Western North American Naturalist 83(1), © 2023, pp. 8–22

Revisiting Great Basin bristlecone pine (*Pinus longaeva*) in the Stansbury Mountains, Utah

David R. Burchfield[1,*], Otto W. De Groff[2], Matthew F. Bekker[3], Stanley G. Kitchen[4], and Steven L. Petersen[2]

[1]*Department of History, Geography, and Political Science, Brigham Young University–Idaho, Rexburg, ID*
[2]*Geospatial Habitat Analysis Laboratory, Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT*
[3]*Department of Geography, Brigham Young University, Provo, UT*
[4]*USFS Rocky Mountain Research Station, Provo, UT*

Abstract.—Great Basin bristlecone pine (*Pinus longaeva* D.K. Bailey) presence in the Stansbury Mountains of north-central Utah has been reported prior to the year 2020, but these reports lack adequate population characterization and the delineation of distinct stands of trees. In summer 2020, we identified and documented the presence of 5 separate stands of bristlecone pine in the Stansbury Mountains. These stands are removed from the nearest bristlecone populations in other mountain ranges by a distance of approximately 120 km; as such, they represent a unique outlier population of the species. We used GPS data to create a geographic information system (GIS) database delineating the 5 stands we identified, and we sampled tree age and size in one of the stands for comparison with other bristlecone pine populations in the Great Basin. We present here 2 hypotheses to explain the occurrence of bristlecone pine in the Stansbury Mountains: first, that this population is a relict from a time when bristlecone pine was widely distributed across the Great Basin; and second, that the species arrived in the range via long-distance dispersal mechanisms at some point during or after the Pleistocene/Holocene transition (ca. 12,000 ^{14}C YBP). *Neotoma* (woodrat) midden data suggest that bristlecone pine was absent or at least not widespread in the northern Bonneville Basin during the late Pleistocene, but midden data are sparse for the Stansbury Mountains and surrounding ranges. Additionally, we present possible migration pathways that the species could have taken to reach the Stansbury Mountains from the southern Bonneville Basin, where it was widespread during the late Pleistocene, using the largest extent of Lake Bonneville as a limiting boundary. Hypothesized migration vectors include windborne long-distance dispersal events or transport by granivorous birds. We also postulate that a small population of bristlecone pine may be present in the Oquirrh Mountains to the east of the Stansbury Mountains based upon the existence of similar habitat characteristics there, as well as our identification of a likely misdetermined 1964 voucher specimen from the Oquirrh Mountains that appears to be of bristlecone pine.

Resumen.—La presencia del pino longevo de la Gran Cuenca (*Pinus longaeva* D.K. Bailey) en las montañas Stansbury del centro-norte de Utah fue registrada antes del año 2020. No obstante, estos reportes carecen de caracterización adecuada de la población y delineación de distintos rodales de árboles. En el verano de 2020, identificamos y documentamos la presencia de cinco rodales separados de pino longevo en las montañas Stansbury. Estos rodales se encuentran alejados de las poblaciones de pinos longevos más cercanas en otras cadenas montañosas, a una distancia de aproximadamente 120 km, y como tales, representan una población atípica única de la especie. Usamos datos de GPS para crear una base de datos del sistema de información geográfica (SIG) que delinea los cinco rodales que identificamos, y tomamos muestras de la edad y el tamaño de los árboles en uno de los rodales para compararlos con otras poblaciones de pinos longevos en la Gran Cuenca. En este trabajo presentamos dos hipótesis para explicar la presencia del pino longevo en las montañas de Stansbury: (1) esta población es un relicto de la época en que el pino longevo se encontraba ampliamente distribuido en la Gran Cuenca, y (2) la especie llegó a la cordillera a través de mecanismos de dispersión de larga distancia (LDD, por sus siglas en inglés) en algún momento durante o después de la transición Pleistoceno/Holoceno (ca. 12,000 14C YBP). Las estadísticas de los yacimientos de neotoma (rata de bosque) sugieren que el pino longevo estaba ausente o al menos no estaba muy extendido en la cuenca del norte de Bonneville durante el Pleistoceno tardío, pero los datos de los yacimientos son escasos en las montañas Stansbury y las cordilleras circundantes. Adicionalmente, presentamos posibles rutas de migración que la especie podría haber tomado para llegar a las montañas Stansbury desde el sur de la cuenca de Bonneville, donde se encontraba muy extendida durante el Pleistoceno tardío, utilizando la mayor extensión del lago Bonneville como límite. Los vectores de migración hipotéticos incluyen eventos LDD transportados por el viento o por aves granívoras. También postulamos

*Corresponding author: burchfieldd@byui.edu

DRB orcid.org/0000-0002-5032-2898 MFB orcid.org/0000-0001-6662-3225 SGK orcid.org/0000-0002-5536-4237
SLP orcid.org/0000-0001-7521-9451

que una pequeña población de pino longevo podría estar presente en las Montañas Oquirrh al este de las Montañas Stansbury ya que el hábitat presenta características similares, así como, nuestra identificación de un espécimen de prueba de 1964 de las Montañas Oquirrh que probablemente no se describió correctamente y que parece ser de pino longevo.

Great Basin bristlecone pine (*Pinus longaeva* D.K. Bailey, hereafter "bristlecone pine") is a subalpine conifer species found in isolated populations across the Great Basin and western Colorado Plateau, USA (Bailey 1970). Bristlecone pine is well known as being the longest-lived tree species on earth (Schulman 1958, Currey 1965). Bristlecone pine primarily grows on limestone- and dolomite-derived soils across an elevation range of 2200 to 3600 m (Bailey 1970). Bristlecone pine is found in Utah, Nevada, and eastern California (Lanner 1984, Welsh et al. 1993, Charlet 1996), with the southernmost population of the species occurring on Mt. Potosi, Nevada (Spring Mountains) (35.97°N), and the northernmost populations in the Ruby Mountains (40.64°N), Spruce Mountain (Pequop Mountains) (40.55°N), and Goshute Peak (Goshute Mountains) (40.50°N) of the central Great Basin in Nevada. In Utah, bristlecone pine extends from the Pine Valley Mountains in Washington County (37.32°N) to the West Tavaputs Plateau in Duchesne County (39.99°N) (see Appendix 1 for voucher information for the aforementioned locations).

D.K. Bailey (1970) described Great Basin bristlecone pine as a separate species from Rocky Mountain bristlecone pine (*P. aristata*). He identified several locations where the environmental conditions were assumed to be suitable for bristlecone pine occurrence, but where vouchers were lacking. One location he identified was the Stansbury Mountains in north-central Utah (Bailey 1970). In 1978, Kay and Oviatt published a report describing a single bristlecone pine individual that they observed along an arête in the central portion of the Stansbury Mountains. This report included a general location and site description of this tree, while explaining that conditions were potentially suitable for additional populations to occur (Kay and Oviatt 1978). Taye (1983) identified isolated stands of bristlecone pine as infrequent but locally dominant on limestone slopes in the range, although he did not provide specific information regarding the location of these stands or individual trees. Additional information about bristlecone pines in the Stansbury Mountains has been recorded in the form of herbarium vouchers—one collected by P. Kay in 1977 (from the tree described in Kay and Oviatt 1978), another collected by A. Taye in 1979, and a third by S. Langer in 1994 (Appendix 1). Taye's and Langer's vouchers were collected within 1 km of Kay's original voucher along ridges on the east side of Deseret Peak, the range's high point. These reports are notable because they describe a population of bristlecone pine that is highly disjunct from other known populations. The nearest known populations are in the Deep Creek Mountains, Utah, ca. 122 km to the west-southwest, and the House Range, ca. 129 km to the south-southwest (Appendix 1). The Stansbury Mountains population is currently the northernmost identified population of bristlecone pine in Utah at 40.47°N, rivaling the latitudes of the aforementioned northernmost populations in Nevada.

