SPECIES: Pinus longaeva

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INTRODUCTORY

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Wheeler Peak, NV. Photo by Glenn and Martha Vargas. © 2004. California Academy of Sciences.

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Howard, Janet L. 2004. Pinus longaeva. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2010, June 21].

FEIS ABBREVIATION:
PINLON

SYNONYMS:

Pinus aristata Engelm. var. *longaeva* D.K. Bailey [63]

NRCS PLANT CODE [132]:
PILO

COMMON NAMES:
Great Basin bristlecone pine
intermountain bristlecone pine
western bristlecone pine

TAXONOMY:
The scientific name of Great Basin bristlecone pine is *Pinus longaeva* D.K. Bailey (Pinaceae) [9,44,62,136].

Great Basin bristlecone pine, Rocky Mountain bristlecone pine (*P. aristata*), and foxtail pine (*P. balfouriana*) share a common ancestor [111,142]. Taxa within the bristlecone-foxtail pine complex (*Pinus*, subgenus *Strobus*, section *Parrya* Mayr, subsection *Balfourianae* Englm.) are distinguished by growth form, bark, and differences in chemical composition [9,30,98,105]. Bristlecone and foxtail pines readily produce fertile hybrids in the laboratory [122,142]. Disjunct distributions, and possibly other factors, prevent natural hybridization among the 3 species. Great Basin bristlecone and southern foxtail pine (*P. b.* ssp. *austrina*) populations seem geographically close enough for limited pollen dispersal (see General Distribution); yet to date (2004), Great Basin bristlecone × southern foxtail pine hybrids have not been found in the field [9,86].

LIFE FORM:
Tree

FEDERAL LEGAL STATUS:
No special status

OTHER STATUS:
The California Native Plant Society (CNPS) places Great Basin bristlecone pine on their watch list (CNPS List 4) as a plant of limited distribution in California [113]. The World Conservation Union's Species Survival Commission (IUCB-SSC) lists Great Basin bristlecone pine as vulnerable, with this classification needing updating [60].

DISTRIBUTION AND OCCURRENCE

SPECIES: Pinus longaeva

- GENERAL DISTRIBUTION
- ECOSYSTEMS
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- KUCHLER PLANT ASSOCIATIONS
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GENERAL DISTRIBUTION:
Great Basin bristlecone pine occurs in a relatively narrow latitudinal range in California, Nevada, and Utah [86,94]. In California it occurs on the summits of the Panamint, Inyo, and White mountains of Mono and Inyo counties [53]. In Nevada it has scattered occurrences on high mountain ranges from the White Mountains in Esmeralda County; north to the southern Ruby Mountains of south-central Elko County; south to the Spring Mountains of west-central Clark County; and east to the Ruby Mountains and Snake Range of White Pine County [31,63,94]. In western Utah Great Basin

bristlecone pine occurs on the western edge of the Colorado Plateau from the Confusion Range of Millard County; north to the Uinta Mountains of Summit, Wasatch, and Duchesne counties; south to the Pine Valley Mountains of Washington County and northern Kane County; and east to the Wasatch Plateau of Emery County [94,136]. The U.S. Geological Survey provides a distributional map of Great Basin bristlecone and Rocky Mountain pines.

The ranges of Great Basin bristlecone, Rocky Mountain bristlecone, and foxtail pines do not overlap. The Colorado-Green River drainage has separated the 2 bristlecone pine species for millennia. There is a 160-mile (260-km) gap between the 2 bristlecone species at their closest point in Utah and Colorado [52]. Inyo Valley, located between the southern Sierra Nevada and the White Mountains, creates a 20-mile-wide (32-km) gap between Great Basin bristlecone and southern foxtail pine populations [32].

ECOSYSTEMS [46]:
FRES20 Douglas-fir
FRES21 Ponderosa pine
FRES23 Fir-spruce

STATES/PROVINCES: (key to state/province abbreviations)
UNITED STATES
CA NV UT

BLM PHYSIOGRAPHIC REGIONS [18]:
4 Sierra Mountains
6 Upper Basin and Range
7 Lower Basin and Range
9 Middle Rocky Mountains
12 Colorado Plateau

KUCHLER [68] PLANT ASSOCIATIONS:
K011 Western ponderosa forest
K012 Douglas-fir forest
K018 Pine-Douglas-fir forest
K020 Spruce-fir-Douglas-fir forest
K021 Southwestern spruce-fir forest
K022 Great Basin pine forest

SAF COVER TYPES [38]:
206 Engelmann spruce-subalpine fir
208 Whitebark pine
209 Bristlecone pine
210 Interior Douglas-fir
211 White fir
219 Limber pine
237 Interior ponderosa pine

SRM (RANGELAND) COVER TYPES [118]:
None

HABITAT TYPES AND PLANT COMMUNITIES:
Great Basin bristlecone pine occurs in montane, subalpine, and timberline communities. Throughout its range, Great Basin bristlecone pine grows in pure stands in timberline and upper subalpine zones and codominates or associates with limber pine (*Pinus flexilis*) at lower elevations [31,133]. Quaking aspen is a consistent associate on mesic sites [82]. Singleleaf pinyon (*Pinus monophylla*) often associates with Great Basin bristlecone pine near Great Basin bristlecone pine's lower elevational limits [52,67]. Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Rocky Mountain white fir (*A. concolor* var. *concolor*) and Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) are

common Great Basin bristlecone pine associates in montane forests of eastern Nevada and Utah [13,52,56,63,86]. Great Basin bristlecone pine communities are surrounded by sagebrush (*Artemisia* spp.) and salt-desert communities at low elevations. Cushion plant communities and bare rock occur above Great Basin bristlecone pine communities[13,56].

California/Nevada White Mountains: Limber pine codominates with Great Basin bristlecone pine except at Great Basin bristlecone pine's highest elevational limits [133]. Shrubs are infrequent in Great Basin bristlecone-limber pine communities in the White Mountains. Shrub associates include big sagebrush (*A. tridentata*), low sagebrush (*A. arbuscula*), curlleaf mountain-mahogany (*Cercocarpus ledifolius*), desert sweet (*Chamaebatiaria millefolium*), wax currant (*Ribes cereum*), gooseberry currant (*R. montigenum*), and green rabbitbrush (*Chrysothamnus viscidiflorus*) [52,59,126,137]. Prairie Junegrass (*Koeleria macrantha*), bottlebrush squirreltail (*Elymus elymoides*), king's sandwort (*Arenaria kingii*), and granite prickly phlox (*Leptodactylon pungens*) are commonly associated herbs [126]. Wright and Mooney [137] provide extensive lists of herbaceous associates in Great Basin bristlecone pine communities of the White Mountains. Great Basin bristlecone pine communities usually merge with low sagebrush or limber pine communities at about 9,500 feet (2,900 m) elevation, but sometimes merge with singleleaf pinyon-western juniper (*Juniperus occidentalis*) woodlands, particularly on Nevada's eastern slope [59,126].

