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Chapter 1

Ecology of Southwestern Ponderosa Pine Forests

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What Is Ponderosa Pine Forest and Why Is It Important?

Forests dominated by ponderosa pine (*Pinus* ponderosa var. *scopulorum)* are a major forest type of western North America (figure 1; Steele 1988; Daubenmire 1978; Oliver and Ryker 1990). In this publication, a ponderosa pine forest has an overstory, regardless of successional stage, dominated by ponderosa pine. This definition corresponds to the interior ponderosa pine cover type of the Society of American Foresters (Eyre 1980). At lower elevations in the mountainous West, ponderosa pine forests are generally bordered by grasslands, pinyon-juniper woodlands, or chaparral (shrublands). The ecotone may be wide or narrow, and a ponderosa pine forest is recognized when the overstory contains at least 5 percent ponderosa pine (USFS 1986). At upper elevations ponderosa pine forests usually adjoin or grade into mixed conifer forests. A mixed conifer stand where ponderosa pine has more overstory canopy than any other tree species or there is a plurality of tree stocking, is an interior ponderosa pine forest (Eyre 1980).

Two distinct ponderosa pine forests occur in the Southwest. The xerophytic (drier) forests have ponderosa pine as a climax tree (reproducing successfully in mid- to late succession) and comprise the ponderosa pine life zone (transition or lower montane forest) (USFS 1991; Dick-Peddie 1993). The mesophytic (wetter) forests have ponderosa pine as a seral tree (regeneration occurs only in early- to mid-succession although older trees may persist into late succession) and are part of the mixed conifer life zone or upper montane forest (USFS 1991; Dick-Peddie 1993).

Ponderosa pine forests are important because of their wide distribution (figure 1), commercial value, and because they provide habitat for many plants and animals. Ponderosa pine forests are noted for their variety of passerine birds resulting from variation in forest composition and structure modified by past and present human use. Subsequent chapters discuss how ponderosa pine forests are associated with different types and number of passerine birds and how humans have modified these forests and affected its occupancy and use by passerine birds. This chapter discusses the ecology and dynamics of ponderosa pine forests and wildlife use in general and describes natural and human induced changes in the composition and structure of these forests.

Paleoecology

The oldest remains of ponderosa pine in the Western United States are 600,000 year old fossils found in west central Nevada. Examination of pack rat middens in New Mexico and Texas, shows that ponderosa pine was absent during the Wisconsin period (about 10,400 to 43,000 years ago), although pinyon-juniper woodlands and mixed conifer forests were extensive (Betancourt 1990). From the late Pleistocene epoch (24,000 years ago) to the end of the last ice age (about 10,400 years ago), the vegetation of the Colorado Plateau moved southward or northward with glacial advance or retreat. Regional temperatures over the Southwest during the glacial advances may have been 6 °C lower and annual precipitation 220 mm higher in the lowlands than today. Ponderosa pine in the mountains of New Mexico occurred about 400 m lower than where it is found today (Dick-Peddie 1993; Murphy 1994).

With the beginning of warming in the early Holocene, ponderosa pine began colonization of the Colorado Plateau. Pinyon-juniper woodlands shifted upward and northward from a low elevation of just over 450 m to 1,500 m. Pinyon pine (*P. edulis)* reached its present upper limit (about 2,100 m) between 4,000 and 6,000 years ago. The present distribution of ponderosa pine forests in the interior West and Southwest was apparently the result of this rapid Holocene expansion, but the exact cause and manner of this expansion is unknown (Anderson 1989; Betancourt 1987).

Climate and Soils

Climates in ponderosa pine forests are similar throughout the interior Western United States. For example, a comparison of climates at Spokane, Washington and Flagstaff, Arizona where ponderosa pine forests occur with a grassy understory, shows that levels of mean annual precipitation (MAP) at Spokane is 41 cm and at Flagstaff is 57 cm.

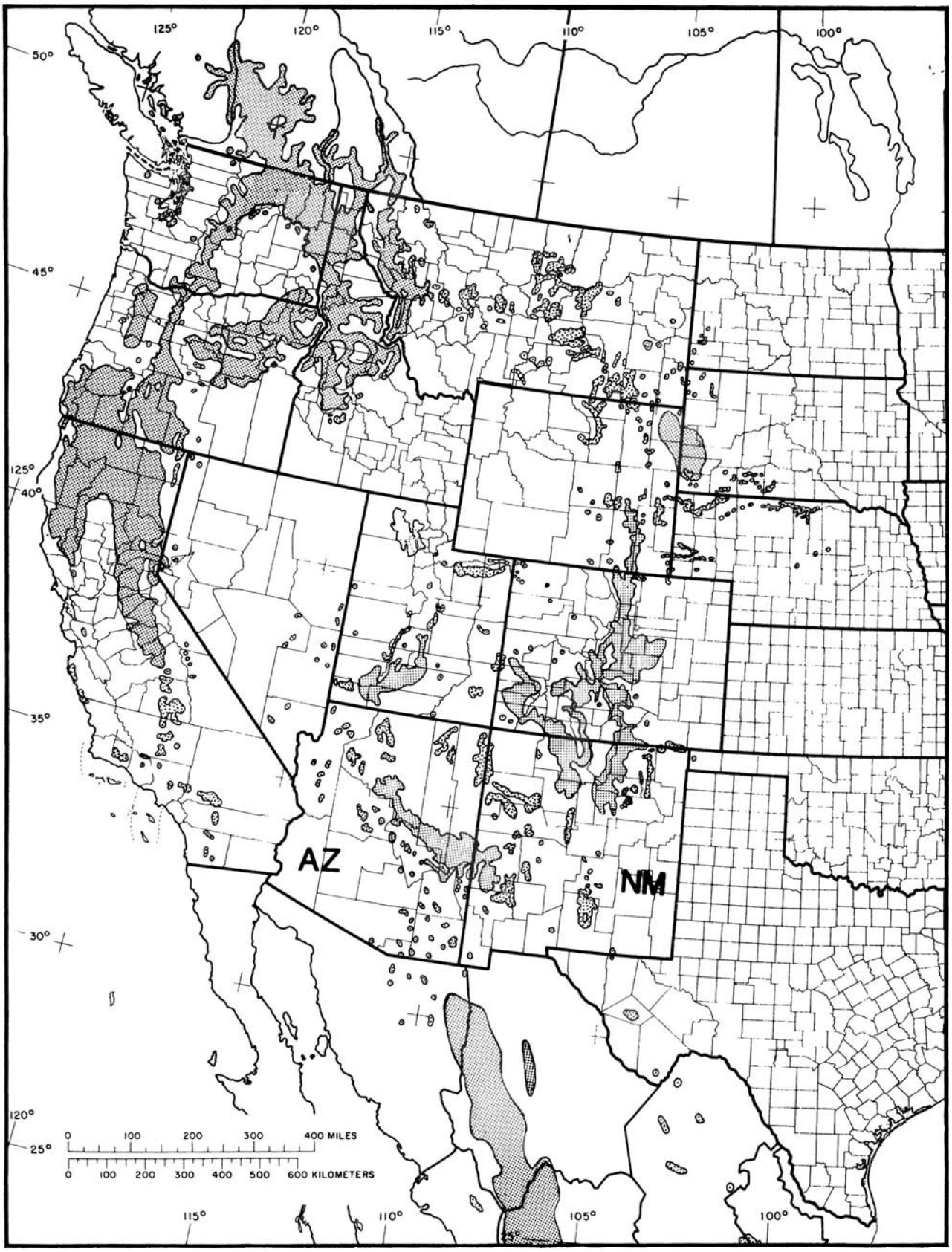

Figure 1. Distribution of ponderosa pine in North America. Arizona and New Mexico comprise the Southwest area discussed in this chapter (Little 1971).

Both locations have a pronounced dry season during several warm months when precipitation is insufficient to maintain plant growth. This drought is in July and August at Spokane and May and June at Flagstaff.

Climates of Arizona and New Mexico are described in the General Ecosystem Survey (USFS 1991; table 1). Ponderosa pine forests mostly occur within the High Sun Cold (HSC) and High Sun Mild (HSM) climate zones (table 1). Mean annual air temperatures (MAAT) for xerophytic and mesophytic forests are 9 °C and 6 °C in the HSM zone, and 5 to 7 °C and 4 °C the HSC zone, respectively (table 1). For these climate zones, mean annual precipitation (MAP) is 520 to 560 mm and 660 mm, respectively (table 1). The climate (figure 2a) for xerophytic forests of ponderosa pine/Arizona fescue (PIPO/FEAR) is near the mid-range of MAAT and MAP at Flagstaff (FLA), Pinetop (PIN), and Ruidoso (RUI). In contrast, ponderosa pine/blue grama (PIPO/BOGR) forests at Los Alamos (LOS) are near the lower limit of MAP, and forests of ponderosa pine/silverleaf oak (PIPO/QUHY) at Mt. Lemmon (MTL) are near the upper limit of MAP. Ponderosa pine/Arizona white oak (PIPO/QUAR) forests at Payson (PAY) have the warmest MAAT and ponderosa pine/mountain muhly (PIPO/MUMO) forests around Jacob Lake (JAC) have the coldest MAAT.

