Synthesis of Lower Treeline Limber Pine (Pinus flexilis) Woodland Knowledge, Research Needs, and Management Considerations

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Abstract—Lower treeline limber pine woodlands have received little attention in peer-reviewed literature and in management strategies. These ecologically distinct systems are thought to be seed repositories between discontinuous populations in the northern and central Rocky Mountains, serving as seed sources for bird dispersal between distinct mountain ranges. Their position on the lower treeline and foothills in semi-arid climate systems is predicted to be particularly vulnerable to climate change. The genetic variation within these stands is viewed as important to conservation geneticists in developing seed sources resistant to blister rust. The isolated locations and different climatic conditions of these woodlands may have provided them some protection in the past from the mountain pine beetle (Dendroctonus ponderosae) and white pine blister rust (Cronartium ribicola) that are threatening upper treeline limber pine forests region-wide. But, recent studies show that the lower treeline woodlands are just as, or more, susceptible to white pine blister rust infections and mountain pine beetle infestations.

Lower treeline woodlands are often thought to be “invading” more desirable sagebrush and grass vegetation types, so eradication via chaining, mastication, and burning have been accepted practices to limit woodland growth or “encroachment.” The lack of economic value has led to the common perception that these lower treeline woodlands are “weeds” which need to be controlled to prevent their expansion into more economically valuable grazing lands. The common perception of these woodlands is that they should be maintained only on steep rocky slopes that will not support other vegetative types. Their expansion into grass and shrublands is thought to be from wildland fire suppression and other management actions such as livestock grazing. This view does not account for the dynamic relationships among vegetation, climate and wildland fire. It also does not take into account that these are ecotones between biomes that move elevationally, based on the above conditions. The conditions and characteristics that are used for baseline vegetation developed during the Little Ice Age conditions from approximately 1300 to 1900; a climatic period that was both wetter and cooler than present conditions. Many of the current models for the areas encompassing the lower treeline limber pine woodlands predict an increase in temperature of between 1° to 7° F in the summer and from 1° to 6° F in the winter, which may increase the growing season evapo-transpiration rates. For much of the area, seasonal changes in precipitation are also predicted, including a summer precipitation decrease from 10 to 50 percent and winter precipitation increase from 10 to 25 percent.

Not enough is known ecologically about the lower treeline limber pine and its relationship to upper treeline populations and the biotic communities dependent upon them, to assume “business as usual” activities and management. In order to change the management paradigms that exist for the lower treeline woodlands, a series of carefully delineated basic and applied research questions need to be formulated for these stands. Answering these questions will provide managers with a fuller understanding of the ecological role(s) of the lower treeline limber pine woodlands, resulting in more informed management decisions on the ground.

Introduction

Limber pine grows across the widest elevational range of any conifer in the Rocky Mountains, ranging from approximately 5,250 feet (1,600 m) to almost 11,000 feet (3,300 m) (Schoettle and Rochelle 2000). This elevational range increases when the isolate found in North Dakota at 2,850 feet (869 m) is considered. The mean daily temperature in areas where limber pine grows also varies considerably (from 22.8° C to 12.6° C) and is linearly related to elevation (Schoettle and Rochelle 2000). Schoettle and Rochelle (2000) concluded that limber pine has a high degree of physiological plasticity in that the fundamental niche, where the tree can grow, and the realized niche, where it competes the best, are very broad.

The limber pine woodlands under discussion in this paper are those woodlands that occupy the lower slopes of the mountains and foothills, and the ecotones bordering the sagebrush/grass biome in Montana, Wyoming, and northern Colorado. Defining the actual elevational range for these lower treeline populations is challenging because the limber pine has such a large elevational gradient and a wide latitudinal range. For the purposes of this paper, the lower treeline limber pine woodland is defined as outside the alpine vegetative community and below 8,500 feet (2,580 M) in elevation (Kearns and Jacobi 2007). It also includes the isolated stands (isolates) that occur within the Western Great Plains biome in Colorado, Nebraska, Wyoming, South Dakota, North Dakota and Montana.