The origin and timing of arrival of bristlecone pine into the Stansbury Mountains remain uncertain. The paleogeography of conifer species in the western United States has been extensively characterized in the literature (Wells 1983, Betancourt 1984, Thompson 1984, Rhode and Madsen 1995, Rhode 2016). A common source of late Quaternary paleobiogeographic records is in the form of vegetation fragments found within the strata of excavated woodrat (*Neotoma* spp.) middens (Wells 1983, Betancourt 1984). *Neotoma* middens typically contain needles, seeds, and other plant matter that can be identified to the species level (Wells 1983). Individual plant fragments are ^{14}C-dated to approximate the time when a particular species was present at the midden location.

Midden records indicate that bristlecone pine was dominant in the southern Bonneville Basin during the late Pleistocene, between at least 37,000 and ~10,000 ^{14}C YBP (Wells 1983, Madsen et al. 2001). Available *Neotoma* midden evidence (Wells 1983, Thompson 1984, Rhode 2016) suggests that the upper Bonneville Basin, including the Stansbury Mountains, was dominated by limber pine during that period and that bristlecone pine might have been absent above about 40°N latitude (Wells 1983, Rhode 2016). More extensive sampling of Pleistocene-aged samples from the region is needed to confirm this hypothesis. An unpublished *Neotoma* midden record of bristlecone pine on Swasey Mountain in the House Range of west-central Utah

(39.380°N, 113.321°W; elevation 2386 m, ~11,000 ^{14}C YBP; data on file USDA Forest Service, Shrub Sciences Laboratory, Provo, UT), combined with a widespread modern distribution, supports a conclusion that this species has had a continuous presence on the northern end of the House Range since at least the late Pleistocene. From these midden records, it could be assumed that a transition from bristlecone pine dominance to limber pine dominance occurred between the House Range and the southern Stansbury Mountains. Unfortunately, there are large gaps in the midden records for the upper Bonneville Basin, and the genesis of the small outlier population on the Stansbury Mountains remains unexplained.

The objective of this paper is to characterize prior ambiguous observations of the extent and structure of extant stands of bristlecone pine in the central Stansbury Mountains by producing a map that delineates the location and size of each stand. Additionally, we speculate regarding 2 possible mechanisms that could explain how and when bristlecone pine arrived at this mountain range:

1. Bristlecone pine was present in the range during much or all of the last (Wisconsin) glacial stage (≈75,000–11,000 YBP), having arrived under much colder-than-modern climate conditions, and the current stands are high-elevation remnants of a larger, earlier population.
2. Bristlecone pine colonized the Stansbury Mountains at approximately its modern elevational range, under warmer climatic conditions of the terminal Pleistocene (Pleistocene/Holocene transition) or during the Holocene (<11,000 YBP) via long-distance dispersal mechanisms.

Methods

Study Area Description

The Stansbury Mountains are located in the eastern Great Basin in Tooele County, 62 km WSW of Salt Lake City, Utah. Like most mountain ranges in the Great Basin, the crest of the range trends from north to south and is bounded on either side by low-elevation semiarid desert valleys, with Skull Valley located to the west and Rush and Tooele valleys to the east (Lanner 1971, Taye 1983). The range extends from Johnson Pass (elevation 1981 m), where it meets the Onaqui Mountains, north to the Great Salt Lake. The range rises to its highest point, Deseret Peak, at 3362 m. Ridgelines extend both north and south of Deseret Peak, forming a high, narrow crest. The total length of the range is approximately 45 km, and it is 21 km wide at its greatest width (Taye 1983). Geologically, the Stansbury Mountains are described as a massive eastward-tilted fault block with a steep western escarpment and more gradual eastern slopes. The core consists of Precambrian Prospect Mountain quartzite, with abundant Paleozoic limestone and dolomite occurring on the north and south ends of the range, and east of Deseret Peak (Rigby 1958).

The distribution and composition of vegetation vary with elevation, slope, and aspect across the range. On west-facing slopes, Utah juniper (*Juniperus osteosperma*) and Rocky Mountain juniper (*J. scopulorum*) grow in scattered stands, with singleleaf pinyon (*P. monophylla*) occurring primarily on north-facing aspects at low and middle elevations. The east side of the range supports riparian ecosystems that follow stream corridors in canyon bottoms. These sites are dominated by narrowleaf cottonwood (*Populus angustifolia*) and boxelder (*Acer negundo*) at lower elevations. Aspen (*Populus tremuloides*) is present along streams and within higher-elevation sites interspersed among montane mixed conifer forests. White fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*) are common in canyons at lower elevations. At middle elevations (between 2350 and 2450 m), limber pine (*P. flexilis*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) are common. Along the crest of the range (above 3050 m), these 3 species are also present, but they often grow as matted stands of krummholz (Lanner 1971). Bristlecone pine is found within this upper high-elevation zone, commonly associated with limber pine, Douglas-fir, subalpine fir, and Engelmann spruce (Lanner 1971, Taye 1983). The summit of Deseret Peak is devoid of trees (Lanner 1971). The ridgeline to the east of Deseret Peak averages between 3000 and 3120 m, with Engelmann spruce, limber pine, and bristlecone pine common along its length. Tree line in the area is between 3200 and 3290 m, with only Deseret Peak rising above this height (Taye 1983).

Assessment of Great Basin Bristlecone Pine in the Stansbury Mountains

We used historic voucher records describing the distribution of bristlecone pine to approximate the locations of potential trees or stands within the Stansbury Mountains. These voucher data were compiled as part of a study mapping and characterizing the overall distribution of bristlecone pine throughout its range (Burchfield et al. 2023). Our search efforts were assisted with information provided by personal communication with S. Langer (personal communication 2019), who had collected voucher specimens of bristlecone pine in the Stansbury Mountains on limestone substrate near Point 10,042, 1.6 km east of Deseret Peak (Point 10,042 refers to an unnamed peak shown on the USGS topographic quadrangle map of the area). Langer provided estimated GPS coordinates of additional sites along the ridgeline north and south of Point 10,042 where bristlecone pines were assumed to be present (Langer personal communication 2019). In June 2020, we conducted an initial scouting trip to the range. In the vicinity of the coordinates provided by Langer, we identified 3 distinct stands of bristlecone pine on east-facing slopes in the upper reaches of the Bear Fork of East Hickman Canyon (hereafter Bear Fork, stand 5) and the White Pine Fork of Box Elder Canyon (hereafter White Pine Fork North and South, stands 3 and 4, respectively) that had not been identified or described previously. Vouchers were collected from stands 3 and 4 and deposited at the S.L. Welsh Herbarium (Appendix 1).

In July 2020, we made a second visit to the ridgeline east of Deseret Peak via the Mill Fork Canyon trail. Observations made of conifers in this area led to the discovery of 2 additional bristlecone pine stands (hereafter Mill Fork West and East, stands 1 and 2, respectively). We visited the area a third time in August 2020 to obtain radial cores from stand 4 to determine the average tree age within the stand. Ten bristlecone pines were opportunistically selected within the stand (randomized sampling proved difficult due to steep slopes), and radial cores were extracted from the trees using a 24-inch Haglöf increment borer (Haglöf, Långsele, Sweden). Slope and aspect were measured for each tree using a TruPulse 360 Rangefinder (Laser Technology, Centennial, CO). Core samples were collected at heights below 1.0 m above ground level through actively growing wood (live cambium) to extract a maximum number of rings available for age estimation. Out of the 10 cores, 3 reached tree pith, while 7 did not. Failure to reach tree pith was a result of either (1) being only slightly off pith (and because of time limitations, samples close to pith were deemed sufficient for the study) or (2) reaching sections of rotted wood during core sampling, which resulted in a partial core of solid wood being obtained. Trees were selected for sampling in an effort to represent total variation in tree size and age classes, as well as differences in terrain characteristics (slope and aspect) within the stand. Two of the trees selected for sampling showed the "strip bark" morphology often observed in high-elevation bristlecone pine individuals (Wright and Mooney 1965). We did not perform a systematic survey of remnant wood that could be used for dendrochronology, but scattered remnant pieces were noted in White Pine Fork South (stand 4).

