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PINYON-JUNIPER WOODLANDS IN ZION NATIONAL PARK, UTAH

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ABSTRACT.—*Juniperus osteosperma–Pinus monophylla* or *P. edulis* (P-J) woodlands are the most widespread plant community in Zion National Park (ZNP), southwestern Utah. These woodlands dominate nearly half of the park's land area. Our study of this vegetational complex is based on a sample consisting of 115 macroplots (each 0.01 ha in area) objectively distributed across the entire area of ZNP. We recognize 3 subtypes within the P-J complex: *Juniperus osteosperma* (Utah juniper) alone, juniper with *P. monophylla* (single-leaf pinyon), and juniper with *P. edulis* (two-leaf pinyon). The 2 pinyon pines rarely occur together, and thus the foregoing subtypes do not overlap geographically to a significant extent. The first 2 subtypes occur primarily below 1800 m elevation, while the latter is most commonly found above that elevation. Because of the scarcity of sizable expanses (over ~10 ha) of well-developed soils in ZNP, the P-J complex occurs primarily on sites where exposed bedrock covers a large portion of the habitat. As a result, over 90% of stands assigned to the P-J complex support less than 50% tree canopy cover (64% have less than 25% tree cover). Shrub cover increases along the woodland successional gradient. Pinyon cover increases faster than juniper cover. Microbiotic soil crust cover is consistently greater in *J. osteosperma–P. monophylla* woodlands than in *J. osteosperma–P. edulis* woodlands, but total living cover increases significantly along the successional gradient in both communities. To enhance plant and animal biodiversity, we recommend that pinyon-juniper woodlands of Zion National Park be managed so that late seral stages do not dominate large tracts.

Key words: habitat types, management, woodland, Juniperus osteosperma, Pinus edulis, Pinus monophylla.

Pinyon-juniper woodlands dominate more than 30 million ha in the western United States (West 1999), making this vegetational type one of the most widespread plant communities in western North America. Pinyon-juniper woodlands are also the most common vegetation type in Zion National Park (ZNP) and across southern Utah. The study area is in the Virgin River basin lying just outside the Great Basin. Within ZNP, pinyon-juniper woodlands cover 46.5% of the total area (Harper 1993). Woodlands in the park are composed of *Juniperus osteosperma* (Torr.) Little (Utah juniper) and *Pinus monophylla* Torr. & Frem. in Frem. (single-leaf pinyon) or *P. edulis* Englem. (two-leaf pinyon). Bailey (1987) segregated single-leaf pinyon into multiple taxa. Under Bailey's classification system, the pinyon of ZNP would be *P. californiarum* D. K. Bailey. Although Langer (1996) reported that *P. californiarum* occurred in southwestern Utah, we have retained the commonly used classification of a solitary single-leaf pinyon (*P. monophylla*) for this study.

Successional studies conducted elsewhere show decreasing species richness as these woodlands approach maturity (West 1984, Everett and Ward 1984, Miller et al. 2000). Tree and shrub species tend to become more dominant as stands age and total vegetative cover increases (Everett and Ward 1984). Mature woodlands are dominated by pinyon and juniper in the canopy with little herbaceous cover in the understory (Tress and Klopatek 1987, West and Van Pelt 1987, Miller et al. 2000). Should wildfire remove pinyon-juniper woodland, bare soil is exposed, resulting in the potential for severe soil erosion. Secondary succession is initiated by the invasion of annual plants and sprouting perennials which may be uncommon in these woodlands (Koniak 1985, Goodrich 1999). Annuals may eventually be displaced by perennial grasses and forbs. Shrubs tend to increase on such sites. Eventually juniper, followed by pinyon, establishes among the shrubs. Ultimately, the site may become a mature pinyon-juniper woodland again, provided alien weeds have not severely shortened the fire-return cycle (Arnold et al. 1964, Erdman 1970). Sites that are reburned after an initial fire often become dominated by

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alien annuals such as cheatgrass (*Bromus tectorum* L.; Goodrich 1999). This stage may be bypassed depending on the amount of understory cover of sprouting perennial herbs or shrubs prior to the initial fire. Successful revegetation of newly burned sites with appropriate perennial species also may preclude dominance by alien annuals (Everett and Ward 1984, West and Van Pelt 1987). Gambel oak (*Quercus gambelii* Nutt.) and other shrubs that are associates of juniper and pinyon on some sites sprout profusely after fire (Floyd et al. 2000). Such sprouts both stabilize soil at the site and hasten the rate at which juniper and pinyon reinvade (Floyd 1982). Gambel oak is an associate of pinyon-juniper in many stands in ZNP.

Pinyon-juniper woodlands support a great variety of wildlife. Mule deer (*Odocoileus hemionus*) are perhaps the most important game animal of the woodlands (Evans 1988). Deer use both juniper and pinyon foliage sparingly, but shrubs and perennial herbs in the understory provide palatable and nutritious forage for them. *Purshia tridentata* (Pursh) DC (antelope bitterbrush), *Cercocarpus montanus* Raf. (birchleaf mountain mahogany), *Purshia mexicana* (D. Don) Welsh (Stansbury cliffrose), and *Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle (mountain big sagebrush) are representative of palatable shrubs for deer in the woodlands (Welch and McArthur 1986, Evans 1988). All of these shrubs occur in some pinyon-juniper woodlands in ZNP. Elsewhere in Utah elk (*Cervus elaphus*) also make considerable use of these woodlands in winter. Larger mammal predators in the woodlands include mountain lions (*Felis concolor*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and badgers (*Taxidea taxus*). Populations of rabbits (*Lepus* and *Sylvilagus* spp.), mice (*Onychomys, Microdipodops, Dipodomys,* and *Peromyscus* spp.), voles (*Microtus* spp.), ground squirrels (*Citellus* spp.), woodrats (*Neotoma* spp.), and porcupines (*Erethizon dorsatum*) also reside in the woodlands. Over 50 species of birds nest in this community type (Balda and Masters 1980, Webb 1999). Paulin et al. (1999) found that pinyon-juniper woodlands are essential for nesting success of 31 species of birds in northeastern Utah. By way of comparison, these authors ascertained that riparian ecosystems are essential for successful reproduction of 49 avian species. Two other ecosystems essential for reproduction of many bird species are ponderosa pine and trembling aspen forests, which are primary reproductive environments for 42 and 38 species, respectively. Some birds aid in dispersal of seeds of both juniper and pinyon, but all feed on insects during the nesting season (Evans 1988). A herd of desert bighorn sheep (*Ovis canadensis*) has been reintroduced into ZNP; they utilize watering sites in the woodlands and forage in more open stands that occur adjacent to steep, barren rock outcrops (Smith and Flinders 1992).

