AN ABSTRACT OF THE THESIS OF

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In the Northwest Great Basin, aspen (*Populus tremuloides*) communities uniquely contribute to the biodiversity of a semi-arid, sagebrush-dominated landscape. In this same region, western juniper (*Juniperus occidentalis*) is encroaching into aspen stands. This study determined the timing, extent, and some of the effects of this expansion.

Aspen stands below 2,133 m elevation were sampled in northwest Nevada, northeast California, and southeast Oregon for density, canopy cover, age, stand structure, and recruitment of western juniper and aspen. Soils and tree litter from both species were collected to analyze the effects of western juniper in areas previously influenced by aspen. Additionally, two large aspen complexes in southeast Oregon were intensively aged to determine disturbance (fire) frequencies.

Western juniper encroachment into aspen stands peaked from 1920 to 1939 with 77% of all juniper trees sampled establishing during this period. Five percent were greater than 100 years and none exceeded 145 years. Three-fourths of aspen stands sampled have established populations of western juniper. Twenty-three percent have a dominant canopy of western juniper. Twelve percent of aspen stands sampled were completely replaced by western juniper. Average density of western juniper was 1,573 trees per hectare of aspen. Seventy percent of aspen stands sampled had zero recruitment of new aspen. Within the study area aspen stands averaged 98 years old. Forty-eight percent of stands were greater than 100 years old. There was an inverse correlation between aspen canopy cover and western juniper canopy cover ($r^2 = .80$, $p = .0001$).

Soils influenced by western juniper had a higher C:N ratio and pH; higher amounts of salts, lime, and sulfate; and lower amounts of magnesium, iron, copper, and manganese ($p < .05$). Aspen litter had a lower C:N ratio than western juniper litter ($p < .05$).

Prior to 1870, the two major aspen complexes sampled had mean fire return intervals of 10 and 11 years. However, the most recent disturbance in either complex was 80 to 90 years ago. This lack of disturbance (fire) coupled with aspen stand decadence and low recruitment levels leaves aspen communities in the Northwest Great Basin vulnerable to western juniper encroachment and replacement.

Western Juniper Encroachment into Aspen Communities in the Northwest Great Basin

by

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Travis G. Wall, Author

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INTRODUCTION

Quaking aspen (*Populus tremuloides*) communities constitute a small portion of the Northwest Great Basin (northern Nevada, northeastern California, and eastern Oregon) but contribute significantly to the biodiversity of wildlife and plant species. For example, there are 56 wild mammal and 136 bird species found in aspen and aspen-conifer mixed forest of the Western United States (Debyle 1985a). Of those bird species, 34 are cavity nesters in the aspen type (Debyle 1985a). In the Great Basin of southeastern Oregon, 84 wildlife species reproduce and 110 wildlife species forage within aspen/grass sites and 95 wildlife species reproduce and 117 wildlife species forage within aspen/mountain big sagebrush sites (Maser et al. 1984). From Maser et al. 1984, one may conclude that only riparian areas exceed aspen sites for the greatest majority of wildlife use proportional to total land area in southern Oregon. Aspen communities are also very productive in terms of herbaceous plant growth and species diversity. Aspen are generally recognized as having more lush undergrowth than neighboring coniferous forests (Mueggler 1985a). This undergrowth can vary from less than 560 kg/ha to over 4,500 kg/ha (Houston 1954, sited by Mueggler 1985b). The herbaceous vegetation occurs as a multilayered mixture of shrubs, forbs, and grasses and consists of a broad combination of over 300 species (Houston 1954, sited by Mueggler 1985b).

The majority of aspen communities in the western U.S. are not considered climax. In the Rocky Mountain region, Utah alone has had an approximate 60% decline in aspen dominated landscapes due to conifer encroachment (Bartos and Campbell 1998). As aspen communities succeed to conifer woodlands then microenvironments and competitive relationships are altered resulting in changes of under-story vegetation (Mueggler 1985a). Conifers more effectively shade the forest floor altering the abundance and composition of understory plant species. Undergowth in aspen communities decreases as conifer dominance increases (Mueggler 1985b). Bartos and Campbell (1997), state that when conifers overtake aspen communities, less water is available to the watershed, under-story biomass vegetation is significantly reduced, and the diversity of wildlife and plant species declines. The greatest concern over conifer invasion is the permanency of aspen exclusion from succession once a climax conifer community persists.

Today, western juniper (*Juniperus occidentalis*) inhabits over 3 million ha in the Northwest Great Basin (Gedney et al. 1999). Extensive studies have shown that western juniper is expanding its range into meadows, shrub-grasslands, riparian areas, and aspen stands (Miller and Wigand 1994, Miller and Rose 1995, Miller 1996). Of particular interest are the aspen communities below 2,133 m in elevation. These stands are the most susceptible to juniper invasion because 2,133 m marks the upper elevation limit for western juniper (subspecies *occidentalis*). On Steens Mountain in eastern Oregon, Miller and Rose 1995, found the greatest densities and cover of western juniper occurred in aspen stands compared to sagebrush community types. In these locations, western juniper are invading and replacing aspen. Due to aspen's limited distribution and ecological importance in the Northwest Great Basin, western juniper encroachment is very alarming.

In the Rocky Mountain region, Utah alone has 650,000 ha of aspen (Mueggler 1988). Utah's aspen dominated lands have decreased by approximately 60% since European settlement (Bartos and Campbell 1997, 1998). In this region, extensive research has been conducted regarding the ecology of the aspen community including studies on distribution, reproduction, soils, under-story vegetation, disturbance roles, wildlife uses, animal impacts, biodiversity, succession, and conifer interaction (Debyle and Winokur 1985). However, very little research has been conducted in aspen communities in the Northwest Great Basin. Due to the lack of research on aspen in the Northwest Great Basin no one knows the extent of aspen loss or the magnitude and effects of western juniper invasion into aspen communities. How will livestock use, soil, erosion, wildlife, herbaceous vegetation, and water be affected? These important issues warrant attention due to the ecological diversity that aspen add to landscapes that are predominately sagebrush and juniper. By gaining a better understanding of western juniper encroachment into aspen communities, land managers can make effective and proper decisions on how to perpetuate and maintain aspen communities in this semi-arid region. This study was designed to gain needed understanding and insight of the effects, magnitude, and history of western juniper invasion into aspen communities in the Northwest Great Basin.

The focus of this study was to determine the extent and ecological effects of western juniper encroachment into aspen stands in the Northwest Great Basin. The objectives of the study with specific questions related to each objective include:

1. Determine the extent of western juniper invasion into aspen stands in the Northwest Great Basin.
2. Determine the structure of aspen stands in the Northwest Great Basin.
3. Assess aspen stand age or time since last disturbance.
4. Determine when western juniper began to significantly invade aspen stands.
5. Determine the effects of aspen stand structure (density, cover, & age) on western juniper encroachment
6. Determine the frequency of disturbance in aspen stands.
7. Determine the effects of western juniper invasion on soils previously influenced by aspen. Soil characteristics to be studied include C, N, and pH.
8. Measure the difference of C and N in aspen and western juniper litter.

LITERATURE REVIEW

Aspen (*Populus tremuloides*)

Distribution

Quaking aspen (*Populus tremuloides*) is the most highly distributed native North American tree (Fowells 1965, cited by Weber 1990; Jones 1985). Aspen thrives from the hardwood forests of eastern North America to the coniferous forests in the Rocky Mountain west. It grows in a wide variety of sites ranging from gentle slopes with deep soils to valley bottoms, riparian areas, and steep high talus ridges (Morgan 1969). Soil types vary from loamy sands to heavy clays (Shepperd 1986).

Mueggler (1988) stated that aspen-dominated woodlands constitute a major portion of forest types in the interior West. He explains that the Intermountain Region contains over 1 million ha of aspen forests. These forests range from small isolated groves to broad expanses of pure and mixed stands.

Utah's extensive stands of aspen occupy more of its forested land (25%) than any other tree species (Mueggler 1988; Jones 1985). Idaho and western Wyoming combined have 323,000 ha of widely distributed isolated stands (Mueggler 1988). Idaho's aspen occupy a greater diversity of geographic areas than in any of the other intermountain states (Jones 1985).

Aspen is associated with montane and subalpine vegetation types along a broad elevational and moisture gradient (Shepperd 1986). Elevation levels of aspen in the Intermountain Region range from a high of 3,350 m in Utah to a low of 914 m in central Idaho (Jones 1985). Across this wide elevation zone annual precipitation ranges from 40 to 100 cm per year, most being received as snow (Shepperd 1986).

Amacher and Bartos (1997) currently estimate that aspen dominated lands in the Intermountain West have decreased by 60% since European development. They feel that this loss of aspen results in decreased water, forage, and biodiversity. Restoration will be needed to ensure that aspen stands remain a part of the landscape.

Comparing seral and stable aspen communities

The main question in regard to succession is whether present-day aspen stands are seral or climax communities. To be considered climax, a species must reproduce within the community and/or provide an environment unfavorable for the successful invasion of a potential climax species (Morgan 1969). In general, aspen has been regarded as a fire-induced successional species that dominates a site until more shade tolerant conifers begin replacing the stand (Mueggler 1985a; Bartos 1973; Morgan 1969). Without periodic fires, these conifers reproduce in their own shade, out-compete aspen, and move the site's composition towards climax.

Long fire intervals are required if conifers are to replace aspen stands. Long intervals enable conifers to establish, reproduce, and become the dominating climax species. However, fire interval length can vary. Depending on the site and the conifer species, conifers can replace aspen stands within a single generation or they take up to a 1,000 years in the absence of fire (Mueggler 1985a). For conifers to replace an aspen stand there must be an initial population to provide a seed source.

Conifers do not reproduce vegetatively like aspen, so without a seed source, they will not establish. The viability, fecundity, and number of seed help ascertain the rate of conifer establishment. A reliable determinant of a seral aspen site is the presence of an uneven-aged conifer under-story (Mueggler 1985a, Peterson and Squires 1995).

An aspen stand classified as a climax community has key indicators of stability. Stands with an uneven-age structure in the canopy over-story indicates trees are reproducing in the absence of disturbance. The fact that the stand is reproducing in its own shade may qualify a stand as climax. However, there must be lack of successional change in the under-story and the absence of more shade tolerant trees (Mueggler 1985a, Shepperd 1986). A stable aspen community may contain a few scattered conifers due too highly unusual and temporary conditions that favored their establishment. However, conifers must be prominent with an uneven-aged under-story to suggest a seral aspen stand (Mueggler 1985a).

Pure aspen stands exist in which no conifers are present. On Steens Mountain in southeast Oregon, no conifers are found above 7,000 ft. Aspen stands above this elevation are exempt from shade tolerant conifers and further successional development. These stands can be classified as climax.

Daubenmire's polyclimax theory suggests that aspen stands that burn at regular fire intervals can be classified as a pyric climax. Regular fire intervals deter conifer development and allow aspen regeneration to continue. Without periodic disturbances, stands are considered seral and succession of conifers will progress (Daubenmire 1968). Environmental conditions determining aspen's role, as a seral or climax species has not been determined (Mueggler 1988).