Sample cores were preserved in paper straws and later glued to wood mounts after drying. Mounted cores were surfaced using progressively finer sandpaper, starting with 150 grit paper and ending with 600 grit paper, using a 53.3 × 7.6 cm belt sander. Subsequently, cores were sanded by hand using 9-micron finishing film until individual cells were distinguishable in cross-section. Growth-ring series were aged using a simple ring count approach at 20–60× microscope magnification to develop estimates of tree ages. In cores that approached but did not intersect pith (i.e., were within 1 cm of pith), the number of missing rings was estimated using a pith indicator (Applequist 1958, Speer 2010). For cores that did not come close to pith (those that ended in rotted wood), estimated age was determined by using DBH measurements to approximate the length of the missing wood (from core end to pith). The average growth rate of each incomplete core's innermost 3 full centuries of growth was then calculated (centuries were measured at even 100-year marks, such as 1500, 1600, etc.). This growth rate was applied to the estimated missing length of wood to pith, giving an approximate total number of rings for each incomplete core. We acknowledge that this method is limited; crossdating is needed to definitively date these trees, but this was impossible due to the small number of core samples we obtained and an apparently large number of missing rings in our samples.

During each visit to the Stansbury Mountains, we collected numerous digital photographs of each bristlecone pine stand we encountered. The photographs were tagged with geographic coordinates (latitude, longitude, and elevation values) and plotted using Google Maps (Google, Mountain View, CA) and ArcGIS Pro (Esri, Redlands, CA) to produce boundary polygons for each stand. For the stands we did not visit due to steep terrain and time constraints (Mill Fork West and Mill Fork East), we used Gaia GPS, a mobile GPS mapping application (Outside, Boulder, CO), to draw estimated boundary polygons. This application offers the capability of precaching topographic maps and high-resolution aerial imagery, such as with sUAS (drone) technology, for use in remote areas where cellular data connectivity is unavailable. We viewed the Mill Fork West and East stands through binoculars from the bottom of Mill Fork Canyon, compared visible terrain features with those present on the precached topographic map in Gaia GPS, and then drew the stand boundaries accordingly.

Compilation of Bristlecone Pine Distribution Data for the Late Pleistocene and Early Holocene

We utilized the USGS–NOAA Packrat Midden Database (USGS 2021a) to compile midden records for bristlecone pine and limber pine within western Utah and eastern Nevada for 12,000 ± 2000 ^{14}C YBP. This time period was chosen because it encompasses much of the Pleistocene/Holocene transition period during which time these species migrated to their modern distributions. Only midden strata that corresponded to this Pleistocene/Holocene transition period were considered, as some middens also included strata that were dated to other time periods. We restricted the analysis to bristlecone pine and limber pine due to their relative dominance (among conifers) in the region compared to other species during this time period (Wells 1983). The midden records were plotted on a map using ArcGIS Pro. Additionally, a GIS file for the maximum extent of Lake Bonneville was obtained (Utah Automated Geographic Reference Center 2021) and plotted in ArcGIS Pro for analysis of possible bristlecone pine migration routes.

RESULTS

Analysis of Surveyed Bristlecone Pine Stands

Four of the 5 stands we mapped are located on limestone or limestone-shale substrates, while the remaining stand grows on Prospect Mountain quartzite, north of the lone tree described by Kay and Oviatt (1978) (Utah Geological Survey 2021). The stand found on quartzite (stand 1) is located north of Point 9841 on the lower, rocky portion of the ridge. These geology types are consistent with substrates found at other bristlecone pine stand locations (Wright and Mooney 1965).

The smallest of the 5 newly identified stands (stand 3) is located approximately 150 m northeast of Point 10,042 and corresponds to the voucher collected by Taye in 1979 (Appendix 1). We counted 8 mature trees and 2 juvenile bristlecone pine individuals in this stand. Trees are growing on steep, rocky limestone slopes positioned above White Pine Fork Canyon. Limber pine is codominant with bristlecone pine in this stand. The 2 stands south of Point 10,042 (stands 4 and 5) are larger in area. The White Pine Fork South stand is located northeast of Point 10,230 on east-facing slopes (Fig. 1). Bristlecone pine is dominant within the stand, with scattered limber pine, Engelmann spruce, Douglas-fir, and subalpine fir present in the vicinity. The White Pine Fork South stand (stand 4) contains a large number of ancient, weathered bristlecone pines (Fig. 2). The southernmost stand we identified (stand 5) lies within the Bear Fork drainage and is similar in size to the White Pine Fork South stand, with a slightly lower mean elevation (Fig. 1, Table 1).

White Pine South (Stand 4) Tree Measurements

Within stand 4, sampled trees ranged in size from 22 to 172 cm diameter at breast height (DBH) (Table 2). Mean DBH for all sampled trees was 80 cm. The mean elevation of the sampled trees was 3053 m. Slope ranged from 52.0° near the north end of the stand to 37.2° near the stand center, with a mean slope of 41.0° among the sample locations. Aspect varied slightly throughout the stand, ranging from 41° to 78° (NE to ENE), with a mean of 59.6° (ENE).

The position of stand 4 appears to be representative of most other portions of the Stansbury ridgeline where bristlecone pine occurs. Trees are generally restricted to steep, east-facing slopes of the ridge. Bristlecone pine rarely reaches the ridge, and when it does, only scattered trees are present and limber pine becomes dominant. These characteristics fit closely with Taye's description of bristlecone pine occurrence in the range (Taye 1983). Additional conifer species co-occurring with bristlecone pine on the ridgeline are common juniper (*Juniperus communis*), Engelmann spruce, and Douglas-fir.

Age Distribution

Estimated ages for sampled trees varied by an order of magnitude, consistent with the wide variability in individual tree DBH. The youngest