Moir and Carton (1987) separate pinyon-juniper woodlands into several different habitat types. They recognize 70 plant associations and 230 ecological site types within these woodlands in western North America. They base these habitat types, in part, on climatic and elevational subzones. West et al. (1998) provide a classification of Great Basin pinyon-juniper woodlands based on the relative composition and dominance of these species as well as dominant shrub and perennial grass species. Another study of pinyon-juniper woodlands on the Manti–La Sal National Forest of central and southeastern Utah classifies pinyon-juniper woodlands into habitat types based on understory characteristics of mature woodlands (Thompson 1999).

The objective of this study was to characterize the pinyon-juniper woodlands of ZNP. Our characterization emphasizes the values of various vegetation assemblages for wildlife habitat, proposes the existence of 9 principal habitat types, and provides some management options.

METHODS

Sampling Vegetation

This report is part of a larger survey of all vegetational types within ZNP. The original survey uniformly sampled 309 section corners and ancillary sites of 0.01-ha circular study plots (Fig. 1; Harper 1993, Harper et al. 2001). Ancillary sites are those areas of ZNP where section lines were projected across rugged, unsurveyed areas on 7.5-minute quadrangle topographic maps to locate sampling points and additional sites from plant communities of limited geographical area (Harper 1993, Harper et al. 2001). Botanical nomenclature follows Welsh et al. (1993). Results for pinyon-juniper woodlands are based on the following 115 study plots (Table 1) that had a minimum of ≤1%

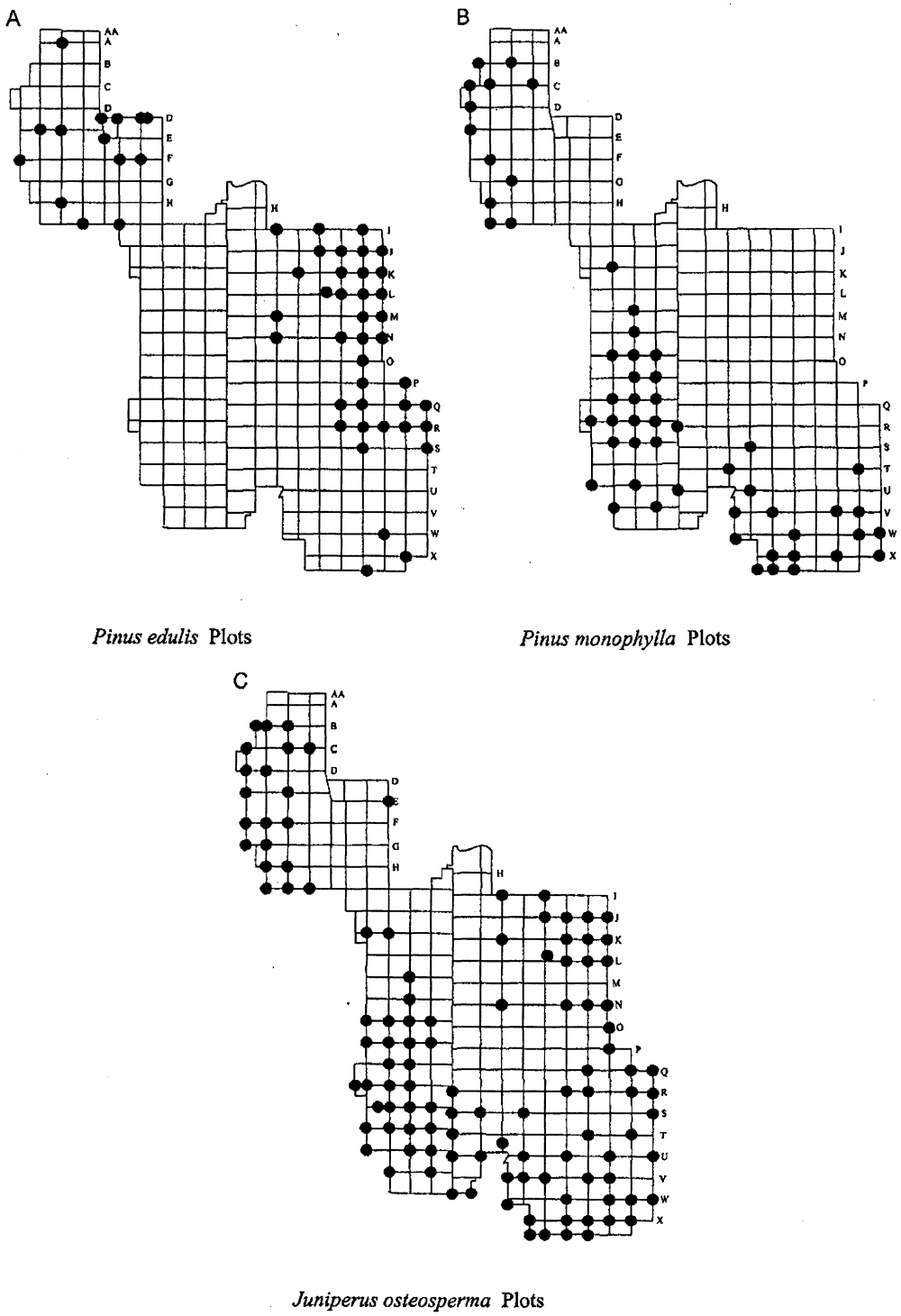

Fig. 1. Occurrence of *P. edulis* (A), *P. monophylla* (B), and *J. osteosperma* (C) in the macroplots taken at section corners in Zion National Park.

TABLE 1. Environmental and vegetational characteristics of 3 community types in the P-J woodlands sampled in ZNP. Standard errors appear in parentheses next to the means wherever possible.

