

Chapter 4

Ponderosa Pine Forest

Abstract Ponderosa Pine Forest is the lowest-elevation, most extensive forest in the American Southwest. It occurs in an elevational band below Mixed Conifer Forest and above Pinyon-Juniper vegetation, Gambel Oak Shrubland, and Interior Chaparral Shrubland. Stands are dominated by ponderosa pine, and are divided into moist, mesic, and dry stand types with decreasing elevation and moisture availability. A historical fire regime of frequent, low-severity surface fires is widely documented, but there is growing evidence of historical mixed-severity and high-severity fires, especially for steep slopes in areas of heterogeneous topography. Other important natural disturbances include insect outbreaks and drought. Late nineteenth century livestock grazing initiated fire exclusion, which was continued by fire management through most of the twentieth century. Other anthropogenic drivers are modern climate change, invasive species, recreation, and nearby land use. Vegetation dynamics are dominated by tree regeneration, thinning, and succession. Historical conditions ranged from open-canopied stands with a well-developed, often grass-dominated understory – more woodland than forest – to denser stands. Stand densities increased during the twentieth century because of the exclusion of surface fires. Vegetation dynamics are illustrated in a nested, three-tiered set of conceptual models. Key conclusions and challenges for researchers and land managers are summarized.

4.1 Introduction

Ponderosa Pine Forest (*Pinus ponderosa*) is the lowest-elevation coniferous forest of the American Southwest (Figs. 4.1 and 4.2). It occurs in an elevational band below Mixed Conifer Forest and above Pinyon-Juniper vegetation (*Pinus-Juniperus*), Gambel Oak Shrubland (*Quercus gambelii*), and Interior Chaparral Shrubland. With this elevational position, Ponderosa Pine Forest has the most extensive, contiguous distribution of any forest in the Southwest. It covers about 49,000 km² (18,900 miles²), which is 6.3 % of the total area of the region (Fig. 4.3; calculations



Fig. 4.1 Landscape of Ponderosa Pine Forest in Santa Fe National Forest, north-central New Mexico (Photograph by Betty J. Huffman)



Fig. 4.2 Landscape of Ponderosa Pine Forest with surface fire in Santa Fe National Forest, north-central New Mexico. Note variation in tree densities (Photograph by Kari Greer/U.S. National Forest)

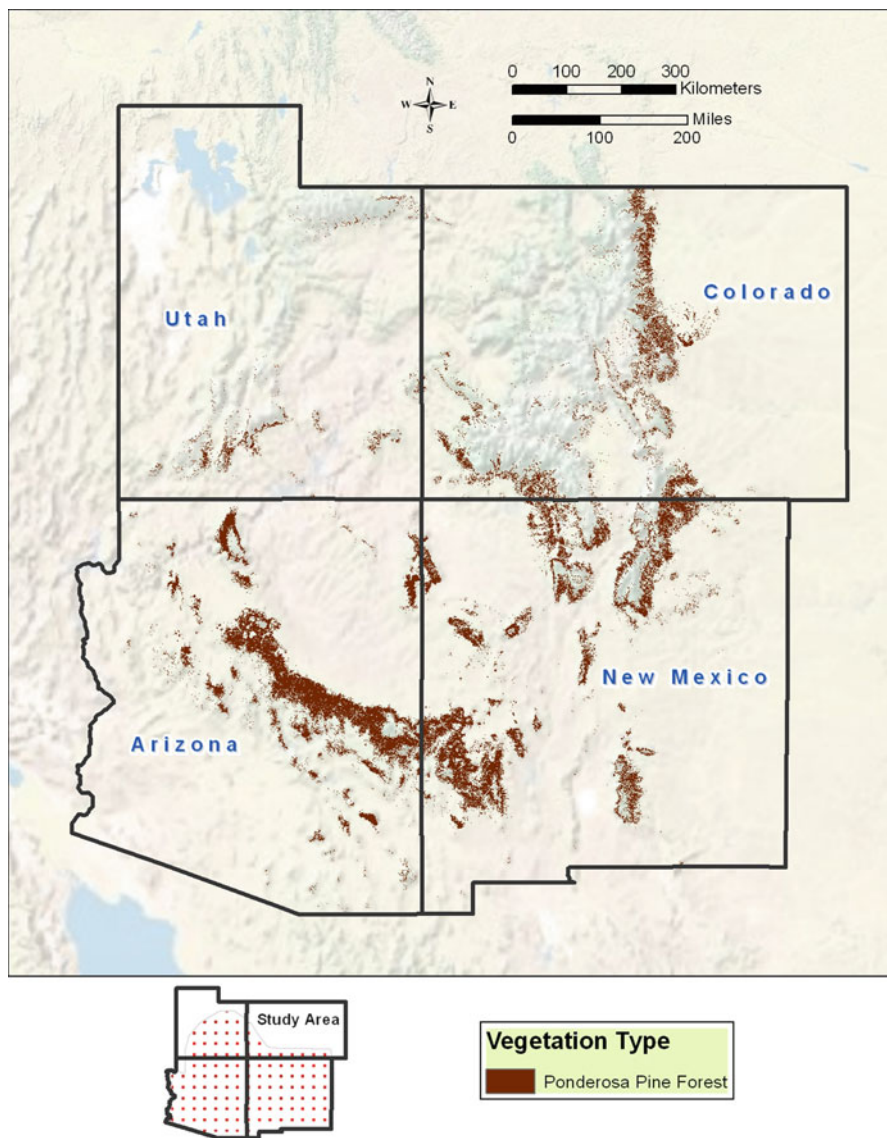


Fig. 4.3 Distribution of Ponderosa Pine Forest in the American Southwest. The map shows all of the states of Arizona, New Mexico, Colorado, and Utah, and the American Southwest is illustrated in red on the small map (Source: U.S. Geological Survey National Gap Analysis Program 2005 Southwest Regional Gap Analysis Project, RS/GIS Laboratory, College of Natural Resources, Utah State University, Logan, Utah. Map prepared by Monica Swihart)

based on Prior-Magee et al. 2007). These values do not include stands dominated by quaking aspen (*Populus tremuloides*), which cover 8,100 km² (3,100 miles²) and 1.0 % of the region. Only approximately 5 % of aspen stands are associated with Ponderosa Pine Forest; the rest occur with Spruce-Fir (*Picea-Abies*) and Mixed Conifer Forests

Table 4.1 Common and scientific names of species in this chapter. Primary sources: Integrated Taxonomic Information System (2012) for plants and animals and Bates (2006) for fungi

<i>Plants</i>	
Apache pine	<i>Pinus engelmannii</i> Carrière
Arizona pine	<i>Pinus arizonica</i> Engelm.
Arizona white oak	<i>Quercus arizonica</i> Sarg.
Cheatgrass	<i>Bromus tectorum</i> L.
Chihuahuan pine	<i>Pinus leiophylla</i> Schiede & Deppe
Colorado pinyon	<i>Pinus edulis</i> Engelm.
Common dandelion	<i>Taraxacum officinale</i> F.H. Wigg.
Common mullein	<i>Verbascum thapsis</i> L.
Common salsify	<i>Tragopogon dubius</i> Scop.
Dalmatian toadflax	<i>Linaria dalmatica</i> (L.) Mill.
Douglas-fir	<i>Pseudotsuga menziesii</i> (Mirbel) Franco
Fir	<i>Abies</i> P. Mill.
Gambel oak	<i>Quercus gambelii</i> Nutt.
Gray oak	<i>Quercus grisea</i> Liebm.
Juniper	<i>Juniperus</i> L.
Kentucky bluegrass	<i>Poa pratensis</i> L.
Manzanita	<i>Arctostaphylos</i> Adans.
New Mexico locust	<i>Robinia neomexicana</i> A. Gray
Oak	<i>Quercus</i> L.
Pinyon	<i>Pinus</i> L.
Ponderosa pine	<i>Pinus ponderosa</i> Douglas ex P. Lawson & C. Lawson
Ponderosa pine dwarf mistletoe	<i>Arceuthobium vaginatum</i> spp. <i>cryptopodum</i> (Engelm.) Hawksworth & Wiens
Quaking aspen	<i>Populus tremuloides</i> Michx.
Southwestern white pine	<i>Pinus strobiformis</i> Engelm.
Spruce	<i>Picea</i> A. Dietr.
Utah juniper	<i>Juniperus osteosperma</i> (Torr.) Little
Wayleaf oak	<i>Quercus X undulata</i> Torr.
White fir	<i>Abies concolor</i> (Gord. & Glend.) Lindl. Ex Hildebr.
Wild lettuce	<i>Lactuca serriola</i> L.
<i>Animals</i>	
Bark beetle	<i>Dendroctonus</i> Erichson, 1846 and <i>Ips</i> De Geer, 1775
Deer	<i>Odocoileus</i> Rafinesque, 1832
Elk	<i>Cervus elaphus</i> Linnaeus, 1758
Ips engraver beetle	<i>Ips</i> De Geer, 1775
Pandora moth	<i>Coloradia pandora</i> Blake, 1863
Pine sawfly	<i>Neodiprion</i> Rohwer, 1918
Sheep	<i>Ovis aries</i> Linnaeus, 1758
Western pine beetle	<i>Dendroctonus brevicomis</i> LeConte, 1876
<i>Fungi</i>	
Armillaria root rot	<i>Armillaria</i> (Fr.:Fr.) Staude
Annosus root rot	<i>Heterobasidion annosum</i> (Fr.) Bref.

(see Sects. 2.1 and 3.1, respectively). The only vegetation type that covers more area than Ponderosa Pine Forest on southwestern mountains and plateaus is Pinyon-Juniper. Southwestern Ponderosa Pine Forest decreases in area northward and becomes uncommon in central Utah (Fig. 4.3).



Fig. 4.4 Example of moist Ponderosa Pine Forest in the North Rim region of Grand Canyon National Park, north-central Arizona (Photograph by Betty J. Huffman)

The structure of undisturbed stands of southwestern Ponderosa Pine Forest is characterized by large ponderosa pines. Overstory cover is often ~15–33 % (e.g., Pearson 1923, 1950; White 1985; Covington and Sackett 1986). Although such an open overstory suggests woodland physiognomy, the large size of the trees and the presence of stands with greater overstory cover result in the vegetation being described as forest. Stand variation results from differences in density of ponderosa pine, as well as species of other canopy trees (at upper elevations), subcanopy trees, and understory plants. Detailed vegetation classifications of Ponderosa Pine Forest are available for different geographic areas within the American Southwest (Layser and Schubert 1979; Hanks et al. 1983; Alexander et al. 1984, 1987; Youngblood and Mauk 1985; DeVelice et al. 1986; Fitzhugh et al. 1987; Muldavin et al. 1996). More generally, stands are divisible into three broad types: moist, mesic, and dry (Vankat 2011).

Moist stands of Ponderosa Pine Forest (Fig. 4.4) are common at relatively high elevation and extend to lower elevation in drainages. They are transitional with Mixed Conifer Forest. Historically, these stands had scattered individuals of white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and southwestern white

pine (*Pinus strobiformis*) in the canopy, quaking aspen in the subcanopy, and Gambel oak in both the subcanopy and shrub layers. Quaking aspen is most abundant in recently disturbed stands.

Mesic stands of Ponderosa Pine Forest (Fig. 4.5) dominate mid elevations. Ponderosa pine is usually the only canopy tree. Gambel oak occurs in the subcanopy and shrub layers.

Dry stands of Ponderosa Pine Forest (Fig. 4.6) occur primarily at low elevations. They also have Gambel oak in the subcanopy and shrub layers. Other subcanopy species are pinyons such as Colorado pinyon (*Pinus edulis*) and junipers such as Utah juniper (*Juniperus osteosperma*). Stands are transitional with Pinyon-Juniper and sometimes other vegetation.

In addition to this elevational, moisture-driven gradation within Ponderosa Pine Forest, there is substantial latitudinal variation. In Utah and southwestern Colorado, Gambel oak and sometimes other shrubs are often more abundant. In southern Arizona and New Mexico, ponderosa pine is replaced in dry forests of similar overstory physiognomy by Apache pine (*Pinus engelmannii*), Arizona pine (*P. arizonica*), or Chihuahuan pine (*P. leiophylla*), and the understory can be dominated by oaks (*Quercus* spp.) such as Arizona white oak (*Q. arizonica*), Gray oak (*Q. grisea*), or wavyleaf oak (*Q. X undulata*).

Ponderosa Pine Forest is also extensive elsewhere in the western United States, as for example in north-central Colorado (Fig. 4.3). However, research findings from other regions are not always applicable to the Southwest, because there are differences in climate, associated species, and other factors. This chapter is based nearly entirely on research done on the mountains and plateaus of the American Southwest, where Ponderosa Pine Forest is the most thoroughly studied vegetation.

4.2 Drivers

Key drivers of southwestern Ponderosa Pine Forest are landscape, climate, soil, animals, natural disturbance, and anthropogenic disturbance. Each driver is important in vegetation dynamics, and therefore all are incorporated in the conceptual models (Sect. 4.5).

4.2.1 Landscape

Ponderosa Pine Forest occurs at approximately 1,800–2,500 m (5,900–8,200 ft) elevation in the mid-latitudes of its distribution in the American Southwest (Fig. 4.7). The topography ranges from relatively level plateaus to steep mountain slopes. At its upper elevational limit, Ponderosa Pine Forest intergrades with Mixed Conifer Forest. In areas of diverse topography, this transition is a mosaic (Plummer 1904; Greenamyre 1913) in which stands of Ponderosa Pine Forest occur on drier sites



Fig. 4.5 Example of mesic Ponderosa Pine Forest in the South Rim region of Grand Canyon National Park, north-central Arizona (Photograph by author)



Fig. 4.6 Example of dry Ponderosa Pine Forest in the South Rim region of Grand Canyon National Park, north-central Arizona (Photograph by Betty J. Huffman)

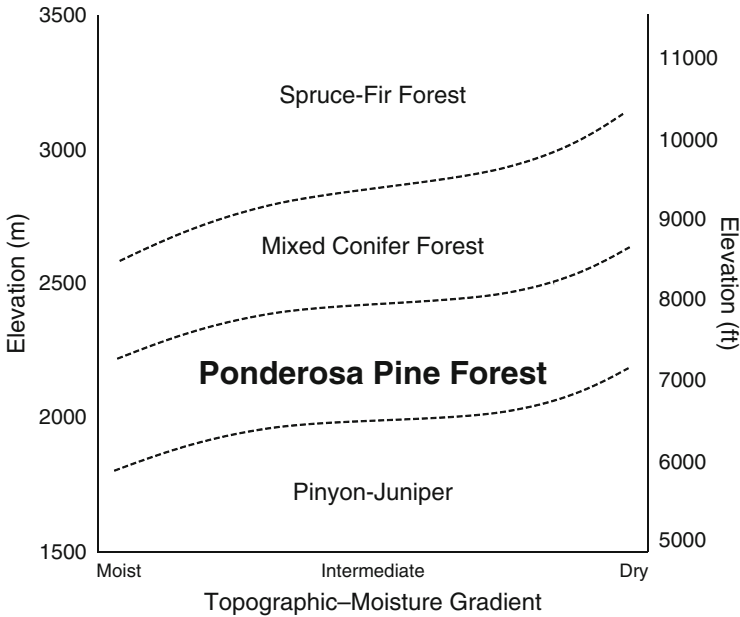


Fig. 4.7 Ecological distribution of Ponderosa Pine Forest on the mountains and plateaus of the American Southwest along gradients in elevation and moisture. Elevations are approximate and generally representative of mid-latitudes of the region, i.e., landscapes in northern Arizona and northern New Mexico

such as south aspects and ridgetops, and stands of Mixed Conifer Forest occur on more mesic sites such as north aspects and drainages. In areas where the topography is less diverse, this transition is gradual. The clarity of the mosaic and position of the transition changed as white fir, which is shade-tolerant and fire-intolerant, increased with fire exclusion during the twentieth century. This essentially converted stands into Mixed Conifer Forest (Dahms and Geils 1997; Swetnam et al. 2001; Mast and Wolf 2004; Evans et al. 2011).

At its lower elevational limit, Ponderosa Pine Forest intergrades primarily with Pinyon-Juniper vegetation but also with Gambel Oak Shrubland and Interior Chaparral Shrubland. These transitions also can be gradual or as a mosaic, but the mosaic is not always clearly related to topography. Fire appears to be the dominant factor determining the mosaic, with patterns both related and unrelated to topography.