Nevada: Elsewhere in Great Basin bristlecone-limber pine forests of Nevada, limber pine tends to dominate in the north, while Great Basin bristlecone pine gains dominance in southern Nevada [82,92]. Great Basin bristlecone pine-limber pine forests are often extensive in northern Nevada [31]. Whitebark pine (*Pinus albicaulis*) associates with Great Basin bristlecone pine in the northern Ruby Mountains; it is the only place where the 3 *Strobus* species (Great Basin bristlecone, limber, and whitebark pine) co-occur [52,81]. Understories are sparse in Great Basin bristlecone pine communities of Nevada. In an inventory of Great Basin bristlecone pine-limber pine community on the Snake Range of east-central Nevada, common juniper (*J. communis*) and singlehead goldenbush (*Ericameria suffruiticosa*) were the most common shrubs; wax currant and gooseberry currant were also present. Although sparse, there was a diverse array of graminoids and forbs. Mutton grass (*Poa fendleriana*), spike trisetum (*Trisetum spicatum*), prickly sandwort (*Arenaria aculeta*), tufted fleabane (*Erigeron caespitosus*), and southern monardella (*Monardella australis*) were among the most common herbs. Overall plant diversity in Great Basin bristlecone pine communities was greater on limestone-derived soils than on quartzite-derived soils [13].

In southern Nevada, Great Basin bristlecone pine-limber pine communities occur just below treeline on the Spring Mountains west of Las Vegas. Associated shrubs and subshrubs are gooseberry currant, broom snakeweed (*Gutierrezia sarothrae*), and elegant cinquefoil (*Potentilla concinna* var. *proxima*). Associated herbs include alpine fescue (*Festuca brachyphylla*), bottlebrush squirreltail, Sandberg bluegrass (*Poa secunda*), Clokey's fleabane (*E. clokeyi)*, Hitchcock's bladderpod (*Lesquerella hitchcockii)*, and Charleston Mountain pussytoes (*Antennaria soliceps*). Charleston Mountain pussytoes is a rare endemic [14].

Utah: Great Basin bristlecone pine-limber pine communities form a mosaic with several other communities in Utah. Except at high elevations, Great Basin bristlecone pine-limber pine is usually a topoedaphic climax community within the Engelmann spruce and interior Douglas-fir zones. Great Basin bristlecone pine-limber pine communities in northern Utah are found above and form stringers into Engelmann spruce-subalpine fir forest and mountain meadow communities. Likewise, Engelmann spruce, subalpine fir, blue spruce (*Picea pungens*), Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*), and white fir may finger into higher-elevation Great Basin bristlecone pine-limber pine communities [140]. Silver sagebrush (*Artemisia cana*), heartleaf arnica (*Arnica cordifolia*), slender wheatgrass (*Elymus trachycaulus*), and Thurber fescue (*F. thurberi*) are common understory associates in Great Basin bristlecone pine-limber pine communities. Fire-disturbed areas are usually occupied by Rocky Mountain lodgepole pine or quaking aspen [12].

Pure Great Basin bristlecone pine stands at high elevations may be species-poor. For example, a Great Basin bristlecone pine community located between 8,900 and 10,000 feet (2,700 and 3,200 m) elevation in Cedar Breaks National Monument is composed of monospecific stands of Great Basin bristlecone pine and a dwarfed paintbrush (*Castilleja* spp.). The understory is otherwise bare [54].Great Basin bristlecone pine-limber pine communities on the plateaus of southern Utah typically have a diverse understory. Common shrub associates include true mountain-mahogany (*Cercocarpus montanus*), curlleaf mountain-mahogany, singlehead goldenbush, wax currant, and Wood's rose (*Rosa woodsii*). Common herbaceous associates include Ross' sedge (*Carex rossii*), slender wheatgrass, Salina wildrye (*Leymus salinus*), western yarrow (*Achillea millefolium*), and timber milkvetch (*Astragalus miser*) [21,140].

In southern Utah, Great Basin bristlecone pine occurs in diverse, mixed-conifer forests at low elevations [54,83]. In the

Bryce Canyon National Park and surrounding areas of Dixie National Forest, Great Basin bristlecone pine occurs in mixed forests also composed of blue spruce, Engelmann spruce, limber pine, interior ponderosa pine (*P. ponderosa* var. *scopulorum*), Colorado pinyon (*P. edulis*), Rocky Mountain Douglas-fir, Rocky Mountain juniper (*J. scopulorum*), Utah juniper (*J. osteosperma*), and Gambel oak (*Quercus gambelii*) [82]. On the Wah Wah Mountain Research Natural Area of southern Utah, Great Basin bristlecone pine occurs in an open, mixed-conifer forest. Interior ponderosa pine dominates the overstory; white fir and Great Basin bristlecone pine form a subcanopy [67]. On some sites in southern Utah, Great Basin bristlecone pine-limber pine forests merge with lower-elevation Rocky Mountain juniper, curlleaf mountain-mahogany, or quaking aspen woodland communities [140].

Vegetation and habitat typings describing Great Basin bristlecone pine communities include:

CA: [59,107,126,127,133]
NV: [92,97]
UT: [2,140]

BOTANICAL AND ECOLOGICAL CHARACTERISTICS

SPECIES: Pinus longaeva

- GENERAL BOTANICAL CHARACTERISTICS
- RAUNKIAER LIFE FORM
- REGENERATION PROCESSES
- SITE CHARACTERISTICS
- SUCCESSIONAL STATUS
- SEASONAL DEVELOPMENT

GENERAL BOTANICAL CHARACTERISTICS:
Morphology: Great Basin bristlecone pine is a native conifer of highly variable growth form. Low-elevation trees are typically tall and upright. At high elevations Great Basin bristlecone pine becomes twisted and contorted. The type locality for Great Basin bristlecone pine is Wheeler Peak, Great Basin National Park, in the Snake Range of eastern Nevada [63]. Great Basin bristlecone pine is rarely shrubby. It does not form timberline krummholz in the White Mountains [77,81,110]; however, some high-elevation sites in eastern Nevada and Utah support Great Basin bristlecone pine krummholz [77]. Trees are typically 30 feet (9.1 m) or less in height. Trees on mesic, low-elevation sites may reach 60 feet (18 m) in height and 5 feet (1.5 m) in diameter [53,63,136].