The soil moisture regime (SMR) of xerophytic forests is ustic (dry) (USFS 1991). At the stations examined (figures 2b–f), seasonal drought is most severe in May and June and understory vegetation, mostly grasses, becomes dry and flammable. Relationships between fire and climate in the Southwest have been studied by Swetnam and colleagues (Swetnam 1990; Swetnam and Baisan 1996; Swetnam and Betancourt 1990). The SMR of mesophytic forests is udic (wet) (USFS 1991); in these forests there is no drought in upper soil horizons during the average growing season. Therefore, at higher elevations where ponderosa pine is a seral tree of mixed conifer forests, the growing season precipitation is usually sufficient to maintain plant growth.

The soil temperature regime (STR) of ponderosa pine forests in Arizona and New Mexico is generally frigid; in the southern portions of these states at lower elevations it is mesic (USFS 1991). This shift to warmer soils, coincident with May through June droughts, is indicated by an understory vegetation of broadleafed, evergreen species such as Emory, gray, wavyleaf and silverleaf oaks (Quercus emoryi, *Q.* grisea, Q. undulata, Q. hypoleucoides), manzanita (Arctostaphylos pungens), madrones (Arbutus xalapensis, A. arizonica), yuccas (Yucca spp.), and other shrubs and trees (table 1). Although Arizona pine (*Pinus arizonica)* replaces *P. ponderosa* on some mesic soils in southeastern Arizona, forest dynamics and structure are similar.

The distinction between xerophytic and mesophytic zones is essential to understand plant succession in ponderosa pine forests in the Southwest. Beschta (1976) described the climate of a single ponderosa pine type in central Arizona without differentiating the ustic zone, where the pine is climax, from the udic zone, where it is seral. Similarly, both zones were combined in early forest inventories in Arizona and New Mexico (Eyre 1980; choate 1966; Spencer 1966) and showed considerably more ponderosa pine cover type than there is today (Johnson 1994).

Winter snow storms do occur in Southwestern ponderosa pine forests. In central Arizona annual snowfall ranges from 130 to 250 mm for the ponderosa pine zone to about 250 to 320 mm in the mixed conifer zone (Beschta 1976). South of the Mogollon Rim, the average annual snowfall is estimated at 90 to 165 mm, but reliable snow measurements are unavailable.

Vegetation

Xerophytic Forests

In the lower montane zone at elevations 2,150 to 2,600 m (elevations vary according to latitude and local conditions), there are 37 ponderosa pine forest types based on associated understory vegetation (Dick-Peddie 1993; Moir

Table 1. Summary of climates of Southwestern ponderosa pine forests (USFS 1991).

Six-month season with more than 1/2 annual precip.	Winter temp.	Climate category	Vegetation indicators	MAAT(°C)		MAP (mm)	
				XERO	MESO	XERO	MESO
High sun (HS) Apr 1 to Sep 30	Mild (M)	HSM	QUGR, QUEM	9	6	600	700
High sun (HS) Apr 1 to Sep 30	Cold (C)	HSC	PIED, QUGA	5-7	4	520–560	660
Low sun (LS) Oct 1 to Mar 30	Mild (M)	LSM	PICA, QUUN	9	7	600	700
Low sun (LS) Oct 1 to Mar 30	Cold (C)	LSC	ARTR	5-7	4	480-560	660

ARTR = *Artemisia tridentata*
PIED = *Pinus edulis*
QUGR = *Quercus grisea*
QUEM = *Quercus emoryi*
PICA = *Pinus californiarum*
QUGA = *Quercus gambelii*
QUUN = *Quercus undulata*
MAAT = *mean annual air temp*
MAP = *mean annual precipation*
XERO = *xerophytic forests*
MESO = *mesophytc forest*

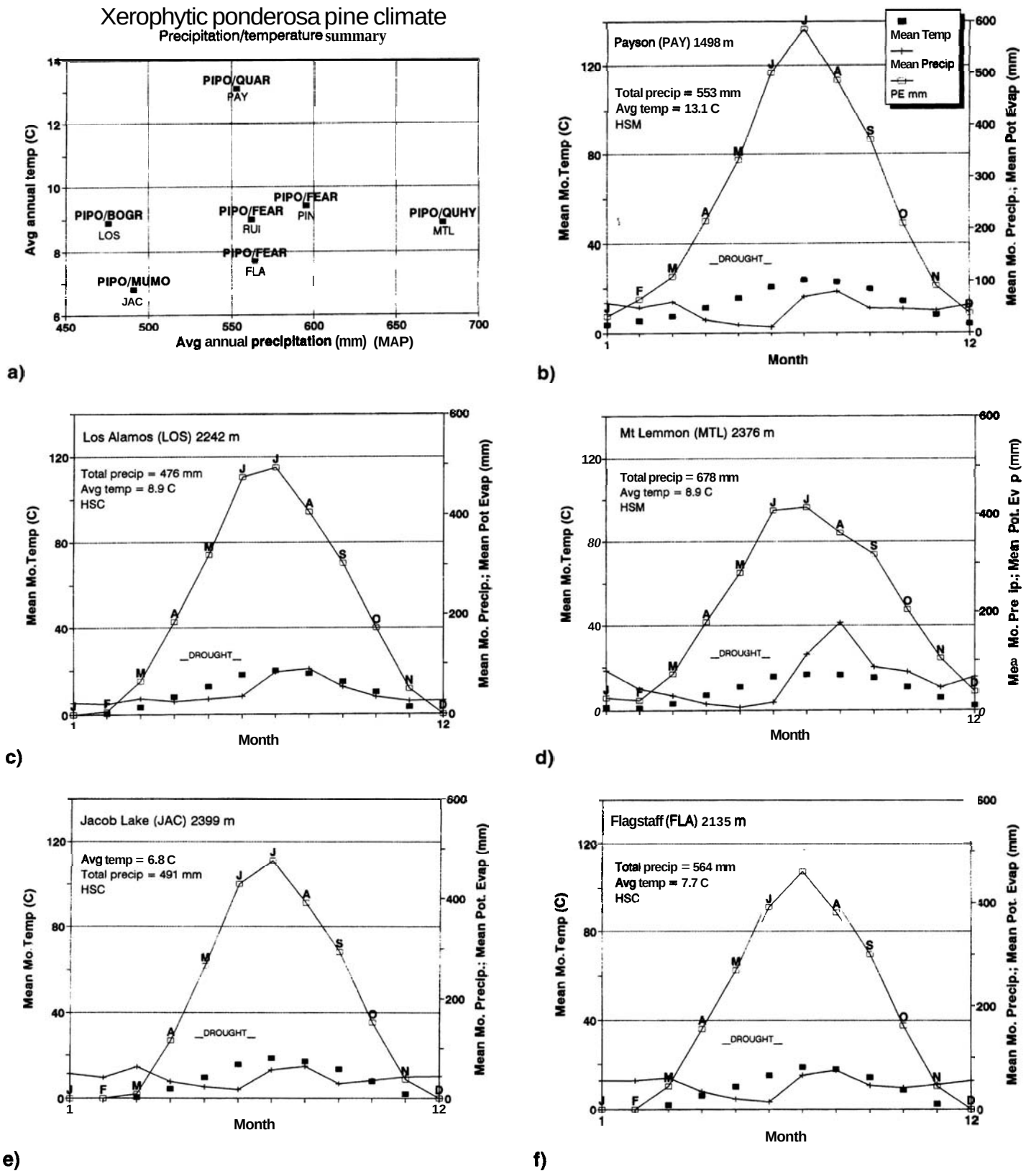

Figure 2. Climate summaries for xerophytic ponderosa pine in North America. PIPO, ponderosa pine; QUAR, Arizona white oak; BOGR, blue grama; FEAR, Arizona fescue; QUHL: silverleaf oak; MUMO, mountain muhly; PAL: Payson; LOS, Los Alamos; RUI, Ruidoso; PIN, Pinetop; MTL, Mt. Lemmon; FLA, Flagstaff; JAC, Jacob Lake.

and Fletcher 1996; USFS 1986, 1987a, 1987b). These types can be combined into 3 major groups, based on similarities in structure, composition, and fire response.

The fringe pine forest types are at dry, warm, lower elevations where ponderosa pine occurs with woody species that are common in the adjoining pinyon/juniper and pinyon/oak/juniper woodlands. Depending on geographic location, typical associated species are *P.* edulis, *P.* discolor, *P. californiarum,* Juniperus spp., Quercus grisea, Q. arizonica, Q. *emoryi,* Arctostaphylos pungens, *Artemisia* tridentata, and Chrysothamnus nauseosus. Associated trees form a mid-level canopy layer below the ponderosa pine overstory (Marshall 1957). These additional species provide resources for a wide variety of animals; discussed in the wildlife section of this chapter. Blue grama (Bouteloua gracilis) is a diagnostic species, and ponderosa pine/blue grama has widespread forest association throughout the Southwest (USFS 1986).