4.2.2 Climate

Climate influences southwestern Ponderosa Pine Forest directly and indirectly. Direct effects include influences of moisture availability on tree recruitment. Indirect

effects occur through influences on disturbances such as fire and insects. The climate is characterized by cool temperatures and relatively long growing seasons of 120–180 days (Schubert 1974; Moir 1993; Pase and Brown 1994), during which moisture likely limits plant growth (Moir 1993). The climate can be considered borderline for forest, because it is among the driest of any forest area in North America (Moir 1993; Pase and Brown 1994). Annual precipitation averages 400 to >760 mm (16–30 in.) and is divided between winter and the summer monsoon season separated by dry springs and moderately dry falls (Pase and Brown 1994; Chambers and Holthausen 2000). Summer precipitation is possibly necessary for the existence of this forest in areas that average <640 mm (25 in.) annual precipitation (Pase and Brown 1994). Winters are relatively mild compared to upper-elevation forest types. Winter precipitation falls mostly as snow, which can prevent deep soil freezing and saturates soils when melting (Schubert 1974). Low-elevation stands have an average annual temperature of 6 °C (43 °F), while mid-elevation stands average 5 °C (41 °F; Moir 1993). Lightning is common; for example, a large area of primarily Ponderosa Pine Forest in the Jemez Mountains of north-central New Mexico received an average of 2.1 cloud-to-ground lightning strikes/ha (0.8 strikes/acre) annually from 1985 to 1994 (Allen 2002). More details on climate are available in Beschta (n.d.).

Modern climate change is described in Sect. 1.6.3 and is treated as an anthropogenic driver of Ponderosa Pine Forest in Sect. 4.2.6.3.

4.2.3 Soil

Ponderosa Pine Forest occurs on a wide range of soils formed from a variety of parent materials (Pase and Brown 1994), but soils are generally deep, permeable, and capable of storing snowmelt. Soils in the southern Rocky Mountains of Colorado and New Mexico range from fine to moderately coarse-textured sandy loams with gravel (Paulsen 1975). Litter and duff depth is lower than in conifer-dominated stands of Mixed Conifer Forest and Spruce-Fir Forest (cf. Cocker et al. 2005, for the San Francisco Peaks of north-central Arizona). The soil moisture regime is ustic, and the soil temperature regime is frigid (Klemmedson and Smith 1979; Moir 1993). Ponderosa Pine Forest soils in Arizona are Alfisols (Typic Eutroboralfs, Typic Glossoboralfs, and Mollic Eutroboralfs) and Entisols (Typic Cryorthents and Typic Ustorthents), with most being well-drained, shallow to deep, and fine- to moderately coarse-textured (Hendricks 1985). Soils in New Mexico are mostly Alfisols with some Mollisols (Maker and Saugherty 1986). Soil characteristics that affect moisture availability are critical to Ponderosa Pine Forest, with porous soils being most productive (Clary 1975; Paulsen 1975).

The soil system also includes root-decay fungi. Species important in vegetation dynamics are annosus root rot (*Heterobasidion annosum*) and Armillaria root rot (*Armillaria* spp.; Dahms and Geils 1997; Moir et al. 1997).

4.2.4 *Animals*

The animals most important to vegetation dynamics of southwestern Ponderosa Pine Forest are insects, especially bark beetles (*Dendroctonus* spp. and *Ips* spp.). Elk (*Cervus elaphus*) and deer (*Odocoileus* spp.) are the common large ungulates. The impacts of animals on vegetation dynamics are described in Sect. 4.2.5.3.

4.2.5 *Natural Disturbance*

The natural disturbance regime of southwestern Ponderosa Pine Forest is dominated by fire. Wind disturbance occurs but is less widespread than at higher elevations (e.g., Sect. 2.2.5.2). Insect outbreaks can have major impacts. Climate variations such as drought are critically important, primarily through interactions with fire and insect outbreaks.

4.2.5.1 *Fire*

Fire is likely to have been a key driver of Ponderosa Pine Forest in the American Southwest for as long as ponderosa pine has dominated landscapes (cf. Weng and Jackson 1999). Ponderosa pine is well-adapted to fire with deep roots, fire-resistant bark, self-pruned lower branches, branches and cones distant from the ground, open arrangement of branches and needles unfavorable to spread of fire, needles with high moisture content, thick bud scales, and longevity of seed production (Moir et al. 1997; Keeley and Zedler 1998; Covington 2003; Kaufmann et al. 2005). These enable trees to survive and regenerate on landscapes with frequent surface fires. Moreover, the open structure of historical stands resulted in a generally warm, dry microenvironment on the forest floor that kept fuel moisture very low, facilitating the ignition and spread of surface fires (Harrington 1982). Fire is more common than in higher-elevation forests. Nearly 80 % of all lightning-ignited fires in forests and woodlands of National Forests of Arizona and New Mexico occurred in Ponderosa Pine Forest (calculated from data in Barrows 1978, for 1960–1974).

Identification of the importance of fire in Ponderosa Pine Forest dates back to the mid nineteenth century, when American expeditions surveyed resources of the region. Economic interest in timber resources led to a negative view of fire, because fire killed trees, reduced lumber quality by scarring trees, and limited tree regeneration. In addition, cultural biases of the time led observers to believe that Native Americans were the primary source of ignitions and that fire was unnatural. This precluded early understanding of the essential role of fire in this forest type (Allen 2002; Swetnam and Baisan 2003). Scientific understanding of fire in southwestern Ponderosa Pine Forest dates to Weaver (1951a), who provided data documenting frequent surface fires and suggested that such fires had been critical to maintaining healthy, open forest.

Today, most authorities concur that the historical fire regime was characterized by frequent, low-severity surface fires (Fig. 4.8; e.g., Weaver 1951a; Swetnam and Baisan 1996) that occasionally crowned in relatively small areas via fuel ladders (Swetnam et al. 2001; Iniguez et al. 2009). Surface fires were carried by fine fuels on the forest floor, especially herbaceous plants but also abundant annual needle fall (3,900 kg/ha or 3,500 lb/acre; Bradley et al. 1992). Given the relatively dry climate, the limiting factor for surface fire was generally fuel, not moisture. Factors that control fires and fire intervals can change over time (e.g., Iniguez et al. 2009). Today, dense stands with thick litter are not fuel-limited; instead fire is limited by moisture, as in higher elevation forests (Holden et al. 2007a).

The importance of fine fuels links fire and weather, because fine fuels dry and pick up moisture quickly (Bradley et al. 1992). The primary fire season is from April or May through June, when there is little precipitation (e.g., Margolis and Balmat 2009), although the fire season can extend into summer (e.g., Fulé et al. 1997). July can be a key month, because fires are more prevalent if the monsoon season is delayed or initially has below-average rainfall (Grissino-Mayer et al. 2004). Years with abundant surface fire are correlated with drought, especially when preceded by 1–3 years of high precipitation during which herbaceous fine fuels increased (Swetnam and Baisan 1996; Touchan et al. 1996; Grissino-Mayer et al. 2004; Allen 2007; Allen et al. 2008; Brown et al. 2008; Margolis and Balmat 2009). During such years, fires are not always synchronous among sites at fine spatial scales within a landscape, where local conditions of site productivity and fuel continuity can be more important, but fire synchrony is apparent at broad spatial scales (Ireland et al. 2012). In contrast, years with little fire are correlated with high precipitation. Given the importance of weather, episodic climatic events such as the El Niño-Southern Oscillation (ENSO; Sect. 1.2.2) have large impacts on fire regimes (Swetnam and Betancourt 1990, 1998; Grissino-Mayer and Swetnam 2000).

A key parameter of fire regimes of southwestern Ponderosa Pine Forest is mean interval for surface fire. Historical intervals determined from fire scars for 31 sites ranged from 4 to 36 years (median of 13 years; ≥ 10 % scarred) from 1700 to 1900 (Swetnam and Baisan 1996). This wide range in intervals is partly accounted for by differences in area and intensity of sampling (Sect. 1.2.5.1). More recent studies in the Southwest have reported intervals that fall into or near this range (e.g., Fulé et al. 1997; Brown et al. 2001; Swetnam et al. 2001; Grissino-Mayer et al. 2004; Allen et al. 2008; Iniguez et al. 2009; Margolis and Balmat 2009). Frequent fires reflect the dryness of the American Southwest in that the annual inputs of organic matter (herbaceous shoots and needles) accumulate because of slow decomposition rates, and these fuels are often sufficiently dry to carry fire.

Mean intervals for historical fires varied temporally, depending on climate (e.g., Swetnam and Baisan 1996; Touchan et al. 1996; Fulé et al. 2000). Intervals also varied spatially, as longer intervals are associated with sites of (a) topographic isolation, which reduces the spread of fires, (b) low elevation, apparently because of lower production of fine fuels to carry fires, (c) high elevation, apparently because of higher moisture levels, and (d) more moisture (Allen et al. 1995; Swetnam and Baisan 1996). Mean fire intervals in Ponderosa Pine Forest of the San Juan

Mountains of southwestern Colorado decreased with elevation from 8–13 years at high elevation to 6–11 years at middle elevation to 6 years at low elevation (Grissino-Mayer et al. 2004). Intervals tend to be longer on less productive sites, because of reduced, less-continuous surface fuels (Rollins et al. 2002).

A second important parameter of fire regimes is the length of individual fire intervals, i.e., gaps in fire occurrence. These fire-free periods also differ temporally and spatially, including among microsites within stands, landscapes within regions, and regions within the American Southwest. For example, historical fire-free periods were up to 11 and 22 years in two areas of the North Rim of Grand Canyon National Park in north-central Arizona (Fulé et al. 2002; ≥ 10 % scarred). Again, such differences are likely partially accounted for by differences in sampling area and intensity. Spatial and temporal variability in fire-free periods is related to the factors that influence mean fire intervals, as described in the preceding paragraph, as well as the vagaries of weather. Another possible factor is differences in the flammability of leaf litter among tree species (e.g., see Abella and Fulé 2008b for Gambel oak having less flammable litter than conifers). The lengths of fire-free periods are important because they affect tree regeneration and persistence. Short periods favor species that develop fire-resistant bark at a relatively young age such as ponderosa pine and Douglas-fir, as well as sprouts of species such as Gambel oak. Longer fire-free periods are necessary for regeneration of species that require more time to develop fire-resistant bark, such as white fir, and for the development and persistence of larger individuals of Gambel oak (Abella and Fulé 2008b). Although the length of fire-free periods was critical to the survival of seedlings and small saplings lacking fire-resistant bark, entire stands did not need to be fire-free, only some sites within stands. This suggests that fire-free periods can be more important at the scale of single trees or clusters of trees than at the scale of stands. Nevertheless, such data are rarely reported in fire-history studies.

The role of crown fire (Fig. 4.9) in the historical fire regime has received much less study. Of course, surface fires resulted in the torching of single trees or small clusters of trees, but the question is whether crowning historically occurred at stand or landscape scales. The consensus has been that large crown fires were absent or rare both temporally and spatially (Woolsey 1911; Cooper 1960; Moir et al. 1997; Fulé et al. 2003); however, evidence of historical crown fire can be difficult to document in southwestern Ponderosa Pine Forest. In forests such as Mixed Conifer Forest, past crown fires are usually identified by post-fire cohorts of early-successional trees, e.g., even-aged stands of quaking aspen (Sect. 3.2.5.1). Even-aged cohorts can be difficult to identify in southwestern Ponderosa Pine Forest, where they have been thinned by frequent surface fires and intermixed with cohorts of regeneration related to climate (Baker 2006; Margolis and Balmat 2009).

Nevertheless, there is evidence of historical crown fire in southwestern Ponderosa Pine Forest. For example, a 60-ha (~150-acres) patch of crown fire was documented for a mixed-severity fire on Rincon Peak in southeastern Arizona in the mid twentieth century (Iniguez et al. 2009). Also, a mixed-severity fire in the late twentieth century that produced crown-fire patches of ~200–500 ha (~500–1,250 acres) was considered similar to fires that occurred before Euro-American settlement in the Animas Mountains



Fig. 4.8 Surface fire in mesic Ponderosa Pine Forest in Grand Canyon National Park, north-central Arizona (Photograph by Fire and Aviation Management, Grand Canyon National Park)



Fig. 4.9 Crown fire in mesic Ponderosa Pine Forest in Gila National Forest, west-central New Mexico (Photograph by Steven Meister and U.S. Forest Service, Gila National Forest)

of southwestern New Mexico (Swetnam et al. 2001). In addition, crown fires have been documented from Holocene charcoal deposits in alluvial sediments at Kendrick Mountain in north-central Arizona (Jenkins et al. 2011). Crown-fire intervals at this site averaged 200–400 years during the last 2,000 years, but this likely underestimates frequency because alluvial sediments do not record all crown fires (nor do they document fire size).

The above evidence suggests crown fire was spatially and temporally limited in southwestern Ponderosa Pine Forest. It also indicates that historical crown fire occurred primarily on steep slopes in areas of heterogeneous topography. Steep slopes have vertically stacked tree crowns that facilitate upslope burning of crown fire (Jenkins et al. 2011) and have been characterized as “breeders of very large fires” (Barrows 1978). Heterogeneous topography results in fuel breaks that limit the spread of surface fires, resulting in isolated stands with infrequent fires and heavy fuels (Swetnam et al. 2001; Iniguez et al. 2009; Jenkins et al. 2011). Crown-fire intervals varied depending on long-term patterns in climate (Jenkins et al. 2011). Crown fires likely occurred after wet periods during which surface fires were reduced, fuel accumulated, and tree densities increased (Roos and Swetnam 2012). Historical crown fires at Kendrick Mountain are thought to have been both fuel- and moisture-limited (Jenkins et al. 2011). Additional research could reveal other sites of historical crown fires, such as drainages where moisture can reduce the frequency of surface fires, resulting in dense stands, high fuel loadings, and vertical fuel continuity.

Determining the prevalence of crown fire (including the crown-fire portion of mixed-severity fire) is challenging for large areas. Evidence of past fire regimes has been extrapolated from vegetation data recorded in historical land surveys dating to circa 1880–1904 in three large areas of north-central and east-central Arizona (Williams and Baker 2011, 2012, 2013). The proportions of small and large trees recorded in the surveys were interpreted as indicating that mixed and high-severity fire structured about 38, 41, 88 % of the three areas and low-severity fire structured 62, 59, and 12 %. The differences among study areas reflect differences in vegetation. For example, Williams and Baker (2013) examined the Coconino Plateau of north-central Arizona, an area of Ponderosa Pine Forest intermixed with Pinyon-Juniper vegetation (only 34 % of the historical landscape was continuous Ponderosa Pine Forest). This intermixing affected the fire regime because differences between Ponderosa Pine Forest and Pinyon-Juniper vegetation limit movement of fire from one to the other (Huffman et al. 2008; Sect. 5.2.5.1).

The fire regime of Ponderosa Pine Forest on the portion of the Coconino Plateau included in the South Rim region of Grand Canyon National Park was examined in greater detail by Dugan (2012). The lack of logging in this area – in contrast to the mostly disturbed areas studied by Williams and Baker (2012, 2013) – enabled (a) censusing fire scars to date past fires and (b) utilizing modern age structures to reconstruct severity levels of past fires. Findings for pre-1880 fires (i.e., prior to fire exclusion) indicated that mixed-severity fire accounted for 23 % of the total area burned and low-severity fire for 77 %. Historical fire turnover times (fire rotations) were 24.9 years in the South Rim area dominated by Ponderosa Pine Forest,

50.4 years in the area where Ponderosa Pine Forest was more intermixed with Pinyon-Juniper vegetation, and 33.2 years overall.

Findings that the fire regimes of the areas studied by Williams and Baker (2012, 2013) and Dugan (2012) included mixed-severity and/or high-severity fires raise a critical question. Why have most other fire-history studies, including some done in portions of the same areas, reported only low-severity fires? One explanation is that other researchers (a) selected small study areas with open stands and numerous fire scars, i.e., areas likely to have been structured by surface fires, and (b) did not link fire-scar and age-structure data (Baker 2009; Dugan 2012).

With surface fires being the focus of most researchers, the effects of surface fires have been extensively researched. High-frequency, low-severity surface fires kept forest structure relatively open. Microsites for tree regeneration were produced as reductions in the herbaceous layer decreased competition for germinating seedlings (Sackett et al. 1996). Cohorts of seedlings and saplings were thinned, but the growth of survivors increased (Dahms and Geils 1997; see also Holden et al. 2007b). Fuel loads were kept relatively low and constant both spatially and temporally. In addition, studies of prescribed burns in modern forests indicate that soil properties were altered. The layer of duff on the soil surface was kept thin and patchy, enhancing moisture availability (Covington et al. 1997; Feeney et al. 1998) and exposing mineral soil. In addition, mineralization was increased (White 1986, 1996), which increased nutrient mobilization (Covington and Sackett 1984) and nutrient concentrations on the soil surface (Covington and Sackett 1990), including nitrogen (e.g., Harris and Covington 1983; Covington and Sackett 1990, 1992). Populations of arbuscular mycorrhizae in the soil possibly increased (Korb et al. 2003).

