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Identification and dendrochronology of wood found at the Ziegler Reservoir fossil site, Colorado, USA

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ABSTRACT

Over 300 wood fossils were collected from the Ziegler Reservoir fossil site near Snowmass Village in central Colorado, USA. Wood fossils range from fragments of stems and branches only a few centimeters in diameter and length to whole logs >50 cm diameter and >10 m length. Many of the fossils were collected from a "beach" horizon, where they appear to have been washed up on the side of the interglacial lake and buried. The wood is mainly fir (*Abies* sp.) or Douglas-fir (*Pseudotsuga menziesii*), with some spruce (*Picea* sp.), pine (*Pinus* sp.), and at least one other unidentified conifer species. Douglas-fir and species of fir, spruce, and pine are common in the area today. Dendrochronological analyses compared annual growth rings in fossil wood to similar data from modern trees. Results suggest that fossil trees from the beach horizon grew under similar environmental conditions and annual climate variability as today. Three Douglas-firs and several fir logs also appear to have been alive at the same time based on crossdating of ring widths and other ring characteristics. These trees may have died at the same time, suggesting a stand mortality event in the surrounding forest that resulted in numerous logs being buried synchronously in the beach horizon.

Introduction

The phenomenal late Pleistocene [Marine Oxygen Isotope Stages (MIS) 5 and 4] faunal and floral assemblage collected from the Ziegler Reservoir fossil site (ZRFS) near Snowmass Village in central Colorado includes over 300 pieces of wood in addition to several thousand bones from dozens of animals species. The site contains an ~10 m sequence of lake and marsh sediments from a subalpine setting at ~2705 m elevation, making it one of the highest elevation collections of fossil diversity ever found (Pigati et al., 2014–in this volume). Wood fossils range from branch or log fragments only a few centimeters in diameter and length to several large logs >50 cm in diameter and >10 m in length. Wood fossils from the ZRFS were able to be prepared and analyzed like modern wood samples, although the fossil wood has been somewhat decayed or deformed by overlying sediments. Many of the fossils, especially the largest logs, were collected from a distinct stratigraphic horizon referred to as the "beach," an obvious strandline where they had washed up on the side of the informally named Pleistocene Lake Ziegler and were later buried by subsequent sediments. Other fossils, mainly smaller diameter and shorter fragments but including some larger pieces were found scattered throughout the sediment profiles.

We report here on both the identification of a representative sample of wood fossils found throughout the sediments and the ages and dendrochronologic characteristics of growth rings in a selection of logs collected from the beach horizon. Analyses of the growth rings in fossil wood can provide important information about the growing conditions and annual variation in climate during the time when the trees were alive (e.g., Péwé et al., 1997, 2009). Dendrochronology involved measuring ring-widths of the trees, both to compare variations in growth to that of modern trees and to estimate past inter-annual environmental and climatic variability. We also used crossdating procedures on the ring-width series to assess the possibility that the ancient trees from the beach horizon grew contemporaneous with each other.

Methods

The ZRFS (39.2075°N, 106.9648°W) was discovered in October, 2010, when the bones of a Columbian mammoth (*Mammuthus columbi*) were unearthed during expansion of an existing lake near Snowmass Village in the central Rocky Mountains of Colorado. Subsequent excavations in 2010 and 2011 were coordinated by the Denver Museum of Nature and Science (DMNS) and yielded a diverse array of bones and other faunal material, plant macrofossils, and pollen (Sertich et al., in this volume; Fisher et al., 2014-in this volume; Anderson et al., 2014–in this volume; Miller et al., 2014–in this volume; Strickland et al., 2014–in this volume). The site comprises a portion of an ~12 ha basin created by a moraine

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formed during the Bull Lake glaciation, ~155–130 ka (Pigati et al., 2014–in this volume). The basin has been occupied by lakes during much of the time since then, with slow filling by mainly windblown silts and clays, intermixed with both floral and faunal organic material.

