AN ABSTRACT OF THE THESIS OF

Chaylon D. Shuffield for the degree of Master of Science in Forest Resources presented on December 21, 2010.

Title: Overstory Composition and Stand Structure Shifts within Inter-mixed Ponderosa Pine and Lodgepole Pine Stands of the South-central Oregon Pumice Zone.

Abstract approved:

John D. Bailey

Ponderosa pine (Pinus ponderosa) and lodgepole pine (Pinus contorta var. murrayana) forests of south-central Oregon have been extensively researched over the last century. However, little information has been reported on overstory composition and stand structure shifts associated with fire exclusion within inter-mixed ponderosa pine and lodgepole pine stands of the south-central Oregon pumice zone. In recent time, the lack of disturbance history and quantitative information needed to reconstruct historic stand conditions has become a growing concern for many ecologists. The need to collect quantitative information from remnant old-growth stands is imperative to improve restoration activities, incorporate stand-level diversity, identify the degree of successional departure, and to ensure valuable data is archived for future reference and ecological analysis.

In Chapter 1, an exhaustive search for published information on early land-use practices specific to our study area was performed to: (1) identify the degree of Native American influence on vegetation; (2) identify direct and indirect Euro-American disturbances involving the loss of natural processes; and (3) establish a reference period for appropriate representation of historic conditions. In Chapter 2, remnant
old-growth stands were analyzed using dendrochronological techniques and statistical comparisons to quantify: (1) shifts in overstory composition and stand structure; (2) growth and development of ponderosa pine and lodgepole pine across time; and to (3) characterize the influence of climate and fire on species recruitment.

Our analysis indicated successional trajectory shifts occurred shortly after the loss of Native American influence beginning around 1850 and associated affects of intensive grazing following 1880. Age reconstruction displayed an exponential pattern of recruitment between 1880 and 1950. Since 1850, our analysis revealed a reduction in average tree basal area growth and height development of understory ponderosa pine and lodgepole pine. Ponderosa pine greater than 150 years old accounted for less than 5.0% of the total contemporary density, but composed 45.0% of the total basal area. Lodgepole pine greater than 100 years old accounted for approximately 3.0% of the total contemporary density and composed 12.8% of the total basal area. Stand density for our study area averaged 25.3 trees per hectare for ponderosa pine greater than 53.3 centimeters diameter at 1.4 meters.

We report low levels of lodgepole pine recruitment (2/hectare/decade) prior to 1880 and suggest the long-term development of less fire-resistant lodgepole pine has been favored since fire exclusion. Furthermore, contemporary settings support conditions associated to atypical mountain pine beetle outbreaks and fire behavior known to cause mortality of large diameter ponderosa pine. Restoration of remnant inter-mixed stands requires the aggressive removal of lodgepole pine and re-introduction of fire to provide long-term sustainability of ecosystem health and preservation of large diameter ponderosa pine.
Overstory Composition and Stand Structure Shifts within Inter-mixed Ponderosa Pine and Lodgepole Pine Stands of the South-central Oregon Pumice Zone

by
Chaylon D. Shuffield

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APPROVED:

______________________________
Major Professor, representing Forest Resources

______________________________
Head of the Department of Forest Engineering, Resources and Management

______________________________
Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

______________________________
Chaylon D. Shuffield, Author
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CHAPTER 1 - INTRODUCTION

Ponderosa pine (*Pinus ponderosa*) forests are widely distributed east of the Cascade Range in Oregon (Franklin and Dyrness, 1988). In the south-central Oregon pumice zone, the transition between pure lodgepole pine (*Pinus contorta* var. *murrayana*) and ponderosa pine is often abrupt. However, where growing conditions are favorable lodgepole pine and ponderosa pine frequently intermix (Franklin and Dyrness, 1988).

Historically, inter-mixed stands separated two distinct fire regimes. Stands where lodgepole pine is the potential vegetation (climax), found on infertile pumice soil and ash derived from the eruption of Mt. Mazama (Crater Lake), experienced an infrequent, moderate-severity fire regime with a mean fire return interval (MFRI) between 60-80 years (Larson, 1976; Agee, 1981; Agee, 1993). The infrequent fire events interacted with other disturbances described by Gieszler *et al.* (1980), whereas the ponderosa pine ecosystem experienced a frequent, low-severity fire regime. Weaver (1959) reported a MFRI of 11-16 years from selected trees within the Warm Springs Indian Reservation, and Bork (1984) reported fire return intervals of 4-11 and 7-24 years, representing wet and dry sites respectively, on the Deschutes National Forest.

Historic fire disturbances in the ponderosa pine ecosystem of the western U.S. maintained processes and functions, and influenced forest composition and structure by reducing competition from fire-sensitive species, understory fuel accumulation, long-term development of an understory shrub component and intraspecific
competition for available resources (Veblen et al., 2000). This relationship was historically evidenced in early reports of central Oregon researchers (Langille et al., 1903; Munger, 1908; Kerr, 1913; Munger, 1914; Kerr, 1917; Munger, 1917), fire history studies (Weaver, 1951; Weaver, 1959; Cooper, 1960; Soeriaatmadja, 1966; Bork, 1984; Swetnam and Dieterich, 1985; Baison and Swetnam, 1990; Agee, 1993; Brown and Sieg, 1996), and circumstantial evidence from 20th Century photographs.

Following a century of Euro-American alterations to the landscape, uncharacteristic fuel loadings and disruption to natural processes in ecosystems adapted to frequent fire have shifted species composition and structure (Covington and Moore, 1994; Covington et al., 1997; Covington, 2003). Contemporary conditions within the inter-mixed stands resemble a mix of characteristics associated with both ponderosa pine and climax lodgepole pine, suggesting a historic mixed-severity fire regime. However, historically inter-mixed stands may have resembled characteristics closely associated with adjacent pure stands of ponderosa pine.

For this study, we identified a reference date specific to our study area based on early land-use practices, settlement and associated loss of natural processes. In the last decade scientists and managers have increased their use of incorporating early land-use records (Swetnam et al. 1999). Reference dates can also fluctuate by dominant forest type and elevation. This information will assist our ability to indirectly correlate temporal reference periods to characterize and distinguish sensitivity between direct and indirect Euro-American disturbances.
Our research objectives for Chapter 1 were to: (1) identify the degree of Native American influence on vegetation; (2) identify direct and indirect Euro-American disturbances involving the loss of natural processes; and (3) establish a reference period for appropriate representation of historic conditions.

Early Research

The Deschutes National Forest was established on July 1, 1908. Land included in the designation was formerly withdrawn from public domain on September of 1893, known as the Cascade Forest Reserve. Land east of the Cascade Forest Reserve was later withdrawn in 1903, which is currently managed by the Bend/Fort Rock Ranger District. Since the establishment of Deschutes National Forest many withdrawals, releases and boundary adjustments have occurred (Baker, 1950).

Following the establishment of the Deschutes National Forest Thorton Munger led the silvics section under the United States Department of Agriculture (USDA) Forest Service’s Regional Office in Portland, Oregon (Langston, 1995). Munger’s first assignment as a researcher was to study the encroachment of lodgepole pine on western yellow pine [ponderosa pine] in the pumice zone of south-central Oregon (Rakestraw, 1991).

Although Munger specifically reported on the encroachment of lodgepole pine, observations of the expansion of species was first discussed in W.H.B Kent’s 1904 report, “The Proposed Wenaha Forest Reserve Washington and Oregon” (Kent, 1904).
In the latter report, Kent described the dominance of lodgepole pine following areas repeatedly disturbed by wildfire in the Blue Mountains of Oregon.

George Bright (1911) also contributed to this idea and noted lodgepole pine was the only tree species that could “invade the territory of the typical yellow pine.” Munger (1908) quickly hypothesized the extent of pure lodgepole pine had encroached beyond the natural geographical range at the expense of ponderosa pine, due to centuries of Native American burning and carelessness of recent Euro-American settlers. The idea of pure stands of ponderosa pine being replaced by lodgepole pine following fire likely originated from the familiarity with serotinous cone taxon (*Pinus contorta var. lattifolia*) of the Rocky Mountains, which depends on infrequent, high-severity fire disturbances to break resinous bonds between cone scales (Clements, 1910; Lotan 1967).

Kerr (1913) acknowledged the encroachment theory, but added the distribution of ponderosa pine was also dependent on water table depths, fire resistance, and seedling capabilities and limitations. Tarrant (1953) later investigated this theory by reviewing published studies and observations and concluded the range of pure lodgepole pine was a factor of soil moisture, rather than a direct result of encroachment following fire disturbances on wet, poorly drained soils, which explains distinct boundaries on well-drained soils with any rise in elevation (Berntsen, 1967). Cochran and Berntsen (1973) also concluded lodgepole pine was more tolerant to low night temperatures in areas associated with frost pockets at the time of seedling
emergence. Stands dominated by pure lodgepole pine were later defined as edaphic and topoedaphic climax (Franklin and Dyrness, 1988).

Inter-mixed stands of ponderosa pine and lodgepole pine were first described by Munger (1908) who stated “There are intermediate areas on which probably both pines have always been present, but in which lodgepole had no silviculture affect on the forest.” Tarrant (1953) was the last investigator to specifically reference inter-mixed stands by concluding the influence of soil moisture and lack of ecological information was not supportive of favoring one species over another and “the best guide as to which is the most desirable species for the site is the condition of thrift crown growth rate of young trees.”

In present time, areas supporting both species should be closely evaluated to identify remnant ponderosa pine stumps when attempting to classify. Plot inventory records from central Oregon have revealed stands classified as lodgepole pine/bitterbrush had sufficient ponderosa pine basal area to be classified as ponderosa pine/bitterbrush (Johnson et al., 2007).

**Pre-Settlement**

Early explorers and fur trappers were the first Euro-American’s to visit the south-central Oregon area. Between 1813 and 1835 fur trappers from the John Jacob Astor Company, and Peter Skene Ogden and Finian McDonald of the Hudson’s Bay Company searched the central Oregon waterways for furbearing wildlife (Tonsfeldt et al., 2004; OHTF, 2010). The date 1813 engraved into a rock south of Bend marks the
beginning of Euro-American presence and influence to this specific landscape (DCHS, 2009).

The central Oregon area was later visited by Nathaniel Wyeth in 1834 and in 1843 by Lt. John C. Fremont, U.S. Army Corps of Topographical Engineers. Fremont’s report to congress provides written description of his journey through central and south-central Oregon (Fremont, 1845; Appendix C, Photo 1):

- December 4th, “…the trail entered a beautiful pine forest” (north of Metolius River)
- December 5th, “Today the country was all pine forest…the timber was uniformly large; some of the pines measuring 22 feet in circumference at the ground, and 12 to 13 feet at six feet above” (south from Metolius River)
- December 8th, “The soil was generally bare, consisting, in greater part, of a yellowish white pumice stone, producing varieties of magnificent pines, but not a blade of grass” (north of Klamath Lake)
- December 12th, “Among the pines here, I noticed some five or six feet in diameter” (east of Klamath Lake).

In 1903, Langille and his investigation team gave the first report on the forest conditions in the Cascade Range Forest Reserve in Oregon. He described the forest floor as being “clean as if it had been cleared, and one may ride or even drive without hindrance.” Where ponderosa pine bordered non-timber areas, Langille estimated 10 percent of the area had burned recently and 90 percent of the forest had evidence of
older fire scars. In 1905, geologist Israel C. Russell who wrote “This forest [central Oregon ponderosa pine forest]……barring the destruction due to fires, nearly everywhere recognizable, still retains its natural wilderness and pristine beauty……yellow pine [ponderosa pine] is the most abundant tree east of the Cascades” (Russell, 1905).

Natural Disturbances

Native American use of fire had more of an ecological impact to the North American landscape compared to lightning ignitions (Stewart, 1956). Native Americans used fire directly and indirectly to facilitate hunting visibility, reduce wildlife hiding cover, gather and drive wildlife, kill insects and rodents, manipulate available forage, stimulate new growth for browsing wildlife and waterfowl, enhance edible plant diversity, improve hunting tactics, maintain travel routes, improve and expand grasslands for horse grazing, drive away predators, increase warfare tactics, signal to enemies or strangers, inhibit natural wildfire spread, and to entertain (Shinn, 1978; Robbins, 1997).

It is also believed Native Americans facilitated type conversion in many ecosystems (Pyne, 1982; Cronon, 1983; Patterson and Sassaman, 1988; Abrahams, 1992 in Stewart, 2002). The seasonality differences between Native American and lightning caused fires influenced genetic variation and adaptations to other plant species. In the Pacific Northwest, seed gathering was also conducted to promote the
establishment of desired species through broadcast seeding after burning (Stewart, 2002).

Evidence of Native American inhabitants in south-central Oregon date back 14, 500 years with the new coprolite discovery found in a cave near Paisley, Oregon during the summer of 2008 (Gilbert et al., 2008; Gilbert et al., 2009; Rasmussen et al., 2009). Other evidence includes the Fort Rock sandals made of sagebrush (Artemisia L.), which date back around 10,000 years (Cressman, 1981). Further north, a wickiup was discovered near the Newberry Caldera dating back at least 9,000 years, and the Odell Lake campsite evidence dates back 10,000 years (Cressman, 1948). Settlement and subsistence patterns were largely influenced by changing moisture levels that included shrinking, expanding, and the disappearance of marshes and lakes in response to broader climatic fluctuations (Wingard, 2001).

