

Fire and High-Elevation, Five-Needle Pine (*Pinus aristata* & *P. flexilis*) Ecosystems in the Southern Rocky Mountains: What Do We Know?

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Abstract—Rocky Mountain bristlecone pine (*Pinus aristata* Engelm) and limber pine (*P. flexilis* James) are high-elevation, five-needle pines of the southern Rocky Mountains. The pre-settlement role of fire in bristlecone and limber pine forests remains the subject of considerable uncertainty; both species likely experienced a wide range of fire regimes across gradients of site productivity and connectivity of fuels and flammable landscapes. In dense stands and more continuous forests, stand history reconstructions provide evidence for infrequent, high-severity fires. Limber pine can be dispersed long distances by Clark's nutcrackers (*Nucifraga columbiana*), and in the high-elevation subalpine forests of the northern Colorado Front Range, it is an early colonist of extensive, high-severity burns. However, this relationship with fire may not be general to the southern Rockies. The degree to which high-severity fire was typical of bristlecone pine, and the spatial extent of such fires, is uncertain. Following fire, bristlecone pine regeneration tends to be constrained to burn edges or beneath surviving trees. In both five-needle pines, regeneration dynamics take decades to centuries. Where open stands border grassy openings both species frequently exhibit fire scars indicative of fairly frequent but low-intensity fire; because of the great ages attained by both species, they offer potentially very long fire history reconstructions in such settings. Whether or not fire suppression has led to declines in either species—through successional shifts to shade-tolerant competitors or by shifts to a stand replacing fire-regime—remains an open question that deserves further inquiry. In any case, re-establishing pre-settlement fire regimes, whatever they were, may not be as important as determining appropriate disturbance regimes given current conditions and management objectives. Both species are highly susceptible to rapid declines caused by white pine blister rust (*Cronartium ribicola*) and mountain pine beetles (*Dendroctonus ponderosae*). In the face of these threats, and uncertain consequences of climate change, fire management (both prevention and application) can be a tool to promote resilient landscapes. Appropriate fire management may be used to conserve valuable stands, promote regeneration and diversify age class structures, and/or alter the balance between these species and their competitors. Many of these themes and questions indicate the need for further basic and applied research.

Introduction

Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*P. flexilis*) are high-elevation, five-needle pines of the southern Rocky Mountains. These tree species frequently occur at the high-elevation and xeric margins of the arborescent life form, and as such they form biological

communities and provide ecological services that cannot be replaced. However, both species are highly vulnerable to large scale changes caused by white pine blister rust (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*). Considerable uncertainty remains surrounding the role of fire in southern Rocky Mountain five-needle pine ecosystems. First, few quantitative studies have explicitly addressed this theme. Secondly, both species can occupy a diversity of ecological settings, and nearly the entire spectrum of fire regimes and their effects probably occurred within their ranges. For this reason, generalizations from any given line of evidence are likely to be inaccurate. For example, based on ordinations of morphological traits, McCune (1988) and Keeley and Zedler (1998) concluded that fire is essentially absent or unimportant for bristlecone and limber pine. While fire may be inconsequential in some settings, there is clear evidence for abundant fire, a diversity of fire regimes, and a significant role of fire in many bristlecone and limber pine ecosystems, as discussed below.

The purpose of this review is to summarize what we do know about fire ecology of the high-elevation, five-needle pine forests of the southern Rocky Mountains, including both published and unpublished data, anecdotal information, and the observations of ourselves and others. The geographic scope of this review is limited to the southern Rocky Mountains, extending from southern Wyoming south through the major ranges of Colorado into northern New Mexico. At the southern end of this region, there appears to be a broad, unresolved transition zone between limber pine and southwestern white pine (*P. strobiformis*; *P. flexilis* var. *reflexa*), which we also discuss briefly, though little work has been done on the fire ecology of these transitional populations. We also include some discussion of the disjunct Rocky Mountain bristlecone pine population in the San Francisco Peaks of northern Arizona. Our primary goals are to review what we know generally about the ecology of these species, fire regimes, effects of fire on stand dynamics, and possible human and climatic influences on fire in these systems. Throughout, we point out deficiencies in our understanding of these systems and suggest possible research directions. Lastly, we consider how the management of fire may be used to promote resilient southern Rocky Mountain five-needle pine ecosystems in a future of certain change of uncertain direction and magnitude.

Overview of Bristlecone and Limber Pine Ecology

Rocky Mountain bristlecone pine (henceforth, bristlecone pine) and limber pine are five-needle pines of *Pinus* subgenus *Strobus*. Within this large group they are not particularly closely related, bristlecone pine is classified in section *Parrya* and limber pine in section *Quinquefoliae* (Gernandt and others 2005). However, they share many morphological and ecological characteristics: both are short-statured, slow-growing, drought- and cold-tolerant tree species that may be very long-lived, and frequently occupy xeric and high-elevation sites where conditions for arborescent growth are marginal and competitors are few. Bristlecone and limber pines rarely achieve heights greater than 15 m or bole diameters greater than 1 m. For both species, radial growth rates of <0.01 mm/year are common on dry, high-elevation sites and rarely exceed 3 mm/year on more mesic or lower-elevation sites (J.D. Coop, unpublished data). Where bristlecone and limber pine co-occur, limber pine typically exhibits greater rates of radial growth with greater variance (J.D. Coop, unpublished data). Both bristlecone and limber pine are well-known for their extreme longevity. The oldest known Rocky Mountain bristlecone pine, found in Colorado, is nearly 2500 years (Brunstein & Yamaguchi 1992), and the oldest known limber pine, found in northern New Mexico, exceeds 1600 years in age (Swetnam & Brown 1992).