Wood fossils were collected from throughout sediment layers at the ZRFS. All samples are still wood with no mineralization evident, although wood has been discolored by sediments and water saturation. Samples of wood were submitted for radiocarbon dating and were found to be at or near the limit of the ^{14}C dating technique (Mahan et al., 2014–in this volume). Many of the samples are short or fragmented pieces of either branches or smaller diameter trees, especially those found scattered throughout much of the excavated area. In the case of smaller samples, generally the entire piece was collected. Other samples are from large, either partial or whole circumference, logs, especially those found in the beach horizon. The largest log found in the beach layer was ~10 m long and ~54 cm diameter at the largest end. Generally a 20–30 cm thick cross-section sample was cut with a chainsaw from larger diameter samples, usually from an area of better preservation or where outside rings appeared to be most intact. Several of the largest logs were cut into sections and the entire log returned to storage facilities at DMNS to be used as possible displays.

Wood samples were wet when collected and dried before processing. Samples were wrapped in plastic stretch wrap before drying to minimize loss of cross section integrity. After drying, two cross sections 3–5 cm in thickness were cut from most samples using a bandsaw or chainsaw. One of these cross sections was used for wood identification and the other for aging and tree-ring analysis. The rest of the sample was returned to storage for future analyses.

Wood identification

The identification of wood samples from the ZRFS was based on microscopic analysis of gross anatomical features of the wood. We prepared radial and tangential sections. Since adequate characteristics for identification could be obtained from the radial and tangential sections, we made only limited attempts to stabilize transverse sections in resin for thin sectioning. Future work will include investigating how to make accurate and permanent mounts of all three section directions.

Samples were prepared by softening and strengthening the wood fibers in a mixture of glycerin and isopropyl alcohol. Samples were sliced from prepared blocks using a #20 surgical scalpel and placed on microscope slides with a cover slip. The slides were then studied using an Olympus BX51 microscope at 200×, 400×, and 1000× magnifications.

We used a suite of characters to identify the samples (Hoadley, 1990). Fir was identified on the basis of possessing nodular end walls on the parenchyma, and taxodioid cross-field pitting, while lacking fusiform rays. Douglas-fir was identified on the basis of possessing nodular end walls of the parenchyma, piceoid cross-field pitting, fusiform rays, and spiral thickening of the longitudinal tracheids. This unique set of characters is exclusive to Douglas-fir, allowing species-level identification. Spruce was identified on the basis of possessing nodular end walls of the parenchyma, piceoid cross-field pitting, and fusiform rays, while lacking spiral thickenings of the longitudinal tracheids. Pine was identified on the basis of possessing pinoid cross-field pits. A fifth unidentified species possessed nodular end walls of the parenchyma, piceoid and cupressoid cross-field pitting, while lacking fusiform rays.

Dendrochronology

We focused dendrochronological analyses on wood from the beach horizon because it was likely that these trees grew more or less contemporaneously at the time of burial based on their stratigraphic association. This gave us a larger sample of ring-width statistics to compare between individual fossil trees, and to compare to modern tree-ring series to characterize past growing conditions and climate variability in relation to current conditions. It is likely that the beach sediment dates to MIS 5c during the Sangamon interglacial (Mahan et al., 2014–in this volume). The setting of the logs at the time of deposition appears to have been a shoreline along the eastern edge of Pleistocene Lake Ziegler. A large concentration of logs, including what appear to be largely main boles (without branches), were intermixed with mastodon bones in this horizon. A total of 17 wood specimens were analyzed in detail from the beach horizon for their ages at time of death and their dendrochronological characteristics. These logs were chosen as they were larger and contained the most rings of the samples collected from this horizon.