As with other forest types in the American Southwest, the portion of the historical fire regime characterized by frequent, low-severity surface fires changed late in the nineteenth century (Sects. 4.2.6.1, 4.2.6.2, and 4.4.1.2).

4.2.5.2 Wind

Windthrows of scattered trees occur (Pearson 1950; Kolb et al. 2001), but there is little in the scientific literature about stand-scale effects of wind on southwestern Ponderosa Pine Forest. Woolsey (1911) described “considerable windfall” when soils were saturated, but possibly was referring to areas that had been partially logged. There also is mention of a major blowdown in the Jemez Mountains (Allen 1989).

A well-documented example of wind damage occurred in north-central Arizona in 2010, when several tornados affected 2,375 ha (5,868 acres) of mostly Ponderosa Pine Forest (Fig. 4.10; U.S. Forest Service 2010). Damage to stands ranged from none to complete blowdown. Within the core area of damage, average stands decreased in density from 1,006 to 12 trees/ha (407 to 5 trees/acre), including 57 to 7 trees/ha (23 to 3 trees/acre) for trees ≥ 51 cm (16 in.) diameter at breast height (dbh), i.e., at 1.4 m (4.5 ft). Basal area decreased from 31 to 2 m²/ha (137– 10 ft²/acre), and canopy cover decreased from 65 to 10 % (U.S. Forest Service 2011a).

Impacts on the forest were such that the paths of individual tornados were evident from aircraft (see Fig. 4.7 in U.S. Forest Service 2010).

4.2.5.3 Biotic Agents

Insects, especially bark beetles, are important disturbance agents in southwestern Ponderosa Pine Forest (Fig. 4.11). Bark beetles affect stand structure and possibly were important historically in maintaining low tree densities, especially following surface fire (cf. Breece et al. 2008) and drought (Allen 1989; Negrón et al. 2009). Bark beetles also have affected vegetation distribution, as they caused mortality of ponderosa pine in the Jemez Mountains that moved the ecotone between Ponderosa Pine Forest and Pinyon-Juniper vegetation upslope (Allen and Breshears 1998).

Stands of Ponderosa Pine Forest in northern Arizona maintain several species of bark beetles, possibly persisting in lightning-scarred trees (Sánchez-Martínez and Wagner 2002). Bark beetles typically attack scattered, small clusters of trees, but larger outbreaks also occur (cf. Douglas and Stevens 1979). Extensive outbreaks have been reported for the Kaibab Plateau of northern Arizona (Lang and Stewart 1910; Wilson and Tkacz 1996), Bandelier National Monument in north-central New Mexico in 1955–1958 (Allen 1989), and much of the Southwest in the first few years of the twenty-first century (U.S. Forest Service 2011b). Insect-caused tree mortality in the twenty-first century outbreak peaked in Ponderosa Pine Forest in 2003 with about 3,087 km² (1,192 miles²) affected in Arizona and New Mexico (U.S. Forest Service 2011b). Ponderosa pine mortality was caused primarily by ips engraver beetles (*Ips* spp.) in Arizona and western pine beetle (*Dendroctonus brevicomis*) in New Mexico (Negrón et al. 2009; U.S. Forest Service 2011b). *Ips* species have greatest impacts on dense stands, at low elevations, and on trees with diameters of 10–35 cm (4–14 in.) dbh, i.e., trees that had established during the period of fire exclusion (Negrón et al. 2009). Western pine beetle appears to impact primarily larger, more mature trees (Miller and Keen 1960).

Inference from stands with different tree densities in north-central Arizona suggested that populations of *Dendroctonus* (but not *Ips*) increased with tree densities during fire exclusion (Zausen et al. 2005). However, the relationship between tree density and outbreaks is unclear. Battaglia and Shepperd (2007) suggested that increased tree density and reduced tree vigor made Ponderosa Pine Forest more susceptible to outbreaks in southern Utah, but Sánchez-Martínez and Wagner (2002) reported no effect of increased tree density on outbreaks in north-central Arizona.

Other important insects include pine sawflies (*Neodiprion* spp.; McMillin and Wagner 1993), but little information is available for the American Southwest. Pandora moth (*Coloradia pandora*) defoliates ponderosa pine at a landscape scale, but does not appear to significantly impact tree growth and vigor (Bennett et al. 1987; Schmid and Bennett 1988; Miller and Wagner 1989).

Another biotic disturbance agent is ponderosa pine dwarf mistletoe (*Arceuthobium vaginatum* spp. *cryptopodum*), a parasite plant that infects approximately one-third



Fig. 4.10 Wind damage caused by a tornado in mesic Ponderosa Pine Forest in Coconino National Forest, north-central Arizona (Photograph by U.S. Forest Service, Coconino National Forest)



Fig. 4.11 Mortality of ponderosa pine (note *reddish-brown color*) caused by engraver beetles in Prescott National Forest, central Arizona (Photograph by Joel McMillin, Forest Health, Arizona Zone, U.S. Forest Service)



Fig. 4.12 Mistletoe-caused growth of a “witches broom” on a ponderosa pine in Coconino National Forest, north-central Arizona (Photograph by Betty J. Huffman)

of the area of Ponderosa Pine Forest in Arizona and New Mexico (Andrews and Daniels 1960). This species causes host trees to accumulate resins and form dense clusters of branches (“witches brooms”; Fig. 4.12). When burned, these increase crown scorching, which is a primary factor in tree mortality following surface fire (Harrington and Hawksworth 1990; Breece et al. 2008). The resins and witches brooms also facilitate the laddering of fire into forest canopies (Alexander and Hawksworth 1975). Research in north-central Arizona determined that severely infected stands had higher total fuel loadings but no differences in canopy fuels (Hoffman et al. 2007). These stands also required lower wind speeds for surface fires to crown than did uninfected stands.

Other biotic disturbance agents are root-decay fungi and large ungulates. Root decay fungi such as annosus root rot and *Armillaria* root rot reduce growth

and weaken trees, which increases the likelihood of bark beetle infestation and windthrow. Interactions of these fungi with insects and pathogens generally accounted for about one-third of tree mortality in several National Forests of Arizona and New Mexico (Wood 1983, in Moir et al. 1997).

Elk and deer, the common large ungulates, likely have affected tree regeneration patterns, especially of quaking aspen, a heavily browsed species (see Sects. 3.2.5 and 3.3.2).

4.2.5.4 Climate Variation

Periodic drought is a critically important disturbance factor affecting Ponderosa Pine Forest. It acts primarily through interactions with other disturbance agents such as fire and insects. The importance of drought in the American Southwest was recognized early in the twentieth century. Woolsey (1911) reported 10 % of the standing trees (all or mostly ponderosa pine) in a large timber sale in Coconino National Forest in north-central Arizona were dead, as “the result largely of unfavorable moisture conditions.” He also noted that drought interacted with insects and pathogens.

Drought in the early twenty-first century in north-central Arizona was associated with a 74 % increase in tree mortality in 2002–2007 (Ganey and Vojta 2011). Mortality was disproportionately greater for Gambel oak and quaking aspen and lower for ponderosa pine. Mortality occurred in 98 % of study plots but the degree of mortality was spatially variable. Mortality was uncorrelated with stand density and elevation (although negative impacts of drought on tree growth are greater in low-elevation forests; Adams and Kolb 2005). Absolute mortality was greater in smaller diameter classes, but relative mortality (i.e., mortality relative to species abundance) was generally greater in larger diameter classes. Relative mortality was lower than in Mixed Conifer Forest (Sect. 3.2.5.4). Drought also increased the elevation of the ecotone between Ponderosa Pine Forest and Pinyon-Juniper vegetation by causing mortality of ponderosa pine by bark beetles (Allen and Breshears 1998; Koepke et al. 2010), as mentioned in the previous section. See Sect. 3.2.5.3 for the role of drought (and other factors) in aspen decline.

4.2.6 Anthropogenic Disturbance

Land use by Native Americans in the American Southwest was concentrated in Pinyon-Juniper vegetation (Sects. 1.5.1.1 and 5.2.6), but Ponderosa Pine Forest was commonly used for hunting and sometimes for settlements (Roos et al. 2010). Major anthropogenic disturbances related primarily to Euro-American land use and affecting relatively undisturbed stands of southwestern Ponderosa Pine Forest are livestock grazing, fire management, modern climate change, invasive species, recreation, and nearby land use. Each of these can be important in vegetation dynamics,



Fig. 4.13 Domestic sheep (*Ovis aries*) grazing in 1925 in mesic Ponderosa Pine Forest, north-central Arizona (Photograph by E.W. Loveridge, U.S. Forest Service, Coconino National Forest)

and therefore all are incorporated in the conceptual models (Sect. 4.5). For a review of several contemporary human uses, see Raish et al. (1997). Logging has been widespread, but is outside the scope of this book.

4.2.6.1 Livestock Grazing

Livestock grazing became widespread in the late nineteenth century and had both direct and indirect effects on southwestern Ponderosa Pine Forest (Fig. 4.13). Direct effects included consumption of palatable plants, which reduced understory cover and altered the competitive balance among plant species, thereby affecting the composition of the forest understory. However, documentation of such effects can be challenging, because changes in forest canopy cover can dominate understory changes (cf. Bakker and Moore 2007). The major indirect effect of livestock grazing was that it reduced the biomass and continuity of the herbaceous layer, which formerly carried surface fires, and thereby caused an abrupt decrease in the frequency of surface fires in the late nineteenth century.

Livestock grazing continues today in many areas, but is generally less intensive (Battaglia and Shepperd 2007) and is not allowed in most protected areas. Long-term light to moderate livestock grazing appears to have little impact (Milchunas

2006). Grazing is most common in stands with quaking aspen (Reynolds 1969; Milchunas 2006), where it reduces aspen regeneration and understory cover, affecting tree-age distributions and understory composition (DeByle 1985; Mueggler 1985; Bartos 2007). Effects of heavy grazing can persist for more than 40 years, even after the withdrawal of livestock (Hanks et al. 1983). Overgrazing also can result in increases in invasive species (e.g., Korb et al. 2005; Battaglia and Shepperd 2007). Study of grazing exclosures over a 25-year period documented that removal of livestock grazing from Ponderosa Pine Forest greatly increased grass cover and regeneration of ponderosa pine (Potter and Krenetsky 1967).

4.2.6.2 Fire Management

Fire management throughout most of the twentieth century focused on preventing and suppressing fires. This continued the exclusion of surface fires that was initiated by livestock grazing (previous section). Just as southwestern Ponderosa Pine Forest was “profoundly shaped by fire” (Romme et al. 2009), it was also profoundly altered by fire exclusion (Fig. 4.14a–c; Sect. 4.4.1.2). Without frequent fires, southwestern Ponderosa Pine Forest increased in tree density, fuel loadings, and horizontal and vertical fuel continuities across landscapes, which led to increased frequency and size of crown fires (Fig. 4.15, e.g., Fulé et al. 2004; Romme et al. 2009). Examples



Fig. 4.14 (a–c) Repeat photography (1909, 1949, and 2012) in old-growth Ponderosa Pine Forest of the Fort Valley Experimental Forest, Coconino National Forest, north-central Arizona. (a) In the 1909 photograph, note absence of seedlings and saplings of ponderosa pine.



Fig. 4.14 (continued) (b) In the 1949 photograph, note ponderosa pine regeneration had occurred, probably in 1919. (c) In the 2012 photograph, note growth but little thinning of ponderosa pine regeneration during the period of fire exclusion (Photographs by W.R. Matton (a) and F.R. Herman (b) courtesy of Fort Valley Experimental Forest Historic Images, U.S. Forest Service, and by author (c))

of large crown fires affecting southwestern Ponderosa Pine Forest in the twenty-first century include the Rodeo-Chediski Fire in east-central Arizona (1,897 km² or 732 miles²), the Whitewater Baldy Fire Complex in the Gila Mountains of west-central New Mexico (1,205 km² or 465 miles²), and the Missionary Ridge Fire in the San Juan Mountains (286 km² or 110 miles²). Shifts in climate could be related to this change in fire behavior, but increased fuel is the principal cause, based on observations of lower fire severity in sites less changed by fire exclusion (Stephens and Fulé 2005) and modeling of fire behavior (Fulé et al. 2004). Fire management practices began to shift focus in the late twentieth century to include management fires (both prescribed and lightning-ignited). This has successfully changed fire behavior in some areas (Fig. 4.16). However, the area affected by management fires has been small, and tree densities, fuel loadings, and fuel continuity continue to result in landscape-scale crown fires in many areas. Fire management during 1979–2011 in the South Rim region of Grand Canyon National Park has been so active that the modern fire rotation is 17.4 years vs. the historical rotation of 33.2 years (moreover, the rotation period was only 10.3 years in 1998–2011; Dugan 2012; see Sect. 4.2.5.1).

4.2.6.3 Modern Climate Change

Modern climate change (Sect. 1.6.3) is implicated in fires, insect outbreaks, and drought. Therefore, it has affected the structure, composition, and dynamics of southwestern Ponderosa Pine Forest. Air pollution is a driver of modern climate change, but pollution sources are more global than regional or local, and direct effects of air pollution on southwestern Ponderosa Pine Forest are understudied. However, there is circumstantial evidence of likely impacts. For example, ozone levels in Grand Canyon National Park (Bowman 2003) have exceeded thresholds for foliar injury on ponderosa pines observed in California (National Park Service 2002). Ozone also can affect quaking aspen (e.g., Karnosky et al. 1999). Nevertheless, with the lack of documentation of direct effects, air pollution is not included in this chapter as a separate anthropogenic driver of southwestern Ponderosa Pine Forest.

4.2.6.4 Invasive Species

Invasive plant species are more abundant and much more thoroughly studied in Ponderosa Pine Forest than in higher-elevation forests. A review of exotic species in Ponderosa Pine Forest in Arizona reported that cover values are typically <10 % (McGlone and Egan 2009). However, the abundance of invasives is highly variable. For example, mean cover of exotic plants in a regional study of ten Ponderosa Pine Forest ecosystem types in central and north-central Arizona ranged from <0.1 to 7 %, and their relative cover was <1 to 16 % (Abella et al. 2012). Mean exotic species richness ranged from ~0 to 1.7 species/m² (species/10.8 ft²). Multiple regression



Fig. 4.15 A century or more of fire exclusion has led to landscape-scale crown fires. Note evidence of past fire in the foreground and a current fire in the background in Gila National Forest, west-central New Mexico (Photograph by Mormon Lake Interagency Hotshot Crew and U.S. Forest Service, Gila National Forest)



Fig. 4.16 Smoke from surface fire in Gila National Forest, west-central New Mexico (Photograph courtesy of U.S. Forest Service, Gila National Forest)

determined that about half of the variation in exotic species cover and richness was related to native species and environmental variables. Moist ecosystem types were most heavily invaded. Disturbance, which usually leads to increases of invasives, only entered the regional-scale regression models when native species were dropped from the analysis. This surprising result is likely accounted for by widespread anthropogenic disturbance, including livestock grazing.

At the stand scale, invasives generally increase following disturbances such as fire, tree thinning for fire management, and livestock grazing (e.g., Sackett et al. 1996; Korb et al. 2005; Battaglia and Shepperd 2007; McGlone and Egan 2009; McGlone et al. 2009a, 2012b; Stoddard et al. 2011). Invasives are generally uncommon in areas of little disturbance (Laughlin et al. 2004; Korb et al. 2005) and abundant where disturbance is severe (Sackett et al. 1996; Crawford et al. 2001; Griffis et al. 2001; Stoddard and McGlone 2008), but some studies have shown no correlation with severity (e.g., Kuenzi et al. 2008). Also, invasives generally decrease with time since disturbance (Stoddard and McGlone 2008). For example, relative cover of exotics dropped from 6 % immediately after disturbance (i.e., understory thinning and prescribed burning) to ~3 % after 6 years (Stoddard et al. 2011), but this can be negated by the introduction of other invasive species (cf. McGlone et al. 2009b).

