Ecological Roles of Five-Needle Pines in Colorado: Potential Consequences of Their Loss

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Abstract—Limber pine (*Pinus flexilis* James) and Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.) are two white pines that grow in Colorado. Limber pine has a broad distribution throughout western North America while bristlecone pine's distribution is almost entirely within the state of Colorado. White pine blister rust (*Cronartium ribicola* J. C. Fisch.) was discovered in Colorado in 1998 and threatens populations of both species. Available information suggests that these species have several important ecological roles, such as (1) occupying and stabilizing dry habitats not likely to be occupied by other, less drought tolerant tree species, (2) defining ecosystem boundaries (treelines), (3) being among the first to colonize a site after fire, especially fires that cover large areas, (4) facilitating the establishment of high elevation late successional species such as Engelmann spruce and subalpine fir and (5) providing diet and habitat for animals. While the rust is not likely to eliminate five-needle pines from Colorado ecosystems, it is likely to impact species' distributions, population dynamics and the functioning of the ecosystems. These changes may well affect (1) the distribution of forested land on the landscape, (2) the reforestation dynamics after fire, (3) the rate and possibly fate of forest succession, and (4) habitat for wildlife. Our incomplete understanding of the ecology, genetic structure and adaptive variation of limber pine and Rocky Mountain bristlecone pine constrain our ability to rapidly develop and implement conservation programs.

Key words: Limber pine, *Pinus flexilis* James, Rocky Mountain bristlecone pine, *Pinus aristata* Engelm., *Cronartium ribicola* J. C. Fisch., regeneration, fire

Limber pine (*Pinus flexilis* James) and Rocky Mountain bristlecone (*Pinus aristata* Engelm.) are two white pine species that grow in Colorado. Limber pine's distribution includes habitats throughout the Rocky Mountains while the distribution of Rocky Mountain bristlecone pine is almost entirely within the state of Colorado. In southern Colorado, it is speculated that a limber pine - southwestern white pine (*Pinus strobiformis*) complex exists. The distribution of southwestern white pine extends south into New Mexico. This paper will focus on limber pine and Rocky Mountain bristlecone pine. These species are white pines (subgenus *Strobus*) yet limber pine is in section *Strobus*, subsection *Strobi* and Rocky Mountain bristlecone pine is in subgenus *Parrya*, subsection *Balfournianae* (Lanner 1990). Their often bushy growth form (fig. 1) and slow growth rate combined with the inaccessibility of the rocky sites that they dominate make them poor timber species and ones that have long been overlooked by the forestry community. The most basic ecological information, such as the forest cover, has not been quantified for these species in Colorado or throughout their ranges.

The impact of white pine blister rust (*Cronartium ribicola* J. C. Fisch.) on commercial North American white pines has been a focus of attention since its introduction from Europe in the early 1900s. In the mid-1980s, the focus expanded to

Figure 1—Limber pine on a dry site with a bushy growth form with upward reaching branches.

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impacts of the disease to the non-commercial whitebark pine (*Pinus albicaulis* Engelm.) as forest practices shifted toward management of ecosystems. White pine blister rust's threat to whitebark pine and the resultant impacts to the habitat of the endangered grizzly bear (*Ursus arctos horribilis*) have brought whitebark pine ecosystems into view by the management and research community (for example, Schmidt and McDonald 1990, Tomback and others 2001). With the recent discovery of white pine blister rust in Colorado on limber pine in 1998 (Johnson and Jacobi 2000) and Rocky Mountain bristlecone pine in 2003 (Blodgett and Sullivan 2004), both limber pine and Rocky Mountain bristlecone pine populations are threatened. To predict the impacts of white pine blister rust on Colorado ecosystems, we must first understand the role of these five-needle pines in the absence of the rust. It is not clear how similar the ecological roles of limber pine and bristlecone pine are to the more studied whitebark pine. Therefore, in the interest of brevity, this paper will focus on research conducted on limber pine and Rocky Mountain bristlecone pine, recognizing that some information from other species may be applicable but will not be summarized here. This paper will discuss what is currently known about the ecology of limber pine and Rocky Mountain bristlecone pine in the central Rocky Mountains and the possible repercussions of white pine blister rust on these ecosystems.

Limber Pine _____

Limber pine is a species whose distribution has changed from continuous to patchy and presently displays metapopulation dynamics (Webster and Johnson 2000, Antolin and Schoettle 2001). Approximately 14,000 years ago, at the last glacial maximum, limber pine was widespread along the eastern slope of the Colorado Front Range in the central Rocky Mountains (Wells and Stewart 1987). Currently limber pine is characterized by a patchy distribution, spanning a broad latitudinal and elevational range (Burns and Honkala 1990) (fig. 2). In the central Rocky Mountains limber pine grows from below the lower tree line up to the upper tree line, from ~ 1600 m in the short grass steppe to > 3300 m at Rollins Pass near the continental divide (Schoettle and Rochelle 2000). Limber pine's elevational range is wider than any of its co-occurring tree species in this region (table 1). In the northern Rocky Mountains and west, limber pine is generally found at lower elevations with whitebark pine occupying the higher elevations. In the southern mountains limber pine grows at high-elevation sites with the lower elevations occupied by southwestern white pine (*Pinus strobiformis* Engelm.).

Limber pine is similar to the stone pines (subsection *Cembrae*) in so much as it has large wingless (or near wingless) seeds that depend on corvid species (for example, Clark's nutcracker, *Nucifraga columbiana* Wilson) for dispersal (Lanner and Vander Wall 1980). In contrast to the stone pines, which have indehiscent cones necessitating animals to extract the seed, limber pine cones open when dry. As for whitebark pine, seeds of limber pine can be an important food source for corvids (Tomback and Kramer 1980), black and grizzly bears (*Ursus* spp.; Kendell 1983, McCutchen 1996), red squirrels (*Tamaisciurus hudsonicus*; Hutchins and Lanner 1982) and other small rodents. The role of limber pine forests as habitat for wildlife species is unknown. The phloem, cones and seeds all provide habitat and diet for arthropod fauna (Hedlin and others 1981, Cerezke 1995, Schoettle and Négron 2001).

Limber Pine Stand Dynamics

Limber pine is often the first species to colonize an area after fire (Donnegan and Rebertus 1999). Clark's nutcrackers can cache seed many kilometers from the parent tree (Vander Wall and Balda 1977), enhancing seed dispersal across the landscape as well as into the central areas of large burns where wind-dispersed seeds of other conifer species are scarce (Tomback and others 1993). The germination of multiple seeds from one cache results in a cluster of seedlings that are often related (Carsey and Tomback 1994). The clustered distribution of seedlings facilitates successful establishment of limber pine (Donnegan and Rebertus 1999). However, as the trees mature, the clustered distribution may reduce the reproductive output (Feldman and others 1999) and lifespan of the individuals (Donnegan and Rebertus 1999) compared to trees growing singly.

The dynamic of stands containing limber pine depends on the site; limber pine form sustainable stands on dry rocky sites and tend to be limited to early succession on more mesic sites. Dry sites can be occupied by limber pine at any elevation within the species range and are often windswept and accumulate little snow. Limber pine dominates xeric sites not because they provide the optimal physical environment for limber pine growth (Lepper 1974, Schoettle and Rochelle 2000) but because the conditions are not suitable for the growth of other species and therefore competition is minimal. Competition is likely to be the largest limitation defining the realized niche of limber pine and the location of sustainable limber pine stands. On dry sites, maximum tree ages have been reported of more than 1500 years for limber pine in Colorado (Schuster and others 1995) and over 2000 years for individuals in Nevada and California (Lanner 1984). The stands tend to be low density, open, and support continual recruitment of limber pine (Knowles and Grant 1983, Stohlgren and Bachand 1997). Upon sexual maturity, which may take over 50 years (personal observation), limber pine on dry sites can produce large cone crops. Loss of apical dominance due to leader damage provides many cone bearing branches per tree. The frequency of mast years, the environmental factors that affect their periodicity, and the repercussions of them on the population dynamics of animal species deserve research attention. In addition to the extreme longevity of individuals, the lack of competing tree species and sustained regeneration, the persistence of these limber pine stands is also possible because catastrophic disturbance (i.e. wildfire) is rare on dry, rocky sites.

