

Seed Dispersal and Seedling Establishment of Piñon and Juniper Species within the Piñon-Juniper Woodland

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Abstract—Understanding the prehistoric and historic dynamics of piñon-juniper woodland requires knowledge of the seed dispersal mechanisms and seedling establishment requirements of the tree species. Here, the types and effectiveness of the different seed dispersers and the environmental requirements for seedling establishment are compared and contrasted for the various piñon and juniper species within the woodlands. The importance of long-distance vs. short-distance dispersal and the roles of ecotones and disturbance in woodland dynamics are discussed. Recommendations for future research are given.

The distribution of piñon and juniper species within the woodlands has undergone dramatic changes in both prehistoric and historic times. Since the end of the Wisconsin Ice Age 12,000 years ago, some species have moved upward in elevation as much as 1,000 to 1,500 m and northwards as much as 6° latitude. For example, singleleaf piñon (*P. monophylla*) has migrated from the warm deserts of southern Arizona and New Mexico and northern Mexico northwards through the Great Basin as far as southern Idaho. Colorado piñon (*P. edulis*) has migrated over most of the Colorado Plateau and southern Rockies (Betancourt 1987). Recent expansions of the woodlands appear to be influenced by human activities. Prior to settlement of the West in the early 1800's, fires burned through much of the woodlands as often as every 50 to 100 years, resulting in a mosaic of early seral grasses, mid-seral shrublands, and late seral woodlands (West and Van Pelt 1987). However, overgrazing by livestock and a severe reduction in fire frequency has resulted in an increase in relatively unpalatable and fire-intolerant shrub and tree species throughout the woodland (West and Van Pelt 1987; Miller and others 1994). Trees are expanding into adjacent grasslands and shrublands throughout their range (Johnsen 1962; Tausch and others 1981; Miller and Rose 1995), and tree density is increasing within existing stands (Tausch and others 1981).

Information on seed and seedling ecology of the tree species is essential for understanding both the long- and

short-term dynamics of piñon-juniper woodlands. Despite the fact that seed dispersal and seedling establishment processes are critical determinants of both the prehistoric migration and historic expansion of the woodlands, relatively little research has focused on this area. Here, we provide an overview of the state of our knowledge of seed dispersal and seedling establishment of piñon and juniper species within the woodlands. We then discuss the importance of long-distance versus short-distance dispersal and the roles of ecotones and disturbance in woodland expansion. Finally, we suggest areas for future research.

Seed Dispersal Processes

To understand plant dispersal processes, information on both the types and behaviors of the seed dispersers and the effectiveness of dispersal for plant establishment is necessary. Disperser effectiveness has been defined as "the contribution a disperser makes to the future reproduction of a plant" population (Schupp 1993). Effectiveness has a quantitative component (the number of seeds dispersed) and a qualitative component (the likelihood that a dispersed seed will survive to produce a new plant in the population). Here, we examine the information on both the types and behaviors of the animals that disperse piñon and juniper and the effectiveness of those dispersers.

Seed dispersal of both piñon and juniper is probably much more complex than the literature to date indicates. We have the best information on seed dispersal of piñon pines by birds. Piñon pines are dispersed by several species of corvids (jays and nutcrackers) that store seeds in shallow caches in the soil (Vander Wall and Balda 1981; Vander Wall 1990). Piñon pine cones and seeds are well adapted for dispersal by birds. The seeds are large and nutritious (Botkin and Shires 1948), and the cones are weakly constructed so that the seeds can be easily extracted by corvids with long pointed beaks, such as Clark's nutcracker (*Nucifraga columbiana*) and piñon jays (*Gymnorhinus cyanocephalus*). Seeds are enclosed in deep pockets and held by thin flanges so that they do not fall readily from the cones. Unlike many conifers, cones are primarily pointed to the side and upward, which not only retards seed loss, but increases the visibility and availability of the seeds to avian dispersers.

Birds typically disperse seeds from several meters to 5 km (Vander Wall and Balda 1981). Differences in dispersal distances exist among different bird species with the more solitary scrub jays (*Aphelocoma coerulescens*) seldom dispersing seeds more than 1 km, the gregarious piñon jays

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carrying seeds slightly farther, and Clark's nutcrackers carrying seeds as far as 22 km. While jays typically place one seed in each cache site, nutcrackers cache from one to 10 seeds with a mean of about four seeds per cache. The total number of seeds cached can be phenomenal. Individual Clark's nutcrackers scatter hoard between 22,000 to 33,000 Colorado piñon seeds (Vander Wall and Balda 1977) or 17,900 singleleaf piñon seeds (Vander Wall 1988) in a good seed crop year. Ligon (1978) estimated that a flock of 250 piñon jays could cache about 4.5 million Colorado piñon seeds over 5 months.