The most widespread species of invasives differ among studies (cf. Sackett et al. 1996; Scurlock and Finch 1997; Sieg et al. 2003; McGlone and Egan 2009; McGlone et al. 2009b). The regional study of Ponderosa Pine Forest ecosystem types by Abella et al. (2012) mentioned above listed the following invasives as having ≥ 20 % frequency values averaged across the types: common dandelion (*Taraxacum officinale*; 42 %), common salsify (*Tragopogon dubius*; 42 %), cheatgrass (*Bromus tectorum*; 36 %), common mullein (*Verbascum thapsus*; 35 %), Kentucky bluegrass (*Poa pratensis*; 33 %), wild lettuce (*Lactuca serriola*; 27 %), and Dalmatian toadflax (*Linaria dalmatica*; 20 %).

The invasive of perhaps greatest concern is cheatgrass (cf. Sieg et al. 2003), an annual with no native ecological equivalent. Its broad ecological amplitude allows it to grow and reproduce in a variety of environments. This and dispersal attached to animals, including humans, give it a wide geographic distribution and the ability to expand it. Cheatgrass is a cool-season species that can capture resources before most native species (but see McGlone et al. 2011, 2012a). Its growth can produce extensive cover of fine fuels every year, giving it the potential to shorten fire intervals. Cheatgrass has had a larger, more-widespread impact on lower-elevation vegetation, including Pinyon-Juniper vegetation (Sect. 5.2.6.4). Nevertheless, it can dominate successional patterns in Ponderosa Pine Forest following restoration treatments (McGlone et al. 2012b). Moreover, its role in promoting fire in Ponderosa Pine Forest in the western United States goes back at least to 1938:

A lush, early spring growth of cheatgrass (*Bromus tectorum*), followed by dry, hot, late spring and early summer weather set the stage for this fire. (Weaver 1959, for north-central Oregon)

Dry, hot weather in late spring and early summer is atypical for north-central Oregon, but is characteristic of the American Southwest (Sects. 1.2.2 and 4.2.2).



Fig. 4.17 Campground illustrating recreation in 1928 near Ruidoso in south-central New Mexico (Photograph by E. S. Shipp/U.S. Forest Service)

4.2.6.5 Recreation

Impacts of recreation are also greater in Ponderosa Pine Forest than higher-elevation forests in the American Southwest. This is because of greater accessibility and use by recreationists (Fig. 4.17). Some impacts are spatially limited (e.g., construction and use of roads, trails, and campsites, but others are more extensive). Fires ignited by recreationists in Ponderosa Pine Forest have included the Chediski portion of the Rodeo-Chediski Fire (Sect. 4.2.6.2) and the Schultz Fire, which burned 61 km² (24 miles²) in the area of the San Francisco Peaks. Recreationists also appear to have introduced and spread invasive plants (invasives are often more common near roads and campsites). In addition, the use of off-highway vehicles by recreationists negatively impacts forest understories and soils.

4.2.6.6 Nearby Land Use

Nearby land use is an important anthropogenic driver. It too has greater effects on Ponderosa Pine Forest than higher-elevation forests. Ponderosa Pine Forest borders more adjacent lands, especially disturbed lands, and has more cities, towns, and housing developments embedded within it. Such proximity facilitates the spread of fires and invasives species into southwestern Ponderosa Pine Forest.

4.3 Processes

Ponderosa Pine Forest of the American Southwest has two major types of vegetation dynamics. One involves the paired processes of tree regeneration and thinning, and the other is succession. Research on both has concentrated on woody plants. These processes play key roles in the conceptual models (Sect. 4.5).

4.3.1 *Regeneration and Thinning*

The process of tree regeneration and thinning in southwestern Ponderosa Pine Forest has been referred to as gap dynamics. This can be misleading, at least for old-growth stands with open canopies, because the process is dissimilar to the gap dynamics of forests such as southwestern Spruce-Fir Forest (Sect. 2.3.2) and broad-leaved deciduous forests of the eastern United States. In such closed-canopied forests, gap dynamics begin with the death of one or a small cluster of canopy trees. The resultant opening in the tree canopy alters the microenvironment below it by increasing light. Smaller trees that were present before or established after gap formation respond with accelerated growth. Within a few decades, the canopy gap is filled by one or more of these trees or by ingrowth of crowns of adjacent canopy trees.

Open-canopied stands of southwestern Ponderosa Pine Forest do not have such gap dynamics. Instead, their woodland-like structure is characterized by persistent spaces between tree crowns. Long-term stability of both open and tree patches is evidenced by the finding that the soils of about 70 % of tree patches within stands in north-central Arizona are Alfisols, and soils in about 70 % of open patches just 5 m (16 ft) away are Mollisols (Scott R. Abella, personal communication). Persistence of open patches contrasts with canopy gap dynamics in which gaps continuously form and close in different locations over decadal time spans. Therefore, the old-growth structure of stands of southwestern Ponderosa Pine Forest depends not on gap dynamics but instead on the on-going processes of tree regeneration and thinning, as described below. Closed-canopied stands can have gap dynamics (Moir et al. 1997), but such stands also depend on regeneration-thinning dynamics.

Discussion of regeneration of ponderosa pine began with forest surveyors and lumbermen in the early twentieth century, who were concerned about the presence of replacement trees after logging:

...mature trees occur among good patches of saplings and poles...isolated or in groups...
Underneath the old trees and in open areas between the groups are often numerous small
seedlings... (Lang and Stewart 1910, for the Kaibab Plateau)

See also Woolsey (1911) for Arizona and New Mexico.

Historical patterns of ponderosa-pine regeneration have been studied by examining dates of recruitment of current trees (Cooper 1960; White 1985; Savage et al. 1996; Mast et al. 1999; Brown and Wu 2005; Sánchez Meador et al. 2009; Dugan 2012).

Findings show broad pulses of recruitment separated by periods of less regeneration (Mast et al. 1999; Brown and Wu 2005). The broad pulses occurred during multi-decadal periods when surface-fire frequency was reduced by wet conditions or by lack of wet/dry oscillations important for the buildup and drying of fuels associated with surface fires (Brown and Wu 2005; Sect. 4.2.5.1). However, regeneration pulses also can be associated with fire and drought (Dugan 2012), which can be associated with overstory mortality and release of resources. The maximum period without regeneration in a stand in north-central Arizona was two decades (Mast et al. 1999; see also Villanueva-Díaz and McPherson 1995).

The last two regional regeneration cohorts (1910s–1930 and mid 1970s–1980s) occurred with wetter conditions and also with fire exclusion and reduced livestock grazing (Fig. 4.18; Kaufmann et al. 2007; see also Dugan 2012). The lack of surface fires increased ponderosa pine establishment by orders of magnitude in a north-central Arizona forest in 1919 (Mast et al. 1999). More-recent seedlings in the same area have died under a now-dense overstory (P.Z. Fulé, personal observation, cited in Mast et al. 1999). Years of abundant regeneration occur with heavy seed crops, moist spring and summer weather, and absence of fire (Pearson 1950; Bradley et al. 1992; Savage et al. 1996). Such years can be infrequent outside of the multi-decadal periods mentioned above, and can be site specific (Cooper 1960). A stand in north-central Arizona went 73 years (1919–1992) between confluences of conditions necessary for abundant regeneration (Savage et al. 1996).

Study of regeneration in a north-central Arizona forest that had been partially logged in the late nineteenth century indicated establishment was highest in canopy gaps and other forest interspaces (Sánchez Meador et al. 2009). Initial recruitment occurred near the center of natural grass openings (livestock grazing had eliminated competition from herbs, according to Pearson 1942). Regeneration later filled in other spaces. Ponderosa pine regeneration in Utah occurs as scattered individuals, scattered clumps, or dense stands (Bradley et al. 1992). Clumps can vary greatly in size, but in the Southwest are generally 0.02–0.3 ha (0.05–0.7 acres), with some as large as 0.8 ha (2 acres; White 1985; Kaufmann et al. 2007).

The thinning portion of the regeneration-thinning vegetation dynamic of south-western Ponderosa Pine Forest historically occurred as surface fire reduced cohorts of seedling and sapling ponderosa pines (Fig. 4.19). Substantial self-thinning from intra-specific competition is not common today, at least within unburned, twentieth century cohorts (personal observation). Surface fires were a density-independent driver of ponderosa pine density, because they occurred largely independently of the density of overstory and understory trees (Brown and Wu 2005). Prescribed fire in east-central Arizona that resulted in the loss of only 0–5 % of trees with a dbh of ≥ 30 cm (12 in.) caused much greater mortality of smaller trees: 98–99 % of seedlings < 30 cm (12 in.) height and 63–76 % of saplings from > 30 cm (12 in.) height up to 8 cm (3 in.) dbh (Gaines et al. 1958).

With the presence of different cohorts, stands were uneven-aged. Regeneration between major pulses of regeneration also contributes to the uneven-age distribution of stands. The age-distribution of individual patches has been reported both as even (Cooper 1960, 1961) and uneven (e.g., White 1985).



Fig. 4.18 Ponderosa pine seedlings and saplings that likely date to a regeneration pulse in 1919. Trees have not been thinned by fire because of fire exclusion. In Coconino National Forest, north-central Arizona (Photograph by Betty J. Huffman)



Fig. 4.19 Fire thinning ponderosa pine regeneration in Grand Canyon National Park, north-central Arizona (Photograph by Fire and Aviation Management, Grand Canyon National Park)

4.3.2 Succession

Succession in Ponderosa Pine Forest of the American Southwest occurs after high-severity, stand-scale disturbance. Despite increases in crown fires following decades of fire exclusion, there is little research on post-fire succession in southwestern Ponderosa Pine Forest. Successional pathways that have been described indicate succession is greatly affected by pre-fire stand composition (e.g., Savage and Mast 2005), especially where sprouting species were present (e.g., Haire and McGarigal 2008). Successional patterns are also influenced by soil erosion, site moisture conditions, elevation, proximity to seed sources, and disturbance during succession.

Succession after crown fire in moist Ponderosa Pine Forest, i.e., at higher elevations, often involves quaking aspen (Bradley et al. 1992; Savage and Mast 2005), a species that root sprouts following fire (Sect. 3.3.2). Herbs and aspen sprouts dominate early in succession (Fig. 4.20), but ponderosa pine seedlings soon appear if seed sources are nearby. Subsequent surface fire favors aspen, until ponderosa pine saplings develop fire-resistant bark. If aspen and ponderosa pine continue to codominate, ponderosa pine eventually overtops aspen and aspen either senesces or remains as a subcanopy species in ponderosa pine-dominated stands. High mortality of aspen in moist Ponderosa Pine Forest, as reported for north-central Arizona (cf. Vankat 2011; Zegler et al. 2012), likely enhances the rate of succession to ponderosa pine (see Sect. 3.2.5.4).

Crown fire in moist and mesic stands of Ponderosa Pine Forest in which Gambel oak is abundant can have successional stands dominated by that sprouting species (Fig. 4.21; Harper et al. 1985; Romme et al. 1992; Bradley et al. 1992; Moir 1993; Savage and Mast 2005; Strom and Fulé 2007; Haire and McGarigal 2008). Gambel oak, sometimes with other shrubs such as New Mexico locust (*Robinia neomexicana*) and manzanita (*Arctostaphylos* spp.), can persist for long periods. Where nearby seeds sources are present, ponderosa pine invades and establishes. Before its saplings develop fire-resistant bark, subsequent fire favors shrubs. After ponderosa pine saplings develop fire-resistant bark, light fires favor it and kill back stems of the shrubs. Succession continues to forest, and the density of trees in late-successional stands negatively affects the density of the understory shrubs that persist (see Sect. 7.3.2).

Stands of dry Ponderosa Pine Forest and related forests with Apache, Arizona, and Chihuahuan pines often have pinyons, junipers, and evergreen oaks such as wavyleaf oak in the understory. After crown fire, the understory species dominate from early- through mid-succession (Bradley et al. 1992; Moir 1993; Barton 2002). Mid-successional stands can persist for long periods, but where seed sources available, pines can invade, establish, and eventually overtop the mid-succession dominants. (see Sect. 8.3.2).

Alternatively, succession in moist, mesic, and dry Ponderosa Pine Forest can be dominated by ponderosa pine, beginning early in succession. This is likely to occur when sprouting trees and shrubs are absent or uncommon before disturbance and when seed sources of ponderosa pine are nearby. Long-distance seed dispersal supplements reseeded of ponderosa pine from edges of burned patches (Haire and McGarigal 2010).

Succession following crown fire in stands in Arizona and New Mexico can lead to a variety of possible outcomes: forests, shrublands, and grasslands (Fig. 4.22a, b; Savage and Mast 2005; Strom and Fulé 2007; Iniguez et al. 2009; Roccaforte



Fig. 4.20 Succession in moist Ponderosa Pine Forest often begins with rapid sprouting of quaking aspen. This six-year-old patch of quaking aspen originated after crown fire in the North Rim region of Grand Canyon National Park, north-central Arizona (Photograph by Betty J. Huffman)



Fig. 4.21 Succession in mesic and dry Ponderosa Pine Forest can involve rapid sprouting of Gambel oak. These approximately two-year-old sprouts originated after forest fire in the North Rim region of Grand Canyon National Park, north-central Arizona (Photograph courtesy of Marc E. Gottlieb)

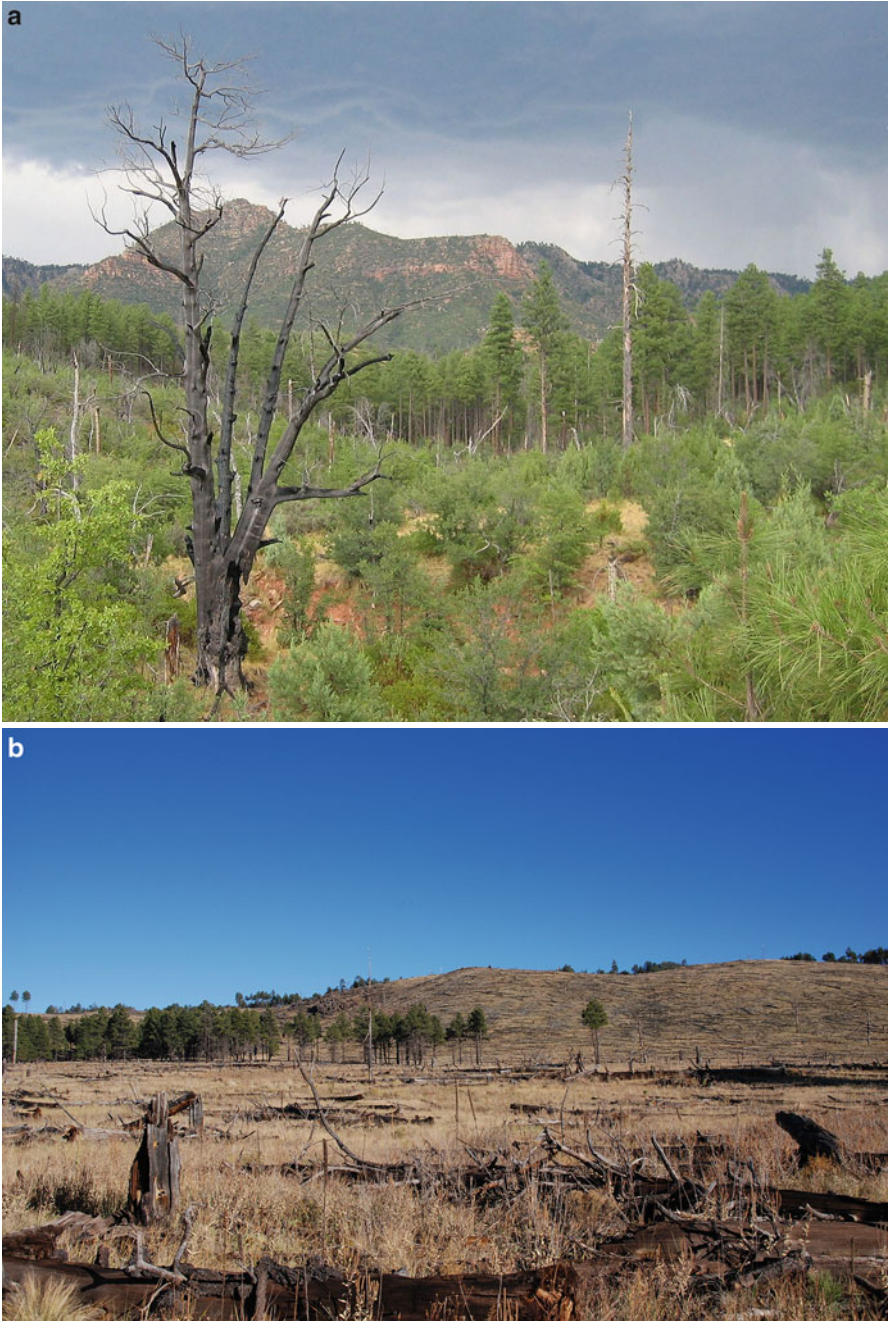


Fig. 4.22 (a, b) Modern landscape-scale crown fires can cause conversion of southwestern Ponderosa Pine Forest into shrublands and grasslands. **(a)** The photograph shows shrubland in the foreground and a patch of unburned Ponderosa Pine Forest in the mid-ground 19 years after fire in Tonto National Forest, central Arizona. **(b)** The photograph shows grassland 15 years after fire in Coconino National Forest in north-central Arizona. There is little or no evidence of succession to forest in either photograph (Photographs by Jackson Leonard/U.S. Forest Service **(a)** and Betty J. Huffman **(b)**)

et al. 2012). Sites that have changed from forest to shrubland or grassland possibly will persist as non-forest if subsequent fire maintains them and/or seed sources of ponderosa pine are distant (Savage and Mast 2005). Also, stands that regrew as forest have little evidence of self-thinning decades later, making them susceptible to future crown fire and possible long-term conversion to grassland or shrubland. Impediments to recovery of sustainable Ponderosa Pine Forest include competition with sprouting species such as quaking aspen, oaks, New Mexico locust, and grasses, long distance to seed sources of ponderosa pine, and modern climate change toward higher temperatures and drier conditions (Roccaforte et al. 2012; see Sect. 1.6.3). Modeling has indicated that it will take centuries before Ponderosa Pine Forest recovers across a landscape burned by crown fire in east-central Arizona (Strom and Fulé 2007).

