west-central Colorado (Fig. 1). Sediments were deposited at this site during recession of the Bull Lake glaciation, during MIS 6 (Pigati et al., 2014–in this volume). The basin sits within a set of nested lateral moraines, deposited by at least one advance of the Snowmass Creek glacier down modern Snowmass Creek Valley that was large enough to overtop the eastern valley wall. This glacier originated in cirques high within the Elk Mountains, being nearly 26 km in length and more than 250 m thick, and terminating at 2315 m elevation (Pigati et al., 2014–in this volume). When the ice retreated, a small basin was formed on top of the ridge between Snowmass Creek and the Brush Creek Valley to the east, which became a small lake, surviving through the subsequent interglacial (MIS 5) and into the beginning of the most recent glacial (MIS 4). Eventually the basin filled with at least 10 m of primarily organic-rich silt/clays and peats above the till basement, transforming first from a lake to a marsh or wetland, and later to an alpine meadow.

Bedrock of the site is largely Paleozoic sand-, silt- and mudstones and shales, with Oligocene intrusives (Ogden, 1979; Pigati et al.,

2014–in this volume). The late Cretaceous Mancos Shale underlies the Quaternary sediments of the ZRFS, while clasts within the enclosing Bull Lake moraines consist in large part of rocks of the Pennsylvanian-Permian Maroon Formation, which outcrops at high elevation as peaks of the Maroon Bells to the south.

The chronology for the ZRFS record consists of a combination of ^{14}C dates on lake sediment organics, a single ^{10}Be date on a boulder located on the enclosing moraine crest, and a series of optically stimulated luminescence (OSL) ages ($n=18$) from different levels within the stratigraphic profile (Mahan et al., 2014–in this volume). OSL ages occurred in stratigraphic order, were based on dose rates that exhibited minimal scatter, and are replicable based on ages obtained from multiple samples from units 10 and 18.

Site setting – modern vegetation and climate

The modern vegetation of the southern Rockies of central Colorado consists of alpine and upland herbaceous plant communities above ca. 3500 m asl, with high-elevation conifer forest and *Populus tremuloides* (quaking aspen) above ca. 2900 m. *Artemisia* (*Seriphidium*; sagebrush) steppe often occurs below this (RSA personal observations; Langenheim, 1962; Jiménez-Moreno and Anderson, 2012). The *Picea engelmannii* (Engelmann spruce)–*Abies lasiocarpa* (subalpine fir) forest generally occurs over the range of ca. 2590 m to ca. 3800 m, but at the highest elevations occurs only as krummholz. It is best developed between ca. 3200 and 3500 m (Langenheim, 1962). Dominant trees include *P. engelmannii* and *A. lasiocarpa*, but also *P. tremuloides* and *Pinus contorta* (lodgepole pine) can be found. *P. tremuloides* often dominates with mixed conifers between ca. 2900 m and 3200 m. Below ca. 2600 m, especially on dry sites or lower valleys is the *Artemisia* steppe community. This community often includes extensive stands of *Quercus gambelii* (scrub oak), as well as *Chrysothamnus* spp. (rabbitbrush) and many other species.

Modern vegetation around the site is dominated by *A. lasiocarpa* and *P. tremuloides*, with minor amounts of *Q. gambelii* and *Artemisia* (*Seriphidium*) cf. *arbusculum* in forest openings. Small populations of *Pseudotsuga menziesii* (Douglas-fir) and *P. contorta* also occur locally. Additional shrubs include *Symphoricarpos rotundifolius* (snowberry), *Padus* (*Prunus*) *virginiana* (chokecherry) and *Rosa woodsii* (rose). Herbs include *Fragaria* cf. *virginiana* (strawberry), *Heracleum spondylium* (cow parsnip), *Lathyrus* sp. (pea vine), *Dephimum* sp. (larkspur), *Geranium richardsonii* (wild geranium), *Taraxacum officinale* (common dandelion), *Lupinus* sp. (lupine), *Thalictrum sparsiflorum* (meadowrue), *Verbascum thapsus* (mullein), *Achillea lanulosa* (yarrow), *Bistorta bistortoides* (bistort), *Maianthemum* (*Smilacina*) *stellatum* (false Solomon's seal), *Corallorhiza* cf. *trifida* (coralroot), *Pteridium*

aquilinum (bracken), and members of Asteraceae, Apiaceae, Lamiaceae and Violaceae. Terminology follows Weber and Wittmann (1996).

The climate of central Colorado is continental, with cold snowy winters and cool moist summers. Winter precipitation arrives predominantly from Pacific frontal storms, while summer precipitation is primarily from convective thunderstorms. Long-term climate data for Aspen, Colorado (Aspen 1 SW; 39°11' N, 106° 50' W; 2487 m; data for 1980 to 2013 CE) ca. 13 km east–southeast of the ZRFS show typical patterns for the central Rocky Mountains (Fig. 2). Average monthly temperature varies from winter lows (DJF; –12.8 to –11.3°C) to summer highs (JJA; 22.6–25.6°C) (Western Regional Climate Center, <http://www.wrcc.dri.edu>, accessed May 2013). Precipitation can occur in any month, with an annual average of 623.8 mm. Average monthly precipitation varies from a high of 65.8 mm in March and April to a minimum of 33.8 mm in June. Measurable snow accumulation has occurred in all months except JJAS (average annual = 2748 mm). Most snow falls during JFM (533, 711, 660 mm, respectively).

Methods

Samples for pollen analysis were collected in June 2011 from several exposures that had been excavated by mechanized excavators, as well as from a sediment core, with pollen samples coming from a number of identified units (see stratigraphy in Pigati et al., 2014–in this volume). Previous to our pollen sampling a total of 18 stratigraphic units were identified in these exposures that could be traced laterally across the basin. Excavation localities included a basinward trench – Locality 51, including units 18 to 15 – as well as a mid-basin exposure – Locality 43, including units 14 to 8. Five sediment cores were drilled to till using a Giddings Soil Probe at Locality 43, which recovered additional units (Unit 7 to basement till). Stratigraphic units are traced easily across the basin but are best exposed where sampled. Because of this the stratigraphic analyses reported here comprise a composite of these units for the two localities. At least 525 bulk sediment samples were collected for pollen at 1- or 2-cm depth intervals throughout the stratigraphy, placed in whirlbags, transported back to the Laboratory of Paleoecology (LOP) at Northern Arizona University (NAU), and placed in cold storage.

In the laboratory 1 cm³ of sediment was subsampled from each of the bags. Two *Lycopodium* tracer tablets were added to each of the samples for pollen concentration calculation. Pollen extraction followed a modified Faegri and Iversen (1989) methodology, including suspension in sodium pyrophosphate (when necessary) for disaggregation of clays, sieving through 8- μm screen, and successive suspension in dilute KOH, HCl, HF and acetolysis solution. The resulting residue was stained with safranin-O and mounted in glycerol. Counting was performed at 400 \times on a compound light microscope at the University of Granada (UGR). Pollen was identified through comparison to the LOP and personal reference collections, as well as using published keys. Percentages were calculated and plotted as a composited diagram.