While rocky ridges and dry slopes are the most obvious habitat occupied by limber pine, scattered occurrence of limber pine throughout the forested region of the Colorado Front Range is typical (Marr 1961, Schoettle and Rochelle 2000). On these more mesic sites, limber pine's early post-disturbance dominance succeeds over time to other conifer species (Rebertus and others 1991). Limber pine acts as a nurse tree, mitigating the harsh open environment after disturbances and facilitating the establishment of Engelmann spruce and subalpine fir (Rebertus and others 1991,
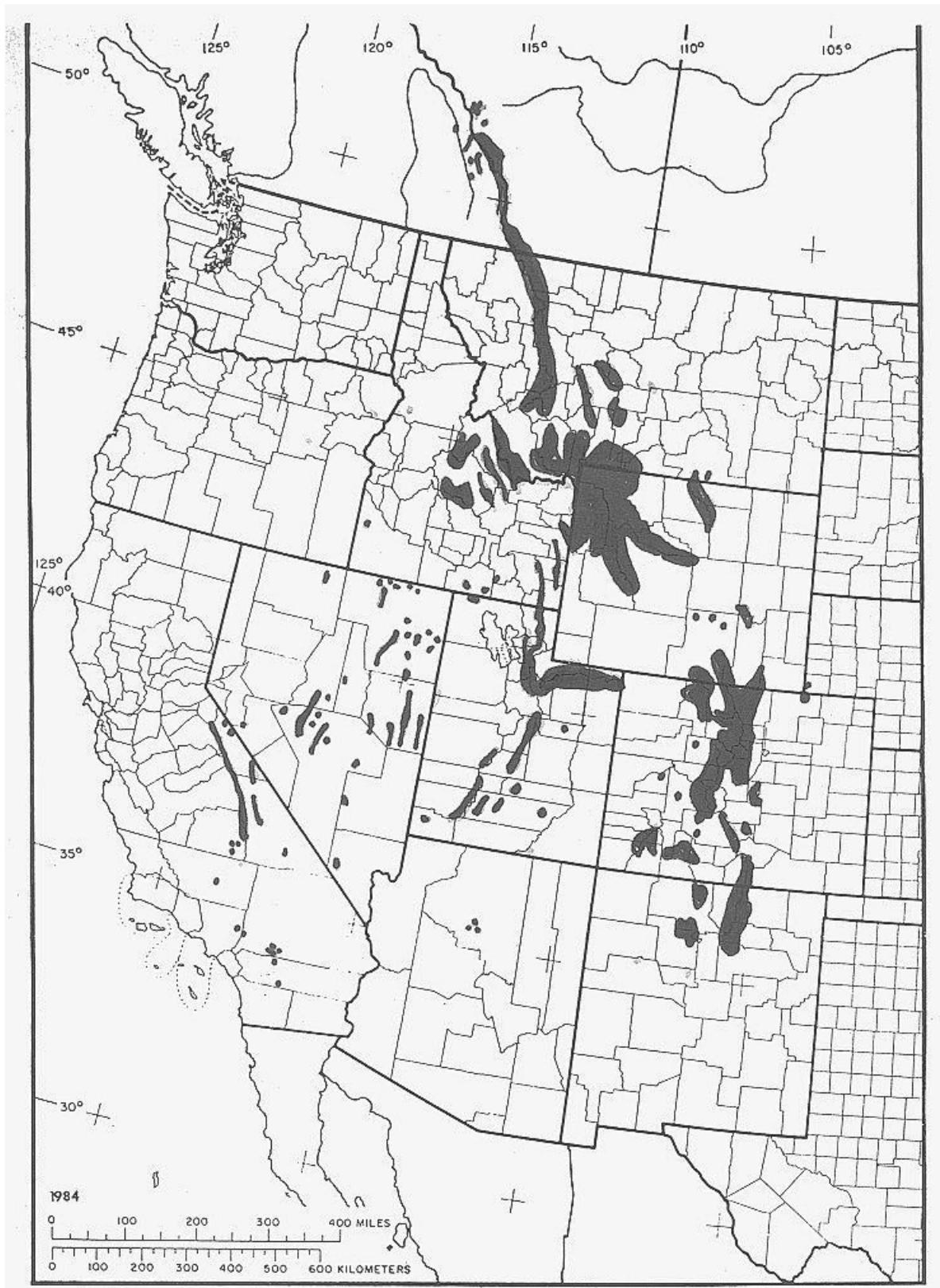
Figure 2—Distribution of limber pine (*Pinus flexilis* James). (From Burns and Honkala 1990)

Table 1—Elevation ranges of tree species in Colorado. Data from Peet (1981) and Baker (1992).

Scientific name	Common name	Elevation range (m)
Pinus flexilis James	Limber pine	1600-3400
Juniperus scopulorum Sarg.	Rocky Mountain juniper	1600-2800
Pinus ponderosa Dougl. ex Laws.	Ponderosa pine	1700-2800
Pseudotsuga menziesii (Mirb.) Franco	Douglas-fir	1700-3000
Populus tremuloides Michx.	Quaking aspen	2000-3400
Pinus contorta Dougl. ssp. *latifolia* Bailey	Lodgepole pine	2300-3300
Picea engelmannii Perry ex Engelm.	Engelmann spruce	2400-3500
Pinus aristata Engelm.	Rocky Mountain bristlecone pine	2750-3670
Abies lasiocarpa (Hook.) Nutt.	Subalpine fir	2500-3500

Donnegan and Rebertus 1999). Such facilitation accelerates limber pine's mortality due to the close proximity of, and competition by, the succeeding species. Seedlings of limber pine occur frequently throughout all stand types along the elevational gradient, yet successful establishment in late successional stands on mesic sites is rare (Stohlgren and others 1998).

Seral limber pine is likely to maintain apical dominance and retain an erect forest tree form and is suspected to produce fewer cones per tree than those trees on drier sites (Lepper 1974). Seed yields for limber pine can also be reduced by some of the same cone and seed insects that affect co-occurring conifer species (Hedlin and others 1981, Schoettle and Négron 2001). Due to the lower seed yields of successional stands, it is unclear what proportion of seed from these sites is consumed on site by animals versus dispersed and cached. Therefore, the relative contribution of progeny from seral compared to persistent limber pine stands to the recolonization of nearby disturbances has not yet been established.

Limber Pine Population Genetics

Despite limber pine's wide range and patchy distribution, it shows little genetic differentiation related to elevational changes (Latta and Mitton 1997, Schuster and others 1989, Schuster and Mitton 1991, 2000). Other species with long distance dispersal of seed by birds show similar apparent lack of genetic structure (Bruederle and others 1998). This is in contrast to species that depend on the wind for dispersal of seed; these species show not only local genetic differentiation, but also differentiation within local populations (see Rehfeldt 1997). Genetic studies of limber pine indicate that within local populations, pollen is dispersed evenly among trees (Schuster and Mitton 2000) but that seed dispersal patterns result in local clusters of related individuals (Schuster and Mitton 1991). Differences in pollen phenology along elevation gradients could limit gene flow via pollen between local populations (Schuster and others 1989), but low between-population differentiation suggests gene flow by stepping-stone pollination across intermediate populations. Long-distance seed dispersal by birds (Lanner and Vander Wall 1980) also contributes to gene flow across the elevation gradient. Currently, the only large genetic differences in limber pine that have been identified are on a

regional geographic scale that may reflect isolation in Pleistocene refugia on the Great Plains east of the Rocky Mountains and in the Great Basin west of the Rocky Mountains (Latta and Mitton 1997; Mitton and others 2000).

Limber pine appears to be a genetic generalist based on presumably selectively neutral genetic markers, yet extensive common garden and genetic by environment interaction experiments have not been conducted to evaluate local adaptation. One common garden study of several seed sources for limber pine suggests some geographic variation in seedling growth characteristics (Heit 1973). Seed transfer rules for limber pine have not been established.