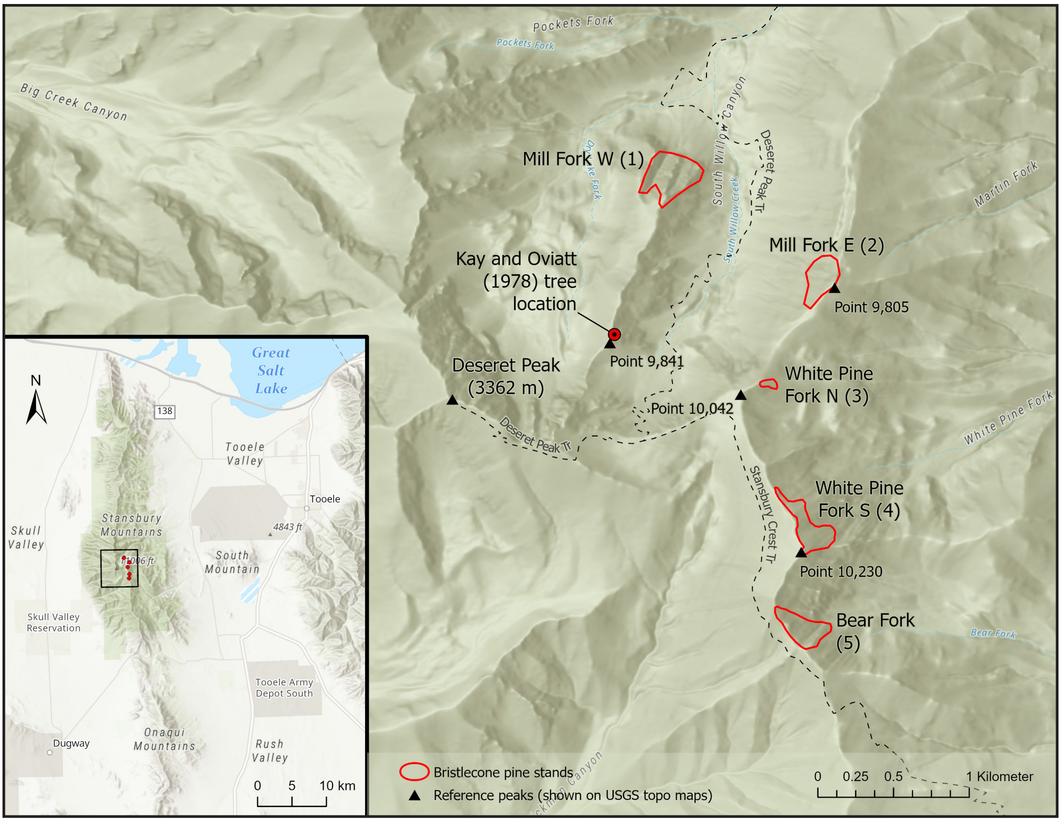

Fig. 1. Map of Great Basin bristlecone pine (*Pinus longaeva*) occurrence in the Stansbury Mountains, Utah (40.4614°N, 112.6224°W).

tree was 80 years old, while the oldest estimated age was 1784 years (this age is an estimate from our best assessment of the available tree rings, which were limited because of internal tree rot; Table 2). Based on our visits to the stand, we estimate that the sampled trees are representative of all trees across the stand. Large trees in the stand (DBH > 80 cm) grow on a wide range of slopes, with some trees on steep, rocky terrain, while others are on more gentle slopes where soil accumulation is evident. The oldest trees in the stand exhibit growth patterns outlined by LaMarche (1969), in which growth is limited to a portion of the tree's circumference (strip bark). This allows old trees (>1500 years old) to maintain a constant ratio of green to nongreen tissue, even when trunk circumference becomes large (>6 m) (Wright and Mooney 1965). Cores from trees 1, 5, and 9 provide the longest history of growth in the stand. Tree ring growth at this elevation (3055 m) is most likely to be precipitation sensitive rather than temperature sensitive (Kipfmueller and Salzer 2010, Salzer et al. 2014). A marked trend toward smaller rings estimated to be from AD 1300 to 1400 could correspond to the drier conditions at the end of the Medieval Warm Period and beginning of the Little Ice Age.

DISCUSSION

Disjunct Nature of the Stansbury Mountains Bristlecone Pine Population

The characteristics of the bristlecone pine population we identified in the Stansbury Mountains are similar to those of other populations in the eastern and central Great Basin. The 5 stands we mapped lie between 2560 m and 3118 m, which is consistent with the species' typical elevation range (Fryer 2004). Dominant soil series in these stands include Lundy, Podmor, and Datemark, which are each found within bristlecone pine stands in the Deep Creek

Fig. 2. Ancient bristlecone pine (*Pinus longaeva*) individuals growing on steep limestone substrate in the White Pine South stand. Photograph courtesy of Otto De Groff.

Mountains to the southwest (California Soil Resource Lab 2021). Vegetation associations are also typical of other bristlecone pine populations in Utah and Nevada (Hiebert and Hamrick 1984). Despite these similarities to other populations, the Stansbury Mountains population is unique because of its large distance from the next closest known populations in the Deep Creek Mountains, the House Range, and the West Tavaputs Plateau.

Paleobiogeography of Bristlecone Pine and Limber Pine in the Bonneville Basin

Modern records of conifers in the Bonneville Basin during the late Pleistocene and early Holocene indicate a low probability of bristlecone pine reaching the Stansbury Mountains, given known dispersal mechanisms. This extant bristlecone pine population in the Stansbury Mountains may be a remnant of an undocumented presence of the species in the northern Bonneville Basin sometime prior to the Pleistocene/Holocene transition, when cooler temperatures facilitated montane conifer presence at low elevations. A warming climate during the early Holocene makes it seem more likely that bristlecone pine reached the Stansbury Range prior to that time, as the suitable habitat area for this species would have declined sharply under warmer conditions. *Neotoma* midden records from the late Pleistocene (ca. 12,000 YBP) suggest that bristlecone pine was dominant in mountains and foothills of the east-central Great Basin (Wells 1983, Thompson 1990). Middens that document bristlecone pine occurrence during the Pleistocene have not yet been discovered in the Stansbury Mountains.

Neotoma midden records from other portions of the Bonneville Basin suggest that bristlecone pine was present on thin or skeletal soils as low as 1660 m at the north end of the Confusion Range in west-central Utah (11,880 ± 170 ^{14}C YBP) (Wells 1983). This elevation is near the maximum level of Lake Bonneville at 1550 m

TABLE 1. Topographic and geologic characteristics of the 5 stands of Great Basin bristlecone pine (*Pinus longaeva*) mapped in the Stansbury Mountains, Utah (USGS 2021, Utah Geological Survey 2021).

Stand name	Stand area (ha)	Mean elevation (m)	Mean slope (degrees)	Mean aspect (degrees)	Geology
Mill Fork W (stand 1)	6.6	2669	42.8	123.3	Prospect Mountain quartzite (Podmor series)
Mill Fork E (stand 2)	3.8	2918	35.9	44.3	Cambrian carbonates and shales (Datemark and Podmor series)
White Pine Fork N (stand 3)	0.4	3014	36.2	118.3	Wheeler Formation and Swasey Limestone (Lundy series)
White Pine Fork S (stand 4)	4.3	3055	37.5	69.0	Pierson Cove Formation (limestone) (Lundy series)
Bear Fork (stand 5)	3.9	2958	38.0	80.0	Pierson Cove Formation (limestone) (Lundy series)

(Wells 1983). The lake maintained this level between 18,600 and 18,000 ^{14}C YBP and later subsided to the Provo Level (1450 m MSL), where it stabilized for 2000 years (ca. 17,000–15,200 ^{14}C YBP) (Benson et al. 2011, Oviatt 2015). Throughout the Provo Level period, Lake Bonneville continued to occupy low passes between the House Range and the Stansbury Mountains. As temperatures gradually increased after the last glacial maximum (ca. 18,000 YBP), subalpine tree species (including bristlecone pine) moved upslope into cool, dry mountain ranges where they are currently located (Betancourt 1984). The Stansbury Mountains offer a relatively small area of suitable habitat for bristlecone pine compared to other ranges (e.g., House Range, Utah; Deep Creek Mountains, Utah; Snake Range, Nevada), which could explain the small, fragmented nature of modern bristlecone pine stands near the highest elevations in the range. Competition from other conifer species in areas with higher-quality soils and shallower slopes may further explain the species' highly restricted distribution (Beasley and Klemmedson 1980). Based on available data, we propose 2 hypotheses to explain both the arrival and modern presence of bristlecone pine in the Stansbury Mountains.