In a report regarding lodgepole pine encroachment, Munger (1908) acknowledged the influence of naturally ignited fires, as evidenced by the abundance of lightning struck trees and indigenous burning. “The significant fact is that there has been an increase in the number of forest fires since the Indians began to occupy the land. It has always been the custom of the aborigines to burn the woods systematically and frequently. Their reason for doing so were to get rid of sticks, underbrush, and young growth to make travel and hunting easier, to improve the grass for their ponies, and to drive smaller game in a hunt. This whole region was certainly ranged over by Indians until the comparatively recent advent of the white man” (Munger, 1908). Munger (1908) also reported every acre in the central Oregon forests
had been visited by fire at least once in the last 20 to 40 years. Appendix B, Map 1 displays large fire history for the Deschutes National Forest between 1909 and 1919. Appendix B, Map 2 displays historic fire occurrences designated by point of ignition to show the frequency and probability of fire potential. Since 1989, the Deschutes National Forest has experienced a conservative average of approximately 203 annual fire starts with a range between 106 and 296 fires (KCFAST, 2010). This report accounted for all wildfires with an associated incident number, regardless of size and cause of ignition.

The arrival of domestic horses by the Spanish in the 16th Century slowly transitioned the Native American culture of the west in which they used horses as a hunting and travelling tool. Most notably, horses were viewed as currency and power over other tribes. Therefore, Native Americans used fire to increase and expand meadow openings for pasture.

However, Native American burning practices in south-central Oregon, although commonly underrepresented, did not significantly shape vegetation at the landscape level compared to western Oregon or the Great Plains. For example, the oak savanna environment of western Oregon was historically dependent on regular burning by the Kalapuya to inhibit the establishment of Douglas-fir (Boyd, 1999). Native American burning in south-central Oregon was likely not as influential as a result of late introduction of horses by the Nez Perce around the 1790’s, abundance and availability of water and food resources with little need to travel long distances, and abundance of lightning caused ignitions to stimulate fire-adapted vegetation.
(Spier, 1930). However, traditional burning was performed in the late summer following berry collection to enhance plant abundance for food and medicinal purposes and to increase browse for deer (Deur, 2008). This also indirectly reduced large woody debris accumulation in the understory of ponderosa pine and mixed conifer forests (Deur, 2008). Northern Paiute and Tenino bands are stated to have regularly practiced burning in the Deschutes River Valley (Shinn, 1978; Stewart, 1936 in Bork, 1984). There is also circumstantial evidence of early ranchers setting fire to hillsides following their return from summer grazing to reduce fuel accumulation that would later inhibit travel the following spring, adapted from the Northern Paiute tradition of broadcast burning (Pyne, 1982; Uran, 2010 personnel communication).

Native American Travel

Based on cultural evidence, we speculate the Yahooskin Band of the Northern Paiute and the Tenino Band of the Walla Wallas (seasonal hunters and gatherers) frequently passed through inter-mixed stands during seasonal travel between Newberry Crater, Davis Lake and the Fort Rock Valley (Bassett et al., 1998; Stern, 1956). There is also supportive evidence to suggest the historic trail that later became Highway 31 was formerly used to connect the Northern Paiute Bands to a popular trade route known as the Klamath Trail (Highway 97), which extended north to The Dalles (Uran, 2010 personnel communication).

Furthermore, early explorers, trappers, settlers and the United States Army followed trail networks created by Native Americans (Deur, 2008). This is likely due
to the fact that Native Americans occupied the land for thousands of years, which gave them an excellent understanding of the diverse landscape, especially through mountainous terrain. Therefore, Euro-Americans likely followed the path of least resistance as it would not have been feasible to construct new trails or roads when tribal networks were already established.

Lt. John C. Fremont provided written evidence to suggest Highway 31 was historically a well travelled Native American trail. Following Fremont’s descent down the north side of Winter Ridge on December 16, 1843 he wrote, “Our course [desired route] would have taken us to the other shore [east side of Summer Lake], and over the highlands beyond [towards Lake Abert]; but I distrusted the appearance of the country, and decided to follow a plainly beaten Indian trail leading along this side [west] of the lake [Summer Lake].”

In 1841, Lt. Charles Wilkes, U.S. Exploring Expedition, created the first map of Oregon displaying the extent of Native American lands (Appendix B, Map 3). This was an important point in history for all western states since Native Americans had already suffered widespread population loss, due to disease epidemics introduced by Euro-Americans beginning as early as the 16th Century. It has been recognized that disease killed massive numbers of Native Americans prior to Euro-American observation. Therefore, early settlers and explorers assumed there were always small, poor bands scattered throughout the west. Smallpox first appeared in southern Oregon around the 1770’s, and in 1801, 1825-25, 1838 and the 1840’s (Boyd, 1990 in Deur,
The 1840’s smallpox epidemic was the result of large numbers of settlers travelling through the Applegate Trail (Deur, 2008).

In 1850, the Oregon Indian Act was passed by congress, allowing the President to negotiate treaties. During this time census records indicated 25,000 to 30,000 settlers entered the Oregon Territory following the Donation Land Act of 1850 (OHS, 2010). By 1864 land once occupied by the native tribes had significantly been reduced. Appendix B, Map 4 displays the original lands purchased from the Native Americans by the U.S. Government and associated location of negotiated reservations. The remaining tribes in the central Oregon area were grouped under the Klamath and Warm Springs Confederated Tribes.

*Settlement and Grazing/Farming*

Following the fur trapper advancement and exploration into south-central Oregon, wagon trains passed through on their way to the Willamette Valley. Stephen Meek presumably led the first wagon train through central Oregon in 1845 (DCHS, 2009). By 1850 industrialized development had taken place in Oregon City, Portland and Salem (Robbins, 1997). An influx of farming settlements later began after newspapers promoted rich, fertile land following the Homestead Act of 1862. However, ranching operations east of the Oregon Cascades were not established until 1864 (DCHS, 2009).

By 1880 Oregon’s population was estimated to be around 174,768 (Robbins, 1997). Most settlers who claimed land in central and south-central Oregon region
were from the Willamette Valley and California. However, the arid environment east of the Cascade Range and lack of irrigation technology heavily impacted those with limited or no access to natural waterways (Foster, 1989; Robbins, 1997). In 1890 the population of Klamath County increased to 2,444 (Robbins, 1997). The next influx of land seekers came after the Carey Act of 1894, which supported the construction of water canals to irrigate arid farmland. Between 1870 and 1897 Oregon’s sheep population increased from 500,000 to 2,604,640 (Colville, 1898). To further off-set the cost of poor crop production on infertile lands the U.S. Congress passed the Enlarged Homestead Act of 1909, which interested settlers from the eastern U.S. (Allen, 2005). Settlers’ fortunate enough to withstand the initial difficulty experienced drought during the early 1900’s (Ramsay, 2003). Despite unfavorable farming conditions the first successful railroad reached Bend in 1911 as demand for transportation of timber increased (DNF 1, 2010).

Euro-American development into this area came at a cost to the land and associated ecological impacts of overgrazing were becoming apparent around the state (Colville, 1898; Appendix C, Photo 2). Reports of rangeland degradation and soil erosion were noted as early as the mid-1880’s (Galbraith and Anderson, 1971). Shrub species began to dominate rangelands as a result of fire exclusion associated to fine fuel consumption (Galbraith and Anderson, 1971). For the remainder of this thesis, we refer to fire exclusion as the beginning of fine fuel consumption by domestic livestock.
Early Forest Management

Privatizing large sections of land from the public domain began around the 1890’s (Robbins, 1997). However, timber claims purchased with the intent of selling to major timber companies did not become common until 1900. News of large diameter ponderosa pine quickly spread to investors as commerce began to strengthen in Oregon. In 1916, the Shevlin-Hixon and the Brooks-Scanlon mill companies began operating in Bend, Oregon. However, small privately owned portable mills were also scattered throughout the forest (Cowlin et al., 1942; Appendix C, Photo 3).

Ecological and social impacts of unsustainable logging practices on private timberland became apparent by the 1930’s (Appendix C, Photo 4, 5, 6). To help balance the demand for timber resources and to indirectly support surrounding businesses, the U.S. Forest Service agreed to allow increased harvesting on public land (Joslin, 2007; Appendix C, Photo 7).

During the middle of the 20th Century the U.S. Forest Service was involved in many land exchanges (Appendix B, Map 5), particularly in cut-over forestland following the Clarke-McNary Act of 1924 (DNF 2, 2010). Other historic logging practices on Forest Service land included high-grading and selective logging of “overmature” timber during the first half through the middle of the 20th Century. Chaffee (1910) proposed a management approach to cut mature and “overmature” timber immediately under a seed tree method with a diameter limit restriction…“overmature and rapidly declining veterans should be considered in one
sub-type and treated first.” During the mid 20th Century management practices favored selective cutting of trees vulnerable to bark beetle attack (Keen, 1943).

**Fire Suppression Policy**

The connection between fire suppression and need to protect “green forests” became the answer for policy makers as economic demand for wood resources began to emerge during the early 1900’s. Many researchers have attributed forest ecosystem health changes to active management and the U.S. Forest Service’s fire suppression policy (Stephens and Ruth, 2005).

Active fire suppression on the Deschutes National Forest likely occurred shortly after designation in 1908. Response time likely improved with the construction of Black Butte, Walker Mountain, Maiden Peak, Paulina Peak and Pine Mountain lookouts between 1913 and 1915 (DNF, 2010). During the early 20th Century the public view to keep “light surface fires” was culturally accepted by the general public to clean the forest floor of debris and to prevent crown fires (Stephens and Ruth, 2005). However, following the Great Fires of Montana and Idaho in 1910 the public view changed and fires natural role was scrutinized. This criticism was encouraged by the press and used as a scare tactic to encourage full suppression of all forest fires. In 1911, F.E. Olmsted was one of the earliest government officials to publically support full suppression for all wildfires and later viewed as a way for the U.S. Forest Service to gain public acceptance (Olmsted, 1911; USDA 1911).
Lodgepole pine in south-central Oregon is fairly intolerant to shade and fire sensitive (Volland, 1984). However, mature lodgepole pine commonly survive radiant heating from nearby ground fires. Cambial scarring should be closely examined to determine the actual cause of injury. Studies in central Oregon have found presumed lodgepole pine fire scars were the result of cambium stripping of mountain pine beetle (Dendroctonus ponderosae), suggesting fire was not a single major disturbance factor in these forests (Stuart et al., 1982). Regeneration following a fire event is usually successful as a result of reliable seed crops and restocking capabilities (Martin and Dell, 1978).

Lodgepole pine can rapidly invade disturbed sites in the presence and absence of fire and disperses seed annually producing between 35,000 and 1.2 million seed per ha (Lotan and Critchfield, 1990 in Burns et al., 1990). A four year study in central Oregon found lodgepole pine seed production varied between 35,000 and 1,250,000 (Dahms, 1963). Abundant seed is produced in 1 to 3 year intervals (Dahms, 1963). The majority of seed in the latter study was released by the beginning of November. Seed germination from viable seed in this region is governed by low nighttime temperatures, frost heaving, high soil surface temperatures and drought, good seed crops and other physical factors (Cochran, 1973).

Climax lodgepole pine occupies a range in elevation between 1,200 and 1,525 meters (m) (Franklin and Dryness, 1988; Appendix B, Map 6). Precipitation in this region ranges between 361 and 676 millimeters (mm) and extreme temperatures
between -3.9° and 29.8° Celsius (C). Appendix A, Table 1 displays the extreme and average climate data compiled from local weather stations near the proximity of our study area separated by dominant vegetation.

Ponderosa pine is a fire-resistant species adapted to withstand low-intensity surface fires. Fire-resistant adaptations include a thick bark layer, exfoliating bark, self-pruning of lower limbs, deep tap roots, high foliar moisture content and insulated bud scales. Ponderosa pine of central Oregon have been estimated to disseminate approximately 825,050 seeds per ha during a favorable year with good seed crop occurring every 4 to 5 years (Oliver and Ryker, 1990 in Burns et al., 1990). Other sapling disturbance agents include damage by American porcupine (*Erithizon dorsatum*), pocket gophers (*Thomomys spp.*), mule deer (*Odocoilius hemionus*), Rocky Mountain elk (*Cervus elaphus nelsoni*) and American black bear (*Ursus americanus*) (Burns et al., 1990). For this study, saplings represented all understory trees < 1.4 m in height.

Species longevity ranges between 300 to 600 years for ponderosa pine and 80-220 years for lodgepole pine (Shuffield and Bailey, 2011 unpublished data). However, most lodgepole pine mortality occurs around 80-100 years as a result of the mountain pine beetle attacks, fungi and fire. Therefore, lodgepole pine of south-central Oregon has the physiological potential of reaching around 250 years within uneven-aged stands. However, longevity is similar to that of *Pinus contorta var. latifolia* as a result of disturbance agents. Ponderosa pine occupies a range in elevation between 1,280 to 2,010 meters, and precipitation range between 355 to 760
Temperatures in the Oregon ponderosa pine belt range between -5.3° to 30.8° C (Franklin and Dyrness, 1988). To better understand soil conditions related to overstory composition Tarrant (1953) summarized soil types based on the range of percent composition for each species (Appendix A, Table 2).

Appendix A, Table 3 displays 90 m mean annual temperature and precipitation climate data downscaled from the original 4 kilometer (km) dataset, and geographic description for individual plots across the inter-mixed ponderosa pine and lodgepole pine stands (Prism Climate Group, 2007; Simpson, 2007). Elevation ranges from 1285 to 2096 m, average annual precipitation ranges between 32.2 centimeters (cm) and 80.6 cm, and an average annual temperature ranging between 5.7 ° and 6.7 °C. Maximum slope for our study area was less than 22.0% with a majority of plots ≤ 5.0%.