Seed caching by corvids has important consequences for the fates of piñon pine seeds. It can be quantitatively effective for piñon pine as large numbers of seeds are cached and, especially in large seed crop years, many are left unrecovered to germinate and possibly establish. Some aspects of bird dispersal are qualitatively effective while others are not. Piñons almost always require burial for establishment, and birds bury the seeds 2 to 4 cm in the soil (Vander Wall, personal observation). However, piñons also have a fairly strict nurse plant and shading requirement, and birds tend to place most seeds in interspace environments, not in more favorable microhabitats under trees or shrubs (Vander Wall, personal observation).

The importance of seed caching of piñon pine by rodents has been largely ignored and probably vastly underestimated. Most rodents, unlike the corvids, forage for seeds on the ground after the seeds have fallen from the tree. In the Pine Nut Range of Nevada, deer mice (*Peromyscus maniculatus*), piñon mice (*Peromyscus truei*), Great Basin pocket mice (*Perognathus parvus*), and Panamint kangaroo rats (*Dipodomys panamintinus*) all scatter hoard singleleaf piñon seeds (Vander Wall 1997). Of 1,000 labeled seeds placed under five source trees, 69 percent were taken by rodents and 24 percent were scatter hoarded 5 to 30 mm deep. Rodents placed 36 percent of these scattered caches under shrubs, 39 percent in the open and the rest (25 percent) at the edge of shrub canopies. At other locations chipmunks, such as cliff chipmunk (*Tamias dorsalis*) and Panamint chipmunk (*T. panamintinus*), are probably important dispersers of piñon seeds. Rodents are qualitatively effective seed dispersers in that they bury the seeds and place most of them (about 60 percent) under or adjacent to shrubs. However, many of the seeds that are harvested are placed in larders where they have little or no chance of establishment (Vander Wall 1990). From a quantitative perspective, they may be less important because, except in heavy seed crop years, most seeds do not fall to the ground before they are harvested by birds.

Relatively little is known about dispersal of juniper species within the woodland. In general, most species of juniper have been assumed to be bird dispersed. Unlike bird dispersal of piñon in which the seeds are scatter hoarded, bird dispersal of junipers is by frugivory in which the seeds are ingested and passed through the gut track. Many bird species are involved in juniper dispersal. At least 12 species of birds feed on fruits and potentially disperse seeds of western juniper (*J. occidentalis*) (Maser and Gashwiler 1978), 13 species are known to disperse Ashe juniper (*J. ashei*) (Chavez-Ramirez and Slack 1994), and 52 species have been observed feeding on eastern red-cedar (*J. virginiana*) (Van Dersal 1938). Of the wide diversity of bird species

involved, the most important for juniper dispersal are probably members of the highly frugivorous subfamily Turdinae (Muscicapidae) such as bluebirds (*Sialia mexicana* and *S. currucoides*), Townsend's solitaire (*Myadestes townsendi*), and American robin (*Turdus migratorius*), and two members of the family Bombycillidae, the waxwings *Bombycilla garrulus* and *B. cedrorum* (Gabrielson and Jewett 1940; Salomonson 1978; Holthuijzen and Sharik 1985; Chavez-Ramirez and Slack 1994). The rounded and more or less fleshy cones of junipers are well suited for frugivorous dispersal, especially by birds (Salomonson and Balda 1977; Salomonson 1978).