Asexual reproduction

Aspen are unique in their ability to reproduce asexually and sexually. They reproduce asexually through suckering, a process in which stems are produced from the underground parent root system. The production of suckers greatly increases when over-story stems are removed by disturbance such as fire, wind, and cutting. Suckers are also produced when over-story stems die from disease or old age. This vegetative method of reproduction results in clones of genetically identical trees and stands can be a single genetic individual. In the Intermountain Region, aspen mainly reproduce asexually through suckering (Shier et al., 1985a).

Sucker development in aspen roots is suppressed by auxins transported from aerial parts of the tree (Shier et al., 1985b). The loss of the over-story stems causes hormonal imbalance and apical dominance is lost. Auxin levels decline and buds located just below the soil surface on lateral roots are stimulated to sprout and grow (Shepperd 1986). Under favorable conditions, almost any section of an aspen root can sucker since lateral roots have thousands of suppressed shoot primordia (Shier et al., 1985b).

Undisturbed aspen stands that contain large numbers of suckers indicate that apical dominance is not absolute (Shier et al., 1985b). Auxins are unstable compounds that are translocated over lengthy distances from buds and young leaves down to roots. As auxins travel down the stems, apical dominance is weakened due to auxin immobilization, destruction, and age (Shier et al., 1985b). Periods can occur in the growing season when apical dominance is weak enough to allow suckering. This allows stands to reproduce without disturbance. This supports the earlier discussion of climax aspen stands.

Elongating suckers depend on parent root reserves until they can photosynthesize. Sucker population of a clone is related to levels of reserved carbohydrates and hormonal growth promoters in the roots (Shier et al., 1985b). Once the sucker begins assimilation of carbon, additional roots sprout from the parent root near its base. The degree of dependence on parent roots declines as these roots develop to provide water, nutrients and support for that specific stem (Jones and DeByle 1985). It is suggested that 10,000 to 20,000 suckers/ha are needed initially to re-establish aspen on burned sites (Bartos et al., 1991).

Soil temperature also affects suckering. Increased temperatures raise cytokinin levels in root meristems and degrade auxin concentrations. Suckering is then stimulated by the higher ratio of cytokinin to auxins (Shier et al., 1985b). Canopy removal allows greater amounts of light to reach the soil surface, which increases soil temperatures, and suckering. Also, stand-replacing fire can leave black soil surfaces that are conducive to light absorption and soil heating.

Sexual reproduction

Aspen is dioecious, with male and female flowers borne on separate trees. Flowering generally occurs in early spring before the appearance of leaves (Jones and DeByle 1985). Aspen seed production and subsequent colonization strongly depends on favorable climatic and microclimatic conditions. Reproductive maturity is reached at 10 to 20 years of age. Peak seed production occurs at 50 years with varying years of light to heavy seed crops (McDonough 1985).

Aspen's ability to produce sufficient seeds for establishment is offset by the exacting conditions required by germinating seed and seedlings (McDonough 1985). Factors involving germination, viability, and water stress, affect seedling growth and survival (McDonough 1985; Shier et al., 1985a; Morgan 1969). Temperatures greater than 25 C at the soil surface inhibit seed germination. Elevated temperatures from fire blackened soil surfaces stimulate sucker sprouting but are not conducive to seed germination. In a dry, warm environment seed viability typically lasts 2-4 weeks after maturation, limiting the time for establishment (McDonough 1985; Morgan 1969). Root hairs from the germinating seed perform the critical water absorbing function until adequate root growth occurs (McDonough 1985). These root hairs dry rapidly if they fail to quickly penetrate the soil surface and make contact with water. These conditions for establishment are delicate and under current climatic conditions in the Intermountain Region are not favorable for sexual reproduction.

Age structure

Aspen stands can be categorized as young, mature, old, and uneven-aged. The following paragraphs describe each age class:

Young stands are found where a recent disturbance or disease has killed the over-story and triggered vegetative reproduction (Shepperd 1986). Disturbance such as fire removes the stand in a single event allowing for uniform sucker growth with an even age distribution. These stands can contain 49,000-75,000 suckers/ha that thin over time because of competition for sunlight (Jones 1976, cited by McDonough 1985).

Mature even-aged stands are 80 to 100 years old with tree height ranging from 9 to 30 m (Mueggler 1985). Heights depend upon site quality and clonal genotype. An estimated two-thirds of the aspen stands in the Intermountain Region exceed 95 years of age (Mueggler 1989).

Stands reaching ages greater than 120 years are classified old (Bartos and Mueggler 1981). Some stands have been reported to persist for more than 200 years (Bartos and Mueggler 1981). At this point, deterioration becomes evident and trees begin to die (Jones and Schier 1985).

Uneven-aged stands contain multiple age levels of young, mature, and old trees. These stands form under stable conditions where the over-story progressively dies from age or disease and is consecutively replaced by suckers (Mueggler 1985). Uneven-aged stands can also be found where individual clones expand and invade into adjacent grass or shrub communities (Mueggler 1988).

Stand dynamics

Mueggler (1988) states that most aspen communities are multi-layered because light penetration into the aspen over-story is sufficient to support abundant undergrowth. This undergrowth is comprised of shrubs, perennial herbs, and annuals. Aspen stands can be complex with several layers of conifers, shrubs, tall forbs, low forbs, and grasses. In contrast, stands can be very simple with even-aged aspen and a general assembly of grasses. He further shares that among the hundreds of plant species present in aspen communities of the Intermountain Region, very few can be considered representative of the aspen type. He feels that this reflects the ability of aspen to serve as an over-story dominant under a broad range of environmental conditions.

In discussing his methods of classifying aspen community types, Mueggler (1988) does generalize those plant species most likely to be found. Shrub genera include: *Symphoricarpos, Rosa, Amelanchier, Prunus*, and *Berberis*. Forb genera include: *Thalictrum, Osmorhiza, Geranium, Aster, Lathyrus, Achillea*, *Galium*, and *Senecio*. Graminoid genera include: *Agropyron*, *Bromus, Elymus, Poa*, and *Carex*. Of 2,100 aspen stands sampled by Mueggler (1988) only four plant species occurred more than half the time. These include: *Symphoricarpos oreophilus, Agropyron trachycaulum*, *Achillea millefolium*, and *Thalictrum fendleri*.

Mueggler (1985) points out that seral stands of aspen giving rise to conifer development become depauperate of previous plant species. When the conifer layer thickens, less light penetrates to lower levels of the under-story and competitive relationships are altered. This results in a progressive decrease of under-story shrubs and herbs.

Soils

Aspen is found on soils derived from basalt, granite, sandstone, and limestone (Berndt and Gibbons 1958, cited by Jones and DeByle 1985). Aspen grow on almost any soil type originating from these parent rocks. This broad amplitude of growth success is attributed more to environmental factors than actual soil types (Jones and DeByle 1985).

According to Jones and DeByle (1985), aspen has been observed on a full spectrum of landforms, including bottoms of draws, tops of ridge crests, and on tops of mesas and plateaus. Aspen have been observed on gley soil next to marshes, on 73% slopes of an old avalanche track, and on old talus with very thin stony soils. This wide spectrum of aspen stand locations explains why numerous types of soils are represented. However, aspen does grow larger and faster at the foot of slopes and on benches. These areas are well suited for aspen because they can contain rich, deep soils with plentiful moisture (Baker 1925, cited by Jones and DeByle 1985).

Bartos and DeByle (1981) state that the annual return of leaf and twig matter to the soil surface is a major contribution to the organic matter and nutrient content of soils under aspen. Their study revealed that nearly 1,800 kg's per hectare of aspen leaves and twigs fell each year from stands with basal areas ranging from 17 to 25 square meters per hectare. Further study revealed that a 42% weight loss in the litter crop occurred after the first year. Such high decomposition rates suggests these communities have rapid nutrient cycling.

Aspen leaves typically have a higher nutrient content than conifer needles and are able to decay faster (Duabenmire 1953, Troth et al. 1976, cited by Jones and DeByle 1985; Bartos and DeByle 1981). Herbaceous undergrowth is usually more productive under aspen than under conifers. This provides for even more litter input to the soil (Morgan 1969).

Soil studies done in northern Colorado found the A1 soil horizon under aspen was darker and contained more organic matter than under adjacent coniferous stands (Hoff 1957, cited by Jones and DeByle 1985). Another study in northern Utah revealed that the top 6 inches of mineral soil under aspen had 4% more organic matter, slightly higher pH, more available phosphorus, and a higher water holding capacity than the soils of adjacent stands of shrubs and herbaceous vegetation (Tew 1968, cited by Jones and DeByle 1985).

Jones and DeByle (1985) believe that if aspen occupies a site for several generations, an aspen type soil develops. If the aspen is seral to conifers, then the soil exhibits influences of the vegetation that occupied the site for the longest period of time. A single generation of conifers may result in a leached, light colored A2 horizon. This layer would be darker and more nutrient rich under aspen dominant sites.

Aspen are excellent nutrient pumps. Their varied rooting depth on deep well-drained soils allows for effective withdrawal of large quantities of available nutrients. These nutrients are incorporated into biomass. A large proportion of that biomass is annually dropped as litter to the soil surface where it decays rapidly and returns those nutrients to the mineral soil. This cycle builds and enhances soil (Jones and DeByle 1985).

Amacher and Bartos (1997) conducted a study where they sampled soils that at one time were dominated by aspen. Due to lack of fire, wildlife use, grazing livestock, or natural succession, conifers or sagebrush had largely replaced them. They measured pH, exchangeable cations, extractable phosphorus, total organic carbon, total nitrogen, and organic matter content of soils developed under conifers, mixed conifer-aspen, and aspen stands. Their studies found no significant differences for these measured soil properties. They felt that the soils had not been altered significantly to inhibit new aspen development.

This raises several questions. How much time is needed for soil genesis to actually change? How long had the conifer stands been established? What were the proportions of aspen to conifers in the mixed stands? Were samples taken under the trees or in the interspace? The study of changes occurring in soil genesis due to loss of the aspen community is fascinating but information in the literature is limited.

Fire

Fire is a natural event in aspen communities that plays an important role in perpetuating stands (Baker 1925, cited by Bartos and Mueggler 1981; Brown and DeByle 1987; DeByle et al., 1989). It is responsible for the abundance of aspen in the West (Jones and DeByle 1985; Romme et al., 1995). Fire stimulates the production of suckers by nullifying apical dominance through the removal of the over-story (Bartos et al., 1991). Prior to European settlement fire occurred regularly at varying intervals. With the settlement of the West, these intervals have lengthened due to fire suppression and alteration of fuel loads. Today fire in aspen stands is considered an unusual event (DeByle et al., 1987). The lack of fire has resulted in old decadent aspen stands throughout the West (Jones and DeByle 1985, DeByle et al., 1989).

DeByle and others (1989), state that the current dominance of aging, decadent aspen stands concerns land managers. Managers desire a more favorable multi-aged mosaic of aspen stands. Therefore steps are being taken to rejuvenate decadent stands on public lands. Re-introduction of fire through prescribed methods kills invading conifers and removes over-aged aspen. Vigorous growth of the new even-aged root suckers enhances the favorability of the community.