An important difference between bristlecone and limber pine is seed morphology and dispersal mode. Bristlecone seeds are small (ca. 20 mg) and winged, typical of wind-dispersal; the large (ca. 100 mg), wingless (or near-wingless) seeds of limber pine are dispersed primarily by Clark's nutcrackers (Woodmansee 1977; Lanner & Vander Wall 1980). Because nutcrackers often deposit numerous seeds in each cache, limber pine seedlings arising from caches often occur as multi-stem clusters (Woodmansee 1977; Lanner & Vander Wall 1980; Carsey & Tomback 1994). Based on frequent stem-clusters and observations of nutcrackers, Lanner (1988) concluded that Great Basin bristlecone pine (*Pinus longaeva*; which produces small, winged seeds similar to those of Rocky Mountain bristlecone pine) is often nutcracker-dispersed, particularly at high elevations. Multi-stemmed Rocky Mountain bristlecone pines also occur occasionally, although whether these trees usually represent single, multi-stemmed individuals or separate individuals arising from a seed caches is not known. However, it is likely that nutcrackers occasionally serve as the dispersal agents for this species as well, though their importance relative to wind has not been studied.

In general, both bristlecone and limber pine are found on xeric sites at moderate to high elevations where competition from other tree species is limited, and are replaced on mesic sites by more rapidly growing competitors—often Engelmann spruce (*Picea engelmannii* var. *engelmannii*). South-facing slopes dominated by five-needle pines usually give way to mixed conifer or spruce-fir forests on north aspects. Both species can form krummholtz at alpine

treeline. Although both five-needle pines are often associated with subalpine and alpine timberline environments (3100–3650 m), both species also commonly occur at lower (2650–3100 m) elevations, often on montane rocky outcrops, or bordering valley- bottom montane and subalpine grasslands. At such lower sites, five-needle pine communities often give way to mixed conifer or spruce-fir forests above. Both species can also be found co-occurring with nearly every other tree species in the region, including piñon pine (*Pinus edulis*), ponderosa pine (*Pinus ponderosa* var. *scopulorum*), lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas fir (*Pseudotsuga menziesii* var. *glauca*), aspen (*Populus tremuloides*), Colorado blue spruce (*Picea pungens*), Engelmann spruce, and subalpine and corkbark fir (*Abies lasiocarpa* var. *lasiocarpa* & var. *arizonica*).

Geographic Distributions and Environmental Settings

Rocky Mountain bristlecone pine is restricted to the southern Rocky Mountains between central Colorado and northern New Mexico, and a small disjunct population on the San Francisco Peaks of north-central Arizona (Fig. 1). Farther west it is replaced by Great Basin bristlecone pine (*Pinus longaeva*), which ranges from the central plateaus of Utah to eastern California. Other than geography, the two species were separated by Bailey (1970) by longer bristles on the cones of Rocky Mountain bristlecone, and the abaxial groove and resin-dotted needles of Rocky Mountain bristlecone which are not present in Great Basin bristlecone pine. While macrofossils preserved in packrat middens indicate that Great Basin bristlecone pine was widespread at low elevations across its range during the last glacial period (Betancourt and others 1990), the Pleistocene distribution of Rocky Mountain bristlecone pine is not documented. Bailey (1970) hypothesized that Rocky Mountain bristlecone pine was distributed across the Mogollon Rim from the San Francisco Peaks through west-central New Mexico during the glacial maximum.

Limber pine is widespread throughout western North America, between the Pacific crest and the Rockies, from British Columbia and Alberta south through at least as far south as the southern Rockies, with several outlier populations east of the Rockies (Fig. 1). At the southern end of its range in the southern Rockies there is a broad transition zone with southwestern white pine, a taller, straight-boled, thick-barked tree that is an important component of southwestern montane mixed-conifer forests. Many populations within this region appear intermediate in ecology and the morphological characteristics used to separate the two species (longer needles and cones, and reflexed cone scales in *P. strobiformis*, stomata present on all leaf surfaces in *P. flexilis* but absent from the abaxial surface in *P. strobiformis*). Limber pine is well-known to have occupied an extensive range during the last Pleistocene glaciation at lower elevations now occupied by piñon pines (*P. edulis* and *P. monophyla*) across the Great Basin (Betancourt and others 1990), along the

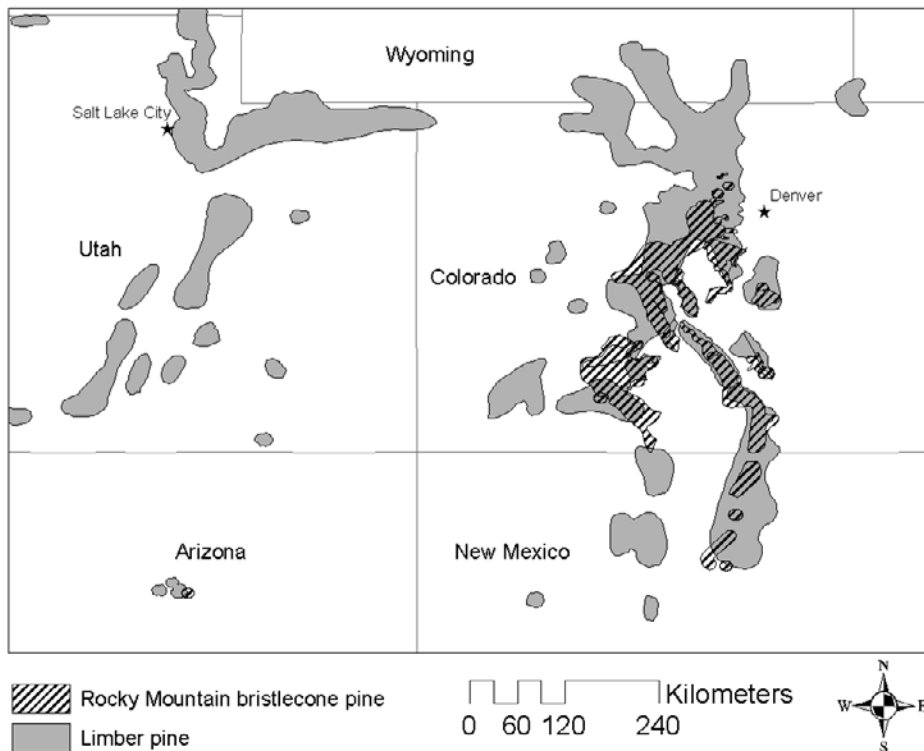


Figure 1. Map showing the ranges of Rocky Mountain bristlecone pine (*P. aristata*) and limber pine (*P. flexilis*) in the southern Rocky Mountains, modified from Little (1971), with several additions by the authors.