A current literature search finds a paucity of information on the lower treeline limber pine (Pinus flexilis) woodlands compared to the upper treeline (above 8,500 feet) whitebark (Pinus albicaulis) and limber pine woodlands. The majority of research that has been done is on the isolates in the Western Great Plains, not on the lower treeline and isolated mountains that form the bulk of the lower treeline limber pine woodlands which serve as ecotones between the sage/grass and forest/woodlands biomes.
The lower treeline limber pine woodlands have a different set of management pressures than the upper treeline limber and whitebark pines. At the higher elevations, insect and disease, fire exclusion, visual resources, wildlife habitat, and climate change issues are at the forefront. The lower treeline woodlands not only have these issues, but also have issues related to livestock grazing, fuels management and energy development. They also entail management of a different set of wildlife species.

These low elevation woodlands are often characterized as “invading” more desirable vegetation types, so eradication via chaining, mastication, and burning have been accepted practices to limit woodland growth or “encroachment”, particularly in the ecotone adjacent to the sagebrush/grassland biome. These low elevation woodlands, because of their position on the landscape as transitional areas between biomes, have a history of movement both up and down the elevational gradient. The limber pine woodland can be considered a functional ecological replacement of the pinyon pine \((\text{Pinus monophylla/edulis})\) woodland. It waxes and wanes with climate and fire, facilitated by the Clark’s nutcracker \((\text{Nucifraga columbiana})\) (Tomback, personal communication) (figure 1).

These are ecologically distinct systems that serve as seed repositories between the upper treeline populations in the northern and central Rocky Mountains. They serve as a seed source for bird dispersal between mountain ranges (Perkins and DeArmond 2009). These lower treeline/foothills systems are thought to be particularly vulnerable to climate change (Aiken and others 2008; Romme and Turner 1991). Additionally, limber pine has been designated a “Regional Plant Species” by the National Phenology Network. Species placed with this designation are considered important in a locale or region of the nation in terms of ecological processes, biological diversity, or conservation (USA National Phenology Network 2010).

**Current State of Knowledge**

**Wildlife Usage**

Schoettle (2004) notes that “The role of limber pine forests as habitat for wildlife species is unknown.” Although many authors (Latta and Minton 1997; Schoettle 2004; Tomback 2009) have tied some specific species to limber pine usage such as the Clark’s nutcracker, grizzly and black bears \((\text{Ursus spp.})\), red squirrels \((\text{Tamiasciurus hudsonicus})\), and other small rodents. But overall, this lack of knowledge remains an important gap in information needed to develop multi-resource management strategies for the lower treeline limber pine.

**Tree Longevity**

Upper treeline limber pine is a very long-lived species with documented reports of live trees ranging from 1,500 to more than 1,600 years of age (Brown 2009; Schuster and others 1995). Studies located in the isolates of Pawnee Buttes/Pine Bluff (Schuster and others 1995), Black Hills (Thilenius 1970) and North Dakota (Potter and Green 1964) found no trees older than 238 years. Goodding (1923) did find three “old” limber pines at the Pine Bluffs site in Nebraska. Millar and others (2007b) found episodic Little Ice Age (from approximately 1300 to 1900) establishment of lower elevation limber pine stands in the eastern Sierra Nevada escarpment, with stands ranging in age from 90 to 200 years old.

The reasons for the difference in oldest age within these isolate woodlands compared to the upper treeline woodlands are not clear. Schuster and others (1995) suggest that it may be due to a more frequent wildland fire disturbance regime in the plains compared with those of the upper treeline woodlands. Other potential reasons include:
• The stands are composed of recent migrants (Latta and Mitton 1997; Millar and others 2007b; Schuster and others 1995).
• Anthropogenic movement of limber pine seeds by the Native Americans that used the seeds as a food source (Potter and Green 1964; Schuster and others 1995).

To date, there have been no studies looking at the age classes and structure of the lower treeline woodlands that occur primarily on Bureau of Land Management (BLM) and private lands in Wyoming, Montana and Colorado.

**Importance to Watershed and as a Nurse Plant**

Upper treeline limber pine woodlands are valued for watershed protection. They provide shade that delays snowmelt, which causes the retention of snowdrifts until early to mid-summer. At the lower treeline, limber pine woodlands influence snow retention and available soil moisture (Perkins and DeArmond 2009). The growth form of the tree with upswept branches provides shade and a windbreak that holds snow on the lee side of the trees. Baumeister and Callaway (2006) found higher soil moistures on the leeward side of the trees compared with the windward side. Beauvais (personal communication) and the author have observed the extended period of vegetative green-up on the lee side of limber pine.