Limber Pine Adaptive Variation

Despite living in metapopulations along a broad elevational gradient, limber pine shows remarkably low morphological variation (Schoettle and Rochelle 2000). The genetic basis for the morphological variation or lack thereof has not yet been assessed. Schoettle and Rochelle (2000) hypothesized that if limber pine lacked elevational races, the environmental effect of elevation on growth and resultant phenotype would be greater for limber pine than for species that have undergone adaptations to local environments. Contrary to this hypothesis, the environmental stress of increasing elevation that is apparent in the growth patterns of other tree species was less obvious for limber pine (fig. 3). Leaf longevity, ranging from 4 to 10 years, was one of the few characteristics to vary along an elevational gradient (Schoettle and Rochelle 2000). Limber pine appears less stressed than other species by the environmental gradients associated with elevation (Schoettle and Rochelle 2000).

How can limber pine uncouple its growth from the environmental differences from the upper to the lower tree line? The rates of most physiological and biochemical processes are a function of temperature. Limber pine seedlings from four of five populations from Wyoming, Nevada and California revealed a typical photosynthetic temperature optimum (15 °C) but an unusually broad response curve with a variation in photosynthetic rate of only 12 percent from the maximum over the temperature range of 10-35 °C (Lepper 1980). This is in contrast to the sharper temperature response of photosynthesis of balsam fir (*Abies balsamea* (L.) Mill., Fryer and Ledig 1972) and Great Basin bristlecone pine (then called *Pinus aristata* Engelm. but now recognized
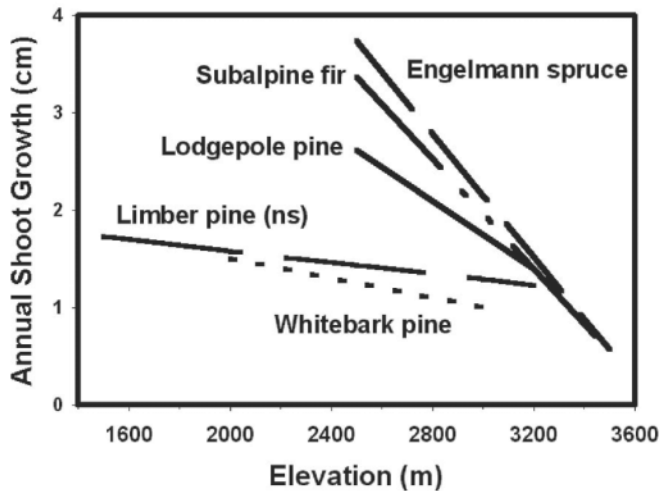
Figure 3—Effect of elevation on the annual twig growth of mature conifers. Data for Engelmann spruce and subalpine fir are from Hansen-Bristow (1986), limber pine are from Schoettle and Rochelle (2000), and lodgepole and whitebark pine are from Schoettle (unpublished data). (Adapted from table 7 of Schoettle and Rochelle, 2000)

as *Pinus longaeva* Bailey) according to Bailey (1970) Mooney and others (1964) where photosynthesis fell 63 percent and 87 percent, respectively, below the maximum rates within the range of 5 °C below and 20 °C above the optimum temperature for photosynthesis (fig. 4). Strong variation in photosynthetic capacity between mature trees at the elevational extremes (Schoettle, unpublished data) also suggests considerable adaptive physiological variation for limber pine. Limber pine also has a high degree of variation in other physiological traits, both among individuals as well as within individuals (Barrick and Schoettle 1996, Schoettle
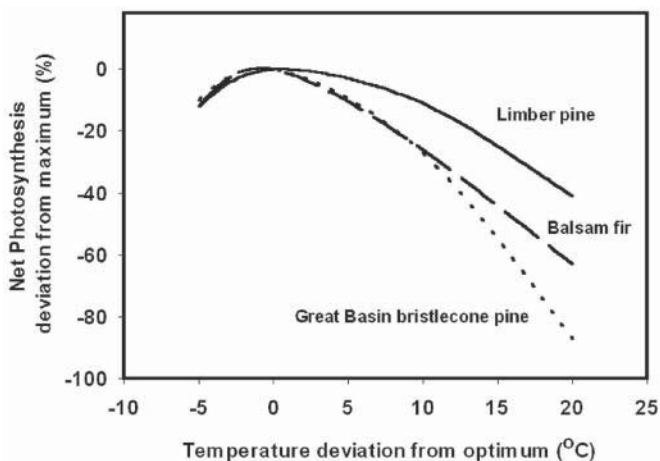

Figure 4—Relative temperature response of net photosynthesis of seedlings of three conifer species. The optimum temperature for photosynthesis for each species is that temperature that the maximum rate of photosynthesis was recorded. To enable comparison among species, photosynthesis is expressed as a percentage reduction from the maximum rate.

and Rochelle 1996). Therefore physiological plasticity or broad physiological tolerances appear to contribute to limber pine's wide fundamental niche with respect to temperature.

Limber pine seedlings, similar to the stone pines, have large root to shoot ratios. How or if this allocation pattern varies among habitats hasn't been studied. This pattern of carbon allocation is often associated with shade intolerance as well as drought tolerance and avoidance. Both limber pine seedlings and mature trees demonstrate drought tolerant behavior, compared to co-occurring species, by maintaining leaf gas exchange even under severe soil drying (Lepper 1980; Pataki and others 2000). The hypothesis that, on xeric sites, the long roots of limber pine are able to access ground water sources not within reach of other conifer species has not been tested. Mature limber pine also demonstrates drought avoidance behavior by closing its stomata more readily than associated species during periods of atmospheric dryness (high vapor pressure deficit) (McNaughton 1984, Pataki and others 2000). Stomatal closure may prevent xylem cavitation but also sacrifices photosynthetic carbon gain; this pattern of water conservation at the expense of carbon assimilation may contribute to limber pine's poor competitive abilities.

Limber pine may be a case where turnover of local populations, combined with high dispersal and gene flow, results in evolution of a generalist lifestyle capable of tolerating a wide variety of environmental circumstances (Schoettle and Rochelle 2000; Antolin and Schoettle 2001). It is unclear at this time if being a poor competitor is the "cost" associated with the generalist lifestyle for limber pine.

Rocky Mountain Bristlecone Pine_____

In 1970, Bailey (1970) split the North American bristlecone pine (*Pinus aristata* Engelm.) into two species, the Rocky Mountain bristlecone pine (retaining the name *Pinus aristata* Engelm.) and Great Basin bristlecone pine (newly named *Pinus longaeva* Bailey). Most of the research on bristlecone pines before 1970 was conducted on Great Basin bristlecone pine; very little research has been conducted on Rocky Mountain bristlecone pine. Both species are recognized as charismatic and are appreciated by the public for their majestic and artistic tree form and their extreme longevity (fig. 5). Great Basin bristlecone pine can reach ages in excess of 4,000 years (Schulman 1958, Curry 1965), while the oldest Rocky Mountain bristlecone pine is just over 2,400 years of age (Brunstein and Yamaguchi 1992). Both species of bristlecone pine have been utilized in dendrochronology studies (such as Kreb 1973, LaMarche and Stockton 1974).