eastern Great Plains (Wells & Stewart 1987) and possibly areas in southern New Mexico, central Colorado, Wyoming, and California (Mitton and others 2000).

Across the southern Rockies, bristlecone pine and limber pine exhibit a latitudinal and elevational shift in dominance (Peet 1978): in the north, limber pine is more abundant and occupies a very wide elevational range, but is gradually replaced by bristlecone pine, at first only at high elevations, but at progressively lower elevations as bristlecone pine increases in importance to the south. The extent to which this apparent displacement is driven by variation in competitive ability, shifting physiological limits by either species along the climatic gradient over which they both occur, or other factors altogether, is unknown.

In southern Wyoming and northern Colorado, north of the range limits of bristlecone pine, limber pine occupies one of the largest elevational ranges of any species in the Rockies (from 1660 to 3300 m; Schoettle & Rochelle 2000), including dry sites at alpine treeline in Rocky Mountain National Park, extensive stands on xeric subalpine slopes and montane ridges across the northern Front Range, foothill sites in intermountain valleys such as North Park and the Great Divide Basin of Wyoming, and even topographic breaks in Great Plains east of the Rockies. At the northern end of the range of bristlecone pine (the Front Range south of Rocky Mountain National Park), bristlecone pine occupies only xeric alpine treeline sites just above stands of limber pine. As one progresses south along the Front Range, bristlecone pine appears to gradually displace limber pine entirely from alpine treeline sites; limber pine is increasingly restricted to south-facing subalpine and montane slopes. In the southern Front Range and throughout much of the Mosquito and Sawatch Range, bristlecone pine forms extensive subalpine

stands and limber pine is mostly confined to lower elevations, being more or less restricted to dry upper montane ridges.

Bristlecone pine is particularly abundant around South Park and along the Cochetopa Hills where it also forms extensive lower treeline stands abutting Arizona or Thurber's fescue (*Festuca arizonica* & *F. thurberi*) grasslands (Ranne and others 1997) of parks and valleys. Other tree species may be excluded from these valley-bottom grassland margins in the southern Rockies by fine-textured soils with extremely low moisture potential during dry periods and frequent temperature inversions causing frost damage to tree seedlings (Coop & Givnish 2008). Frequently, bristlecone pine at these lower-treeline settings gives way to species with more mesic affiliations at higher elevations. Along the eastern margins of South Park, bristlecone pine occasionally exhibits a bimodal distribution, coexisting with ponderosa pine at low elevations, absent from the montane lodgepole pine zone, then reappearing at high elevations with spruce. Some bristlecone pine stands reach essentially unbroken from lower treeline up to alpine treeline. Limber pine is much less frequent in these areas, and may be limited to unusual topo-edaphic conditions such as limestone ridges. Throughout its range in the Wet Mountains, the Sangre de Cristos, and the eastern San Juans in Colorado, bristlecone pine may occur in patches at alpine treeline, in extensive subalpine forests, at the margins of subalpine grasslands, and isolated stands in dry, rocky sites at lower elevations. In northern New Mexico, bristlecone pine extends along the length of the Sangre de Cristo range, but does not occur farther west in the San Juan or Jemez Mountains. Around the Valle Vidal in northern New Mexico, bristlecone pine is particularly abundant, reaching from montane grasslands to

alpine treeline. Bristlecone pine decreases in abundance toward the southern terminus of the Sangres, where it is more often associated with montane and subalpine grasslands, and occurs only rarely at alpine treeline.

At the approximate location of a SW-NE trending diagonal line through the southern San Juans, the northern Sangre de Cristo range, and the Wet Mountains, there is an apparent transition zone from limber pine to southwestern white pine, with morphologically and taxonomically variable populations. Interestingly, the region of this transition also represents the southern range limit of lodgepole pine and the approximate location of the shift from subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*) to corkbark fir (*Abies lasiocarpa* var. *arizonica*). The apparent *P. flexilis*/*P. strobiformis* intermediates in this region occur in both dry montane mixed-conifer forests, often associated with Douglas fir, and also occasionally form small, monodominant stands on exposed settings such as low summits, ridges, and rocky outcrops. Taxonomic affinities to southwestern white pine increase to the south (J.D. Coop, personal observation). In some areas, such as the Jemez Mountains, more limber pine-like trees can be found on exposed sites, and more southwestern white pine-like trees occur in mixed conifer forests.

Bristlecone Pine Fire Regimes and Stand Dynamics

The most geographically extensive characterization of bristlecone pine stands was carried out by Baker (1992), who collected size-class data and dated the oldest trees in 65 stands dominated by bristlecone pine between 2700 and 3700 m elevation across Colorado and concluded that many of these stands were initiated following stand-replacing fire. Two stands had burned recently and contained many seedlings and saplings. In nineteen stands the oldest trees were dated to 1900-1925 or 1625-1700, which Baker inferred were periods of stand-initiating wildfire activity. The abundance of aspen in some of these stands may also be indicative of an infrequent, stand-replacing disturbance regime. However, direct evidence for wildfire was not presented in this research, and other stand-initiating disturbance and/or climatic drivers may also be important. Baker concluded that stand-replacing fire was the primary disturbance regime for bristlecone pine, with a fire rotation interval of approximately 300 years. Though this estimate undoubtedly masks considerable variation, it is apparent many stands can reach canopy densities sufficient to support crown fire, particularly on relatively mesic settings where bristlecone co-occurs with other conifer species. In these settings, an important unanswered question is what spatial scale typified such burns.