Where precipitation is greater than about 480 mm, blue grama is absent or minor and ponderosa pine occurs with understory bunchgrass species, mainly Festuca arizonica, Muhlenbergia montana, and/or M. virescens. There may be a mid-level canopy of shrubs, copses of oaks, or even an occasional oak tree (Kruse 1992), but these are minor vegetation components. Fires, either lightning- or human-caused, are frequent in these dry forests. Southwestern pine forests can be grouped with ponderosa pine forests in other areas of in the Western United States that share a similar fire ecology. Southwestern ponderosa pine/bunchgrass forests are similar to warm, dry forests in Idaho, Montana, and Utah (Davis et al. 1980; Crane and Fischer 1986; Fischer and Bradley 1987; Bradley et al. 1992). Numerous descriptions of presettlement forests in the Southwest (Woolsey 1911; reviews Cooper 1960; Covington and Moore 1994; Moir and Dieterich 1988) apply to this group of forests.

The third group of xerophytic ponderosa pine forests are those with understories dominated by shrubs and mid-level trees. Bunchgrasses may still be abundant, especially as patches in open areas. Common woody associates include Quercus gambelii, Q. undulata, Robinia neomexicana, Cercocarpus *montana,* and Symphoricarpos oreophilus. These forests are similar in structure and fire responses to the warm, moist ponderosa forests of central Idaho and Utah (Crane and Fischer 1986; Bradley et al. 1992).

Mesophytic Forests

In mesophytic forests at elevations 2,400 to 3,000 m (elevations vary according to latitude and local conditions), ponderosa pine is a major seral tree in 11 forest associations (USFS 1986, 1987a). These forests are identified by increasing importance of Pseudotsuga menziesii (Douglas-fir), Abies *concolor* (white fir), Picea *pungens* (blue spruce), and *Pinus strobiformis* (Southwestern white pine) as climax trees (Dick-Peddie 1993; USFS 1986, 1987a, 1987b; figure 3). Thousands of hectares of ponderosa pine-dominated mixed conifer forest existed in the Southwest in the early- to mid-20th century and were inventoried as part of the ponderosa pine cover type (Johnson 1993, 1994; Eyre 1980). Ponderosa pine and the other conifers were often associated with aspen (Populus *tremuloides),* which occurs where previous fires favored its regeneration (Jones 1974; Abolt et al. 1995). Without recurring fires, however, conifers !eventually replace aspen (Moir and Ludwig 1979; Dick-Peddie 1993). The aspen and coniferous mesophytic forests of the Southwest have structures and fire responses similar to those of mesic forests in the central and northern Rocky Mountains (Crane and Fischer 1986; Fischer and Bradley 1987, Bradley et al. 1992).

A number of mesophytic forest types in the Southwest include a bunchgrass understory of Festuca arizonica, Muhlenbergia montana, and/or M. virescens. In these types, ponderosa pine, Douglas-fir, and sometimes Southwestern white pine are the most important trees. The occasional white fir or blue spruce in these forests are evidence of the udic soil depicted in figure 3. Counterparts in western Montana and central Idaho are the warm, dry Douglas-fir forest types (Fischer and Bradley 1987; Crane and Fischer 1986).

Ponderosa pine and other conifers also occur with an understory of shrubs or mid-level trees such as Quercus gambelii, Robinia neomexicana, Symphoricarpos oreophila, Holodiscus *dumosus,* or Salix scouleriana (for more complete lists of associated species see Moir and Ludwig 1979). Rather than bunchgrasses, the herbaceous layer is composed of mesic species such as *Bromus* richardsonii, *Artemisia franserioides, Osmorhiza* chilensis, Geranium *richardsonii,* and Viola canadensis. Similar forests of moist Douglas-fir occur in Idaho (Crane and Fischer 1986), western Montana (Fischer and Clayton 1983), and Utah (Fischer and Bradley 1987; Bradley et al. 1992).

Finally, there are mixed conifer forests in the Southwest where ponderosa pine is minor or absent. These are the cold coniferous forests (Dick-Peddie 1993; USFS 1986, 1987a, 198%) where stand-replacing fires favor regeneration to aspen or tall shrubs such as Acer glabrum, Salix scouleriana, or Holodiscus *dumosus.* The coniferous species of these forests are Douglas-fir, white fir, blue spruce, Southwestern white pine, and sometimes bristlecone pine (*Pinus* aristata).

Fire

In the last decade forest fires have increased in Arizona and New Mexico (figure 4). Fire, the most important natural abiotic disturbance in ponderosa pine forests (Moir and

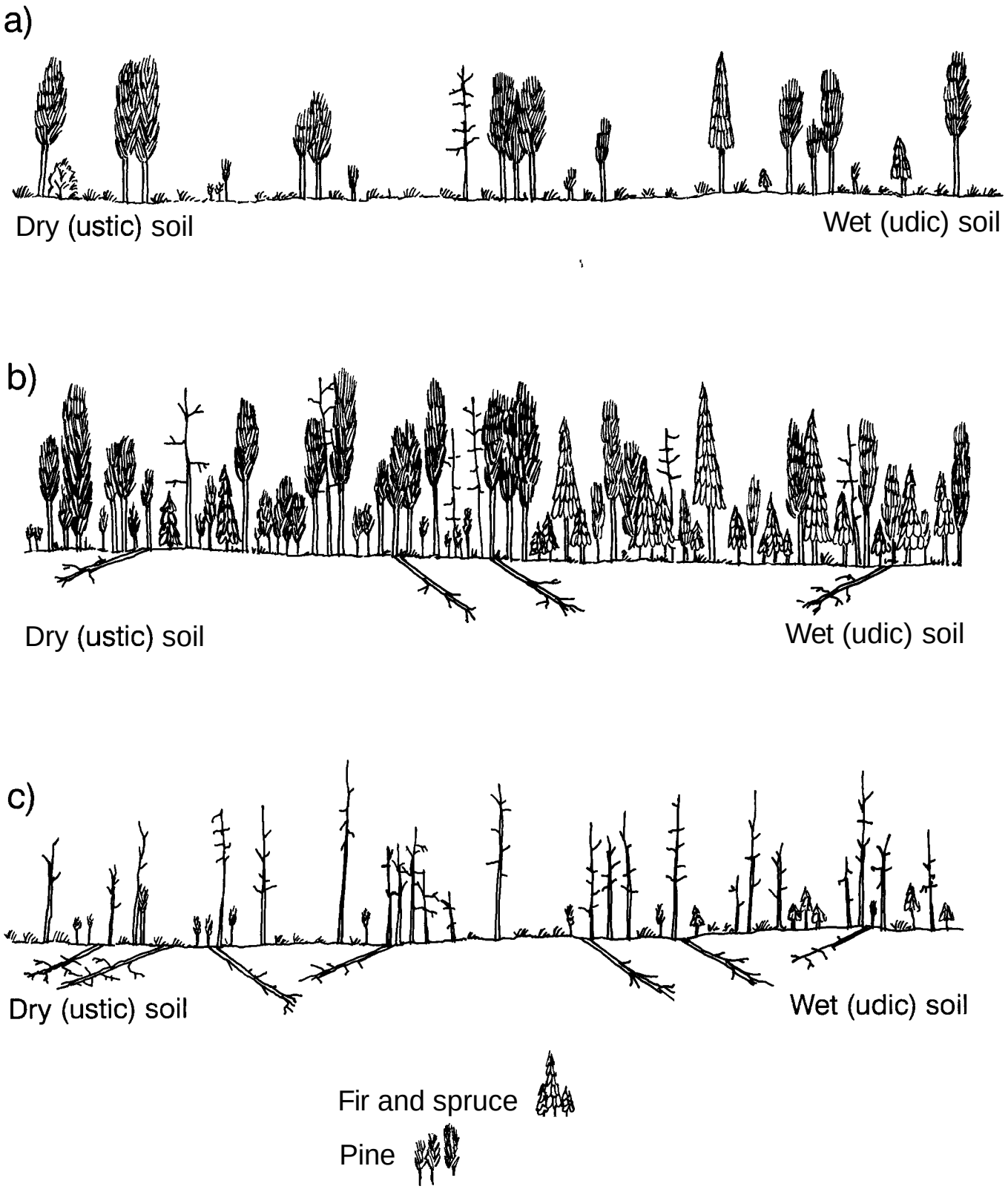

Figure 3. Generalized climate-differentiated ponderosa pine forests in Arizona and New Mexico. Diagram a) depicts the open, grassy pine forests described around the turn of the century (1890 to 1925). The open forest has a grassy understory, sparse ponderosa pine regeneration in the dry end, and, as precipitation increases, poor regeneration of ponderosa pine, Douglas-fir, blue spruce, or white fir. Diagram b) illustrates the same forest under average conditions in the 1990s (Johnson 1993, 1994). Diagram c) depicts the same forest 10 to 15 years after a fire holocaust. Natural or managed reforestation is occurring, although understory grasses may not be the same composition or density as that in diagram a) (Foxx 1996). Artwork by Joyce Patterson.