Aspen stands require certain conditions for fire to occur. They do not readily burn as other vegetation types that have evolved flammable characteristics (Mutch 1970, cited by Jones and DeByle 1985; Bailey and Anderson 1980). A dense under-story of conifers or shrubs combined with dry conditions favor a hot fire with rapid spread. However, many aspen stands lack these larger fuel loads and only have fine herbaceous material, fallen leaves, occasional downed stems, and a few shrubs or conifers (Jones and DeByle 1985). Fires that occur in these fuel loads are generally lower intensity creeping ground fires and not the higher intensity fires of conifer/shrub stands.

Key factors that influence fire temperatures include kind, quantity and spatial distribution of fuels and weather conditions prior to and during burning (Bailey and Anderson 1980). Aspen is not readily flammable, but because its bark is thin and green without protective corky layers, it is very sensitive to fire heat. Fire kills trees or inflicts damaging scars that lead to root and heart rot (Baker 1925, cited by Jones and DeByle 1985). Fire that is able to kill the over-story stimulates profuse suckering (Bartos and Mueggler 1981). In Wyoming, severely burned sites generated the most suckers 2 years after the fire. Moderate to light burned sights produced the most suckers 1 year after the burn. On Both sites, these suckers numbered from 29,900 to 150,000 stems per hectare (Bartos 1979, cited by Jones and DeByle 1985). Aspens sensitivity to fire negates the difficulty for these stands to burn and allows for vigorous sucker regeneration (Jones and DeByle 1985).

Animal impacts

Aspen communities regularly produce more that 2,000 kg's of forage per hectare (Houston 1954, cited by DeByle 1985a). This rivals the production of grasslands and can exceed neighboring conifer communities by 10 times (Reynolds 1969, cited by DeByle 1985a). Young aspen is nutritious, and when abundant, will make up a substantial portion of livestock and wild ungulate diets (Mueggler 1985b). Today the primary consumptive use of aspen growth and under-story is grazing by cattle and sheep (DeByle 1985a).

In a given area, the proportion of aspen acreage is relatively small when compared to the overall acreage available for livestock use. However, these stands can be and have been greatly affected by livestock herbivory. Cattle and sheep contribute different methods of disturbance. Utilization of 50-60% of the palatable forage by cattle has negligible affects in both mature and young sucker stands of aspen. In contrast, similar levels of grazing by sheep will damage and kill the aspen suckers (Sampson 1919, cited by DeByle 1985a). Sheep browsing directly impacts aspen in the early sapling stage by reducing growth, vigor, and numbers (DeByle 1985a). Repeated over-browsing will eliminate an aspen stand.

As a growing season progresses, cattle increase use of herbaceous species in aspen stands as the availability of forage outside the stands declines (Fitzgerald et al., 1986). On the other hand, sheep select for the forage in these stands regardless of the season. Despite season of use and foraging, cattle do negatively impact these sites by seeking shade and constantly trampling stands. Repeated sucker damage progressively deteriorates the stand until only a few decadent trees remain.

Reduced fire intervals in aspen stands is partially attributed to removal of under-story vegetation by livestock (Jones and DeByle 1985). Normally this vegetation dries in the fall allowing for potential fuel loads to carry fire. Stands that do burn must be protected to ensure sucker survival. Fencing or piling slash can be used to deter livestock use. This gives the suckers opportunity to establish and grow to a needed height of 1.5 m to protect the terminal meristems from damage caused by ungulate use (Jones and DeByle 1985).

Wild ungulates, such as deer and elk, seasonally rely upon aspen stands. The season of primary use is during fall and winter when elk and deer seek food and thermal cover. Deer browse heavily at this time. Their average diets include 74% trees and shrubs (Kufeld et al., 1973, cited by DeByle 1985a). Deer reside in and around aspen stands during fall and early winter until snowpack depth in the aspen zone forces them to lower elevations. Elk are larger and able to remain in aspen zones during most winters (DeByle 1985a). Their evidence of residency is regularly depicted due to elk "barking" mature aspen stems. This barking is the process of gnawing or stripping the bark for food. Elk are the primary barkers of the West, but rabbits, hares, mice, voles, and porcupines also contribute. Excessive barking can girdle trees or allow pathogenic fungi and canker to infect and adversely affect the aspen stand (DeByle 1985a; Romme et al. 1995).

Excessive or highly concentrated populations of deer and elk are a major concern to the health and longevity of the aspen community. Aspen communities found on winter ranges receive the most damage (Romme et al. 1995). The combination of human encroachment on winter range and subsequent fire suppression has resulted in concentrated animal numbers relying on decadent aspen stands. When a stand does burn and sprout suckers, it is utilized too heavily due to the scarcity of suckers on the landscape. If the suckers are continually over utilized, the stand will eventually disappear from the landscape.

Insects and diseases

Aspen is host to many insects and diseases, but only a few result in significant damage. Western tent caterpillar (*Malacosoma californicum*), found through out the Intermountain West, can defoliate large acreage of aspen in years when population densities are high. This defoliation can become severe enough to cause tree mortality. Species of boring insects that damage or kill aspen include: poplar borer (*Saperda calcarata*), poplar twig borer (*Saperda moesta*), poplar branch borer (*Oberea schaumii*), poplar butt borer (*Xylotrechus obliteratus*) and bronze poplar borer (*Agrilus liragus*). These bores can cause severe physical damage or mortality to aspen. They also provide openings that allow cankers, fungus, and disease to infect, deform, and kill trees (Jones, Debyle, and Bowers 1985).

Sooty canker (*Cenangium singulare*) is considered the most lethal canker and is a major cause of aspen mortality in the West. Black cankers (*Ceratocystis fimbriata*) are large slow growing cankers that are seldom fatal, but cause considerable deformity. *Cryptospaeria* is a recently discovered canker that grows rapidly and can kill stems in a few years (Hinds 1985, Shepperd 1986). Shepperd (1986) feels that the most serious cause of mortality in aspen stands is decay. Stems older than 100 years of age have the highest rate of infection. A false tinder fungus that enters through a wound to the sapwood or heartwood can cause this decay. *Phellinus tremulae* is the predominant aspen trunk rot fungus in North America (Hinds 1985).

Western juniper (*Juniperus occidentalis*)

Distribution

Western juniper (*Juniperus occidentalis* spp. *occidentalis*) is found across arid regions of northeastern California, northern Nevada, eastern Oregon, southwestern Idaho, and southern Washington. It occupies an estimated 3.25 million ha (Gedney et al. 1999) as expansive woodlands, scattered groves, individual trees and open savannas.

Western juniper elevation limits range from a low of 183 to 549 m along the Columbia River (Sowder and Mowat 1958), to a high of 2,120 m on Steens Mountain in southeastern Oregon. It is commonly found on plateaus between 915 and 1,222 m in central Oregon and between 1,220 and 1,982 m in southeastern Oregon and northeastern California (Miller and Rose 1995, Miller 1996).

Climate

A cool, semiarid climate with cold wet winters and dry hot summers is found across the geographic distribution of western juniper. Typical annual precipitation levels range between 25 and 35 cm, but western juniper grows in areas with as little as 23 cm and in areas with greater than 70 cm. Precipitation is received as snow in November, December, and January, and as rain in March through June (NOAA 1993, Miller 1996).

Soils

A broad array of soils occur within the geographical distribution of western juniper. Mollisols that support juniper include Haploquolls, Cryoborolls, Argixerolls, Durixerolls, and Haploxerolls (Driscoll 1964 a & b, Green 1975, Dyksterhuis 1981, Pomerening et al 1983 and Simonson 1986, Josaites 1991). Aridisolls include Duragids, Haplargids, and Camborthids (Miller 1996).

Miller (1996), states that western juniper grows in little to no soil by rooting in the cracks of rocks, but trees also thrive in a range of soil depths including Haploxerolls deeper than 2 m. Sandy, clay, and silt loams, as well as silty clay loams, dominate the upper 10-25 cm in soils supporting western juniper. Below 25 cm, clay and clay loams are prevalent.

Reproduction

Western juniper are described as being submonecious with half the trees being monecious. Female pollinated cones develop into small glaucous-blue berries with 1-3 seeds and approach maturation after approximately two years of development on the tree (Vasek 1966, Hitchcock 1969). Miller and Rose (1995) found that western juniper nears full reproductive potential at 50 years of age. Key seed dispersal mechanisms appear to be wildlife (primarily birds) and down-slope transport (e.g. water transport over frozen ground) (Gabrielson and Jewett 1970, Johnsen 1962, Miller and Wigand 1994).

Stand dynamics

Western juniper woodlands can be separated into two age classes, old growth juniper that established before European settlement and stands of young post-settlement trees (Eddleman et al. 1995). Old growth juniper are typically greater than 150 years old with trees ranging from 400 to 700 years old (Holmes et al. 1975, Miller 1996). Western juniper over a 1000 years old have been recorded (Miller, file data). Stands of post-settlement trees are dominated by young trees less than 100 years old (Miller 1996). In Oregon less than 3% of western juniper woodlands are comprised of trees greater than 100 years old (USDI-BLM 1990).

Disturbance

Fire is the primary disturbance for western juniper. Young trees less than 50 years old are most susceptible and easily killed by fire (Burkhardt and Tisdale 1976). Trees found in rocky outcroppings have the greatest potential of reaching old growth status due to the lack of fine fuels that could carry a fire of sufficient strength to kill trees (Miller and Wigand 1994, Miller and Rose 1995). Typical old growth stands of western juniper can be found in such areas. Insects and disease are found in western juniper stands but cause little mortality (Eddleman et al. 1995). Wood cutting for firewood, fence materials, crafts and furniture occurs but is generally localized and small scale.

Expansion

Since the late 1800s western juniper has been increasing in both density and distribution (Burkhardt and Tisdale 1976, Miller and Wigand 1994, Miller and Rose 1995). Invasion of western juniper is occurring into mountain big sagebrush (*Artemisia tridentata* subsp.*vaseyana*), low sagebrush (*Artemisia arbuscula*), bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus ledifolius*), quaking aspen (*Populus tremuloides*), and riparian communities (Eddleman 1987, Miller and Wigand 1994, Miller and Rose 1995). The expansion and invasion of western juniper affects native plant communities in species composition, site productivity, water, soils, and wildlife. Reasons for expansion include: optimum climatic conditions at the turn of the century, reduced fire intervals resulting from European settlement with subsequent livestock use and fire suppression, and an increased seed source (Miller and Wigand 1994, Miller and Rose 1995, 1999, Miller 1996).