The distribution of Rocky Mountain bristlecone pine is primarily in Colorado and extends south into New Mexico along the Sangre de Cristo Mountains and includes a disjunct population on the San Francisco Peaks in central Arizona (fig. 6). It is thought that during the Pleistocene glacial periods there was nearly continuous habitat for bristlecone pine between the New Mexico and Arizona stands, suggesting that the Arizona stand is a relic of a formerly larger distribution (Bailey 1970). The current southern distribution of bristlecone pine appears limited by suitable habitat, however it is not known what limits bristlecone pine
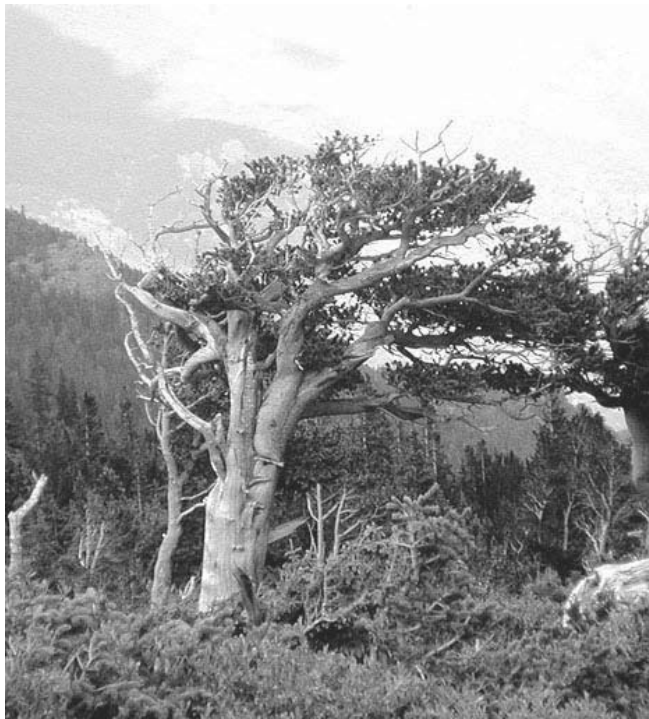
Figure 5—Rocky Mountain bristlecone pine near treeline in central Colorado. Note partial cambial dieback (see fig. 7).

from occupying apparently suitable habitat to its north. The distribution of this species may reflect a dependence on summer monsoons, restricting it from occupying higher elevation sites in northern Colorado. Rocky Mountain bristlecone pine (referred to as bristlecone pine hereafter) has a narrow elevation range and is primarily a high elevation species occupying dry sites from 2750 to 3670 m elevation (Baker 1992). Bristlecone pine forests may contain limber pine, Engelmann spruce, subalpine fir, quaking aspen, and Douglas fir.

Bristlecone Pine Stand Dynamics

The origin of bristlecone pine stands throughout Colorado is related to episodes of drought and presumably peak fire occurrence (Baker 1992). Bristlecone pine is a long-lived species that regenerates well after fires. Bristlecone pine has been identified as a component of two climax vegetation types (DeVelice and others 1986). The first is dominated by bristlecone pine with or without Engelmann spruce with an understory of *Festuca*. These sites are open and park-like. This habitat type transitions into one where bristlecone pine succeeds to the more shade tolerant spruce's competitive edge on moister sites (Moir and Ludwig 1979). On lower elevation sites, bristlecone pine dominates or co-dominates stands with Douglas fir. Using a different approach based on environmental variables and species distributions, Baker (1992) characterized sixty-five bristlecone pine stands into 6 forest structures that are distinguished by (1) the time since the last disturbance (age of the oldest tree in the stand),

(2) presence of young quaking aspen, and (3) relative amounts and sizes of Engelmann spruce and subalpine fir (Baker 1992). Baker (1992) reports that bristlecone pine regenerates well only on recently burned sites and therefore attributes the persistence of old stands of bristlecone not to climax stand dynamics but to the long lifespan of the individual pioneer trees in the absence of competition and fire. However, Baker's data reveal some bristlecone pine regeneration in most of the sampled bristlecone pine stands. This raises the question of how much regeneration is necessary to sustain bristlecone pine on sites with little to no competition.

Regardless of whether one subscribes to climax vegetation theory or not for very long-lived species, it is clear that the rate of succession from bristlecone pine to other species varies with site and the transition may proceed very slowly (>1000 yrs) on dry high elevation sites and may be pre-empted by disturbance. Ranne and others (1997) followed up on Baker's work and characterized the vegetation characteristics of the six bristlecone pine forest groups. Vegetation in bristlecone forests is influenced primarily by elevation and soil pH and secondarily by substrate, soil texture, topographic position, and geographic location (Ranne and others 1997).

The relative role of wind versus animal-dispersal of seeds for bristlecone pine regeneration within existing stands and colonization of burned areas is not known. Bird-dispersal of seeds appears common at higher elevations while wind-dispersal may predominate at lower elevations for Great Basin bristlecone pine (Lanner 1988). Clustered individuals, indicative of animal-mediated seed dispersal, are apparent in mature high elevation Rocky Mountain bristlecone pine stands in central Colorado (Torick and others 1996), as well as in the young seedlings establishing in those stands (personal observation, 2001). The frequency of clustered individuals on sites that have been recently burned, those at lower elevation stands or those in southern Colorado has not been assessed. Therefore it is not clear if long-distance animal-mediated seed dispersal of bristlecone pine plays a major role in recolonization of disturbed areas.

Although bristlecone pine is a pioneer species after fire, its role in mediating the environment to facilitate the establishment of late successional species has not been fully explored. At the forest - alpine ecotone, bristlecone pine growing in the krummholz form facilitate the establishment of Engelmann spruce and subalpine fir (personal observation). In the subalpine zone, bristlecone pine forests tend to have relatively clear boundaries with bristlecone pine densities abruptly falling as elevation decreases and moisture regimes change.

Although bristlecone pine has delayed sexual maturity, its extreme longevity enables each tree to be a seed source for many years. During a good cone year, cone production per tree appears to increase with increasing elevation within a stand, including good production by krummholz trees at tree line (Schoettle, unpublished data, 2001). The gradient in cone production may be a function of differences in the number of cones initiated or rates of cone damage or abortion. Cone insects were common on low elevation trees and absent from trees growing at the higher elevations (personal observation, 2001), similar to the findings for limber pine (Schoettle and Négron 2001). As with limber pine, squirrels are very efficient at harvesting bristlecone pine cones and create large cone caches within the forests. Again, similar to
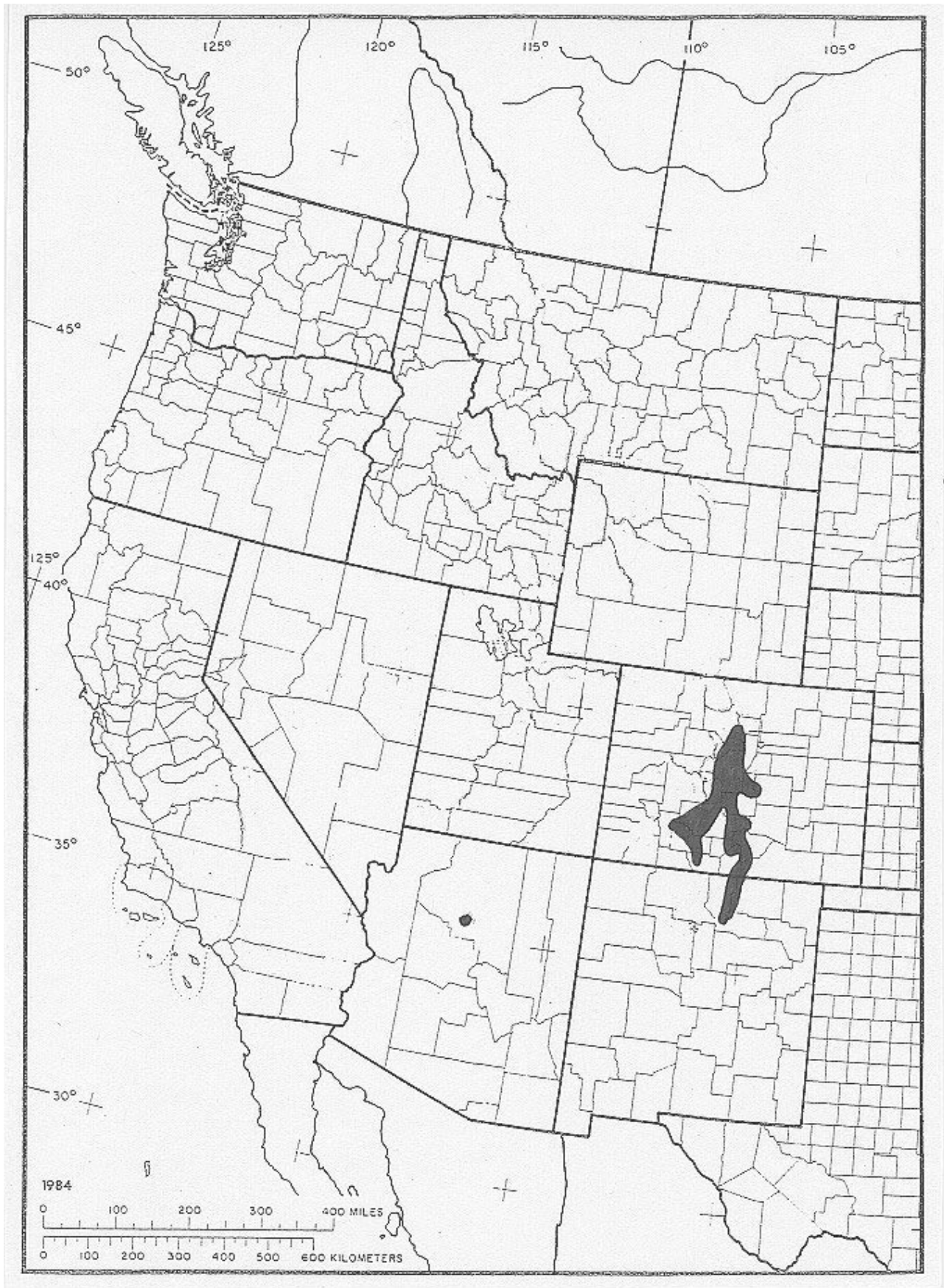
Figure 6—Perimeter of the distribution of Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.) based on data from Bailey (1970), Brunstein and Yamaguchi (1992) and Ranne and others (1997).