Characteristic	Community type		
	Juniperus osteosperma	*Pinus monophylla*	*Pinus edulis*
Sample size (macroplots)	19	58	38
Elevation (m)	1601 (66.0)	1578 (28.1)	1926 (20.8)
Slope steepness (%)	33.8 (7.0)	35.1 (2.9)	41.7 (3.7)
Direct solar radiation/yr (pot. lanleys/cm²/yr)	298.9	305.5	249.0
Topographic shading index[a]	1.4	1.4	1.4
Cover			
Living (%)	58.1 (7.97)	60.2 (4.42)	61.8 (5.38)
Bare soil (%)	28.7 (4.3)	24.6 (2.7)	18.9 (2.4)
Litter cover (%)	25.4 (4.4)	29.5 (2.6)	46.2 (4.0)
Vegetational composition (% total cover)			
Trees	28.8	31.4	38.2
Shrubs	43.5	37.4	50.0
Herbs	8.3	9.4	4.4

[a]A value of 1 represents a flat surface with no topographic shade during the day. A value of 4 represents a site at which direct sunlight reaches for less than 4 hours per day.

pinyon-juniper cover: 38 study plots that fell on habitat dominated by *J. osteosperma* and *P. edulis*, 58 plots that were dominated by *J. osteosperma* and *P. monophylla*, and 19 plots that had neither pinyon but did have *J. osteosperma*. Two study plots supported both *P. edulis* and *P. monophylla* and were analyzed as part of the samples for both pinyon-juniper types. This subset of Figure 1 plots is representative of the 3 principal pinyon-juniper community types (*J. osteosperma* and *P. edulis*, *J. osteosperma* and *P. monophyla*, and *J. osteosperma* alone as the dominants). The higher number of plots in Figure 1 includes all plots of the larger study (Harper 1993, Harper et al. 2001) that include pinyon and juniper regardless of cover criteria.

In each sample plot we surveyed vegetation using a procedure developed by the Zurich-Montpellier school of phytosociology (Braun-Blanquet 1932). We recorded all species rooted within the plot and assigned them a cover value based on an ocular estimate. Living cover and cover of litter and rock were estimated independently and often overlapped; thus, their sum sometimes exceeded 100%. A sociability index (the degree to which individuals of a species are clumped in space) was also assigned to each recorded species. For each macroplot we recorded the Universal Traverse Mercator Grid location and photographed the plot using color print film. Elevation, aspect, slope, and geologic parent material were recorded for each study plot. We also observed each plot for evidences of prior use by humans and attempted to classify site condition (intensity of previous disturbances and resultant damage to the system) and trend (recovering or continuing to deteriorate) for each plot. Direct solar radiation estimates were made using tables compiled by Frank and Lee (1966), which consider slope steepness, aspect, and latitude of a site.

Soil Sampling

Scientists from the U.S. Department of Agriculture, Natural Resource Service Conservation Service, have classified soils in the region covered by this study (Mortensen et al. 1977). We took soil samples from 3 pinyon-juniper study plots of vegetational composition considered to be near average for ZNP pinyon-juniper sites. Soil samples were analyzed for important physical and chemical characteristics by the Soil and Plant Analytical Laboratory, Department of Agronomy and Horticulture, Brigham Young University, using standard procedures outlined by Horowitz (1980) and Brady and Weil (1996).

Analysis of Vegetation

Vegetational data in this study are based on prevalent species only. Curtis (1959) proposed that the number of prevalent species recognized for a community should equal the average number of species per study macroplot placed in that community. This number is called species density. In our study we identified prevalent species by arranging all species encountered in the community in decreasing order of percent occurrence in the study plots.

TABLE 2. Prevalent species of *J. osteosperma*, *P. monophylla/J. osteosperma*, and *P. edulis/J. osteosperma* community types. Modal prevalents in each community are marked with an asterisk, and names of introduced species are followed by (I). Species are prevalent in communities where frequency of occurrence is in italics.

Species	Community type		
	Juniperus osteosperma	*Pinus monophylla*	*Pinus edulis*
	% of occurrence		
Amelanchier utahensis Koehne	41	56	84*
Astragalus L. sp.	*41*	14	19
Arctostaphylos patula Greene	18	26	59
Arabis perennans Wats.	*47*	*60**	*49*
Aristida purpurea Nutt.	*24*	12	0
Artemisia tridentata Nutt.	35	30	14
Artemisia ludoviciana Nutt.	*24*	19	8
Bromus rubens L. (I)	*41*	26	3
Bromus tectorum L. (I)	*71*	*54*	*38*
Carex rossii F. Boott	6	4	*30*
Cercocarpus montanus Raf.	0	9	*43*
Chaenactis douglasii (Hook.) H. & A.	6	14	*27*
Chrysothamnus nauseosus (Pallas) Britt.	29	5	11
Cryptantha Lehm. species (annual)	35	39	11
Descurainia pinnata (Walter) Britt.	18	25	8
Draba verna L.	29	28	8
Elymus elmoides (Raf.) Swezey	*47*	23	19
Erigeron utahensis Gray	29	33*	19
Eriogonum davidsonii Greene	*24*	21	16
Erysimum asperum (Nutt.) DC	18	23	*30*
Euphorbia albomarginata T. & G.	12	2	22
Fraxinus anomala Torr. ex Wats.	12	*32*	22
Gilia inconspicua (J. E. Sm.) Sweet	53	*49*	*43*
Gutierrezia sarothrae (Pursh) Britt. & Rusby	*35*	*42*	22
Haplopappus scopulorum (Jones) Blake	0	18	22
Hilaria jamesii (Torr) Benth.	*41*	*30*	3
Juniperus osteosperma (Torr.) Benth	*94**	*86*	*76*
Opuntia macrorhiza Engelm.	*41*	*46*	*59**
Pachystima myrsinites (Pursh) Raf.	6	2	*27*
Phlox austromontana Cov.	12	11	22
Pinus edulis Engelm.	0	4	*100**
Pinus monophylla Torr. & Frem. in Frem.	0	*100**	5
Poa fendleriana (Steudel) Vasey	*47*	*68*	*73*
Purshia tridentata (Pursh) DC	6	5	*35*
Quercus gambelii Nutt.	18	*25*	*57*
Quercus turbinella Greene	*29*	*35**	14
Senecio multilobatus T. & G.	6	*26*	*65*
Shepherdia rotundifolia Parry	*24*	18	0
Stipa hymenoides R. & S.	*47*	*23*	*38*
Stipa speciosa Trin. & Rupr.	*24**	16	0
Streptanthus cordatus Nutt. Ex T. & G.	12	*32*	*41**
Swertia albomarginata (Wats.) Kuntze	*24*	11	0
Symphoricarpos oreophilus Gray	0	5	*24*
Tradescantia occidentalis (Britt.) Smyth	*24*	9	3
Vulpia octoflora (Walter) Rydb.	*47*	*40*	16

Prevalent species were then selected from the top of the species list in a number equal to species density. In cases where the last species on the species density list had a percentage frequency value equaled by several other species in the community, we listed those species as prevalent (Table 2). As a result, the number of prevalent species listed for a community may exceed the species density value for the community. In the pinyon-juniper communities of ZNP (including all plots dominated by either juniper or pinyon or both), prevalent species represented about 27% of all species encountered in the entire pinyon-juniper sample.