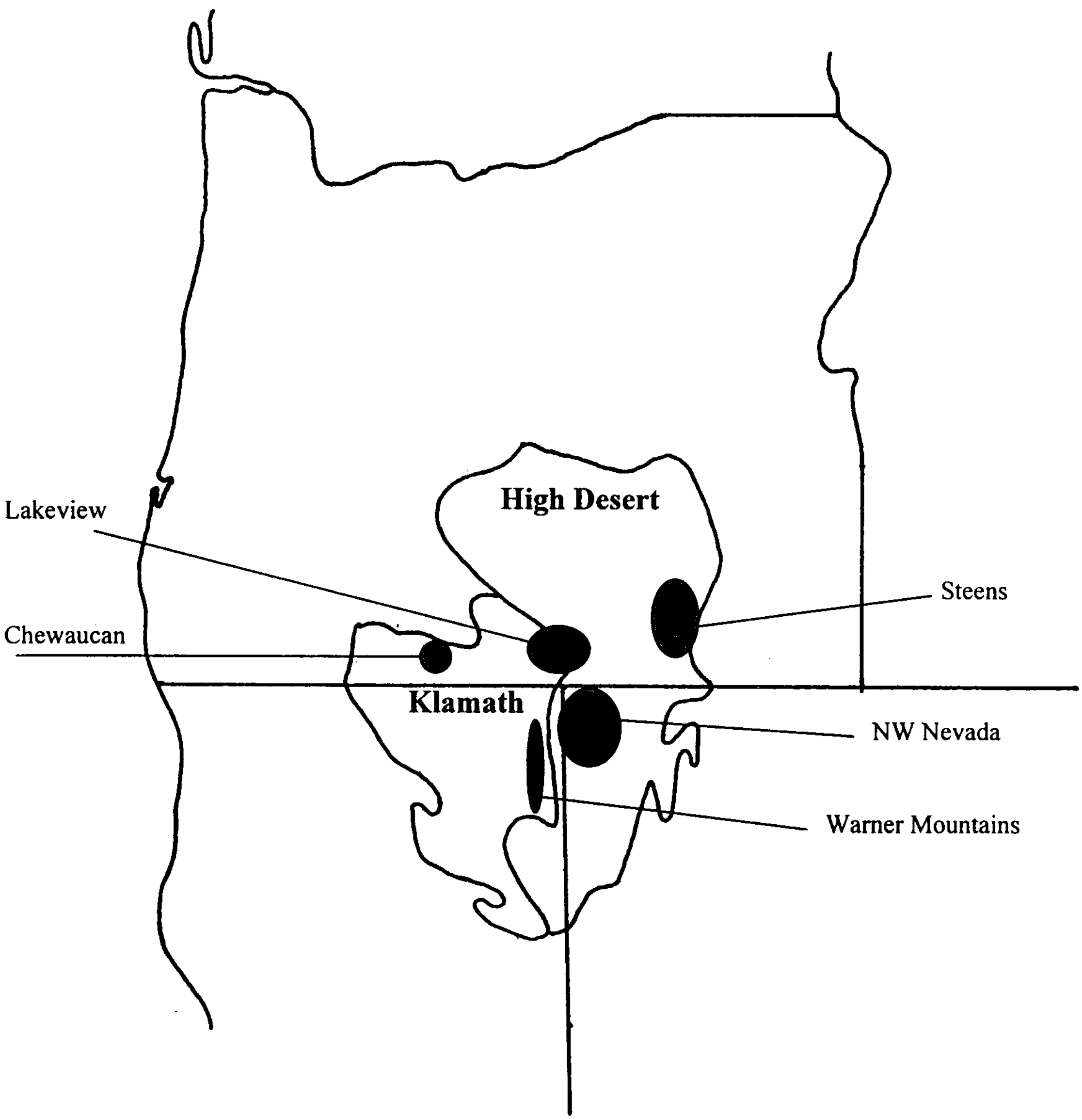
STUDY AREA

The study was located in the High Desert and Klamath Ecological Provinces (Anderson 1956, Cronquist et al. 1972, and Bailey 1994) in southeast Oregon, northeast California, and northwest Nevada (Figure1). Geographic regions sampled include: 1) Chewaucan River watershed; 2) Lakeview regions of Abert Rim, Fish Creek Rim, Coleman Rim, and Long Canyon; 3) Steens Mountain; 4) Northwest Nevada regions of Sheldon National Antelope Refuge, Bald Mountain Canyon, and Mosquito Lake; and 5) Northern California Warner Mountain regions of Cedar Creek, Selic Canyon, Nelson Corral, and McDonald Peak. Desert basins, uplands, canyons, and fault block mountains typify the geography of these regions. Shrub-grass communities are predominantly mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana*) with various degrees of low sagebrush (*Artemisia arbuscula*), rabbitbrush (*Chrysothamnus* spp.), bitterbrush (*Purshia tridentata*) and snowberry (*Symphoricarpos oreophilus*) with fescues (*Fescue* spp.), wheatgrasses (*Agropyron* spp.), and needlegrasses (*Stipa* spp.) Tree communities include western juniper (*Juniperus occidentalis*), mountain mahogany (*Cercocarpus ledifolius*), and aspen (*Populus tremuloides*). Climate is cool and semi-arid characterized by cold wet winters and dry hot summers. Precipitation falls as snow in November, December, and January and as rain in March through June.

Aspen stands typically reside along the north and northeast base of ridges where wind deposition causes excess snow accumulation. Elevation of aspen stands varied between a high of 2,133 m to a low of 1,494 m. Within this elevation, yearly precipitation varies from 30 to 40 cm. However, excess snow accumulation increases available moisture enabling these sites to sustain aspen in an otherwise semi-arid environment.

Aspen stands can be complex with several layers of shrubs, tall forbs, low forbs, grasses, and annuals. In contrast, stands can be very simple with even-aged aspen and a general assembly of grasses. Shrub genera typically found within aspen stands include: *Symphoricarpos, Rosa, Amelanchier, Prunus*, and *Berberis*. Forb genera include: *Thalictrum, Osmorhiza, Geranium, Aster, Lathyrus, Achillea*, *Galium*, and *Senecio*. Graminoid genera include: *Agropyron*, *Bromus, Elymus, Poa*, and *Carex*. Soils located within aspen stands were formed from igneous rock (basalt) and are typically deep loamy Haploxerolls.

Figure 1. Study Area (ecological provinces derived from Anderson 1956, Cronquist et al. 1972, and Bailey 1994).



METHODS

Stand selection and plot layout.

Aspen stand selection for this study was limited to non-riparian stands greater than 0.5 ha located on public lands. All stands reside within the Klamath and High Desert Ecological Provinces. Additionally, only stands under 2,133 m were chosen since this is the upper elevation limit for western juniper (*Juniperus occidentalis* spp. *occidentalis*) in this region.

In stands sampled, a circular plot 15 m in diameter was positioned inside the stand, away from the edge to represent the stand. In stands greater than 1 ha several plots were used to characterize the aspen community. Inside this plot, age, density, and overstory canopy cover of both aspen and western juniper were measured. Overstory canopy cover was defined as cover higher than 1.5 meters from the ground. Percent bare ground and herbaceous plant cover was visually estimated within the 15 m circular plot. A total of 91 aspen stands were sampled using this method.

Stand data collection

Within each 15 m circular plot all live and dead stems of juniper and aspen were counted and assigned to a height class. Height class designation was expressed on a percent ranking relative to the maximum height of trees on that site (e.g. 100-90, 89-75, 74-60, 59-45, 44-30, 29-15, 14-5, <5). Adult aspen were defined as trees equal to or greater than 75% of stand height. Aspen trees considered to have potential for recruitment were equal to or greater than 2 m tall up to 75% of stand height. Trees less than 2 m in height were typically browsed, so recruitment potential into the stand was assumed to be very limited.

In every stand sampled, five of the largest aspen and five of the largest western juniper were measured for height, diameter, and cored with an increment wood corer. This was to establish the age of the dominant aspen trees and approximate time of initial juniper encroachment. Trees that were too small to core were cut at ground level to obtain a cross-section slab. Diameter measurements of all trees were measured at the location the tree was cored or cut. Wood cores and slabs were mounted, stained with phloroglucinol, sanded, and then aged by counting growth rings under a dissecting microscope. Because of the height at which trees were cored, not all growth rings were included. For instance, a core collected from a tree at 50 cm does not include the growth rings before the tree reached that height. To compensate, small juvenile trees correlating with various core sample heights were cross-sectioned at ground level and aged. These ages were then added to the growth ring counts of the trees cored to approximate actual ages of trees.

The degree of western juniper presence in each aspen stand sampled was numerically rated. Numbers are based solely on observation and researcher intuition.

5 - Dominant: Larger presence of western juniper than aspen.

4 - Co-dominant: Equal presence of western juniper and aspen.

3 - Common: Western juniper common.

2 - Present but not common: Only a few trees present in the plot.

1 - Rare: Only a few trees present in the stand.

0 - Absent: No juniper exist in the stand.

To determine if aspen community characteristics influence juniper encroachment, aspen and juniper canopy cover, canopy height, stand age, aspect, slope, and elevation data were collected. A spherical densiometer was used to measure overstory canopy cover for aspen and western juniper within the 15 m circular plot. Densiometer measurements were recorded for five locations; one reading in the center of the 15 m circular plot and additional readings at the north, south, east, and west edge of the circular plot. From the five locations, an overall measurement of separate overstory canopy cover for aspen and juniper was derived. Tree height was determined by measuring length of dead fallen trees in combination with visual estimates of live trees. Aspect, slope, and elevation were recorded for every site sampled. Aspect was determined using a compass. A clinometer was used to measure slope. Elevation was derived from USGS topographic maps. With this information, statistical correlations were computed between juniper canopy cover and density versus aspen overstory canopy cover, canopy cover height, stand age, aspect, slope, and elevation.

Disturbance interval data collection.

To determine fire disturbance intervals in aspen within the Northwest Great Basin, two areas with the largest stands were located and sampled. The first, a continuous 71 hectare stand, is located along Eusabio Ridge and Ankle Creek on the southern end of Steens Mountain. The second, a series of adjacent stands totaling approximately 35 hectares, grows on the Fish Creek Rim and Cox Springs located north of Adel, Oregon.

The Eusabio stand was systematically sampled from top to bottom by walking several transects from toe-slope to the ridge crest. Transects were placed every 80 to 100 meters across the length of the stand. Along these transects, plots were established every 25 to 50 meters. The variation in distance between plots was determined by stand structure; i.e., plots were centered in sites with similar tree density and tree size and not placed to overlap areas of varying stand structure. The broad distribution of plot locations captured the variability of aspect, elevation, and slope within the stand. Within each plot, ten aspen trees were sampled using an increment wood corer to determine age distributions within the stand. Within the entire 71 hectare stand on Eusabio Ridge, a total of 100 plots and 1,000 aspen were sampled.

The series of stands located on Fish Creek Rim and Cox Springs were growing along a northwest to southeast series of ridges approximately 11 kilometers long. Starting at the northwest end and working southeast, each individual aspen stand was sampled. Again due to variability in stand shape, stand size, aspect, elevation, and slope, plots were placed arbitrarily along single transects to ensure proper sampling. Similarly, ten aspen trees were sampled with an increment wood corer within each plot. A total of 28 plots with 280 aspen were sampled covering approximately 35 hectares.

All aspen cores were mounted, sanded, aged, and reviewed on a plot by plot basis. Since aspen sprouts after a fire, the oldest tree in each plot revealed the approximate timing of the last fire at that specific location within the stand. All plots where assessed to determine timing of fire in an entire aspen complex. A pre-settlement (pre-1865) mean and range of years between fires was calculated for each aspen complex sampled.

Soil data collection

Soils were sampled using a randomized block design with five blocks. These five blocks were placed in aspen stands greater than 1.5 hectares growing on Steens Mountain in southeast Oregon. Block size depended on aspen stand characteristics, such as distance between treatments and shape of aspen stands. Each block had the following two treatments.