While stand-replacing fire may have been prevalent in some settings, at least some stands may be best characterized by a low-severity fire regime. Fire-scarred bristlecone pines in open, low-density stands with grassy understories occur nearly throughout the range of the species, particularly where stands abut montane and subalpine grasslands, such as around South Park, in the Cochetopa Hills, the Wet



Figure 2. Fire-scarred bristlecone pines near Bobcat Pass in the Sangre de Cristo range, northern New Mexico.

Mountains, and the Sangre de Cristo range (J.C. Coop, personal observation; Fig. 2), and numerous fire histories have been reconstructed from bristlecone pines scarred by low-severity fires (Table 1). Donnegan and others (2001) collected fire scar data from several stands dominated by bristlecone pine around South Park, Colorado between 2865-3108 m elevation. These authors reported mean fire intervals (MFIs) in some bristlecone pine stands < 20 years, similar to fire frequencies from lower elevation (1996-2865 m) stands of ponderosa pine reported in the same study. Sherriff and others (2001) also relied on several primarily bristlecone pine sites to reconstruct fire history from high-elevations (>3100 m) in the Colorado Front Range. These sites, representing some of the northernmost locations of bristlecone pine, also showed abundant, low severity fires, two with MFIs of 13 and 15 years. In the southern Sangre de Cristo range in New Mexico, a fire-scarred bristlecone pine stand bordering subalpine grasslands in the Pecos Wilderness yielded a reconstructed MFI of 59 years (C.D. Allen, unpublished data). In the disjunct bristlecone pine population of the San Francisco Peaks of northern Arizona, Coker and others (2005) noted large, old trees with multiple fire scars, and cited unpublished data indicative of both low-severity fire and small patches of high-severity fire.

Bristlecone pine stands exhibit substantial variation in composition and structure and occur across a wide range of ecological conditions, so a variety of disturbance regimes is not unexpected. Large gradients in stand conditions can occur over short distances. For example, open bristlecone pine stands bordering montane grasslands that likely experienced a frequent, low-severity fire regime can give way abruptly to dense, mixed species forests above that would be more likely to experience stand-replacing fire (Fig. 3). Stand conditions and fire regimes may also change over time, as at Packer Gulch, a bristlecone site in the Puma Hills bordering South

Table 1. Low-severity fire sites in bristlecone and limber pine stands that have been used to reconstruct fire histories, from north to south across the southern Rocky Mountains, and mean fire intervals (MFI).

Site	Region	Authors	Species	Trees*	Period	MFI†
Lake John	Northern CO	Brown & Schoettle 2008	<i>Pinus flexilis</i>	6	1464-1832	41
Wild Basin	Northern CO	Sherriff and others 2001	<i>Pinus flexilis</i> , <i>Pinus contorta</i> , <i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	74	1559-1996	7
Hidden Valley	Northern CO	Sherriff and others 2001	<i>Pinus flexilis</i>	31	1298-1988	23
Arapaho NF	Northern CO	Sherriff and others 2001	<i>Pinus aristata</i> , <i>Pinus flexilis</i> , <i>Picea engelmannii</i>	48	1288-1986	15
Mt. Evans	Northern CO	Sherriff and others 2001	<i>Pinus aristata</i> , <i>Pinus flexilis</i> , <i>Picea engelmannii</i>	33	1266-1986	13
Packer Gulch	Central CO	Brown & Schoettle 2008	<i>Pinus aristata</i> , <i>Pinus flexilis</i> , <i>Picea engelmannii</i> , <i>Pseudotsuga menziesii</i>	26	1106-1824	103
Badger Mtn.	Central CO	Donnegan and others 2001	<i>Pinus aristata</i> , <i>Pinus flexilis</i> , <i>Pinus ponderosa</i> , <i>Pseudotsuga menziesii</i>	58	1456-1920	67
BSA Shortcut	Central CO	Donnegan and others 2001	<i>Pinus flexilis</i> , <i>Pinus ponderosa</i>	15	1727-1920	33
Crooked Cr.	Central CO	Donnegan and others 2001	<i>Pinus aristata</i>	12	1532-1920	56
39 Mile Mtn.	Central CO	Donnegan and others 2001	<i>Pinus aristata</i>	13	1622-1920	19
Round Mtn.	Northern NM	C.D. Allen unpubl.	<i>Pinus aristata</i>	19	1580-1923	59

* Total number of fire-scarred trees sampled.

† Number of trees used for calculation of MFIs as follows: Allen, ≥ 2 ; Brown and Schoettle, not provided; Donnegan and others, ≥ 2 ; Sherriff and others, >2 .

Park, used to reconstruct fire history and stand dynamics over the last ca. 1000 years by Brown & Schoettle (2008). This site experienced low-severity fire, apparently maintaining an open canopy, at intervals of 5-155 years from 1106 to 1824. However, fire frequency decreased and tree recruitment of both bristlecone pine and other species increased from the 1600s-1800s, leading to stand density sufficient to support a high-severity fire in 1978 that was outside the range of variation of at least the ca. 1000 years (Brown & Schoettle 2008).