Dieterich 1988; Moody et al. 1992; Covington and Moore 1994), determines plant composition, succession, and forest structure. Fire ecology, especially since the 1930s and in the xerophytic ponderosa pine/bunchgrass forests, is well studied (Weaver 1943 and 1967; Biswell 1972; Cooper 1960; Ahlgren and Ahlgren 1960; Biswell et al. 1973; Habeck and Mutch 1973; Wright 1978; Moir and Dieterich 1988; Morgan 1994; Pyne 1996; Allen 1996). Forest succession under different fire regimes is generalized in the papers cited above and should be considered as hypotheses. Although they present sequences of species replacement and stand structure, these models generally do not specify the time between stages.

Frequent, low-intensity fires were part of the ecology and evolutionary history of ponderosa pine forests. Crown fires seldom occurred or were confined to small thickets (Woolsey 1911; Pyne 1996). Fires in the xerophytic pine forests occurred every 2 to 12 years and maintained an open canopy structure and a variable, patchy tree distribution (White 1985; Cooper 1961; Covington and Moore 1994; figure 3). The open, patchy tree distribution from fires and other disturbances, such as bark beetles and mistletoe, reduced the risk of fire holocausts. Downed woody material was sparse, and fires before about 1890 were fueled mostly by herbaceous material that accumulated at the end of the annual drought period. These low-intensity, surface fires reduced ground fuel, thinned smaller trees, and invigorated the understory maintaining the open forest structure (Ahlgren and Ahlgren 1960; Ffolliott et al. 1977).

Understory burns occurring over millennia helped forest vegetation adapt to fire (Habeck and Mutch 1973; Rapport and Yazvenko 1996). For example, the thick, corky bark of mature (15 to 20 cm diameter at breast height [dbh]) ponderosa pine and Douglas-fir insulates the cambium

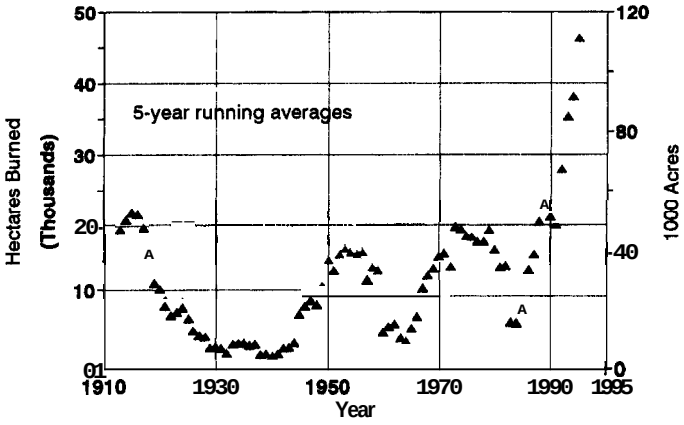

Figure 4. Forest fires in Arizona and New Mexico, 1910–1995 (U.S. Department of Agriculture, Forest Service, Southwest Region).

from killing temperatures. Another adaptation to fire, as well as drought, is the longevity of seed trees. Successful tree reproduction occurs only when heavy seed crops and germination coincide with moist springs and summers and a long fire-free period (Pearson 1950). Because these factors only occasionally occur simultaneously, tree reproduction is episodic. Decades may pass before conditions for reproduction and seedling survival are favorable (White 1985). However, ponderosa pine and Douglas-fir are long-lived (4 to 5 centuries) and over that time numerous opportunities for reproduction and establishment exist (Pearson 1950). Although ponderosa pine and Douglas-fir have high genetic diversity over broad areas, human impacts, primarily by harvest and fire suppression, may have modified their fitness for future environments and human uses (Ledig 1992).

Many other plants of ponderosa pine forests are either fire resistant or fire dependent. For example, since most fires begin near the end of a warm season drought, understory species whose seeds have long dormancy and whose germination is stimulated by high soil temperatures (Arctostaphylos *pungens* and Ceanothus fendleri), are unaffected or benefitted by fire. Another fire adaptation is rapid sprouting after fire. Examples include oaks (Quercus spp.), alligator juniper (*Juniperus* deppeana), aspen, maples (*Acer* spp.), Scouler willow (Salix scouleriana), and serviceberry (*Amelanchier alnifolia*).

The length of fire-free intervals is an important attribute of an area's fire regime. Long fire-free periods allow trees to grow adequately thick bark to protect the cambial cells of the lower stem and root crown from the lethal temperatures of the next surface fire. But during a long interval between fires, woody fuels and mistletoe brooms (dense, woody structures that develop in tree crowns parasitized by dwarf mistletoe) accumulate, increasing the probability that the crown will be scorched and/or the roots killed (Harrington and Sackett 1992). To prevent destructive, high-intensity fires, tree thinning and manual fuel removal (especially around the base of large trees) is performed as part of fuel-reduction burn prescriptions (Kurmes 1989; Brown et al. 1994; Covington and Moore 1992; Harrington and Sackett 1992).

Much current research is dedicated to estimating fire frequencies in the xerophytic and mesophytic ponderosa pine forests of the Southwest (Swetnam and Baisan 1996). Working in a ponderosa pine/Arizona white oak stand surrounded by chaparral in Arizona, Dieterich and Hibbert (1990) reported that low-intensity, surface fires occurred somewhere within the 87 hectare (ha) study site in 67 of the years between 1770 and 1870. In similar open pine forests of the Rincon Mountains, Baisan and Swetnam (1990) reported a mean fire interval (MFI) of 7 years in the century before 1890; these were low-intensity, surface fires. In the earliest study of a mixed conifer forest containing ponderosa pine, Dieterich (1983) reported a 22-year MFI

(combining fires in several forest communities) in the Thomas Creek drainages in Arizona before 1890. The lack of fire since then allowed shade tolerant trees, such as white fir and Engelmann spruce, to establish and increase overall tree density in the study area.

There is evidence that ponderosa pine forests with grassy understories in the xerophytic or mesophytic zones have similar fire regimes. Unpublished data from the Sacramento and White Mountains, New Mexico (Huckaby and Brown 1996) reveal high fire frequencies in Douglas-fir and white fir forests where grasses were a major component of the forest understory. Between 1712 and 1876, a Douglas-fir climax site on James Ridge had 25 fires (MFI = 7 years). Between 1790 and 1890, the MFI was 4.5 years for a white fir climax site (white fir/Arizona fescue association) on Buck Mountain. Fires at each of these sites were low-intensity, surface fires that maintained an open forest structure. High fire frequencies (low MFIs) were also found in a wide variety of other ponderosa pine and mixed conifer forest types, with or without present-day grassy understories.

Data indicating frequent ground fires before the 20th century have been collected for the Pinaleno Mountains, Arizona (Grissino-Meyer et al. 1995), the Jemez Mountains, New Mexico (Allen et al 1995; Touchan et al. 1996), the Mogollon Mountains, New Mexico (Abolt et al. 1995), and the Sandia and Manzano Mountains, New Mexico (Baisan and Swetnam 1995b). In all cases, the MFI before 1890 was 12 years or less. Savage and Swetnam (1990), Abolt et al. (1995), and Touchan et al. (1995) suggest that continuity of understory fuels, especially the grass layer, maintained high frequencies of low-intensity, surface fires along the entire gradient from woodlands to the spruce-fir forests. This hypothesis is supported by evidence that forests with grassy understories were once extensive and continuous over a large elevational range. Descriptions of forests around the turn of the century noted open, large areas not confined to xerophytic pine forests. Most ecologists agree that hot, crown fires were not extensive in these open ponderosa pine forests, although small thickets would have been destroyed by spot crown fires. Because fires have been suppressed in the last 100 years, much of the area classified as ponderosa pine cover type was previously within the mesophytic mixed conifer climate (Beschta 1976; Johnson 1994; Covington and Moore 1994).

Other Natural Disturbances

Although only a few species of forest insects and pathogens described are the principal natural agents of change in Southwestern ponderosa pine forests, they interact with each other and with other abiotic factors to generate forests with varying species composition and landscape patterns (Lundquist 1995a). Some of these organisms have coevolved with host trees, while others, such as white pine blister rust, were recently introduced (Wilson and Tkacz 1996). Each insect or pathogen attacks only certain host species and parts (foliage, stems, roots) and is controlled by various host and environmental conditions. Tree competition, drought, lightning strike, wind damage, site conditions, and fire can stress a tree and increase its vulnerability to opportunistic insects and fungi. The initial attack can lead to invasion by other insects and pathogens, tree death, and deterioration. Many insect and pathogen species do not require the host tree to be stressed before attack, instead they proceed rapidly as host resistance is overcome (Franklin et al. 1987). Injury from biotic agents can also increase damage from abiotic factors. For example, decay increases the likelihood of stem failure, and mistletoe brooms provide fuel continuity from the ground to the crown.