Vegetation Potential

The concept of a plant association has commonly been used in management to interpret the vegetation potential for a particular area in the absence of disturbances (Daubenmire, 1968). Therefore, careful consideration should be made when referencing historic conditions because this classification system does not account for the historic role disturbance processes played at maintaining composition and structure. Furthermore, uncertainty associated with a lack of disturbance history has inhibited our full understanding of disturbance interactions in many ecosystems.
Throughout this thesis we considered reference conditions based at the ecosystem level, but incorporated current classification systems when appropriate to identify our study area. We recognized four major dominant vegetative zones within the south-central Oregon pumice zone: (1) climax lodgepole pine; (2) pure ponderosa pine; (3) inter-mixed ponderosa pine and lodgepole pine; and (4) inter-mixed stands where lodgepole pine has facilitated ponderosa pine seedling development.

For this study, climax lodgepole pine was defined as areas dominated by uneven-aged lodgepole pine with no evidence of recruitment or potential of ponderosa pine. We defined climax as the ability of a species to self-regenerate based on physiological tolerances to extreme edaphic and topoedaphic conditions too harsh for the development and growth of other conifer species (Volland, 1984; Cochran, 1985). Climax lodgepole pine is separated from seral lodgepole pine forests by the absence of other tree species and few shrub species in the understory (Agee, 1993). As a result of limited understory fuel accumulation, historic fires within climax lodgepole pine were closely linked to the dynamic of coarse fuel accumulation associated to mortality by past fire events, mountain pine beetle and fungi (Gara et al., 1985). Under current climax trajectories, the effects of fire exclusion have increased age structure homogeneity and associated threat of atypical mountain pine beetle outbreaks.

Pure stands of ponderosa pine were defined as areas not supporting evidence of potential lodgepole pine. The term disclimax is usually associated with this ecosystem and used to describe a stable ecosystem maintained by repeated disturbances.
Inter-mixed stands were defined as areas supporting continuous replication of favorable growing conditions for both ponderosa pine and lodgepole pine. There has been an assumed level of knowledge regarding fires natural role at inhibiting the long-term development of lodgepole pine within inter-mixed stands. Under contemporary conditions areas supporting ponderosa pine and lodgepole pine have been referred to as a transitional area or an ecotone because there has been maximum opportunity for the recruitment and long-term development of both species. However, historically ponderosa pine likely had a competitive advantage over lodgepole pine due to the development of a thick bark layer and associated resistance to frequent, low-intensity surface fires. Additionally, we acknowledged pockets of mature lodgepole pine were likely present across the landscape created by the absence of a fire cycle or as a result of rare, spatially restricted high-severity fire events (Morrow, 1985).

The last vegetation zone we identified, but did not include in this study were areas unfavorable for the early development of ponderosa pine in the absence of a lodgepole pine overstory. In these stands, lodgepole pine has acted as a facilitator of ponderosa pine. Ponderosa pine seedling development is benefited in the form of thermal covering against low-nighttime temperatures. Historically, these stands likely experienced an infrequent, mixed-severity fire regime. Independence from lodgepole pine occurred once openings were created in the overstory canopy layer as a result of beetle activity, windthrow, fungi or fire. Ponderosa pine likely withstood multiple fire events or multiple rotations of lodgepole pine once ponderosa pine penetrated through the lodgepole pine overstory.
**Historic Reference Conditions**

Reference dates are generally site specific and can vary widely depending on the homogeneity of the forest, but represent changes to a landscape, such as pre and post fire exclusion in ponderosa pine forests (Danzer et al., 1996). Early forest records and documentation commonly overlooked indirect Euro-American disturbances.

In Chapter 2, we defined a reference date of 1850 to identify the initial loss of Native American influence to the landscape and analyzed our data for statistical comparisons where appropriate. However, because remnant data prior to this period was limited due to species longevity, fire and decomposition, we also reference reconstructed 1880 conditions. This time period included indirect effects of Euro-American disturbances and loss of natural processes, but was prior to direct Euro-American disturbances in the form of logging, mining, overgrazing, farming, settlement and fire suppression. Furthermore, both dates were used for the enhancement of ecological interpretation.
CHAPTER 2 - OVERSTORY COMPOSITION AND STAND STRUCTURE SHIFTS WITHIN INTER-MIXED PONDEROSA PINE AND LODGEPOLE PINE STANDS OF THE SOUTH-CENTRAL OREGON PUMICE ZONE

ABSTRACT

We examined overstory composition and stand structure shifts during the last 160 years within inter-mixed ponderosa pine and lodgepole pine stands of the south-central Oregon pumice zone displaying old-growth structural components. These transitional areas historically separated two distinct fire regimes between climax stands of lodgepole pine, reported to have experienced mixed-severity fires every 60-80 years, and pure stands of ponderosa pine reported to have experienced low-intensity surface fires every 4-24 years. The purpose of this study was to reconstruct historic reference conditions using direct structural evidence to examine the spatial and temporal expansion of lodgepole pine since fire exclusion. Remnant stands were analyzed using dendroecological reconstruction and quantitative statistical comparison techniques.

Prior to 1880 our age reconstruction indicated relatively low levels of lodgepole pine recruitment (2 trees/ha/decade), however revealed an exponential increase of ponderosa pine and lodgepole pine between 1880 and 1950. Quantitative basal area analysis congruently displayed a decreasing trend during this period. Contemporary understory conifer dynamics revealed ponderosa pine requires an average of 30.2 years to obtain breast height and 27.1 years for lodgepole pine,
compared to 18.4 years for trees pre-dating 1850. By examining overstory composition and stand structure shifts we identified the direct effects of fire exclusion, which has resulted in increased stand density, overall long-term development of less fire-resistant lodgepole pine and resultant shifts in overstory composition. These shifts have driven broad ecosystem alterations including the risk of stand-replacing fire behavior and atypical insect outbreaks. We support a need to reflect historic stand-level diversity when applying broad restoration concepts. However, the long-term sustainability and preservation of large diameter ponderosa pine within remnant inter-mixed stands requires the restoration of fire as a process to inhibit long-term lodgepole pine development.
INTRODUCTION

In fire adapted ecosystems of the western United States, fire disturbances influenced and maintained transitional areas by inhibiting the long-term development of less fire-resistant species, which resulted in a high level of biodiversity (Arno and Greull, 1982). However, fire exclusion has reduced biodiversity in transitional areas by favoring plant succession under a climax trajectory (Franklin et al., 1971; Dickman, 1978; Bock, 1984; Arno et al., 1986; Mast et al., 1998; Miller and Rose, 1999; Bai et al., 2004; League and Veblen, 2006; Strand et al., 2007).

Fire history studies within the central Oregon landscape have suggested climax lodgepole pine historically experienced mixed-severity fires every 60-80 years, whereas the ponderosa pine ecosystem experienced low-intensity surface fires every 4-24 years prior to 1900 (Bork, 1984; Agee, 1981; Stuart, 1984 in Agee, 1993). These studies suggest transitional inter-mixed ponderosa and lodgepole pine stands historically separated two distinct fire regimes.

We hypothesized inter-mixed ponderosa pine and lodgepole pine stands experienced low-intensity fires synchronized with the timing of fire occurrences within adjacent pure ponderosa pine. Fire would have eventually spread into adjacent climax lodgepole pine along dead-down logs, particularly along decayed logs remnant from the last fire event (Agee, 1993). Numerous fire scars observed on large diameter ponderosa pine and remnant stumps combined with a high density of young lodgepole pine in the understory support this dynamic. We defined large diameter to be \( \geq 53.3 \) cm diameter at breast height (DBH).
Currently, there is an assumed level of knowledge pertaining to the natural role fire played at inhibiting lodgepole pine development within inter-mixed stands. During the last century an extensive amount of work has been published from studies within inter-mixed stands (Munger, 1908; Kerr, 1913; Munger, 1914; Tarrant, 1953; Dyrness and Youngberg, 1966; Cochran and Berntsen, 1973; Sorenson and Miles, 1974; Cochran, 1984; Morrow, 1985; Volland, 1985; Seidel, 1989; Simpson, 2007). However, specific ecological information referencing shifts in species composition and stand structure since Euro-American influence to this specific landscape is limited.

 Significant Euro-American alterations (e.g. clear-cut logging, seed-tree management and intensive grazing) and the associated disruption of natural processes have limited our ability to research undisturbed sites. Presently, no landscape-level research has been conducted to enhance our ecological understanding of successional departure from historic conditions within remnant inter-mixed ponderosa pine and lodgepole pine stands of the south-central Oregon pumice zone.

Research Objectives

Age reconstruction using dendrochronological techniques have been used to reconstruct species composition, and stand structure, to indicate disturbance history, competition and climatic variation across time (Fritts and Swetnam 1989; Mast et al., 1999). Because accurate mortality measurements are often limited, researchers commonly examine pulses in cohort establishment to better understand fluctuations in
seedling recruitment across time (Allen, 1998; League and Veblen, 2006). The incorporation of direct evidence (e.g. dead-down logs, standing dead, stumps and pre-1850 live trees) is important in order to accurately represent stand structure changes across time (Fulé et al., 1997). Mast et al. (1999) reported the reconstructed pre-settlement age structure of Gustav A. Pearson Natural Area would have been misinterpreted if only live trees had been sampled.

Our primary research objectives were to quantify: (1) shifts in overstory composition and stand structure; (2) growth and development of ponderosa pine and lodgepole pine across time; and to (3) characterize the influence of climate and fire on species recruitment. For this study, remnant was defined as stands currently supporting old-growth ponderosa pine structural components.

We hypothesized the extent of inter-mixed stands were historically less spatially expansive as a result of frequent fire disturbances. These frequent disturbances controlled overstory composition and stand structure by inhibiting the long-term development of lodgepole pine, as well as the density of ponderosa pine. Scattered mature lodgepole pine would have remained low during extended warm and dry, and cool and wet climatic periods, although regeneration was likely favored during cool and wet periods. However, surface fuel accumulation would have also increased accordingly during associated wet periods, which would have increased surface fuel homogeneity and fire spread potential. Lodgepole pine likely persisted as a result of non-serotinous capabilities and ability to prolifically seed, regardless of fire and fire frequency.
Under contemporary climax conditions, areas where mortality has resulted from maximum longevity, disease and insect activity lodgepole pine breaks-down in the understory of ponderosa pine creating a jack-straw of entangled logs. Through time new cohorts established as resources became available. This cycle was repeated if the stand was spared from high-severity fire and atypical mountain pine beetle outbreaks. Figure 1 displays a simplified state-and-transition model in an attempt to display the effects of fire exclusion within remnant inter-mixed stands.

However, stand complexity is highly dependent on environmental controls, physiological capabilities, disturbance history, availability and distance of ponderosa pine seed sources and climate. Our state-and-transition model was limited to stands where growing conditions supported the dominance of ponderosa pine in the overstory and understory.
Figure 1. Simple state-and-transition model for inter-mixed ponderosa pine and lodgepole pine stands of the south-central Oregon pumice zone. **L** - Increased lodgepole pine sapling density between frequent, low severity fire events. **M** - Lodgepole pine inhibited from long-term development due to frequency of low-severity fire. **N** - Long fire-free periods may lead to increased stand density and long-term development of lodgepole pine. **O** - Thinning and removal of lodgepole pine followed by the reintroduction of fire restores pre-fire suppression conditions. **P** - Dominant overstory ponderosa pine mortality continues as a result of inter and intra-specific stress. Lodgepole pine competes with ponderosa pine in the understory. Following a high-severity fire event lodgepole prolifically recruits in dense patches. Loss of seed-bearing ponderosa pine inhibits regeneration, which leads to dominance of lodgepole pine and alters overstory composition compared to historic reference conditions. Some large diameter ponderosa pine would likely remain that survived high-severity fire, but at low densities and not in every stand. The crossing of this threshold leads to a mixed-severity fire regime at the landscape-level and increased threat of insect outbreak (assumes no management intervention).
During extended warm and dry, fire-free periods, lodgepole pine would have displayed long-term development in areas missed by fires or had an opportunity to develop bark thickness resistant to low-intensity surface fires. Mature lodgepole pine would have increased fire resistance acting as a seed source for future cohorts.

Mortality by fire was likely significant for both species, although survival of ponderosa pine would have been more prevalent due to adapted resistance of low-intensity fire. In a southwestern U.S. ponderosa pine study, all saplings >5.0 cm diameter at stump height and > 2.0 m total height were reported to have survived surface fire with evidence of scorch at their bases (Bailey and Covington, 2002). Lodgepole pine seedling establishment has likely always been more abundant near stand edges adjacent to climax lodgepole pine. Reasons include distance to seed source and unfavorable ponderosa pine seedling development requirements. We also hypothesized the effects of fire exclusion have increased stand density, reduced diameter growth and increased long-term survival and density of lodgepole pine.

Secondary effects include the increased threat of stand-replacing fire behavior, insect outbreak, and inter and intra-specific competition induced mortality, resulting in a loss of large diameter ponderosa pine and direct quantitative data linking contemporary to historic reference conditions.
METHODS

Study Area

Our study area was located on the east slope of the south-central Oregon Cascade Range on the Bend/Fort Rock and Crescent Ranger Districts of the Deschutes National Forest, Silver Lake Ranger District of the Fremont-Winema National Forests and LaPine State Park (Appendix B, Map 7). In our study area, inter-mixed stands occurred across the High Cascades, High Lava Plains, and Basin and Range physiographic and geological provinces.