Nevertheless, prevalent species accounted for over 57% of all species occurrences in the sample.

Modal species, as defined by Curtis (1959), are also identified for the 3 pinyon-juniper communities. Modal species reach maximum regional abundance in the community type of concern. We computed indices of homogeneity and distinctiveness for each of the pinyon-juniper (P-J) community types as suggested by Curtis (1959). The index of homogeneity is computed by dividing the sum percent presence of prevalent species by the sum percent presence of all species encountered in the study plots. This index shows how similar the flora of one study plot is likely to be to that of another in the same community. The index of distinctiveness is computed by dividing the number of modal species in a community by the number of prevalent species in the same community and expressing the quotient as a percentage. This index shows the proportion of prevalents that achieve maximum regional abundance in the community of concern. Communities having a high distinctiveness value have many species that reach maximum regional commonness in that community. Since genetic diversity in a species is usually tied to its abundance, communities having large values of distinctiveness can also be expected to be rich reservoirs of genetic diversity (Wright 1931, Dobzhansky 1951, Harper et al. 2001).

A similarity matrix was constructed for the 3 pinyon-juniper types in ZNP. The percent presence values for component species is used to calculate percent similarity between communities. To express similarity we used the Ruzicka index (Ruzicka 1958). This index is computed by dividing the summation of the minimum percentage presence values for all prevalent species by the summation of maximum percentage presence values for all prevalents in the 2 communities being compared and expressing the quotient as a percentage.

Analysis of Secondary Succession

Seral status of each macroplot was assigned based upon tree canopy cover on the plot. Plots having 0–25% tree cover were designated as early seral, those with 25.1–50% tree cover as mid-seral, and those with 50.1% or more tree cover as late seral plots. We recognize that our assignment of successional position to individual stands is arbitrary and may be influenced by site quality as well as by autogenic processes induced by pioneer species over long periods of time. Trees in some stands were clearly very old and showed no evidence of recent fire- or human-related disturbances, but because of rocky substrates, living cover was sparse (<25%). Other stands with trees of comparable apparent age may show evidence of heavy use by domestic grazers and/or localized logging or burning induced by lightning strikes. In these cases stand age could be great, but autogenic processes may have had little impact on associated species. We finally decided that amount of tree cover alone is perhaps the best indicator of autogenic successional processes for our purposes. Our observations convinced us that, given a more-or-less complete soil cover across the surface of sites within ZNP, juniper and/or pinyon trees would invade the site and eventually develop canopy cover over most of the surface. Such encroachments are often slow and require long time periods (many decades) on more arid sites and/or very fine-textured soils. On sites with great amounts of exposed bedrock, vegetation may be confined to crevices and be unable to develop enough canopy to overshadow more than a few percent of the site's surface area. Dense tree canopies rather than age of tree stands or absence of disturbance thus seem most likely to control autogenic vegetation changes customarily considered to be associated with forest succession in the P-J woodlands.

Regression analyses and group comparison tests were used to determine which vegetational characteristics were correlated with seral stage in each community type (Steel and Torrey 1960).We computed the average performance of various prevalent species and vegetative parameters for each seral stage (early, mid-, and late) to discover in which stage a species or vegetative characteristic could be expected to perform best.

Recognition of Vegetational Subtypes

Plots for these community types were assigned to different habitat types based on criteria similar to those used by Stuever and Hayden (1996), West et al. (1998), and Thompson (1999). Characteristics of geologic substrate,

vegetation, and inferred climate are described for each habitat type recognized.

RESULTS

Abiotic Environment

Environmental and vegetational data for the 3 community types recognized are given in Table 1. Average elevation (1926 m) of the *P. edulis* type is significantly higher than that recorded for *J. osteosperma* and *P. monophylla* communities (1601 and 1578 m, respectively). As has been found in P-J stands elsewhere (Lanner 1981), *P. edulis* is restricted to higher elevation plots, while *P. monophylla* and *J. osteosperma* are dominant trees at lower elevations. Our *P. monophylla* plots did not, however, occur at intermediate elevations between juniper and *P. edulis* as reported by Lanner (1974) and Gafney and Lanner (1987). Our data show no significant difference in elevation between plots co-dominated by *P. monophylla* and *J. osteosperma* and plots dominated by *J. osteosperma* alone. *Pinus edulis* plots receive less direct solar radiation than the other 2 community types, since most of them are located on north-facing slopes. All 3 community types have equivalent topographic shading indices (1.4); thus, shading from surrounding landscape prominences is of brief to moderate duration at all sites.

The three P-J community types differed in respect to their proportional occurrences on various geologic substrates (Table 1). *Pinus monophylla* and *J. osteosperma* stands occur primarily on sandstone (*P. monophylla*, 36% Keyenta, 20% Navajo, 10% Moenhave; *J. osteosperma*, 30% Navajo, 24% Moenhave, 12% Keyenta), whereas *P. edulis* stands are located primarily on limestone (40% Carmel, 30% Temple Cap) substrates. Based on a small but representative 3-sample data set, soils in pinyon-juniper woodlands of ZNP are of low salinity (0.6 ± 0.15 mmhos $\cdot$ cm^{-1}), predominantly sandy ($52.2 \pm 16.0\%$ sand, $23.7 \pm 5.6\%$ silt, $24.1 \pm 11.4\%$ clay), and have a near neutral pH (7.2 ± 0.18). Other soil mineral characteristics are available P (ppm as extracted by 0.2 N acetic acid), 32.9 ± 19.9, and exchange cations ppm as extracted with neutral 1.0 N ammonium acetate: Ca, 2856.5 ± 1351.7; Mg, 263.5 ± 131.2; K, 312.8 ± 138.6; Na, 16.0 ± 9.2; Zn, 0.8 ± 0.1; Fe, 5.1 ± 0.6; Mn, 1.9 ± 0.4; and Cu, 0.5 ± 0.1. The small sample size for soil parameters provides no basis for discerning edaphic differences between the 3 broad vegetational types considered here.