4.4 Historical Changes

4.4.1 Overstory

4.4.1.1 Pre-Euro-American Settlement

Most descriptions of nineteenth century southwestern Ponderosa Pine Forest characterize it as open and park-like, with large, widely spaced trees and a dense, grass-dominated herbaceous understory. Such descriptions are typically justified by reference to historical accounts such as:

We came to a glorious forest of lofty pines...every foot being covered with the finest grass, and beautiful broad grassy vales extended in every direction. The forest was perfectly open... (Beale 1858, for east of the San Francisco Peaks)

All the morning passing through a fine open forest of tall pines, with extensive open glades and meadows at short distances. (Beale 1858, for the Zuni Mountains of northwestern/west-central New Mexico)

The trees are large and noble in aspect and stand widely apart... Instead of dense thickets where we are shut in by impenetrable foliage, we can look far beyond and see the tree trunks vanishing away like an infinite colonnade. (Dutton 1882, for the Kaibab Plateau)

The lofty pine forest...is a noteworthy forest, not alone on account of the size and beauty of the single species of tree of which it is composed (*Pinus ponderosa*), but also because of its openness, freedom from undergrowth, and its grassy carpet... (Merriam 1890a, for the region of the San Francisco Peaks)

...the history of the forests of Arizona...gather[ed] from many of the oldest reliable pioneers, is that when first invaded by the white man the forests were open... (Holsinger 1902)

See similar comments by Ives (1861) for near Bill Williams Mountain in north-central Arizona, Rothrock (1875) for the Zuni Mountains, Powell (1890) for the San Francisco Peaks and near the South Rim of the Grand Canyon in north-central Arizona, Bailey (1904; in Allen 2002) for the Jemez Mountains, and Pinchot (1947) for north-central Arizona in 1900.

It has been argued that ecologists and land managers have overemphasized historical descriptions of open forests and underemphasized descriptions of dense forests (Pollock and Suckling 1997). While this is possibly true, Beale's (1858) comments such as "a heavy forest of pine" can be misinterpreted, because "heavy" can refer to an abundance of large trees, not to overall stand density (cf. Woolsey 1911). In addition, failure to differentiate between Beale's (1858) observations of Ponderosa Pine Forest and Pinyon-Juniper vegetation can lead to confusion. Perhaps it is more likely that early observers, many of whom were more familiar with dense forests of the eastern United States, focused on what was unfamiliar to them, i.e., open stands.

Regardless of that debate, some historical accounts indicated variation in density:

...thick woods, which for the sake of our wagons we were obliged to avoid as much as possible... (Möllhausen 1858, for the area of the San Francisco Peaks)

On small areas in various places in these mountains the stand is much more dense [sic]. (Kellogg 1902, for the Chiricahua Mountains of southeastern Arizona)

although open stands were indicated to be predominant in some areas:

The pine forest is...rarely crowded. (Merriam 1890a, for the area of the San Francisco Peaks)

The pine occurs mostly in open stand[s] park-like or even isolated in character. Practically all of the [Ponderosa Pine Forest] is open... (Lang and Stewart 1910, for the Kaibab Plateau)

Historical descriptions also included an overview of stand structure:

The stand embodies all age classes in varying density and proportions [with] the old trees fairly uniformly distributed among the young growth over which they tower with large spreading crowns... (Lang and Stewart 1910, for the Kaibab Plateau)

as well as a quantitative description of stand structure:

...pines standing at intervals varying from 50 to 100 feet [15 to 30 m]... (Dutton 1882, for the Kaibab Plateau)

Whether this estimate was based on measurement or visually estimated, there is reason to accept it as the first quantitative description of southwestern Ponderosa Pine Forest structure and the only quantitative description dating to near the beginning of Euro-American influence. The source, Clarence Edward Dutton, was experienced with observation and measurement. He previously had served as an army ordnance officer, published multiple scientific papers, and participated in lengthy field expeditions to describe and map geological features in the western United States (Longwell 1958). Using Dutton's (1882) estimate of the mean distance between trees, density of canopy pines in Ponderosa Pine Forest on the Kaibab Plateau in the late nineteenth century was 11–43 trees/ha (4–17 trees/acre). Therefore, it too indicated variation in stand density.

There are few nineteenth century photographs of undisturbed southwestern Ponderosa Pine Forest (see Figs. 4.23a, b and 4.24). They and later photographs through at least the first decade of the twentieth century indicate open stand structure, but with variation among and within stands (Fig. 4.25). Of course, any extrapolation to Ponderosa Pine Forest throughout the American Southwest is risky, because

a



b



Fig. 4.23 (a) Photograph taken in 1873 showing southwestern Ponderosa Pine Forest on the plateau and slopes across the canyon. (b) The open structure of this forest is more apparent in the enlargement of a portion of the image. Location is given as North Fork Cañon, Sierra Blanca Creek, Arizona, but this place name is not currently used. Likely in east-central Arizona (Photograph by Timothy H. Sullivan; enlargement by author. Source: U.S. National Archives and Records Administration)



Fig. 4.24 Photograph taken in 1885 showing variation in density of southwestern Ponderosa Pine Forest near the San Francisco Peaks in north-central Arizona. Open areas are Subalpine-Montane Grassland (Photograph by J. K. Hillers. Source: U.S. Geological Survey)



Fig. 4.25 Stand of mesic Ponderosa Pine Forest in 1909 in the Fort Valley Experimental Forest, Coconino National Forest, north-central Arizona. Although surface fires ended with fire exclusion approximately 30 years earlier, the stand has remained open because of the lack of a regeneration pulse of ponderosa pine and possibly because of livestock grazing (Photograph by G. A. Pearson, courtesy of Fort Valley Experimental Forest Historic Images, U.S. Forest Service)

the sample is small and non-random (open stands likely were considered more photogenic than dense, closed stands).

Detailed quantitative descriptions are in forest surveys dating to the early twentieth century. Lang and Stewart (1910) sampled Ponderosa Pine Forest on the Kaibab Plateau in 1909 and reported the average density of trees ≥ 15 cm (6 in.) dbh was 111 trees/ha (45 trees/acre). However, Lang and Stewart (1910) underestimated density because they did not sample quaking aspen, pinyon, juniper, or Gambel oak, apparently because they lacked value for lumber. They also possibly included samples that extended into treeless meadows (Vankat 2010, 2011). In addition, their data do not reflect conditions prior to Euro-American influence, which began with livestock grazing and resultant fire exclusion about 30 years earlier (Vankat 2011). In fact, their data indicate ingrowth of fire-sensitive fir (probably white fir), which accounted for only 6 % of trees but 37 % of seedlings and saplings < 15 cm (6 in.) dbh. Therefore, Lang and Stewart's (1910) data for larger trees better reflect conditions prior to Euro-American influence: the density of ponderosa pines > 46 cm (18 in.) dbh was 30 trees/ha (12 trees/acre), which falls near the middle of the range extrapolated from Dutton (1882).

Another early report included densities of Ponderosa Pine Forest in Arizona and New Mexico. Woolsey (1911) described "average" stands in Tusayan (now part of Kaibab) and Coconino National Forests in north-central Arizona as having 27 and 40 pines/ha (11 and 16 pines/acre), respectively, for individuals ≥ 15 cm (6 in.) dbh. Variation in stand structure was indicated by his characterization of the 764-ha (1,888-acres) area averaged for Coconino National Forest as "frequently very dense". Considering pines > 46 cm (18 in.) dbh, Tusayan and Coconino National Forests averaged 12 and 22 pines/ha (5 and 9 pines/acre), respectively, values within the range extrapolated from Dutton (1882).

Nineteenth century structure and composition of Ponderosa Pine Forest also have been estimated by forest reconstruction. This approach usually involves analyzing rings of living trees and using decay classes to estimate ages of snags and downed logs currently on the site to determine/estimate which were alive and at what dbh on a selected date in the past. This method has been used for southwestern Ponderosa Pine Forest primarily in north-central Arizona (e.g., Covington et al. 1997; Fulé et al. 1997, 2002; Menzel and Covington 1997; Mast et al. 1999; Abella and Denton 2009; Sánchez Meador et al. 2010), but also see Romme et al. (2009) for southwestern Colorado and Heyerdahl et al. (2011) for Utah. Reconstruction studies often differ in terms of minimum diameters reported, preventing direct comparison of reconstructed densities. In addition, most reconstruction studies do not include diameter-class data that would facilitate comparison of results of different studies and enable inference of nineteenth century stand dynamics.

The accuracy of tree-ring-based forest reconstruction depends on evidence of all trees from the historical date, e.g., 1880, persisting to the modern sampling date in the form of living trees, snags, downed logs, etc. Forest reconstructions underestimate historical density and basal area when evidence of trees has been lost by combustion or decomposition (Fulé et al. 2002, 2003) or is otherwise missing. Combustion is a factor on some sites of reconstruction studies of southwestern

Ponderosa Pine Forest (Moore et al. 2004), but of course not where fire has been totally excluded. Decomposition is a factor for young trees and small trees, as well as species with decay-susceptible wood, including pinyons (Kearns et al. 2005), quaking aspen (Gosz 1980; see Sect. 2.4.1.1), and white fir. Losses by tree cutting are important if evidence such as stumps is no longer present.

The accuracy of reconstruction of southwestern Ponderosa Pine Forest has been examined by resampling study plots where tree stems >9.1 cm (3.6 in.) dbh and other structures such as stumps had been mapped in the early twentieth century. Moore et al. (2004) relocated 91 % of the mapped tree structures and therefore suggested that reconstruction in southwestern Ponderosa Pine Forest is reliable within 10 %. The authors acknowledged that trees too small to have been included on the original stem maps and no longer evidenced in the plot were a source of additional error (therefore, the accuracy of the many reconstructions that include trees with a dbh of ≤ 9.1 cm/3.6 in. is unexamined). Also, Moore et al. (2004) included stump holes as evidence of mapped tree structures, even though structures that cannot be dated would have limited use in reconstructions where historical stem maps are unavailable. In addition, thinning of mature trees in the study plots near the time of the original mapping likely increased the vigor of the remaining trees and thereby increased persistence of structural evidence. Nevertheless, reconstructions of nineteenth century southwestern Ponderosa Pine Forest apparently are more accurate than reconstructions of Mixed Conifer and Spruce-Fire Forests (see Sects. 2.4.1.1 and 3.4.1.1, respectively).

Reconstruction studies of densities and basal areas of nineteenth century southwestern Ponderosa Pine Forest have produced widely different results. This is partly because of differences in minimum diameters included (at least for densities), but it also reflects differences in sites. The effects of site conditions were highlighted by a study in north-central Arizona in which sites were randomly selected within nine Ponderosa Pine Forest ecosystem types that reflected a broad range of soils (Abella and Denton 2009). Each site was sampled for reconstruction using a 1 ha (2.5 acres) plot. Among the ecosystem types, mean tree densities reconstructed for 1880 ranged from 5 to 99 trees/ha (2 to 40 trees/acre) for individuals ≥ 9 cm (3.5 in.) dbh (diameter limit: Scott R. Abella, personal communication). Moreover, there was substantial variation among sites within the same ecosystem type: 54–85 trees/ha (22–34 trees/acre) in the least-variable type and 39–143 trees/ha (16–58 trees/acre) in the most-variable. Statistical analysis of factors influencing density indicated that soils and climate variables were more important than topography (including elevation).

Two other studies also reported high variation in forest density circa 1880–1900 across two large areas in north-central and one in east-central Arizona (Williams and Baker 2012, 2013). Mean tree densities reconstructed from original land survey records were remarkably similar among the areas: 142–144 trees/ha (57–58 trees/acre) for trees >10 cm (4 in.) dbh. Densities varied within each the areas: 19–33 % of the areas had open forests (<100 trees/ha; 40 trees/acre) and 15–17 % had dense forests (>200 trees/ha; 81 trees/acre), suggesting spatially complex forests. Another study based on land survey records dating to 1878–1879 also indicated substantial

variation in forest density across a large area of mostly Ponderosa Pine Forest near Flagstaff, Arizona (Arundel 2000).

Tree-ring-based reconstructions done on the Kaibab Plateau are of particular interest, because other historical data are available from the area (cf. Dutton 1882; Lang and Stewart 1910; Vankat 2011), and some areas have been considered reference sites for late nineteenth century conditions (as discussed below). Reconstructions of stand structure to 1879 were done for three protected, relatively remote sites on the North Rim of Grand Canyon National Park, where surface fires had burned during the twentieth century (Fulé et al. 2002). Total densities were 153–160 trees/ha (62–65 trees/acre) and total basal areas were 17–21 m²/ha (74–91 ft²/acre) for trees ≥ 2.5 cm (1 in.) dbh. Ponderosa pine accounted for ≥ 96 % of the density and basal area. Ranges for individual plots indicated great stand heterogeneity. Fulé et al. (2002) acknowledged that their reconstructed 1879 values were likely underestimates because of loss of evidence in surface fires. They reported reconstructed densities for ponderosa pines >15.2 cm dbh (6 in.) as 125–141 pines/ha (51–57 pines/acre), but erroneously stated that this range matched historical data. Lang and Stewart (1910) actually reported 99 pines/ha (40 pines/acre).

Another protected forest approximately 130 km (80 miles) to the south is the Gus Pearson Natural Area, which has been the site of extensive research on Ponderosa Pine Forest (e.g., Biondi 1996; Mast et al. 1999; Wallin et al. 2004). Ponderosa pine density reconstructed for 1876 was 57 pines/ha (23 pines/acre; for trees >0 dbh; Covington et al. 1997). Basal area was 26 m²/ha (112 ft²/acre), as calculated from diameter-class data provided by Covington et al. (1997). Therefore, reconstructed density was much lower, and basal area was higher than the North Rim sites. The density of pines ≥ 51 cm (20 in.) dbh was reported as 44 pines/ha (18 pines/acre), slightly above the range extrapolated from Dutton (1882). The stand had not burned since before the reconstructed date of 1876.

A second approach to estimating nineteenth century structure and composition of southwestern Ponderosa Pine Forest is through sampling relict stands little disturbed by Euro-Americans. The three North Rim sites described above were said to provide "...a contemporary example of the forest characteristics that might have been extant..." without Euro-American influence (Fulé et al. 2002). However, this conclusion was challenged because mean fire intervals at the sites increased by ~4 to 9 times during 1880–1997 (Vankat 2011). In addition, sampling of contemporary forests at the sites indicated substantial increases in tree densities and basal areas over reconstructed values (Fulé et al. 2002; see next section). Such increases would not be expected for true relict sites.