Our study area was limited to the ponderosa pine/bitterbrush, ponderosa pine/bitterbrush/Idaho fescue, ponderosa pine/greenleaf manzanita, ponderosa pine/long-stolon sedge plant associations described by Simpson (2007) within ponderosa pine dry plant association groups. Understory vegetation was mostly dominated by antelope bitterbrush, Ribes cereum, Achnatherum occidentale, Elmus elymoides and Carex rossii (Simpson 2007). Other common understory species included: Ceanothus velutinus, Arctostaphylos patula, Carex rossii, Fragaria virginiana platypetala, Sitanion hystrix.

Site-Selection

Our study sites contained multi-aged stands discernible from adjacent single-aged stands that were created by aggressive early 20th Century logging on former private land or stand-replacing wildfires on federal land. Evidence of historic logging activity to reduce the threat of insect, disease and wildfire on federal land was
common throughout our study area, evidenced by scattered large diameter ponderosa pine stumps. Remnant stands were observable by the presence of large diameter, multi-aged ponderosa pine and lodgepole pine, and multi-story canopies as a result of ingrowth over the last century. We incorporated the entire extent of inter-mixed ponderosa pine and lodgepole pine because stands displaying old growth characteristics are rare and in decline.

Forest and stand-level data is limited from the late 19th Century and Federal and State land not impacted by some form of historic logging activity is rare. Areas currently displaying old-growth structural components missed by early aggressive logging activities are now at risk of stand-replacing fire behavior or have already been consumed by uncharacteristic, stand-replacing fire events. The combination of these factors has left scientists and researchers with limited opportunities to recreate historic conditions using stand reconstruction.

During the 1930’s, many Research Natural Areas were designated in Oregon to preserve ecosystems in relatively pristine conditions. RNA’s were recommended by forest officials and set aside to conduct non-destructive research for the purpose of providing information to land managers and to contribute to science (Greene et al., 1986). Scientists have used RNA’s to study structural shifts and spatial relationships to infer results for the purpose of aiding restoration objectives to neighboring stands (Morrow, 1985). Multiple RNA’s have also been used to broaden the scope of inference to the larger landscape (Youngblood et al., 2004). However, recent restoration activities within RNA’s have further limited our ability to implement new
research dependent on the absence of human intervention, although these activities are well justified to maintain their unique features (Wilson et al., 2009).

Although remnant stands in our study area displayed evidence of historic logging to improve stand susceptibility to insect outbreak, our study design allowed us to capture historic quantitative data while also incorporating and representing contemporary conditions (Keen, 1943). All plots were established on the Deschutes National Forest, Fremont-Winema National Forests and LaPine State Park.

Remnant stands were identified based on overstory structure using aerial photographs. Stands were later evaluated to determine whether the following research criteria were met:

- Mature ponderosa pine dominating the overstory with some combination of understory ponderosa pine and lodgepole pine;
- No evidence of recent fire activity;
- Minor evidence of Euro-American disturbance.

We classified ponderosa pine as mature based on visibly deep bark furrows and flat or rounded crowns (Van Pelt 2008; Keen 1943). Stands were disregarded if overstory trees consisted solely of “black bark” ponderosa pine (<100 years old). Evidence of disturbance was based on: (1) presence of stumps and mechanical displacement, (2) missing diameter and height classes, (3) presence of charcoal on soil surfaces suggesting evidence of recent fire and (4) close proximity of remnant railroad
grades (Figure 2). A total of fifteen sites were selected for this study. Each site was composed of many individual stands separated by road systems. All neighboring stands suggested our study sites was spared during regionally heavy logging activity as a result of presumed low productivity, ownership and federal land management practices. Careful interpretations should be considered when data from this study is compared to historic quantitative information. Site names used in this study were unofficial and based on major geographic locations. Therefore, site names did not necessarily correlate to close proximity of a major geographic site.

Figure 2. Remnant railroad grade visible by the elevated berm and wood ties covered by needle cast and vegetation.
Field Methods

Polygons were created in ArcMAP/ArcGIS 9.3.1 to define stand boundaries (ESRI, 2009). Hawth’s Analysis software was used to randomly generate a center point for each sample plot (Beyer, 2004). Within each stand a 150 meter buffer was placed around all roads and stand edges and a 300 meter buffer was placed around all sampling points. Four random plot centers were located within each site to define a 0.1 ha circular sampling plot (17.8 m radius). Therefore, 15 sites * 4 plots = 60 total plots. Plot centers were located in the field using a handheld Global Positioning System (GPS) unit. A plot size of 0.10 ha was used because the sampling area was sufficient enough to capture old-growth structural components, and was easily expandable for data analysis and interpretation.

All field sampling was conducted during the summer and fall months of 2008 and 2009. Sampling procedures included measuring tree DBH in cm, tree height in m and height to crown ratio in m of each tree ≥ 1.4 m in height. We also recorded tree species, presence of western dwarf mistletoe (Arceuthobium camphyopodium), presence of tree damage, type of crown characteristics and presence of cones. Ponderosa pine and lodgepole pine saplings were tallied in each plot to evaluate understory abundance.

Tree increment cores were collected at breast height (1.4 m above ground) to create an age-diameter regression model used to predict breast height age from DBH. An increment borer was used to core every 10th live tree in each plot, regardless of species. Field technicians also cored every ponderosa pine > 60.0 centimeters at
breast height and every lodgepole pine > 30.0 cm DBH to ensure adequate representation of large diameter classes. We cored approximately 13 trees per plot on average. The number of associated increment cores per plot fluctuated because tree density varied and the first tree in each plot was randomly selected. Tree cores were stored in the field using paper art straws to prevent mold, labeled by site, plot number, and tree number with a fine tip permanent marker adapted from a method described by Maeglin (1979). Trees ≤ 4.0 cm diameter at root collar (2-5.0 centimeters above mineral soil) were cut at root collar using destructive sampling techniques to improve tree aging accuracy.

Two root collar cross sections (disks) were collected from saplings < 1.4 m in height within 11 randomly selected sites across our study area to: (1) examine height development and estimated years to breast height and (2) compare contemporary sapling age-height relationships against historic quantitative sapling information. Individual sapling root collar disks were collected in suppressed, open and intermediate understory conditions. Saplings with evidence of wildlife damage were not selected for sampling.

In each plot 4 ponderosa pine and 4 lodgepole pine paired root collar and breast height disk samples were collected from trees ≥ 1.4 m in height, but ≤ 16.5 cm DBH using destructive sampling techniques. All trees were subjectively selected by dividing our plot area into 4 quadrants. Quadrants were identified from plot center and marked with flagging along perimeter angles at 0°, 90°, 180° and 270°. In each quadrant, we selected the first sampled tree between 0 - 4.9 cm DBH, 5.0 - 9.9 cm
DBH and 10.0 - 16.5 cm DBH. However, tree clumping patterns representing the same diameter class range, inhibited us from collecting 3 disk pairs per quadrant. Each disk pair was labeled by site, plot number, tree number and position on tree (e.g. breast height /root collar) using a permanent marker. Each disk was incorporated into our age-diameter regression model and radial growth analyses. Root collar and breast height disks were used in our analysis to estimate average number of years to obtain breast height.

Large diameter ponderosa pine snags are rare and protected in our study area. Therefore, we did not incorporate large diameter snags into our destructive sampling design. However, all dead-down logs were destructively sampled at root collar and 1.4 m from each bole base (herein referred to as breast height for all dead-down samples). Ideally, these samples would have been sampled within each plot perimeter. Data from dead-down logs were not included in our age-diameter regression models because they were sampled outside of our plots. Furthermore, bark was absent or loosely intact on approximately 80.0% of our samples which inhibited us from collecting a DBH measurement. Data from dead-down samples were used to determine year of establishment and later incorporated into our age to breast height analysis, whereas data from all breast height disks were incorporated into our basal area growth analysis.

Each disk pair was wrapped in plastic and labeled by site and tree number with a broad tipped permanent marker. GPS coordinates of all dead-down large diameter ponderosa pine were collected to archive tree location records (Appendix B, Map 8).
Root collar and breast height disks were air dried in central Oregon’s environment under covered conditions for several weeks during both field seasons to avoid mold. Age to breast height data was collected by subtracting total number of rings on each root collar disk from paired breast height disks. This step allowed us to determine total number of years required for each sample to obtain breast height.

Data Preparation and Processing

Increment cores were prepared for sanding by gluing individual samples into grooved wooden blocks with each tree center (pith) vertically aligned. All increment cores were sanded using a belt sander beginning with 120-grit followed by a 320-grit sanding paper. A 400-grit sanding paper was used last as a finish to obtain optimum tree-ring clarity. All breast height and root collar disks were prepared with a belt sander using 80-grit, followed by a 120-grit sanding paper, and finished with a 320-grit or 400-grit, depending on tree-ring clarity. If additional clarity was needed, cores and disk samples were hand sanded with a 600-grit sanding paper. Each disk pair was sanded together and re-wrapped with plastic after sanding. Decomposition in some disk samples inhibited us from determining age. Furthermore, heartwood decay in some large diameter trees also inhibited us from extracting complete increment cores.

Tree core age estimates were determined by hand counting individual tree-rings under a binocular dissecting microscope. Missing years were estimated using a pith locator when core samples did not intercept tree center (Applequist, 1958). Tree cores not within 5 years of tree center were removed from our analysis.
Large diameter ponderosa pine breast height disks were aged and cross-dated using a master chronology from near our study area to determine year of mortality and to check for missing and false tree-rings (Speer et al., 2001). Large diameter lodgepole pine breast height disks were not cross-dated, due to a lack of correlation between key years, and formal published lodgepole pine master chronology for our study area. Therefore, we used total number of annual rings from each root collar sample and subtracted from 2009. Although there is an error associated with establishment date, we were able to successfully determine specific years that each sample pre-dated. All disks collected from dead-down logs were either touching the ground or lightly suspended above mineral soil. Samples were not collected if technicians determined the level of decomposition would inhibit tree ring analysis.

Because 50.0% of lodgepole pine biomass decomposition is reached around 26 years our age estimates for dead-down samples likely underestimated the true establishment year for dead-down samples (Busse, 1994). Conservative establishment estimates may also arise from the lag time between standing dead and dead-down logs. In a central Oregon study, 90.0% of lodgepole pine killed by mountain pine beetle fell within 12 years in thinned stands, and 14 years in unthinned stands, regardless of tree size (Mitchell et al., 1998).

During data collection dead-down logs were only collected from large diameter samples because small diameter material had already decomposed. Age distributions can sometimes misrepresent the historic density of young, small diameter trees (Mast et al., 1999). However, studies from dry regions of the west indicated
historic young tree survival has been accurately represented as a result of slow
decomposition combined with natural mortality caused by high fire frequency (Fulé et
al., 1997; Everett et al., 2007).

Lodgepole pine is a relatively short-lived species compared to ponderosa pine,
usually succumbing to insect, disease and fire before the longevity of the species is
reached (Gieszler et al., 1980). However, Swezy and Agee (1991) reported lodgepole
pine reaching 200 years with distinct age class peaks around 160 to 180 years, 100 to
120 years and 40 to 60 years in climax stands within Crater Lake National Park. Other
studies within climax stands report lodgepole pine age estimates of 140 years within
the central Oregon pumice zone (Littke et al., 1986).

Radial growth data from tree core and breast height disks were incorporated
into our basal area analysis (Bonham, 1989). Ring widths were measured to the
nearest 0.001 mm using Measure J2X with a binocular microscope and incremental
measuring unit (Voorhees, 2000). COFECHA was used to correct for dating problems
associated with false or missing annual growth rings (Holmes, 1983; Grissino-Mayer
and Holmes, 1993; Grissino-Mayer, 2001). Based on a tree core subsample (20.0%) and
breast height subsample (23.0%), we found a 2.0% age associated error, which
was not significant enough to affect the results of this study.

All root collar data with an associated diameter were used for our age
reconstruction analysis, excluding dead-down samples. Total age for all root collar
samples were obtained by subtracting date sampled from the associated establishment
date. Sapling root collar data was used for our understory development in conjunction
with our years to obtain breast height analysis. Due to tree-ring identification
difficulties, we could not accurately age all saplings < 1.4 m.

We used R statistical software for all of our statistical analyses (R
Development Core Team, 2006). Tree height and height to crown ratio data were not
used as a predictor for tree age in this study. Preliminary analysis revealed these
variables, including any combination in conjunction with DBH, did not significantly
increase our aging accuracy. However, we acknowledge DBH is a poor predictor of
age in suppressed stands and old trees (Van Pelt, 2008).

Regression Fits

We fit a simple linear regression (SLR) model to our lodgepole pine age-
diameter relationships. The SLR model was fit to our tree core and breast height disk
data to estimate breast height age from DBH for trees with only a DBH measurement.
All assumptions of this model were met and transformations to the data did not change
or improve correlation between breast height age and diameter.

We fit a weighted least squares regression (WLSR) model to our ponderosa
pine age-diameter relationships. A WLSR model was fit to our ponderosa pine age-
diameter relationship. Our test of non-constant variance in our SLR model was
violated. Residuals from the SLR model were used to estimate weights and refit to
our model using predicted weights, which resulted in nearly constant variance. We
then used the weighting function to estimate standard error (SE).
Tree core and breast height disk samples were fit using a SLR model based on our breast height data and root collar data to estimate total age from breast height. Age structure is commonly analyzed and reported in histograms displaying frequency by 10 or 20-year age classes to depict broad recruitment patterns across time and to reduce the amount of stand-level discreetness within a single year. Therefore, we also analyzed our data by frequency per 10 and 20-year age classes.

