Abstract—Categories of papers in the “Ecological Session” were history and ecological change, distribution, classification, ecology and physiology, succession and diversity, and disease. Substantial changes have taken place in pinyon-juniper woodlands over the past 150 years. Coinciding with and following early extensive localized harvesting, these woodlands have been dramatically expanding and thickening. Several authors predicted future large, severe fires. Ecological research reported included seed dispersal and banks, seedling establishment, and ecophysiological relations of pinyon and juniper. One model presented illustrated the process of increases in tree density and cover and corresponding decreases in understory. This model would explain most of the processes and results reported in the other papers.

I discuss the plenary and poster papers in the “Ecological Session” in six broad and somewhat uneven categories, with considerable interrelations among them: (1) History and Ecological Change, (2) Distribution, (3) Classification, (4) Ecology and Physiology, (5) Succession and Diversity, and (6) Disease. I analyze strengths, weaknesses, and gaps in coverage of the ecology of the pinyon-juniper type in this symposium. Except where noted, all author references here refer to papers in this section of these proceedings, and the reader is encouraged to study the entirety of each paper.

History and Ecological Change

Trends since Pleistocene

Tausch outlined the landscape position held by juniper and pinyon in the Great Basin from the Pleistocene to the present. He emphasized that climatic change influences the key ecological processes that drive vegetation change. Vegetation types such as pinyon-juniper have shifted hundreds of miles north and south and also up and down in elevation during glacial cycles.

The fact that substantial changes have taken place in the pinyon-juniper woodlands in the past 150 years is one of the reasons for this symposium. According to Tausch, this period was characterized by: (1) a warming climate following the Little Ice Age, (2) the period of the heaviest use by European livestock, and (3) a decrease in wildfire frequency. These factors, in combination, enabled trees (juniper and pinyon) to establish in and then dominate new communities, expand to both higher and lower elevations, and, more recently, dramatically thicken in tree densities and canopies of both existing and new stands.

Harvesting After Settlement

Young and Svejcar summarized the history of tree harvesting in the pinyon-juniper woodlands in the late 19th century—harvesting that mainly provided energy for mining, industries, and domestic purposes. All over the Great Basin, use of pinyon and juniper wood for home heating and cooking was widespread until use of fossil fuels became common after World War II.

In the 1860’s, the existing pinyon or juniper trees in the vicinity of large mining operations in Nevada and California were quickly exhausted. The demand for charcoal was so great that deforestation became a severe problem. In Nevada, Young and Svejcar estimated that 4,000 to 5,000 acres of woodland had to be cut annually to supply the Eureka District. By 1874, the mountain slopes around Eureka were denuded of accessible pinyon and juniper for 20 miles, and the average hauling distance from charcoal pit to smelter was estimated to be 35 miles. This 70 mile diameter cutting circle covered about 2.5 million acres of which 0.6 million acres may have been pinyon-juniper woodlands.

On a much smaller scale, Creque and others examined vegetation patterns and change in the past 120 years in the Upper Tintic Valley in Utah. Although their study could not define presettlement conditions, massive harvesting of pinyon-juniper also took place for early mining, domestic, and agricultural activities. Domestic fuelwood consumption from 1870-1900 was estimated to be as much as 74,000 cords. Total woodland harvest in the Tintic Valley from 1870 through 1900 may have been as high as 86,000 ha, with 74,000 cords cut for domestic fuelwood. All of these figures represent the maximum possible wood removed and not all are well documented.

The early period of widespread tree harvesting was followed by the significant region-wide woodland expansion in the recent past (Creque and others). West stated that current conditions are far from the presettlement situation when much more savanna and less woodland and forest existed in the area where relatively dense pinyon-juniper stands now exist.
Role of Fire in Pinyon-Juniper Systems

Gruell studied fire history based on fire-scarred trees in three areas showing a history of repeated fires. Presettlement fire intervals ranged from a mean of 8 years in the Walker River area of Nevada, 13 years at the Hart Mountain and Sheldon Refuges in Oregon, to 50 to 100 years in the Great Basin National Park in Nevada. In the past, fires occurred more frequently on deeper soils which produced an abundance of fine fuels. Less frequent fires were found on shallow soils and rocky sites which produced less fine fuel.