In addition to the high-severity Packer Gulch fire, several other recent historic fires also attest to variability in bristlecone

pine fire regimes in the southern Rocky Mountains. The Badger Mountain (near South Park) and Maes Creek (in the Wet Mountains) fires, also occurring following extremely dry conditions in 1978, led to near-complete mortality in many bristlecone pine stands (Coop & Schoettle 2009). In 2000, the 11760-ha Viveash Fire was primarily a moderate- or high-severity fire in ponderosa pine, mixed conifer, and spruce-fir forests in the southern Sangres. However, the fire was less severe where it entered bristlecone pine stands in the headwaters of Cow Creek. Many of these stands are very open and intermixed with subalpine *Festuca thurberi* grasslands on steep, south-facing slopes. Only scattered



Figure 3. High variation in bristlecone pine stand structure and recent disturbance over short spatial distances in the Cochetopa hills of southern Colorado. This small drainage contains isolated fire-scarred bristlecone pines bordering montane grasslands, a recent (2007) 21-ha., mixed-severity burn and evidence of small patches of historic stand-replacing fire in mixed bristlecone pine, Douglas fir, and spruce stands on more densely forested summits.

individuals and patches of bristlecone pine were killed, leaving most trees undamaged or with scorch marks and/or fire scars (J.D. Coop, personal observation). In the Cochetopa Hills of Colorado, the 21-ha Lujan Ridge fire in 2007 was a mixed-severity burn that appeared to preferentially kill spruce and aspen in a mixed bristlecone pine stand (J.D. Coop, personal observation).

The regeneration response of bristlecone pine to fire also appears to be the subject of some uncertainty. While Baker (1992) concluded that bristlecone pine is a “long-lived pioneer that regenerates primarily after fire”, Brown and Schoettle (2008) found regeneration to be associated with long fire-free intervals, and Cocks and others (2005) reported nearly continuous regeneration over ca. 400 years. It may be these apparent contradictions can be reconciled when the very gradual tempo of regeneration dynamics of this species is considered, particularly at the least productive sites. Open conditions that favor five-needle pine seedling establishment may persist for decades to centuries after disturbance in xeric, high-elevation settings in the southern Rockies (Shankman & Daly 1988; Coop and others 2010). Coop & Schoettle (2009) examined patterns of bristlecone pine regeneration three decades after the stand-replacing fires at Badger Mountain and Maes Creek. Regeneration in these burns was generally poor, and bristlecone pine populations were substantially depressed in burn interiors relative to unburned stands. However, relative to both unburned stands and burn interiors, seedling numbers were elevated near or beneath surviving trees, and total density (of all size classes) was increased in these partially burned patches. This is likely due to propagule limitations related to wind-dispersal, and suggests that mixed-severity or small (≤ 15 m) patches of high-severity fire would be most likely to promote bristlecone pine regeneration. Seedlings also showed strong affinities to “nurse objects” (rocks, fallen logs, live or dead standing boles) that may provide sheltered microenvironments for establishment.

Limber Pine Fire Regimes and Stand Dynamics

The role of fire in limber pine ecosystems in the southern Rockies is perhaps even less well understood than that of bristlecone pine, with the important exception of its ecology in dry subalpine forests of the northern Front Range of northern Colorado. In the Front Range, limber pine is well-known to be an early colonist of high-severity burns, where it forms stable, self-replacing stands on xeric sites and successional stands that over time give way to spruce and fir on more mesic sites (Peet 1981; Veblen 1986; Rebertus and others 1991; Donnegan & Rebertus 1999). Limber pine appears to require a mosaic of successional stages across the landscape generated by infrequent, stand-replacing fire. This ecological role of limber pine is analogous to that described for whitebark pine (*Pinus albicaulis*) in northern Rockies of the continental U.S and southern Canada (Arno 2001). Both species are dispersed by Clark’s nutcrackers, who may

preferentially cache seeds in open sites such as the exposed interiors of large burns (Tomback 2001 and references cited therein). Limber pine stands in this setting display meta-population dynamics, with patches constantly undergoing episodes of colonization, contraction, extinction, and recolonization (Webster and Johnson 2000, Antolin and Schoettle 2001).

Veblen (1986) reconstructed forest development from age cores from several subalpine stands recovering from high-severity fire in the northern Front Range of Colorado. In the two most xeric stands, limber pine was the first post-fire colonist, and dominated recruitment for up to a century before substantial establishment next by lodgepole pine, then Engelmann spruce, and later, subalpine fir. As these other tree species became abundant, limber pine recruitment ceased, probably due to dense shading by competitors. Rebertus and others (1991) also reconstructed temporal and spatial patterns of stand development in ca. 100- and 250-year old burns in the northern Front Range, and found that colonization by limber pine began very soon after fire and continued for at least a century; spruce and fir recruitment lagged behind by several decades. Two old-growth limber pine stands did not show any evidence of stand-replacing disturbance, and showed essentially continuous, albeit limited recruitment, throughout the ca. 400-1000 years for which stand history could be reconstructed. Finally, Donnegan & Rebertus (1999) mapped and collected nearly two thousand increment cores from 25 subalpine forest plots in two watersheds in the northern Front Range to reconstruct spatial and temporal patterns of stand development, and found limber pine was the initial colonist following an extensive (at least ca. 1000 ha.) stand replacing fire that occurred over their entire study area around 1700. Succession to spruce and fir was most rapid on more mesic sites, decreasing with site aridity. Spruce and fir seedlings became preferentially established beneath limber pine trees. Successional rates peaked with high limber pine mortality around 200 years post-fire, which was highest for multi-stemmed limber pine clusters and limber pines that had high spruce and fir establishment in close spatial proximity (Donnegan & Rebertus 1999).