1. Soils influenced by aspen.
2. Soils once influenced by aspen but now dominated and influenced by western juniper.

Five sub-samples were collected two thirds inward from the drip line of the present dominant canopy in each treatment. The top 10 cm of soil was sampled. A total of ten soil sub-samples were collected in each block with 50 total sub-samples for the five blocks (n = 25 for each treatment). The soil sub-samples were sent to a soils lab and analyzed for C:N ratio, pH, CEC, %lime, %OM, and plant available C, N, P, K, Ca, Mg, Na, Zn, Fe, Mn, Cu, B, and sulfate. Additionally, at each soil sub-sample collection site for juniper dominated treatments, juniper were cored and aged to determine duration of their influence over the site.

At each sub-sample collection site, resident litter depth was measured. This totaled 50 measurements for the five blocks. Furthermore, a litter trap approximately 40 x 90 cm was placed under each treatment in all five blocks for a total of 10 litter traps. These traps collected current litter fall from August 1st to November 1st, 1998. The two litter types were sampled with a carbon-nitrogen analyzer to determine differences in carbon and nitrogen content and C:N ratios.

Data analysis

SAS was used for all statistical analysis. Stepwise multiple regression was used to determine if aspen overstory canopy cover, canopy cover height, stand age, aspect, slope, and elevation affected western juniper canopy cover and density. The soil data were analyzed as a randomized block with two treatments. Simple linear regression was used to determine if soil variables of C:N ratio, pH, CEC, lime, organic mater, and plant available nutrients differed between the two treatments. Simple linear regression was also used to determine if aspen and juniper litter variables of C:N ratio, carbon, and nitrogen differed. To determine pre-settlement fire intervals the mean and range of all events recorded prior to 1870 were calculated for the two sites sampled. In tables 1, 2, 3, 4, and 6, calculated means only include

l the variable of interest (e.g. mean juniper densities

l sites that contained juniper). All other tables and

ıpled.

RESULTS

western juniper encroachment into aspen.

encroachment into aspen stands has occurred throughout the e 91 aspen stands sampled, 86 (or 95%) contained various iiper. Twelve percent of the stands sampled were completely iniper and in 23%, western juniper was the dominant tree canopy. Western juniper was common but not yet dominating in 42% of aspen stands sampled. The average density of western juniper was 1,573 trees per hectare (Table 1). Sixty-two percent of aspen stands contained between 100 and 2,000 western juniper per hectare and 10% contained 2,500 or more per hectare (Figure 2).

Western juniper canopy cover averages 21% across the 86 aspen communities containing juniper (Table 2). Fifty-one percent of aspen stands had greater than 10% western juniper canopy cover and 21% had greater than 40% canopy cover (Figure 3). Based on percent composition between western juniper cover and aspen cover, western juniper constitutes 33% of the total overstory canopy cover in aspen stands across the study area (Table 2).

Table 1. Mean densities and standard error of all western juniper tree sizes in aspen communities across the five geographic regions.

Location	Mean Density (tree#/ha)	SE
Entire study area	1573	133.71
Geographic regions:		
Chewaucan	1368	143.44
Lakeview	1382	175.82
Steens	1745	209.44
NW Nevada	1669	525.76
Warners	1012	246.05

Table 2. Mean western juniper canopy cover, standard error, and percent composition of the tree canopy in aspen communities across the five geographic regions.

Location	% Juniper canopy cover	SE	% Juniper composition based on canopy cover
Entire study area	21%	2.46	23%
Geographic regions:			
Chewaucan	36%	4.66	54%
Lakeview	22%	4.93	29%
Steens	25%	3.55	29%
NW Nevada	13%	6.42	18%
Warners	2%	1.20	3%

Figure 2. Frequency of occurrence of different levels of western juniper densities across all aspen stands sampled.

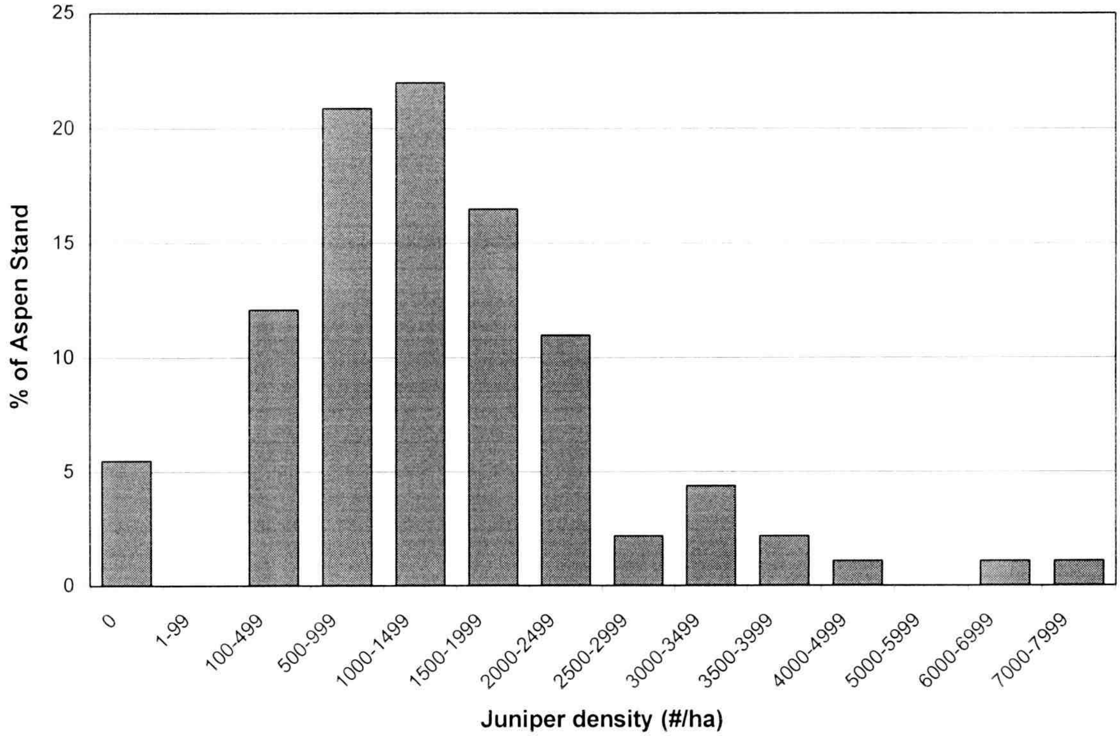
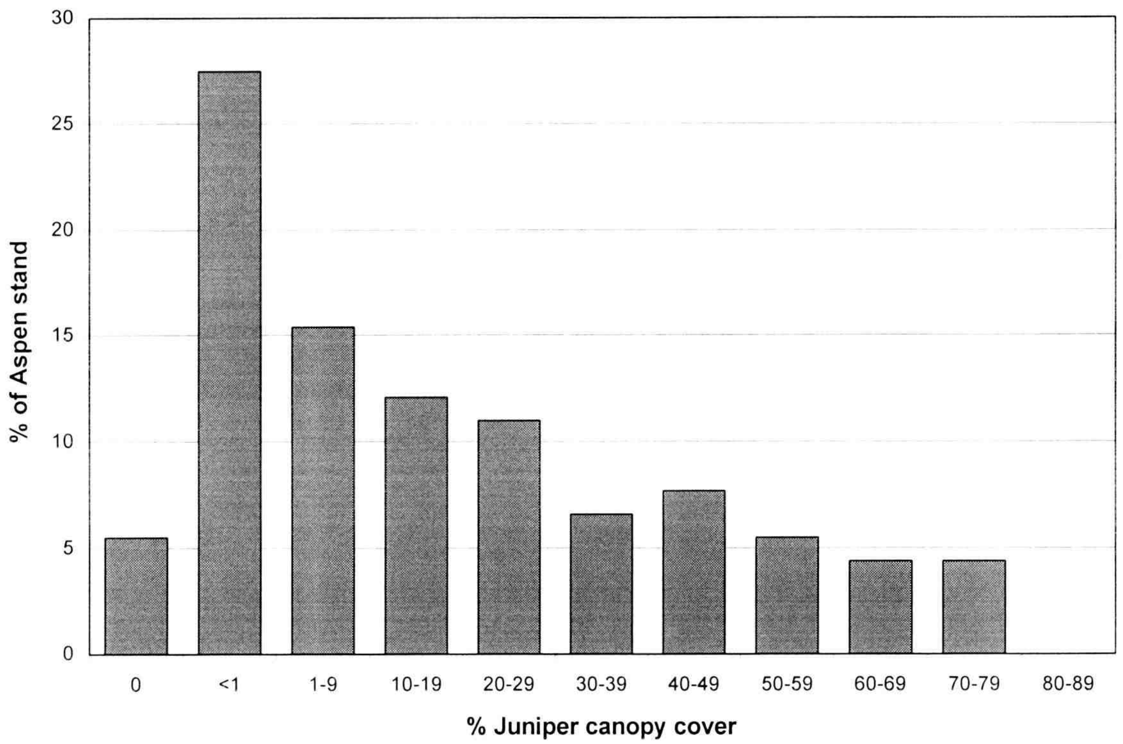


Figure 3. Frequency of occurrence of western juniper canopy cover levels across all aspen stands sampled.



Western juniper encroachment into aspen peaked between 1900 to 1939 with 77% of all trees sampled establishing during this 39 year period (Figure 4). Across the study area, 60% of western juniper sampled were greater than 70 years old. However only 5% were greater than 100 years old and none exceeded 107 years (Table 3).

Aspen stand age.

Aspen stands sampled across the study area average 98 years old with 85% of the stands varying between 70 and 130 years old (Table 4, Figure 5). Forty-eight percent of the aspen stands still surviving were greater than 100 years old and 9% were locally extinct (no live trees present).

Mean aspen stand density of adult live trees across the study area was 966 trees per hectare (Table 5). Sixty-six percent of stands had greater than 500 trees per hectare and 11% greater than 2,000 trees per hectare (Figure 6).

Aspen stand density of adult dead trees averaged 123 trees per hectare (Table 5). Aspen stand density of recruitment trees averaged 143 trees per hectare (Table 5). However, 70% of aspen stands sampled had 0 recruitment and 21% had between 100 and 500 recruitment trees per hectare (Figure 7).

Table 3. Mean ages and standard error of largest western juniper in aspen communities across the five geographic regions.

Location	Age (yrs.)	SE
Entire study area	72	1.95
Geographic regions:		
Chewaucan	104	0.33
Lakeview	73	3.82
Steens	73	2.20
NW Nevada	73	4.56
Warners	46	9.40

Table 4. Mean ages and standard error of largest aspen across the five geographic regions

Location	Age (yrs.)	SE
Entire study area	98	3.23
Geographic regions:		
Chewaucan	119	8.21
Lakeview	93	7.47
Steens	96	4.47
NW Nevada	103	8.94
Warners	111	6.11

Figure 4. Frequency of occurrence of western juniper establishment periods across all aspen stands sampled.