Gruell concluded that presettlement fires were common in the pinyon-juniper woodlands of the Great Basin. This fire regime was dramatically altered after settlement because of fire suppression and of heavy grazing, which removed fine fuels. This has resulted in increased density and crown cover of pinyon-juniper along with a more recent buildup of ground fuels. This has resulted in a shift from more frequent, low intensity, small fires, to less frequent but larger, high intensity fires. Gruell contended that “considering the extent of the fuel buildup, severe fires in the Great Basin will continue and perhaps become more frequent.” West also stated that “The future holds increased probability of crown-fires, invasion by introduced annuals and short-lived perennials, and then repeated burning and permanent site degradation unless seeding of desirable understory takes place expeditiously.” Tausch predicted the same future scenario.

Distribution

Area Covered by Pinyon-Juniper

Estimates of total area covered by pinyon and juniper varied considerably in the papers in the symposium. Some, but not all, of the discrepancies are because of differences in area considered.

<table>
<thead>
<tr>
<th>Author</th>
<th>Acres</th>
<th>Area Considered</th>
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<tbody>
<tr>
<td>West</td>
<td>75 million</td>
<td>SW U.S. and Mexico</td>
</tr>
<tr>
<td>Nowak and others</td>
<td>74 million</td>
<td>Not specified</td>
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<tr>
<td>Weber and others</td>
<td>99-124 million</td>
<td>SW U.S.</td>
</tr>
<tr>
<td>Horman &amp; Anderson</td>
<td>60 million</td>
<td>Nevada, Utah, Colo. New Mexico, Arizona</td>
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<tr>
<td>O’Brien &amp; Woudenberg</td>
<td>45.3 million</td>
<td>Intermountain West</td>
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<tr>
<td>Bunting and others</td>
<td>42 million</td>
<td>NW Great Basin &amp; S. Columbia Basin</td>
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Mitchell and Roberts probably reported the most accurate figures, based on satellite imagery. They estimated that pinyon-juniper covered 55.6 million acres in the entire Western United States.

Altitudinal Distribution

Drought and frost during the growing season limits distribution of pinyon-juniper woodlands to relatively narrow altitudinal belts on the sides of mountains. In western Utah, Harper and Davis found that elevation of pinyon-juniper sites on granite averaged 1,926 m while those on sandstone averaged 1,341 m. Lei reported pinyon-juniper woodland occupied the area from approximately 1,250 to 2,600 m in elevation in southern Nevada. West stated that pinyons are less tolerant of drought and early spring frosts than junipers and usually dominate the middle elevations while juniper tend to dominate both the higher and lower elevations of the woodland belt.

Nowak and others reported that juniper has greater drought tolerance and that pinyon is more responsive to increased water and nitrogen. Lei studied the environmental variables of a pinyon-juniper woodland along an elevational gradient in a canyon in southern Nevada. Four primary species groups were identified with increasing elevation: blackbrush, big sagebrush, singleleaf pinyon, and ponderosa pine. Species distribution was associated with elevation, soil moisture, air temperature, percent bare soil and rock cover, and soil depth.

In contrast to these reported results and published elsewhere, West and others reported that in the western part of the pinyon-juniper range, pine dominates or is the only tree in the upper elevations of these woodlands. (West N. E., Tausch, R. J. and Tueller, P. T. 1998. A management-oriented classification of pinyon-juniper woodlands of the Great Basin. Gen. Tech. Rep. RMRS-GTR-12. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.)

Classification

Tausch stated that “The understory is central to understanding the ecology and ecosystem function of a site.” Within the Great Basin, pinyon-juniper woodlands represent multiple communities and ecosystems that are better identified by the understory species. This complexity is increased and often obscured by successional stages of each community. West stated that juniper-pinyon savannas and woodlands have understories that are floristically and structurally more variable than the overstory. Generally, the understory is compositionally similar to that of adjacent grasslands, shrub steppes, chaparral, and forests.