We also collected modern pollen samples both from moss polsters around the ZRFS and from modern high-elevation lake-core tops from 41 sites within 60 km of the site. These lakes ranged from 2869 m elevation in the *Picea* – mixed conifer zone to above treeline at 3893 m. These pollen samples were processed in the same manner as the fossil samples except without the sodium pyrophosphate treatment and counted at 400 \times at NAU.

Results

Modern pollen assemblages

The vegetation directly around Ziegler Reservoir today is dominated by *P. tremuloides* and *A. lasiocarpa* (see above), with only minor amounts of *Pinus* trees and *Quercus* and *Artemisia* shrubs. However, the modern pollen assemblage reflects the relative differences in pollen productivity

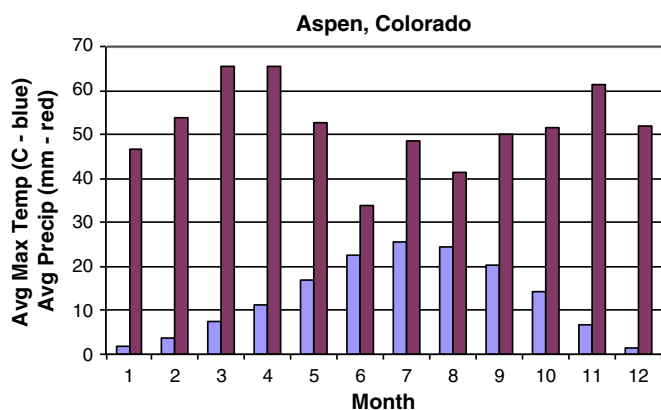


Figure 2. Climate data (average maximum temperature and precipitation) for Aspen, Colorado. The Aspen 1 SW recording station (2487 m) is ca. 13 km east–southeast of Snowmass Village and the Ziegler Reservoir fossil site. Data accessed from Western Regional Climate Center, 23 May 2013.

Table 1
Modern lakes that provided core tops used in the modern pollen calibration.

| Lake name | Code | Elevation (m) | Latitude (°N) | Longitude (°E) | Depth (m) |
|-----------------------|-------|---------------|---------------|----------------|-----------|
| American | AML | 3450 | 39.056434 | −106.830143 | 10.5 |
| Anderson | AND | 3584 | 39.020381 | −106.627456 | 3.5 |
| Bear | BRL | 3351 | 39.296418 | −106.415324 | 4.6 |
| Brady | BRD | 3353 | 39.368328 | −106.500557 | 2.1 |
| Cathedral | CAT | 3598 | 39.027824 | −106.842861 | 6.7 |
| Cleveland | CVL | 3609 | 39.421108 | −106.490829 | 6.7 |
| Constantine | CNS | 3472 | 39.450279 | −106.455002 | 3.7 |
| Crater | CRL | 3053 | 39.085133 | −106.967266 | 3.3 |
| Diemer | DMR | 2869 | 39.334721 | −106.606941 | 2.6 |
| Eagle | EGL | 3074 | 40.210831 | −105.650284 | 2.0 |
| Galena South | GAL-S | 3364 | 39.296689 | −106.420133 | 3.1 |
| Grizzly | GRZ | 3788 | 39.050385 | −106.594205 | 13.7 |
| Half Moon North | HFM-N | 3705 | 39.181211 | −106.496153 | 5.3 |
| Half Moon South | HFM-S | 3648 | 39.178212 | −106.492944 | 5.6 |
| Hard Scabble | HRD | 3070 | 39.231250 | −107.100606 | 4.1 |
| Hunky Dory | HDY | 3452 | 39.421669 | −106.483612 | 2.5 |
| Independence | IND | 3785 | 39.143998 | −106.567429 | 6.9 |
| Linkin | LNK | 3639 | 39.128484 | −106.588388 | 9.0 |
| Lost Man | LMN | 3775 | 39.153144 | −106.568847 | 16.7 |
| Maroon | MRL | 2903 | 39.097028 | −106.945398 | 3.1 |
| Missouri Adjacent | MLA | 3524 | 39.399236 | −106.515367 | 2.5 |
| Missouri Central | MLC | 3488 | 39.396400 | −106.515328 | 3.2 |
| Missouri North | MLN | 3513 | 39.396400 | −106.511150 | 5.9 |
| Missouri South | MLS | 3477 | 39.387139 | −106.515500 | 3.6 |
| Native | NTV | 3403 | 39.225326 | −106.459205 | 0.9 |
| Petroleum | PTL | 3729 | 39.026322 | −106.636675 | 20.0 |
| Seller | SLR | 3119 | 39.323608 | −106.584717 | 3.6 |
| Seven Sisters Central | SSC | 3755 | 39.441256 | −106.481147 | 5.8 |
| Seven Sisters North | SSN | 3612 | 39.443272 | −106.487361 | 5.6 |
| Seven Sisters South | SSS | 3708 | 39.436539 | −106.483056 | 1.2 |
| Seven Sisters West | SSW | 3893 | 39.431906 | −106.487269 | 6.9 |
| Sopris | SOP | 3364 | 39.371109 | −106.502502 | 5.4 |
| St. Kevin | SKL | 3580 | 39.310593 | −106.426860 | 6.8 |
| Tabor Creek | TCL | 3588 | 39.053913 | −106.647472 | 24.0 |
| Thomas North | TL-N | 3089 | 39.272701 | −107.143641 | 9.5 |
| Thomas South | TL-S | 3114 | 39.269965 | −107.140331 | 5.7 |
| Timberline | TMB | 3275 | 39.298019 | −106.475281 | 10.4 |
| Tuhare East | TLE | 3691 | 39.448739 | −106.470111 | 11.0 |
| Tuhare West | TLW | 3775 | 39.450614 | −106.478136 | 25.5 |
| Weller | WLL | 2894 | 39.115076 | −106.720923 | 8.7 |
| Whitney | WHT | 3321 | 39.426186 | −106.450547 | 7.8 |

and dispersal in alpine systems. It is dominated by *Pinus* (24.8%; mostly *P. contorta*-type), *Abies* (23.8%), *Picea* (10%), *Quercus* (10.3%), *Artemisia* (14.5%), with only minor amounts of *P. tremuloides* (1.6%), *P. menziesii* (0.3%), Poaceae (1.9%) and *Atriplex*-type (1.9%). Other herbs total 6.6% of the sum.

Important characteristics of the high-elevation lakes comprising the modern pollen dataset for this study are shown in Table 1. While changes in many pollen species occur with elevation, others – such as *Juniperus*, *Artemisia*, *Ambrosia*, *Sarcobatus*, Asteraceae and Poaceae – show little variability (Fig. 3). In general, herbaceous pollen types are more abundant within the *Picea*–*Abies*–*P. contorta* zone and above (Fig. 3).