limber pine, the frequency of mast years, the environmental factors that affect their periodicity, and the repercussions of them on the population dynamics of animal species deserve research attention.

Bristlecone Pine Population Genetics

Very little is known about the population genetics of bristlecone pine. Recent research has shown that stands as close as 11 km from one another near the northern extreme of the species distribution differed from one another in allele frequencies and the distribution and presence of certain alleles, suggesting a strong founders effect (Oline 2001). This pattern may suggest that long-distance transport of seed by birds for this otherwise wind-dispersed species may play a significant role in the establishment of bristlecone pine stands. As mentioned above, the caching behavior of birds also results in fine scale genetic structure for bristlecone pine, similar to that of the other bird-dispersed pines (Torick and others 1996). As with limber pine, common garden and genetic by environment interaction experiments have not been conducted for bristlecone pine.

Bristlecone Pine Adaptive Variation

Phenotypic variation associated with elevation has been observed for bristlecone pine (Ewers and Schmid 1981) yet the genetic basis for the differences has not been studied. Bristlecone pine has several traits that may contribute to its longevity. This species has considerable plasticity with respect to leaf longevity, ranging from 7 to over 15 years, and has the unusual ability to maintain high physiological function of leaves as they age. Both of these traits may contribute to the absence of growth declines in aging bristlecone pine trees that are commonly observed in other species (Schoettle 1994). Bristlecone pine and limber pine both express partial cambial dieback, resulting in a strip of dead bark extending from dead roots to dead branches (fig. 7) (Schauer and others 2001). It is speculated that partial cambial dieback contributes to the exceptional longevity of individuals by effectively isolating damaged roots, stem or branches from remaining healthy tissues and thereby maintaining a favorable photosynthetic to non-photosynthetic tissue ratio (Schulman 1954, LaMarche 1969).

Similar to limber pine, bristlecone pine seedlings allocate a large amount of resources below ground. How this allocation pattern affects the performance of seedlings regarding stress tolerance or competitive abilities has not been studied, yet this pattern is usually reflective of poor shade tolerance (Tilman 1988).

Threat of White Pine Blister Rust _____

The most immediate threat to limber pine and bristlecone pine is the exotic disease white pine blister rust caused by the fungus *Cronartium ribicola* J.C. Fisch. This pathogen was introduced into North America in the early 1900s and has caused significant impacts to white pines throughout North America. For a summary of the biology of the rust and
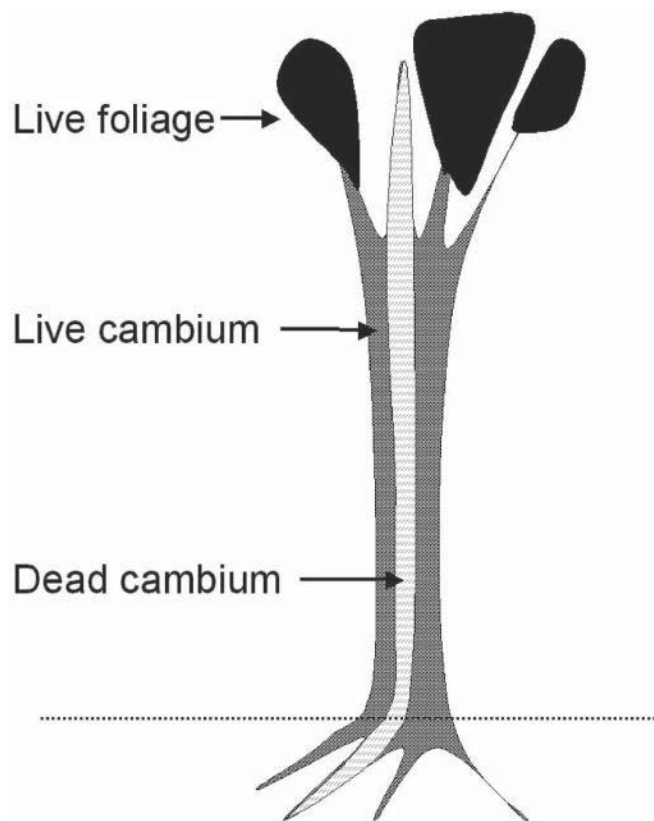

Figure 7—Schematic of partial cambial dieback. Note that the dead cambial strip connects a dead root with a dead branch.

the impacts of this disease to white pines, see McDonald and Hoff (2001). The rust has been affecting limber pine since 1945 in the Northern Rocky Mountains and down into southern Wyoming since the 1970s (Brown 1978) and was identified in Colorado in 1998 (Johnson and Jacobi 2000). White pine blister rust was first reported on Rocky Mountain bristlecone pine in 2003 in the Sangre De Cristo Mountains of Colorado (Blodgett and Sullivan 2004).

The white pine blister rust spores enter trees through the stomatal openings of young leaves (McDonald and Hoff 2001). The effectiveness of older leaves as infection sites needs to be assessed for Colorado white pines since more than 90 percent of their foliage is greater than 1 year old (Schoettle 1994). The rust causes cankers that girdle the infected branch or stem killing the distal tissue. Cankers on the main stem of a tree will usually kill the individual. Branch cankers often will not kill the tree until the reduction in leaf area is so great that the tree cannot survive or the canker grows to affect the main stem. The contribution of rust-caused branch mortality to an increase in sensitivity of the tree to other stresses such as drought, competition, and bark beetle attacks deserves research attention to fully assess the impacts of the disease. Very old trees that have significant partial cambial dieback, such that all of the tree's surviving foliage is supported on a few branches, may be rapidly killed by white pine blister rust. Alternatively, it is possible that those trees that support foliage on many

upwards-reaching branches may prolong the time between canker formation and tree mortality.

Effects of white pine blister rust on recolonization of disturbed areas may well precede the mortality of existing, mature white pine trees (fig. 8). While a tree may survive with white pine blister rust cankers it is likely to experience substantial branch mortality and reduced cone and seed production. If seed yields are low, it is unclear if Clark's nutcrackers will visit and cache seeds from these stands. In addition, even if seed is available for colonization and regeneration, white pine blister rust exerts strong selective pressure at the seedling – sapling stage and can cause high rates of seedling mortality within several years of infection.