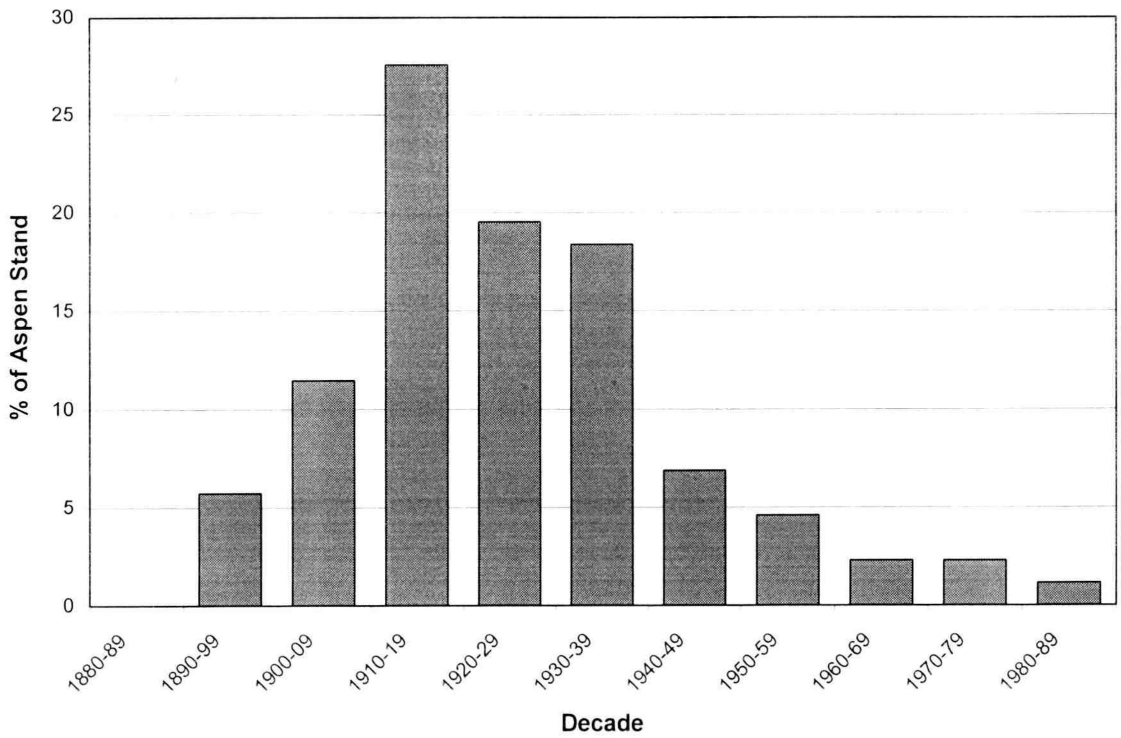


Figure 5. Frequency of occurrence of dominant aspen ages across all aspen stands sampled.

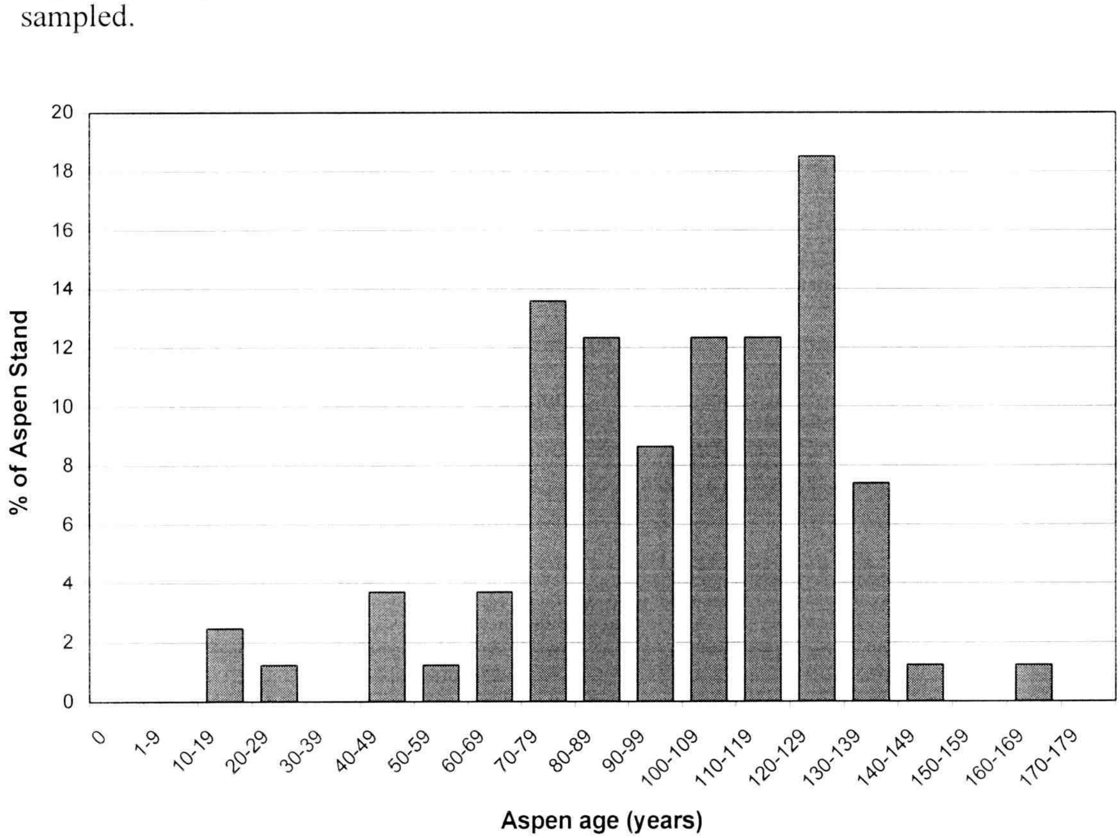


Table 5. Mean and standard error of adult live aspen, adult dead aspen, and recruitment aspen per hectare of aspen. Adult live trees are trees greater than 75% of stand height. Recruitment trees are greater than 2 m tall and up to 75% of stand height.

Location	Adult live trees	SE	Adult dead trees	SE	Recruitment trees	SE
Entire study area	953	88.09	123	18.87	143	50.12
Major regions:						
Chewaucan	361	50.26	456	205.51	0	0
Lakeview	684	120.84	143	40.19	316	194.06
Steens	948	115.01	102	23.80	81	36.85
NW Nevada	1496	504.07	71	38.46	36	23.93
Warners	1340	216.78	143	37.31	270	166.44

Figure 6. Frequency of occurrence of dominant live aspen per hectare across all aspen stands sampled.

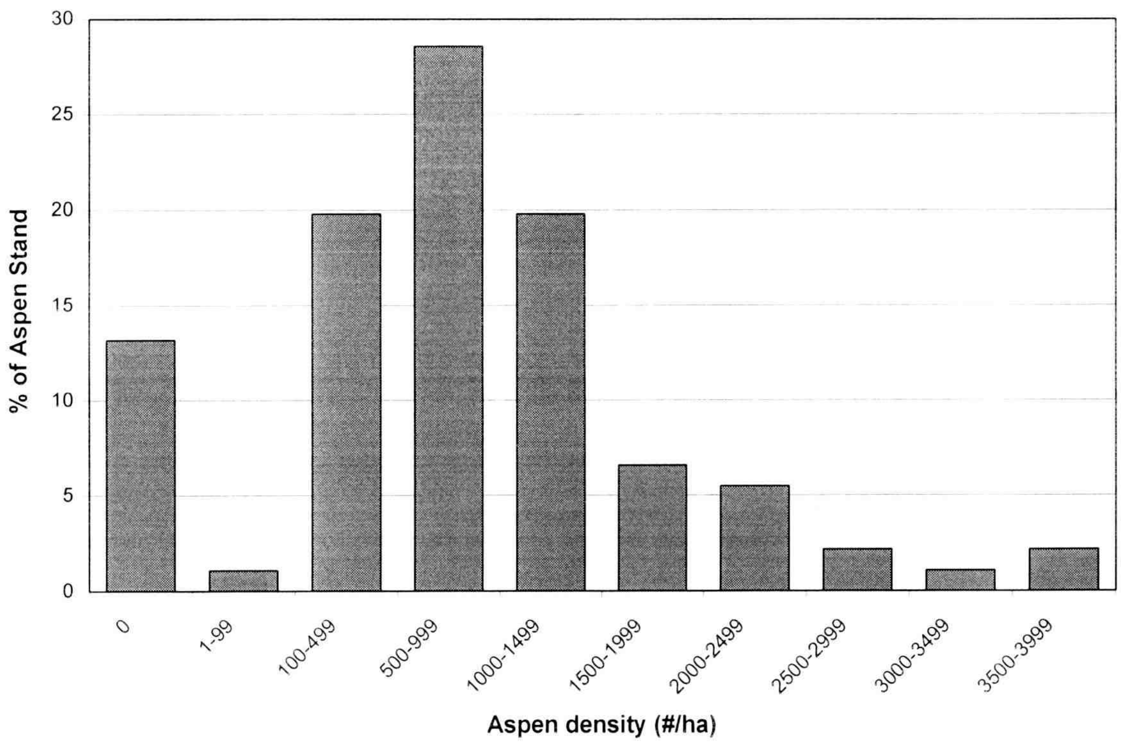
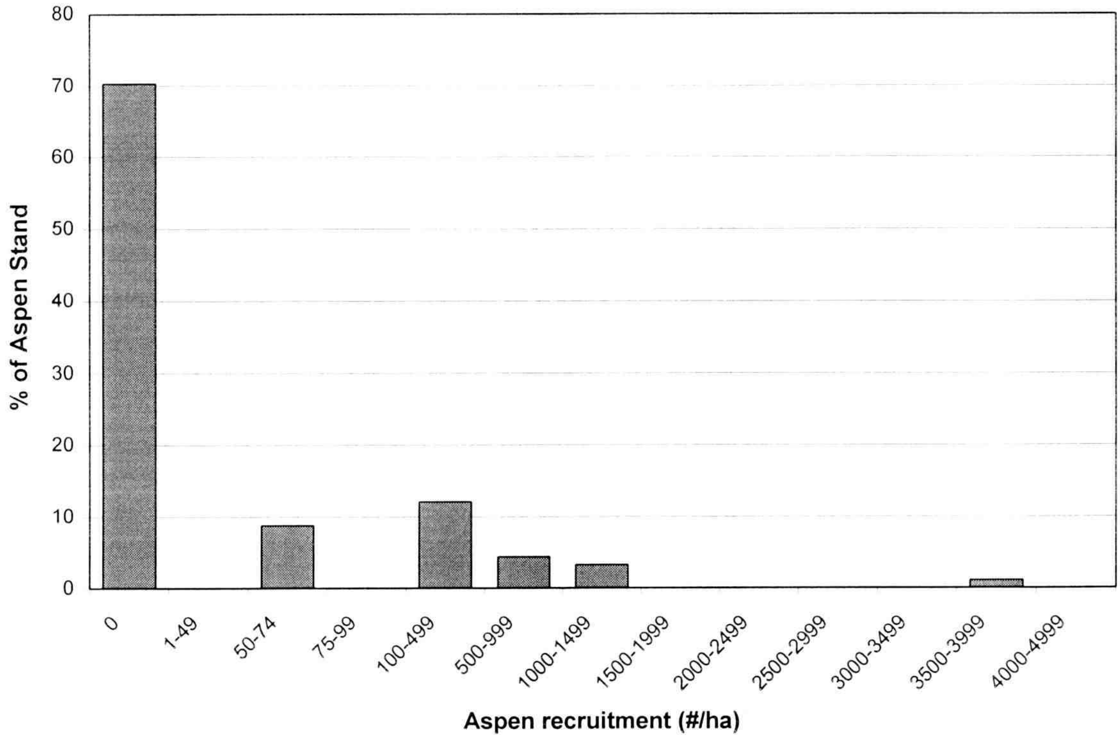


Figure 7. Frequency of occurrence of aspen recruitment density per hectare across all aspen stands sampled. Recruitment trees were defined as subcanopy aspen greater than 2m tall but less than 75% of the dominant tree canopy height.