In addition to fire, important abiotic factors affecting ponderosa pine in the Southwest are drought, lightning, winter drying, and hail (Rogers and Hessburg 1985). Droughts several years long occur periodically across the region and are frequently severe. Pine mortality is usually associated with secondary bark beetles at the end of the drought (Lightle 1967). Lightning is a common cause of mortality for large ponderosa pine, especially in certain geographic areas with high lightning frequency such as the Mogollon Rim, Arizona (Pearson 1950). Winter drying is the result of foliage desiccation when soil and roots are frozen (Schmid et al. 1991). The affect on ponderosa pine can be devestating but most trees recover, as in 1985 in northern New Mexico (Owen 1986). Violent summer thunderstorms can produce severe hail, stripping trees of much of their foliage. Such a storm occurred on the Mescalero Apache Indian Reservation in the 1950s (Shaw et al. 1994).

Insects

Although many insect species feed on nearly every part of ponderosa pine (Furness and Carolin 1977), ecologically the most severe are the defoliators and bark beetles. Conifer sawflies (Diprionidae) and various moths, especially the pandora moth (Coloradia pandora), occasionally reach outbreak status; however, although foliage is removed, trees usually recover. In the mesophytic ponderosa pine zone, the western spruce budworm (*Choristoneura occidentalis*) can induce a temporary increase in ponderosa pine growth while depressing the growth of competing Douglas-fir and white fir, which are the principal budworm hosts (Swetnam and Lynch 1993). Pine bark beetles (Dendroctonus and Ips) feed on the cortex and cambium and introduce fungi that promote rapid tree death and decay.

The roundheaded pine beetle (D. adjunctus) is the most common bark beetle that attacks pines in the Southwest (Chansler 1967; Furness and Carolin 1977). This beetle infests ponderosa and related pines from Colorado and Utah south to Guatemala (Massey et al. 1977). Outbreaks have occurred periodically and killed large numbers of pole-and sawtimber-sized ponderosa pine (trees larger than 23 cm dbh), especially in the White and Sacramento Mountains in 1950, 1960s, 1970s, and 1990s (Lucht et al. 1974; Chansler 1967; Flake et al. 1972). Eruptions of roundheaded pine beetle are often accompanied by the western pine beetle, Mexican pine beetle, and Ips beetles, which establish on poor sites or in mistletoe infested areas. Trees are attacked in groups of 3 to over 100; smaller trees and those in dense thickets are most likely to be attacked. Killed trees rapidly develop a brown cubical decay and break near the groundline.

The western pine beetle (D. *brevicomis*) is most damaging in the far western United States and British Columbia, but its range extends into the Southwest and Mexico (DeMars and Roettgering 1982). This beetle usually occurs in one or a few widely scattered trees already weakened by drought, lightning, stagnation, root disease, or other disturbances. Although it usually creates small canopy gaps, the western pine beetle can cause significant mortality and increased fire hazard in drought and competition-stressed stands; an outbreak occurred near Flagstaff, Arizona from 1980 to 1982 (Telfer 1982).

The mountain pine beetle (*D.* ponderosae) is the most extensive bark beetle to attack ponderosa pine in western North America. In the Southwest, however, outbreaks have been restricted to the north Kaibab Plateau (Parker 1980). Like the roundheaded pine beetle, the mountain pine beetle can develop large populations in dense stands and then disperse to kill large numbers of otherwise vigorous trees.

The Arizona five-spined engraver beetle (Ips lecontei) is the most common bark beetle in central and southern Arizona. Although this beetle usually occurs in slash and small, weakened trees, it has multiple generations per year that allow populations to build quickly (Parker 1991).

Dwarf Mistletoe

Southwestern dwarf mistletoe (Arceuthobiurn *vaginatum* subsp. *cryptopodum*) is a widely distributed parasitic plant that causes severe damage and mortality to its principal host, ponderosa pine (Hawksworth and Wiens 1995). Southwestern dwarf mistletoe occurs throughout the range of ponderosa pine in New Mexico and Arizona and extends into neighboring states. Other infected pines include Arizona pine, Apache pine (*Pinus engelmannii*), and Colorado bristlecone pine (P. aristata). Region-wide, 40 percent of the commercial pine forest is infested. Infection is more common in some forests; 70 percent of the stands in the Lincoln National Forest are infested (Maffei and Beatty 1988). Growth loss and mortality from this mistletoe in the Southwest is estimated at 150 to 200 million board feet per year (Walters 1978). The severity of growth loss for infected trees is related to disease intensity (Hawksworth 1977). Radial growth increment is reduced by 9 percent, 23 percent, or 53 percent for trees moderately infected (class 4), heavily infected (class 5), or very heavily infected (class 6), respectively (Hawksworth 1961). Survival of infected trees is also reduced; 10-year mortality rates of 9 percent, 12 percent, and 38 percent for trees rated class 4, 5, and 6, respectively, have been observed (Hawksworth and Lusher 1956). Other effects of mistletoe infestation include reduced reproductive output (Koristan and Long 1922) and increased likelihood of attack and mortality from bark beetles and pandora moth.

In mesophytic forests, selective loss of ponderosa pine from dwarf mistletoe can accelerate conversion to Douglas-fir or white fir. However, Douglas-fir in ponderosa pine stands is a principal host for the Douglas-fir dwarf mistletoe (Arceuthobium douglasii), which is very damaging to that species. The dense swollen and branching structures resulting from mistletoe infection, known as witches' brooms, often form near the ground. Broomed trees are more readily killed by even a low-intensity fire, and these brooms provide a fuel ladder into the crown (Alexander and Hawksworth 1974; Harrington and Hawksworth 1990). Mistletoe spread and intensification is greatest in stands with a multiple story structure.

Although there is evidence that mistletoe abundance has increased in the last century (Maffei and Beatty 1988), it has long been an important natural disturbance (figure 5). In addition to mistletoe shoots and associated insects providing wildlife forage, infections and brooms are especially suitable for roosting and nesting birds. Dead tops and snags created by mistletoe also enhance wildlife habitat (Bennetts et al. 1996; Hall et al. this volume; Rich and Mehlhop this volume). Although mistletoe infestation can increase canopy and wildlife diversity (Mathiasen 1996), the desired amounts or tolerable levels for resource objectives other than timber production are unknown.

Plant Pathogens

Root disease fungi, including Arrnillaria ostoyae and Heterbasidion *annosum*, are a major cause of tree mortality and growth loss in the Western United States. In the Southwest, 446 thousand ha are seriously affected by root diseases (DeNitto 1985), which reduce growth by 10 percent region-wide or by 25 percent in severely damaged stands (Rogers and Hessburg 1985). Complexes of root disease with insects and pathogens were associated with 34 percent of the mortality in all stands (Wood 1983). Root disease is more common in the mesophytic than xerophytic ponderosa pine zone. *Armillaria* is generally found in stands 10 to 25 years old, but in the Jemez Mountains,

New Mexico, 50 years of selective logging intensified disease severity and lead to extensive mortality in all ages of ponderosa pine (Marsden et al. 1993). *Annosus* root disease also infects ponderosa pine throughout the Southwest but is less common than other diseases. Like the mortality patches caused by dwarf mistletoe, centers of root disease reduce high canopy densities and increase patchiness. As discussed in the wildlife section of this chapter, these changes to forest structure are important to wildlife. Many of the organisms described here contribute to gap dynamics, forest structural diversity, and wildlife use in ponderosa pine forests (Lundquist 1995a, 1995b).

Figure 5. Stand of ponderosa pine June 4, 1990, Tonto Basin, Arizona. The multistory structure and high incidence of dwarf mistletoe disturbance is evidenced by the many large brooms in lower crowns and progressive dieback of upper crowns. Giffort Pinchot, the photographer, noted the sparsity of understory vegetation, consisting of only a little lupine.

The white pine blister rust caused by the fungus *Cronartium* ribicola, was discovered in the Sacramento Mountains of New Mexico in 1990. This fungus infects Southwestern white pine but has an indirect impact on ponderosa pine because as these tree species compete in mixed conifer forests, southwestern white pine is less susceptible to insects and diseases than ponderosa pine. Rust mortality of Southwestern white pine could possibly decrease its buffering affect on various other disturbances and will have a major impact as the disease progresses (Wilson and Tkacz 1996); at present the ecological consequences are speculation.

Wood Decay Fungi

Although there are many wood decay fungi (Basidiomycetes) of ponderosa pine (Gilbertson 1974), a few species commonly cause trunk rot. Red rot (*Dichomitus* squalens) is a major stem decay fungus of live ponderosa pine in the Southwest (Andrews 1955). An estimated 15 to 25 percent of the gross volume in old-growth ponderosa pine was decayed by red rot (Andrews 1955; Lightle and Andrews 1968). Common decay fungi that cause brown cubical rots of ponderosa pine include Phellinus pini (red ring rot), *Fomitopsis officialis*, Phaeolus schweinitzii (more common on Douglas-fir), Veluticeps berkeleyi, and *Lentinus lepideus* (usually associated with fire scars). In addition to their important roles in nutrient recycling and organic decomposition, decay fungi provide the soft wood habitat in snags that is required by numerous cavity-dependent species as discussed in later chapters.