Fruits are conspicuously colored blue or reddish and are easily accessible on the outer layers of the foliage. The fleshy portion of a one-seed juniper (*J. monosperma*) cone has an energy content of 1.32 kJ making it a reasonably rich energy source. Also, the thick hard seed coat allows seeds to pass undamaged through the guts of most birds and mammals. Dispersal distances and patterns vary depending on the bird species and the juniper species (Holthuijzen and Sharik 1985; Chavez-Ramirez and Slack 1994). The effectiveness of birds as dispersal agents varies among species of junipers. For species such as western juniper, birds appear to disperse the majority of the seeds and, thus, are quantitatively important. Bird dispersal is often qualitatively effective as most birds deposit seeds primarily in more favorable under shrub or tree microhabitats and only occasionally carry seeds to open microsites. Also, seeds tend to be deposited singly or in small groups and, thus, may be less likely to die from density-dependent seed predation or competition (Chavez-Ramirez and Slack 1993; Schupp 1993). However, some bird species, such as cedar waxwings, travel in flocks and use the same perches repeatedly resulting in high seed densities under single trees. Another limitation of bird dispersal is that seeds are deposited on the soil surface and are dependent on other mechanisms of burial.

Mammals, considered to be unimportant dispersers of juniper seeds in the past, may be quite important for certain juniper species. Mammals that consume and disperse juniper seeds include woodrats (*Neotoma* spp.), Virginia opossum (*Didelphis virginiana*), Nuttalls cottontail (*Sylvilagus nuttallii*), desert cottontail (*S. auduboni*), black-tailed jack-rabbit (*Lepus californicus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), black bear (*Ursus americanus*), ringtail (*Bassariscus astutus*), raccoon (*Procyon lotor*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and assorted livestock (Miller 1921; Parker 1945; Martin and others 1951; Johnsen 1962; Maser and Gashwiler 1978; Salomonson 1978; Chavez-Ramirez and Slack 1993; Willson 1993; Schupp and others 1997a, b). All species pass at least some seeds intact and, in some cases, seed germination is increased (Miller 1921; Johnsen 1962; Schupp and others 1997a).

Mammals may be quantitatively more important for some species of juniper than others. Western juniper is dispersed by several different bird species, but coyotes appear to be one of the few important mammalian dispersers (Schupp and others 1997b). In contrast, Utah juniper (*J. osteosperma*) appears to be dispersed primarily by cottontail rabbits and jackrabbits, and less so by birds (Schupp and others 1996; 1997a). This would seem to indicate that for the fleshier, moister species of junipers, coyotes and, perhaps in some

species, foxes are the major mammalian dispersers. These are also the species fed on mostly by birds. In contrast, the woodier, drier juniper species may be dispersed largely by rabbits. In general, mammalian endozoochorous dispersal may not be effective for plant establishment. Seeds are deposited on the soil surface, often in high densities, and usually in the open and not in more favorable shaded environments. One advantage of mammalian seed dispersal is that passage through the gut track can be relatively slow resulting in long transport distances.

As for piñon pines, the role of scatter hoarding rodents in the dispersal of juniper has probably been greatly underestimated. Rodents commonly cache tree seeds (Vander Wall 1990; 1997), and clumps of juniper seedlings have been observed emerging from caches in the spring (Vander Wall 1990; Schupp unpublished data). In west-central Utah, a minimum of 16 to 33 percent of all natural Utah juniper recruits less than or equal to 2.0 m tall emerged from rodent caches. To quantify the role of rodents in the dispersal of Utah juniper, 500 labeled seeds were placed under four different source trees in the Pine Nut Range, Nevada, and seed fates were monitored (Vander Wall unpublished data). Slightly less than half of the seeds were taken (41 percent) and of those 27 percent were found in caches. Although a relatively low percentage of seeds were cached, the study was conducted in mid-summer when other, possibly more desirable shrub and forb seeds were available.

In general, the low preference for juniper seeds may result in low recovery of cached juniper seeds and, thus, a high potential for seed germination and establishment. Also, many juniper seeds are available under the trees on a year-around basis potentially resulting in more caching activity than this single study indicates. As described for piñon pine, seed caching by rodents may be highly effective in that many of the seeds are placed in favorable environments and have a high potential for establishment.

Seedling Establishment Processes

Both the seed characteristics and the types of microhabitats in which seeds are placed are important in determining seed fates after dispersal. In general, piñon pines have short-lived seeds with little innate dormancy (Meewig and Bassett 1983). Thus, they form only a temporary seed bank with most seeds germinating the spring following dispersal. Density of seeds in the seed bank is highly dependent on the current year's cone crop. Piñon pines exhibit regionwide synchrony in cone production with singleleaf piñon masting every 2 to 3 years and Colorado piñon every 5 to 7 years (Tueller and Clark 1975). The potential for a large temporary seed bank is high during mast years, especially since many seeds probably remain unrecovered by animals. During nonmast years, the seed bank is probably quite sparse. For piñon, germination and establishment are most likely when favorable growing season conditions follow a mast year.