Aspen canopy cover averaged 59% (Table 6). Fifty-one percent of stands had greater than 60% canopy cover. Aspen canopy in 9% of the aspen stands was greater than 90% (Figure 8).

Effects of aspen stand structure and geography on western juniper encroachment.

There were significant correlations ($p<.05$) among site and stand variables (Table 7). Juniper and aspen cover expressed the strongest relationship. As aspen cover decreased juniper cover increased. Other parameters reported were significant but their R^2 values indicated they explained only a small degree of the variability. Elevation was the only site variable that was significantly correlated to a tree parameter. As elevation increased juniper cover decreased.

Simple regression revealed that as juniper cover increased in aspen stands, herbaceous plant cover decreased ($p = .0001$) and bare ground increased ($p = .0018$).

Disturbance

Within the 71 hectare Eusabio/Ankle Creek aspen complex, pre-settlement fire (prior to 1870) occurred at a mean interval of 10.3 years with a range from 6 to 13 years. The last recorded fire occurred in 1918 affecting 54% of the entire aspen complex (Figure 9). Pre-settlement fire within the Fish Creek Rim/Cox Springs aspen complex, occurred at a mean interval of 11.3 years with a range from 5 to 18 years. The last recorded fire occurred in 1910 affecting 13% of the entire aspen complex.

Table 6. Mean and standard error of canopy cover for aspen.

Location	% canopy cover	SE
Entire study area	59%	2.95
Geographic regions:		
Chewaucan	31%	4.66
Lakeview	49%	7.21
Steens	62%	3.87
NW Nevada	59%	9.37
Warners	76%	4.60

Table 7. Statistical analysis (multiple regression) of aspen, western juniper, and geography variables.

Variables	R-square	P-value
Juniper cover vs. aspen cover	.80	.0001
Juniper cover vs. aspen density	.19	.0001
Juniper cover vs. elevation	.13	.0004
Juniper density vs. aspect	.04	.0365
Juniper density vs. aspen cover	.04	.0313
Juniper density vs. aspen density	.06	.0187
Aspen age vs. aspen cover	.32	.0001

Figure 8. Frequency of occurrence of overstory aspen canopy cover across all aspen stands sampled.

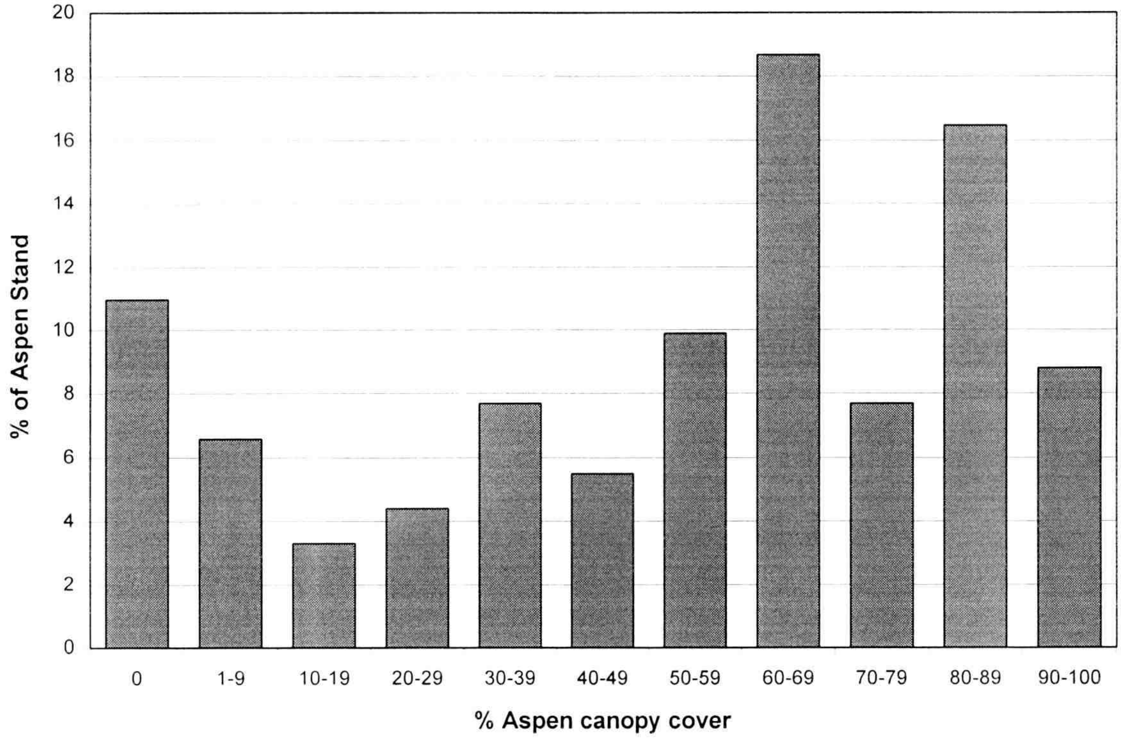
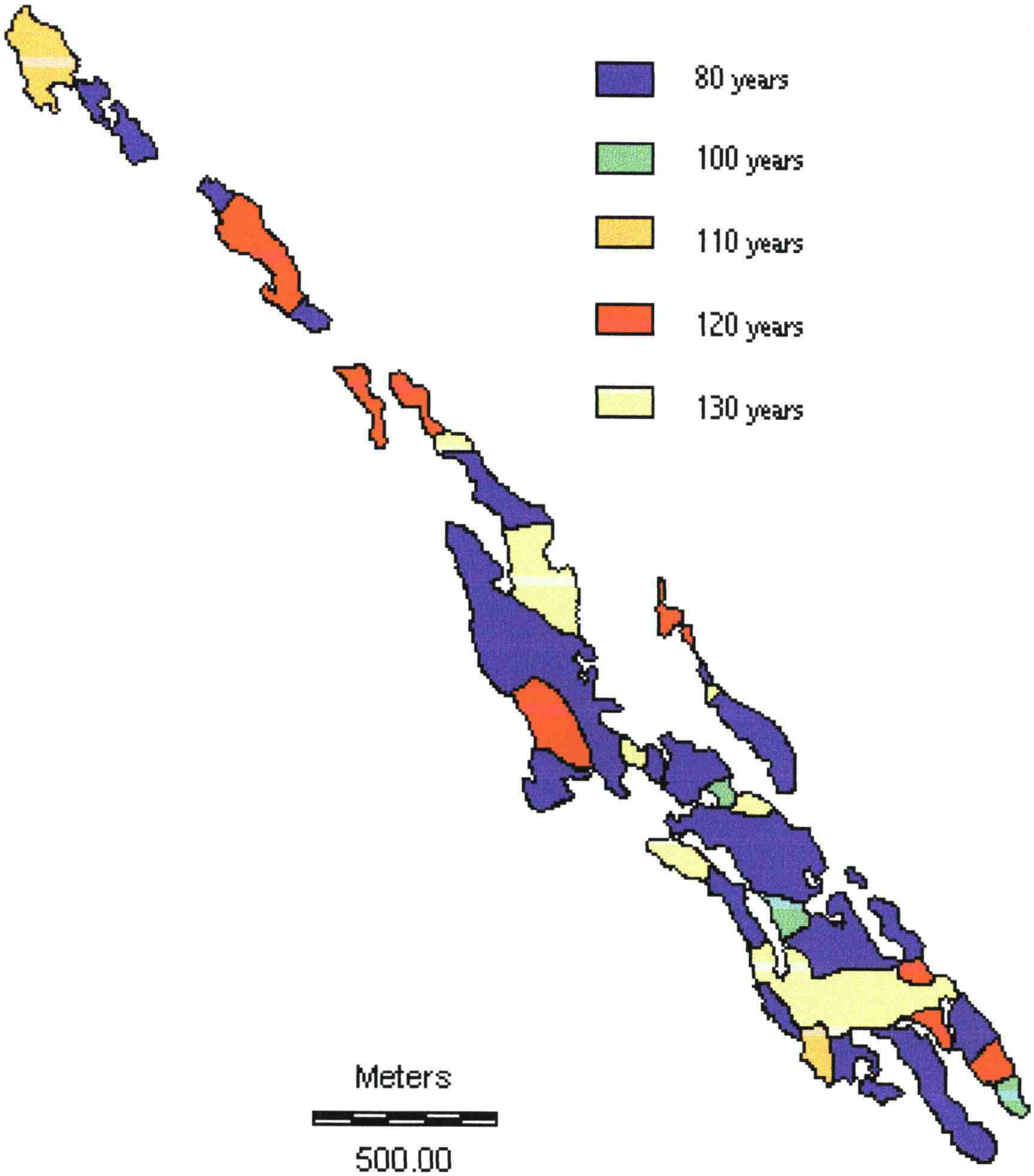


Figure 9. Seventy-one hectare aspen complex on Eusabio Ridge, Steens Mountain, Oregon. Different colors illustrate the variation of age of overstory canopy throughout the stand.



Effects of western juniper encroachment on soil previously influenced by aspen.

Soil conditions evaluated were: 1) soils influenced by aspen, and 2) soils once influenced by aspen but now dominated and influenced by western juniper. Western juniper across the five blocks ranged from 75 to 85 years old. These trees showed signs of crown lift (lower canopy branches dying). Average juniper litter depth across the juniper influenced plots was 10 cm. The average litter depth for aspen influenced soils was 3 cm.

There was no significant difference in soil carbon and nitrogen content between the two treatments. However, the C:N ratio and pH proved to be significantly greater in the juniper than in aspen plots (Table 8). Soils influenced by western juniper also had higher amounts of salts, lime, and sulfate, and lower amounts of magnesium, iron, manganese, and copper. Aspen and juniper litter was also significantly different (Table 9). Carbon and nitrogen content were greater and C:N lower in aspen litter than in juniper litter.

Table 8. Mean, standard error, and P-value for aspen and western juniper soil treatments.