Baumeister and Callaway (2006), Rebertus and others (1991) and Tombreck (2009) have found that limber pine serves as a nurse tree facilitating tree and shrub growth underneath as well as on the lee side for multiple species including: fir (Abies spp.), spruce (Picea spp.), Douglas fir (Pseudotsuga menziesii), and currant (Ribes spp.). This nurse tree function also is true for other species such as ponderosa pine (Pinus ponderosa) and curl leaf mountain mahogany (Cercocarpus ledifolius).

**Genetics**

There has been a limited amount of work on the genetics of the isolates included within the lower treeline limber pine woodlands. Latta and Mitton (1997) compared the genetic variation in the Pawnee Buttes isolate in Northeastern Colorado (including the Pine Bluffs isolate in Wyoming/Nebraska) to upper treeline limber pine stands found on the eastern slopes of the Rocky Mountain National Park (RMNP). Their analysis noted little genetic difference between the isolate and the RMNP stands. Only the southern-most stand located several hundred kilometers away outside of Fairplay, CO, was significantly differentiated.

The USDA Forest Service (1999) performed a similar study comparing the North Dakota isolate with other isolated stands in Montana (proximate to Terry) and South Dakota (Black Hills) as well as with two upper treeline alpine limber pine stands in south central Montana (Crazy and Pryor mountains) samples which are located within the contiguous range of limber pine in Montana. Their data suggested that the North Dakota stand has a closer relationship to the Montana stands than the geographically closer Black Hills stand. All three of the isolates exhibited less genetic variation than the Pryor and Crazy mountains. Latta and Mitton (1997) also noted the same lack of genetic variation in the Pawnee Buttes stand as compared to the more contiguous RMNP stands. These findings suggest a recent genetic bottleneck or a recent founding event.

Schoettle and Rochelle (2000) noted that different molecular genetic analyses produce different answers on estimates of limber pine gene flow between the upper treeline and the lower treeline/isolate populations. No common method has yet been used with which one may compare results among the different studies.

To date, reciprocal transplant studies (common garden) to examine the potential differing genetics of different elevational zones have not been conducted. Schoettle and Rochelle (2000) performed on-site measurements of limber pine to approximate this method. Because current genetic testing methods only analyze neutral variation, the common garden experiments are needed to evaluate the adaptive genetic traits of varying populations.

**Insects and Disease**

Many authors have documented the three primary insect and disease agents acting on limber pine: white pine blister rust (WPBR; Cronartium ribicola), mountain pine beetle (MPB; Dendroctonus ponderosae), and limber pine dwarf mistletoe (Arceuthobium cyanocarpum) (Kearns and Jacobi 2007; Millar and others 2007b; Schoettle 2004). Although these are the most important, other recognized insects include the ponderosa pine cone worm (Dioryctria auranticella) (Potter and Greene 1964; Schoettle and Negron 2001), the western conifer seed bug (Leptoglossus occidentalis), and the cone beetle Conophthorus contortae (Schoettle and Negron 2001).

To date, Hoff and McDonald (1993) has conducted the only known greenhouse trial of seedling susceptibility to WPBR. In that study, limber pine appears to have less resistance to blister rust than the other North American white pines. Limber pine had infection levels as high as 98 to 100 percent. In the three years of the study, limber pine mortality due to WPBR was 75 percent. In comparison, mortality in whitebark pine was 33 percent.

Since limber pine grows in very dry areas, ecologists hoped that WPBR would not be able to substantially spread into limber pine stands. It is now apparent that it may be just a matter of time before the necessary climatic conditions combine to produce a large wave of infection, even in the southern dry climates within the limber pine range (Kinloch and Dulitz 1990).