Classification Systems

Winward reported that, because of the complex geology and terrain, past climatic fluctuations and human disturbances, past attempts at classification of pinyon-juniper communities have only been marginally successful. He proposed the following step-down (hierarchical) classification:

Geographic Units (as homogeneous as possible)
- Series-Level based on dominant tree species
  - Associations based on a dominant understory shrub species
  - Sub-Associations based on prominent herbaceous species

West and others (cited earlier in this paper) published a hierarchical approach to classification of pinyon and juniper woodlands that appears similar to, but perhaps more comprehensive than, the one presented in the proceedings by Winward.
Rust used a similar system to classify pinyon-juniper woodlands on 12 research natural areas in southeastern Idaho. He identified four series: singleleaf pinyon, Rocky Mountain juniper, Utah juniper, and curl-leaf mountain-mahogany. Within these series he described 23 plant associations based on differences in understory species.

Forest Inventory

About 40 percent of the 45.3 million acres of the pinyon-juniper and juniper woodlands in the Intermountain West occur in Nevada and Utah (O’Brien and Woudenberg). Net volume of wood was estimated at more than 10 billion cubic feet or about 137.5 million cords. About 53 percent of the woodland stands in Utah and 67 percent in Nevada were estimated to be between 40 and 120 years old. Only 20 percent of stands in Utah and 9 percent in Nevada are more than 200 years old.

Ecology and Physiology

Seed Dispersal of Pinyon and Juniper

Chambers and others studied seed dispersal and seedling establishment of pinyon and juniper species. Birds disperse pinyon seeds a distance of several meters to 5 km. Some birds and rodents make caches of pinyon seeds, which are important sources of new tree seedlings. Many mammals consume and disperse juniper seeds including rodents, rabbits, predators, deer, and livestock. All pass some seeds intact, which can enhance germination.

Chambers and others found that pinyons have relatively short-lived seeds that form only temporary seed banks. Junipers have a rather continuous seed bank because of long-lived seeds with germination being delayed by impermeable seed coats, immature or dormant embryos, or germination inhibitors. Pinyon seedlings often require a nurse plant to survive, while juniper seedlings survive in open spaces almost as well as under the canopy of shrubs or trees. Areas under shrubs and trees often have higher concentrations of nutrients and organic matter and higher infiltration rates, making microenvironmental conditions favorable for many conifers. Ecotones between woodlands and adjacent shrublands or grasslands often provide favorable microhabitats for seedling establishment. Over time, and without periodic fires, this process would help to explain the expansion of the boundaries of pinyon-juniper woodlands in many areas.

Seed Banks of Non-Tree Species

Poulsen and others studied the soil seed bank of all species in pinyon-juniper sites in central Utah ranging from closed stands with minimal understory to open stands with excellent understory communities. As tree cover increased, the numbers of understory species and seeds in the soil seed bank decreased. The composition shifted from perennial grasses and shrubs in the moderately depleted and nondepleted understories to annuals and perennial forbs in the depleted understory.

Ecophysiological Patterns of Pinyon and Juniper

Nowak and others examined the ecophysiological patterns of pinyon and juniper and found that these trees generally are conservative in their acquisition and use of resources. Maximum assimilation and conductance rates and tolerance to severe water stress are considerably less for pinyon and juniper than for sagebrush. These conservative ecophysiological traits of pinyon and juniper do not, in themselves, provide for success but may benefit the conifer species by enhancing establishment and growth under nurse plants. The relatively low nutrient content per unit of foliage may allow the conifers to produce more foliage biomass per unit of ground area than sagebrush. These traits coupled with greater longevity allow the conifers to establish under nurse plants and then grow and ultimately outsize and outlive the shrub competitors.

Succession and Diversity

Relation of Tree Density to Species Diversity

The development of mature pinyon and especially juniper woodlands has often resulted in decreases in the herbaceous and shrub understory components. Bunting and others studied the effects on species richness caused by thickening of Western juniper stands and encroachment onto deeper soils in the northwestern portion of the Great Basin. Development of Western juniper woodland vegetation resulted in reductions of shrub and herbaceous plant cover and species richness. Many perennial herbaceous species were associated primarily with early to mid-seral communities and not found in the late seral communities dominated by trees. Maximum landscape species richness and species diversity would occur when all structural and seral stages are represented within a watershed. This emphasizes the need to reintroduce or include smaller scale disturbances, such as fire, as a process in landscape dynamics.

In northeastern Utah, Huber and others also found that both alpha and beta diversity were highest in seral communities where pinyon and juniper canopy cover did not exceed 20 percent. In woodland communities where canopy exceeded 30 percent, both understory cover and diversity were severely depressed.