Great Basin bristlecone pine may have single or multiple trunks [83,87]. Unlike foxtail pine, which has very thick bark, Great Basin bristlecone pine bark is thin [141]. Great Basin bristlecone pines on harsh sites have a high proportion of dead trunk- and branchwood. Old trunks and exposed roots have thick, vertical ribbons of dead wood. Between the dead ribbonwood, thin strips of living root and stem tissue support living branches [84]. In younger trees, branches are long and pendulous, forming an irregular crown [124]. The *Balfourianae* complex is unique among pines in that about half of their branches originate from within the needle fascicles [26,35]. Great Basin bristlecone pine needles are 1 to 1.6 inches (2.5-4 cm) long, with 5 needles per fascicle. Needles may be retained for 35 or more years [29,36,141]. Staminate cones are 0.4 to 0.5 inch (10-12 mm) long. The dehiscent female cones are 2 to 5.5 inches (5-14 cm) long and armed with an incurved, bristly prickle. Seeds are 6 to 8 mm in length; the seed wing is slightly longer than the seed [13,63,84,85,86,110,136].

The Great Basin bristlecone pine's root system is mostly composed of highly branched, shallow roots [90]. A few large, branching roots provide structural support. In old age, structural roots may buttress when denudation exposes large lateral roots [71]. A soil trench dug in the White Mountains revealed root profiles of Great Basin bristlecone pine extended 20 inches (51 cm) below ground, where an impervious carbonate layer prevented further root penetration. Most roots were 0.5 to 2 inches (1.3-5.1 cm) in diameter and 2 to 7 inches (5-18 cm) below the soil surface [45]. Bidartondo and others [19] identified some of the ectomycorrhizal associates of Great Basin bristlecone pines in the White Mountains.

Physiology: Great Basin bristlecone pine is highly drought tolerant [13,124]. Both its morphology and physiology confer drought tolerance. Branched, shallow roots maximize water absorption. Waxy needles and thick needle cuticles also aid in water retention [29]. Old needles remain functional: 35-year-old needles of Great Basin bristlecone pines in the White Mountains retained their ability to regulate water loss and photosynthesize [29]. On limestone soils of Wheeler Peak, Great Basin bristlecone pine maintained lower leaf water potentials than associated limber pine and curlleaf mountain-mahogany. Favorable leaf water potential probably lowers internal water stress, enabling Great Basin bristlecone pine to dominate on harsh timberline sites [16]. Mooney and others [106] compared metabolic functions (transpiration, net photosynthesis, and dark respiration) of big sagebrush and Great Basin bristlecone pine in the White Mountains. They found Great Basin bristlecone pine was less sensitive to changing weather conditions than big sagebrush, enduring June snows and extended summer drought without showing large changes in rates of photosynthesis and transpiration. Big sagebrush showed marked changes in metabolic response during the growing season. It photosynthesized more efficiently at higher temperature than Great Basin bristlecone pine, and decreased growth and water losses during drought. The authors concluded that Great Basin bristlecone pine was better adapted to colder, high-elevation sites, while big sagebrush was better adapted to the warmer temperatures typical of lower elevations.

Ancient Great Basin bristlecone pine have difficulty maintaining a favorable carbon balance [65]. Low amounts of photosynthesizing tissue reduce the ability of old Great Basin bristlecone pines to acquire carbohydrates. Unlike other high-elevation pines, Great Basin bristlecone pine has high rates of winter respiration. Schultze and others [117] estimated that Great Basin bristlecone pine uses at least half of its annual carbohydrate accumulation in a normal winter.

Stand structure: Great Basin bristlecone pine communities are very open at high elevations, and understories are sparse. At low elevations, Great Basin bristlecone pine occurs in denser, mixed forests. In the White Mountains, Bidartondo and others [19] described Great Basin bristlecone pines in the Ancient Bristlecone Pine Botanical Area as "widely spaced, surrounded by their own litter," and "separated from neighboring trees by little or no vegetation amidst the gravel and bare rock." Downed wood may persist for thousands of years on high-elevation sites [76]. Stand density is usually proportional to site severity, with trees on the harshest sites showing the most open canopies [82]. Bare [13] documented the following structure on sites in the Snake Range:

Location	Understory plant cover (%)	Mean tree basal area (square feet/acre)				Tree spacing (milacres/tree)
		Bristlecone pine	Engelmann spruce	Limber pine	Total tree cover	
Wheeler Peak (n=6)	3.52	56	50	28	134	12.1
Bastian Peak (n=2)	10.51	67	17	28	112	21.56

Hiebert and Hamrick [54] found east-west clinal variation in Great Basin bristlecone pine stand structure. Eastern populations tended toward greater conifer species richness. To the west, stands became less diverse but had a corresponding increase in altitudinal range. Stand boundaries of Great Basin bristlecone pine and other conifer types became less abrupt to the west, and habitats were less restricted to poor soils. From east to west, Great Basin bristlecone pine stand densities (trees/ha) and approximate number of individuals on 3 sites in Utah and Nevada and were:

Altitudinal zone*	Cedar Breaks (CB), UT	Wheeler Peak (WP), NV	Egan Range (ER), NV
upper	138	57	51
middle	138	99	94
lower	224	75	102
Population mean	163	72	77
Number of individuals	17,000	8,500	14,000

*Upper zones are 3,200 m for CB and ER, 3,500 m for WP; mid-zones are 2,950 m for CB and ER, 3,375 m for WP; lower zones are 2,700 m for CB and ER, 3,250 m for WP.

Stand structure is affected by aspect. Trees on northern slopes tend to be very open, with twisted, gnarled forms, while trees on south aspects are more upright, and tend to form denser stands [15,90]. Bryson and others [23] found that Great Basin bristlecone pines in the Schulman Grove of the White Mountains occurred in pure stands on north-facing slopes. South-facing slopes were occupied mostly by limber pines, with few or no Great Basin bristlecone pines.

Age structure: Great Basin bristlecone pine stands are usually multi-aged [21]. Ancient trees generally compose the smallest age class and seedlings the largest, but relative proportion of the seedling age class may vary greatly. In a White Mountain study, seedlings comprised 27%-71% of individuals within a population [134]. Age class structure may change somewhat with elevation, with high-elevation sites having proportionately more old trees. Hiebert and Hamrick [54] found the lower and mid-zone populations at the 3 sites in the table above were strongly skewed toward younger age classes (<875 years). Populations in the upper zone still had a preponderance of individuals in the younger age classes, but there were more trees older than 875 compared to mid- and low-elevation sites. Aspect may influence stand age classes. In the White Mountains, Great Basin bristlecone pines on north-facing slopes tended to be older (mean age was 2,000 years) than Great Basin bristlecone pines on south-facing aspects (mean age was 1,000 years) [23].