To better examine current age structure against historic conditions we compared data from a logged 16 ha stand of virgin ponderosa pine collected near Embody, Oregon in 1917 (Appendix B, Map 9). This site is located near the southeast portion of our study area. Historic contemporary data displays the number of trees by age class per decade for trees over 100 years old (Munger, 1917). All data was displayed in histograms using SigmaPlot 11 (Systat Software Inc., 2010).

*Diameter Distribution and Basal Area Growth*

Diameter distributions for our study area was analyzed and displayed as frequency of trees by 5 cm diameter class. For this analysis, we included all live samples with associated DBH measurements. To better analyze diameter shifts across time, we compared our results to quantitative diameter distribution information also provided by Munger (1917). Data was prepared and displayed as frequency by 5 cm diameter class. Historic data was collected from representative central Oregon stands using a 30 acre tract as a basis and converted to trees per acre (Munger, 1917). Data from Munger’s (1917) second site was collected near LaPine, Oregon. This stand was
also representative of central Oregon conditions using a 40 acre tract as a basis and converted to TPH (Munger, 1917). Contemporary and historic diameter distribution information was incorporated into a frequency by diameter class histogram and a smoothed value age-diameter relationship using SigmaPlot 11.

Basal area comparisons were separated by establishment date to determine trends in stand density and competition across time. We did not consider first 5 years of growth for our basal area analysis in order to increase our sample size by including all tree core samples, particularly samples where a pith locator was used to estimate number of years to tree center. Clumpy seedling establishment from rodent caching, root development, climate, browse and fire would have increased confounding variables within the first 5 years of establishment (Cooper, 1960). Basal area was calculated as follows:

\[
\text{Tree basal area (BA)} = 0.0000758 \times (\text{Radius}_i \times 2)^2
\]

(Where, \(i = ith\) sample)

Basal area groups were later separated by ponderosa pine establishing: (1) Group A “pre-1850”, (2) Group B “post-1850, pre-1920”, (3) Group C “post-1920”; and lodgepole pine establishing (4) Group D “pre-1920” and (5) Group E “post-1920.” We based our group selection on our identified reference date, historic logging activities and other land-use practices specific to our study area.

Pairwise comparisons between basal area groups were analyzed using Analysis of Variance (ANOVA) non-repeated measures in R. Log transformations to our data
were performed to adhere to model assumptions. A Tukey Honestly Significant Differences (HSD) test was then performed to further determine differences between groups. We then computed a 95.0% family-wise confidence level comparison between groups with their adjusted p-values. Basal area comparisons were calculated from a 32.0% ponderosa pine sub-sample and a 37.0% lodgepole pine sub-sample randomly selected from all samples used in our age-diameter regression analysis. This included all dead-down logs collected using destructive sampling techniques.

We determined a subsample ≥30.0% was sufficient enough to capture and appropriately represent our total population and associated growth trend. Results were then incorporated in a box-and-whiskers plot displaying median basal area growth in log (cm²) units by associated groups. Basal area comparisons were between 30 and 50 years of growth was selected as an assumed age for long-term survival and less confounding variables associated with understory development.

*Understory Conifer Development*

Because there has been a presumed shift in number of years required to obtain breast height for trees > 1.4 m across time, we also analyzed a separate age-height relationship for saplings < 1.4 m in height. This analysis was performed to better examine understory development and predicted number of years to obtain breast height. Our data was then compared to historic quantitative sapling information provided by A.F. Kerr (1913) and Munger (1917), as well as more recent sapling quantitative information provided by Morrow (1985). All historic quantitative sapling
information was collected in stands representative of our study area. We also fit a
SLR model to our sapling age-height relationship. All model assumptions were met
and transformations to the data did not improve age-height relationships.

Age-height relationships were based from differences in number of years
between ponderosa pine and lodgepole pine root collar disk and core height disk
samples. All samples were collected within Pringle Falls Research Natural Area
(RNA) using destructive sampling techniques. All samples for both 2009 and 1985
models were collected within suppressed conditions, semi-suppressed and open
conditions.

*Influence of Climate and Fire on Species Recruitment*

Temporal recruitment patterns were analyzed against Palmer Drought Severity
Index (PDSI) values from a south-central Oregon gridpoint near our study area (Cook
*et al.*, 2004). PDSI values were smoothed to reveal 20-year low-pass values based on
original data using SigmaPlot 11. Recruitment patterns were reconstructed and
analyzed by displaying frequency of trees by 10-year age class against 20-year
smoothed PDSI values. Our climate analysis was also conducted to examine recent
recruitment associated to a cooling and wet period during the early 1900’s.

Additionally, to determine the influence of fire on species recruitment we
selected two known large fires within our study area to compare recruitment between
two study sites for the purpose of identifying general post-fire recruitment patterns.
Post-fire recruitment of ponderosa pine and lodgepole pine was carefully examined and analysis was further highlighted to show frequency of recruitment by year of establishment. The purpose of this analysis was to distinguish post-fire effects between species. Figure 3 displays a flow-chart summarizing the type of data collected and how our data was eventually analyzed in our study.
Figure 3. Ponderosa pine flow-chart summary of data collected and where data was used in our study. The same flow-chart was also used for lodgepole pine with the exception of a SLR model to estimate age at breast height.
RESULTS and DISCUSSION

Age-Diameter Relationships

Our ponderosa pine and lodgepole pine age-diameter relationships yielded the following models to estimate breast height age from DBH for all samples with only a DBH measurement.

Ponderosa pine age-diameter relationship (Figure 4):

\[
\text{Ponderosa pine breast height age} = 25.47 + 2.93 \times \text{DBH}_i \text{ (cm)}
\]

(WLSR: n = 490, (SE_{wls} = SE_{slr}/wts = SE_{slr}*(86.7*DBH))

(\text{where, } wts=1/var(\text{tree}_i)), P < 0.001; \text{ DBH} = \text{diameter at breast height}; i = \text{DBH for } i\text{th tree})

Figure 4. Age-diameter relationship for ponderosa pine within remnant inter-mixed stands of the south-central Oregon pumice zone. A Weighted Least Squares Regression (WLSR) model was fit to our age-diameter relationship. Standard error was modeled to account for increased variance for each one-unit increase in DBH. Ponderosa pine breast height age = 25.47 + 2.93 *DBH (n=489, r^2 = 0.66, P < 0.001).
Lodgepole pine age-diameter relationship (Figure 5):

\[
\text{Lodgepole pine breast height age} = 29.96 + 1.94 \times \text{DBH}_i \text{ (cm)}
\]

(SLR: \( n = 434, r^2 = 0.49, \text{SE} = 21.52, P < 0.001; \text{DBH} = \text{diameter at breast height}; i = \text{DBH for } i\text{th tree})

Figure 5. Age-diameter relationship for lodgepole pine within remnant inter-mixed stands of the south-central Oregon pumice zone. A Simple Linear Regression (SLR) model was fit to our age–diameter relationship. Lodgepole pine breast height age = 29.96 + 1.94*DBH (n=434, \( r^2 = 0.49, P < 0.001 \)).

Typically, 5 to 10 years is an assumed estimate to account for missing years to obtain breast height for ponderosa pine (Youngblood et al., 2004). We added 18.4 years (standard deviation (SD) = 8.3 years) to ponderosa pine estimated to be greater than 160 years at breast height, 30.2 years (SD = 8.6 years) to ponderosa pine estimated to be less than 160 years at breast height and 27.1 years (SD = 9.6 years) for
all lodgepole pine (Shuffield and Bailey, 2011). Our reference date of 1850 was incorporated to separate between pre and post historic reference conditions. We averaged all lodgepole pine age to breast height records due to our small sample size pre-dating 1850 (Appendix A, Table 4). Furthermore, based on our observations and analysis, an open grown sapling does not always reflect exceptional height growth compared to saplings growing in the understory of a semi-closed canopy, which is why a statistical average of all samples was incorporated.

Our age to breast height estimates were based on the average difference in the number of annual growth rings between breast height and root collar disk samples, earlier described in the methods section. This step was performed on samples with only a DBH measurement and no direct breast height age related record. Figure 6 displays the average number of years to obtain breast height across time for our study area. Additional time periods were incorporated based on Euro-American disturbances to provide supplementary information relating to shifts in height growth following indirect influences and aggressive logging activities on private land around the 1920’s (Appendix A, Table 4; Figure 6). Both species displayed an increasing trend in number of years to obtain breast height between 1850 and 1920. Following 1920, ponderosa pine displayed a continued increasing trend, while lodgepole pine displayed a continued decreasing trend in height growth.
A total of 663 ponderosa pine samples were aged using techniques described in our methods section. Three hundred and eighty-two samples consisted of tree cores with roughly a 21.0% success rate of capturing the pith. A total of 147 paired ponderosa pine root collar and breast height disk samples were used to estimate the average number of years to obtain breast height across time and later fit to SLR models for estimating total age from breast height age for all tree core and unpaired breast height disk samples (39.0%). One hundred and ninety-seven samples were root collar disks, which were further used in our age reconstruction.

A total of 540 lodgepole pine tree core and breast height disk samples were aged using techniques described in our methods section. Three hundred and thirty of those samples consisted of tree core samples with roughly a 20.0% success rate of
capturing the pith. A total of 100 root collar samples and 110 paired lodgepole pine root collar and breast height disk samples were analyzed for this study.

An additional 21 paired root collar and breast height disk samples and 15 dead-down lodgepole pine paired root collar and breast height disk samples were also analyzed. Together, only 132 paired root collar and breast height disk samples were incorporated into our SLR model to estimate total age from breast height age for all 330 tree core and breast height disk samples (40.0%). Therefore, 489 ponderosa pine tree core samples were analyzed to estimate tree age at breast height for 6,690 trees (~8.0 %). Four hundred and thirty-four lodgepole pine samples were analyzed to estimate tree age at breast height for 4,323 trees (10.0%).

The difference in number of annual growth rings between our paired breast height and root collar disk samples yielded the following SLR models to estimate total age from breast height age for all tree core and unpaired breast height disk samples:

**Ponderosa pine age** $= 35.02 + 0.95\times BHA_i$ (SLR: $n = 147$, $r^2 = 0.98$, $P < 0.001$)

**Lodgepole pine age** $= 28.05 + 0.94\times BHA_i$ (SLR: $n = 132$, $r^2 = 0.92$, $P < 0.001$)

(Where $BHA = \text{breast height age in years}; i =$ ith breast height age sample)

Figure 7 and Figure 8 display frequency of trees aged (aged samples) and tree age estimates (total age estimated from model) against 10-year age class by establishment year. Tree estimates based solely on diameter did not seem to significantly shift our age reconstruction or general recruitment trends when compared to our age reconstruction based solely on aged samples.
Figure 7. Ponderosa pine aged (Pipo) and estimated ages (Pipo Est.) by 10-year age class. Tree age data collected from remnant inter-mixed ponderosa pine and lodgepole pine stands of the south-central Oregon pumice zone.

Figure 8. Lodgepole pine aged (Pico) and estimated ages (Pico Est.) by 10-year age class. Tree age data collected from remnant inter-mixed ponderosa pine and lodgepole pine stands of the south-central Oregon pumice zone.
Overstory Composition and Age Structure

Our age reconstruction revealed an average of 2,036 live ponderosa pine and lodgepole pine greater than 1.4 m in height per ha (ponderosa pine = 1,225.5/ha, lodgepole pine = 810.5/ha) over our study area. Remnant inter-mixed ponderosa pine and lodgepole pine stands revealed evidence of sensitivity to indirect Euro-American disturbances evidenced in our age and growth reconstruction analysis.

A significant influx of recruitment occurred between 1880 and 1950 with an exception of one general peak ponderosa pine recruitment period occurring during the 1860’s. Recruitment per ha was achieved by summing total sample size divided by total study area (6 ha) per age class for each species. Total sample size population over our entire study area consisted of 7,353 ponderosa pine and 4,863 lodgepole pine for a grand total of 12,216 samples.

Our results revealed ponderosa pine established at an average rate of 1.1 TPH/decade (Range: 0 to 6.5 TPH/decade), prior to 1850. During this time, ponderosa pine density was low (~44.2/ha), but increased to 71.5 TPH based on 1880 reconstruction. However, between 1800 and 1900 ponderosa pine established at a rate of 8.8 TPH/decade (Range: 3.2 to 24.2 TPH/decade). On average, ponderosa pine greater than 150 years accounted for 53.0 TPH.

Lodgepole pine accounted for approximately 1.3 TPH with an associated average recruitment of 0.3 TPH/decade (Range: 0 to 0.8 TPH/decade) for our study area prior to 1850. Prior to 1850, lodgepole pine accounted for roughly 2.8% of the total tree density and roughly 9.2% of the total tree density per ha prior to 1880. Age
reconstruction revealed lodgepole pine recruitment was relatively low (~7.3/ha) prior to 1880. Lodgepole pine accounted for approximately 40.0% of the total tree density per ha. However, between 1850 and 1900 lodgepole pine accounted for approximately 31.5 TPH, of which, 48.0% established during the 1890’s. Therefore, between 1800 and 1900 lodgepole pine average recruitment consisted of 3.2 TPH/decade. Based on our age reconstruction reference conditions (1850 to 1880) lodgepole pine accounted for approximately 6.0 TPH with an associated recruited rate of 2.0 TPH/decade (Range: 1.2 to 3.7).