Nine core top pollen samples (2869–3119 m) come from the *Picea*–*Pinus*-mixed conifer forest, with dominant species *P. engelmannii*, *P. tremuloides*, *Salix* and *Alnus*, with minor amounts of *Picea pungens* (Colorado blue spruce), *A. lasiocarpa* or *A. concolor* (white fir), *P. contorta* and numerous herbaceous species. Pollen assemblages from these samples are dominated by *Pinus* (18–76%; median = 43.4), *Picea* (4–34%; median = 15.4), *Quercus* (2–14%; median = 5.7) and Amaranthaceae (cf. *Atriplex*, 1–9%, median = 3.9). Pollen of *P. menziesii* (0–2.6%; median = 0.3) is primarily found in the zone, as is *Ephedra* (0–1.4%; median = 0.6), *Salix* (0–2.7%; median = 1.3) and Brassicaceae (0–1.7%; median = 0). *P. contorta*-type is at a minimum at this elevation (0.7–10.6%; median = 3.8).

Fifteen samples (3275–3524 m) came from *Picea*–*Abies*–*P. contorta* forest where *P. engelmannii*, *P. contorta* and *P. tremuloides* dominate

with a diverse herbaceous understory. Total *Pinus* (42–63%; median = 55.2) dominates samples from this elevational range. *Picea* remains important (6–30%; median = 11.4). *P. contorta*-type increases (2–10.5%; median = 7.1), while *Abies* (0.3–5.2%; median = 1.2), *Alnus* (0–0.6%; median = 0.3) and *Populus* (0–1.0%; median = 0.3) reach their highest pollen percents in this group. Those pollen types that decline include *P. menziesii*, *Salix*, *Quercus*, *Ephedra* and Amaranthaceae.

Ten samples come from the *P. engelmannii*-dominated krummholz zone with elevations 3580 to 3705 m. *Salix*, Cyperaceae, *Dryas* and other alpine herbs also occur here. *Pinus* continues to dominate (51–71%; median = 59.3) with somewhat diminished *Picea* (7.4–20.3%; median = 11.1), *P. contorta* (2.2–8.7%; median = 4.9), *Abies* (0.3–1.0%; median = 0.6), *Alnus* (0–0.6%; median = 0.1) and *Quercus* (0–3.3%; median = 1.1). High-elevation herbs continue to be important in the pollen of this elevation range.

Lastly, eight samples were taken from lakes above treeline (3708–3893 m) in the alpine zone where dwarf *Salix*, Cyperaceae, *Dryas*, *Pedicularis*, Ranunculaceae and members of the Asteraceae dominated. Again, *Pinus* continues to dominate (55–67%; median = 62.1), while *P. contorta*-type increases slightly as well (4.6–15.8%; median = 8.7). *Picea* pollen percents are comparable to the krummholz values. *Abies* is reduced, while *Quercus* and *Alnus* dwindle to trace amounts. Herbaceous pollen is most important in this zone (Fig. 3).

Using the 41 pollen assemblages from the core tops we calculated a ratio of spruce:pine (*Picea:Pinus*; S:P ratio) (Fig. 4). This ratio has been used in several studies in the southern Rockies (Markgraf and Scott,

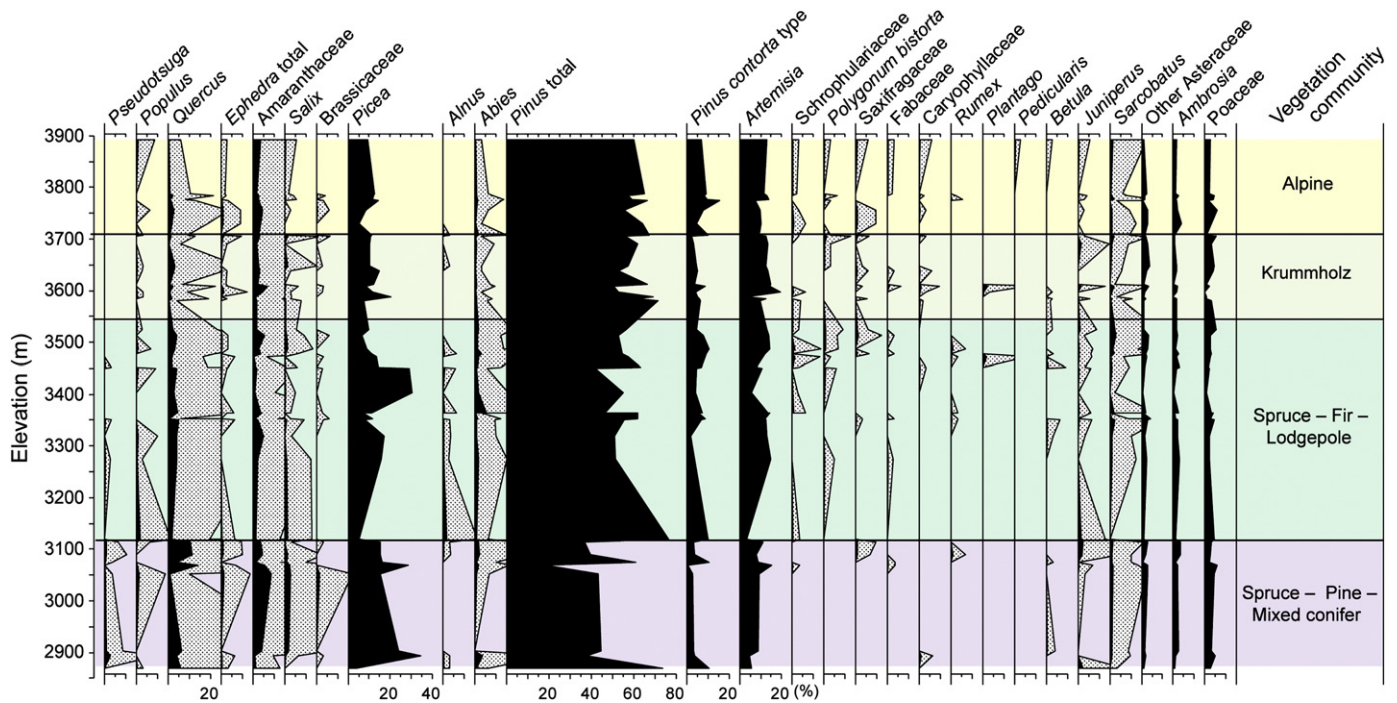


Figure 3. Modern pollen surface samples from high-elevation lakes near the Ziegler Reservoir fossil site. Lake tops were collected as part of the chironomid calibration network of Haskett and Porinchi (2014—in this volume). Sites range from 2869 m in *Picea*–*Pinus* – mixed conifer forest to above treeline at 3893 m.

1981; Carrara et al., 1984; Fall, 1997; Reasoner and Jodry, 2000; Toney and Anderson, 2006; Jiménez-Moreno et al., 2008, 2011) to track the density of the *Picea* forest. For our modern pollen data, the ratio is often near or above 0.4 within the *Picea* dominated forests below ca. 3500 m (Fig. 4). It is always below 0.3 within the *Picea* krummholz, and below 0.2 in the alpine zone where no trees are present.