Two isolated mesa tops without livestock grazing have been examined as relict areas with Ponderosa Pine Forest in Zion National Park in southwestern Utah (Madany and West 1980, 1983, 1984). Forest structure was described as a savanna, with an open canopy and herb-dominated groundlayer (Madany and West 1984). Tree density was 163 trees/ha (66 trees/acre) for individuals >5 cm (2 in.) dbh (Madany and West 1984). It is questionable whether the data are broadly representative of southwestern Ponderosa Pine Forest. The mesa tops are only 85 and 150 ha

(210 and 370 acres) in area (and included other vegetation types). The total sample was only 0.21 ha (0.5 acres). In addition, the mean fire interval of 69 years on the one mesa researched for fire history was much longer than the typical interval of approximately 4–36 years reported in Sect. 4.2.5.1. The long interval likely reflects limited ignitions and spread of lightning fires on the small mesa top.

Stands of Ponderosa Pine Forest in El Malpais National Monument in west-central New Mexico have been mentioned as possible relict sites (e.g., Covington 2003). These stands have been studied primarily for climate and fire history (e.g., Grissino-Mayer and Swetnam 1997; Grissino-Mayer et al. 1997). Use as relict sites is inappropriate because partial fire exclusion began in ~1880 and altered forest structure (Lewis 2003).

In conclusion, southwestern Ponderosa Pine Forest before Euro-American influence was more varied than many historical accounts suggest. Open, park-like conditions were common, but apparently so were sites where trees were denser. Stands were uneven-aged and consisted of clusters of ponderosa pines that established during widely separated periods of exceptional regeneration and were thinned by surface fires (Sect. 4.3.1). Historical forest structure and composition are best approximated by forest reconstructions, but reconstructions based on tree rings likely underestimate late nineteenth century densities and basal areas.

4.4.1.2 Post-Euro-American Settlement

Stands of southwestern Ponderosa Pine Forest – even stands in protected areas such as National Parks – have greatly changed since the late nineteenth century (e.g., Weaver 1951a; Harrington and Sackett 1990; Covington and Moore 1994a, b; Fulé et al. 2002; Vankat 2011). There are many facets to the changes, including changes in forest density, diameter distribution, structural diversity, tree vigor, and species composition.

Increases in tree density have been attributed to fire exclusion, which began when livestock grazing consumed herbaceous fuels that had carried surface fires (Sect. 4.2.6.1). It continued throughout most of the twentieth century because of fire-management-suppression activities (Sect. 4.2.6.2). Possible roles of other factors such as direct impacts of livestock grazing, wildlife population dynamics, tree cutting, and climate fluctuations were considered by Fulé et al. (2002) for Grand Canyon National Park, but they concluded that forest structure had changed primarily because of fire exclusion. Climate appears to have been an additional, essential factor in some areas. For example, although the fire regime was altered when livestock grazing began in the Chuska Mountains of northeastern Arizona and adjacent New Mexico in about 1830, forest structure didn't change until the early twentieth century. At that time, warm, wet weather coupled with the lack of surface fires enabled tree regeneration (Savage 1991). Many areas of the Southwest experienced a major pulse of regeneration in 1919 (Moir 1993) that was correlated with uncommon seasonal and interannual climatic factors, along with the decline of livestock grazing and ongoing fire exclusion (Savage et al. 1996).

Research on changes in southwestern Ponderosa Pine forest has focused on tree density – it is visually obvious and easily quantified. A common approach has been to compare data from reconstructions of nineteenth century forest structure to recent samples from the same sites. Nearly all such studies have reported large increases in density (e.g. Covington and Moore 1994a; Menzel and Covington 1997; Sánchez Meador et al. 2009), but see Abella (2008) for a dry stand that was stable. The results of broad-scale reconstructions by Abella and Denton (2009) and Williams and Baker (2012) do not provide insight into changes in relatively undisturbed forest, because their research areas were extensively logged in the late nineteenth and twentieth centuries.

Reconstruction studies done in protected areas include Fulé et al. (2002) for the three relatively remote North Rim sites mentioned in the previous section. These sites had surface fires (but at reduced frequencies) during the twentieth century. Densities at these sites in 1997–1998 were 2.5–5.9 times reconstructed values, with modern values of 389–936 trees/ha (157–379 trees/acre) for trees ≥ 2.5 cm (1 in.) dbh. These values include high densities of Gambel oak and New Mexico locust, species that are not amenable to accurate reconstruction because individuals are generally small and prone to decay (Fulé et al. 2002). Considering ponderosa pine only, densities at the three sites were 1.3–1.6 times reconstructed values, with modern values of 193–249 pines/ha (78–100 pines/acre). Basal areas were similarly 1.4–1.6 times reconstructed values, with modern values of 22–31 m²/ha (96–135 ft²/acre). The accuracy of these estimates of increases were affected by twentieth century surface fires that removed evidence of some of the trees that had been present in 1879 (Fulé et al. 2002), resulting in over-estimation of change. Nevertheless, the large differences in density and basal area between 1879 and 1997–1998 suggest these North Rim sites should not be considered relict areas. The sites might be relictual with regard to larger trees, but the absence of data on diameter distributions prevents assessing this.

Estimation of change at the protected, unburned Gus Pearson Natural Area gave a very different result for ponderosa pine density: it was 55 times the reconstructed value, with 3,099 pines/ha (1,254 pines/acre) in 1992 (Covington et al. 1997). The result for basal area was similar to the North Rim sites: 1.3 times the reconstructed value, with 34 m²/ha (148 ft²/acre; calculated from diameter-class data in Covington et al. 1997). This indicates that the large increase in density of ponderosa pine was due to small-diameter trees (see below).

Changes with Euro-American influence also have been examined by resampling permanent plots. The oldest known plots are ~50 that were established in 1909–1913 in National Forests in Arizona and New Mexico to study forest recovery after cutting (Moore et al. 2004; Bell et al. 2009; Sánchez Meador et al. 2010). Resampling these plots has been insightful for various purposes, but because of cutting they are not directly applicable to determining changes in protected stands.

Resampling of plots dating to 1935 in Grand Canyon National Park has proven useful for this purpose (Vankat 2011). Total density remained constant from 1935 to 2004, as an apparent decrease was not statistically significant. Basal area decreased from 50 to 37 m²/ha (218 to 161 ft²/acre). Ponderosa pine was constant in density,

but its basal area decreased from 42 to 33 m²/ha (183 to 144 ft²/acre). In addition, Vankat (2011) combined data sets from various dates in Grand Canyon National Park and found evidence suggesting that Ponderosa Pine Forest had increased in sapling density since the late nineteenth century, apparently as a result of fire exclusion. He concluded that, depending on forest subtype and variable being examined, Grand Canyon stands had reached or passed a peak in forest density and basal area. Dry Ponderosa Pine Forest was likely near peak density and basal area when sampled in 2004, because it lacked statistically significant increases or decreases in either parameter. Both mesic and moist Ponderosa Pine Forests appear to have passed peak values, with decreases in total density and/or basal area. Decreases were likely due to the interaction of density-dependent mortality and exogenous factors such as climate change and prescribed fires (Vankat 2011).

When density changes are examined by diameter class, it is clear that diameter distributions have changed, with increases in smaller classes (e.g., Covington et al. 1997; Fulé et al. 1997, 2002; Menzel and Covington 1997; Vankat 2011) and in some cases decreases in larger classes (e.g., Covington et al. 1997; Vankat 2011). The overall increases in density and greater homogenization of diameter classes among stands have decreased structural diversity of stands (Dahms and Geils 1997) and landscapes (Allen et al. 2002).

Data in Covington et al. (1997) enable insight into changes in tree-diameter distribution from 1876 to 1992 at the Gus Pearson Natural Area. The estimated density increase of 55 times stated above, which was based on reconstructed density for 1876, was accounted for by seedling and sapling ponderosa pines <30 cm (12 in.) dbh. Although a major increase in these pines undoubtedly occurred, accurate estimation of the increase is impossible because most small pines present in 1876 would have died and decomposed by 1992, resulting in an underestimate of 1876 values (previous section) and therefore an overestimate of change. Also, it is unknown if the 1876 density of small pines – only 5 pines/ha (2 pine/acre) for trees in the above diameter class – was typical or abnormally low for the site. The dates of prior regeneration pulses are unknown (only establishment pulses are known; cf. Mast et al. 1999), yet the timing of regeneration pulses would affect interpretation of density increases. In contrast to the large increase in seedlings and saplings, the density of larger pines (i.e., dbh ≥30 cm/12 in.) was nearly unchanged, with 52 and 49 pines/ha (21 and 20 pines/acre) in 1876 and 1992, respectively. However, all three diameter classes ≥81 cm (32 in.) decreased in density and combined for a decrease from 25 to 5 pines/ha (10–2 pines/acre). Vankat (2011) also reported that small ponderosa pines increased in density and large ponderosa pines decreased; however, the magnitudes of the changes were much smaller (and the time period of 1935 to 2004 was much shorter).

With the increased density of small trees, tree vigor decreased across diameter classes. Tree growth rates declined in all diameter classes, with increased shade and root competition and decreased moisture and nutrients because of thicker litter (Clary and Ffolliott 1969 in Harrington and Sackett 1990; Biondi 1996). It appears that reduced vigor has been especially damaging to older, larger trees, as earlier predicted by Pearson (1950) and Weaver (1951a). Data suggest that competition

from smaller, younger trees reduced the vigor of larger, older trees (Feeney et al. 1998; see also Graybill and Rose 1992). Reduced vigor of older trees is inferred from results of ecophysiological measurements following thinning of smaller, younger trees in north-central Arizona; canopy growth, insect-resistance characteristics, and uptake of water, nitrogen, and carbon by older trees all increased with thinning (Stone et al. 1999; Wallin et al. 2004; Zausen et al. 2005). Circumstantial evidence is that many sites have experienced decreased density of larger trees (e.g., Covington et al. 1997; Vankat 2011; see also Crocker-Bedford et al. 2005b). Elevated mortality rates of large trees in Grand Canyon National Park have been related to older trees being more susceptible to pathogens, drought, and injury because of increased stress through increased competition (Kaufmann and Covington 2001).

In contrast to large changes in forest structure, changes in tree composition in protected areas have been minor, except at relatively high elevations in Ponderosa Pine Forest (see below). Although forest reconstructions have indicated increased relative abundance of Gambel oak and/or New Mexico locust, this could partly reflect the above-mentioned issues in reconstructing small, decay-prone individuals of these species (Fulé et al. 2002; Abella and Fulé 2008a). Remeasurement of historical plots in Grand Canyon National Park found suggestions of increases in Gambel oak and New Mexico locust from 1935 to 2004, but none were statistically significant (Vankat 2011).

Data from the remeasurement of historical plots showed that post-1935 changes in species composition were generally limited to increases of white fir and decreases of quaking aspen (Vankat 2011). Changes were different among dry, mesic, and moist Ponderosa Pine Forest. Dry stands exhibited no statistically significant differences in any species from 1935 to 2004. Mesic stands had an increase in density of white fir in the smallest diameter class (10 to <30 cm / 4 to <12 in.), and the species' relative density increased from <1 to 9 % (all diameter classes combined). Moist stands, which are primarily at high elevations, also had an increase in density of white fir in this diameter class, as well as large decreases in density and basal area of quaking aspen. As a result, white fir increased in relative density from 4 to 24 %, and aspen decreased from 64 to 15 %. Changes in moist stands reflect large changes in forest composition reported for stands transitional with Mixed Conifer Forest (Mast and Wolf 2004; Crocker-Bedford et al. 2005a). Such high-elevation stands historically had seed sources of shade-tolerant, fire-sensitive conifers such as white fir within and near stands. As suggested in Sect. 4.2.1, compositional shifts in these stands have changed them into Mixed Conifer Forest (Dahms and Geils 1997; Swetnam et al. 2001; Mast and Wolf 2004; Evans et al. 2011).

In summary, stands of southwestern Ponderosa Pine Forest greatly changed with the influence of Euro-Americans because of a confluence of livestock grazing, fire management, and one or more regeneration pulses of ponderosa pine. All three factors were necessary. Without livestock grazing, some surface fires would have occurred even with fire management. Without fire management, regeneration pulses would have been thinned by fire as livestock grazing declined. Without regeneration pulses, there would have been no dramatic increase in stand densities. Changes in

southwestern Ponderosa Pine Forest include increases in tree density, shifts in diameter distributions toward smaller trees, reductions in tree vigor, and shifts in species composition in higher-elevation stands.

4.4.2 Understory

A review of understory vegetation of southwestern Ponderosa Pine Forest concluded that reference conditions are difficult to identify (Korb and Springer 2003). Euro-American impacts have been so widespread that there are no known, broadly representative relict sites (Sect. 4.4.1.1). Also, little nineteenth century understory plant material has persisted, although archeological data have been used in combination with ethnobotanical records (Alcoze and Hurteau 2001) and phytoliths have been studied (Kerns et al. 2003).

Brief historical descriptions of past understory conditions are available:

...every foot being covered with the finest grass... (Beale 1858, for east of the San Francisco Peaks)

...we walk nearly waist-deep in fine pasture grasses... (Rusby 1889, for the San Francisco Peaks)

There is no undergrowth to obstruct the view, and after the rainy season the grass beneath the trees is knee-deep in places, but the growth is sparse on account of the rocky nature of the surface. (Merriam 1890b, for the San Francisco Peaks)

...the ground was well set with perennial grasses and other herbage... It was not an uncommon thing for the early settlers to cut native hay in the pine forests... (Holsinger 1902 for Arizona)

...hundreds of tons of hay were cut under the actual spread of the forest trees during the [eighteen] sixties and seventies... (Holsinger 1902 for near the city of Prescott in central Arizona)

The underbrush is very heavy, chiefly oak brush, choke-cherry, scarlet thorn, and wild rose. (DuBois 1903, for San Juan National Forest in the San Juan Mountains; in Romme et al. 2009)

See similar comments by Ingersoll (1885) for the vicinities of the towns of Pagosa Springs and Ignacio in southwestern Colorado.

Photographic evidence of historical conditions is very limited. The landscapes in Figs. 4.23a, b and 4.24 are too distant to show the understory, and livestock grazing modified understories at early dates (Sect. 4.2.6.1).

There is universal agreement that understory conditions changed with Euro-American influence. The changes have been linked to livestock grazing, fire exclusion, increases in tree density, and increases in litter depth (e.g., Arnold 1950; Cooper 1960; Pase and Brown 1994; Sackett et al. 1996; Korb and Springer 2003; Battaglia and Shepperd 2007; Romme et al. 2009). For example, surface fire – by thinning tree regeneration – generally had favored understory plants by reducing competition, increasing nutrient availability, and changing soil-water relationships (Moir et al. 1997).

Today (and presumably in the past), the understory of southwestern Ponderosa Pine Forest is highly variable (Romme et al. 2009). Factors influencing the variability

include soil parent material, soil texture, litter depth, precipitation, elevation, topography, fire history, and canopy cover (Laughlin et al. 2005; Abella and Covington 2006; Laughlin and Abella 2007; Romme et al. 2009). Mean understory cover values on isolated, relatively undisturbed sites on the North Rim are ~25 % for ponderosa pine sites and ~47 % for ponderosa pine-Gambel oak sites at somewhat lower elevation (Laughlin et al. 2005). Cover values for individual plots ranged from ~3 to 77 %. At the regional level, shrub species are usually not abundant in most relatively undisturbed stands in northern and central Arizona and New Mexico, but are more abundant in the southern portions of those states and include various oaks (Moir 1993; Pase and Brown 1994; Barton 2002). Shrubs are also abundant in Utah and southwestern Colorado, where Gambel oak is widespread (Bradley et al. 1992; Romme et al. 2009).

Understory species composition has been quantitatively characterized for specific locations (e.g., Laughlin et al. 2004, 2005). Regional characterizations include Hanks et al. (1983), Alexander et al. (1984, 1987), Youngblood and Mauk (1985), DeVelice et al. (1986), Fitzhugh et al. (1987), Moir (1993), Pase and Brown (1994), and Muldavin et al. (1996).

With the scarcity of direct information, understory dynamics must be inferred from various types of research, including studies of the effects of forest thinning and prescribed burning designed to initiate restoration of historical conditions. Long-term results from thinning and burning are not yet available, and inferences from these and other studies can be problematic. Even research on contemporary understories accounts for only 58 % of the variation in plant cover, 22 % of the variation in composition, and 38 % of diversity in Ponderosa Pine Forest on the North Rim (Laughlin et al. 2005). Moreover, historical understory dynamics are likely to have been complex and to have differed among regions (cf. Laughlin et al. 2005). The following paragraphs assess the dynamics of understory cover, species composition, and diversity. All studies are from north-central Arizona, unless otherwise noted.