Great Basin bristlecone pine has the longest life span of any nonclonal species in the world. The oldest known living Great Basin bristlecone pine had 4,862 countable annual rings when it was cut on Wheeler Peak in 1974 [33,79,104]. A few downed trees in the White Mountains lived over 5,000 years before they fell [41,42,76,77]. Schulman [115] suggested that longevity of bristlecone pines is directly related to site adversity. A high proportion of dead:live wood reduces respiration and water loss, extending life span [65,137]. Wright and Mooney [137] noted a relationship between tree age and proportion of dead stemwood, hypothesizing that the great ages attained by some bristlecone pines are related to their capacity to survive partial die-back while maintaining a constant ratio of photosynthesizing and nonphotosynthesizing live tissue.

RAUNKIAER [109] LIFE FORM:
Phanerophyte

REGENERATION PROCESSES:
Great Basin bristlecone pine reproduces from seed [82]. There is no evidence of vegetative reproduction [87]. Regeneration requirements for successful Great Basin bristlecone pine establishment are rarely met [20,65], but as an extremely long-lived species, Great Basin bristlecone pine has centuries to millennia to wait for favorable regeneration conditions. Few studies have examined long-term Great Basin bristlecone pine population stability. For the 3 sites listed in the table above, Hiebert and Hamrick [54] found the Cedar Breaks and Egan Range populations were growing, while the Wheeler Peak population was stable.

Breeding system: Great Basin bristlecone pine is monoecious. Its mating system is predominantly outcrossing [55,89]. Great Basin bristlecone pines on desert "sky islands" are susceptible to inbreeding due to poor pollen and seed dispersal [87].

Few studies have been conducted on Great Basin bristlecone pine population genetics. In the White Mountains, Johnson and Critchfield [61] noted a high degree of polymorphism in pollen and female cone characteristics of trees in the Sherman Grove. Hiebert and Hamrick [55] conducted allozyme tests on 5 Great Basin bristlecone pine populations across eastern Nevada and western Utah. They found normal to high levels of genetic variation in Great Basin bristlecone pine compared to other pine species. Most variation occurred within, rather than among, populations. Polymorphic loci and number of alleles per loci were average for pines; level of heterozygosity was above average. The authors attributed high levels of heterozygosity to wind pollination, Great Basin bristlecone pine's multiple-age class structure, and its wide geographic distribution in the Pleistocene.

Populations in the White Mountains may be less genetically diverse than eastern Great Basin bristlecone pine populations. In the Ancient Bristlecone Pine Botanical Area, allozyme and DNA tests showed slightly lower than average genetic variation for Great Basin bristlecone pine compared to most pine species. Genetic variation at the population level was about average for pine species ([89] and references therein).

Pollination: Great Basin bristlecone pine is pollinated by wind [86]. Germinability of Great Basin bristlecone pine pollen may be low. In the laboratory, Conner and Lanner [29] studied germination of pollen collected on high-elevation sites (9,300 feet (2,835 m)) in the White Mountains and lower-elevation sites (8,400 feet (2,560 m)) on the Dixie National Forest. Germinability ranged from 0%-66% (μ=13.4) and did not differ by either site (r^2=0.061) or tree age (r^2=0.085) factors.

Seed production: Great Basin bristlecone pine does not mast, but is a steady cone and seed producer [83]. For example, Great Basin bristlecone pines on the Snake Range produced a cone crop every year during 1982-1986 (personal communication from Conner 1987, in [83]). About 90% of Great Basin bristlecone pine cones have a dark purple cast, which probably helps warm the cones and hastens seed ripening. Cones that lack the anthocyanin pigment and stay green may not develop their seed [86]. Seed production continues well into old age. On Wheeler Peak, trees over 3,000 years old produce viable seed. In the White Mountains, the Alpha tree continues to produces viable seed at 4,300+ years of age [82]. Total number of seeds produced decreases with tree age, however. As Great Basin bristlecone pines age, their total number of living branches decreases [29].

Seed dispersal: Seed is dispersed by wind [84].

It has been suggested, but not proven, that Clark's nutcrackers disperse Great Basin bristlecone pine seeds [83,85,87]. If it occurs, such a method of seed dispersal has important implications for Great bristlecone pine's genetic structure and ability to establish on disturbed sites such as burns. Clark's nutcrackers bury seeds in caches. A growth form of clumped trees that fuse at the stem is characteristic of establishment resulting from Clark's nutcracker seed dispersal [83]. Great Basin bristlecone pine clumps are common at high elevations of the White Mountains [85]. For example, the Patriarch, a 36-foot- (11-m) diameter specimen that may be the world's oldest living tree, is composed of 7 to 9 stems [87]. In a study across Great Basin bristlecone pine's range, Lanner [83] noted a range of 13% occurrence of mutistemmed clumps at an 8,300-ft (2,530-m) site in Great Basin National Park to 80% clumping at a 9,810-ft (2,990-m) site in Cedar Breaks National Monument.

When an individual tree has multiple stems, genetic marker tests show that each stem is genetically identical. If several individual trees fuse at the base as a result of close planting by Clark's nutcrackers, forming a multi-stemmed tree clump, individual stems retain their separate genetic identities. Genetic marker tests can show if fused stems are genetically identical or different [129]. To date (2004), only 1 genetic marker study has been conducted on Great Basin bristlecone pine. This Ancient Bristlecone Pine Botanical Area study did not support the bird-dispersal hypothesis; instead, it showed that most Great Basin bristlecone pine clumps were composed of a single tree with multiple stems. Of 204 tree clumps tested, only 6 were composed of genetically different stems. Stems of the Patriarch were genetically identical, indicating that it is a single tree [89]. However, a single study does not rule out the possibility of Clark's nutcracker dispersal of Great Basin bristlecone pine seeds. Torick [130] observed Clark's nutcrackers caching Rocky Mountain bristlecone pine seed in Colorado. Further studies are required across Great Basin bristlecone pine's range to determine the influence, if any, of Clark's nutcrackers on Great Basin bristlecone pine's mating system and seedling establishment.

Seed banking: No information is available on this topic.

Germination: Seed is immediately germinable [86]. Few seed trials on Great Basin bristlecone pine seed viability have been published. Germination trials of Great Basin bristlecone pine seeds in the U.S. Forest Service Nursery in Placerville, California, have shown 90% germinability [19]. Conner and Lanner [29] found a wide range of germination rates in Great Basin bristlecone pine seeds collected from the Methuselah Grove of the White Mountains and from a site on Mammoth Creek on the Dixie National Forest. Mean germination rates in the laboratory were 57% (range, 20%-86%) and 51% (range, 29%-79%) on the Methuselah and Mammoth Creek sites, respectively. Seed germinability was not significantly correlated with tree age (r^2=0.087); at ~4,713 years of age, the Methuselah tree produced the most viable seeds (μ=85% germination) in the study.