Extensive subalpine stands dominated by limber pine or mixed limber pine/spruce/fir are less common out of the northern Front Range, and it seems unlikely this successional sequence is general of limber pine elsewhere in the southern Rocky Mountains. However, only one other limber pine stand history has been developed anywhere else in this region. Brown & Schoettle (2008) reconstructed nearly 600 years of stand development and fire history of isolated limber pine woodland bordering sagebrush-bunchgrass steppe in North Park. The early part of record shows numerous low-severity fires with a gradual decrease in the 1600’s and 1700’s (MFI = 41 years). The last fire in this stand occurred in 1832, apparently following an episode of mortality caused by bark beetles. Abundant recruitment occurred through the 1800s and early 1900s, stand density increased dramatically, and no further fire in occurred in this stand through the period of settlement, livestock grazing, and fire suppression (Brown & Schoettle 2008).

Frequent, low-severity fires in limber pine stands were also recorded in mixed, high-elevation bristlecone and limber pine stands around South Park by Donnegan and others (2001), and several limber pine-dominated subalpine stands in the Front Range by Sherriff and others (2001; Table 1). As with the bristlecone pine fire chronologies discussed previously, these stands were subjectively chosen for sampling based on the presence of fire scars, and the extent to which any of these are representative of limber pine disturbance regimes across the southern Rockies cannot be determined without substantially more research. Few fire history reconstructions have focused specifically on intermediate *P. flexilis-strobiformis* populations occurring within the broad transition zone between limber pine and southwestern white pine in the San Juans, the Sangres, and the Jemez Mountains. These populations frequently occur as a component of mixed-conifer forests also including ponderosa pine, Douglas fir, and white fir. There is strong evidence for a low-severity, high-frequency fire regime in such forests in the Jemez Mountains, where many fire history reconstructions have included fire-scarred *P. flexilis-strobiformis* intermediates, and indicate a return interval of ca. 4-12 years (Allen, 1989). These ranges are similar to those reported from mixed-conifer stands farther south in Arizona that include a substantial component of *P. strobiformis*. In the Rincon Mountains, MFI's for "open pine forests" (including ponderosa and southwestern white pine) ranged from 6.7-7.3 years and were 9.9 years in mixed conifer forests containing southwestern white pine (Baisan & Swetnam 1990); mixed conifer forests with a southwestern white pine component in the Pinaleño Mountains had an MFI of 6.24 years (Grissino-Mayer and others 1995).

The 1978 Ouzel fire caused stand-replacing tree mortality across a broad swath of Rocky Mountain National Park east of the continental divide, including many areas dominated by limber pine. Consistent with stand reconstructions from the northern Front Range described above, limber pine regeneration has been extensive and ongoing on dry slopes and high elevations in the burn interior, even hundreds of meters from possible seed sources (Coop & Schoettle 2009; Fig. 4). Within thirty years post-fire, limber pine population density in the high-severity burn interior exceeded that in either adjacent or unburned or incompletely burned stands. However, in the 1978 Badger Mountain and Maes Creek burns (near South Park and in the Wet Mountains, respectively, discussed previously) limber pine regeneration in burn interiors was far lower (Coop & Schoettle 2009). At Badger Mountain, where limber pine is mixed with bristlecone pine and Engelmann spruce, recent limber pine regeneration and total population were greatest in burn margins. Limber pine forms monotypic stands on rocky outcrops at moderate elevations at the Maes Creek burn; at this site regeneration was greater outside of the burn perimeter than within. This apparent shift in limber pine regeneration pattern from north to south was not associated with any changes in the frequency of multi-stem clusters and distance from probable seed sources, but was accompanied by a decrease in limber pine seedling height growth (J. D. Coop, unpublished



Figure 4. Recent post-fire limber pine seedling establishment in the interior of the 1978, stand-replacing Ouzel burn, Rocky Mountain National Park, northern Colorado.

data). Thus, rather than any change in dispersal mechanism, variation in post-fire regeneration pattern across these three burns appears more likely related to some fundamental shift in limber pine physiological performance that may be also correspond with the elevational shift across the southern Rockies described by Peet (1978).

Anthropogenic and Climatic Influences on Fire in Bristlecone and Limber Pine Ecosystems

Have recent changes in human land use, including fire suppression, driven changes in stand conditions and fire regimes in southern Rocky Mountain five-needle pine ecosystems? Based on the few fire- and stand-history reconstructions that have been completed, no clear trends emerge, and any effects appear to be variable and context-specific. Where bristlecone and limber pine stands typically experienced infrequent, high-severity fire (such as bristlecone stands characterized by the 300-year rotation interval estimated by Baker 1992 and successional limber pine forests of the northern Front Range), direct fire suppression over

the last century is unlikely to have led to stand-level shifts in structure and composition outside of historic ranges of variation. However, the extent to which fire suppression has driven landscape-level changes in the distribution of mosaics of different successional stages remains an open question. In forest types that experienced infrequent stand-replacing fire, suppression may have reduced the proportion of early-successional landscapes that promoted five-needle pines, leading to decreases in the proportion of five-needle pines across the landscape. This is an important topic in need of further inquiry.

Stands that experienced more frequent, low-severity or mixed-severity fires are more likely to have experienced structural or compositional changes in the absence of recent fire. However, the extent to which such changes have occurred is unknown. In bristlecone, limber, and ponderosa pine stands that recorded many low-severity fires around South Park, Colorado, Donnegan and others (2001) noted increases in fire frequency that began with the large influx of settlers into the region in the mid-late 1800s, followed by a pronounced decline in fire frequency contemporaneous with the onset of fire suppression in the 1900's. However, reductions in fire in the 1900's also correspond with a period of reduced climatic variability (Donnegan and others 2001), and the relative importance of these two factors cannot be determined. Contrasting these findings, subalpine stands that recorded frequent fire in the Front Range (primarily composed of limber pine, but also some bristlecone pine and other tree species, see Table 1) generally showed increased fire in the 1900s compared with the 1800s (Sherriff and others 2001). Only one limber pine stand showed 20th century reductions in fire frequency consistent with anthropogenic fire suppression.