Understory cover would have changed with overstory successional dynamics. The finding that understory cover was higher on sites burned by high-severity fire vs. lower-severity fire in east-central Arizona (Kuenzi et al. 2008) suggests understory cover is high in early stages of succession (although management reseeding can complicate findings; cf. Foxx 1996; Kuenzi et al. 2008). As succession continues to stages where trees are present, it is likely that understory cover decreases. This is suggested by findings of negative relationships between understory cover and both canopy cover (Arnold 1950) and ponderosa pine basal area (Laughlin et al. 2005, 2011), as well as between understory production and tree density (e.g., Moore and Deiter 1992). These relationships also suggest that understory cover decreased with increased tree densities during fire exclusion. Additional evidence supporting this dynamic is that understory cover is negatively related to time since surface fire (Laughlin et al. 2005), and understory cover and productivity increase with forest restoration treatments of tree thinning and/or management burning (Fig. 4.26; e.g., Huffman and Moore 2004; Laughlin and Fulé 2008). However, some studies



Fig. 4.26 Well-developed herbaceous layer following manual thinning of trees and seeding of herbs near Flagstaff in north-central Arizona (Photograph by Betty J. Huffman)

have shown little relationship between restoration treatments and understory cover (e.g., Korb et al. 2005; Fulé et al. 2005).

Composition of the understory also would have changed with successional dynamics, but this has received little study, except for increases in invasive species following modern, high-severity crown fire (e.g., Crawford et al. 2001; Griffis et al. 2001). Understory composition also changed following fire exclusion (although findings can be inextricably associated with livestock grazing). Grass cover decreased (Cooper 1960; Covington and Moore 1994b; Covington et al. 1997; Fulé et al. 1997; Kerns et al. 2003). This is supported by forest restoration treatments of tree thinning and/or management burning that favored grasses (Weaver 1951b; Sackett et al. 1996; Griffis et al. 2001; Korb and Springer 2003; Moore et al. 2006). In addition, fire exclusion (along with livestock grazing) appears to have led to increases in shrubs, at least in southern Utah (Battaglia and Shepperd 2007).

Changes in understory diversity during succession also have received little study and can be confounded by management reseeding after fire. Understory species richness can be high early in succession (cf. Crawford et al. 2001). It is likely that richness declines as succession continues to stages dominated by trees, as inferred from a negative relationship of understory richness and ponderosa pine basal area

(Laughlin et al. 2005; Laughlin and Grace 2006) and findings that richness is lower in denser forests in Arizona (Clary 1975) and lowest with greatest overstory cover (Laughlin et al. 2007). These findings also indicate that understory richness decreased with increases in tree densities during fire exclusion. Additional evidence of this dynamic is that richness increases following surface fire (Laughlin et al. 2004), is negatively related to time since surface fire (Laughlin et al. 2005; Laughlin and Grace 2006), and decreases without fire (Laughlin et al. 2011). But some studies have found little difference following restoration thinning and burning (e.g., Fulé et al. 2005; Laughlin and Fulé 2008). The decline in understory richness with time since fire can be attributed to post-fire stimulation of seed germination in understory plants, followed by declining understory abundance and increasing ponderosa pine basal area (Laughlin and Grace 2006).

In summary, understory dynamics include increases in understory cover with high-severity disturbance, decreases during succession, and decreases as tree density increased during fire exclusion. Species composition also is dynamic, with decreases in abundance of grasses during succession and with fire exclusion. Species richness increases with high-severity disturbance and decreases during succession and with fire exclusion.

4.5 Conceptual Models

The following nested, three-tiered set of conceptual models is based on my interpretation of best-available information on Ponderosa Pine Forest of the American Southwest. The models summarize and synthesize material on drivers (Sect. 4.2) and processes (Sect. 4.3) of vegetation dynamics, and they account for historical changes (Sect. 4.4). Their format is explained in Sect. 1.7. The models can be used to facilitate understanding of the past and the present. They also can provide insight into effects of future changes in the environment and outcomes of alternative land-management decisions. Moreover, they can guide the development of quantitative models.

4.5.1 *Ecosystem-Characterization Model*

The ecosystem-characterization model for southwestern Ponderosa Pine Forest emphasizes *Vegetation* (a biotic component) and *Disturbance* (a driver; Fig. 4.27a, Table 4.2). Key aspects of *Vegetation* are structure, fuel, herbaceous cover, and species composition, and these affect various aspects of *Disturbance*. The primary agents of *Disturbance* are fire, drought, and insect outbreaks, and these affect tree mortality, vegetation structure, fuel, and species composition. The two other biotic components are *Soil System* and *Animals*, including insects that cause disturbance.

A second driver is *Weather & Climate*, which causes fires and drought and influences fire behavior, plant vigor, and fuel and soil moisture. The third driver is *Landscape*, with its primary feature being elevation. It influences weather and climate, as well as spread, pattern, and severity of fire and impact of drought. The model also includes six anthropogenic drivers (Fig. 4.27b, Table 4.2): *Livestock Grazing*, *Fire Management*, *Modern Climate Change*, *Invasive Species*, *Recreation*, and *Nearby Land Use*.

4.5.2 *Vegetation-Dynamics Models*

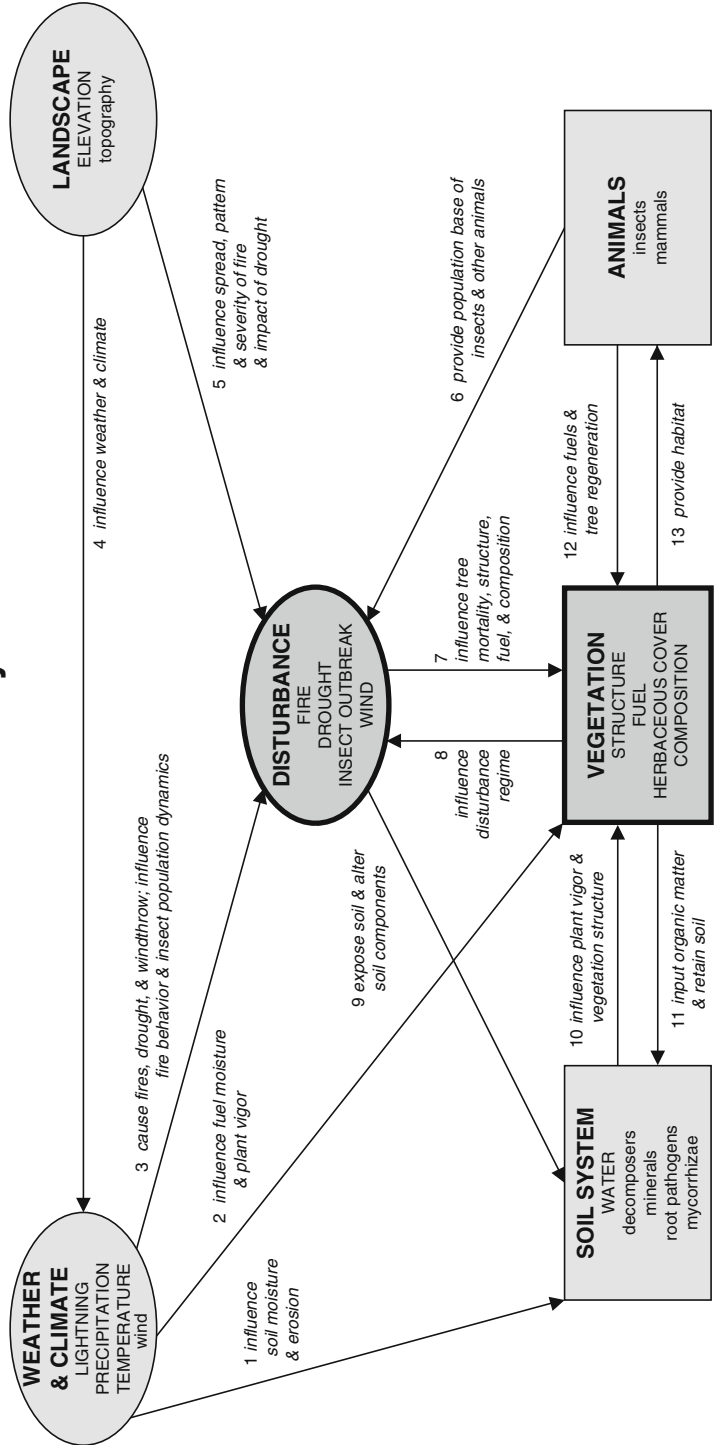
Separate models are needed to illustrate the vegetation dynamics of moist, mesic, and dry southwestern Ponderosa Pine Forest. The models have similar structure, but there are important differences in species composition of communities. Each vegetation-dynamics model is accompanied by a bar graph to show estimated relative shifts in abundances of the community types from circa 1870 (prior to widespread Euro-American land use) to circa 1970 (end of strict fire exclusion policy) to the present. The estimates are based on my understanding of vegetation dynamics and should be interpreted as showing relative differences and not interpreted quantitatively (hence the absence of a scale for abundance). Although not shown on the graphs, relative abundances shifted prior to circa 1870 as a result of variation in climate and disturbance. Localized differences also have been and are present, but are beyond the scope of these generalized bar graphs.

4.5.2.1 **Moist Ponderosa Pine Forest**

The vegetation-dynamics model for moist Ponderosa Pine Forest has four states, nine communities, and three transitions (Fig. 4.28, Table 4.3). All occurred historically. *State A* has been more common than the other states, and it encompasses the three most characteristic moist Ponderosa Pine Forest communities, all of which are dominated by ponderosa pine, white fir, and quaking aspen. Community *A1 Old Growth*, which is maintained by tree regeneration coupled with surface fire, was the most common community circa 1870 and included a wide range of stand densities. With reduced frequency of surface fires, community *A1* forms *A2 Old Growth with Dense Understory*. Therefore, *A2* greatly increased with past fire exclusion as ponderosa pine and white fir became more abundant in the understory in the absence of thinning by frequent surface fire. Surface fire can return community *A2* to *A1*, and consequently *A2* decreased since circa 1970 because of management fires. Continued reduced frequency of surface fire results in the maturation of understory trees and changes community *A2* into community *A3 Denser Old Growth*. Moderate tree mortality, as for example with some insect outbreaks, changes community *A3* into *A1* or *A2*.

Base Ecosystem

a



b Proximate Effects of Anthropogenic Drivers on Base Ecosystem

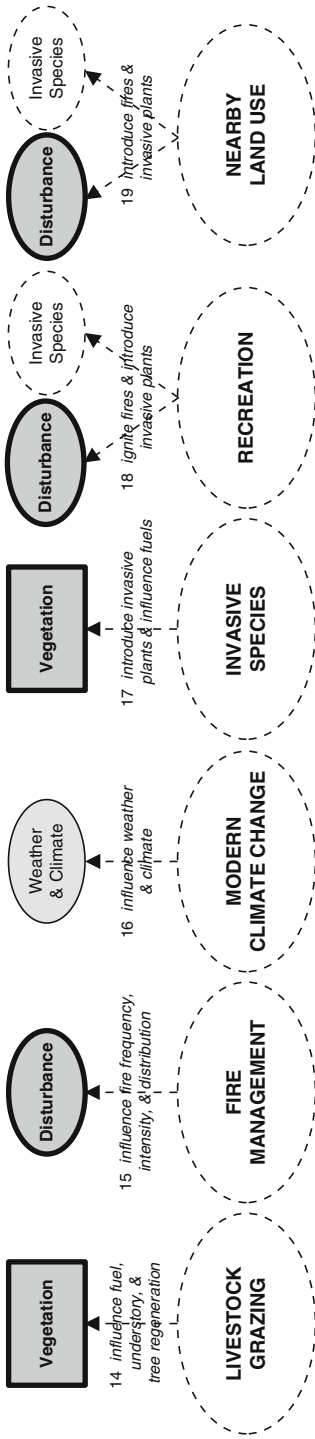


Fig. 4.27 (a, b) Ecosystem-characterization model for Ponderosa Pine Forest. In the base model (a), biotic components are shown as *rectangles* and drivers as *solid ovals*. Text within them identifies major features in *upper case* and other important features in *lower case*. Disturbance and Vegetation are *highlighted*, because they are the basis for the vegetation-dynamics models (Figs. 4.28, 4.29, and 4.30). In the anthropogenic supplement to the base model (b), drivers are shown as *dashed ovals*. Relationships in (a) and (b) are shown as *solid* and *dashed arrows*, respectively, and are described in Table 4.2

Table 4.2 Relationships in the ecosystem-characterization model of southwestern Ponderosa Pine Forest (Fig. 4.27a, b)

Relationships	Circa 1870	Present
1	Precipitation increases soil moisture and can cause soil erosion. Winter precipitation is critical for recharging soil moisture	Same, but infiltration of precipitation, especially summer monsoonal rain, can be reduced by thicker layer of litter and duff, where unburned. Infiltration is reduced and soil erosion can be increased where this layer has been lost in high-severity fires. In addition, climate change increases the severity and duration of drought
2	Precipitation and temperature largely determine fuel moisture and are important to plant vigor	Same, but climate change increases drought and insect outbreaks of drought
3	Lightning ignites fires. Consistently low precipitation and high temperature cause drought and affect insect population dynamics. Wind influences fire behavior	Same, but climate change increases drought and insect outbreaks
4	Topography influences weather and climate	Same, but the effects on forest microclimate can be reduced with dense tree cover
5	Fire patterns are influenced by elevation and topography	Same, but the effects of elevation and topography are reduced in areas with higher fuel loadings and more continuous fuels
6	Increases in populations of bark beetles can result in outbreaks	Same
7	Frequent surface fires thin tree regeneration and keeps fuel loadings low. Crown fires kill trees in all size classes. Bark beetles kill scattered large trees, producing coarse fuels. Drought increases stress in trees, surface fire frequency, probability of patchy crown fires, and outbreaks of bark beetles	Same, except past fire exclusion resulted in increased tree densities, fuel loadings, fuel continuity, and homogeneity of vegetation patterns. Surface fires are more likely to crown, and crown fires are more likely to burn across landscapes. Crown fires kill trees in all size classes. Drier climate results in expansive stands of stressed trees and increased probability of fires and bark beetle outbreaks
8	Horizontally continuous fine fuels, light fuel loadings, and vertically discontinuous fuels result in fire regime dominated by frequent, low-severity surface fires. Crown fires occur in areas of heterogeneous topography and steep slopes	Increased fuel loadings and more vertically continuous fuels result in greater probability of extensive crown fires

9	Surface fires partially and patchily expose soil surface and alter soil properties	Past fire exclusion resulted in thicker, more extensive litter and duff and likely altered other soil properties. Hotter, larger fires likely have greater effects on soil properties
10	Water and minerals in soil affect plant vigor and growth and forest structure	Same, but less water is available because of drought, higher temperatures, and thicker litter and duff. Minerals can be less available because of greater sequestering in organic matter
11	Plants add organic matter to soil and stabilize soil, except in areas of crown fires	Same, except areas of crown fires are larger
12	Herbivory influences fuels and tree regeneration	Same, but livestock and increased deer and elk populations have greater effects
13	Vegetation is habitat for animals	Same, but animal populations are changed where habitat is changed
14	Not applicable	Late nineteenth century livestock grazing reduced herb cover and likely influenced tree regeneration. The reduction in herb cover reduced the frequency of surface fires. Impacts of twenty-first century grazing are poorly known
15	Not applicable	Past fire management attempted to suppress fires throughout most of the twentieth century. This resulted in large changes in forest structure and composition. Beginning in the late twentieth century, fire management included prescribed and lightning-ignited management fires
16	Not applicable	Modern climate change affects weather and climate, raising temperature and increasing the frequency and extent of drought
17	Not applicable	Invasive plants have potential to modify the understory and change fire patterns
18	Not applicable	Recreationists ignite fires and introduce and spread invasive plants
19	Not applicable	Nearby land use that initiates fires and colonization by invasive plants can introduce fires and invasives into Ponderosa Pine Forest