Ponderosa pine recruitment was represented in most age classes, except noticeable absences between 1660 and 1670, 1580 and 1570, 1550 and 1520, and 1490 to 1450. Lodgepole pine was present in all age classes following 1800 except an absence between 1830 and 1820. Lodgepole pine recruitment increased 3.5 times during the 1880’s compared to 1870’s. Recruitment again increased approximately 1.6 times during the 1890’s compared to 1880’s, approximately 2.3 times during the 1900’s compared to 1890’s, approximately 2-fold during the 1910’s compared to 1900’s and approximately 1.6 times during the 1920’s compared to 1910’s. Trends in tree establishment prior to 1700 were vague due to our small sample size.

Overall, tree establishment was observed in every age class with no significant evidence of distinctive multimodal pattern of ponderosa pine recruitment following 1670. Tree recruitment continued to increase following 1850, regardless of observed climatic fluctuations with > 95.0% of the trees less than 160 years old. General peaks in ponderosa pine recruitment occurred during the 1860’s, 1820’s, 1760’s, 1730’s,
1710’s and 1630’s. Our pattern of lodgepole pine recruitment was limited to 1800 due to our small sample size, resulting from species longevity and decomposition. However, because an exhaustive search was performed to find all dead-down logs, we feel historic lodgepole pine recruitment following 1850 is well represented.

During the 1950’s our age reconstruction revealed 3.2 times less ponderosa pine and 4.6 times less lodgepole pine recruitment compared the 1940’s. During the 1940’s there was 1.7 times more ponderosa pine and 1.7 times more lodgepole pine recruitment compared to the 1930’s. This pattern of understory tree species development and associated increase in fire-intolerant species has been observed in other fire-excluded forests of the western U.S. (Arno et al., 1995). Differences in species recruitment becomes apparent following the 1950’s as lodgepole pine increased recruitment by a magnitude of 2-fold over ponderosa pine and continued to recruit at a higher rate up to present time, excluding saplings <1.4 m (Figure 9 and Figure 10). Figure 10 was includes sapling prevalence per ha between species at a separate scale compared to Figure 9.
Figure 9. Age reconstruction of ponderosa pine (Pipo) and lodgepole pine (Pico) from remnant inter-mixed ponderosa pine and lodgepole pine stands displaying frequency of ponderosa pine and lodgepole pine by establishment date.
Figure 10. Age reconstruction of ponderosa pine (Pipo) and lodgepole pine (Pico) from remnant inter-mixed ponderosa pine and lodgepole pine stands displaying frequency of ponderosa pine and lodgepole pine by 10-year age class, including saplings (<1.4 m).
Age structure is also commonly reported and displayed as frequency by 20-year age class to depict broad recruitment patterns across time and to reduce the amount of stand-level discreetness within a single year. Therefore, we also analyzed our data as frequency by 20-year age class (Figure 11). However, little evidence suggested broad recruitment patterns were needed for this study.

Broad recruitment patterns revealed a similar increase in recruitment during the last century, but masked the general increase of ponderosa pine recruitment during the 1860’s. We determined decadal representation was best fit when analyzing our study areas sensitivity to Euro-American influence and loss of natural processes. Furthermore, decadal representation was needed to target temporal patterns of disturbance associated to shifts in overstory composition and stand structure across time.
Figure 11. Age reconstruction of ponderosa pine (Pipo) and lodgepole Pine (Pico) within remnant inter-mixed ponderosa pine and lodgepole pine displayed as frequency by 20-year age class used to analyze age structure.
Historic quantitative information for ponderosa pine greater than 100 years old reported as frequency by 10-year age class revealed contemporary remnant stands displayed similar age-frequency patterns for trees greater than 250 years old (Munger, 1917). This supports our observation that remnant stands were spared from most historic logging activity. Shifts in ponderosa pine frequency by age class were observable and evidenced in older cohorts. For example, trees around 500 years old in contemporary stands were reported to be around 408 years old in 1917.

Approximately 48.0% of ponderosa pine density was historically represented between 150 to 250 years old (Figure 12). In contemporary stands, ponderosa pine around 150 to 250 year old accounted for approximately 18.0% of the total density. However, there were approximately 3.6 times more ponderosa pine in this age group compared to historic conditions. Approximately 76.0% of ponderosa pine was less than 150 years old. Contemporary stands also revealed a higher frequency of older age classes, particularly between 200 and 300 years old. We speculate the higher density of ponderosa pine greater than 200 years old was the result of our site selection criteria.
Figure 12. Ponderosa pine age distribution from two sites within south-central Oregon’s pumice zone displayed as frequency by 10-year age class.
Species abundance fluctuated by site across our study area (Appendix A, Table 5). However, general trends showed higher lodgepole pine density on drier sites compared to wet sites along associated precipitation gradients for our study area. Ponderosa pine greater than 150 years old accounted for less than 5.0% of the total contemporary density, whereas lodgepole pine greater than 100 years old accounted for approximately 3.0%.

The oldest living ponderosa pine sampled near Crane Prairie was 566 years old (establishment date = 1443) and the oldest living lodgepole pine sampled near Red Butte was 200 years old (establishment date = 1809). Our oldest living lodgepole pine samples were collected from arid sites, whereas a majority of the oldest ponderosa pine samples were collected from relatively moist sites. Although there was a general pattern of finding older ponderosa pine on sites with higher average annual precipitation and lodgepole pine on drier sites, there was not an observable pattern between tree density and associated east to west precipitation gradient (Figure 13). This reflects the importance and influence of environmental diversity on vegetation heterogeneity at the stand and landscape-level.
Dead-Down Logs

Nineteen of our 20 ponderosa pine paired root collar and breast height disk samples were successfully cross-dated. The oldest dead-down ponderosa pine was 546 years old at root collar and 524 years old at breast height. This sample was determined to have died in 1996 from uprooting due to windthrow (establishment date = 1450).

The oldest dead-down lodgepole pine sampled near Big Hole Butte was estimated to be 219 years old at root collar and 213 years old at breast height (establishment date = \(\geq 1790\)). Our 219 year old lodgepole pine point sample survived 6 fires with a fire return interval of 36.7 years, evidenced by heavy charcoal.
accumulation between discontinuous growth rings. Decomposition of this sample slowed since death as a result of heavy pitch accumulation. We also provided evidence of a 195 year old lodgepole pine sampled near Finley Butte.

Out of our 45 paired root collar and breast height disk samples, we were only able to successfully estimate age records of 20 samples. Our histogram of dead-down logs revealed lodgepole pine pre-dating 1850 was scarce, but was still present on the landscape. In addition to our ability to opportunistically sample all dead-down lodgepole pine, our results suggested recruitment patterns were well represented following 1850. Furthermore, the addition of dead-down samples would not have altered our recruitment patterns across time (Figure 14).
**Stand Structure**

Diameter at breast height measurements from all 7,354 ponderosa pine and 4,863 lodgepole pine > 1.4 m in height were displayed in a histogram showing frequency per ha by 5 cm diameter class (Figure 15). Our contemporary diameter distribution from across the study area revealed a reverse J-shaped distribution. Ponderosa pine diameters ranged between 0.3 and 122.6 cm with 2.1% of live tree > 53.3 cm. Lodgepole pine diameters ranged between 0.2 and 53.1 cm with 10.0% of live trees greater than 20.3 cm DBH. Small diameter trees < 10.0 cm DBH at breast height accounted for 77.6% of all ponderosa pine and 64.7% of all lodgepole pine.

Diameter growth trajectories displayed excellent development for ponderosa pine up to around 150 years (Figure 16). Following this time diameter growth progresses, but at a slower pace, flattening around 350 to 400 years of age for Lapine (1) 1917, Lapine (2) 1917 and Embody 1917. The 2009 data displayed slow diameter growth compared to the 1917 and then rapid growth development between 200 and 300 years of age, but still within the range of historic growth variability for ponderosa pine greater than 200 years old.

These data suggested ponderosa pine developing in the last 2 centuries have slowed diameter growth compared to historic conditions, especially during the first 150 years. The 2009 smoothed regression model showed tree establishment prior to 1800 had developed under a different diameter growth trajectory compared to trees that established following 1800. The trajectory of ponderosa pine younger than 200 years of age, if plotted separately through time, will follow a projected trend.
consisting of reduced diameter growth under current suppressed conditions. Our results supported the concept that a given unit area of land is only capable of supporting a maximum leaf area index, as a result of annual precipitation and associated soil productivity compared to the importance of sunlight availability in semi-closed canopy systems.
Figure 15. Ponderosa pine (Pipo) and lodgepole pine (Pico) diameter distribution displayed as frequency per ha by 5 cm diameter class for trees sampled on 60-0.1 ha circular plots from within remnant inter-mixed ponderosa pine and lodgepole pine stands of the south-central Oregon pumice zone.
Figure 16. Smoothed-regression of ponderosa pine age-diameter relationships collected from 4 sites within remnant inter-mixed ponderosa pine and lodgepole pine stands of the south-central Oregon’s pumice zone. Data from LaPine (1) 1917, LaPine (2) 1917 and Embody 1917 collected in 1917 by Munger (1917). All historic quantitative data was collected near contemporary remnant inter-mixed ponderosa pine and lodgepole pine stands.
Diameter distributions from historic records provide evidence of departure from historic conditions (Figure 17). Munger (1917) labeled non-ponderosa pine species as “others,” which given this geographic range was likely white fir (*Abies concolor*), however smaller diameter classes could have been lodgepole pine. Historic quantitative information suggested the largest diameter class for tree species not labeled as ponderosa pine “others” were approximately 61.0 cm and 46.0 cm for the second largest diameter class. Our largest lodgepole pine measured 53.1 cm at DBH. Additionally, two other lodgepole pine measured greater than 50.0 cm at DBH. Therefore, our data provides evidence of lodgepole pine reaching 53.1 cm DBH for this area, especially given historic open growing conditions with low competition on productive sites.

Stand structure shifts included a 10-fold increase in TPH and roughly a 746.0% increase for species labeled as “others” in 1917 compared contemporary lodgepole pine density. Stand density averaged 25.3 trees per ha (SD = 10.6) for ponderosa pine greater than 53.3 cm DBH compared to range between 24.6 TPH (LaPine 1917) and 37.3 TPH (Embody 1917) reported from historic stand conditions near our study area.
Figure 17. Shifts in diameter distribution across time displaying a range in variability from 2 historic ponderosa pine stands (collected near Embody, OR), and (LaPine, Oregon) to contemporary diameter data collected from contemporary remnant inter-mixed ponderosa pine and lodgepole pine stands (Munger, 1917).
Basal Area Growth

Basal area growth of ponderosa pine separated by: (1) Group A “pre-1850”, (2) Group B “post-1850, pre-1920”, (3) Group C “post-1920”; and lodgepole pine separated by: (4) Group D “pre-1920” and (5) Group E “post-1920” between 30 and 50 years of growth displayed a decreased growth trends across time. Using Group A as our reference group, our Analysis of Variance (ANOVA) non-repeated measure pairwise comparison between groups revealed Group C was significantly different (P <0.001).

Our analysis further suggested a Tukey HSD test to determine if any other groups were significantly different (F = 7.21) from each other. The Tukey HSD test and associated 95.0% Family-Wise confidence intervals revealed Group C was also significantly different from Group B (P <0.04), Group D (P <0.001) and Group E (P <0.001). Confidence interval means were back-transformed to form confidence intervals of the medians and confidence intervals of the differences were back-transformed to produce confidence intervals of ratios for each group.

This analysis suggested that competition as a result of increased tree density has resulted in reduced basal area growth and subsequent diameter growth since 1850. Although the mean BA ratio of Group C was statistically different from all other groups, there was a noticeable decreasing trend for all groups since 1850. Basal area growth of lodgepole pine also followed a similar trajectory as the ratio between Group D and Group E (P = 0.89) was not statistically significant. Furthermore, Group E showed a median BA growth of 63.5 cm², which was greater than Group A with a
median BA growth of 61.6 cm². Although lodgepole pine had reduced BA growth following 1920, the average BA growth was still greater than Group A (Figure 18).

Between 30 and 50 years of age the results from our Family-Wise BA comparisons revealed Group A accumulated 0.85 times more BA compared to Group B with a median of 52.3 cm² (95.0% CI: 0.46 to 1.58, Group A median = 61.6 cm², Group B median = 52.3 cm²). Group A also accumulated 0.44 times more BA compared to Group C (95.0% CI: 0.25 to 0.76, Group C median = 27.1 cm²), 1.23 times less BA than Group D (95.0% CI: 0.70 to 2.18, Group D median = 75.9 cm²), and 1.03 times less BA compared to Group E (95.0% CI: 0.63 to 1.69, Group E median = 63.5 cm²). Group B accumulated 0.52 times more BA compared to Group C (95% CI: 0.27 to 0.98), 1.45 times less compared to Group D (95.0% CI: 0.75 to 2.80) and 1.21 times less compared to Group E (95.0% CI: 0.67 to 2.20). Group C accumulated 2.81 times less BA compared to Group D (95.0% CI = 1.55 to 5.09) and 2.35 times less than Group E (95.0% CI: 1.39 to 3.96). Group D accumulated 0.84 times more BA compared to Group E (95.0% CI: 0.49 to 1.44).

Lodgepole pine basal area growth does not seem to be as heavily impacted by increased stand density. Average basal area growth estimates revealed lodgepole pine basal area estimated median growth of 63.5 cm² prior to 1920 developed at a rate higher than pre-1850 ponderosa pine at a median growth rate of 75.9 cm², and similar basal area growth following 1920 with a median growth of 61.6 cm².