The best documentation of changes in bristlecone and limber pine stand structure attributable to fire suppression is the work done by Cocks and others (2005) in the San Francisco Peaks of northern Arizona. These authors compared modern stand structure (2000) with a dendroecological reconstruction of historic stand structure (1876) along a gradient from low to high elevation to assess the effects of over a century of livestock grazing, timber harvest, and fire suppression. The high-elevation bristlecone pine stands they assessed were the least-changed of any forest type, but the changes were not insubstantial. Bristlecone-dominated forests showed a 92 percent increase in density (from 282.9 to 546.2 trees/ha). These changes were driven primarily by increased abundance of Engelmann spruce which expanded from 19.3 to 169.5 trees/ha; bristlecone density increased from 258.7 to 342.6 trees/ha. Tree density in mixed-conifer forests composed of limber pine (noted to be possible limber-southwestern white pine hybrids) and Douglas fir also showed large increases. All these changes were attributed in large part to fire suppression over the last century (Cocks and others 2005).

Brown and Schoettle (2008) provide clear evidence of gradual infilling of both a bristlecone and limber pine stand following reductions in fire severity. At the Lake John limber pine site, frequent, low-severity fires ended and increases

in stand density began in the mid-1800s and may have been reinforced by livestock grazing and direct fire suppression in the 1900s (Brown & Schoettle 2008). At Packer Gulch, gradual reductions in fire frequency coupled with increased tree recruitment appear to have led to stand conditions conducive to the 1978 high-severity wildfire. These changes began in the 1600s—probably associated with cooler and wetter climatic conditions—and effects of modern fire suppression appear inconsequential at this site (Brown & Schoettle 2008).

The longevity of both bristlecone and limber pine and the presence of fire-scarred trees across the region suggest considerable potential to reconstruct southern Rocky Mountain fire chronologies and assess both human and climatic influences over multi-century time scales. Comparisons of the handful of fire chronologies that have been developed from these species (included Table 1) hint at some regional synchronicity in periods of reduced fire (ca. 1780-1830) and increased fire activity (late 1800's-ca. 1900). However, no fire years appear common to all studies, though samples within particular regions indicate some shared fire years. Donnegan and others (1991) found only three years that showed fire across multiple sites: 1748, 1851, and 1871. However, Sherriff and others (1991) found many years in which fire was recorded across > 20 percent of their sites, including one year (1880) that was recorded by trees in seven of 13 sites. Both of these authors noted that fires occurred primarily in years of decreased precipitation (typically La Niña years), particularly those that followed years of enhanced precipitation (typically, El Niño). Several of these authors also reported fire scars found in latewood or dormancy, suggesting late summer or fall burns. It would undoubtedly be interesting to develop additional chronologies from elsewhere within these species' ranges in the southern Rocky Mountains.

Fire and Management for Resilient Southern Rocky Mountain High-Five Ecosystems

Our knowledge of the role of fire in bristlecone and limber pine ecosystems is substantially incomplete, and further research is necessarily for more informed management. Significant questions remain as to what kinds of pre-settlement fire regimes best characterized these ecosystems generally, how these have changed, and what kinds of fire regimes are most likely to promote these ecosystems. High variability in historic and current stand conditions and characteristic disturbance regimes also suggests there is no "one-size-fits all" prescription for suitable burning regimes in these ecosystems, which may be highly localized and context-dependent.

Regardless of any anthropogenic changes to fire in these systems, re-establishing or maintaining pre-settlement fire regimes may not be as important as determining appropriate disturbance regimes to meet management and conservation objectives given current and projected changes to these

systems. Both bristlecone and limber pine are highly susceptible to declines caused by white pine blister rust and mountain pine beetles (Schoettle 2004; Schoettle and others 2008), as with the rapidly collapsing whitebark pine ecosystems farther north (e.g., Keane & Arno 1993; Logan & Powell 2001). Southern Rocky Mountain five-needle pines are beginning to display the consequences of this vulnerability: by 2010, blister rust had been recorded in both species in Colorado, and limber pine stands across northern Colorado were experiencing high rates of mortality from mountain pine beetles (Burns, personal communication). There appears to be little reason to expect either five-needle pine not to decline substantially across the entire region. Under this scenario, combined with probable warming and drying conditions projected under anthropogenic climate change, there are pressing needs to develop management strategies for resilient bristlecone and limber pine ecosystems. Resilience is the ability of a system, such as a forest ecosystem, to absorb change and persist (e.g., Holling 1973). The appropriate application and prevention of fire may be important tools to promote regeneration, diversify age class structures, alter the balance between these species and their competitors, and conserve valuable stands and seed sources.

In areas currently affected by mountain pine beetle and/or blister rust, there appear to be few management options other than 1) retaining any surviving five-needle pines as seed sources for post-disturbance regeneration and/or 2) replanting five-needle pines where feasible. Mortality from disease and insects may in fact generate suitable habitat for five needle pine regeneration—ranging from small canopy openings to entire beetle-killed landscapes—however, subsequent recolonization is likely to be severely constrained by propagule availability and/or blister rust-induced seedling mortality. Conserving seed sources may require active management to prevent crown fire; reintroducing fire into already heavily impacted systems could be harmful. For example, high-severity fire in areas that have been decimated by beetles or rust might kill surviving seed sources, impeding regeneration, and worse, eliminating valuable genotypes with proven survival capacity. Particularly in areas impacted by white pine blister rust, any surviving trees are likely to have genetic resistance to the pathogen, and their conservation should be a priority. Strategies to protect stands containing valuable seed sources from high-severity fire may include reducing surface fuels and crown density, increasing the height to living branches, and retaining large, fire-resistant trees (e.g., Agee & Skinner 2005). Individual disease-resistant trees can also be protected by removing fuels in their immediate vicinity, water dropping, wet lining, or foil wraps (Murray 2007). As an example, possible disease-resistant whitebark pine trees were identified by field surveys in advance of the Bybee Complex Fire in Oregon; 26 trees were protected by the removal of dead and down fuel and the establishment of hand lines at each tree crown's drip line (Murray 2007). Surviving trees in areas impacted by white pine blister rust may not only benefit from reduced fire risk

but also protection from other hazards—such as mountain pine beetle, for example, through the use of verbenone (e.g., Bentz and others 2005).