Cross sections from each sample were first glued to a backing board to provide sample stability and then sanded using a belt sander to 400 grit (very fine) sandpaper. Distinct growth rings were obvious in all samples examined (Figs. 1 and 2). Some tracheid degradation was apparent in all of the samples, and many of the samples were distorted by overlying sediments (Fig. 1). A few were less flattened or distorted (Fig. 2). Ring numbers were counted on one or more radii on each section, and a diameter estimated. On flattened sections, diameters were estimated as an average of both the short and long distances.

Ring widths were measured along selected radii on most samples using a Velmex™ measuring stage (precise to 0.001 mm) interfaced to a computer running MeasureJ2X™ software. Two or more radii were measured on some cross sections and averaged for the sample. Four descriptive statistics were calculated for each individual ring width radius and used to quantify and compare variation in individual tree and inter-annual growth rates. The statistics are: 1) maximum ring width, 2) mean ring width, 3) first-order autocorrelation, and 4) a statistic unique to dendrochronology, mean sensitivity (Douglass, 1936; Fritts, 1976). These statistics are often used to compare tree-ring series from different sites or species to assess both site productivity and annual variability in growing conditions (Fritts, 1969; Fritts and Shatz, 1975; Fritts, 1976; Péwé et al., 1997, 2009). Maximum and mean ring widths reflect relative overall productivity of an individual tree. Differences in productivity arise from varying environmental conditions of the microsite where a tree was growing (e.g., soil moisture or nutrients) or the canopy position of the tree (e.g., both maximum and mean ring widths will be relatively larger if a tree was dominate in the stand, and not shaded or competing with other trees). First-order autocorrelation and mean sensitivity are measures of how much variability there was in climatic or other environmental conditions that affected annual tree growth, or how responsive the tree was to that annual variability. First-order autocorrelation is the cross-correlation of the ring widths lagged by one year. Mean sensitivity is the mean first difference in a time series. Higher autocorrelation and lower mean sensitivity typically result from less annual variability in growing conditions, while the opposite patterns result from greater annual variability. Program COFECHA (Holmes,

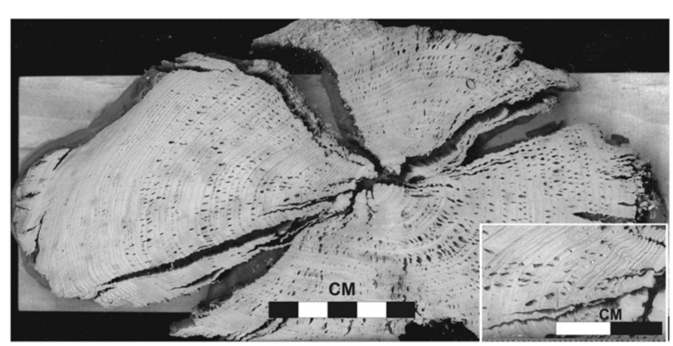

Figure 1. Cross section of a sample of fir (*Abies* sp.; sample id 47-61b) collected from the beach horizon. Inset: Close-up view of rings showing ring distortions and erosion.

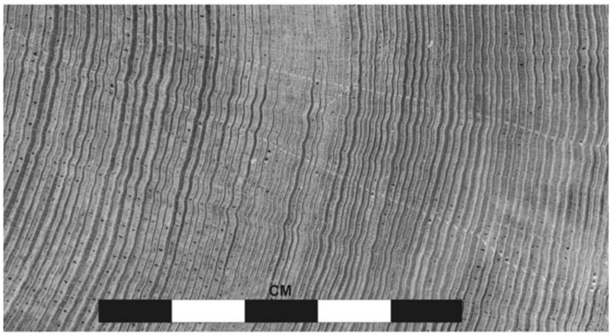

Figure 2. Cross section close-up view of a sample of Douglas-fir (*Pseudotsuga menziesii*; sample id 47-74) collected from the beach horizon.

1983; Grissino-Mayer, 2001) was used to calculate statistics for each measured radius.