Biotic Relationships

The 3 primary woodland species that are the focus of this report have different distribution patterns. *Pinus edulis* occurs primarily in the northern and northeastern portions of ZNP where elevations are higher (Fig. 1A). *Pinus monophylla* is located at lower elevations in the Kolob section of the park and in the southwestern portions of ZNP (Fig. 1B). *Juniperus osteosperma* is distributed more uniformly in the park (Fig. 1C). However, P-J community types were found to be indistinct from other community types in the ZNP area (index of distinctiveness of 7.4%, 17.4%, and 16.0% for *Juniperus osteosperma*, *Pinus monophylla*, and *P. edulis*, respectively). The *J. osteosperma* community was the least distinctive of the 3 types; thus, these communities have many species found in other communities elsewhere in the park. These community types are also compositionally variable from one place to another (index of homogeneity of 49.2%, 44.3%, and 55.0% for *Juniperus osteosperma*, *Pinus monophylla*, and *P. edulis*, respectively). In this respect, our results are similar to those of West et al. (1998).

Pinus edulis had substantially less bare soil (~19%) than the other 2 types. Litter cover was greatest in *P. edulis* (46.2%), likely the result of greater tree cover in that type and lower annual temperatures that would tend to slow litter decomposition by microorganisms. Absolute cover (living cover × total cover) of shrubs was greatest in the *P. edulis* community type (~31%) and somewhat lower in the *J. osteosperma* and *P. monophylla* types (22–25%). Herbaceous cover was limited (<10%) everywhere but was approximately twice as great in juniper-only (8.3 %) and *P. monophylla* (9.4 %) woodlands as in the *P. edulis* (4.4%) types. We believe that relationship is probably reflective of a uniformly later seral stage in the *P. edulis* woodland type due to less frequent fires.

Communities of arid environments often have microbiotic soil crusts that tend to stabilize soils against erosion and contribute nitrogen via fixation by numerous cyanobacterial components of the crusts (Harper and Marble 1988). Such crusts also are known to enhance

TABLE 3. Response of various parameters along successional gradients in 2 vegetational types within the woodlands of ZNP. Mean values are followed by their standard errors in parentheses. Microbiotic cover represents cover of nonvascular plants on soil surfaces.

	Community type					
	Juniperus osteosperma–Pinus monophylla			*Juniperus osteosperma–Pinus edulis*		
Parameter	Early	Mid-seral	Late	Early	Mid-seral	Late
Sample size	51	22	4	23	11	4
Ave. tree cover (%)	10.3 (1.0)	32.5 (0.9)	58.0 (2.5)	10.5 (1.6)	35.2 (2.1)	67.3 (11.2)
Total living cover (%)	48.7 (4.0)	77.3 (7.0)	88.3 (11.6)	46.3 (5.8)	77.4 (7.4)	83.7 (9.2)
Ave. litter cover (%)	23.1 (2.1)	41.6 (4.8)	33.3 (17.4)	38.8 (4.4)	53.2 (7.9)	70.0 (10.8)
Ave. bare soil (%)	30.8 (2.9)	14.0 (2.0)	11.7 (1.7)	19.7 (3.1)	18.2 (4.7)	16.3 (2.4)
Ave. rock cover (%)	32.8 (3.5)	38.8 (5.3)	10.0 (2.9)	34.7 (6.3)	17.7 (4.0)	18.8 (17.1)
Juniperus cover (%)	4.3 (0.8)	10.9 (2.3)	14.6 (8.1)	1.9 (0.7)	7.2 (2.3)	17.0 (7.6)
Pinus cover (%)	4.7 (1.0)	10.3 (1.5)	26.3 (11.3)	6.0 (1.4)	17.8 (3.2)	24.5 (14.7)
Shrub cover (%)	21.2 (2.2)	32.1 (5.1)	50.3 (10.3)	24.7 (5.1)	35.6 (4.9)	53.5 (4.5)
Annual plant cover (%)	2.6 (0.2)	1.8 (0.3)	1.5 (0.9)	1.0 (0.2)	2.0 (0.5)	0.3 (0.1)
Microbiotic cover (%)	9.4 (2.0)	17.6 (4.3)	20.0 (16.7)	4.5 (1.4)	5.3 (2.3)	2.8 (1.3)
Ave. no. vascular plant per 0.01 ha	21.6 (1.0)	23.1 (1.5)	20.5 (2.9)	20.1 (1.8)	23.5 (2.6)	17.5 (1.7)

the nutrient status of surface soils and increase uptake of several bioessential nutrients in addition to nitrogen by associated herbs (Harper and Belnap 2001). In the *J. osteosperma* and *P. monophylla* community types, cryptogamic cover (living × total) averaged 11–13% (Table 1). In the *P. edulis* zone, the low absolute (living × total) percentage cover of microbial crust (4.6%) is probably related to the heavy litter layer and to shading by trees.

Species richness was approximately equal among the 3 woodland subtypes recognized, with an average of 21–23 vascular species per 0.01 ha. Likewise, richness for different plant life-forms was similar (trees, 1.0–1.9; shrubs, 5.3–6.3; graminoids, 2.8–4.6; and forbs, 9.8–11.6 species per 0.01 ha.) Although herbs contributed little cover, 61–72% of prevalent species in those communities were herbaceous. Dicotyledonous herb species accounted for over 2.5 times as many species as monocotyledonous herbs in the communities. Considering that West et al. (1998) ignored annual plants, our species density values are similar to theirs, even though their macroplots were 10 times larger than ours (~1000 m^2 versus 100 m^2).