In contrast to piñon pines, junipers often have long-lived seeds. Tests of stored juniper seeds showed that 45-year old Utah juniper still had 17 percent germination, 21-year-old one-seed juniper had 54 percent germination, and 9-year-old

alligator juniper (*J. deppeana*) had 16 percent germination (Johnsen 1959). The long-lived seeds are often highly dormant with germination being delayed by impermeable seed coats, immature embryos, embryo dormancy, or the presence of inhibitors (Fisher and others 1987). Consequently, junipers have highly persistent seed banks with germination of a single seed cohort extending over many years.

Although seed production is highly variable among both individuals and years, junipers exhibit less pronounced masting than piñon. The result is a more or less continuous input of seeds into the seed bank. For juniper, germination and establishment can occur whenever favorable environmental conditions exist.

A common assumption concerning the establishment of piñon and juniper is that they require a nurse plant for establishment. However, there is little establishment data that directly follows the fates of piñon or juniper seedlings. Most establishment studies have examined the locations of seedlings in communities with varying tree and shrub cover without considering the pattern or effectiveness of dispersal or the requirements for establishment. Usually, higher numbers of piñon and juniper seedlings are found under shrubs or adult trees than in interspace environments (Johnsen 1962; Burkhardt and Tisdale 1976; Everett and others 1986a.; Eddleman 1987; Callaway and others 1996). In fully stocked stands of one-seed juniper, singleleaf piñon, and western juniper, higher number of seedlings occur under trees than in interspace environments (Johnsen 1962; Everett and others 1986a; Miller and Rose 1995). However, in areas where western juniper is expanding into sagebrush communities, higher numbers of seedlings occur under sagebrush (52 to 65 percent) than under trees (17 to 31 percent).

A more detailed examination reveals large differences in the nurse plant requirement both among and within species. Piñon seedlings rarely establish in interspaces or open environments (Everett and others 1986a; Callaway and others 1996). This is well illustrated by the total lack of first-year survival of singleleaf piñon seedlings in interspace microhabitats in the Pine Nut Range, Nevada (Chambers unpublished data). In contrast, juniper seedlings are capable of establishing in these environments under the proper conditions. First-year survival of Utah juniper seedlings in the Pine Nut Range in interspace microhabitats was less than in undertree sites, but was as high or higher than in under sagebrush sites (Chambers unpublished data). In Tintic Valley, Utah, emergence of Utah juniper seedlings differed among open, shrub, and tree microhabitats and also among years (Schupp and Gomez, unpublished data). The undershrub microhabitat had the highest emergence in one year, the lowest in a second, and was intermediate in two other years. Survival differed for only one emergence year, being least under shrubs and highest under trees. In expanding western juniper populations, 18 to 47 percent of established seedlings occurred in interspaces (Burkhardt and Tisdale 1976; Miller and Rose 1995). For Utah juniper on stabilized Lake Bonneville sand dunes in Utah, most of the few natural seedlings occurred in interspaces (Schupp unpublished data). Also, in the Southwestern grasslands and shrublands, juniper seedlings readily establish in open environments (Johnsen 1962; Salomonsen 1978). Differences between piñon and juniper in the nurse plant requirement may be related to their physiological characteristics.

Juniper species have greater drought tolerance and a higher capacity to obtain water resources for interspace microhabitats and shallow soils (Nowak and others, proceedings). This may enable seedlings to establish in unshaded interspaces with higher soil temperatures.

Higher establishment of juniper in open or interspace environments in the southwestern portion of the woodlands may be due to differences in precipitation patterns. While much of the Great Basin and more northern areas receive most precipitation during winter, the southwestern grasslands and shrublands receive moderate winter precipitation and monsoonal summer rains. Summer precipitation in the Southwest may offset the beneficial microenvironmental effects of nurse plants for seedling establishment in the Great Basin and more northern areas.