Stratigraphic pollen

Based on the OSL chronology, our pollen record spans the upper part of MIS 6 time (to ~140 ka) to the lower part of MIS 4 time (at least ~70 ka). However, we describe the pollen assemblages below as biostratigraphic zones rather than as time stratigraphic zones. It appears that our pollen zones (PZ) correlate strongly with the marine oxygen isotope stages, and we number them in a similar fashion. However, the equivalence is not exact (Table 2), with the offset in age increasing with increasing depth. Here, the similar numbering schemes are for convenience of discussion. We analyzed 123 pollen samples in

this ~69,700-yr record, corresponding to an average sampling interval of ~570 yr. This relatively high-resolution record is comparable to the Jiménez-Moreno et al. (2007) study from Bear Lake, UT/ID, where the average sampling interval was ~600 yr. Individual pollen zones are described below, in ascending stratigraphic order.

PZ 6 (1019–991 cm; 141–138 ka)

Pollen analyses from this interval were from samples taken near the bottom of the Giddings drill core ZR-3C (at Locality 43, including units 3 and 4), where sediment is a dark brown clay with fine silt, existing immediately above till (Pigati et al., 2014—in this volume). Pollen assemblages in this group are dominated by non-arboreal (NAP) pollen, principally by *Artemisia* (31–60%) (Fig. 5), with minor amounts of *Amaranthaceae* (cf. *Atriplex*; 2–6%), *Poaceae* (grasses; 3–6%), and *Asteraceae* (4–6%). Conifer pollen is dominated by *Pinus* (16–23%), with the greatest proportion identifiable as high-elevation *Pinus* (*P. cf. haploxylon*) (Fig. 5). *Picea* pollen is 3–9% of the sum, while *Abies*, *Juniperus* and *Quercus* are all >1% of the sum.

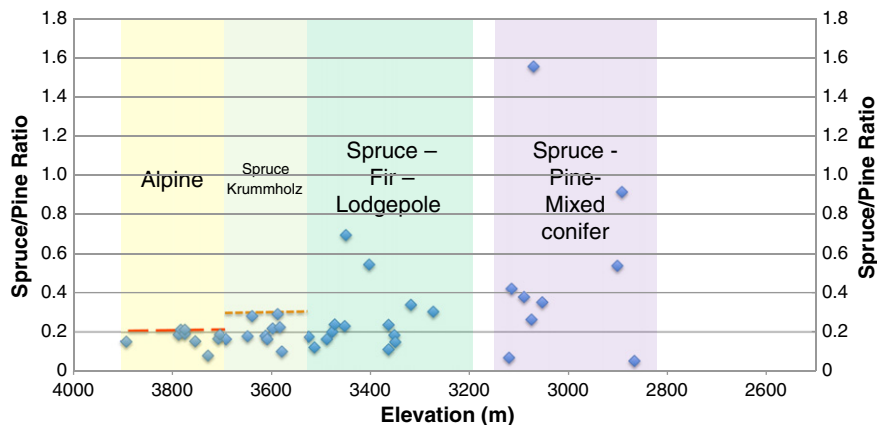


Figure 4. Ratio spruce to pine (*Picea*:*Pinus*; S:P) pollen percentages for the modern pollen surface samples shown in Fig. 3. Note that for those samples located within the modern *Picea* krummholz zone the ratio is <0.3, and for those within the modern alpine zone it is <0.2.

Table 2

Comparison of ages and uncertainties for the MIS 6/5 and 5/4 boundaries and MIS 5 substages from the SPECMAP and LR04 isotopic records (Martinson et al., 1987; Lisiecki and Raymo, 2005) with the pollen record from the Ziegler Reservoir fossil site (this study; Mahan et al., 2014–in this volume).

| MIS boundary | SPECMAP age, (ka) | Uncertainty, $\pm 1\sigma$ (ka) | LR04 age, (ka) ^a | This study age (ka) ^b | Uncertainty, $\pm 1\sigma$ (ka) |
|--------------|-------------------|---------------------------------|-----------------------------|----------------------------------|---------------------------------|
| MIS 5/4 | 73.9 | 2.5 | 71 | 77.0 | 3.4 |
| 5a (peak) | 79.2 | 3.5 | 82 | 83.1 | 4.0 |
| 5b (peak) | 90.0 | 6.8 | 87 | 94.4 | 3.9 |
| 5c (peak) | 99.3 | 3.4 | 96 | 103.5 | 5.1 |
| 5d (peak) | 110.7 | 6.2 | 109 | 117.7 | 8.4 |
| 5e (peak) | 123.8 | 2.6 | 123 | 133.2 | 11.3 |
| MIS 6/5 | 129.8 | 3.0 | 130 | 137.7 | 13.1 |

^a Uncertainty in the LR04 age model is ± 4 ka from 1 to 0 Ma (Lisiecki and Raymo, 2005).

^b Ages for the MIS 5 substages were defined as follows (Fig. 7): MIS 5e: maximum values in *Quercus* and *Pseudotsuga*. MIS 5d: minimum central value in arboreal pollen (AP); MIS 5c: peak in AP; MIS 5b: peak central value in *Artemisia*. MIS 5a: peak in AP, minimum value in *Artemisia*. Even if our dates for the different climatic events seem to be older, they fall within the age uncertainty of the different age models.

PZ 5e (991–902 cm 138–129 ka)

Pollen analyses from in this interval also came from samples taken in the lower part of drill core ZR-3C (including units 4–6). Sediment is described as organic-rich silt with sparse carbonate lenses near the base, grading upward into a laminated silty clay in the middle of the unit, and overlain by an organic-rich silt with abundant plant remains (Pigati et al., 2014–in this volume). Major changes in the pollen assemblages occur in this zone, including a significant decline in *Artemisia* (~5–20%) and a change to dominance by arboreal pollen (AP). Conifer pollen is again dominated by *Pinus* (14–31%), of which the majority identified is *P. haploxylon*-type. *Picea* increases substantially (up to 25% of the sum), and *Quercus* also increases to a maximum of 21% (Fig. 5). Pollen of *P. menziesii* (to 3%), *Abies* (generally <1%) and *Juniperus* (up to 3%) increases, as does pollen of Asteraceae (4–20%). Amaranthaceae (probably *Atriplex*) increases to nearly 12% in the lower part of the interval, but declines in the upper part. Poaceae pollen declines, while pollen percentages of *Sarcobatus* are largely unchanged from below. Cyperaceae increases to over 7% of the pollen sum within this zone (Fig. 5).