Species Composition

A combined list of prevalent species for the 3 P-J community types in ZNP shows *J. osteosperma* to be the most common species (Table 2). *Pinus monophylla* and *P. edulis* both occur with *J. osteosperma* but rarely together (twice only in this data set). Most species listed in Table 2 occur in all 3 community types, but with widely varying occurrence values. The weedy bromes (cheatgrass [*Bromus tectorum*] and red brome [*B. rubens* L.]) both occur on lists for the 3 communities and are tenacious reminders of decades of domestic animal grazing in the P-J zone prior to the establishment of ZNP. These 2 bromes are the only introduced species on prevalent species lists. All other prevalents are native to the ZNP area.

Cover-class Dynamics

Shrub cover increases along the successional gradient in woodlands of ZNP (Table 3). Pinyon cover tends to increase somewhat faster than juniper cover along the successional gradient. Later seral stands in both community types regularly support equal amounts of cover of the small tree oaks (*Quercus gambelii* [Gambel oak] and *Q. turbinella* Greene [Turbinella live-oak]) and juniper and pinyon (Table 4).

Microbiotic soil crust cover is consistently greater in *J. osteosperma–P. monophylla* woodlands than in *P. edulis* woodlands (Table 3). Annual plants tend to be minor components of plant cover in both community types. Dead plant tissue (litter) on the soil surface tends to increase strongly along the successional gradient in both woodland types (Table 3). Sites with heavy tree cover (late seral by our criteria) apparently are on less rocky sites and thus have better-developed and more continuous soil covers (Table 3).

TABLE 4. Cover of some common understory species along the successional gradients in *J. osteosperma–P. monophylla* and *J. osteosperma–P. edulis* woodlands in ZNP. For this analysis, stands of *J. osteosperma* only were pooled with those of the *J. ostersperma–P. monophylla* type. Average cover values are followed by their standard error shown in parentheses.

	Community type					
	J. osteosperma only and *J. osteosperma–P. monophylla*			*J. osteosperma–P. edulis*		
Species[a]	Early	Mid-seral	Late	Early	Mid-seral	Late
Amelanchier utahensis	3.2 (0.76)	4.1 (1.81)	6.0 (4.59)	4.4 (1.22)	5.6 (1.85)	6.0 (3.0A
Arabis perennans	0.3 (0.07)	0.4 (0.05)	0.3 (0.17)	0.2 (0.05)	0.3 (0.08)	0.5 (0.00)
Arctostaphylos patula	3.5 (1.21)	7.0 (3.44)	10.0 (5.01)	6.4 (2.79)	6.3 (2.12)	3.9 (3.71)
Aristida purpurea	0.2 (0.07)	0.3 (0.20)	5.0 (5.01)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)
Artemisia tridentata	1.6 (0.85)	0.8 (0.28)	0.2 (0.17)	0.2 (0.13)	0.05 (0.05)	0.0 (0.00)
Bromus rubens	0.4 (0.10)	0.1 (0.02)	0.2 (0.17)	0.0 (0.00)	0.05 (0.05)	0.0 (0.00)
Bromus tectorum	3.1 (1.47)	0.5 (0.19)	1.2 (0.93)	0.2 (0.05)	1.1 (0.34)	0.0 (0.00)
Carex rossii	0.03 (0.02)	0.0 (0.00)	0.2 (0.17)	0.3 (0.13)	0.2 (0.08)	0.0 (0.00)
Cercocarpus montanus	0.5 (0.31)	0.0 (0.00)	0.0 (0.00)	3.4 (1.17)	4.4 (2.08)	4.5 (3.57)
Elymus elymoides	0.2 (0.03)	0.07 (0.04)	0.0 (0.00)	0.1 (0.04)	0.2 (0.08)	0.1 (0.13)
Erigeron utahensis	0.2 (0.03)	0.4 (0.14)	0.0 (0.00)	0.1 (0.04)	0.05 (0.05)	0.1 (0.13)
Haplopappus scopulorum	1.5 (0.58)	0.5 (0.23)	1.0 (1.00)	0.2 (0.13)	0.1 (0.07)	0.8 (0.75)
Hilaria jamesii	1.8 (0.58)	0.2 (0.14)	0.0 (0.00)	0.0 (0.00)	0.05 (0.05)	0.0 (0.00)
Opuntia macrorhiza	0.8 (0.3)	0.8 (0.24)	1.2 (0.93)	0.8 (0.25)	2.1 (1.33)	4.6 (3.52)
Pachystima myrsinites	0.0 (0.00)	0.02 (0.02)	1.0 (1.00)	0.8 (0.66)	3.7 (3.39)	4.6 (3.52)
Poa fendleriana	2.0 (0.84)	9.6 (3.63)	5.2 (4.95)	3.5 (1.78)	5.0 (1.97)	8.3 (3.95)
Quercus gambelii	0.7 (0.4)	4.4 (1.50)	21.8 (20.4)	2.0 (0.89)	8.3 (2.33)	23.3 (8.59)
Quercus turbinella	1.6 (0.6)	7.6 (2.18)	12.5 (12.5)	0.8 (0.66)	1.4 (1.36)	3.8 (3.25)
Stipa hymenoides	0.4 (0.11)	0.3 (0.14)	1.0 (1.00)	0.3 (0.13)	0.4 (0.30)	0.1 (0.13)
Streptanthus cordatus	0.1 (0.03)	0.2 (0.05)	0.0 (0.00)	0.2 (0.05)	0.09 (0.06)	0.1 (0.13)
Symphoricarpos oreophilus	0.0 (0.00)	0.8 (0.71)	1.0 (1.00)	0.8 (0.66)	0.9 (0.41)	0.9 (0.72)
Tradescantia occidentalis	0.1 (0.02)	0.2 (1.05)	0.0 (0.00)	0.02 (0.02)	0.0 (0.00)	0.0 (0.00)
No. of stands averaged	50	21	3	23	11	4

[a]Species authorites are given in Table 2.

Total living cover increases significantly along the successional gradient in both community types (Table 3). That increase is attributed primarily to trees (an inescapable consequence of our criteria for advanced seral stages) and shrubs. Increased shrub cover is strong and significant across all stages of the arbitrarily designated seral stages based on tree cover (Table 3). Herb cover appears to decline across the gradient.