We compared statistics from the ZRFS trees to the same statistics from individual modern trees from six Douglas-fir chronologies downloaded from the International Tree-Ring Data Bank (ITRDB; http://www.ncdc.noaa.gov/paleo/treering.html; accessed March 26, 2013; Table 2). Trees in these sites were growing at the same general elevation and in the same area of Colorado as the ancient wood. We only examined data from Douglas-fir wood as we were not sure of the species of the fir and there are very few fir collections in the ITRDB (only one in Colorado of *Abies lasiocarpa*). In general, fir has not proven useful for dendrochronological study owing to fir trees' generally younger ages, presence in closed-canopy forests, and lack of consistent climate response. We also did not assess data from the spruce since we only had one sample from the beach sediment.

Finally, COFECHA was used to compare ring-width series on different samples in an effort to assess crossdating. Crossdating is the process of cross-matching in-common patterns of ring widths between trees (e.g., Fritts, 1976). Ring patterns co-vary because of synchronous climate effects on tree growth. We assumed that crossdating between trees would imply that they grew contemporaneously with each other since the trees came from the same stratigraphic layer. COFECHA first segmented each radius into 50-yr overlapping periods. Each segment was then compared against another sample radius one year at a time, with the 11 highest correlations reported. Possible crossdating was indicated when COFECHA output specified the same systematic dating position for most or all of the segments of a radius and the correlations associated with these suggested placements were statistically significant. Crossdating was then checked between the two samples by visual examination of the wood underneath a microscope (7× to 30× magnifications). Other ring characteristics (e.g., latewood thickness) also may match between samples as a result of climate synchronization of growth, and are not captured by the ring-width measurements alone. We used visual examination as a check on crossdating suggested by COFECHA outputs. Once we had series that appeared to crossdate with each other, we added those together into a single "master" chronology. Additional radii from other samples were then compared to the master chronology one at a time. Any that had high and consistent correlations between individual segments and the master chronology were confirmed by visual crossdating and added to the master chronology.

Table 2
Douglas-fir chronologies downloaded from the International Tree-Ring Data Bank used to compare to the three Ziegler Reservoir beach area Douglas-fir trees.

Chronology name	ID no.	Elevation (m)	Latitude	Longitude
Wagon Wheel Gap	CO502	2743	37°48′N	106°50′W
Antonito Site A	CO046	2637	37°04′N	106°11′W
Cathedral Creek	CO593	2895	38°05′N	107°00′W
Douglas Pass	CO599	2591	39°36′N	108°48′W
Dillon	CO597	2880	39°36′N	105°54′W
McGee Gulch	CO609	2743	38°51′N	106°01′W

Results and discussion

Wood identification

Fir (*Abies* sp.) was the most commonly identified taxon with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) the second most common (Table 1). The fir wood could not be identified to species, although subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) is a common species in the forest surrounding the site today. However, another possibility would be white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.). Miller et al. (2014–in this volume) identified fossil cones from the ZRFS sediments as belonging to *A. concolor* and none from *A. lasiocarpa*, and therefore it is likely that most if not all of the fossil wood was also from this species. Miller et al. (2014–in this volume) also identified a total of 59 cones from Douglas-fir which matches well with the wood identification. Also identified in the wood samples was spruce (*Picea* sp.; Table 1). Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) is abundant in the area today, as well as blue spruce (*Picea pungens* Engelm.), albeit generally at lower elevations (1830 to 2740 m; Burns and Honkala, 1990). Miller et al. (2014–in this volume) assigned 94 cones as belonging to *P. engelmannii* and another 19 cones as belonging to an unknown species of *Picea*. This unknown species exhibits some similarities to *P. pugens* but possibly is from an extinct species. In general, fir (*Abies* sp.) and spruce (*Picea* sp.) samples appeared to be more distorted or flattened by overlying sediments (e.g., Fig. 1) than those of Douglas-fir (e.g., Fig. 2).