Kearns and Jacobi (2007) confirmed this with their study of 13 areas in Wyoming and Colorado. They found that the lower treeline limber pine has a significantly greater incidence of WPBR than the upper treeline limber pine. They found that plots at elevations of less than 8,500 ft (2,590 m) had an infection rate of 82 percent while those above 8,500 ft (2,590 m) had an infection rate of 30 percent. They also found that plots located at the bottom of slopes had higher incidences of WPBR infection than midslope,
When populations are lost due to WPBR infections, the limber pine becomes functionally extinct in the local area for hundreds of years until rust-resistant types emerge (Kendall 1997).

Unlike some pine species such as lodgepole (Pinus contorta), limber pine did not co-evolve a normative relationship with the mountain pine beetle (Logan and Powell 2001). The upper treeline five-needle pines evolved at higher elevations that did not support consistent MPB presence that is an important disturbance component of the ecology of other pine species. Consequently, the limber pine has limited or no resistance to the MPB. Of the 13 tree species attacked by MPB, limber pine shows some of the least resistance (Six 2010). Widespread MPB infestations in the upper treeline limber/whitebark pine communities have occurred previously. For example, above average temperatures in the 1930’s led to widespread MPB infestations and mortality in the upper treeline woodlands in Idaho (Logan and Powell 2001; Perkins and Swetnam 1996). This susceptibility to MPB along with the potential of limber pine shifting its species range to lower elevations where there is a higher potential for contact with MPB may lead to significant MPB outbreaks in the lower treeline limber pine woodlands, impacting the species’ distribution and abundance on the landscape.

In addition to the above factors, because the lower treeline limber pine woodlands tend to be younger and more densely stocked than the upper treeline alpine woodlands, their susceptibility to MPB is increased. Perkins and Roberts’ (2001) work in whitebark pine stands as well as Millar and others’ (2007b) work in limber pine stands provide evidence that younger and denser limber pine stands exhibit increased susceptibility to MPB. The author has observed MPB-caused mortality in the lower treeline limber pine stands in Wyoming (figure 2).

**Ecotonal Dynamics**

Ecotones are the boundaries between ecosystems and/or biomes (Allen and Breshears 1998). They are subject to movement dependent upon many local and regional factors, including drought, changing climate and management practices. The semiarid ecotones (where the lower treeline limber pine is located) are considered to be among the most sensitive to change (Intergovernmental Panel on Climate Change 1996). The low elevation woodland ecotones have moved both up- and down-slope throughout the Holocene (approximately 11,500 years BP to present) driven by changes in the above factors.

Allen and Breshears (1998) have documented rapid ecotone woodland/forest movement on the Frijolito Mesa in the Jemez Mountains of New Mexico. They documented a drought-induced shift over a five-year period of more than two kilometers, which has persisted over the last 40 years. They attributed this rapid movement and resulting persistence on the landscape to climate, primarily through drought. They also noted that management activities such as fire suppression had amplified this climate-induced ecotone shift by modifying the disturbance intervals.

Millar and others (2007b) studied limber pine sites on the eastern escarpment of the Sierra Nevada. Their work indicates that the upper treeline woodlands vary considerably in age and structure from the lower treeline woodlands. The lower elevational woodlands were established during the Little Ice Age and are much denser than the upper treeline stands. Eckert and Eckert’s (2007) research on another five-needle pine, foxtail (Pinus balfouriana), in the Klamath Mountains of California, has also shown downhill expansion (using diameter class as a surrogate for age).

Recent droughts, temperature increases, and the attendant increase in insect and disease mortality have thinned the Sierra Nevada stands and have had the net effect of increasing their health and resistance to drought while maintaining them on the landscape. Although Eckert and Eckert (2007) did not specifically look at climate in their analysis, they conclude that although historic climate change could be a driver, habitat heterogeneity and ecological context are critical factors. Millar’s (2007b) conclusion that these stands may retreat downslope into new microsites, in effect shifting the species range downslope, on the landscape in response to a series of complex climatic, environmental and disturbance variables is important and reinforces the diversity of change agents involved in species range movement (figure 3).
Climate change modeling and field observations indicate that these downslope microsites and their microclimates may well become wetter and cooler than the up-slope sites, creating the conditions for a downward shift in limber pine species range (Millar, personal communication). Recent work by Daly and others (2009) shows a de-coupling of nocturnal cold air drainage from normal synoptic patterns in complex topography and shows that the temperature changes due to this may well be less that those changes predicted by regional and global climate models. They suggested that these cold air drainages may act as refugia in times of changing climatic conditions. McLachlan and others’ (2005) and Pearson’s (2006) analyses show that tree species movements in periods of rapid climate change are closely tied to spread from refugia throughout the range of the species.