Pleistocene Refugium Mechanism

Extant bristlecone pine stands in the Stansbury Mountains could be a relict population that was continuously present in the range during all or much of the Wisconsin Glacial Stage (75,000–11,000 YBP). During the late Pleistocene (ca. 12,000 YBP) and into the Pleistocene/Holocene transition (warming) period, midden records indicate that bristlecone pine was widespread within montane environments in the central and southern Great Basin (Wells 1983, Thompson 1990). However, midden data from calcareous soils in the northern Bonneville Basin are sparse, and bristlecone pine material is absent from the single Pleistocene-aged midden record from the Stansbury Mountains (at Devil's Gate at the south end of the range, 1825 m elevation), which only contains material from subalpine fir and limber pine from 12,370 ± 60 ^{14}C YBP (USGS 2021b). Limber pine was the dominant conifer in the northern Bonneville Basin during this period, while bristlecone pine transitioned to dominance in the southern portion of the basin (Fig. 3). Complex relationships between multiple conifer species and climatic

TABLE 2. Measurements from the 10 bristlecone pine (*Pinus longaeva*) individuals sampled within White Pine South (stand 4). Additional samples are needed to facilitate cross-dating and the development of a climate chronology from this population. Estimated ages are in years.

Core number	Ring count	Estimated inner ring year (AD)	DBH (cm)	Radius estimate (cm)	Core length (cm)	Estimated age (years)
1	997	1023	94.7	47.4	33.9	1320
2	446	1574	95.3	47.6	13.1	1784
3	515	1505 (pith)	41.2	20.6	18.9	515
4	335	1685	59.2	30.0	29.9	345
5	1147	873	130.8	65.4	44.0	1516
6	80	1940 (pith)	22.0	11.0	10.5	80
7	542	1478	92.5	46.2	27.6	858
8	507	1513	172.3	86.2	23.4	1767
9	869	1151	70.4	35.2	30.3	995
10	113	1907 (pith)	25.7	12.8	13.2	113

changes during this period make it difficult to determine both the timing and migration route of bristlecone pine to the Stansbury Mountains. Additionally, a near absence of bristlecone pine in *Neotoma* middens north of the Confusion Range in western Utah during the Pleistocene/Holocene transition further complicates the task of identifying both the timing and route of bristlecone pine migration to the Stansbury Mountains. The aforementioned unpublished midden record from the northern House Range is evidence that the species was present in upland areas north of the Confusion Range during this period, though it is impossible to determine the northern extent of the distribution without additional midden data from the Pleistocene/Holocene transition period.

Long-distance Dispersal (LDD) Mechanism

Alternatively, if bristlecone pine was not present in the vicinity of the Stansbury Mountains during the Pleistocene, we hypothesize that seeds could have traveled to the range via long-distance dispersal (LDD) mechanisms at some time during or after the Pleistocene/Holocene transition. This mechanism seems to be the most likely cause of bristlecone pine's arrival in the Stansbury Mountains, regardless of whether the migration occurred in the Pleistocene or Holocene, but the timing and possible migration pathways are important to consider.

Bristlecone pine seeds are small (6–8 mm in length), winged, and typically spread across short distances via wind dispersal (Lanner 1988, Fryer 2004). Clark's Nutcracker (*Nucifraga columbiana*) forages for pine seeds and caches them at longer distances, particularly in higher-elevation stands, which results in germination in a small percentage of caches (Lanner 1988, Chambers et al. 1999). While the LDD capability of bristlecone pine under typical conditions has not been studied extensively, the likelihood that seeds from the nearest populations in the Deep Creek Mountains, House Range, or West Tavaputs Plateau could reach the Stansbury Mountains in a direct linear path seems very low, based on seed dispersal research from other pine species (McCaughey et al. 1985, van Wilgen and Siegfried 1986, Benkman 1995). However, studies have shown that tree species can move rapidly via uncommon dispersal events, which can cause seeds to travel greater distances than would be expected within a specific time period (Clark et al. 1998, Powell and Zimmerman 2004).

Dispersal mechanisms may include interactions with high winds, water movement, or transport by birds (Clark et al. 1998)—the latter seeming quite likely with bristlecone pine during the late Pleistocene, when Lake Bonneville covered valley bottoms around the Stansbury Mountains and other mountain ranges where bristlecone pine is now present. Clark's Nutcracker has been shown to disperse seeds some 30 km (Schaming 2016), and it seems feasible that seed transport to the Stansbury Mountains from nearby ranges could have occurred over several generations. Because of bristlecone pine's affinity for limestone soils (Bailey 1970), it appears probable that dispersal of seeds may have occurred as a series of LDD events that delivered seed from one suitable habitat area to the next across an unknown time frame.

A likely scenario is that bristlecone pine could have reached the Stansbury Mountains via wind- or bird-borne seed dispersal through a series of desert mountain ranges extending northward from the House Range. Following this route, migration would have occurred via a