Overstory-Understory Relationships

General

Rather than directly affecting passerine birds, land managers manipulate forest composition and structure. To understand why and how the environment of passerine birds in ponderosa pine forests is always changing, it is necessary to comprehend the interactions that determine forest composition and structure. Plant succession in ponderosa pine forests is a complex of overstory-understory (O-U) dynamics responding to disturbances. Overstory-understory refers to the effects of tree canopies (overstory) and ground-layer plants (understory) including shrubs, herbaceous vegetation, cryptogams (mostly mosses and lichens) on the soil surface, and tree seedlings. The heights that species display canopies is a continuum, so there is no precise definition the O and U classes. Trees, shrubs, herbs, and nonvascular plants (such as mosses and lichens) are usually easily distinguished, and their canopy levels can be assigned to local condition classes. Competition also occurs in the soil; for example, as root competition for soil water or the mycorrhizal differences between herbaceous and coniferous vegetation (Kendrik 1992; Klopatek 1995). Figure 6a, a generalized model, shows O and U competing, but their affects cannot be separated from other abiotic and biotic factors such as prescribed or wild fires, forest insects and pathogens, and soil microorganisms. At any location, both climate and soil influence the reactions shown in figure 6b. This climate, soil, vegetation influence is the basis of ecosystem classification, mapping, and interpretation used by the USDA Forest Service Southwest Region (USFS 1991). Plant succession, which after a fire holocaust killed virtually all of the aboveground vegetation, has been studied quantitatively, most notably after the La Mesa fire near Los Alamos, New Mexico (Foxx 1996)

A large class of O-U relationships are associated with tree death and falls (Denslow and Spies 1990). Canopy gaps operate on individual trees, especially the larger dominant or codominant trees. In open, low density pine forests before European settlement, gap processes may have been unimportant because recurrent fires determined tree and understory spatial patterns. However, in this century as tree densities greatly increased, new spatial patterns were created by expanding root rot pockets (Wood 1983) and other diseases, increased abundance of dwarf mistletoe, insect outbreaks, and rapid filling of former open areas by tree regeneration (Allen 1989). Today, especially in xerophytic forests, canopy gap processes may be dominant in O-U dynamics (Lundquist 1995b, 1995c).

In mesophytic pine forests, the death of large trees may be important to maintain shade intolerant trees such as ponderosa pine, aspen, and gambel oak. Forest pattern is determined by combinations of patchy, natural fires (Jones 1974) and other gap-creating factors that stress trees and expose them to numerous mortality agents (Franklin et al. 1987; Lundquist 1995c). In both xerophytic and mesophytic pine forests, silvicultural (Schubert 1974; Oliver and Ryker 1990) or disturbance management (Geils et al. 1995) are used to create or maintain gaps in the absence of fire. In mesophytic forests, however, small canopy gaps are usually filled by shade tolerant trees (Dieterich 1983; Ffolliott and Gottfried 1991). Small gaps do not ensure that shade intolerant trees, such as ponderosa pine, gambel oak, or aspen, or herbs, will be maintained (Moir 1966).

Understory Influence on Trees

Research has focused on competition between the herbaceous layer, particularly grasses and tree seedlings

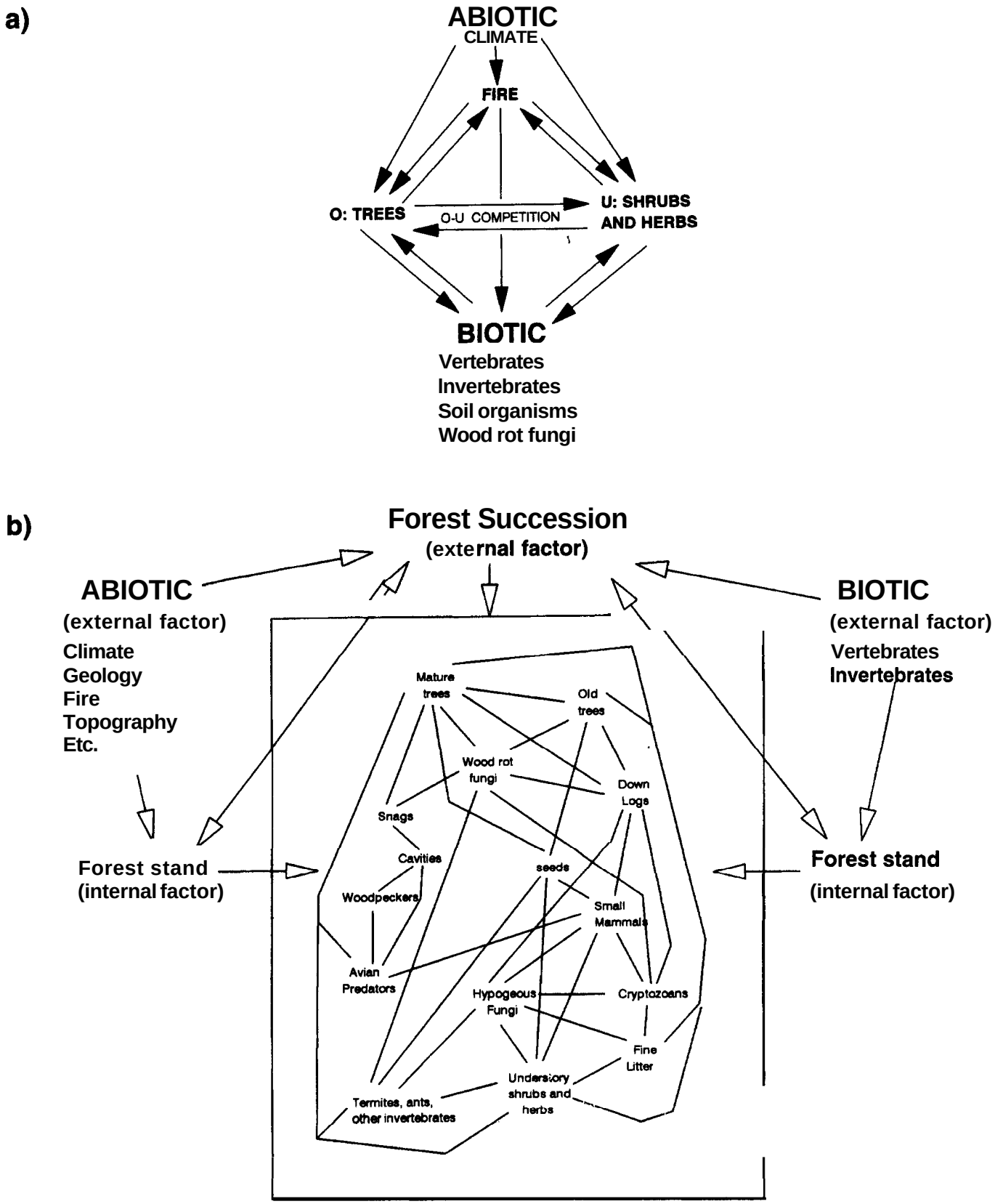

Figure 6. a) Simplified, schematic representation of overstory–understory relationships and ecological associations (Verner et al. 1992). b) A forest stand (internal factors) and the surrounding environment (external factors) that influence the nature and intensity of stand dynamics.

(figure 6a). Competition can be for light (Moir 1966), nutrients (Elliott and White 1987; Moir 1966), water (Larson and Schubert 1969; Embry 1971; Miller 1988), and combinations of these (Moir 1966). Sometimes, shrubs can lessen tree seedling survival or diameter growth (White 1987; Rejmanek and Messina 1989). In the Southwest, *Festuca arizonica* is particularly competitive because it consumes soil moisture during the drought season of April and May (Pearson 1931, 1942, 1950). Allelopathy (compounds produced by one plant species that inhibit the establishment or growth of another species) has also been suggested as a means of tree control (Rietveld 1975; Stewart 1965); however, this subject has received little recent attention. The detrimental effects of understory vegetation on tree establishment can be mitigated by grazing and burrowing animals. Browsing, grazing, or burrowing animals create microsites where reduced herb or shrub competition and exposed mineral seedbeds enhance pine seed germination, seedling survival, and growth (Rummell 1951; Doescher 1987).

Fire also has direct affects on small trees and ground cover (figure 6a). Generally, fire stimulates the understory while killing tree seedlings, saplings, or entire thickets. Fire is the principal means of restoring cover and grass vigor and maintaining or invigorating shrubs (Martin 1983; Harper and Buchanan 1983; Biswell 1972; Bunting et al. 1985; Pearson et al. 1972; Harris and Covington 1983; Andariese and Covington 1986; Ffolliott et al. 1977; Moir 1966). Fire favors understory vegetation by reducing tree competition for sunlight, moisture, and nutrients, accelerates the nutrient cycle, and, by killing trees, changes the soil-water relationship usually to the benefit of ground vegetation. In the past, fire was often carried by extensive and continuous understory vegetation, resulting in small-tree mortality over large areas (Abolt et al. 1995). Before European settlement, recurrent fire was the principal agent maintaining the relationship between overstory trees and understory vegetation. When the herbaceous or herb-shrub vegetation became depleted by overgrazing (Touchan et al. 1995; Savage and Swetnam 1990), heavy tree seedling occurred in the Southwest and elsewhere. The effects of grazing are discussed in Chapters 2, 3 and 6. Fuel reduction and reduced competition between trees and the understory have resulted in increasing tree densities during this century (Pearson 1950; Allen 1989; Savage and Swetnam 1990; Brown et al. 1994; Touchan et al. 1996; Moir and Fletcher 1996).