Seedling establishment: Seedling establishment is a rare event for Great Basin bristlecone pine. Since Great Basin bristlecone pine primarily grows on dry, nutrient-poor soils, conditions favorable to Great Basin bristlecone pine germination and growth are infrequent [20,65].

Wild burro browsing and trampling can damage or kill Great Basin bristlecone pine seedlings [96].

Growth: Growth rates of Great Basin bristlecone pine on harsh sites are very slow. Wright [138] reported heights of 5.9 inches (15 cm) for 40-year-old "seedlings" in the White Mountains. Diameter growth rate of Great Basin bristlecone pines on Wheeler Peak, Nevada, is estimated at 1 inch (2.5 cm) per century [63]. Mature trees on harsh sites often cease height growth after reaching 15 to 30 feet (4.6-9.1 m); however, trunks continue to expand throughout life [82]. Factors slowing growth include high elevation, extreme temperatures, dry, nutrient-poor soils, strong winds, south and west aspects, and high amounts of solar radiation [15]. Great Basin bristlecone pine shows rapid growth on good sites [56]. Bare [13] reported relatively rapid growth and good form (upright and conical) of Great Basin bristlecone pine on deep limestone soils near the gently sloping summit of Bastian Peak, east-central Nevada. East- and north-facing slopes supported best growth and highest Great Basin bristlecone pine densities. In the White Mountains, stem diameter gain per year (averaged over 3 growing seasons) was greatest on low-elevation sites with sandstone or granitic soils (μ=0.53 mm/year) and least on high-elevation, north-facing sites on dolomite soils (μ=0.39 mm/year) [45].

Great age does not necessarily slow growth. Conner and Lanner [27] found that on sites in the Dixie National Forest and White Mountains, stem shoots from old trees did not show reduced growth compared to shoots of younger trees. Tree age varied from 14 to 2,052 years in southern Utah sites and from 824 to 4,712 years in the White Mountains. Variations in shoot length, stem unit production, and stem unit length were not significant when regressed with tree age (r^2=0.010-0.237); neither were xylem and phloem production (r^2=0.001-0.147) [28].

Senescence and death: Great Basin bristlecone pine growing on high-elevation sites age very slowly. Lanner and Conner [79] tested several parameters of plant aging (vascular system function, photosynthetic balance, and mutation loads in pollen, seed, and seedling progeny) in Great Basin bristlecone pines on the Inyo and Dixie National Forests. Tree ages ranged from 23 to 4,713 years. None of the parameters had a statistically significant relationship to tree age. The authors concluded "the concept of senescence does not apply to these trees."

High-elevation, arid environments are poor habitats for insects and root-decaying fungi, so Great Basin bristlecone pines in those environments succumb to disease very slowly. Most high-elevation Great Basin bristlecone pines eventually die from root rot decay or soil erosion, which exposes and kills roots [86]. Localized fire may kill a few trees (see Immediate Fire Effect on Plant). Lower-elevation Great Basin bristlecone pines succumb more quickly to various agents of mortality (see Other Management Considerations).

Barriers to regeneration: Great Basin bristlecone pine populations are sensitive to fluctuations climate [11]. Hiebert [56] found low seedling establishment of eastern Nevada populations during cool, dry periods approximately 900 and 2,500-3,000 BP. LaMarche [69] noted poor Great Basin bristlecone pine seedling establishment during the Little Ice Age. Effects of current climatic conditions on Great Basin bristlecone pine regeneration are uncertain. On dolomite soils in the White Mountains, seedlings are establishing beyond both the current upper and lower elevational limits of mature Great Basin bristlecone pines. Regeneration is sparse, and within current elevational limits of mature trees, on shale soils [134]. However, Lanner [81] cautions that climate warming is hindering Great Basin bristlecone pine regeneration on sites in the interior Great Basin.

SITE CHARACTERISTICS:
Great Basin bristlecone pine has low requirements for moisture and nutrients but high requirements for light [13,54]. It grows on very dry, mid- to high-elevation, exposed slopes and ridges [82]. Great Basin bristlecone pine experiences desiccating, often gale-force winds [13,82]. Slopes are typically steep on Great Basin bristlecone pine sites. Percent slope ranged from 10% to 50% on 8 Great Basin bristlecone pine sites on the Snake Range [13]. In the White Mountains, Bryson and others [23] found slopes of 30 degrees or more were most likely to be forested with Great Basin and limber pines, while more gentle slopes were usually occupied by shrubs and herbs. Great Basin bristlecone pine is most common on south and west aspects, although it can occur on any aspect with well-drained, droughty soil [13,21,52].

Soils: Great Basin bristlecone pine is most common on thin, rocky substrates. Soils are usually derived from limestone or dolomite [53,63,82,136], although some populations grow on sandstone or quarzite [86]. In the White Mountains, Great Basin bristlecone pine communities occur on dolomite soils with a rock content of 50% or more. Dolomite soils are alkaline, high in calcium and magnesium, and low in phosphorus. Those factors tend to exclude other plant species. On the other hand, dolomite soils are light-colored, reflect more light, are cooler, and have a higher total water storage capacity (~20%) than surrounding soils, and those factors favor Great Basin bristlecone pine establishment [137]. For

example, limber pine codominates or associates with Great Basin bristlecone pine on dolomite soils in the White Mountains, but becomes the dominant species on granitic soils [45]. Some Great Basin bristlecone pine populations on Wheeler Peak occur on quartzite and monzonite soils, although most are on limestone [13,55,56,82]. Bare [13] found that on Wheeler Peak, Great Basin bristlecone pine dominated on high-elevation, limestone-derived soils, but was unable to compete with curlleaf mountain-mahogany on high-elevation monzonite-derived soils. On the Colorado Plateau of western Utah, Great Basin bristlecone pine grows on limestone and, more infrequently, glacial till substrates that are "extremely low" in available nutrients. Except at highest elevations, the more nutrient-rich, mesic soils are occupied by Engelmann spruce [55]. Isolated Great Basin bristlecone pines may occur on open mesic sites throughout the species' range [54,137].

Elevation: Across its range, Great Basin bristlecone pine occurs from 7,200 to 12,000 feet elevation [53,86]. Ranges by state are:

State	Range
California	7,200-12,000 feet (2,200-3,700 m) [53]
Nevada	8,000-10,800 feet (2,400-3,300 m) [13,63]
Utah	(7,200-10,700 feet (2,195-3,265 m) [136]

Elevational range of Great Basin bristlecone pine has varied over time and space [78]. Hiebert and Hamrick [54] noted a downward shift in the current elevational range of 3 populations in southern Utah and eastern Nevada, with snags and cone-bearing trees, but no seedlings or saplings, above Great Basin bristlecone pine's present elevational zone of establishment. LaMarche [70] noted a downward population shift on sites in the White Mountains. Great Basin bristlecone pine's zone of establishment has been expanding downward in the White Mountains since around 1850. Great Basin bristlecone pine's elevational range may also be shifting upwards in the White Mountains [134].