White pine blister rust has its own set of environmental constraints as influenced by the tolerances of its biology as well as the distribution of its two hosts, the five-needle pines and *Ribes* spp. The degree of overlap between the rust's potential habitat with that of limber pine and bristlecone pine's distributions has not been fully defined. While the selective pressure exerted by the rust on these five-needle pines will not be uniform across their distribution, existing information on *Ribes* distributions suggests that it may be extensive; three-fourths of the limber pine sites sampled along the elevation gradient of Colorado's Front Range contained *Ribes* spp. (8 of 12 stands; Schoettle and Rochelle 2000) and more than half of the bristlecone pine sites evaluated by Ranne and others (1997) contained *Ribes* spp. (27 of 50 stands). Many of these stands support *Ribes cereum* Douglas, a species that has been thought to be a poor

alternate host for white pine blister rust in other parts of North America (Van Arsdel and others 1998), yet it may serve as a host for the disease in Colorado, southern Wyoming and South Dakota (Lundquist and others 1992, Johnson and Jacobi 2000). *Ribes* spp. may also be present and be potential sources of blister rust spores near white pine stands that do not support it directly. Long-distance dispersal of white pine blister rust spores needs research attention before it will be possible to assess the risk to white pine patches based on the spatial relationships among hosts and the rust.

The white pine populations in other parts of North America that have been severely affected by white pine blister rust have all shown some level of genetic resistance to the disease (e.g. Hoff and others 1980, Kinloch and Dupper 2002, Sniezko and others this proceedings). A bulk seed lot from one Colorado Front Range limber pine population showed evidence of the presence of a hypersensitive reaction to the rust at moderate frequencies, although the bulk seed lot precluded an estimation of the incidence or inheritance of the resistance mechanism within the population (Kinloch and Dupper 2002). No data is currently available on the presence of other resistance mechanisms in limber pine. The loss or near loss of limber pine on xeric sites will likely transition the sites to treeless vegetation communities with currently unknown implications on slope stability, hydrology and wildlife. The impact of the loss of nurse trees on the establishment success of late successional species on mesic sites has yet to be understood. Exclusion of limber pine from some
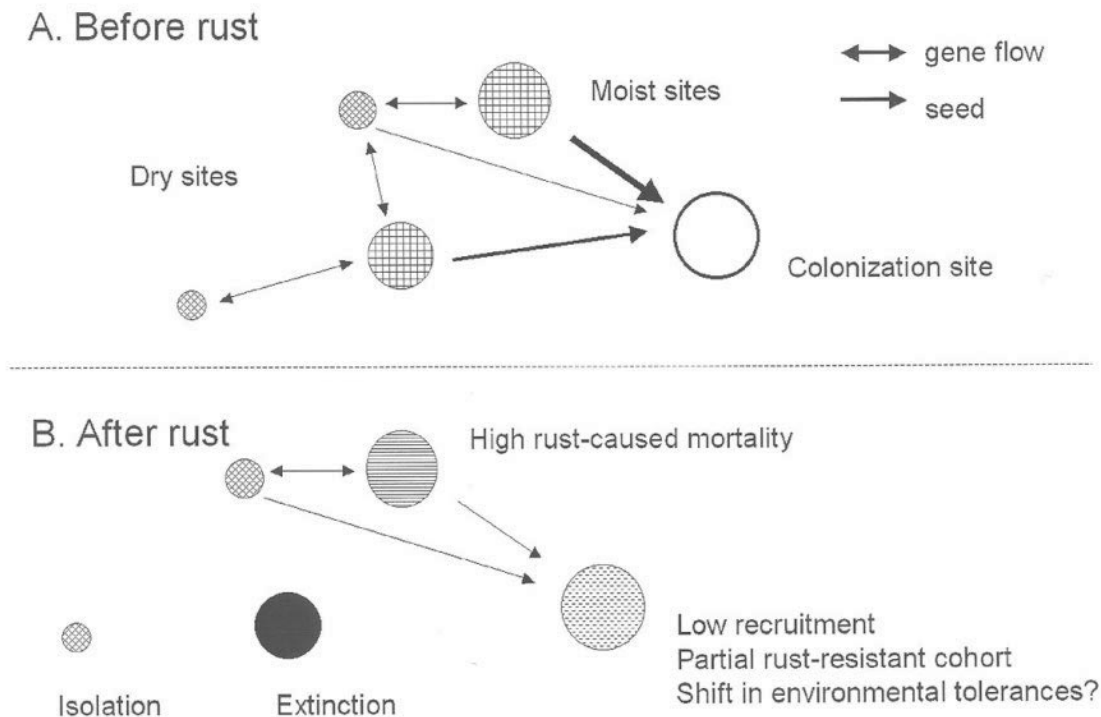

Figure 8—Schematic of potential effects of white pine blister rust on limber pine and bristlecone pine populations. The rust may cause extinction of some stands and isolation of others while also affecting reforestation of disturbed sites. See text for further discussion.

habitats by the selective pressure of the blister rust may isolate surviving patches with implications on gene flow among patches and recolonization success of forest disturbances (fig. 8). As a result, the extinction rate of limber pine patches, although already different for persistent and seral patches, is likely to be disrupted by this exotic disease with implications on the genetic structure of the limber pine metapopulation. The impacts of white pine blister rust on high elevation stands of bristlecone pine will likely lower treeline in those locations and transition the cover to a subalpine understory/alpine species mixture. The presence, nature, and geographic distribution of resistance mechanisms in bristlecone pine have not been studied.

In addition to the obvious population effects of rust-caused tree mortality, the rust may also affect the environmental tolerances of the future rust-resistant population. It is well known in plant ecology that the allocation of resources to defense, be it from herbivory or pests and pathogens, diverts resources from other plant functions. It is not known if the physiological cost on the part of the white pines associated with expressing resistance to white pine blister rust may alter a tree's sensitivity to environmental stresses, potentially causing the rust-resistant trees to have a different fundamental niche from that of the original population. After being challenged by white pine blister rust, the resultant populations of limber pine and bristlecone pine may have a different suite of environmental tolerance and competitive abilities than we see today.

Interaction of Five-Needle Pines, White Pine Blister Rust, and a Changing Fire Regime

The effects of white pine blister rust on five-needle pines will interact with the changing fire regimes in the Rocky Mountains. As fire regimes get more frequent and unpredictable due to past fire suppression and forest practices, large wildfires may jeopardize the usually less-flammable five-needle pine ecosystems on dry sites. In addition, branch and tree mortality caused by white pine blister rust may contribute to fuel loading in white pine stands, increasing the susceptibility of these stands to sustain and be consumed by fire. In the event of larger fires, especially those covering a larger area than can be seeded effectively by wind dispersal mechanisms, the loss of bird-dispersed pines as colonizers may be especially pronounced. Alternatively, if fires do not burn five-needle pine dominated stands and white pine blister rust does not affect Clark's nutcracker dispersal and caching behavior, burned areas offer recolonization opportunities for the establishment and natural selection of rust resistant pine genotypes (fig. 8).

Fire regimes may also change as a result of climatic changes in temperature and precipitation patterns. Again depending on the availability of seed and the scale and location of the fires, this may isolate stands or provide colonization opportunities. However, because persistence of limber pine stands is so sensitive to the competitive ability of co-occurring species, the indirect effects of climatic change on the performance of other species may alter the distribution of persistent versus seral limber pine.

Conservation Strategies _____

In the case of Colorado white pines, there are at least two possible conservation goals: (1) conservation of the genetic diversity within each species and (2) attempt to maintain the species' existing distribution by accelerating the establishment of white pine blister rust resistant genotypes across the landscape. It is unclear if selection for rust resistance will result in the loss of some physiological traits from these species; as a result conservation of genetic diversity of each species may be critical for future breeding stock to attempt to restore the traits that confer stress tolerance in these species in the future. Both bristlecone pine and limber pine have the extraordinary capability of surviving in very harsh environments and it is not known if the selective pressure of the blister rust may cause the loss of any of these traits from the surviving populations. Because white pine blister rust has only just entered Colorado and has contributed little to mortality at this time, the opportunity to conserve the full genetic diversity of Colorado limber pine and bristlecone pine populations exists. However, the feasibility of this task is another matter. Until the genetic structures of the natural populations and seed transfer rules have been defined, the only option is to immediately collect and archive seed and pollen from throughout each species geographic range. Concurrent with this approach, seed storage protocols for the species will need to be developed.