An additional three wood samples were identified as pine (*Pinus* sp.). Several species of pines grow in the area today, including lodgepole pine (*Pinus contorta* Dougl. ex Loud.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and limber pine (*Pinus flexilis* James). Lodgepole pine is the most common species in the area at this elevation today. A fifth distinct but as yet unidentified conifer genus also was present in the assemblage. Tentative identification of this genus is either juniper (*Juniperus* sp.) or hemlock (*Tsuga* sp.). Utah Juniper (*Juniperus osteosperma* (Torr.) Little) is present at lower elevations in central Colorado while hemlock is not found in modern Colorado forests. Interestingly, no quaking aspen (*Populus tremuloides* Michx.) or other

Table 1
Numbers of wood samples by species identified from the Ziegler Reservoir fossil site, Colorado. "All other" localities are not separated by stratigraphic unit but rather lumped together owing to small numbers of trees identified from throughout the excavation. Future work will attempt to resolve species identifications by stratigraphic unit to better examine species distributions through time.

Locality	*Abies* sp.	*Picea* sp.	*Pseudotsuga menziesii*	*Pinus* sp.	Unidentified species
47 (Beach)	27	0	3	0	0
All other	13	8	7	3	3

hardwood species (e.g., willow; *Salix*) wood was identified in the fossil assemblage. Aspen is probably the most common tree species found in the modern forest surrounding the ZRFS, with willow found along streams and wetlands in the general area. It may be that aspen or other hardwoods were not present in the forests surrounding Pleistocene Lake Ziegler, or that these woods were not preserved in sediments at the lake.

Douglas-fir and Engelmann spruce are common species of the modern forests at or near the ZRFS, and are found extensively throughout forests at this elevation in the central Rocky Mountains. Douglas-fir today has the greatest latitudinal range of any conifer in western North America and one of the largest elevational ranges (Burns and Honkala, 1990). Two varieties of Douglas-fir are recognized, *P. menziesii* (Mirb.) Franco var. *menziesii* that grows mainly in Pacific coastal ranges from California to British Columbia, and *P. menziesii* var. *glauca* (Beissn.) Franco that occurs along the Rocky Mountain cordillera from Canada to Mexico. In Colorado, Douglas-fir is found mainly between 2440 and 2900 m elevation, although in mesic or cooler sites it can grow at lower elevations and on warmer sites it may grow higher (Burns and Honkala, 1990). Engelmann spruce also is very widely distributed throughout higher elevation forests in Colorado and the central and northern Rocky Mountains. It generally has a higher elevation range in the central Rockies than the ZRFS (2705 m), from 2740 m up to treeline, which currently is at ~3400–3500 m (Burns and Honkala, 1990). However, along cold air drainages or more mesic locations, Engelmann spruce may extend down to as low as 2440 m. The prevalence of these two species in the ZRFS deposits suggests that climate conditions were comparable to those of the site today, albeit slightly cooler if most of the wood was from Engelmann spruce.

Conversely, the presence of white fir at the ZRFS is outside its current range, with its present northern limit located 50–100 km to the south at this longitude in the Central Rocky Mountains (Burns and Honkala, 1990). The main variety of white fir (*A. concolor* var. *concolor*) has a very widespread distribution throughout the southern Rocky Mountains and Southwest extending into northern Mexico. It also occurs at lower elevations than the ZRFS throughout most of its range, between 2100 and 2700 m (Burns and Honkala, 1990). Thus, we have some evidence of slightly altered species composition during the time of fossil deposition but overall the composition was very similar to modern forests [see also Miller et al. (2014–in this volume) for further discussion of biogeographic implications].

Dendrochronology of the beach wood

The majority of the wood (31 of 35 samples) recovered from the beach horizon was fir. Three of the largest logs, including one over 10 m in length, were Douglas-fir. A single sample of spruce also was identified. Other stratigraphic horizons in the lake yielded the same taxa, but at somewhat more uniform distribution (Table 1). Fir was slightly more prevalent than other taxa over the rest of the sediments, but it did not overwhelmingly dominate the sample as in the beach horizon.