In those ecosystems with little summer rainfall, undertree and shrub microhabitats appear to provide favorable conditions for establishment of both piñon and juniper. Many environmental characteristics under trees and shrubs are more favorable for seedling establishment than those in interspaces. Shrubs and trees in arid or savanna ecosystems have been described as "islands of fertility." The microhabitats under both shrubs and trees often have higher concentrations of limiting nutrients, higher organic matter and total nitrogen, lower bulk densities, higher infiltration and soil water holding capacities, and higher rates of nutrient cycling (Everett and others 1986b; Doescher and others 1987; Klopatek 1987). They are also characterized by lower irradiance and soil temperatures (Stark 1994) — microenvironmental conditions favorable for many conifers. Although these areas receive less effective precipitation than interspace areas, they experience higher relative humidity and delayed dry down relative to open areas and grasslands (Johnsen 1962; Vetaas 1992; Stark 1994).

Although nurse plants facilitate seedling establishment, they also compete for available resources. Lowered seedling growth rates may be a tradeoff for favorable microenvironmental conditions beneath nurse plants. Piñon and juniper seedlings exhibit higher seedling survival under artificial shading (Meagher 1943), but seedlings in full sun have higher growth rates than those beneath shrubs (Burkhardt and Tisdale 1976; Miller and Rose 1995; Callaway and others 1996). Favorable water relations may also increase seedling survival underneath adult trees or nurse plants. Seedlings of western juniper have tighter stomatal control over water use than adult trees and are more responsive to environmental changes (Miller and others 1992). Singleleaf piñon seedlings associated with sagebrush exhibit reduced stomatal conductance as the summer progresses, while sagebrush water use continues to increase reaching levels up to five times greater (per unit leaf area) than associated piñon (Drivas and Everett 1988).

The effects of competition from grasses and other herbaceous vegetation on piñon and juniper seedling establishment are not clear because of the lack of experimental data. It appears that competition from annual forbs and grasses can reduce the seedling survival of Utah juniper and singleleaf piñon during the first year after emergence (Chambers, personal observation). Also, competition from established grasses reduces the initial establishment of one-seed juniper (Salomonson 1978). However, once seedlings are established (that is, greater than 1 or 2 years old) competition appears

to have little effect on subsequent survival. In western Oregon, western juniper seedlings were capable of establishing into the community regardless of grass cover or range condition (Miller and others 1994)

Short-Distance Versus Long-Distance Dispersal

Highly effective seed dispersal and seedling establishment processes have been key elements in both the long-distance migration and local expansion of piñon and juniper species within the woodlands. Recently, it has been suggested that local population growth, short-distance dispersal, and long-distance migration are all interdependent (Clark and others 1998). Although rapid migration is driven by occasional, long-distance dispersal events, the likelihood of such long-distance events occurring increases with seed availability at the existing front. The greater the local population growth and the greater the seed production, the higher the probability that some seeds will be dispersed long distances. Thus, it is important to consider both the local component of seed dispersal that is responsible for local population growth and expansion, and the long-distance component of seed dispersal that is responsible for species migration.

In piñon and juniper, different classes of dispersers are responsible for local versus long-distance dispersal. In piñon, relatively short-range dispersal is accomplished largely by rodents, scrub jays, Mexican jays, and piñon jays that often or always cache seeds within a few hundred meters of the source tree (Vander Wall and Balda 1981; Vander Wall 1997). Unrecovered caches produce new recruits, resulting in population growth and local range expansion. Relatively long-range dispersal is achieved by birds that often carry seeds long distances to new habitats. These birds include nutcrackers, piñon jays, and Steller's jays. Seed dispersal out of the piñon-juniper woodland introduces the species to habitats that may or may not be suitable for establishment. If suitable, the cached seeds can establish a founding colony from which a new stand may eventually arise.

The two extreme spatial scales of dispersal are not as obvious for juniper as for piñon. Depending on the juniper species, local dispersal within stands leading to seedling recruitment is probably due to birds, lagomorphs, and scatter hoarding rodents. Most birds have short gut-retention times and, thus, dispersal is probably within or near the woodland. Birds frequently fly only short distances to perches where they sit and process fruit before returning to the same tree or moving to a nearby fruit source (Schupp 1993). Although rodents and lagomorphs are capable of moving seeds hundreds of meters, they probably cache or deposit most seeds within or near the woodland (Schupp and others 1997b). Long-distance dispersal of junipers is likely by birds and large frugivorous mammals. Although most seed dispersal by birds is probably local, some seeds are potentially dispersed longer distances by flocks of robins, bluebirds, and waxwings, which are widely ranging in fall and winter (Gabrielson and Jewett 1940). Large frugivorous mammals are likely candidates for long-distance dispersal because they have long gut-retention times and can travel long distances over diverse terrain (Willson 1993; Clark and others 1998).