Conifer movement downslope is also supported with long term “common garden” ponderosa pine experiments at the Fort Valley Experimental Station (DeWald and Mahalovich 2008) showing that ponderosa pine from higher elevations grew well at lower elevations but not vice versa.

Allen and Breshears (1998) propose that the unprecedented rapid change in climatic conditions will produce rapid and extensive shifts in the woodlands’ associated ecotones. The range of the lower treeline limber pine in Montana, Wyoming and Colorado is within the area forecasted by Rehfeldt and others (2006) to be extramural climates, i.e. “having no contemporary analogs among the communities of today,” within the next 80 years. These extramural climates may change not only the distribution of genetic variability across the landscape, but also invoke evolutionary processes related to migration, selection and recombination (Rehfeldt and others 2006).

In the past, ecotone movement has been connected to changing climatic conditions. The current period promises change at a more rapid rate than what has been seen in the past. Recurring droughts in the west have synchronized forest composition, structure and the associated functions across broad landscapes, which then become vulnerable to climate shifts (Millar and others 2007a). The shifting ecotones may well provide important refugia for species such as the limber pine, maintaining population levels to survive rapid change.

We may be able to adapt to present and future conditions by promoting diversity within and across the landscapes and managing the ecotones in their early successional movement. The proactive approach of modifying the ecological trajectories of the ecotones is preferential to overreacting to change based on past conditions.

Wildland Fire

There is a lack of research targeting wildland fire disturbances in limber pine. Much of the information must be derived from similar whitebark pine studies. The fire regimes in limber pine are highly variable (Tomback 2009), ranging from low severity surface fire to high severity crown fires depending on elevation and stand structure. At the upper treeline, disturbance by fire was rare and not an important ecological driver in the high elevation old-growth stands (Millar and others 2007b). On more mesic sites where limber pine stands were intermingled with other tree species, the mixed severity to high severity fires probably occurred much like the fire histories of whitebark pine in similar locations (Keane 2010). The lower treeline woodlands and isolates are thought to have a more frequent disturbance regime (Schuster and others 1995). Changing Fire Return Intervals (FRI) in low elevation limber pine may be assisting their survival and expansion by reducing the frequency of disturbance (Tomback 2009).

Information from LANDFIRE (2007) in zones 21, 22, and 29, where most of the lower treeline limber pine occurs, has FRI that vary widely depending on where the limber pine is found. FRI ranges from 100 to 1000+ years, with the shortest being 100-200 years in Wyoming big sagebrush (Artemesia tridentata ssp. wyomingensis) and up to

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**Figure 3.** Limber pine downhill movement in drainages, Beaver Divide, WY. Elevation is 6,360 ft (1940 m).
1,000 years in Rocky Mountain (*Juniperus scopulorum*) and Utah (*Juniperus osteosperma*) juniper with discontinuous fuels.

While LANDFIRE and the Fire Regime and Condition Class (FRCC) have provided important new information about vegetation and its potential relationship with wildland fire disturbance regimes, this information is limiting in two respects:

- Many field personnel use this as static information, which fixes the disturbance return interval and does not allow for the movement of vegetation, especially ecotones on the landscape.
- LANDFIRE was developed using historic conditions as the desired reference point and does not include changing climate and its effect on the vegetation in its modeling.

Recent research shows that while understanding the relatively recent past provides important insights, the paleo-ecological record shows that the fire frequency has changed continually over the Holocene in response to changes in the climate (Whitlock and others 2003). The variability in the record of fire history is important because it contradicts the idea of a static fire return interval (Whitlock and others 2003). As Littell (2010) noted, fire frequency and the area burned are controlled by climate more so than by weather and fuels. Also, fire regimes are not static, but dynamic, changing over time and space.

The conditions that we generally use for baseline vegetation and fire—were developed under the Little Ice Age conditions, a period of wetter and cooler conditions. These conditions are something we will probably never see again. The present communities are relatively young having only developed over the last few millennia with shifts in species distribution and characterized by both range contraction and expansion (Whitlock and others 2003).