PZ 5d (902–704 cm 129–113 ka)

Pollen analyses in PZ 5d were from samples taken from the top of drill core ZR-3C (including units 6–8). Sediments in these units include organic-rich silts at the base, grading into a sandy silt with scattered carbonate lenses, and finally into another organic-rich silt (Pigati et al., 2014–in this volume). In PZ 5d, %AP declines such that the AP:NAP ratio becomes essentially 1:1. This increase in NAP is not due to increasing *Artemisia*, but instead due to significant increases in both Amaranthaceae (*Atriplex*; 5–16%) and Asteraceae (11–21%) pollen (Fig. 5). *Pinus* and *P. haploxylon*-type pollen are slightly diminished, but continue to dominate the conifers. However, *Pinus* percentages decline by almost half from the base of the interval to its top. *Picea* pollen remains largely unchanged from PZ 5e below. *Abies* pollen increases (to nearly 6%), *Juniperus* remains relatively unchanged, but *Pseudotsuga* declines to 1% or less (Fig. 5). Within the hardwood pollen component, *Quercus* percentages remain relatively high at 8–19%. Cyperaceae percentages and the amount of *Pediastrum* cell nets also increase relative to their previous abundances.

PZ 5c (704–543 cm 113–100 ka)

Sixteen pollen analyses in this zone were made from samples taken from units 8–12 exposed in vertical section in the highwall at Locality 43 (Pigati et al., 2014–in this volume). Sedimentary textures within this zone transition from organic silt in Unit 8 to mottled brown silt in Unit 9, which is overlain by yellowish-brown bedded silt with abundant fibrous organic remains, seeds, twigs and wood in Unit 10 (informally referred to as the “yellow brick road”). These are overlain by a weakly banded silt with organics in Unit 11, and finally an organic mat with remains of Cyperaceae leaves and wood in Unit 12. Pollen assemblages from this period are characterized by a slight increase in the arboreal pollen percentages, largely a result of increases in *Abies* (from 4% to

>20% at the top of the zone) and *Juniperus* (to 9% by mid zone, but declining upsection). This zone also includes low but consistent occurrences of both *Pinus edulis*-type (Colorado piñon) and *Cercocarpus* (mountain mahogany), as well as a slight increase in Poaceae. Several pollen types yielded high percentages that declined upward through the zone, including *Pinus* (16–8%), *Quercus* (14–3%), Asteraceae (19 to ca. 10%) and Amaranthaceae (15–6%). Cyperaceae also declines. *Artemisia* percentage does not differ greatly from its occurrence in lower zones. Peaks in *Abies* and *Picea* are associated with sediments of Unit 10. *Pediastrum* cell nets are at their highest percentages during PZ 5c, and *Botryococcus* increases substantially higher in the zone.

PZ 5b (543–338 cm; 100–87 ka)

Nineteen pollen samples were analyzed from units 13 and 14 at Locality 43. These sediments are banded (dark yellowish brown and very dark grayish brown) silty clays in Unit 13 overlain by massive grayish brown silty clays in Unit 14 (Pigati et al., 2014–in this volume). Pollen of PZ 5b is characterized by an abrupt and sustained increase in *Artemisia* pollen, from 36% to over 64%. This maximum abundance is similar to *Artemisia* abundances observed in PZ 6. Amaranthaceae (from 6 to 14%), Poaceae (5–11%) and *Sarcobatus* (2–5%) are other principle pollen types that increase in this zone. All other pollen – *Picea*, *Pseudotsuga*, *Abies*, *Quercus*, *Juniperus* and Asteraceae – decline. *Pinus* is highly variable, with abundances exceeding 16% low in the zone. Percentages of colonial algae – *Pediastrum* and *Botryococcus* – reach near maximum values.

PZ 5a (338–215 cm; 87–77 ka)

Nineteen pollen samples were analyzed from units 15 and 16 at Locality 51. Sediment in Unit 15 is a peaty silt, while Unit 16 is a very dark brown peat with little mineral matter (Pigati et al., 2014–in this volume). The lower part of this zone shows slight increases in both *Quercus* and *Abies*, but less than their relative abundances observed in PZ 5c. *Picea* increases rapidly from <1% to >26% between two stratigraphically adjacent samples; however while *Picea* increases in abundance upward through the zone, both *Quercus* and *Abies* decline. *Pinus* increases gradually from nearly 10–20% by zone's end. The only other major pollen type to increase is Cyperaceae (Fig. 5). All other pollen types, especially *Artemisia*, decline during PZ 5a. This also includes the limnic indicators, *Pediastrum* and *Botryococcus*.

PZ 4 (215–146 cm; ~77–at least 70 ka)

Only twelve pollen samples were taken and analyzed from units 17 and 18, owing to increasingly poor preservation upsection in Unit 18. Samples from this zone were derived from Locality 51. Sediments consist of a clayey silt in Unit 17, grading upward to a mottled light gray clay in Unit 18 (Pigati et al., 2014–in this volume). Pollen of this zone shows increases in *Pinus* and NAP (non-arboreal pollen), especially *Artemisia*, and Cyperaceae reaches its maximum observed abundance in this entire record (Fig. 5). *Picea* percentages decline upsection in this zone