In the northern Rockies, ponderosa pine density and presence of fire-intolerant tree species were reported to be higher in fire excluded, logged stands compared to fire
excluded, unlogged stands (Naficy et al., 2010). Due to the amount of historic logging activity within our study area, it is likely recruitment patterns since the 1920’s reflect tree density increases accordingly. This effect may have accounted for the statistically significant ponderosa pine basal area growth of Group C.
Figure 18. Box-and-whisker plots displaying basal area growth data (log cm$^2$) collected from radial tree-ring data between 30 and 50 years of growth for ponderosa pine establishing: A = pre-1850, B = post-1850, pre-1920, C = post-1920 and lodgepole pine establishing: D = pre-1920 and E = post-1920. All data collected from remnant inter-mixed ponderosa pine and lodgepole pine stands of the south-central Oregon pumice zone.
**Understory Conifer Development**

Our sapling age-height relationships yielded the following models, now referred to as the 2009 models, to estimate age from height for all saplings < 1.4 m (Figure 19):

\[
P\text{onderosa pine } < 1.4 \text{ m} = 6.10 + 0.19\times h_t\text{(cm)} \quad (\text{SLR: } n = 42, R^2 = 0.53, SE = 5.5, P < 0.001)
\]

\[
L\text{odgepole pine } < 1.4 \text{ m} = 9.22 + 0.11\times h_t\text{(cm)} \quad (\text{SLR: } n = 40, R^2 = 0.34, SE = 4.5, P < 0.001)
\]

(Where \( h_t = \text{height of the } i\text{th sample in cm} \))

Historic sapling age-height data were collected from dominant ponderosa pine growing in open overstory conditions collected from the Blue Mountains of Oregon, earlier described in our methods section. Seedlings were noted to have similar growth patterns to seedlings in central Oregon (Munger, 1917). Munger’s (1917) age-height relationship was reported using the following model (Figure 19):

\[
\text{Seedling Age} = 0.93 + 0.16\times h_t\text{(cm)}, \; n = 1,182
\]

(Where \( h_t = \text{height of the } i\text{th sample in cm} \))
Figure 19. Scatterplot displaying ponderosa pine sapling age-height relationships. Data collected from remnant inter-mixed ponderosa pine and lodgepole pine stands of the south-central Oregon pumice zone. Historic data collected around 1917 from the Blue Mountains of Oregon.

All 2009 sapling data fit to our SLR model revealed uniform variance in age for each one unit increase in height. Using Munger’s (1917) sapling age-height model, we achieved an estimate of approximately 23.0 years to obtain breast height. Our ponderosa pine 2009 models revealed saplings will require 32.7 years to obtain breast height for ponderosa pine and 24.6 years for lodgepole pine. Therefore, we revealed a difference of 9.7 years to obtain breast height between our ponderosa pine 2009 model estimate and historic estimates. Whereas, our SLR models fit to our root collar and breast height data estimated 35.0 years for ponderosa pine and 28.1 years for lodgepole pine to obtain breast height. This analysis revealed saplings have become more stagnant in height growth over time.
Sapling age-height comparisons between A.F. Kerr (1913), Munger (1917) and our 2009 ponderosa pine models revealed Munger’s (1917) age-height data aligned well with the “open” overstory condition provided by A.F. Kerr (1913). However, our 2009 model followed an age-height growth trajectory that aligned between the 1913 “full shade” overstory condition model, which estimated age to be around 40 years at 120 cm, and the 1913 “open” overstory condition model (Figure 20). This analysis revealed that although sapling age-height relationships showed slower growth than previously assumed (i.e. 5 to 10 years to breast height) there was not a considerable difference when compared to the average historic growth trajectory.

Figure 20. Ponderosa pine age-height data (< 1.4 m) sampled in south-central Oregon around 1913, 1917 and in 2009 from open and semi-closed canopy conditions. Contemporary data (2009) collected from within remnant inter-mixed stands of the south-central Oregon pumice zone (A.F. Kerr, 1913; Munger, 1917).
Morrow’s (1985) sapling age-height models, now referred to as the 1985 models, used to correct for time to grow to core height “as close to the ground as possible,” were reported as:

Ponderosa pine age = 2.4 + 0.2744 \(ht\). (SLR: \(n = 65\), \(R^2 = 0.81\), \(P < 0.001\))

Lodgepole pine age = 1.94 + 0.34 \(ht\). (SLR: \(n = 54\), \(R^2 = 0.75\), \(P < 0.001\))
(Where \(ht\) = height of the \(i\)th sample in cm)

We revealed there was an approximate age estimate difference of 8 years to obtain breast height for ponderosa pine between our 2009 model compared to the 1985 model estimate (2009 model = 33 years, 1985 model = 41 years). However, an approximate difference of 25 years for lodgepole pine (2009 model = 25 years, 1985 model = 50 years; Morrow, 1985).

Our analysis revealed that if an assumed 5 to 10 year estimate of years to obtain breast height was applied in our study, ponderosa pine age estimates would be underrepresented by more than 20 years. Additionally, our age to breast height analyses and observations revealed growth between tree-rings at breast height is a poor indicator of tree growth and development at root collar. Figures 21 and Figure 22 display photographs of root collar disk cross-sections collected from saplings less than 1.4 m in height using destructive sampling techniques. Photographs are displayed to show the close proximity and clear visibility of annual growth rings.
Figure 21. Ponderosa pine sapling (<1.4 m) collected using destructive sampling techniques. This particular sample measured 83.0 cm in height with an estimated age of 14 years (Establishment data = 1995). Scale reference in mm (ID: #IC01PP).

Figure 22. Lodgepole pine sapling (<1.4 m) collected using destructive sampling techniques. This particular sample measured 132.0 cm in height with an estimated age of 20 years (Establishment date = 1989). Scale reference in mm (ID: #PL03LP).
Interaction of Climate on Species Recruitment

There did not appear to have been any major precipitation or temperature shifts across the time of our 566-year species recruitment record, except an extended drought period between 1450 and 1600. Furthermore, reconstructed PDSI values suggested there was not a strong relationship between species recruitment and climate. General ponderosa pine recruitment peaks occurred during the 1860’s, 1820’s, 1760’s, 1730’s, 1710’s and 1630’s and correlated to the end or beginning of a warm and dry climatic period, represented by negative PDSI values (Figure 23). The only exception to this pattern occurred during the 1880’s when ponderosa pine increased recruitment during an associated cool and wet climatic period. Higher recruitment of lodgepole pine compared to ponderosa pine following 1950 was also correlated with a cool and wet period, suggesting favorable growing conditions as a factor of climate and physiological competiveness following fire exclusion.

Conservative fire disturbance history estimates for this area likely explain the range in recruitment variability prior to 1850. Overall, climate does not seem to be a single driving force of recruitment. However, we cannot discredit the interaction between fire and climate. In south-central Oregon, large fire frequency years were reported to have occurred during associated wet and cool years prior to dormancy (Pohl et al., 2006). This analysis should not be used to infer generalities between species recruitment and climate. Rather, this was a single analysis used to investigate possible patterns in recruitment and climate based on our age reconstruction.
Figure 23. Species age reconstruction by 10-year age class for ponderosa pine (Pipo) and lodgepole pine (Pico) (top) associated to 20-year smoothed Palmer Drought Severity Index (PDSI) values (bottom). PDSI values (Y-axis) in red (negative) associate to warm and dry periods, whereas values in blue (positive) associate to cool and wet periods.
**Influence of Fire on Species Recruitment**

It is now widely accepted that vegetation shifts since fire exclusion in fire-adapted ecosystems has resulted in the long-term development of fire-sensitive and shade tolerant species (Parsons et al., 1979; Arno, 1980). During the past 160 years overstory composition and stand structure shifts have transitioned from the conditions expected under a natural frequent fire regime trajectory (Covington et al., 1997).

To examine and characterize fine-scale lodgepole pine recruitment in response to fire, we used two sites (DL and MB) within our study area known to have experienced turn of the 20th Century large-scale fire events. Species recruitment patterns from the DL site following the South Ice Cave fire of 1915, which burned 4,046 ha, revealed post-fire ponderosa pine recruitment was favored the following year (~13/ha).

Recruitment patterns from the MB site following the Rim Rock Butte fire of 1918, which burned approximately 1,537 ha, revealed lodgepole pine recruitment was most successful 2 years following the fire disturbance (7/ha) (Figure 24). Lodgepole pine also displayed the same 2 year trend (~23/ha) within the DL site (Figure 25). Other similarities between sites included the absence of ponderosa pine recruitment in 1910. However, between 1911 and 1923 ponderosa pine recruitment (~5/ha) and lodgepole recruitment (~2/ha) appeared to have been stable, with the exception of an absence in lodgepole pine recruitment during 1924 within the MB site. Although some trends in post-fire recruitment were made from this analysis, little information has been provided to infer broad-scale post-fire effects on species recruitment.
Furthermore, this analysis did not account for discrete variability in pre and post-fire climate.

According to the central Oregon fire and fuels program, lodgepole pine regeneration following 3 prescribed fire treatments since the late 1980’s is currently recruiting in the form of seedling (≤ 0.1 DBH) establishment within the Pringle Falls RNA (Riegel and Johnson, 2011 unpublished data).
Figure 2. Ponderosa pine and lodgepole pine recruitment by 10-year age class per ha from the MB study site. Annual recruitment between 1910 and 1920 highlighted to display post-disturbance response following the Rim Rock Butte fire of 1918 on the Bend/Fort Rock Ranger Districts of the Deschutes National Forest.
Figure 25. Ponderosa pine and lodgepole pine recruitment by 10-year age class per ha from the DL study site. Annual recruitment between 1910 and 1920 highlighted to display post-disturbance response following the Ice Cave fire of 1915 on the Bend/Fort Rock Ranger Districts of the Deschutes National Forest.
Examining broad landscape recruitment patterns against climate and fire has proven difficult due to the diversity and complexity of stand-level vegetation patterns across the south-central Oregon pumice zone. The mosaic of neighboring lodgepole pine likely acted as a fire barrier during early years of succession in some locations. Based on our study, we support the theory that fire within our study area historically burned frequently in synchrony with pure stands of ponderosa pine, since they share similar dominant understory vegetation capable of carrying low-intensity surface fires. In a productive area near our DL site a collection of 10 fire scars (pending cross-dating) were estimated to have a fire return interval of 12 years (Heyerdahl, 2010 unpublished data). Further research and analysis of the interactions between fire history and climate is needed to address recruitment patterns at the landscape-level within inter-mixed stands.

The complex interactions over our age reconstruction period may have incorporated Native Americans burning prior to 1850, but cannot be separated from the role natural wildfires played at shaping and maintaining historic composition and structure. Fire disturbances occurred both spatially and temporally, which created structural and compositional heterogeneity at the stand and landscape-level. Based on a MFRI of 4-24 years, fires returned to an area following seedling establishment, but prior to reaching breast height, associated to the development of a bark layer capable of resisting low-intensity surface fires. Species physiology and our age to breast height data further support this theory.
Bork (1984) reported high fire frequency years during 1705, 1711, 1762, 1842, 1843, 1862, 1863 and 1886 with an associated decrease in regeneration occurring between 1721-1741, 1762-1781, 1842-1861 and 1882-1901 near our study area. Mast et al., (1999) suggested ponderosa pine seedling establishment was historically favored during warm and dry periods when fine fuel accumulation was limited, thus inhibiting fire spread. Our age reconstruction corresponded well with this conclusion based on above average recruitment of ponderosa pine during the 1710’s, 1760’s, 1860’s and 1880’s. Age reconstruction data from bitterbrush has also revealed increased abundance of older cohorts on dry sites compared to wet sites in the pumice zone of south-central Oregon, due to less historic fire activity as a result of reduced fine fuel accumulation (Riegel, 2010 personnel communication).

Furthermore, based on our age reconstruction data and spatial and temporal heterogeneity of historic fire events, we suggest few mature lodgepole pine persisted per ha within the inter-mixed stands prior to significant Euro-American disturbance to the landscape. Frequent fires would have reduced understory ponderosa pine and lodgepole pine sapling density, while mature lodgepole pine would have remained as a seed source for future recruitment. As time progressed, younger cohorts would have replaced mature lodgepole pine uprooted by wind or killed by mountain pine beetle (Littke and Gara, 1986).

Natural stands of lodgepole pine become susceptible to mountain pine beetle attack when the oldest cohorts reach approximately 100-120 years old. Once mountain pine beetles have occupied an area they will target lodgepole pine greater
than 22.0 cm DBH and the outbreak will last until all large diameter trees within the stand have been infected (Eglitis, 2010 personnel communication). In recent time, uncharacteristic mountain pine beetle outbreaks have occurred within mixed conifer forests of south-central Oregon. However, the dynamic leading to these conditions likely began shortly after fire exclusion, which led to the ingrowth and subsequent intraspecific stress of lodgepole pine on ponderosa pine (Eglitis, 2010 personnel communication). Atypical mountain pine beetle outbreaks have involved significant mortality of large diameter ponderosa pine and pockets of mortality within ponderosa pine plantations consisting of trees less than 22.0 cm DBH (Eglitis, 2010 personnel communication).

We suggest mature lodgepole pine density was historically not capable of creating stand conditions susceptible to large insect outbreaks. Mortality caused by mountain pine beetle would have been isolated to small pockets of trees. Reasons for this include low stand density, open growing conditions and associated tree vigor (Larsson, 1983; Mitchell, 1983).