Variable	p-value	Aspen soil Trt Mean	SE	Juniper soil Trt Mean	SE
C:N ratio	0.0102*	12.360	0.254	13.284	0.204
pH	0.0001*	6.800	0.042	7.380	0.043
Salts	0.0190*	0.352	0.026	0.432	0.020
CEC	0.0036*	17.690	0.394	16.720	0.248
% Lime	0.0016*	0.620	0.044	0.820	0.049
% OM	0.1918	5.256	0.122	5.088	0.098
C mg kg	0.6500	7.040	0.320	7.255	0.366
N mg kg^{-1}	0.3444	0.568	0.022	0.542	0.022
P mg kg^{-1}	0.1168	56.800	4.926	47.960	2.602
K mg kg^{-1}	0.6445	549.560	25.373	536.880	38.254
Ca mg kg^{-1}	0.1032	2786.400	110.027	2560.800	140.207
Mg mg kg^{-1}	0.0074*	245.080	2.064	228.040	6.592
Na mg kg^{-1}	0.2858	86.080	5.660	79.160	5.429
Zn mg kg^{-1}	0.6396	3.448	0.386	3.712	0.624
Fe mg kg^{-1}	0.0001*	29.016	3.060	13.936	0.539
Mn mg kg^{-1}	0.0001*	5.920	0.622	2.980	0.221
Cu mg kg^{-1}	0.0071*	0.524	0.040	0.408	0.030
B mg kg^{-1}	0.2261	0.364	0.015	0.344	0.015
Sulfate mg kg^{-1}	0.0029*	5.280	0.212	6.720	0.464

* Significant difference of treatments at $p < .05$

Table 9. Mean, standard error, and p-value for aspen and western juniper litter treatments.

Variable	P-value	Aspen litter Trt	SE	Juniper litter Trt	SE
C:N ratio	0.0036*	45.310	7.191	76.637	4.458
% C	0.0337*	51.036	0.581	48.802	0.503
% N	0.0179*	1.228	0.163	0.646	0.040

* Significant difference of treatments at p < .05

DISCUSSION

Juniper expansion

Since the 1870's, western juniper (*Juniperus occidentalis*) has been actively invading aspen stands below 2,133 m in the Northwest Great Basin. This study indicates over 90% of the aspen stands below 2,133m are being encroached by western juniper. Across this geographic region, western juniper density typically exceeded 500 trees per hectare, with approximately one third of aspen stands sampled being replaced or dominated by western juniper.

Conifer expansion into aspen is widespread across the Western United States. In most instances aspen is considered a seral species replaced by more shade tolerant conifers such as Douglas fir (*Pseudotsuga menziesii*), Engelman spruce (*Picea engelmanii*), and sub-alpine fir (*Abies lasiocarpa*) in the absence of disturbance (Mueggler 1985a). Encroachment of these conifers has contributed to a 60% decline in aspen dominated landscapes on National Forests across Utah (Bartos and Campbell 1998). Although western juniper is a drought-adapted conifer, its expansion into aspen is comparable to that of the higher elevation conifers.

Between 1900 to the 1939, juniper encroachment into aspen communities peaked in the Northwest Great Basin with only a few stands being invaded prior to the turn of the century. The periodicity of western juniper encroachment into aspen parallels western juniper expansion across sagebrush steppe regions of the Northwest Great Basin (Miller and Rose 1999) and the pinyon-juniper woodlands in Nevada (Tausch et al.1981). Timing of juniper expansion coincides with changes in fire return intervals, optimal climatic conditions for juniper seed production and establishment, and introduction of livestock (Miller and Wigand 1994, Miller and Rose 1995, Miller 1996).

Disturbance issues

Fire has been reported to be an important factor in facilitating the long-term presence and health of aspen across the landscape (Baker 1925, cited by Bartos and Mueggler 1981; Brown and Debyle 1987; Debyle et al., 1989; Jones and Debyle 1985). European settlement has altered fire regimes through fire suppression, livestock grazing, introduction of exotic plant species and urbanization of the West (Miller and Rose 1996, 1999). Lack of fire is a key factor in the recent expansion of juniper into aspen in the Northwest Great Basin.

Age structure in the Eusabio Ridge (Figure 9) and Fish Creek Rim aspen complex indicated the presence of reoccurring disturbance during the 19th century. These disturbances typically occurred within a portion of these two stands on an average of every 10 and 11 years. Disturbances were most likely stand replacing fires. Romme et al. (1996), found that fire caused total aspen stand replacement of a 77km^{2} study area in 58 years. Fire occurred in their study area nearly every decade from the 1760's to the 1870's. In the Eusabio and Fish Creek Rim aspen complex, western juniper began to appear after the last disturbance event around 80 years ago. The lack of pre-settlement western juniper suggests that aspen stands where void of juniper when fire occurred regularly.

In the Chewaucan region of south-central Oregon, fire scar data reveals that fire intervals ranged from 12 to 15 years prior to 1897, with no scars evident after 1897. Hence, no recorded fire has occurred for a century (Miller and Rose 1999). All aspen sampled for age in the Chewaucan region date to the approximate time of the last largest fire in 1870. Western juniper established about twenty-five years later in the mid 1890's within these aspen communities. With the lack of fire for the past century, Chewaucan aspen stands linger in a state of decline. Established western juniper are on the brink of completely replacing these stands.

Besides the lack of fire, long-term browsing of aspen regeneration by wild and domestic ungulates has also been attributed to the scarcity of aspen recruitment into the stand. Continuous or heavy grazing of sprouting aspen suckers jeopardizes the health, recruitment, and longevity of the stand (Bartos and Mueggler 1981; Bartos et al., 1991; Debyle 1985a; Romme et al., 1995). If regenerating suckers are unable to overcome grazing pressure, then aspen stands cannot sustain viable populations and persist amid the compounding effects of western juniper invasion and replacement. To illustrate, 70% of all aspen stands sampled had no active recruitment. The remaining 30% of aspen stands had active recruitment, but only averaged 143 juvenile trees per hectare (Table 5). Mueggler (1989) suggests that mature or over-mature aspen stands with less than 1,235 suckers per hectare may have regeneration problems. In essence, as adult aspen grow decadent and die in the Northwest Great Basin, densities of juvenile aspen escaping from large ungulate use are not adequate to maintain the stand. We observed terminal leader growth on aspen suckers was usually absent due to browsing across the plots. Lack of regeneration due to excessive ungulate grazing of aspen suckers may allow western juniper to establish and accelerate the successional process to the development of juniper woodlands. Aspen stands that are burned and subsequently sprout high densities of suckers could also be eliminated under heavy grazing pressure regardless of conifer encroachment (Bartos et al., 1994).

Pattern of western juniper encroachment.

The direct correlation between juniper and aspen canopy cover indicates a pattern of juniper encroachment into aspen stands. As aspen canopy cover decreased, juniper canopy cover increased ($p = .0001$). A direct observation of juniper growth rings may demonstrate this correlation. While aspen canopy cover is intact, juniper growth rings are very tight often with 30-40 rings per centimeter. Within the same complex, as aspen canopy cover decreases, individual juniper ring growth increases up to one centimeter for one year of growth. Additionally as aspen become old, aspen canopy cover declines ($p = .0001$) allowing more light to reach juniper in the understory. Thus, aspen decadence may indirectly facilitate an increase in juniper growth. The fact that 75% of aspen stands sampled are greater than 90 years old suggests a decline in aspen canopy cover across the Northwest Great Basin, is likely occurring (Figure 5).

Several environmental factors are related to the degree of juniper encroachment. Elevation had some effect on juniper canopy cover. As elevation increased, juniper canopy cover decreased. Since juniper are limited by upper elevation restraints of severe winter weather conditions and are not typically found above 2,120 m, this correlation was expected (Miller et al. file data). Additionally aspen stands that faced east or south-east had slightly higher densities of juniper than aspen stands that faced north or north-east. Slope, and aspen height did not have any significant effects on western juniper densities or canopy cover. The relationship with elevation and aspect suggest juniper encroachment is more aggressive on the warmer sites.

The above correlations set forth geomorphic and biologic conditions that predispose a stand to juniper encroachment. These symptoms are: 1) Open aspen canopy cover (<70%), 2) Mature to over-mature stands (>90 years), 3) Elevational location below 2,120 m, 4) East or southeast facing stands.

In aspen stands sampled throughout the Northwest Great Basin in which juniper exhibits no influence on the overstory, stand structure is 3,021 aspen trees/ha with a 72% aspen canopy cover. Typically, herbaceous plant cover is 21%. However, in stands that experience co-dominant to dominant juniper in the overstory, aspen density is 1,425 tree/ha with a 20% canopy cover and 11% herbaceous plant cover. Thus, understory vegetation in stands encroached upon by western juniper contrast sharply with the lush, green understory once present. They have higher amounts of bare ground and less herbaceous cover than non-invaded aspen. Although no data are available, lower density of understory vegetation and increased bare ground may be less desirable to wildlife. Studies on wildlife use and diversity in invaded stands verses pure aspen stands are needed.

Effects on soils

Soils influenced by western juniper had a higher carbon to nitrogen ratio and a higher pH than strictly aspen influenced soil (Table 8). A higher carbon to nitrogen ratio, means that there is less nitrogen in the soil. This higher carbon to nitrogen ratio in soils can be attributed to the effect of western juniper litter on soils; juniper litter also has a higher carbon to nitrogen ratio than aspen litter.

Additionally, western juniper probably sequesters nutrients within the tree, not recycling them back into the soil as quickly as aspen. This difference is a result of the deciduous nature of aspen and the coniferous growth form of juniper. Other studies found that aspen leaf litter lost 42% of its weight during the first winter after leaf fall. In comparison, western juniper needle litter lost only 17% of its mass over two years. Aspen also shed approximately 1.4 times more leaves annually than western juniper (Bartos and Debyle 1981, Bates 1996). Thus, aspen produces more litter that decomposes faster than western juniper resulting in a higher rate of nutrient cycling.

In addition to influencing soils, juniper encroachment may impact hydrologic cycles. Western juniper more effectively intercepts rain and snow than does aspen. Additionally, less water occurs in the snowpack under mixed aspen-conifer stands than under pure aspen (Johnston 1971, cited by Debyle 1985b, Debyle 1985b, Larsen 1993). Conifers also use more water per year than aspen (Gifford et al., 1983, 1984; Jaynes 1978, cited by Debyle 1985b). Further study is required to determine the effects and changes in hydrologic cycles in aspen sites overtaken by western juniper.

Management implications

Three-fourths of the aspen communities below 2,133 m elevation in the Northwest Great Basin have either been replaced, are being replaced, or have establishing populations of western juniper. The magnitude of western juniper encroachment demands immediate action. Without active management stands of aspen in the Northwest Great Basin will continue to decline and possibly be permanently lost. Since establishment of aspen from seed is rare under current climatic conditions in the Intermountain Region, stands that are totally replaced by western juniper have likely past a threshold from a deciduous to conifer woodland. Only immediate planning and proactive management will allow for the restoration and maintenance of this resource. Key questions that need further study for stands replaced by juniper are: 1) At what point is an aspen stand beyond the threshold of restoration, and 2) How long will the parent root system stay intact and viable once no aspen trees are present?

Lack of fire since the turn of the century and excessive herbivory on aspen regeneration are two key reasons for western juniper encroachment into aspen. To sustain or reclaim aspen, prescribed fire or allowed natural fire are the best tools for eliminating young juniper and inducing aspen regeneration. In advanced cases, fine fuel levels may be too low to carry adequate fires. Also, high fuel moisture commonly limits fire. These circumstances necessitate cutting western juniper within the stand one year prior to burning in order to use their dried foliage to carry a fire. Additionally, precautions to protect young aspen suckers from excessive herbivory need to be taken. The continued growth in elk populations in the

Northwest Great Basin will likely increase the browsing pressure on young aspen trees. Further studies on the degree and extent of herbivory in aspen stands as well as on effective means of control would help direct management in efforts to maintain aspen communities in the desert landscape.

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