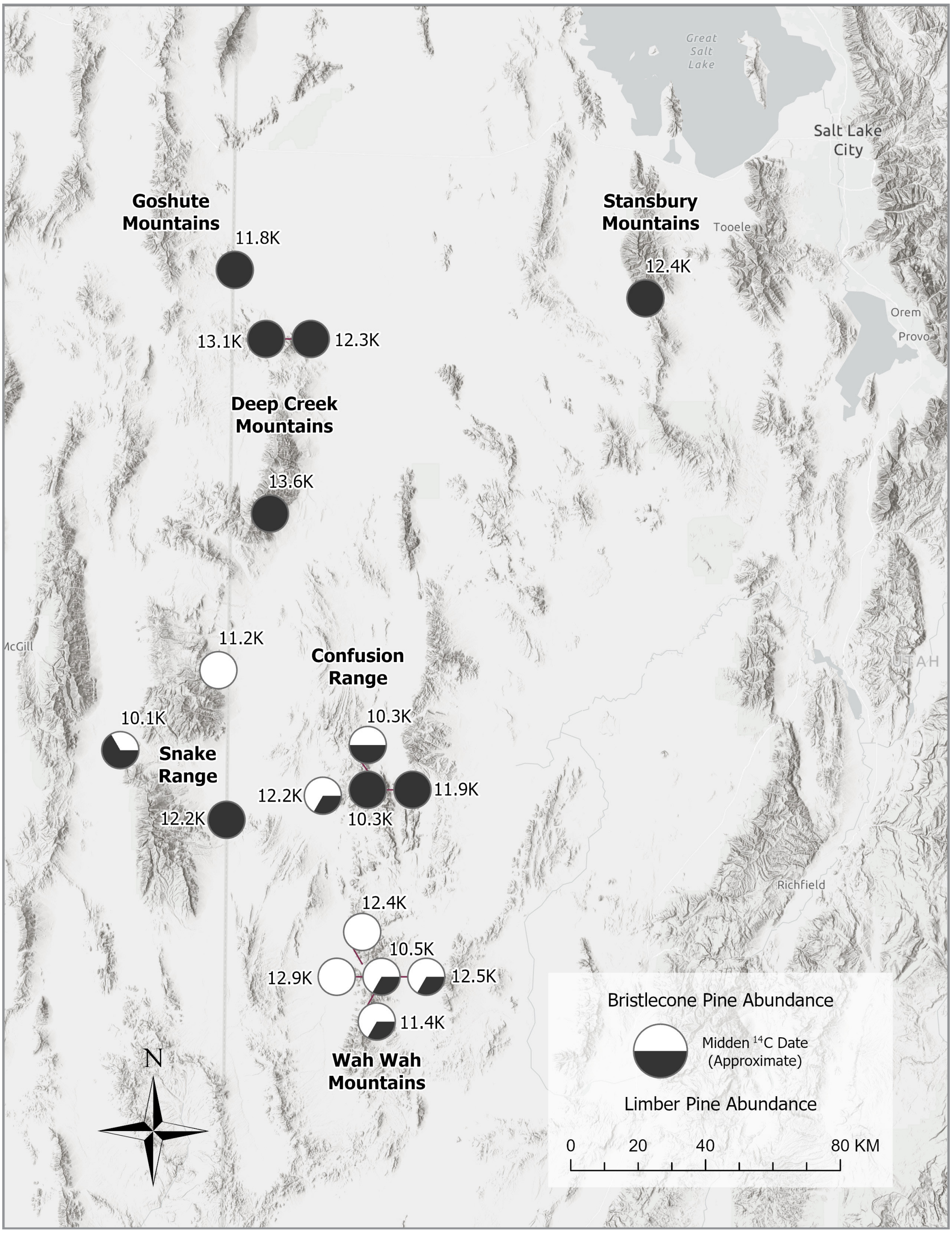

Fig. 3. Map of relative abundance of bristlecone pine (*Pinus longaeva*) and limber pine (*P. flexilis*) material in individual *Neotoma* midden strata dated to the Pleistocene/Holocene transition period (12,000 ± 2000 ^{14}C YBP) in the Bonneville Basin. Bristlecone pine transitions from dominance in the south to absence in records from the northern portion of the basin. Labels indicate the approximate radiocarbon date of each midden record (e.g., 12.4K = 12,400 ^{14}C YBP). Data courtesy of the USGS–NOAA North American Packrat Midden Database and Esri. Approximate central coordinate locations are provided here for the Deep Creek Mountains (39.91408°N, 113.88361°W), the Snake Range (39.14795°N, 114.22736°W), the Confusion Range (39.07491°N, 113.43615°W), and the Wah Wah Mountains (38.67291°N, 113.56441°W).

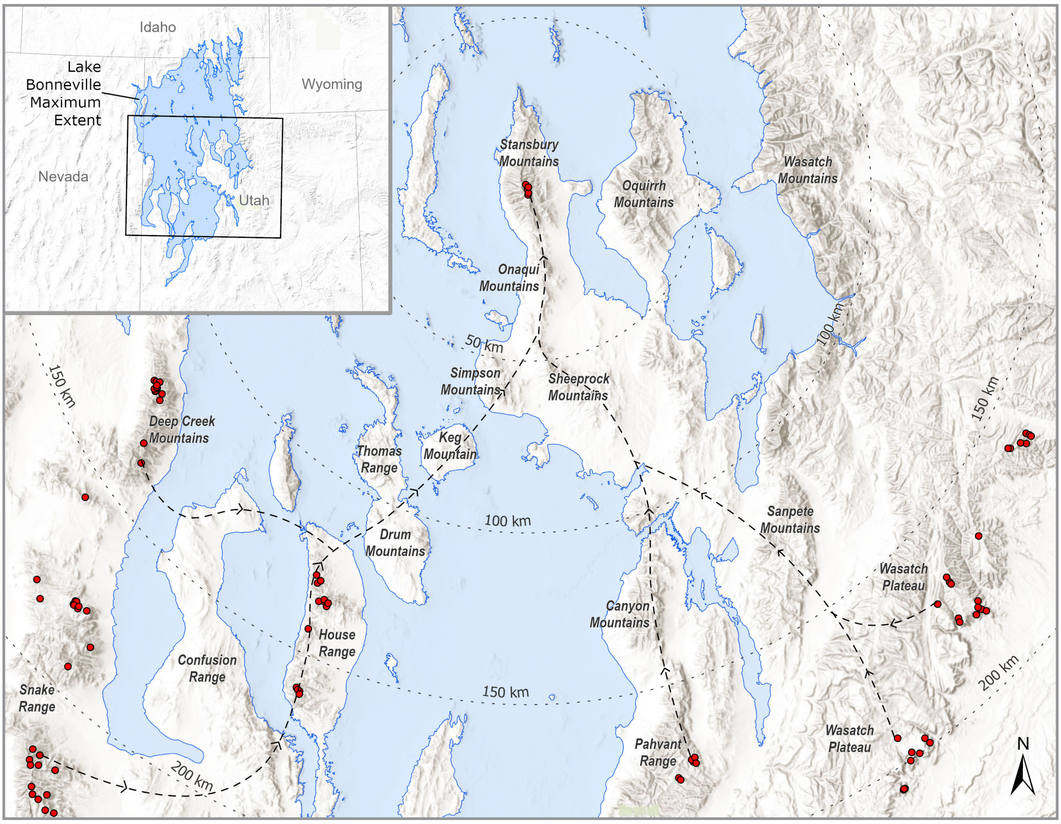

Fig. 4. Hypothetical bristlecone pine (*Pinus longaeva*) migration routes to the Stansbury Mountains, Utah (dashed lines with directional arrows). Known extant stands of bristlecone pine are displayed as red points (Burchfield et al. 2023). The maximum shoreline elevation of Lake Bonneville (1550 m MSL) is shown (Chen and Maloof 2017, Utah Automated Geographic Reference Center 2021). The central coordinate location for this image is 39.85450°N, 112.54335°W.

series of separate establishment events beginning at the vicinity of Swasey Mountain in the House Range (where the species has been present since at least 11,000 ^{14}C YBP), arriving at the Stansbury Mountains through a linear sequence of mountain ranges including the Thomas Range, Drum Mountains, Keg Mountain, Simpson Mountains, Sheeprock Mountains, and Onaqui Mountains (Fig. 4). The lowest elevation along this route is found at the Old River Bed (feature shown on 1:24,000 USGS topographic quadrangle) between Keg Mountain and the Simpson Mountains, at around 1386 m (USGS 2021a). During the maximum level of Lake Bonneville, this pass would have been submerged at a depth of approximately 160 m. Access between the House Range and the Stansbury Mountains would have been possible only by crossing 3 channels of the lake between the House Range and the Simpson Mountains (Fig. 4). Geology appears favorable for this pathway, with the substrate formations (or similar formations) mentioned in Table 1 repeated in the Drum Mountains, Sheeprock Mountains, and Onaqui Mountains (Croft 1956, Cohenour 1957, Hintze 1978, Dommer 1980), although bristlecone pine is apparently not extant in these ranges, or at least it has not been documented. Despite the favorable geological characteristics in these ranges, modern climatic conditions may not be suitable for bristlecone there. If bristlecone pine did establish there in a past climate, it has become extirpated under the modern climatic regime.

Bristlecone pine could also have conceivably reached the Stansbury Mountains via a southeastern approach, coming from either the Wasatch Plateau or Pahvant Range, where the species exists today (Fig. 4). This route minimizes dispersal across Lake Bonneville. To determine which of the 2 options (a southwest or southeast approach) is more likely, a comparison of genetic samples from bristlecone pine populations at multiple sites (the Stansbury Mountains, House Range, Wasatch Plateau, and Pahvant Range) would be required. However, taking weather patterns into account—prevailing winds move from west to east across the Great Basin—bristlecone migration via the southwest approach is more plausible under a wind dispersal scenario, as arrival at the Stansbury Mountains would likely be facilitated by prevailing weather patterns.

Potential for Bristlecone Pine Occurrence in Neighboring Ranges

The Stansbury Mountains have likely served as a refuge for bristlecone pine, as the elevation range of bristlecone pine occurrence has narrowed since the end of the Wisconsin Glacial Stage (Wells 1983). The Oquirrh Mountains, located 45 km east of the Stansbury Mountains, are another location in the northern Bonneville Basin where other small, isolated stands of bristlecone pine could be present. These stands could be of a similar origin to those found in the Stansbury Mountains. A bristlecone pine voucher was collected in 1964 from the Oquirrh Mountains by Col. Lynn Mitchell, a USFS forest ranger (Appendix 1), and was later redetermined to be limber pine without any stated evidence or justification (Thomsen 2011). Upon careful inspection of this voucher via digital photograph, we question the accuracy of this determination as limber pine and suggest that it is most likely a bristlecone pine based on morphological characteristics, including the lengthy needle retention that is characteristic of this species. Unfortunately, the ambiguous location description of the voucher (at an elevation of 2745 m in the Oquirrh Mountains) gives insufficient information to locate the vouchered tree without an extensive search of the range. The northern and central Oquirrh Mountains are composed of Paleozoic limestone (Tooker and Roberts 1962), and as such would offer suitable habitat for bristlecone pine. The Onaqui Mountains, south of the Stansbury Mountains, provide another possible location of undiscovered bristlecone pine stands. Although this range is lower in its maximum elevation (2750 m), the Onaqui Mountains lie along a possible migration route of bristlecone pine to the Stansbury Mountains during the Pleistocene or Pleistocene/Holocene transition (Fig. 4). A thorough search of both ranges is needed to determine whether additional populations might be present. Additionally, *Neotoma* midden records from these ranges from the Pleistocene/Holocene transition are needed to establish whether bristlecone pine was present in these areas during that period.