Management to accelerate the establishment of white pine blister rust resistant genotypes across the landscape may require silvicultural treatment and identifying resistant individuals and collecting and planting the seed or seedlings from those individuals in disturbed areas (Schoettle, in press). Identifying resistant individuals can be done, as has been done for other white pines, by field assessment in areas already challenged by white pine blister rust or by screening seedlings in nursery trials with artificial inoculations (Sniezko and Kegley, this proceedings).

Summary _____

In summary, both limber pine and bristlecone pine are long-lived species that regenerate well after fires. They can persist on xeric sites and may facilitate establishment of late successional species on more mesic sites. Disturbances throughout the elevational gradient of forested lands open habitat for limber pine and are recolonized by the effective bird dispersal of limber pine seed. Disturbances in the higher elevations open possible habitat for bristlecone pine. The genetic structure has not been defined for either species, yet limber pine may be more of a genetic generalist than bristlecone pine, and displays metapopulation dynamics. Both species are poor competitors and dominate sites that are not suitable for other species. It is unclear at this time if being a poor competitor is the "cost" associated with the stress tolerant behavior of both species and the generalist lifestyle for limber pine.

The currently available information on limber pine and bristlecone pine suggests that these species have several important ecological roles in Colorado ecosystems. (1) These white pines are exceptionally stress tolerant and occupy and

stabilize habitats not likely to be occupied by other, less tolerant tree species. (2) Often these species define ecosystem boundaries (treelines). (3) These species are among the first to colonize a site after fire, especially fires that cover large areas. (4) Limber pine, and possibly bristlecone pine, facilitate the establishment of high elevation late successional species such as Engelmann spruce. (5) The seeds of both five-needle pines provide a dietary component for several animal species, and the stands likely also provide habitat for other species.

The recent discovery of white pine blister rust in Colorado threatens limber pine and bristlecone pine populations. While the rust is not likely to eliminate the five-needle pines from Colorado ecosystems, it is likely to impact species' distributions, population dynamics and the functioning of the ecosystems. The rust may cause local population extinctions as well as greatly reduce genetic diversity and alter environmental tolerances of the species. The reduction in effective population numbers may hinder the evolutionary development or render local populations even more subject to risk. Changing fire regimes resulting from management or climatic changes will contribute to determining the future importance of the ecological role of white pines. In addition, change in the competitive interactions among Rocky Mountain conifers as a result of climatic changes may affect the future of these landscapes. The interaction of these factors with the stress of this exotic pathogen may well affect (1) the distribution of forested land on the landscape, (2) the reforestation dynamics after fire, (3) the rate and possibly fate of forest succession, and (4) habitat for wildlife. Our incomplete understanding of the ecology, genetic structure and adaptive variation of limber pine and bristlecone pine constrain our ability to rapidly develop and implement conservation programs.

References _____

Antolin, M.F. and Schoettle, A.W. 2001. Fragments, extinctions, and recolonization: the genetics of metapopulations. Pp. 37-46 *in* D. Joyce and J.D. Simpson, eds. Proceedings of the 27th Biennial Conference of the Canadian Tree Improvement Association. Natural Resources Canada, Fredricton, NB Canada.

Bailey, D.K. 1970. Phytogeography and taxonomy of *Pinus* subsection *Balfourianae*. Ann. Mo. Bot. Gard. 57:210-249.

Baker, W.L. 1992. Structure, disturbance, and change in the bristlecone pine forests of Colorado, USA. Arctic and Alpine Research 24:17-26.

Barrick, K. A. and Schoettle, A.W. 1996. A comparison of the foliar nutrient status of elfinwood and symmetrically formed tall trees, Colorado Front Range, USA. Canadian Journal of Botany 74: 1461-1475.

Blodgett, J.T. and Sullivan, K.F. 2004. First report of white pine blister rust on Rocky Mountain bristlecone pine. Plant Disease 88:311.

Brown, D.H. 1978. Extension of the known distribution of *Cronartium ribicola* and *Arceuthobium cyanocarpum* on limber pine in Wyoming. Plant Disease Reporter 62:905.

Bruederle, L.P., Tomback, D.F., Kelly, K.K. and Hardwick, R.C. 1998. Population genetic structure in a bird-dispersed pine, *Pinus albicaulis* (Pinaceae). Can. J. Bot. 76: 83-90.

Brunstein, F.C. and Yamaguchi, D.K. 1992. The oldest known Rocky Mountain bristlecone pines (*Pinus aristata* Engelm.). Arctic and Alpine Research 24:253-256.

Burns, R.M. and Honkala, B.H. 1990. Silvics of North America, vol. 1, Conifers. USDA Forest Service Agricultural Handbook 654.

Carsey, K. S. and Tomback, D.F. 1994. Growth form distribution and genetic relationships in tree clusters of Pinus flexilis, a bird dispersed pine. Oecologia 98: 402-411.

Cerezke, H.F. 1995. Egg gallery, brood production, and adult characteristics of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), in three pine hosts. The Canadian Entomologist 127:955-965.

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

DeVelice, R.L., Ludwig, J.A., Moir, W.H. and Ronco, F. 1986. A classification of forest habitat types of northern New Mexico and southern Colorado. USDA Forest Service General Technical Report RM-131, 59 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Donnegen, J.A. and Rebertus, A.J. 1999. Rates and mechanisms of subalpine forest succession along an environemtal gradient. Ecology 80:1370-1384.

Ewers, F.W. and Schmid, R. 1981. Longevity of needle fascicles of Pinus longaeva (bristlecone pine) and other North American pines. Oecologia 51:107-115.

Feldman, R., Tomback, D.F. and Koehler, J. 1999. Cost of mutualism: competition, tree morphology, and pollen production in limber pine clusters. Ecology 80: 324-329.

Fryer, J.H. and Ledig, F.T. 1972. Microevolution of the photosynthetic temperature optimum in relation to the elevational complex gradient.. Can. J. Bot. 50:1231-1235.

Hansen-Bristow, K. 1986. Influence of increasing elevation on growth characteristics at timberline. Canadian Journal of Botany 64: 2517-2523.

Hedlin, A.F., Yates III, H.O., Tovar, D.C., Ebel, B.H., Koerber, T.W. and Merkel, E.P. 1981. Cone and seed insects of North American conifers. Canadian Forestry Service, United States Forest Service, and Secretaria de Agricultura y Recursos Hidraulicos, Mexico. 122 pp.

Heit, C.E. 1973. Testing and growing limber and Mexican border pines. American Nurseryman 137 (11): 8-9 and 64-74.

Hoff, R.J., Bingham, R.T., McDonald, G.I. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology 10:307-316.

Hutchins, H.E. and Lanner, R.M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55:192-201.

Johnson, D.W., Jacobi, W.R . 2000. First report of white pine blister rust in Colorado. Plant Disease 84:595

Kendell, K.C. 1983. Use of pine nuts by black and grizzly bears in the Yellowstone area. International Conference on Bear Research and Management 5: 166-173.

Kinloch, B.B. Jr. and Dupper, G.E. 2002. Genetic specificity in the white pine/blister rust pathosystem. Phytopathology 92[3]: 278-280.

Knowles, P. and Grant, M.C. 1983. Age and size structure analyses of Engelmann spruce, pondersoa pine, lodgepole pine, and limber pine in Colorado. Ecology 64:1-9.

Kreb, P.V. 1973. Dendrochronology of bristlecone pine (*Pinus aristata* Engelm.) in Colorado. Arctic and Alpine Research 5:149-150.

LaMarche, V.C. 1969. Environment in relation to age of bristlecone pines. Ecology 50:53-59.

LaMarche, V.C. and Stockton, C.W. 1974. Chronogies from temperature-sensitive bristlecone pines at upper treeline in western United States. Tree-Ring Bulletin 34:21-45.

Lanner, R.M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pine. IN B. P. Dancik and K. O. Higginbotham [eds.], Proceedings of sixth North American Forest Biology Workshop, 15-48. University of Alberta, Edmonton, Alberta, Canada.

Lanner, R.M. 1984. Trees of the Great Basin. University of Nevada Press, Reno, NV.