Overstory/Understory Relationships

Miller and others presented a model of the conversion of shrub steppe to juniper woodlands in the absence of fire in eastern Oregon and northeastern California. Perennial forb/grassland and shrub steppe communities are fire driven systems. During the early stages of tree establishment, the transition is reversible, mainly by fire. Shrub die as the woodlands approach mid development, which decreases the probability of a fire intense enough to kill the large juniper trees. By the mid to late stages of this transition, a threshold is crossed where reversal to a shrub steppe community is unlikely (See figure 2 in Miller and others).
Crossing the mid to late development threshold often is characterized by a loss of native herbaceous species, possibility of dominance by alien annuals, the potential loss of surface soil, and the loss of habitat for many wildlife species, which are abundant in the shrub-steppe communities. Tausch discussed other thresholds important to the understanding of woodland dynamics. The relationships illustrated in the Miller and others’ model help explain the results of many of the papers in this session. The model also would be quite helpful in evaluating potential resource problems, determining wildlife habitat values, and setting realistic goals and time frames for management. Svejcar, in the “Management Implementation Session,” also suggested that state-and-transition models be developed for pinyon-juniper systems.

Horman and Anderson studied the effects of removal of juniper tree canopy and litter on the understory in Utah. In undisturbed woodlands, cover, understory plant abundance, and seedling emergence were quite low but were higher in the under the tree canopy than in the interspaces. Canopy removal decreased plant abundance and seedling emergence in the canopy zone but had no effect in the interspace. Litter removal had no significant effect on perennial species. This study was conducted only for 3 years, possibly too short a time for the effects of canopy removal to become evident. More likely, this site had crossed the threshold referred to by Miller and others, and the understory had lost the ability to respond to the canopy removal.

Naillon and others studied the relation of understory species frequency between canopy and interspaces between trees at different tree densities. As tree density increased, associated herbaceous cover and species diversity decreased. Sandberg bluegrass had higher frequency values under tree canopy than in the interspace at low tree densities. No difference occurred at high tree densities. At all tree densities, cheatgrass frequency values were higher under the canopy than in the interspaces.

### Alien Annual Species in the Understory

Goodrich and Gale studied frequency of cheatgrass (*Bromus tectorum*) on two relic sites within a pinyon-juniper belt in northern Utah. The sites were protected by cliffs and steep slopes and probably had little or no historic livestock use. One area had burned about 80 years ago and the other had an open stand of trees even though it had not burned in the past 150 years. Cheatgrass was by far the dominant understory species on both sites. Its abundance indicates a capacity to drive plant community dynamics both after fire and in areas that had not recently burned, and even in areas where human and domestic livestock activities have been low. They concluded that the concept of potential natural communities based on only native species is seriously challenged by the dynamics of cheatgrass. Refusing to recognize cheatgrass within the site potential will not reduce its presence nor its potential to dominate a community. Tausch reported that the dominance of cheatgrass represents a recognizable threshold in pinyon-juniper woodlands.

Svejcar, in the “Management Implications Session,” also discussed the invasion of cheatgrass and other weeds in disturbed areas. If a good cover of perennial species exists before disturbance, cheatgrass and other weeds often are not a problem. If considerable annuals are present, they likely will dominate the site after a disturbance, and seeding of adapted species may be required (Tausch). A state-and-transition model, including situations with presence and absence of cheatgrass and other annuals, would help managers make more informed decisions.

Jones and others studied drought tolerance of small burnet (*Sanguisorba minor*) and six cultivars of alfalfa (*Medicago sativa*), two nonnative species that might be suitable for planting on specific sites. Small burnet was more drought tolerant than alfalfa.

### Changes Over Time in Mature Stands

While large changes have occurred in areas where trees have invaded or thickened, re-surveys of mature pinyon-juniper stands reported in this session showed little change, at least over relatively short periods. Austin found little change over 23 years (1974 through 1997) in trees, shrubs, grasses, or forbs in a mature pinyon-juniper community in northeastern Utah. In a relict area in Grand Canyon National Park, Brian and others found only slight changes in a mature pinyon-juniper woodland over 38 years (1958 through 1996).