The mean number of rings in the 14 largest fir logs that were analyzed in detail was 68 ± 27, with a range from 32 to 126 rings. The numbers of rings in the three Douglas-fir logs were 259, 228, and 175. However, almost none of the samples contained complete radii, and in places it was difficult to see or count the rings owing to ring distortions or wood erosion. We could not be sure that outermost rings were present on any of the cross sections, although we believe in several cases that the outermost rings were or were very near the tree death dates (especially on the Douglas-fir logs; see further discussion below).

Ring-width measurement statistics from the three ZRFS Douglas-fir logs fit within ranges of similar statistics from 188 modern Douglas-fir trees downloaded from the ITRDB (Fig. 3). Maximum ring widths are within the range of modern wood but above the 75th percentile, while mean sensitivities are also within the range but below the 25th percentile. Slightly higher maximum ring widths suggest that the fossil trees were growing in locations with relatively good environmental conditions, either in terms of factors such as optimal soil moisture or nutrients or in terms of less competitive interactions with surrounding trees. Lower mean sensitivity suggests that the fossil trees either were not as strongly affected by annual variations in climate conditions (as would be the case in a good location for growth) or that annual climate fluctuations were not as great as today. However, another consideration is that trees in ITRDB data sets were generally selected to maximize climate stress for purposes of reconstructing past climate variations (the so-called "principle of site selection in dendrochronology"; e.g., Fritts, 1976; Fritts and Shatz, 1975; Speer 2010). Thus, the comparison of the ZRFS fossil trees with modern trees (Fig. 3) is somewhat biased by the lack of a full range of possible sites and growing conditions where Douglas-fir is found today. However, overall, it appears that the growing conditions and annual variability in climate were similar in the forest surrounding Pleistocene Lake Ziegler as they are in the forests of central Colorado today. This result, combined with the species composition of the fossil wood collection and other observations about vegetation in the interglacial (Miller et al., 2014–in this volume; Anderson et al., 2014–in this volume; Strickland et al., in this volume), suggests that tree growing conditions and annual climate regimes during MIS 5 were similar to modern conditions.

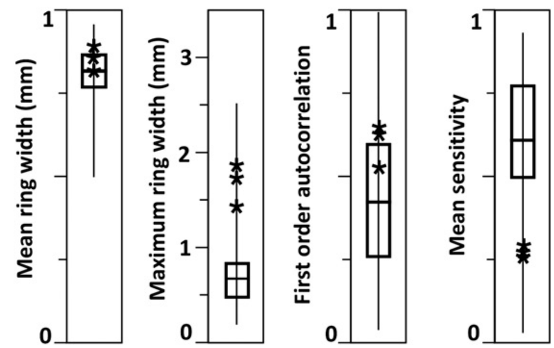

Figure 3. Ring width statistics from three Ziegler Reservoir Douglas-fir logs (asterisks) compared to similar statistics from 188 modern Douglas-fir trees (box-and-whiskers plots; ranges are light lines, 25th and 75th percentiles are bottom and top lines of boxes; means are lines within boxes). Modern trees were collected from sites in central Colorado at approximately the same elevation as the Ziegler Reservoir samples (downloaded from the International Tree-Ring Data Bank; Table 2).

We were able to crossdate several of the logs growing in the beach area with some confidence. The three Douglas-fir logs matched extremely well, both in terms of their high-frequency (annual) and low-frequency (multi-annual) variability (Fig. 4). Inter-series correlations between overlapping segments of ring widths of measured radii on these three logs ranged from 0.82 to 0.87. In fact, these three radii matched so closely that it is possible that these were from the same tree. However, the logs were separated from each other in the beach horizon, and were of different sizes and number of rings (although this could be because they were from different heights on the same tree bole). On the other hand, support for the hypothesis that these are different trees is that we also were able to crossdate with some confidence at least two of the 14 fir logs that were measured (Fig. 4 shows one of these series). Correlations of these two logs with the three Douglas-fir logs were 0.40 and 0.54. Other fir logs also had significant correlations with the master chronology but were lower than these two or did not have consistent correlations between different segments of the measured radii. Modern fir trees, in general, do not have as strong of an inter-series correlation as do other species, such as Douglas-fir, because of their propensity for growing as understory trees. Crossdating is not as strong because the trees are responding more to individual tree environmental factors and less to a common factor such as climate variation.