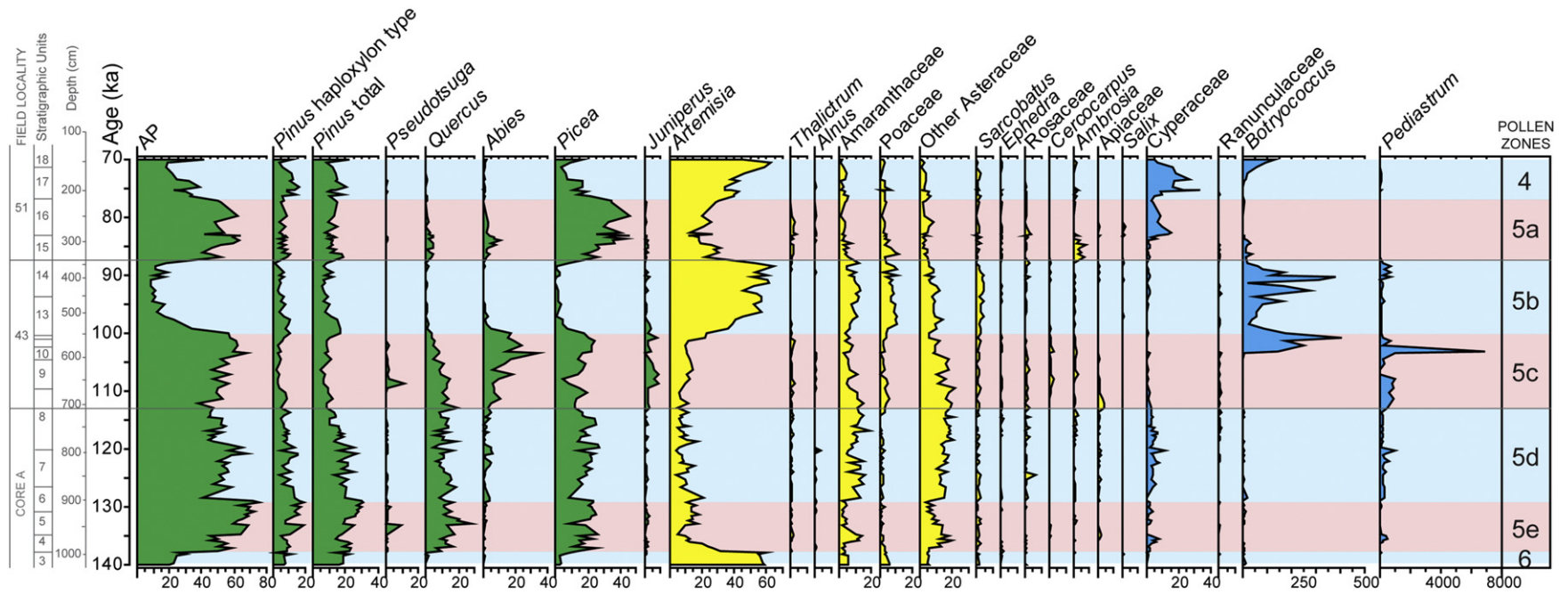


Figure 5. Summary of major stratigraphic pollen percentage assemblages from the Ziegler Reservoir fossil site, Colorado. Arboreal pollen shown in green curves; non-arboreal pollen shown in yellow; aquatic and wetland pollen and spores shown in blue.

precipitously while other conifers (*Abies*, *Juniperus*, *Pseudotsuga*) and hardwoods (*Quercus*) exhibit minimal occurrences. Shrubby taxa, including *Sarcobatus*, Asteraceae and Amaranthaceae, along with Poaceae, also approach minimum values for the entire record.

Discussion

Analyses of sediments at the ZRFS from samples taken from a series of cut faces, pits and drill cores have provided a unique opportunity to investigate the history of vegetation changes from a high-elevation location during what appears to be the transition from the previous glacial (Bull Lake, MIS 6) through the penultimate interglacial (MIS 5e) and into the beginning of the most recent glacial (MIS 5d–4). To our knowledge, this ~2705 m elevation site is the highest-altitude locality in western North America to provide a high-resolution record of vegetation change for this time period. The chronology consists primarily of OSL ages (Mahan et al., 2014–in this volume). This chronology has also allowed us to examine the structure of the previous interglacial independent of global curves such as Martinson et al. (1987). However, our dating scheme tends to systematically over-estimate the generally accepted age boundaries, with increasing departure from Martinson et al. (1987) with depth (Table 2).

Deposition at the site appears to have begun at the end of the Bull Lake glaciation (Bryant and Martin, 1988). One lateral moraine formed the north, east and south boundaries of the basin, while a second formed the west boundary (Pigati et al., 2014–in this volume). When the ice retreated it left a small, enclosed basin that was not overridden by glaciers during the Pinedale glaciation. A limited drainage basin with no inflowing streams and slow input of eolian sediments allowed the lake to exist for up to 70,000 yr before infilling arrested any significant amount of subsequent deposition.

Today the site is surrounded by conifer–*Populus* forest. Interpretation of the pollen from the ZRFS is facilitated by comparison to two modern pollen datasets, including 41 modern core-top samples from lakes at 2869 to 3893 m elevation (this study), and 46 core-top and polster samples from 2470 to 3780 m elevation near Cottonwood Pass to the south (Fall, 1992), and two nearby high-elevation pollen records. Pollen from the bottommost samples of the record is dominated by non-arboreal pollen, predominantly *Artemisia*. This suggests steppe-like vegetation, where trees such as *Picea* and even *Pinus* may have been sparse to absent. During that time, which we interpret to be temporally equivalent to latest MIS 6, *Artemisia* attains 60%. No modern pollen samples in either this study or in the Fall (1992) datasets have such high *Artemisia* percentages, although the lowest elevation *Artemisia* steppe samples of Fall (1992) approach this. The closest fossil analogs to this come from the Last Glacial Maximum (LGM; MIS 2) pollen spectra of Tiago Lake (2700 m elevation; ca. 155 km

north) and Kite Lake (3665 m elevation, ca. 70 km east). In both cases *Artemisia* percentages reach 40–60% of the sum (Jiménez-Moreno et al., 2011; Jiménez-Moreno and Anderson, 2012) and were interpreted as representative of alpine tundra. Such an interpretation also is supported by the low S:P ratio, where ratios of <0.3 suggest *Picea* krummholz ecotype (Fig. 6).

The transition out of MIS 6 time about 138 ka into the MIS 5 time interglacial showed a rapid increase in tree species pollen during PZ 5e, manifested first by *Picea* and then by *Pinus* (Fig. 5). This is closely analogous to the late-glacial – early Holocene vegetative transition at Tiago Lake – and to a lesser extent the vegetative transition observed in sediments at the higher elevation Kite Lake. The S:P ratio during this interval at the ZRFS suggests the presence of a moderately dense *Picea* forest (Fig. 6). Although the pollen records for Tiago and Kite Lakes exhibit millennial-scale abrupt warmings and coolings that have been interpreted to correlate directly to the Bølling – Allerød and Younger Dryas oscillations, no analogous warm-to-cold-to-warm millennial-scale deglaciation pattern could be confirmed in our PZ 6–PZ 5e transition at the ZRFS.

The major difference between our interpreted PZ 5e data and those from MIS 1 at Tiago and Kite Lake is in the importance of *P. menziesii* here, but especially in *Quercus* during this period. *Quercus* is most abundant at the ZRFS during the early interglacial, peaking in the middle of PZ 5e time. Although *Quercus* is most abundant during the mid-Holocene at Tiago Lake it never exceeds ca. 10% (Jiménez-Moreno and Anderson, 2012) compared to 21% in the ZRFS record. *Quercus* is never significant at the much higher Kite Lake site (Jiménez-Moreno et al., 2011). Similarly, although a few modern samples from the *Picea*-mixed conifer zone (Fig. 3) exceed 10%, *Quercus* never exceeds 5% of the pollen sum in the Fall (1992) dataset. This suggests the importance of *Quercus* in the local vegetation around the ZRFS during the Last Interglacial Period, a situation that may have no known analog for this elevation today, and supports the contention that MIS 5e was warmer than the present interglacial (Kukla et al., 2002; CAPE Last Interglacial Project Members, 2006; Jiménez-Moreno et al., 2007).

The transition to MIS 5d, here dated to about 129 ka, is suggested by subtle changes in the pollen record, with increasing non-arboreal pollen types, specifically in Amaranthaceae (probably *Atriplex*) and Asteraceae. The S:P ratio suggests initially the forest was sparser than during PZ 5e time (Fig. 6). The fact that *Quercus* pollen percentages declined little – only to ~10% or so – suggests to us that temperatures were probably only slightly cooler than in PZ 5e. These pollen assemblages are very similar to modern pollen from the *Picea*-mixed conifer forest of today (Fig. 3).