Climate: Great Basin bristlecone pine occurs in arid climates that are cold in winter and droughty in summer. Within Great Basin bristlecone pine's geographic range, climate becomes increasingly dry from the Wasatch Range of eastern Utah to the White Mountains of western Nevada and eastern California. Growth of Great Basin bristlecone pine populations in eastern California and extreme western Nevada is affected by California's mediterranean climate. More interior populations are influenced by the interior continental climate, which has summer monsoons. Correspondingly, eastern populations tend to be larger, denser, and have a greater range in their lower elevational limits [56].

The White Mountains lie directly behind the rain shadow of the Sierra Nevada, in the highest portion of the Sierra Nevada's range. Summer rain is scarce; most precipitation falls as winter snow. Mean precipitation is 12 inches/year (300 mm/yr) [82], about 2.5 inches (64 mm) of which is rainfall during the growing season [77]. In July and August, mean monthly temperatures average 50 °F (10 °C). Mean monthly temperatures are below freezing from November through April. In contrast, mean annual precipitation on Great Basin bristlecone pine sites in the Snake Range of eastern Nevada is about twice that of Great Basin bristlecone pine sites in the White Mountains (Pace and others 1968, as cited in [77]). The ability of Great Basin bristlecone pines to grow to full stature up to treeline in the White Mountains, while forming krummholz at treeline in eastern Nevada, is probably due to differences in climate. Physiological and morphological adjustments made in the needles in response to summer drought in the White Mountains also protect trees from winter desiccation, which is largely responsible for inducing krummholz growth [77].

In geologic time, Great Basin bristlecone pine showed best population expansion with cool temperatures. Best development of Great Basin bristlecone pine forests occurred during the Pleistocene. In the Great Basin, extensive Great Basin bristlecone pine Pleistocene forests extended down mountain slopes to near Lake Bonneville's ancient shoreline. Great Basin bristlecone pines also occupied Mojave Basin mountain slopes, where they are now absent [125,126,135]. Great Basin bristlecone pine populations on marginal sites of the interior Great Basin are threatened by climate change. Already forced to mountain tops by global warming, these populations have run out of suitably cool, moist conditions for seedling establishment [56,87,135].

SUCCESSIONAL STATUS:
Great Basin bristlecone pine is both a pioneer species and, on open harsh sites, a climax species. Great Basin bristlecone pine establishes and shows rapid, vigorous growth on open mesic sites [52]. However, it competes poorly for water and

nutrients, and is usually excluded from good sites [15,56]. It is considered a topoedaphic climax species on droughty sites with nutrient-poor soils [21]. The limestone soils that favor Great Basin bristlecone pine are too low in phosphorus to support potential competitors [137]. On these dry, nutrient-poor sites, Great Basin bristlecone pine outcompetes associated species including limber pine. In east-central Nevada, Bare [13] found that compared to its early successional competitor, curlleaf mountain-mahogany, Great Basin bristlecone pine maintained a more favorable water potential than mountain-mahogany on dry limestone soils (-2.27 mP vs. -2.84 mP, respectively). Curlleaf mountain-mahogany competitively excluded Great Basin bristlecone pine on other soil types. In California and western Nevada, big sagebrush excludes Great Basin bristlecone pine from early seres, except on limestone soils [52,65].

Great Basin bristlecone pine is shade intolerant and cannot establish in dense forest [13,17,82]. On low-elevation sites in eastern Nevada and Utah, Engelmann spruce, and to a lesser extent, limber pine, successionally replace Great Basin bristlecone pine on mesic, relatively nutrient-rich soils [13,17].

SEASONAL DEVELOPMENT:
Growing seasons are short for Great Basin bristlecone pines. Depending upon elevation and year, the growing season may extend to 3 months or be as short as 6 weeks [104]. Time of bud break ranges late June to early July [37,45]. Pollen is shed from mid-July to late August [82,86]. New stem buds are fully formed by mid-August [37]. Female cones open and disperse seed from late September to early October of their 2nd year [86].

In the White Mountains, pollen shed occurred from approximately July 20 to August 8, depending on elevation. Needles were almost totally elongated at time of pollination [45,61]. Needles emerged from July 28-July 30th on low-elevation sites, and 8 days later on high-elevation sites [45].

FIRE ECOLOGY

SPECIES: Pinus longaeva

- FIRE ECOLOGY OR ADAPTATIONS
- POSTFIRE REGENERATION STRATEGY

Fire-scarred tree on White Mt. Photo by Sherry Ballard. © California Academy of Sciences.

FIRE ECOLOGY OR ADAPTATIONS:

Fire adaptations: As a thin-barked pine [141], Great Basin bristlecone pine is adapted to survive only low-severity surface fires. The Great Basin bristlecone pine pictured above shows damage from low-severity fire. On low-elevation Wheeler Peak, fire-scarred Great Basin bristlecone pines grow in association with interior ponderosa pine [86]. Great Basin bristlecone pines also survive mixed-severity fire in patches where fire severity is low.

As of this writing (2004), methods of Great Basin bristlecone pine postfire seedling establishment are undocumented. Clark's nutcracker dispersal of Great Basin bristlecone pine seed onto burns, if such dispersal occurs, would greatly enhance Great Basin bristlecone pine's ability to regenerate after fire [83,85,87]. Even without Clark's nutcrackers, Great Basin bristlecone pine seeds can colonize burns through wind dispersal [86]. The postfire competitive ability of Great Basin bristlecone pine seedlings is largely unknown. Research is needed on postfire succession in Great Basin bristlecone pine communities and in mixed-conifer forest communities where Great Basin bristlecone pine is important.

Fire regimes: Fire is infrequent on high-elevation sites dominated by Great Basin bristlecone pine. Stands are very open, and productivity is low. When fires do occur at high elevations, they are usually small, low-severity surface fires [21]. Stand dynamics in high-elevation Great Basin bristlecone pine communities are more influenced by climate and seed dispersal patterns than by fire [21,80,82,83]. LaMarche and Mooney [76] note that in the White Mountains, "The low density of trees and the sparsity of litter and flammable ground-cover preclude widespread burning of the sub-alpine forest near timberline."