Individual species responses across the successional gradient are unclear for most taxa because of their sporadic occurrence. *Amelanchier utahensis, Pachystima myrsinites* (Pursh) Raf (mountain lover), *Poa fendleriana, Quercus gambelii,* and *Q. turbinella* appear to be increasers across the gradient (Table 4). Nevertheless, assignment of an increaser response for the latter 2 species is questionable since their cover was used to assign seral status. Later seral stands (those with heavy tree cover) were often assigned to that successional state because of heavy cover contributions from the oaks in addition to juniper and pinyon cover. Accordingly, our late seral stage sites may merely be sites where the ecological requirements of juniper, the pinyons, and the oaks overlap.

Other species seem to respond as decreasers. *Artemisia tridentata* (big sagebrush), *B. tectorum, Carex rossii* F. Boott (Ross sedge), *Hilaria jamesii* (Torr.) Benth. (galleta), *Purshia tridentata,* and *Tradescantia occidentalis* (prairie spiderwort; Table 4) appear to respond as decreasers in advanced seral stands in our sample.

DISCUSSION

Prevalent Species Considerations

The value of recognizing 3 community types within the pinyon-juniper woodlands of ZNP is reflected in the fact that slightly over half the species listed in Table 2 are designated as prevalents in but 1 of the communities. Only 8 of the 45 species considered in Table 2 are designated as prevalents in all 3 communities. Those widespread and abundant species include *Amelanchier utahensis* Koehne (Utah serviceberry), *Arabis perennans* Wats. (common rockcress), *Bromus tectorum, Gilia inconspicua* (J.

E. Sm.) Sweet (shy gilia), *Gutierrezia sarothrae* (Pursh) Britt. & Rusby (broom snakeweed), *J. osteosperma*, *Opuntia macrorhiza* Engelm. (plains prickly pear), and *Poa fendleriana* (Steudel) Vasey (muttongrass).

Compositional similarity among the 3 pinyon-juniper community types in ZNP is based upon percent occurrence of the prevalent species as shown in Figure 2. *Pinus monophylla* and *J. osteosperma* types were more similar to each other than to the *P. edulis* type. The fact that *P. monophylla* and *J. osteosperma* types occur at about the same elevation perhaps explains vegetation similarities of those communities. For this reason we pooled *J. osteosperma* and *P. monophylla* community types to analyze the successional process for P-J woodlands in ZNP.

Prevalent species are abundant and well adapted to the environments they define. Use of prevalent species lists can provide an efficient system for training naive workers employed for survey or monitoring duties in particular plant communities. While it is almost impossible to familiarize such workers with all species they may encounter in a community, familiarization with prevalent species can be achieved without great stress, and less common species can be dealt with on an "as needed" basis. Only a few prevalent species of the P-J woodlands of ZNP are known to be nitrogen-fixers (Table 2): *Astragalus* L. (milkvetch) species, *Cercocarpus* (mountain mahogany) species, *Purshia tridentata*, and *Stipa hymenoides* R. & S. (Indian ricegrass; Wullstein 1980, Paschke 1997, Bothe et al. 1998). None are widespread or dominant components of the vegetative cover of these woodlands. Because the microbiotic cover in the woodlands is rich in cyanobacteria (Harper and Belnap 2001), it is thus an important source for fixed-N in these plant communities.

Among 17 woody prevalent species (Table 2), only 4 sprout consistently after fire [*Chrysothamnus nauseosus* (Pallas) Britt. (rubber rabbitbrush), *Quercus gambelii*, *Q. turbinella*, and *Symphoricarpos oreophilus* Gray (mountain snowberry)]. Several other woody species may sprout and regrow if fires are not excessively hot or the site is well watered. Among these potential sprouters, only *Q. gambelii* ever becomes a dominant component of the community cover after fire.

Several community dominants may trigger severe allergic responses in people upon exposure to their windblown pollen, particularly *Artemisia* species and Utah juniper. A few species may become troublesome allergens as their seeds are harvested for reseeding other wildlands in similar ecological zones: *Purshia mexicana* (Stansbury cliffrose) is especially noteworthy. Its abundant stylar bristles, the allergenic agent, become airborne in seed-harvesting procedures.

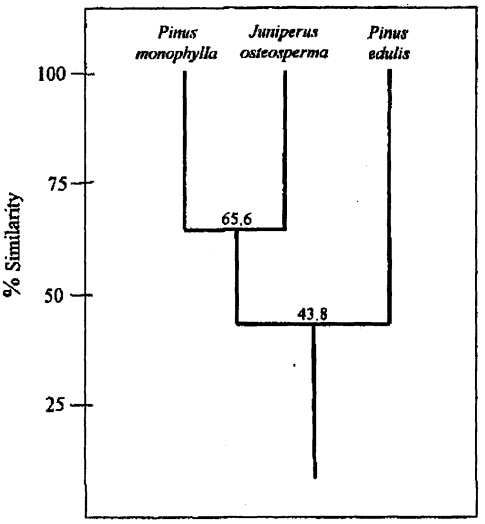

Fig. 2. Similarity of vegetational stands dominated by *J. osteosperma* (no *Pinus* present), *P. monophylla*, or *P. edulis* in Zion National Park. Percentage similarity is based on percentage occurrence of prevalent species (Table 2) in macroplots assigned to 3 woodland types described above. Ruzicka's (1958) similarity index was used.

Only a few P-J prevalents (Table 2) pose a poison threat for animals that forage in these woodlands. Most *Astragalus* species now appear to be poisonous to foraging animals if ingested in significant amounts (Williams and James 1978, Williams 1982). The oaks have a long history of toxicity via their content of tannins (Harper et al. 1988). Similarly, *Gutierrezia* species have long been know to be toxic, but the poisonous agent remains unidentified (Brotherson et al. 1980). Fortunately, animals tend to avoid toxic agents as long as palatable nontoxic alternative forages are available (Holechek et al. 1998).

Vegetative Cover

Percent living plant cover is relatively similar for the 3 community types (*Pinus edulis–*

Juniperus osteosperma, P. monophylla–J. osteosperma, and *J. osteosperma* alone as dominant trees) recognized (58–62%; Table 1). Living cover for this study is thus greater than reported for Great Basin pinyon-juniper woodlands by West et al. (1998). These differences are at least partially explained by our cover values including both microphytic cover on soils and annual seed plants. Those cover categories were not considered by West et al. (1998). The greatest amount of bare soil (28.7%) was found in the *J. osteosperma* type and is likely due to greater disturbance from domestic grazers and/or wildfires at lower elevations early in the 20th century (Gruell 1999). The *P. monophylla–J. osteosperma* type also had a high percentage (~25%) of bare soil.