Role of Ecotones

Ecotones between woodlands and adjacent shrublands and grasslands frequently provide favorable microhabitats for seedling establishment and are often particularly active zones of seed dispersal. Because shrubs provide favorable establishment microhabitats, expansion into shrublands along ecotones or transitional areas is common. Most juniper and piñon seedlings occur under shrubs and, as trees mature, they over-top the shrubs and the shrubs die. In southwestern grasslands, grasses may inhibit initial seedling establishment, but once established seedlings experience little competition. In contrast, in fully stocked stands most seedlings establish under adult trees forming "seedling banks" with little chance of maturing unless the adult tree is removed or dies.

Ecotones are often used by animal dispersers that occur exclusively in one area or the other as well as by those that occur in both areas. Following fire in piñon and juniper woodlands in Nevada, ecotonal areas had the highest rodent species diversity (richness), were actively used by frugivorous mammals, and had the highest bird use (Mason 1981). Even rodent species such as piñon mice that depend on the presence of trees and species such as Great Basin pocket mice and chipmunks (such as, *Tamias* spp.) that prefer some tree or shrub cover use ecotones once vegetation has established. Species such as deer mice that prefer more open habitats occur in both the woodlands and ecotonal areas. Frugivorous mammals frequently forage 100s of meters out of the woodland, and lagomorphs are known to deposit seeds in grasslands up to 1.6 km from the nearest woodland (Schupp and others 1997b). Important avian dispersers of piñon, such as the corvids, depend on the woodlands, but utilize the ecotonal areas (Mason 1981). Because avian dispersers of juniper, such as the Turdinae and waxwings, are more likely to use larger trees or snags as perches, they may be more important for dispersal within the woodlands or after disturbances that leave some trees in place.

Importance of Disturbance

In piñon-juniper woodlands, as in other ecosystems, characteristics of the disturbance and life history attributes of the species determine establishment probabilities of seeds and seedlings. Most tree seedlings are killed by fire, but seeds of both piñon and juniper, especially those that are cached, have a reasonable probability of survival depending on cache microhabitat. Undershrub and tree microhabitats often experience higher soil temperatures than interspace areas, especially if the entire shrub or tree and the duff burn (Wells and others 1979) and would be expected to exhibit the highest seed mortality after fires.

Mechanical disturbances such as chaining have a much different effect on seed and seedling fates than fires. Tree seedlings frequently survive mechanical disturbances, and because a significant "seedling bank" can exist under mature trees, they can be released from competition after overstory removal. Seeds that have already arrived on the soil surface are left in place, although redistribution or burial may occur due to the equipment. Establishment

probabilities depend on the characteristics of the microhabitats after treatment. If downed trees and understory shrubs are left in place, more shaded microhabitats and nurse plants for seedling establishment will be available. If trees are piled and burned and understory shrubs are removed, fewer desirable microhabitats for seedling establishment will remain.

Disturbances that remove both trees and understory shrubs in piñon-juniper woodlands have a relatively greater effect on the establishment of piñon than juniper. Because piñons have short-lived seeds and a nurse plant requirement, piñon seeds and seedlings that survive the disturbance have a minimal chance of survival. In contrast, because junipers have long-lived seeds and less strict nurse plant requirements, their seeds and seedlings have a higher probability of establishment. Also, piñon seedlings appear to be less tolerant of competition from grasses and other herbaceous vegetation than juniper seedlings (Burkhardt and Tisdale 1976; Miller and Rose 1994). Consequently, initial establishment of juniper seedlings is frequently higher than that of piñon seedlings following disturbance in the singleleaf piñon-juniper woodland (Tausch and others 1981) and probably other woodland types.

Future Research

Several areas relating to the seed dispersal and seedling establishment of piñon and juniper require additional research if we are to understand the dynamics of the woodlands. We need more information on: (1) types and behaviors of rodent dispersers of piñon and of all dispersers of juniper; (2) effectiveness of different types of animal dispersers for seedling establishment; (3) environmental requirements for seedling establishment; and (4) the differences in seed dispersal and seedling establishment among species and regions. Ecotones appear to be particularly promising for increasing our understanding of ecosystem disturbance and woodland dynamics.

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