Reforestation may also be a useful and/or necessary option to restore southern Rocky Mountain five-needle pine stands in landscapes heavily impacted by insects and disease. Further work identifying and protecting rust-resistant individuals, collecting seeds, developing rust-resistant stock, and outplanting seedlings appear essential. Guidelines for bristlecone and limber pine planting—as have been advanced for whitebark pine (Scott & McCaughey 2006)—may also require development and testing. Spatial associations in recent burns suggest seedlings of both bristlecone and limber pine will benefit when planted adjacent to objects, especially in areas affording shelter by several objects (Coop & Schoettle 2009). In some cases, light burning may be useful to prepare sites for outplanting, though further research specific to bristlecone and limber pine planting is needed.

In stands not yet affected by mountain pine beetle or white pine blister rust, management must balance current concerns with the forecast for significant future declines in five-needle pines due to beetles and/or rust. Proactive management strategies can be developed to mitigate some of the dramatic changes these agents are likely to produce (Schoettle & Sniezko 2007). Rust-resistance screening, protection of rust-resistant populations, and outplanting can be carried out before blister rust arrives at a site. Diversifying age-class structure, particularly through increased abundance of younger cohorts, may serve the twin purposes of 1) facilitating more rapid selection for rust resistance (Schoettle & Sniezko 2007), and 2) ensuring the presence of many small-diameter individuals likely to survive mountain pine beetle attack. The abundant post-fire limber pine regeneration present in the three-decade-old Ouzel burn in Rocky Mountain National Park will represent one of the largest populations of this species remaining at high elevations in the Front Range if current rates of mountain pine beetle mortality in mature trees continue. As such, the appropriate use of burning or mechanical treatments may be useful in boosting regeneration and populations of both five-needle pines prior to the arrival of insects or disease. Treatments that disproportionately remove competing tree species from stands will be most beneficial for five-needle pines. Small openings (< 15 m diameter) are likely to be most effective for promoting bristlecone pine regeneration; much larger openings may be more beneficial for limber pine (Coop & Schoettle 2009). However, the protracted regeneration response to disturbance suggests positive responses of either species may require decades or centuries to be realized. While the current mountain pine beetle outbreak is likely to have played itself out long before then, management to increase regeneration may still mitigate some of the projected consequences of white pine blister rust, which is a longer-term threat. Conversely, in some settings, ongoing, gradual increases in stand density in the absence of fire may best serve the purpose of augmenting five-needle pine populations in

advance of projected disease- or insect-caused mortality. Equally as important, settings that currently hold high densities of younger age classes may prove valuable in the context of mountain pine beetle and blister rust even if they represent recent regeneration that would historically have been constrained by fire. For example, recent and ongoing expansion of bristlecone pine into subalpine grasslands in northern New Mexico is widely held to be a symptom of a collapsed low-severity fire regime, and it may be desirable from a management perspective to return more frequent fire into these systems to conserve these ecologically (and economically) valuable grasslands. However, these populations of bristlecone pine seedlings and saplings may also be considered as a potential buffer against future mountain pine beetle or blister rust mortality.

Concluding Thoughts

Our knowledge of the role of fire in southern Rocky Mountain bristlecone and limber pine ecosystems is substantially incomplete, revealing many directions and opportunities for further research. Bristlecone pine stands appear to have experienced a range of low- to high-severity fire. What proportion of the bristlecone pine ecosystem could be best characterized by any of these regimes, their spatial extent, and how they may have been affected by fire suppression, remain open questions. In some settings, open stands bordering grassy valley bottoms and experiencing one fire regime can give way over short distances (and also over time) to dense, mixed-dominance stands that experienced another. Post-fire regeneration responses tend to be concentrated beneath or near seed sources, and may be protracted over decades. In the absence of fire, stands are likely to exhibit gradual infilling by five-needle pines and more shade-tolerant tree species. Many of these same questions and themes apply to limber pine. While the role of fire in promoting successional stands of limber pine is well known in the Colorado Front Range, this role is unlikely characteristic of the species elsewhere in the southern Rocky Mountains, where limber pine occurs in quite different ecological settings, and very little quantitative research has been conducted. As with bristlecone pine, post-wildfire regeneration dynamics of limber pine also take place on the time scale of decades to centuries.

Management in response to current threats to high-elevation five-needle pines in the southern Rocky Mountains, particularly white pine blister rust and mountain pine beetles, will need to balance a range of concerns and may include both the application and prevention of fire. Restoring pre-settlement fire regimes where they have been altered may be less important than determining the appropriate use of fire in response to current concerns. These concerns also suggest the need for further research. Under the scenario of continued expansion and intensification of white pine blister rust, what would be an optimal age-class distribution for mitigating severe losses in these communities and the services they provide during selection for rust

resistance? How should this distribution be spread across the landscape—diversity at the stand level or in a mosaic of different patches each of uniform age distribution? How would this ideal be different under the scenario of mountain pine beetle attack and/or climate change? Finally, how might management tools, including fire (or the lack thereof), be best used to encourage such conditions? Applied research is needed to gain insight into these questions.

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