In Nevada and Utah, Great Basin bristlecone pine occurs at high elevations that experience infrequent surface fire, but also occurs in mixed-conifer lower subalpine and mid-elevation sites that experience mixed-severity fire. Fires are more frequent, and are sometimes of greater severity, in mixed forests. Fuels are much heavier in mixed forests compared to sites where Great Basin bristlecone pine is the dominant tree. Historically, fires at mid-elevations in the mixed-conifer zones of Nevada and Utah burned in a pattern of different severities. This included patches where most of the fire-susceptible conifers such as Great Basin bristlecone pine survived [4], and patches where fire-sensitive conifers were killed [100]. Mixed-severity fire regimes create a forest mosaic of stands with varied structures, species compositions, and seral stages. Little is known of the postfire stand dynamics in mixed-conifer forests with a Great Basin bristlecone pine component. It is ironic that Great Basin bristlecone pine, which has yielded such rich tree-ring chronologies on high-elevation sites (see Other Uses), has been the subject of little dendrochronological research on mixed-conifer sites where Great Basin bristlecone pine may require more active fire management. Fire history studies of Great Basin bristlecone pine-limber pine-Engelmann spruce and other lower subalpine and montane forests of the Great Basin are badly needed. Further research is required for best management of these threatened communities.

Fuels: With low productivity and widely spaced stands, there are usually not enough fuels to carry fire on high-elevation Great Basin bristlecone pine sites [13,21,65,82]. Bidartondo and others [19] state "the spread of fire from lightning is most unlikely" in high-elevation Great Basin bristlecone pine stands. Fuels are sufficient to carry fire in denser, low-elevation sites where Great Basin bristlecone pine occurs in mixed forests with limber pine and/or Engelmann spruce [19].

Flammability of Great Basin bristlecone pine has not been examined. The wood and foliage are highly resinous [8,17,90]. Although fire may not spread at high elevations, individual trees may ignite relatively easily.

The following table provides fire return intervals for important plant communities and ecosystems where Great Basin bristlecone pine is sometimes an important component of the vegetation. Except for whitebark pine, Great Basin bristlecone pine often occurs at the upper elevational limits of the communities listed below, so fire return intervals are most likely on the long end of these ranges. For further information on the fire regimes of these plant communities and ecosystems, see the FEIS species summaries for the dominant species below.

Community or Ecosystem	Dominant Species	Fire Return Interval Range (years)
Engelmann spruce-subalpine fir	*Picea engelmannii-Abies lasiocarpa*	35 to > 200 [4]
whitebark pine*	*Pinus albicaulis*	50-200 [1,3]
interior ponderosa pine*	*Pinus ponderosa* var. *scopulorum*	2-30 [4,10,88]
Rocky Mountain Douglas-fir*	*Pseudotsuga menziesii* var. *glauca*	25-100 [4,5,6]

*fire return interval varies widely; trends in variation are noted in the species summary

POSTFIRE REGENERATION STRATEGY [123]:
Tree without adventitious bud/root crown
Initial off-site colonizer (off-site, initial community)

FIRE EFFECTS

SPECIES: Pinus longaeva

- IMMEDIATE FIRE EFFECT ON PLANT
- DISCUSSION AND QUALIFICATION OF FIRE EFFECT
- PLANT RESPONSE TO FIRE
- DISCUSSION AND QUALIFICATION OF PLANT RESPONSE
- FIRE MANAGEMENT CONSIDERATIONS

This bristlecone stand in the White Mts. is dense enough to carry a patchy fire. Photo © Br. Alfred Brousseau, Saint Mary's College.

IMMEDIATE FIRE EFFECT ON PLANT:
Great bristlecone pines can survive low-severity surface fires. Surviving trees may show fire scars. Moderate-severity surface or crown fires kill Great Basin bristlecone pines [76,83].

DISCUSSION AND QUALIFICATION OF FIRE EFFECT:
Mixed-severity fire regimes kill some Great Basin bristlecone pines and leave others scarred or undamaged. On mid-elevation sites in southern Utah, where the fire regime is mixed, fire-scarred Great Basin bristlecone pines grow in association with scarred interior ponderosa pines and later-succession Rocky Mountain white firs. In contrast, Great Basin bristlecone pines on high-elevation sites of Wheeler Peak, where fires are very rare, show no evidence of fire damage [86].

PLANT RESPONSE TO FIRE:
Because Great Basin bristlecone pine is a sun-tolerant, early seral species [13,17,82], postfire establishment seems likely on high-elevation sites. Postfire establishment may also be favored on burned Great Basin bristlecone pine-mixed conifer ecotones, lower-elevation limestone soils, and other sites that are marginally productive for other conifer species but relatively good for Great Basin bristlecone pine. As of this writing (2004), documentation of Great Basin bristlecone pine postfire establishment, growth rate, and successional role is lacking. Research is needed on the fire ecology of Great Basin bristlecone pine.

DISCUSSION AND QUALIFICATION OF PLANT RESPONSE:
In Great Basin National Park, a crown fire on Mt. Washington killed a stand composed of mostly multiple-stemmed Great Basin bristlecone pine. The stand may have originated from Clark's nutcracker caches [83]. Further research is needed on methods of Great Basin bristlecone pine establishment after fire.

FIRE MANAGEMENT CONSIDERATIONS:
Because Great Basin bristlecone pine is a highly valuable species threatened by white pine blister rust (see Blister rust), active management may be necessary in the near future. In high-elevation environments where fires are rare and of small extent, Great Basin bristlecone pine probably needs little fire management beyond fire suppression in ancient groves. However, larger fires that kill some Great Basin bristlecone pine stands are inevitable in lower subalpine and montane forests with mixed-severity fire regimes. There is much yet to learn about the basic ecology of Great Basin bristlecone pine. Given Great Basin bristlecone pine's early successional role, fire may favor Great Basin bristlecone pine establishment on some sites. Fire management for Great Basin bristlecone pine is difficult to plan without basic knowledge of the species' fire ecology. Post-wildfire studies can provide instruction on Great Basin bristlecone fire ecology. Monitoring and documenting Great Basin bristlecone pine's mortality rate under various fire severities; its methods and rate of postfire establishment; postfire growth rate, and successional role after fire can help managers implement fire management plans for Great Bain bristlecone pine. Specific questions that remain unanswered are:

- How well does Great Basin bristlecone pine seed in after fire? Does viable seed fall from on-site, burned trees? How effectively does wind carry Great Basin bristlecone pine seed onto burned sites?
- What is the seedbank ecology of Great Basin bristlecone pine?
- What role, if any, do Clark's nutcrackers play in postfire Great Basin bristlecone pine regeneration? (Digging up Great Basin bristlecone pine seedling clusters to see if the stems have their own root systems can help in this regard.)
- How well does Great Basin bristlecone pine compete with other sun-tolerant associated species, such as limber and ponderosa pines, in early postfire succession in mixed-conifer communities? Long-term studies on succession in mixed-conifer communities are also needed.