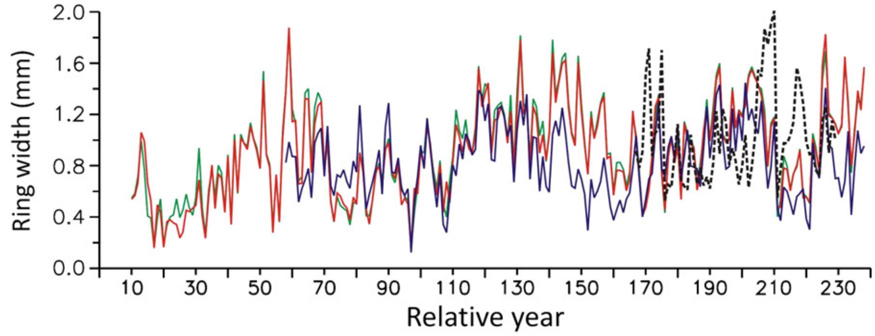

Figure 4. Ring widths measured from three ZRFS Douglas-fir logs (solid color lines) and one fir log (dashed line) crossdated relative to each other based on significant correlations in program COFECHA.

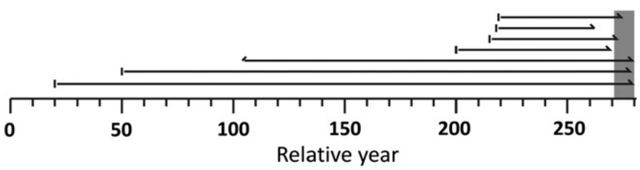

Figure 5. Time spans of three ZRFS Douglas-fir (bottom three lines) and four fir (top four lines) logs trees crossdated relative to each other based on significant correlations in program COFECHA. Vertical straight lines at left side of time spans represent pith dates, while slanted line on the third series from top represents an unknown number of rings to pith. Vertical slanted lines on right represent unknown number of rings to death date. Vertical gray bar on right represents possible period of synchronous death dates for all seven trees.

Matches suggested by the correlations also place the outermost rings of all of the series at near the same date (Fig. 5). Although we cannot be certain that these are the death dates for the trees because of possible erosion of outermost rings, we suspect that they are or are very close to death dates because of our subjective assessment of ring attributes, including particularly the nearly continuous nature of the outermost rings on the circumference of several of the samples. The possibility that at least some of the beach trees died at the same time suggests a possible catastrophic event in the forest surrounding Pleistocene Lake Ziegler that caused synchronous tree mortality. Such an event may have been an ecological disturbance, such as wildfire (although no charcoal was noted on any of the logs), bark beetle outbreak, or windthrow, or a geological disturbance, such as an earthquake or landslide into the lake.

Conclusion

Wood fossils recovered from the Ziegler Reservoir fossil site and especially from the beach horizon suggest that both forest composition and the growing conditions for individual trees were similar to those of modern trees growing at similar elevations in central Colorado. Fir and Douglas-fir were the most common species found, with spruce, pine, and at least one other unidentified conifer species also present. Conversely, aspen is a common species in the current forest but appears to have been either absent, rare, or not preserved in the fossil assemblage. Ring-width data from logs found in the beach horizon also suggest that tree-level and annual variability in growing conditions were very similar to those under which modern trees are growing. In sum, evidence provided by the fossil wood suggests that the environment, growing conditions, and annual climate variations affecting trees at the time they were alive were largely analogous to modern conditions.

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