Future Work

This study represents only a preliminary analysis of this disjunct population of bristlecone pine. More data are needed to understand the paleobiogeography of this species in the Stansbury Mountains. Genetic characteristics of this population should be compared with the nearest populations in the Great Basin to the south and west, and the Utah high plateaus to the southeast, in order to more accurately characterize potential migration routes. Furthermore, the discovery of additional *Neotoma* middens nearby may shed further light on bristlecone pine distribution in the Stansbury Mountains and adjacent ranges during the Pleistocene and early Holocene. Finally, further work should be performed on producing a cross-dated climate chronology using living and remnant bristlecone pine wood from the Stansbury Mountains (Salzer et al. 2019). Remnant wood has been used in other locations to extend tree-ring reconstructions of climate and improve understanding of the longer-term establishment dynamics of forest stands (Lesser and Jackson 2012). The climate history contained within the Stansbury Mountains bristlecone pine population should also be of prominent interest to the human population living within the Wasatch Front region, as this information can provide invaluable insight into potential climate change patterns and influence of human-related activities on endemic forest stands.

ACKNOWLEDGMENTS

The authors wish to express our gratitude to the Charles Redd Center for Western Studies for funding our travel to the Stansbury Mountains. Additionally, we express deep appreciation to David Charlet for his proofreading assistance and to Theresa Whitesell for her insightful review of literature concerning seed dispersal by Clark's Nutcracker (*Nucifraga columbiana*).

LITERATURE CITED

APPLEQUIST, M.B. 1958. A simple pith locator for use with off-center increment cores. Journal of Forestry 56: 138–143.

BAILEY, D.K. 1970. Phytogeography and taxonomy of *Pinus* subsection Balfourianae. Annals of the Missouri Botanical Garden 57:210–249.

BEASLEY, R., AND J. KLEMMEDSON.1980. Ecological relationships of bristlecone pine. American Midland Naturalist 104:242–252.

BENKMAN, C.W. 1995. Wind dispersal capacity of pine seeds and the evolution of different seed dispersal modes in pines. Oikos 73:221–224.

BENSON, L.V., S.P. LUND, J.P. SMOOT, D.E. RHODE, R.J. SPENCER, K.L. VEROSUB, L.A. LOUDERBACK, C.A. JOHNSON, R.O. RYE, AND R.M. NEGRINI. 2011. The rise and fall of Lake Bonneville between 45 and 10.5 ka. Quaternary International 235:57–59.

BETANCOURT, J. 1984. Late Quaternary plant zonation and climate in southeastern Utah. Great Basin Naturalist 44:1–35.

BURCHFIELD, D.R., S.L. PETERSEN, S.G. KITCHEN, D.A. CHARLET, D.H. PAGE, C.O. MILLAR, O.W. DE GROFF, AND G.W. TAYLOR. 2023. Unpublished distribution data for Great Basin bristlecone pine (*Pinus longaeva*).

CALIFORNIA SOIL RESOURCE LAB. 2021. SoilWeb: an online soil survey browser. [Accessed 24 April 2021]. https://casoilresource.lawr.ucdavis.edu/gmap/

CHAMBERS, J., S.B. VANDER WALL, AND E. SCHUPP. 1999. Seed and seedling ecology of piñon and juniper species in the Pygmy Woodlands of western North America. Botanical Review 65:1–38.

CHARLET, D.A. 1996. Atlas of Nevada conifers: a phytogeographic reference. University of Nevada Press, Reno.

CHEN, C., AND A. MALOOF. 2017. Revisiting the deformed high shoreline of Lake Bonneville. Quaternary Science Reviews 159:169–189.

CLARK, J.S., C. FASTIE, G. HURTT, S.T. JACKSON, C. JOHNSON, G.A. KING, M. LEWIS, J. LYNCH, S. PACALA, C. PRENTICE, ET AL. 1998. Reid's paradox of rapid plant migration: dispersal theory and interpretation of paleoecological records. BioScience 48:13–24.

COHENOUR, R.E. 1957. Geology of the Sheeprock Mountains, Tooele and Juab Counties, Utah. Doctoral dissertation, University of Utah, Salt Lake City, UT.

CROFT, M.G. 1956. Geology of the northern Onaqui Mountains, Tooele County, Utah. Master's thesis, Brigham Young University, Provo, UT.

CURREY, D.R. 1965. An ancient bristlecone pine stand in eastern Nevada. Ecology 46:564–566.

DOMMER, M.L. 1980. The geology of the Drum Mountains: Millard and Juab Counties, Utah. Brigham Young University Geology Studies 27:55–72.

FRYER, J. 2004. "*Pinus longaeva*." U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory; [Accessed 29 December 2020]. www.fs.fed.us/database/feis/plants/tree/pinlon/all.html

HIEBERT, R., AND J. HAMRICK. 1984. An ecological study of bristlecone pine (*Pinus longaeva*) in Utah and eastern Nevada. Great Basin Naturalist 44:487–494.

HINTZE, L.F. 1978. Western Utah. Brigham Young University Geology Studies 25:11–24.

KAY, P., AND C. OVIATT. 1978. *Pinus longaeva* in the Stansbury Mountains, Utah. Great Basin Naturalist 38:49–50.

KIPFMUELLER, K.F., AND M.W. SALZER. 2010. Linear trend and climate response of five-needle pines in the western United States related to treeline proximity. Canadian Journal of Forest Research 40:134–142.

LAMARCHE, V. 1969. Environment in relation to age of bristlecone pines. Ecology 50:53–59.

LANNER, R.M. 1971. Conifers of the Bear Lake area and mountains south of the Great Salt Lake. Great Basin Naturalist 31:85–89.

LANNER, R.M. 1984. Trees of the Great Basin: a natural history. 1st edition. University of Nevada Press, Reno, NV.

LANNER, R.M. 1988. Dependence of Great Basin bristlecone pine on Clark's Nutcracker for regeneration at high elevations. Arctic and Alpine Research 20: 358–362.

LESSER, M.R., AND S.T. JACKSON. 2012. Making a stand: five centuries of population growth in colonizing populations of *Pinus ponderosa*. Ecology 93:1071–1081.

MADSEN, D.B., D. RHODE, D.K. GRAYSON, J.M. BROUGHTON, S.D. LIVINGSTON, J. HUNT, J. QUADE, D.N. SCHMITT, AND M.W. SHAVER III. 2001. Late Quaternary environmental change in the Bonneville Basin, western USA. Palaeogeography, Palaeoclimatology, Palaeoecology 167:243–271.

MCCAUGHEY, W.W., W.C. SCHMIDT, AND R.C. SHEARER. 1985. Seed-dispersal characteristics of conifers in the Inland Mountain West. Proceedings of the Conifer Tree Seed in the Inland Mountain West Symposium, Missoula, Montana, August 5–6, 1985.