The terms that we have traditionally used to describe fire and vegetation relationships as being in equilibria are inconsistent with our current understanding of the nature of the relationships among fire, climate, vegetation and fuels, which are highly dynamic and very transient in time. Current research suggests that ecosystems are non-equilibrium systems subject to driving factors at multiple scales (Littell 2010).

### Management Issues

The lower treeline limber pine woodlands have a different set of use and management pressures than the upper treeline limber pine and other five-needle pine species. Because of the ecotone fluctuations, these woodlands are often thought to be “invading” more desirable sagebrush and grass vegetation types, so eradication via chaining, mastication, and burning have been accepted practices to limit woodland growth or “encroachment.”

The common perception, reinforced in part by the static nature of commonly used planning tools, is that limber pine woodlands should be maintained only on steep rocky slopes that will not support other vegetative types. Their expansion into grasslands and shrublands is viewed as a result of management activities such as grazing and wildland fire suppression, not as a natural movement up- and downhill based on a much more complex set of factors.

As an example, during a recent presentation to a group of resource management specialists, describing the rationale behind the decision to place limber and whitebark pine on the BLM sensitive species list there was much discussion and some resistance to this idea. The response of one resource specialist was telling: “I've got 1940’s aerial photos showing that the area was a grass/sagebrush stand and I'm going to burn all the limber pine to return it to that condition, and I'm doing a presentation tomorrow on how to burn limber pine that way.”

Appropriate management strategies, including maintenance of forest and woodland structure and function as well as restoration, require an understanding of the structural and ecological conditions in order to adequately determine and prioritize management actions. Additional management actions must be based on the appropriate historical and potential future contexts when the objectives include maintenance of “natural” conditions. There is a need to perform assessments of the actual distribution of the lower treeline limber pine, insect and disease levels, population levels, genetic variability, wildlife habitat provided by limber pine, and potential range shifts among species.

### Research Needs

Sound resource management on public lands depends upon a solid understanding of the ecological context on which to base decisions. In order to develop management strategies for the lower treeline limber pine woodlands, the scientific and land management communities must develop, prioritize and address research questions for these woodlands. Among the suggested research topics are the following:

- Perform common garden studies to evaluate the genetic basis of limber pine distribution and the potential of the ex situ movement of lower treeline stock to upper treeline woodlands. Elevationally-derived experiments such as Rehfeldt (1990) are needed to quantitatively measure the genetic differences in the limber pine elevational gradient.
- Measure the gene flow between the upper and lower treeline limber pine communities.
- Develop limber pine seed zone maps based on common garden and genetic studies.
- Document vegetative composition changes in the Great Plains isolated stands that were initially surveyed from 1923 to 1970 in Colorado, Nebraska, South Dakota and North Dakota.
- Determine the ecological role of lower treeline limber pine woodlands with respect to wildlife habitat, and watershed and hydrologic function.
- Define the spatial distribution of the lower treeline limber pine woodlands and determine the extent of insect infestations and disease infections in these stands.
• Develop predictive models of the potential movement of lower treeline limber pine woodlands in response to changing climatic conditions.

Conclusions

Until some of these critical research needs are filled, it will be difficult for land managers to recognize lower treeline limber pine woodlands as a valuable, unique ecosystem that requires management to maintain its long term viability across the landscape.

We must emphasize to land managers the suggestions of Millar and others (2007a) that we cannot reply on past forest conditions to provide us with the information to maintain forests sustainably into the future. The complexities of changing climate, insect and disease, changing land use patterns, etc. will create new unique environmental conditions. Our incomplete understanding of the ecology and adaptive genetic traits of lower treeline limber pine woodlands greatly constrain our ability to manage and conserve this ecosystem in a changing world.

Managing these unique woodlands in the face of uncertainty requires a non-deterministic management strategy which emphasizes vegetative diversity and multiple sequential pathways leading to multiple outcomes. Adoption of options that accommodate change rather than holding woodlands to a previously accepted norm will ultimately reduce costs. Most importantly it will improve the land managers' chances of successfully facilitating these systems adaptive response to environmental change.

Literature Cited