Pollen spectra from PZ 5c time – beginning ~113 ka – show an increasingly dense *Picea* forest (increasing S:P ratios; Fig. 6), suggesting

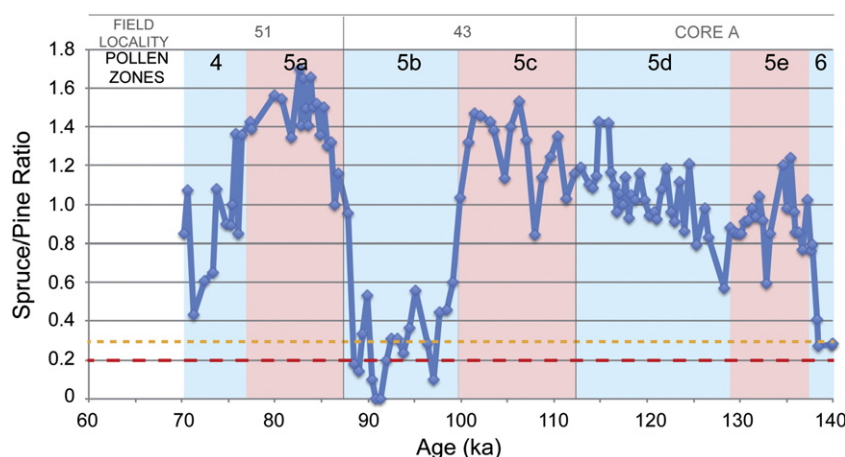


Figure 6. Pollen ratio (S:P) of *Picea* to *Pinus* percentages for the Ziegler Reservoir site fossil pollen assemblages. Based on the relationships shown in Fig. 4, the ratios suggest that during PZ 6 time the site was near treeline, and within PZ 5b time it might have been above treeline.

a more boreal-type (*Picea* dominant) vegetation community. This shift would be consistent with declines in *Quercus*, Asteraceae and cf. *Atriplex*, presumed to grow lower in elevation. However, the ratio is equally influenced by increases in *Picea* or by declines in *Pinus* (Fig. 5), the latter of which appears to have been replaced around the ZRFS by *Abies* near the top of the zone. In both the Fall (1992) modern pollen dataset as well as in our own (Fig. 3), *Abies* is more abundant in the *Picea* – *Abies* – *P. contorta* forest. In no case does *Abies* ever exceed 10% of the pollen sum in these modern samples. In contrast, during the temporal equivalent of MIS 5c *Abies* comprises 15–30% of the sum (Fig. 5). This suggests that *Abies* was a major component of the forest around the lake between ca. 105 and 100 ka, much like it is today, where it is the dominant conifer in the forest and produces nearly 24% of the modern pollen from a polster collected around the lake. High percentages of the algal species *Pediastrum* and *Botryococcus* (Fig. 5) suggest that either the lake was dessicating during this time or that a threshold was achieved in which the lake was infilling at an increasingly rapid rate. A slight increase in

the sediment accumulation rate (SAR) during this time supports the latter explanation.

The pollen spectra from PZ 5b, beginning by ~100 ka, suggest very cool and/or dry conditions prevailed at the site for nearly 12,000 yr. Pollen of *Artemisia* once again dominates the assemblages, and the overall spectra are nearly identical to those from PZ 6 (Fig. 5). Increases in Poaceae occur, as well as in Amaranthaceae (cf. *Atriplex*) and *Sarcobatus*. These pollen types are most common at lower elevations today and their deposition during this time suggests that the vegetation around the ZRFS was quite open, a conclusion that is supported by the S:P ratio as well (Fig. 6). The S:P ratio of fully half of the individual pollen assemblages during this period is either below 0.3 (orange shorter dashed line in Fig. 6; threshold for *Picea* krummholz vegetation) or 0.2 (red longer dashed line in Fig. 6; threshold for alpine vegetation). We interpret this period as being at or near treeline, which suggests a lowering of treeline during PZ 5b of ca. 800–1000 m. Data from the ZRFS suggesting PZ 5b was as cool as PZ 6 was unanticipated. The SPECMAP $\delta^{18}\text{O}$ curve of

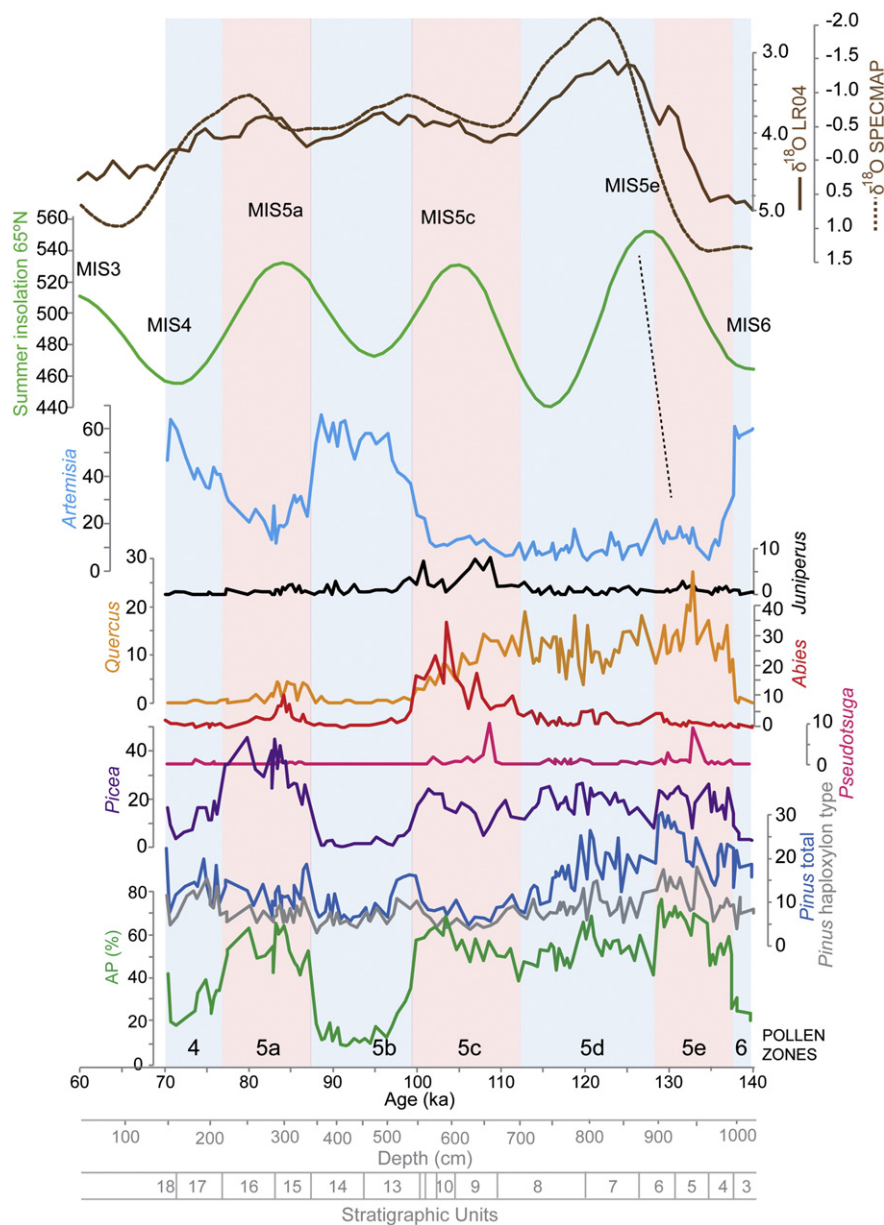


Figure 7. Selected pollen percentages from the Ziegler Reservoir fossil site in comparison to the summer insolation (Laskar et al., 2004) and SPECMAP and LR04 oxygen isotope curves (Martinson et al., 1987; Lisiecki and Raymo, 2005). MIS stages are placed following the Martinson et al. (1987) nomenclature. Relatively warm and cold pollen zones are shown with light red and blue shading, respectively. A tentative correlation between the maxima in summer insolation during MIS 5e and the pollen record (PZ 5e) is shown through a dashed line.