### Disease

Only two papers dealt with diseases of pinyon and juniper. Weber and others reported that a number of pathogens occur on *Pinus edulis* and *Juniperus osteosperma*. The most frequent pathogens on junipers are rust fungi. Mistletoe is more common on pinyon than juniper but occurs on both species. Mold/mildew diseases, wood rot, needle blight, shoot dieback and needle cast are common in juniper.

In southern Nevada, Lei found that taller Utah juniper trees were more likely to be infected by parasitic mistletoe than shorter trees. Mistletoe significantly reduced leaf water potentials, vigor, viability, and reproductive success of the host tree.

### Discussion

Substantial changes have taken place in pinyon-juniper systems over the past 150 years. Tausch provided the historical basis for the Ecological Session by pointing out that this period was characterized by a warming climate, heavy livestock grazing, and a decrease in fire frequency. After the early exploitation of these woodlands for wood, these factors enabled pinyon and juniper to establish and then dominate new communities as well as thicken in existing stands. Young and Svejcar summarized the heavy tree harvesting for industrial and domestic purposes since 1900 before the current expansion and stand thickening.

Gruell provided evidence of pre- and postsettlement fire history for three areas. This type of research needs to be repeated all over the Great Basin and other areas where pinyon-juniper woodlands now exist. Gruell, West, and Tausch indicated that large severe fires covering large areas in the future will be the result of crown closure or fuel buildup.
The greatest lack of agreement among authors concerned the total area covered by pinyon-juniper woodlands. Figures presented ranged from 45 million to 120 million acres. The 55.6 million acre figure of Mitchell and Roberts probably was the most accurate because it was developed from satellite imagery.

Tausch stated that the understory is key to the understanding of the ecology and ecosystem function in pinyon-juniper woodlands. The hierarchical classification systems of Winward, Rust, and West and others (cited previously) start with some large geographic unit, then to the dominant tree species, and only then to the dominant shrub and herbaceous species. If the understory is, indeed, the key to understanding pinyon-juniper systems, then classification systems need to recognize that fact in a more positive manner.

Ecological and physiological research reported in this symposium that should lead to a better understanding of how pinyon-juniper woodlands function included seed dispersal and seedling establishment mechanisms of pinyon and juniper, understory seed banks, ecophysiological mechanisms of pinyon and juniper species, and species diversity at different seral stages. The papers by Miller and others and Tausch probably provided the most useful synthesis of the processes involved in the conversion of shrub steppe to juniper woodland. Miller and others suggested a model showing increase in tree density and corresponding understory changes. If a system crosses a threshold of tree cover and density, the process cannot be reversed, and the site becomes a woodland. This model explains the results of a great many papers in this session and should be read by anyone interested in the ecology or management of pinyon-juniper. Svejcar, in the "Management Implications Session," recommended that one or more state-and-transition models be developed for pinyon-juniper systems. The model proposed by Miller and others along with the thresholds defined by Tausch, could be developed into a state-and-transition model.

The Goodrich and Gale paper also is quite important to the understanding of the ecology of pinyon-juniper woodlands as well and many other ecosystems. They found that an alien species, cheatgrass, was the dominant species on two pinyon-juniper stands in Utah that had little or no historic disturbance by livestock or humans and 80 to 150 years since the last fire. They pointed out that a prevalent concept in management is that preservation of native plant communities will prevent or eliminate cheatgrass (and perhaps other alien annuals). This is not consistent with reality in many situations. If a woodland with an understory dominated by cheatgrass burns, the site then is dominated by cheatgrass and other annuals. Because such sites may re-burn every 3 to 5 years (West and others), they often are permanently converted from a woodland to an alien grassland. Thus, the domination of cheatgrass is a recognizable and important threshold in these woodlands (Tausch).

Similar management concepts, such as those that permit seeding of only native species in severely disturbed pinyon-juniper stands, likewise may be questionable. Site adapted native species are not available in sufficient amounts to adequately restore extensive disturbances. To prevent erosion and keep alien annuals from invading, adapted, drought-tolerant introduced species often will be required to stabilize disturbances until suitable native species become available. In this situation, it seems ecologically undesirable and economically unwise to insist that only native species be seeded. This is especially true if rather large areas have to be seeded to prevent erosion or cheatgrass invasion following extensive wildfires, and if the large sums of money required to purchase expensive native seed are not available.