MANAGEMENT CONSIDERATIONS

SPECIES: Pinus longaeva

- IMPORTANCE TO LIVESTOCK AND WILDLIFE
- VALUE FOR REHABILITATION OF DISTURBED SITES
- OTHER USES
- OTHER MANAGEMENT CONSIDERATIONS

IMPORTANCE TO LIVESTOCK AND WILDLIFE:
Great Basin bristlecone pine-limber pine communities are high-use habitat for small birds and mammals including chickadees, nuthatches, flycatchers, sapsuckers, finches, dark-eyed juncos, mountain bluebirds, Clark's nutcrackers, and ground squirrels [82]. Medin and others [103] provide a census of bird species found along an elevational gradient in the Snake Range that includes Great Basin bristlecone pine mixed-conifer and subalpine zones. Great Basin bristlecone pines provide food. Mountain bluebirds, chickadees, and other wildlife eat the seeds [90]. Great Basin bristlecone pines also contribute to community diversity. For example, they are hosts to 2 species of bark beetles that to date (2004) have only been collected in the White Mountains [22].

Palatability/nutritional value: Great Basin bristlecone pine is listed as unpalatable to mule deer in Utah [7].

Cover value: Great Basin bristlecone pines are a major source of cover for wildlife in high-elevation ecosystems [95]. White-breasted and other nuthatches nest in Great Basin bristlecone pine [86].

VALUE FOR REHABILITATION OF DISTURBED SITES:
Great Basin bristlecone pine provides watershed protection on harsh sites were other vegetation establishes poorly [95,100].

OTHER USES:
Great Basin bristlecone pine is invaluable to dendochronologists. It provides the longest continual and some of the most climatically sensitive tree-ring chronologies on the planet [8,42,45,74,78,110]. By cross-dating millennia-old Great Basin bristlecone pine debris remnants, some Great Basin bristlecone pine chronologies exceed 9,000 years BP [8,40,41,42,86,90]; eventually, Great Basin bristlecone pine chronologies may reach back 10,000 years [42,43]. Besides dendrochronology, the long chronologies obtained from Great Basin bristlecone pines have been applied in other fields of science including archaeology, environmental chemistry, climatology, geology, and astronomy [17,34,39,40,72,73,74,75,121]. Great Basin bristlecone pine has been called "the tree that rewrote history." Its tree-ring chronologies allowed the carbon-14 dating technique to be accurately calibrated and consequently, human artifacts accurately dated [15,90,91,108]. Best chronologies are obtained from slow-growing Great Basin bristlecone pines on harsh sites. Beasley and Klemmedson [15] provide site and tree-growth criteria for recognizing Great Basin bristlecone pine sites with potential for yielding good tree-ring samples. The University of Arizona's Laboratory of Tree-Ring Research provides information on many aspects of dendrochronology.

Rate of exposure of ancient Great Basin bristlecone pine buttress roots can be used to estimate rates of soil denudation over millennia [71].

Great Basin bristlecone pine communities have high recreational value. The gnarled, twisted forms of ancient Great Basin bristlecone pine are aesthetically pleasing [21,25].

Wood Products: Great Basin bristlecone pine wood is harder and denser than the wood of most conifers [8], but the species is not commercially important [63]. Great Basin bristlecone pine-limber pine forests in the White Mountains were heavily logged in the 1860s for mine and structural timber [82,139].

OTHER MANAGEMENT CONSIDERATIONS:
Great Basin bristlecone pines are vulnerable to insect attacks, parasites, and fungi. Miller's [104] Ancient bristlecone pine website provides information Great Basin bristlecone pine ecology.

Damaging agents: Great Basin bristlecone pine is susceptible to mountain pine beetle infestations throughout its range [81]. Logan and Powell [95] provide information on the ecology and management of mountain pine beetles in high-elevation ecosystems. Western dwarf mistletoe (*Arceuthobium camylopodum*) infests Great Basin bristlecone pines in southern Nevada and Utah [51,52,99]. Wood decay fungi infest Great Basin bristlecone pine and may eventually kill them. However, the cold, dry sites that high-elevation Great Basin bristlecone pines inhabit slow fungal growth and wood decay. Survival of the oldest Great Basin bristlecone pines is partially attributable to poor fungal growth in those individuals. Lindsey and Gilberton [93] identified some of the wood-rot basidiomycetes infecting Great Basin bristlecone pine in Cedar Breaks National Monument.

Blister rust: Great Basin bristlecone pine is susceptible to white pine blister rust, an exotic fungus that infects 5-needle white pines (*Strobus* spp.). To date (2004), arid climate has protected most Great Basin bristlecone pines from infection. A 1995-1997 blister rust survey across the West showed an incidental level of infection in the Wasatch Mountains of Utah; otherwise, blister rust was not detected within Great Basin bristlecone pine's range. However, the potential for blister rust to spread into arid zones should not be underestimated. Blister rust's geographical range tends to spread only during wet years, when environmental conditions are favorable for infection of 5-needle pines [119]. Blister rust has spread into the Sacramento Mountains of New Mexico, infecting southwestern white pine (*Pinus strobiformis*) [47,48], and has been detected in Rocky Mountain bristlecone pines in northern Colorado [131]. Great Basin bristlecone pine populations in the White and Inyo Mountains, which lie close to moderately high infection centers in the Sierra Nevada, may currently be at greatest risk for blister rust infection and spread [119].

Blister rust-infected white pines such as Great Basin bristlecone pine may take from 2 years to decades to succumb, but infection is always fatal [57,58]. Gooseberries and currants (*Ribes* spp.) are the primary host of white pine blister rust. Life cycle of white pine blister rust is complex. Gitzendanner and others [49] and McDonald and Hoff [101] provide details of the rust's life history and ecology. Hoff [57] provides a diagnostic guide to aid managers in recognizing symptoms of blister rust infection in white pines. There are no known methods of controlling blister rust [64]. Fungicide application, pruning infected tree branches, and/or removing *Ribes* spp. have neither eliminated nor controlled white pine

blister rust [24,101], and such treatments have undesirable ecological effects [64]. For further information on management of white pine blister rust, see Samman and others [112], Tomback and others [128], and Sniezko and others [120].

Levels of resistance of Great Basin bristlecone pine to blister rust are unclear, since Great Basin bristlecone pine in the field have apparently not yet been subjected to the rust's spores. In a laboratory study, all Great Basin bristlecone pine seedlings tested lacked key alleles that confer genetic resistance to blister rust; however, sample size (120) was small [66]. Inventories are underway to detect and monitor levels of blister rust in Great Basin bristlecone pine and other white pine stands, and to identify Great Basin bristlecone pines with phenotypic resistance to blister rust. If blister rust outbreaks become severe, resistant Great Basin bristlecone pines can be used as seed sources for transplanting programs that use blister rust-resistant seed stock [102,114].

"When research has been carried far enough in these Methuselah pines, perhaps their misshappen and battered stems will give us answers of great beauty" [116].

Pinus longaeva: References

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