Habitat Types Recognized

We recognize 9 habitat types (HT) within the pinyon-juniper woodlands of ZNP. These habitat units are comparable to vegetational associations recognized by Moir and Larson (in Stuever and Hayden 1996), West et al. (1998), and Thompson (1999). They are dependent, in part, on elevational differences and associated climatic changes. In the *P. edulis* community, we recognize the following habitat types: (1) *P. edulis/Quercus gambelii,* (2) *P. edulis/Cercocarpos montanus–Q. gambelii,* (3) *P. edulis/Arctostaphylos patula* (greenleaf manzanita), and (4) *P. edulis/C. montanus.* The *P. edulis/Q. gambelii* HT occurs at higher elevations on primarily sandy soils. The *P. edulis/C. montanus–Q. gambelii* HT also occurs at higher elevations, but on shale substrates. The *P. edulis/C. montanus* HT occupies rocky areas at moderate elevations. Warmer, lower elevational sites with limey sand substrates are more conducive to the *P. edulis/Arctostaphylos patula* HT. These types differ markedly in response to fire: HTs 1 and 2 are heavily dominated by Gambel oak for decades after fire, whereas HT 3 is an early to late mid-seral type that is eventually replaced by other vegetation. HT 4 provides good foraging habitat for deer, and fire rarely occurs on such sites.

In the *P. monophylla* community type, we recognize 5 habitat types. *P. monophylla/Quercus turbinella* (HT 5) occurs predominantly at lower elevations on rocky sites with sandy soils. *P. monophylla/Q. turbinella, Arctostaphyos patula* Greene (HT 6) is found at low-elevational and predominantly sandy sites that have burned within the past century. *P. monophylla/Q. gambelii* (HT 7) is located at higher elevations on sites that receive considerable topographic shading. We also recognize *P. monophylla/Coleogyne ramossima* Torr. (blackbrush) (HT 8), which occurs on sunny, lower elevational sites. The last type recognized is *J. osteosperma/Artemisia tridentata* (HT 9), which occurs at lower elevations and on deeper, well-developed loamy soils.

Large Ungulate Considerations

The most common large ungulates in ZNP are mule deer and bighorn sheep. Managers will inevitably be forced to consider pinyon-juniper woodlands as habitat for these species. Studies have shown that desert bighorn sheep actively seek burned pinyon-juniper areas near rugged, rocky escape areas (Smith et al. 1999). More open pinyon-juniper woodlands may also provide adequate visibility for bighorn sheep. If charred trees remain standing in P-J woodlands, bighorn sheep may still avoid such areas because horizontal visibility is reduced. Managers may choose to maintain some pinyon-juniper woodland pioneer successional stages with sparse tree cover as habitat for bighorn sheep. Burned areas that support an abundance of graminoids would be preferred, since grasses constitute a major portion of bighorn sheep diet (Smith 1992, Smith and Flinders 1992).

Mule deer, on the other hand, favor patches of dense P-J woodland for escape and thermal cover. They do not take to cliffy places, as bighorn sheep do, to escape predators, but rely on dense woodlands that also provide needed thermal cover during winter. Browse and broad-leaved herbs are major components of the mule deer diet. Mule deer would, no doubt, utilize areas burned to enhance habitat for bighorns. Since we found shrub cover to be everywhere abundant and to increase from pioneer to late seral communities, mule deer would have access to browse forage in all seral stages. In addition, they would have access to both dense P-J stands for escape and thermal cover as well as a variety of palatable shrubs in later seral stages.

Shrubs such as *Purshia tridentata,* which are nutritious and palatable to mule deer, occur in greatest abundance in early seral

stages. *Cercocarpus montanus* (curl-leaf mountain mahogany) and *Artemisia tridentata* ssp. *vaseyana,* which are also palatable to mule deer, are most abundant in later seral communities. Therefore, these woodlands would be enhanced in value for bighorn sheep and deer if prescribed burns were used to create scattered open areas. In areas where landscapes support primarily dense P-J stands, interspersing open and more dense woodlands would provide escape cover and late seral forage plants for mule deer. Such judicious placement of managed burns would also enhance local biodiversity and scenic qualities of the landscape (Huber et al. 1999).

Management Recommendations

We recommend that the National Park Service manage the pinyon-juniper vegetational type in such a way that late seral stages do not dominate large areas. Mid-seral stages produce more forage and adequate escape cover for wildlife while maintaining a diverse understory of native herbs and shrubs (Gruell et al. 1994, Huber et al. 1999). Prescribed burns may be necessary to create landscape mosaics consisting of patches of P-J woodland of differing ages, floristic diversity, and tree density. Such varied landscapes will ensure local availability of foraging and escape areas in the woodlands.

An attempt should be made to confine managed burns to areas where slopes are gentle and severe erosion is unlikely during periods immediately after fire. Late seral woodlands can be expected to lose many of the understory species present in early seral stages, seriously reducing local biodiversity (Huber et al. 1999) and largely eliminating usable nutritious forage, since wild ungulates make little use of juniper and pinyon foliage. A mosaic of woodlands of variable successional stages can also be expected to enhance local diversity of plants and both vertebrate and invertebrate animals. Late seral woodlands dominated by juniper and pinyon species also may develop gullies as a consequence of greatly diminished understory cover (West and Van Pelt 1987, Roundy and Vernon 1999). Such gullies reduce water infiltration on-site and produce sediments that are carried into associated waterways.

It must be recognized that prescribed burns in P-J woodlands within ZNP will probably require seeding immediately after fires. We recommend using native plant species that are becoming more available (Roundy et al. 1997, McArthur and Young 1999). Without seeding, burned areas may become dominated by alien weeds such as cheatgrass (*Bromus tectorum* L.) that have the capacity to greatly shorten the fire-return cycle and thus perpetuate themselves indefinitely on the sites (Roberts 1999). Artificial seeding after fire will not require on-site disturbance, since seed can be placed by aerial vehicles and heavy equipment should not be required to cover seed thus deposited. Sources of seed from locally adapted species that normally are common in early seral situations in the P-J woodland of ZNP will need to be established prior to the use of prescribed fire (Goodrich and Rooks 1999).

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