Tree Influence on Understory

Once past their seedling stage, continued growth of pines or other trees reduces cover, vigor, density, and biomass of many understory species. Particularly affected are species that grow best in open meadows or full sunlight (Ffolliott and Clary 1982). However, O-U dynamics vary greatly among sites and forest types, so generalized statistical models are unsatisfactory (Mitchell and Bartling 1991). Gap processes may be important, depending on fire history, gap size, and gap microclimate. Dense thickets of conifers in their sapling or pole stages of succession can extinguish understory vegetation. In livestock grazing allotments, the adverse influence of trees on ground vegetation is well-known in ponderosa pine/bunchgrass and ponderosa pine/blue grama rangelands (Arnold 1950; Reid 1965; Clary and Ffolliott 1966; Currie 1975; Johnson 1953; Smith 1967; Brown et al. 1974). Biswell (1972), citing data from research in the Black Hills, reported declines in herbage biomass from 1,860 kg/ha in openings to 39 kg/ha under closed ponderosa pine canopies. In northern Arizona pine/bunchgrass ranges, Jameson (1967), using negative exponential equations to fit tree basal areas to herbage harvest data, showed declines from 784 kg/ha in areas without trees to less than 56 kg/ha where pine basal areas exceeded 23 m^2/ha. Working in ponderosa pine stands with a grassy understory in eastern Washington, Moir (1966) reported that low supplies of nitrogen and reduced light acted additively and interactively under developing pine thickets to suppress *Festuca idahoensis*. Moir found reduced inflorescence production in stressed grasses followed by reduced foliar cover.

Oaks are a valuable resource used by numerous birds and mammals. The adverse relationships between pines and oaks can be severe. Neither deciduous nor evergreen oaks tolerate shade. They grow best in full sunlight and are often quickly started by hot, stand-replacing fires that induce sprouting. Sprouts grow rapidly, soon dominate burned sites, and often suppress pine regeneration and growth (Hanks and Dick-Peddie 1974; Harper et al. 1985). However, oaks are suppressed and die back once conifers overtop them. In open stands where oaks and junipers form a distinctive mid-layer canopy, such as the pine-oak woodlands of Marshall 1957 and ponderosa pine/gambel oak forests, oaks persist as mid-level trees or as groups of clustered stems if the density or basal area of taller, emergent pines is low. But as pine canopies close during advanced stages of forest succession, oaks die back and are maintained as suckers from below-ground rootstock. Suckering can take place for decades until the next crown fire occurs (USFS 1986, 1987a, 1987b). Oaks growing in full sunlight will coppice from basal portions of the stem and grow rapidly if fire or cutting kills the overstory trees. Both coppicing and suckering are adaptations to fire. If large oak trees, those greater than a specified diameter and taller than a specified height, are part of the desired landscape, then overtopping by conifers must be prevented until the desired heights and diameters of oak are attained. Before about 1890, recurrent surface fires helped maintain oak and pine codominance (Dieterich and Hibbert 1990; Moir 1982; Swetnam et al. 1992). Marshall (1963) claimed that the grassy pine-oak savannas in northern Mexico were maintained by natural fires, whereas

comparable, densely stocked and grass deficient pine-oak forests in the United States were due to aggressive fire suppression programs.

Plant-Animal Relationships

Overstory-understory relationships are directly and indirectly linked by numerous food webs. Some of the more well-known relationships are mentioned in this chapter. Nearly all ponderosa pine forests in the Southwest contain livestock grazing allotments (Raish et al. this volume; Finch et al. this volume) and many areas contain elk and deer. Mitchell and Freeman (1993) discuss the complex interactions of fire, deer, livestock, predators (especially mountain lions), and understory vegetation on the North Kaibab Plateau, which contains extensive ponderosa pine forests (Madany and West 1983). Herbivores directly affect tree structures by trampling or browsing on tree seedlings and saplings (Cassidy 1937; Currie et al. 1978; Eissenstat et al. 1982; Pearson 1950; Crouch 1979).

Browsing on small trees may affect both conifers and deciduous trees. Aspen regeneration is a preferred food by domestic livestock, elk, and deer; severe browsing prevents regeneration where small aspen patches are part of a larger landscape (Crouch 1986). By contrast, aspen regenerates well in mesophytic forests after extensive stand-replacing fires as, for example, the Escudilla Mountain burn in Arizona. Browsing can also affect other important understory species such as gambel oak (Quercus *gambelii*), antelope bitterbrush (Purskia tridentata), junipers, snowberry (Sympkoricarpos spp.), and deerbrush (*Ceanothus* fendleri) (Harper et al. 1985; Harper and Buchanan 1983; Kruse 1992).

Bark damage by bears, porcupines (whose principal food in winter includes pine phloem), antlered animals, and humans affects individual trees. Feeding impacts on selected ponderosa pines by porcupines and Abert's squirrels may have substantial affect on tree genetics (Linhart et al. 1989). The Abert's squirrel was described by Pearson (1950) as "one of the most destructive of all animals" because of twig cutting, seed and cone herbivory, and defoliation of terminal twigs of ponderosa pine. As mentioned, animals feeding on understory shrubs and herbs increase tree densities and dominance by reducing understory competition. Doescher (1987) and others suggested livestock grazing practices that create a favorable balance between livestock numbers and season of grazing, forest or plantation pine growth, and maintenance of understory productivity.

Animals have an important role through mycophagy (fungus eating) in forest regeneration and tree growth. Hypogeous fungi (fruiting below ground) are a major source food of small rodents, deer, and javelinas (Kotter and Farentinos 1984a, 1984b; Hunt and Z. Maser 1985; Fogel and Trappe 1978). Nitrogen fixing bacteria and germinating spores of mycorrhizal fungi in the fecal pellets of these animals can enhance pine seedling survival and growth. Given the important but complex roles of mycorrhizal fungi, trees, and understory vegetation (Brundrett 1993; Klopatek 1995; States 1985), animals that disperse fungal spores, including small mammals, grasshoppers, worms, ants, wasps, and some birds, play an indirect but significant role in O-U relationships.

As tree strata develop they modify the composition, cover, and density of understory shrubs and herbs. As the understory changes, so does the composition of prey species dependent on it. Examples are the predator-prey relationships of the Mexican spotted owl and northern goshawk during various stages of forest succession (figure 6b). Both of these raptors are found in ponderosa pine forests of the Southwest. Their persistence may involve treatment of tree structure and density to ensure that understory shrubs and herbs have cover characteristic~ needed by prey populations (Ward and Block 1995; Reynolds et al. 1992, 1996). The complexity of these ecological interactions (figure 6b) was described for the California spotted owl by Verner et al. in 1992 but also applies to the Mexican spotted owl in the Southwest.

Hidden Diversity Organisms

Hidden diversity organisms (soil and litter invertebrates, plant pollinators, cone and seed predators, wood decay organisms, vertebrate parasites, mycorrhizal fungi, and other seldom studied organisms) are important in nutrient cycling and plant-water relationships in ponderosa pine forests (Castellano 1994; Mason 1995; Gilbertson 1974; Maser and Trappe 1984; States 1985). Some of these organisms are related to decay processes in litter and coarse woody debris. However, their role in ecosystem dynamics of litter and coarse woody debris has changed from what it was before European settlement. Recurrent ground fires in pine forests before about 1890 kept pine-derived fuels to a minimum. Ponderosa pine snags may have persisted for a time, but downed fuels were mostly burned off by frequent surface fires. Early settlers described grassy pine savannas, not woody ground debris, although some old photos do show some logs (Woolsey 1911; figure 5). Wood decay organisms and their associated food webs were present in pre-1900 forests, but their abundance and their roles in fire-adapted forests is unknown. The stand replacing fire holocausts experienced in the past 10 years burned the aboveground vegetation and destroyed mycorrhizae in scorched soils (Klopatek 1995; Klopatek and Klopatek 1993; Vilarino and Arines 1991). However, plant succession after these stand replacing fires has hardly been studied (see Foxx 1996).

There is concern that diversity in forest ecosystems is decreasing. Wilson (1992) discusses this situation for tropical forests, and it is also relevant to ponderosa pine for-

ests. Among functions, such as in carbon and nutrient cycles, hidden diversity organisms possibly contribute to ecosystem resilience, which is the ability of ecosystems to recover or adjust to disturbances. Management should maintain hidden and other kinds of diversity of native organisms to restore or sustain pine ecosystems (Kauffman et al. 1994; Opler 1995; Maser and Trappe 1984; Reynolds et al. 1992; Rapport and Yazenko 1996).

Wildlife

Ponderosa forests provide habitat for birds, mammals, reptiles, and amphibians including threatened or endangered species, neotropical migratory birds, and game species. Detailed information about ponderosa pine forest habitat use by passerine birds is in Chapters 3 and 6. The following section reviews the importance and use of successional stages in ponderosa pine forests by vertebrates.