Martinson et al. (1987) documents a progressively cooler MIS 5b than MIS 5d, with neither being as cold as MIS 6 (Bull Lake) or MIS 2 (Pinedale). One possibility is that this might reflect local conditions within the study area, perhaps particularly dry conditions, which opened the forest more than any other time during MIS 5 time, and allowed for greater deposition of pollen from shrubby taxa, both locally (probably *Artemisia*, perhaps *Poaceae*) and from lower elevations (*Atriplex* and *Sarcobatus*). This interpretation is supported in part by the abundance of the algae *Botryococcus* during this time, which suggests low water levels in the lake.

The transition from PZ 5b to PZ 5a at ca. 87 ka is abrupt and dramatic, as arboreal pollen increases substantially, in *Picea*, *Abies*, *Pinus* and *Quercus* (Fig. 5). We note that this transition also represents a sub-basin site change in our record, from Locality 43 to 51. However, we do not attribute the shift in observed pollen signal to the shift in locality (effectively placed here at 346 cm depth in our composite record) because of the physical correlation of laterally pervasive sedimentological units. Such high percentages of *Picea* are characteristic of subalpine forest (this study; Fall, 1992). The S:P ratio suggests a mostly closed *Picea* (and *Abies*?) forest existed around the ZRFS. The characteristics of the sediments (largely peats) and increases in Cyperaceae pollen suggest that the lake had by this time transitioned to a shallow-water marsh, and the high *Picea* percentages suggest that trees may have begun to encroach onto the margins of the site. The progressively smaller amounts of *Quercus* may be a result of the closed nature of the forest, or due to generally cooler temperatures.

Only a few pollen samples in our dataset document the onset of PZ 4, and they generally record a considerable increase in non-arboreal pollen, primarily *Artemisia*. The S:P ratio suggests much more open conditions than in PZ 5a, but not as open as in PZ 5b. Based on minimum occurrence of other tree species – *Abies*, *Pseudotsuga*, *Quercus* – combined with moderate abundances of *Picea* and *Pinus*, we suggest a mosaic of subalpine *Picea* and *Pinus* with more abundant *Artemisia*, all suggesting cooler and drier conditions. Cyperaceae pollen reaches its abundance maximum of the entire composite record, and it is during this time that we interpret the former lake to have completed its transition to a wet meadow.

Conclusions

Our analysis of the ~70 ka pollen record from the Ziegler Reservoir fossil site in central Colorado has allowed us to determine vegetation sequences of glacial–interglacial–glacial transitions from a site with great sensitivity to climate change. While several other sites have documented characteristics of the previous interglacial, these have come primarily from large lakes at lower elevations in western North America (see compilation in Jiménez-Moreno et al., 2007). To our knowledge the ZRFS pollen record is unique in its length and antiquity for high-elevation sites within the Rockies. In this regard, it is important to examine as many records of interglacial conditions as possible so that we are able to document the range of natural variability inherent in local sequences while placing them into a hemispheric or global context.

In our interpretations we have benefitted greatly from an internally-derived chronology for this depositional record (Mahan et al., 2014–in this volume). This has allowed us to interpret vegetation change within an independent temporal framework, which does appear in general accord with the SPECMAP chronology (Martinson et al., 1987) – but with increasingly older ages with depth (Table 2) – and with variability in summer seasonal solar insolation (Fig. 7). But there exist significant differences (below).

The transition in the early part of the record – essentially correlated to MIS 6 to MIS 5e – is strikingly similar to the MIS 2–MIS 1 record from Tiago Lake (Jiménez-Moreno et al., 2011), a lake presently at nearly the same altitude (Ziegler Reservoir = 2705 m; Tiago Lake = 2700 m). Both sites today occur in conifer–*P. tremuloides* forest. In both records, glacial-

age pollen assemblages are dominated by *Artemisia* and *Poaceae*, but by the earliest part of the transition to the subsequent interglacial, *Picea* and *Pinus* became the dominant vegetation in both cases. Other differences include the greater component of mixed conifer forest at Tiago Lake (greater *Pinus*, where *P. contorta* prevails; *Abies*; *P. menziesii*) and considerably greater importance of *Q. gambelii* at the ZRFS. On the other hand, both sites document early-to-middle interglacial increases in *Amaranthaceae* and *Juniperus*, which we attribute to be derived from pollen from the lower elevation *Atriplex* flats and *Juniperus* woodland.

The paleoenvironmental implications of both PZ 5d and PZ 5b pollen assemblages were unanticipated and counterintuitive. Although MIS 5d is generally considered to be cooler than MIS 5e, the arboreal pollen record is little different between the two temporally analogous zones at Ziegler Reservoir (Fig. 5). For example, although there is a slight increase in *Pinus* and *Abies* and a slight decline in *Quercus*, the primary changes are in pollen types of lower elevation, e.g., *Amaranthaceae* (cf. *Atriplex*) and *Asteraceae* (Fig. 5). This suggests an actual expansion of *Atriplex* scrub, since the S:P ratio remains much the same as before (Fig. 6), again, suggesting little change in the characteristics of the forest at the ZRFS during that time. In contrast, PZ 5b appears to be nearly as cold as latest PZ 6, but these changes might reflect local drying during PZ 5b. In any event, temperature interpretations for both PZ 5d and PZ 5b are somewhat at odds with relative trends in the $\delta^{18}\text{O}$ record from Greenland (Johnsen et al., 2001).

Although it is important to understand the late Pleistocene vegetation shifts suggested by the pollen assemblages from the ZRFS, pollen analysis remains only one of several proxy studies relevant to reconstructing the former environments of this high-elevation site (Johnson et al., 2014–in this volume). Studies of the proboscideans (Fisher et al., 2014–in this volume), plant macrofossils (Brown et al., 2014–in this volume; Miller et al., 2014–in this volume; Strickland et al., 2014–in this volume), insects (Elias, 2014–in this volume), chironomids (Haskett and Porinchi, 2014–in this volume), snails and ostracodes (Sharpe and Bright, 2014–in this volume) and other organisms will be combined with the pollen data to provide a more complete paleoenvironmental picture of the ZRFS over its ~70,000-yr history.

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