In remnant intermixed stands, fire exclusion has provided a competitive advantage for lodgepole pine and increased susceptibility to uncharacteristic high-severity fire behavior and insect outbreak (Larsson et al., 1983; Hessburg et al., 2005; Sugihara et al., 2006). Canopy closure associated with ingrowth has also resulted in a reduction of understory plant species abundance and biodiversity, which has altered the nature and structure of historic biotic interactions and processes (Peek et al., 2000). Historically, fires in ponderosa pine ecosystems influenced understory species
composition and enhanced understory growth conditions by maintaining an open overstory, reducing competition between species and limiting fuel accumulation (Wright and Bailey, 1982; Agee, 1993; Carr, 2007).
CHAPTER 3 – CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This is an observational study and our scope of inference is limited to remnant inter-mixed ponderosa pine and lodgepole pine stands of south-central Oregon pumice zone displaying old-growth structural components. However, our conclusions about species composition shifts and decline in forest health as a result of fire exclusion has been well documented and supported by other research in many forest types.

We collected age and size structure data to assist our age reconstruction of overstory composition and stand structure shifts across time. Such components have been used to reveal important ecological information to aid restoration within ponderosa pine forests throughout the western U.S. (Moore et al., 2004; Covington et al., 1997). Direct evidence linking contemporary structure to historic reference conditions within remnant inter-mixed stands threatened by stand-replacing fire behavior and insect outbreak is not only ecologically important, but an opportunity to preserve data for future reference and analysis.

Our study area extends across a range in environmental gradients and diversity in land-use history, which has contributed to the compositional and structural mosaic at the landscape-level. Many studies including the first large-scale restoration experiment within ponderosa pine forests of the southwest were conducted within stands representing diversity in land-use history, vegetation and topography (Waltz et al., 2003).
This study provides the first landscape-level approach to quantitatively analyze overstory composition and stand structure shifts based on stand reconstruction where current knowledge is limited. Our study design allowed us to achieve landscape-level representation to ensure all remnant stands were identified to capture sufficient data representative of each site to the best of our ability, given economic constraints. This allowed us to meet our objectives and preserve data for future reference. We examined compositional and structural shifts across time to improve our ecological understanding involving the spatial and temporal expansion of lodgepole pine since fire exclusion.

**Future Concerns**

Contemporary conditions within remnant stands reveal lodgepole pine has been given a competitive advantage in the absence of fire, which is causing competition induced mortality of large diameter ponderosa pine. Fire exclusion has also shifted historic single-story structure with pronounced vertical fuel stratification to multi-story conditions with increased ladder fuels and accumulation of coarse woody debris in the understory.

Due to the competitive advantage of lodgepole pine and continued loss of remnant old-growth, the future sustainability of large diameter ponderosa pine is a concern for managers. Large diameter ponderosa pine are ecologically significant for their importance to wildlife, aesthetics, and cultural and spiritual values. The longevity of this species also provides a signature across the south-central Oregon
landscape. Another important concern is the threat of mountain pine beetle activity on stressed, large diameter ponderosa pine. In recent time, mountain pine beetle outbreaks have occurred in atypical settings throughout most of the Fremont-Winema National Forests (Figure 26).

Figure 26. Large diameter ponderosa pine mortality within a mixed-conifer stand following atypical mountain pine beetle activity on the Winter Rim Zone of the Fremont-Winema National Forests. Large diameter ponderosa pine mortality is evident by the light rust colored crowns (Photograph provided by Andy Eglitis).
Need for Continued Monitoring and Future Research

Restoration of fire-adapted ecosystems involves the re-introduction of fire to maintain long-term forest health (Walstad et al., 1999). Therefore, there is a need to improve quality and quantity of monitoring efforts across the landscape to improve our understanding of diversity at the stand-level (Noss et al., 2006). The application of new and improved research and monitoring tools will allow us to make informed and ecologically sound decisions in the future when direct evidence pre-dating 1850 is absent from the landscape. These tasks may be as simple as mapping remnant stumps and dead-down logs prior to the implementation of prescribed burning, since observation shows only 1-3 repeated burns are needed to completely eliminate remnant legacy components from the landscape. Figure 27 displays an example of stem mapping displaying ponderosa pine spatial patterns related to age within the Deadlog Environmental Impact Statement (EIS) to identify historic cohort clumping patterns at the stand-level.
Figure 27. Stem map from Deadlog EIS displaying live trees used to help aid restoration objectives (source: The Nature Conservancy, Oregon Field Office, Bend OR. Stem map results provided by Daren Stringer, Senior Project Manager, Integrated Resource Management, Philomath, OR).
We recognize remnant stands used in this study are insufficient to portray the full historic and contemporary inter-mixed gradient between pure ponderosa pine and climax lodgepole pine. Therefore, we acknowledge stand-level diversity resulting from topography, precipitation, fire history, and soil type and depth. These complex interactions continue to drive compositional and structural heterogeneity throughout the south-central Oregon pumice zone.

Conclusions from this study also reveal further ecological questions worthy of scientific pursuit, such as long-term response of lodgepole pine to repeated fire, number of years to obtain breast height between ponderosa pine and lodgepole pine following different management treatments and post-wildfire settings. Our focus is to help guide and support management activities based on restoring stands threatened by uncharacteristic stand-replacing fire behavior, insect outbreak, drought and competition induced mortality. We suggest future research should involve the modeling of successional transitions and associated trajectories (state-and-transition models) within inter-mixed stands. Future research in this area will prove worth of pursuit as we continue to comprehend landscape-level interactions.
REFERENCES


Riegel, Gregg., 2010. Personnel Communication. USDA Forest Service. Central and South-Central Area Ecologist. Bend, OR


Appendix A

Tables
Table 1. Climate data compiled from local weather stations representative of the south-central Oregon area (Franklin and Dyrness, 1988) with additional weather data compiled from Remote Automated Weather Stations (RAWS) near the ponderosa pine/lodgepole pine inter-mixed stands (NOAA National Weather Service, 2010).

<table>
<thead>
<tr>
<th>Location</th>
<th>Years Collected</th>
<th>Elevation</th>
<th>Extreme max.</th>
<th>Extreme min.</th>
<th>Avg. Annual</th>
<th>Average total</th>
<th>Summer average total</th>
<th>Average total snowfall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pine Mountain</td>
<td>1958-1981</td>
<td>35.0</td>
<td>-28.9</td>
<td>4.9</td>
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<td>281.2</td>
<td>54.5</td>
<td>228.6</td>
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<td>Fremont S</td>
<td>1909-1996</td>
<td>42.8</td>
<td>-41.1</td>
<td>5.8</td>
<td></td>
<td>267.7</td>
<td>46.2</td>
<td>106.2</td>
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<tr>
<td>Bend, Oregon</td>
<td>1901-2009</td>
<td>1105</td>
<td>41.1</td>
<td>-22.2</td>
<td>8.1</td>
<td>302.5</td>
<td>47.8</td>
<td>84.2</td>
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<tr>
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<td>246.6</td>
<td>47.2</td>
<td>49.5</td>
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<td>6.3</td>
<td></td>
<td>441.0</td>
<td>43.0</td>
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<table>
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<th>Location</th>
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<th>Elevation</th>
<th>Extreme max.</th>
<th>Extreme min.</th>
<th>Avg. Annual</th>
<th>Average total</th>
<th>Summer average total</th>
<th>Average total snowfall</th>
</tr>
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<tr>
<td>Wicklup Dam</td>
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<td>6.4</td>
<td>524.3</td>
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<td>Crescent Lake Junction</td>
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<td>28.2</td>
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<td>361.0</td>
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</tr>
</tbody>
</table>
Table 2. Soil data correlated to ponderosa pine and lodgepole pine occurrences within the Pringle Falls Research Natural Area (Tarrant, 1953).

<table>
<thead>
<tr>
<th>Soil Type</th>
<th>Stand Level Dominant Vegetation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lapine loamy coarse sand 15-25% slope</td>
<td>Pure ponderosa</td>
</tr>
<tr>
<td>Lapine loamy coarse sand 0-2% slope</td>
<td>Pure ponderosa; open lodgepole, even mixture of both species</td>
</tr>
<tr>
<td>Lapine loamy coarse sand &gt;2% slope</td>
<td>Predominately Ponderosa pine</td>
</tr>
<tr>
<td>Lapine loamy coarse sand over compact subsoil 0-2% slope</td>
<td>Predominately Lodgepole pine</td>
</tr>
<tr>
<td>Wicklup loamy coarse sand 0-1% slope</td>
<td>Dense Lodgepole pine</td>
</tr>
<tr>
<td>Wicklup silt loam 0-1% slope</td>
<td>Dense or very dense pure lodgepole pine</td>
</tr>
</tbody>
</table>
Table 3. Mean annual temperature and precipitation data based on the original 4 km Prism Dataset including geographic descriptions for individual plots across the ponderosa pine/ lodgepole pine inter-mixed stands (Volland, 1985; Prism Climate Group, 2007; Simpson, 2007).

<table>
<thead>
<tr>
<th>Stand</th>
<th>Plot</th>
<th>Elevation (m)</th>
<th>Slope (%)</th>
<th>Aspect</th>
<th>Surface Soil/Buried Soil</th>
<th>Depth to Bedrock (cm)</th>
<th>Understory Ground Cover</th>
<th>Mean Annual Precipitation (cm)</th>
<th>Mean Annual Temperature (°C)</th>
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<tr>
<td>BND 1</td>
<td>1250</td>
<td>0.5 W</td>
<td></td>
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<td>pumice loamy sands/ sandy loams</td>
<td>70 to 127</td>
<td>Bitterbrush, Idaho fescue, needlegrass, squinotail</td>
<td>52.2</td>
<td>6.7</td>
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<tr>
<td>BND 2</td>
<td>1288</td>
<td>0.5 W/SW</td>
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<td>Bitterbrush, Idaho fescue, needlegrass, squinotail</td>
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<td>1907</td>
<td>0.5 NE</td>
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<td>Bitterbrush, Idaho fescue, needlegrass, squinotail</td>
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<tr>
<td>BND 4</td>
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<td>Bitterbrush, Idaho fescue, needlegrass, squinotail</td>
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<tr>
<td>BHB 1</td>
<td>1960</td>
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<td>BHB 2</td>
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</tr>
<tr>
<td>CP   2</td>
<td>1870</td>
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Table 3 (Continued). Mean annual temperature and precipitation data based on the original 4 km Prism Dataset, including geographic descriptions for individual plots across the ponderosa pine/ lodgepole pine inter-mixed stands (Prism Climate Group, 2007; Simpson, 2007).

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<th>Plot</th>
<th>Elevation (m)</th>
<th>Slope (%)</th>
<th>Aspect</th>
<th>Surface Soil/Sieved Soil</th>
<th>Depth to bedrock (cm)</th>
<th>Understory (ground cover)</th>
<th>Mean Annual Precipitation (cm)</th>
<th>Mean Annual Temperature (°C)</th>
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Table 4. Summary of years to obtain breast height (AVG), standard deviation (SD) and standard error (SE) for ponderosa pine (Pipo) and lodgepole pine (Pico).

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<td>Range</td>
<td>SD (yrs)</td>
<td>SE (yrs)</td>
<td>Avg. (yrs)</td>
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<td>Range</td>
<td>SD (yrs)</td>
<td>SE (yrs)</td>
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<th>Avg. DNA</th>
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Table 6. Additional summary of years to obtain breast height based on 3 methods from 2 data sources. Saplings < 1.4 m, SLR model: root collar and breast height disk samples and average estimate of years to obtain breast height based on root collar and breast height disk samples.

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<th>SLR model: Root Collar/Breast Height Disks (yrs)</th>
<th>Average: Root Collar/Breast Height Disks (yrs)</th>
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Appendix B

Maps
Map 1. Large fire history (1908 to 1919).
Map 3. Estimated Native American territory in 1841 (Oregon Historical Society OrHi 986847).

Map 4. Oregon Native American Reservations in 1864 (Oregon Historical Society CNo 85680).
Map 6. Mount Mazama ash spread/depth and Newberry Crater (Newberry) ash spread/depth (source: Crater Lake Institute, 2010).
Map 7. Study area.
Map 8. Location of disk pairs collected from dead-down ponderosa pine.
Map 9. Approximate location of Embody, Oregon.
Appendix C

Photos
Photo 1. Early photograph taken near central Oregon depicting what John C. Fremont may have encountered during his 1843 Expedition through the Metolius Basin ca. 1913 (Deschutes County Historical Society photograph).
Photo 2. Early photograph of a forest meadow grazed by sheep (Deschutes County Historical Society photograph).
Photo 3. Early logging equipment representative of small mill operations in northern California and south-central Oregon during the late 1800’s and early 1900’s (Jerry Grove collection. Cedarville, California.).
Photo 5. Aggressive logging and burning on private land (2) in central Oregon ca. 1939 (Deschutes National Forest Heritage Program photograph).
Photo 6. Aggressive logging on private land (3) near Finley Butte in central Oregon ca. 1938 (Deschutes National Forest Heritage Program photograph).
Photo 7. Early to mid-20th Century advertisement promoting a selective harvesting and sustainable yield Approach to forest management (Deschutes National Forest Heritage Program photograph).
Photo 8. Logging equipment used to push over hazardous snags. Background shows a dominant ponderosa pine overstory with a mixed ponderosa pine and lodgepole pine understory ca. 1938 (Deschutes National Forest Heritage Program).