Overstory Tree Influence on Wildlife

The overstory structure and plant diversity of ponderosa pine forests affect their use by wildlife. Important forest features include age, size class, and of canopy cover trees, patch size of tree groups, multiple or single canopy layers, and presence of other vegetation such as gambel oak and juniper. Review of the literature and analysis of R3HARE, which is a computerized wildlife relational database for Southwestem forests (Patton 1995), document wildlife use patterns of these ponderosa pine forest structures (Benoit 1996). The following descriptions of forest structural stages mention a few of the vertebrates associated with the stages.

Structural Stages

Six vegetative structural stages, VSS1 to VSS6 (Thomas 1979; Moir and Dieterich 1988), occur within ponderosa pine forests through timber harvest, wild or prescribed fires, diseases, insects, or windfall, which all affect the dynamics of overstory and understory of forest succession. The VSS stages apply to forest stands during succession or stand development; each stage is important to different species of wildlife for feeding, cover, or reproduction. Canopy cover classes of trees (A=0 to 40 percent, B=40 to 60 percent, C=60 percent and over) within each stage also influence how the area is used. Cover includes thermal, hiding, and reproductive cover. Many habitat generalists, such as bear, turkey, elk, mule deer, bobcat, coyote, and northern goshawks, use all structural stages.

Openings (VSS1) occur after significant disturbance, such as fire or timber harvest (Hoover and Wills 1984), or gap processes (Lundquist 1995b). Openings may be maintained as meadows or parks in pine savannas where recurrent surface fires occur and may include a snag stage after a stand replacing fire (Moir and Dieterich 1988). Deer and elk rely heavily on openings for forage (Hoover and Wills 1984). Openings provide primary habitat for numerous other vertebrates that use grasses for shelter or feed on grasses, seeds, or insects.

Seedlings and saplings (VSS2, trees <12.7 cm dbh) provide some hiding cover but may have little forage value depending on tree density (Hoover and Wills 1984). Small tree seedlings of low density often grow in an herbaceous or shrubby environment, which can provide some forage and cover and are used primarily by habitat generalists, some of the VSSl species, and shrub nesting birds. As seedlings grow to saplings the tree canopies close and forage declines.

Young stands (VSS3, trees 12.7 to 30.2 cm dbh) are usually dense and clumped in unmanaged stands. Tree canopy cover often exceeds 70 percent. Stands have sparse herbaceous understory, few snags, and single-storied structure (Hoover and Wills 1984). Denser stands provide thermal cover for habitat generalists and some raptors, but their value for forage and hiding cover is minimal. With sparse understories there is little use by other vertebrates, except possibly animals feeding on fungi.

Mid-aged stands (VSS4, trees 30.5 to 45.5 cm dbh) begin cone production, tend to be multi-storied, and provide small snags suitable for some cavity nesters (Hoover and Wills 1984). Species other than generalists in this stage include squirrels, pygmy nuthatches, and various raptors.

Mature stands (VSS5, trees< 45.5 cm dbh) may be single or multi-storied, with more litter and dead and downed debris in stands without fire for a long period. Mature stands may contain larger snags than in the VSS4 stage. These stands provide a good seed crop and are used for thermal cover by big game (Hoover and Wills 1984). Species found in the VSS4 stage also use mature stands, In addition, mature stands have high value for feeding and/ or cover for flickers and some owls, hawks, eagles and passerine birds.

Old growth forests (VSS6) provide single and multiple stories with many mature trees and dense canopies (>40 percent) in stands not experiencing ground fires in their VSSl and VSS2 stages. Old, yellow-pine forests, which were extensive before European settlement, are open and relatively devoid of coarse woody debris. In ponderosa pine/ bunchgrass environments before about 1890 in Arizona and New Mexico, ponderosa pine required at least 300 years beyond the herbaceous or burned snag stages to develop old growth characteristics (Moir and Dieterich 1988). Today old growth stands are heavily stocked, have much dead and downed material and numerous large snags, and contain trees that are >61 cm dbh (Moir 1992). Without restoration, most of these decaying, old growth stands are at risk of fire holocaust similar to the La Mesa

and other large burns in the last few decades (figure 4; Allen 1996; Moir and Dieterich 1988). Large trees and snags provide the best source of cavities for vertebrates. The primary users of this stage are passerine birds (Hall et al. this volume; Rich and Mehlhop this volume) and raptors.

Understory Tree Influence on Wildlife

All plants contribute to the ecology of ponderosa pine forests and influence the number of vertebrates and invertebrates. Gambel oak (Quercus *gambelii*) and alligator juniper (*Juniperus* deppeana) are often associated with ponderosa pine and provide additional structural diversity, food, thermal and hiding cover, and nest sites for numerous species. The numbers of species below are from R3HARE (Patton 1995) and Nagiller et al. (1991).

Gambel oak provides a key habitat component for birds in pine-oak forests and offers valuable alternate cavity nesting sites when pine snags are limited (Rosenstock 1996). All stages of oak, but especially large trees, are important to wildlife (Kruse 1992). Mature trees benefit the most species with regard to food and nesting sites. Shrubby oaks result from suckering and coppicing, as discussed above. The sprouts and trunks provide food, hiding and thermal cover for deer, elk, and numerous birds (Nagilleret al. 1991). Areas of brush and sprouts may provide important fawning grounds for deer, and cover and foraging habitat for rabbits and rodents (Kruse 1992).

Taller clonal oak groups provide habitat for foliage nesting birds (Szaro and Balda 1979). Foliage and buds provide food for deer, elk, and birds (mourning dove, band-tailed pigeon, turkey, rufous-crowned and chipping sparrows, and spotted towhee). Arthropods living in the foliage and on twigs provide food for birds such as the screech owl, pygmy and white-breasted nuthatches, and brown creeper (Patton 1995).

Some clonal oak and mature trees produce acorns that feed 21 species of mammals and 20 species of birds such as corvids and woodpeckers (Patton 1995). Acorns are the preferred food of Abert squirrels, band-tailed pigeons, turkeys, deer, elk, and acorn woodpeckers. Acorn crops may influence the numbers of these species. Large trunks provide hiding and thermal cover for deer, elk, rabbits, and birds (Nagiller et al. 1991). As the trees age and become less vigorous, acorn production drops, but hollow boles and limbs offer cavities sheltering 10 species of mammals and 19 species of birds such as bats, squirrels, racoons, owls, woodpeckers, and passerine birds (Nagiller et al. 1991).

Young alligator junipers provide hiding cover for elk, deer, rabbits, turkey, small mammals, and birds (Nagiller et al. 1991). Large trees provide nesting cover for birds such as pinyon jays, scrub jays, and blue-gray gnatcatchers (Degraff et al. 1991); thermal cover for deer, elk, and small mammals (Abbott 1991); and juniper berries as food for several species of birds and small and large mammals. Alligator juniper provides food and cover for wildlife all year long and is critically important when deep snows make other food sources unavailable.

Wildlife Communities

Although overstory and understory tree structure and diversity provide important habitat components for wildlife, no particular structure or species can satisfy the needs of the entire wildlife community. Wildlife community use of Southwestern ponderosa pine forests is illustrated using the R3HARE database (Patton 1995) and the Coconino National Forest. This forest has xerophytic and mesophytic ponderosa pine stands and numerous other habitats such as desert scrub, pinyon-juniper, riparian, mixed conifer, and grasslands (Benoit 1996). Of the 435 species that occur in the Coconino National Forest, 50 percent use ponderosa pine forests to meet some or all of their habitat needs. This includes 56 percent of the mammals, 46 percent of the birds, 61 percent of the reptiles, and 54 percent of the amphibians. Eighteen percent of Coconino species (mainly mammals, reptiles, and amphibians) use the ponderosa pine habitat year round. Thirteen percent use it in summer only, 2 percent in winter only, and 17 percent as fringe habitat or transient habitat. The majority of birds (75 percent) use it as fringe, transient or summer habitat (Benoit 1996).

Overall vegetative structural stage use by wildlife (Patton 1995; Benoit 1996) is fairly evenly distributed with slightly higher use in mature and old growth forests and B (40 to 60 percent) and C (60 percent and over) canopies. Young stands and A (0 to 40 percent) canopies are used the least. The distribution is also somewhat uniform across all stages for species for which certain vegetative structural stages have high value. Use by threatened, endangered, sensitive, or dependent species (those that depend on certain structures in ponderosa pine for survival), and birds is also fairly uniform across all stages. Mammals follow an opposing pattern, with higher use occurring in openings, seedlings, and saplings than in mature or old growth areas. Forest indicator species occur predominately in mid-aged and mature stands, and do not indicate overall use patterns in the community or those of species of special concern. Information on structural stages use by amphibians and reptiles is limited, but they appear to prefer VSS1 and 2 and probably respond primarily on the microsite level.

Sixty-one percent of birds using ponderosa pine in the Coconino National Forest are passerines (Patton 1995; Benoit 1996). Use is primarily in summer (44 percent) or as fringe habitat (23 percent). Passerine use is highest in mature and especially old growth stands. Eight of the 12 dependent species are passerine birds associated with old

growth. Use by canopy density is evenly distributed with a slight preference for B canopies.

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