OVIATT, C.G. 2015. Chronology of Lake Bonneville, 30,000 to 10,000 yr BP. Quaternary Science Reviews 110:166–171.

POWELL, J.A., AND N.E. ZIMMERMANN. 2004. Multiscale analysis of active seed dispersal contributes to resolving Reid's paradox. Ecology 85:490–506.

RHODE, D. 2016. Quaternary vegetation changes in the Bonneville Basin. Pages 420–441 *in* C.G. Oviatt and J.F. Shroder, editors, Lake Bonneville: a scientific update. Volume 20, Developments in Earth Surface Processes. Elsevier.

RHODE, D., AND D.B. MADSEN. 1995. Late Wisconsin/Early Holocene vegetation in the Bonneville Basin. Quaternary Research 44:246–256.

RIGBY, J.K. 1958. Geology of the Stansbury Mountains, eastern Tooele County, Utah. Guidebook to the Geology of Utah. 134 pp.

SALZER, M.W., E.R. LARSON, A.G. BUNN, AND M.K. HUGHES. 2014. Changing climate response in near-treeline bristlecone pine with elevation and aspect. Environmental Research Letters 9(11): p.114007.

SALZER, M.W., C.L. PEARSON, AND C.H. BAISAN. 2019. Dating the Methuselah Walk bristlecone pine floating chronologies. Tree-Ring Research 75:61–66.

SCHAMING, T.D. 2016. Clark's Nutcracker breeding season space use and foraging behavior. PLOS ONE 11(2): e0149116.

SCHULMAN, E. 1958. Bristlecone pine, oldest known living thing. National Geographic 113:355–372.

SPEER, J.H. 2010. Fundamentals of tree-ring research. University of Arizona Press, Tucson, AZ.

TAYE, A. 1983. Flora of the Stansbury Mountains, Utah. Great Basin Naturalist 43:619–646.

THOMPSON, R.S. 1990. The Quaternary vegetation and climate in the Great Basin. Pages 200–239 *in* J.L. Betancourt, T.R. Van Devender, and P.S. Martin, editors, Packrat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson, AZ. 469 pp.

THOMPSON, R.S. 1984. Late Pleistocene and Holocene environments in the Great Basin. Doctoral dissertation, University of Arizona, Tucson, AZ.

THOMSEN, C. 2011. Ancient souls: the search for Tooele County's oldest tree. Tooele County Magazine. http://tooeleonline.com/ancient-souls/#:~:text=The%20search%20for%20Tooele%20County's,Stansbury%20bristlecone%20tree%20in%201977.

TOOKER, E.W., AND R.J. ROBERTS. 1962. Comparison of Oquirrh Formation sections in the northern and central Oquirrh Mountains. U.S. Geological Survey Research, Professional Paper 450E: E32–E39.

[USGS] UNITED STATES GEOLOGICAL SURVEY. 2021a. 3D Elevation Program. [Accessed 4 January 2021]. https://www.usgs.gov/core-science-systems/ngp/3dep

[USGS] UNITED STATES GEOLOGICAL SURVEY. 2021b. USGS/NOAA North American Packrat Midden Database. [Accessed 24 April 2021]. https://geochange.er.usgs.gov/midden/

UTAH AUTOMATED GEOGRAPHIC REFERENCE CENTER. 2021. "Historic Lake Bonneville." [Accessed 25 April 2021]. https://gis.utah.gov/data/water/historic-lake-bonneville/

UTAH GEOLOGICAL SURVEY. 2021. Interactive Geologic Map Portal. [Accessed 4 January 2021]. https://geology.utah.gov/apps/intgeomap/

VAN WILGEN, B.W., AND W.R. SIEGFRIED. 1986. Seed dispersal properties of three pine species as a determinant of invasive potential. South African Journal of Botany 52:546–548.

WELLS, P.V. 1983. Paleobiogeography of montane islands in the Great Basin since the Last Glaciopluvial. Ecological Monographs 53:341–382.

WELSH, S.L., N.D. ATWOOD, S. GOODRICH, AND L.C. HIGGINS, EDITORS. 1993. A Utah flora. 2nd edition, revised. Brigham Young University, Provo, UT. 986 pp.

WRIGHT, R.D. AND H.A. MOONEY. 1965. Substrate-oriented distribution of bristlecone pine in the White Mountains of California. American Midland Naturalist 73:257–284.

Received 4 February 2022
Revised 5 August 2022
Accepted 29 September 2022
Published online 23 June 2023

Appendix follows on page 22.

APPENDIX 1. Voucher information for referenced plant collections.

Location	Mountain range	State	Latitude	Longitude	Elevation (m)	Collector	Herbarium/a	Year	Species
1.2 mi ESE of Deseret Peak (stand 4)	Stansbury Mountains	UT	40.4511	−112.6046	3063	De Groff 18	BRY	2020	*Juniperus communis*
1.2 mi ESE of Deseret Peak (stand 4)	Stansbury Mountains	UT	40.4511	−112.6046	3063	De Groff 19	BRY	2020	*Picea engelmanii*
1.2 mi ESE of Deseret Peak (stand 4)	Stansbury Mountains	UT	40.4511	−112.6046	3063	De Groff 17	BRY	2020	*Pinus flexilis*
1.0 mi E of Deseret Peak (stand 3)	Stansbury Mountains	UT	40.4604	−112.6075	3048	De Groff 28	BRY	2020	*Pinus flexilis*
Thomas Creek Canyon	Ruby Mountains	NV	40.6426	−115.4058	2743	Holmgren 6273	BRY	1972	*Pinus longaeva*
Spruce Mountain	Pequop Mountains	NV	40.5509	−114.8270	3109	Williams 81-84-1	BRY	1981	*Pinus longaeva*
Burger Peak	Pine Valley Mountains	UT	37.3224	−113.5030	3100	Higgins 14398	BRY	1984	*Pinus longaeva*
Right Fork Lake Canyon	West Tavaputs Plateau	UT	39.9921	−110.7377	2365	Goodrich 25877	BRY	1998	*Pinus longaeva*
Ridge between Mill Fork and Dry Lake Fork	Stansbury Mountains	UT	40.4622	−112.6166	2957	Kay s.n.	UT	1977	*Pinus longaeva*
White Pine Fork drainage	Stansbury Mountains	UT	40.4602	−112.6078	3018	Taye 589	BRY NY	1979	*Pinus longaeva*
White Pine Canyon	Stansbury Mountains	UT	40.4602	−112.6078	2987	Langer s.n.	BRY	1994	*Pinus longaeva*
Goshute Canyon	Deep Creek Mountains	UT	39.9274	−113.8429	2743–3200	Warburton s.n.	BRY	1974	*Pinus longaeva*
1.4 mi S of Tatow Knob	House Range	UT	39.4331	−113.3400	2537	De Groff 346	BRY	2020	*Pinus longaeva*
1.2 mi ESE of Deseret Peak (stand 4)	Stansbury Mountains	UT	40.4511	−112.6046	3063	De Groff 16	BRY	2020	*Pinus longaeva*
1.0 mi E of Deseret Peak (stand 3)	Stansbury Mountains	UT	40.4604	−112.6075	3048	De Groff 26	BRY	2020	*Pinus longaeva*
Oquirrh Mountains, elevation 9000 ft.	Oquirrh Mountains	UT	—	—	2743	Mitchell s.n.	UT	1964	*Pinus longaeva*
Potosi Mountain	Spring Mountains	NV	35.9691	−115.5030	2499	Bailey 75-113	COLO	1975	*Pinus longaeva*
1.0 mi E of Deseret Peak (stand 3)	Stansbury Mountains	UT	40.4604	−112.6075	3048	De Groff 29	BRY	2020	*Pseudotsuga menziesii*