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

Lanner, R.M. 1990. Biology, taxonomy, evolution, and geography of stone pines of the world. Proceedings – Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. General Technical Report INT-270, Intermountain Research Station, Ogden UT. pp. 14-24.

Lanner, R.M. and Vander Wall, S.B. 1980. Dispersal of limber pine seed by Clark's nutcracker. Journal of Forestry 78: 637-639.

Latta, R.G. and Mitton, J.B. 1997. A comparison of population differentiation across four classes of gene marker in limber pine (*Pinus flexilis* James). Genetics 146: 1153-1163.

Lepper, M.G. 1974. *Pinus flexilis* James and its environmental relationships. Ph.D. dissertation, University of California Davis, Davis, California, USA.

Lepper, M.G. 1980. Carbon dioxide exchange in *Pinus flexilis* and *Pinus strobiformis* (Pinaceae). Madroño 27: 17-24.

Lundquist, J.E., Geils, B.W. and Johnson, D.W. 1992. White pine blister rust on limber pine in South Dakota. Plant Disease 76:538.

Marr, J.W. 1961. Ecosystems of the eastern slope of the Front Range in Colorado. Series in Biology No. 8. University of Colorado Press, Boulder, Colo.

McCutchen, H.E. 1996. Limber pine and bears. Great Basin Naturalist 56(1): 90B92.

McDonald, G.I. and Hoff, R.J. 2001. Blister rust: an introduced plaque. *In* Whitebrak Pine Communities, *edited* by D.F. Tomback, S.F. Arno and R.E. Keane. Island Press, Washington, D.C. pp193-220.

McNaughton, G.M. 1984. Comparative water relations of *Pinus flexilis* at high and low elevations in the Central Rocky Mountains. Master's thesis, University of Wyoming, Laramie, Wyoming, USA.

Mitton, J.B., Kreiser, B.R. and Latta, R.G. 2000. Glacial refugia of limber pine (*Pinus flexilis* James) inferred from the population structure of mitochondrial DNA. Mol. Ecol. 9: 91-97.

Moir, W.H. and Ludwig, J.A. 1979. A classification of spruce-fir and mixed conifer habitat types of Arizona and New Mexico. USDA Forest Service Research Paper RM-207, 47 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Mooney, H.A., Wright, R.D. and Strain, B.R. 1964. The gas exchange capacity of plants in relation to vegetation zonation in the White Mountains of California. American Midland Naturalist 72: 281-297.

Oline, D.K. 2001. Allozyme variation in the Rocky Mountain bristlecone pine (*Pinus aristata*) at the regional and local scales. Published abstract. International IUFRO Conference on Breeding and Genetic Resources of five-needle pines: Growth, adaptability and pest resistance. Medford, OR. July 23-27, 2001. 1p.

Pataki, D.E., Oren, R. and Smith, W.K. 2000. Sap flux of co-occurring species in a western subalpine forest during season soil drought. Ecology 81:2557-2566.

Peet, R.K. 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. Vegetatio 43: 3-75.

Ranne, B.M., Baker, W.L., Andrews, T. and Ryan, M.G. 1997. Natural variability of vegetation, soils and physiography in the bristlecone pine forests of the Rocky Mountains. Great Basin Naturalist 57:21-37.

Rebertus, A.J., Burns, B.R. and Veblen, T.T. 1991. Stand dynamics of *Pinus flexilis*-dominated subalpine forests in the Colorado Front Range. Journal of Vegetation Science 2: 445-458.

Rehfeldt, G.E. 1997. Quantitative analysis of the genetic structure of closely related conifers with disparate distributions and demographics: the *Cuppressus arizonica* (Cuppressaceae) complex. Am. J. Bot. 84: 190-200.

Schauer, A.J., Schoettle, A.W. and Boyce, R.L. 2001. Partial cambial mortality in high-elevation *Pinus aristata* (Pinaceae). Am. J. Bot. 88:646-652.

Schmidt, W.C. and McDonald, K.J., compilers. 1990. Proceedings – Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. General Technical Report INT-270, Intermountain Research Station, Ogden, UT.

Schoettle, A.W. 1994. Influence of tree size on shoot structure and physiology of *Pinus contorta* and *Pinus aristata*. Tree Physiol. 14:1055-1068.

Schoettle, A.W. in press. Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of a non-native pathogen. In: Shepperd, Wayne, Compiler. Silviculture in special places: Proceedings of the 2003 National Silviculture Workshop. 2003 September 7-11. Granby, CO. Proceedings RMRS-P-XX. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Schoettle, A.W. and Negron, J.F. 2001. First report of two cone and seed insects on *Pinus flexilis*. Western North American Naturalist 61:252-254.

Schoettle, A.W. and Rochelle, S.G. 1996. Effect of light on shoot structure and function of mature subalpine conifer trees. IN C. Edelin [ed.], L'ARBRE Biologie et Developement. Naturalia Monspeliensia, Montpellier, France.

Schoettle, A.W. and Rochelle, S.G. 2000. Morphological variation of *Pinus flexilis* (Pinaceae), a bird-dispersed pine, across a range of elevation. Am. J. Bot. 87: 1797-1806.

Schulman, E. 1954. Longevity under adversity in conifers. Science 119:396-399.

Schulman, E. 1958. Bristlecone pine, oldest known living thing. Natl. Geogr. Mag. 113:355-372.

Schuster, W.S.F., Mitton, J.B., Yamaguchi, D.K. and Woodhouse, C.A. 1995. A comparison of limber pine (*Pinus flexilis*) ages at lower and upper treelines east of the Continental Divide in Colorado. Am. Midl. Nat. 13:101-111.

Schuster, W.S.F., Alles, D.L. and Mitton, J.B. 1989. Gene flow in limber pine: evidence from pollination phenology and genetic differentiation along an elevational gradient. Am. J. Bot. 76: 1395-1403.

Schuster, W.S.F. and Mitton, J.B. 1991. Relatedness within clusters of a bird-dispersed pine and the potential for kin interactions. Heredity 67: 41-48.

Schuster, W.S.F. and Mitton, J.B. 2000. Paternity and gene dispersal in limber pine (*Pinus flexilis* James). Heredity 84: 348-361.

Stohlgren, T.J. and Bachand, R.R. 1997. Lodgepole pine (Pinus contorta) ecotones in Rocky Mountain National Park, Colorado, USA. Ecology 78:632-641.

Stohlgren, T.J., Bachand, R.R., Onami, Y. and Binkley, D. 1998. Species environment relationships and vegetation patterns: effects of spatial scale and tree life stage. Plant Ecology 135:215-228.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, N.J. 360 p.

Tomback, D.F. and Kramer, K.A. 1980. Limber pine seed harvest by Clark's nutcracker in the Sierra Nevada: timing and foraging behavior. Condor 82:467-468.

Tomback, D.F., Sund, S.K. and Hoffmann, L.A. 1993. Post-fire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. Can. J. For. Res. 23:113-119.

Tomback, D.F., Arno, S.F. and Keane, R.E., editors. 2001. Whitebark Pine Communities. Island Press, Washington, D.C. 440 p.

Torick, L.L., Tomback, D.F. and Espinoza, R. 1996. Occurrence of multi-genet tree clusters in "wind-dispersed" pines. Am. Midl. Nat. 136:262-266.

Van Arsdel, E.P. Conklin, D.A., Popp, J.B. and Geils, B.W. 1998. The distribution of white pine blister rust in the Sacramento Mountains of New Mexico. Finnish Forest Research Institute Research Papers 712: 275-283.

Vander Wall, S.B. and Balda, R.P. 1977. Coadaptation of the Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. Ecol. Monogr. 47:89-111.

Webster, K.L. and Johnson, E.A. 2000. The importance of regional dynamics in local populations of limber pine (*Pinus flexilis*). Ecosci. 7: 175-182.

Wells, P.V. and Stewart, J.D. 1987. Cordilleran-boreal taiga and fauna on the central Great Plains of North America, 14,000 - 18,000 years ago. Am. Midl. Nat. 118: 94-106.