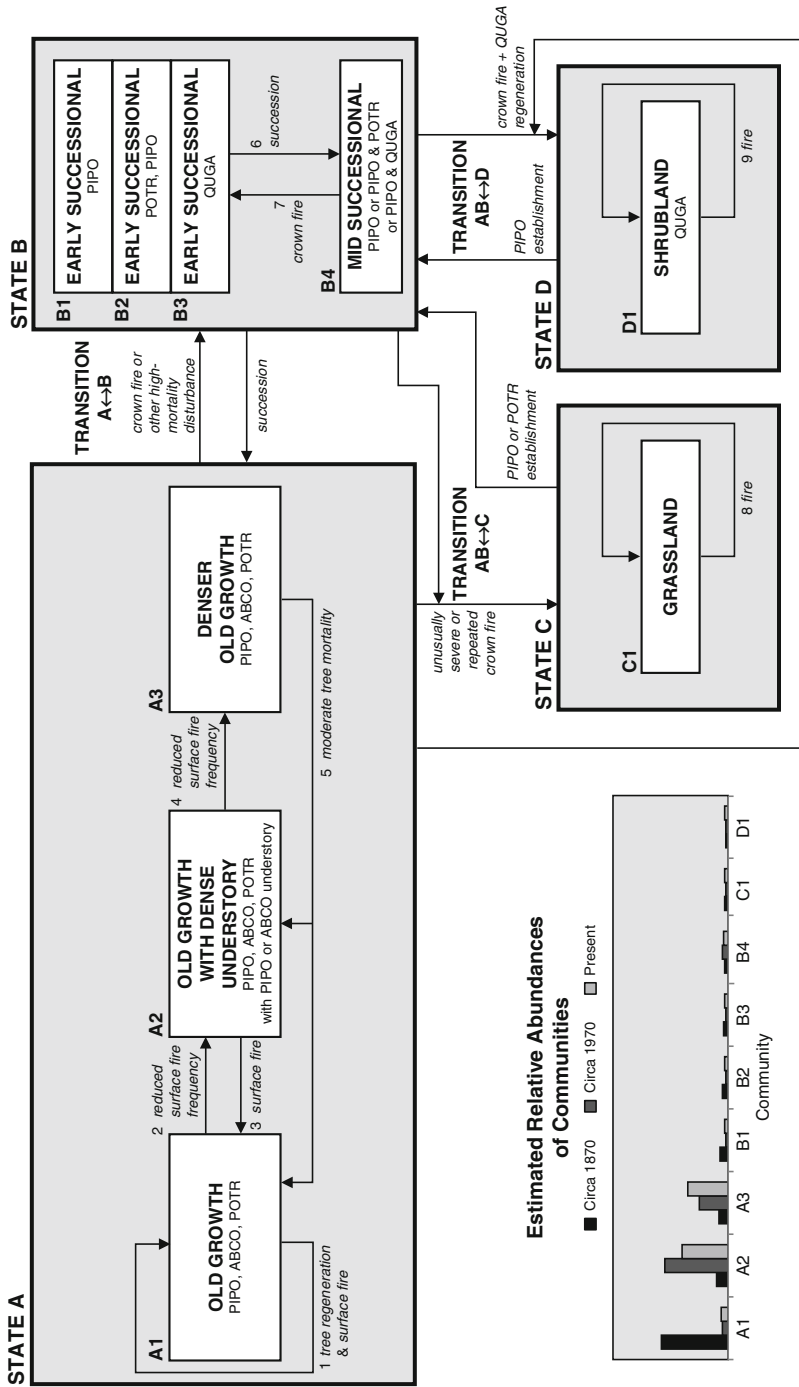


Fig. 4.28 Vegetation-dynamics model for moist Ponderosa Pine Forest. Model provides details on the vegetation-disturbance portion of the ecosystem-characterization model (Fig. 4.27a, b) by showing communities (*smaller, open rectangles*) within states (*larger, shaded rectangles*), processes that form the communities, and transitions between states. Text along *arrows* identifies pathways that are described in Table 4.3. *Bar graph* shows estimated relative shifts in abundances of the community types from circa 1870 (see Sect. 4.5.2). Species: *ABCO* white fir, *PIPO* ponderosa pine, *POTR* quaking aspen, *OUGA* Gambel oak

Table 4.3 Relationships and transitions in the vegetation-dynamics model of moist Ponderosa Pine Forest (Fig. 4.28)

Relationships and transitions	Circa 1870	Present
1	Periodic tree regeneration is thinned by surface fire, which maintains old growth structure and composition	Same, but surface fire is less frequent
2	Periods of reduced frequency of surface fire leave tree understory unthinned, producing old growth with dense understory	Same and surface fire is less frequent
3	Surface fire thins tree understory, changing stands into old growth without a dense understory	Same, but surface fire is less frequent
4	Periods of reduced frequency of surface fire allow understory trees to grow into the canopy, changing stands into denser old growth	Same and surface fire is less frequent
5	Moderate tree mortality, such as with some insect outbreaks, reduces density of canopy trees, changing stands into old growth or old growth with dense understory	Same and insect outbreaks are more frequent
A ↔ B	Crown fire or other high-mortality disturbance changes old growth communities of State A into early successional communities B1, B2, or B3, depending on the abundance and vigor of quaking aspen and Gambel oak in the old growth stands. Reversion to State A requires succession	Same and crown fire is more common
6	Succession changes early successional stands into mid successional community	Same
7	Crown fire changes mid successional stands into early successional communities B1, B2, or B3, depending on the abundance and vigor of quaking aspen and Gambel oak in the mid successional stands	Same and crown fire is more common
AB ↔ C	Unusually severe or repeated crown fire converts some stands from States A and B into State C. Reversion to State B requires invasion and establishment of ponderosa pine or quaking aspen to form early successional communities B1 or B2, depending on the invading species. Reversion to State A has to be via State B	Same, but unusually severe and repeated crown fire is more common. Larger size of crown fire limits invasion of ponderosa pine and quaking aspen
8	Fire maintains stand structure and composition	Same, but fire is less frequent
AB ↔ D	Crown fire followed by regeneration of Gambel oak converts some stands from States A and B into State D. Reversion to State B requires invasion and establishment of ponderosa pine to form early successional community B3 transitioning into B4. Reversion to State A has to be via State B	Same, but crown fire is more common. Larger crown fire limits invasion of ponderosa pine
9	Fire maintains stand structure and composition	Same, but fire is less frequent

Transition A ↔ B changes *State A* to *State B* with crown fire or other disturbance that results in high mortality of trees. One of three *Early Successional* communities is formed: *B1* with ponderosa pine, *B2* with quaking aspen and ponderosa pine, or *B3* with shrubs of Gambel oak. The community formed largely depends on the pre-fire abundance and vitality of aspen and Gambel oak. Succession changes *B1*, *B2*, and *B3* into community *B4 Mid Successional* dominated by either (a) ponderosa pine, (b) ponderosa pine and quaking aspen, or (c) ponderosa pine and Gambel oak. Crown fire changes *B4* into *B1*, *B2*, or *B3*, also depending on the pre-fire abundance and vitality of aspen and Gambel oak. *Transition A ↔ B* can be reversed by succession.

Unusually severe or repeated crown fire can change *States A* and *B* into *State C* via *Transition AB ↔ C*. *State C* is made up of community *C1 Grassland*, which is maintained by fire. *Transition AB ↔ C* can be reversed by invasion and establishment of ponderosa pine and/or aspen, converting *C1* into either *B1* or *B2* depending on the invading species. Reversion to *State A* occurs only via *State B*.

Crown fire followed by regeneration of Gambel oak can change *States A* and *B* into *State D* via *Transition AB ↔ D*. *State D* consists of community *D1 Shrubland*, which is dominated by Gambel oak and maintained by fire (Gambel oak sprouts after fire). *Transition AB ↔ D* can be reversed by invasion and establishment of ponderosa pine, converting *D1* into *B3* transitioning into *B4*. Reversion to *State A* occurs only via *State B*.

4.5.2.2 Mesic Ponderosa Pine Forest

The vegetation-dynamics model for mesic Ponderosa Pine Forest has four states, eight communities (one fewer than moist and dry Ponderosa Pine Forest), and three transitions (Fig. 4.29, Table 4.4). All occurred historically. *State A* has been more common than the other states, and it encompasses the three most characteristic mesic Ponderosa Pine Forest communities, all of which are dominated by ponderosa pine. Community *A1 Old Growth*, which is maintained by tree regeneration coupled with surface fire, was the most common community circa 1870 and included a wide range of stand densities. With reduced frequency of surface fires, community *A1* forms *A2 Old Growth with Dense Understory*. Therefore, *A2* greatly increased with fire exclusion as ponderosa pine became more abundant in the understory in the absence of thinning by frequent surface fire. Surface fire can return community *A2* to *A1*, and consequently *A2* decreased since circa 1970 because of management fires. Continued reduced frequency of surface fire results in the maturation of understory trees and changes community *A2* into community *A3 Denser Old Growth*. Moderate tree mortality, as for example with some insect outbreaks, changes community *A3* into *A1* or *A2*.

Transition A ↔ B changes *State A* to *State B* with crown fire or other disturbance that results in high mortality of trees. One of two *Early Successional* communities is formed: *B1* with ponderosa pine or *B2* with shrubs of Gambel oak. The community formed largely depends on the pre-fire abundance and vitality of Gambel oak.

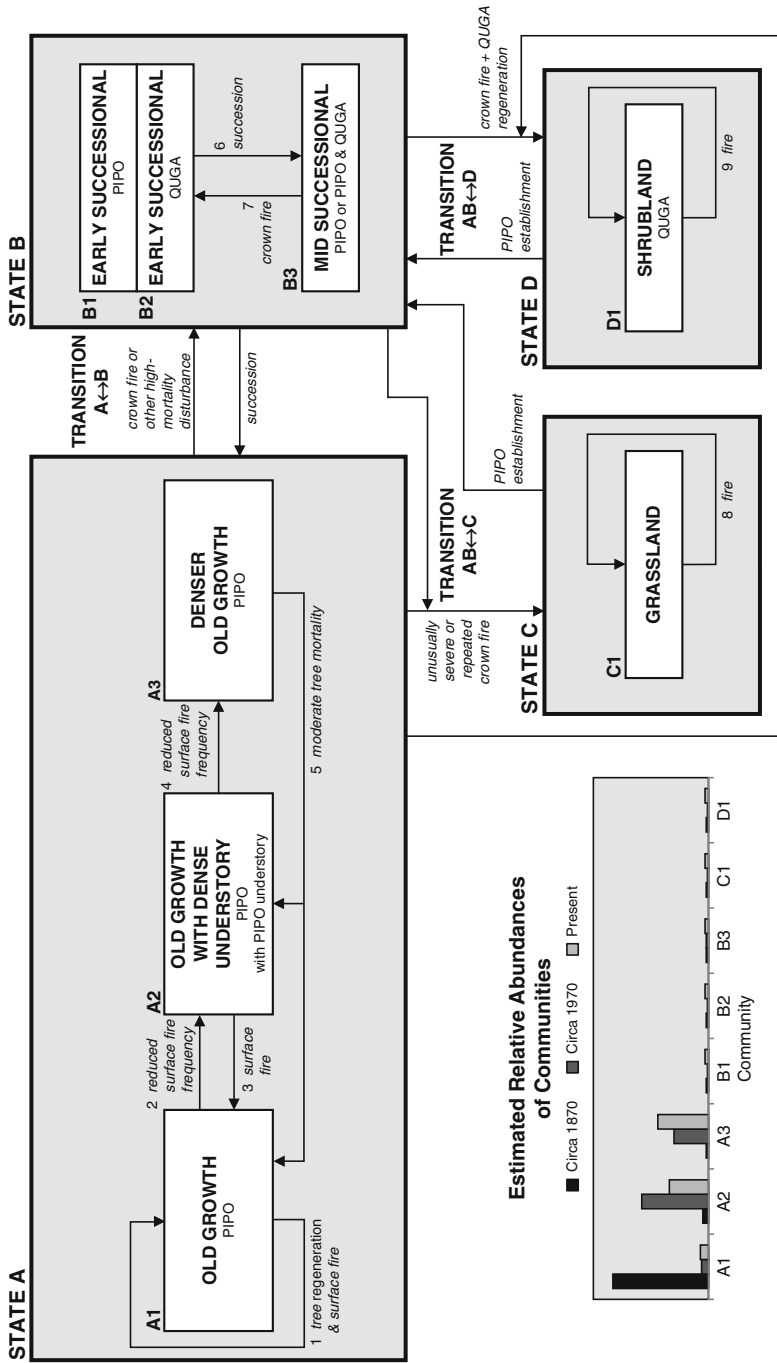


Fig. 4.29 Vegetation-dynamics model for mesic Ponderosa Pine Forest. Model provides details on the vegetation-disturbance portion of the ecosystem-characterization model (Fig. 4.27a, b) by showing communities (smaller, open rectangles) within states (larger, shaded rectangles), processes that form the communities, and transitions between states. Text along arrows identifies pathways that are described in Table 4.4. Bar graph shows estimated relative shifts in abundances of the community types from circa 1870 (see Sect. 4.5.2). Species: PIVO ponderosa pine, QUGA Gambel oak

Table 4.4 Relationships and transitions in the vegetation-dynamics model of mesic Ponderosa Pine Forest (Fig. 4.29)

Relationships and transitions	Circa 1870	Present
1	Periodic tree regeneration is thinned by surface fire, maintaining stand structure and composition	Same, but surface fire is less frequent
2	Periods of reduced frequency of surface fire leave tree understory unthinned, producing old growth with dense understory	Same and surface fire is less frequent
3	Surface fire thins tree understory, changing stands into old growth without a dense understory	Same, but surface fire is less frequent
4	Periods of reduced frequency of surface fire allow understory trees to grow into the canopy, changing stands into denser old growth	Same and surface fire is less frequent
5	Moderate tree mortality, such as with some insect outbreaks, reduces density of canopy trees, changing stands into old growth or old growth with dense understory	Same and insect outbreaks are more frequent
A ↔ B	Crown fire or other high-mortality disturbance changes old growth communities of State A into early successional communities B1, B2, or B3, depending on the abundance and vigor of quaking aspen and Gambel oak in the old growth stands. Reversion to State A requires succession	Same and crown fire is more common
6	Succession changes early successional stands into mid successional community	Same
7	Crown fire changes mid successional stands into early successional communities B1 or B2, depending on the abundance and vigor of Gambel oak in the mid successional stands	Same and crown fire is more common
AB ↔ C	Unusually severe or repeated crown fire converts some stands from States A and B into State C. Reversion to State B requires invasion and establishment of ponderosa pine to form early successional community B1. Reversion to State A has to be via State B	Same, but unusually severe and repeated crown fire is more common. Larger size of crown fire limits invasion of ponderosa pine
8	Fire maintains stand structure and composition	Same, but fire is less frequent
AB ↔ D	Crown fire followed by regeneration of Gambel oak converts some stands from States A and B into State D. Reversion to State B requires invasion and establishment of ponderosa pine to form early successional community B2 transitioning into B3. Reversion to State A has to be via State B	Same, but crown fire is more common. Larger crown fire limits invasion of ponderosa pine
9	Fire maintains stand structure and composition	Same, but fire is less frequent

Succession changes *B1* and *B2* into community *B3 Mid Successional* dominated by either ponderosa pine or ponderosa pine and Gambel oak. Crown fire changes *B3* into *B1* or *B2*, also depending on the pre-fire abundance and vitality of Gambel oak. *Transition A ↔ B* can be reversed by succession.

Unusually severe or repeated crown fire can change *States A* and *B* into *State C* via *Transition AB ↔ C*. *State C* is made up of community *C1 Grassland*, which is maintained by fire. *Transition AB ↔ C* can be reversed by invasion and establishment of ponderosa pine, converting *C1* into *B1*. Reversion to *State A* occurs only via *State B*.

Crown fire followed by regeneration of Gambel oak can change *States A* and *B* into *State D* via *Transition AB ↔ D*. *State D* consists of community *D1 Shrubland*, which is dominated by Gambel oak and maintained by fire (Gambel oak root sprouts after fire). *Transition AB ↔ D* can be reversed by invasion and establishment of ponderosa pine, converting *D1* into *B2* transitioning into *B3*. Reversion to *State A* occurs only via *State B*.

4.5.2.3 Dry Ponderosa Pine forest

The vegetation-dynamics model for dry Ponderosa Pine Forest has four states, nine communities, and three transitions (Fig. 4.30, Table 4.5). All occurred historically. *State A* has been more common than the other states, and it encompasses the three most characteristic dry Ponderosa Pine Forest communities, all of which are dominated by ponderosa pine with pinyons and junipers in the understory. Community *A1 Old Growth*, which is maintained by tree regeneration coupled with surface fire, was the most common community circa 1870 (its range of stand densities was likely narrower than for moist and mesic Ponderosa Pine Forest). With reduced frequency of surface fires, community *A1* forms *A2 Old Growth with Dense Understory*. Therefore, *A2* greatly increased with past fire exclusion as ponderosa pine became more abundant in the understory in the absence of thinning by frequent surface fire. Surface fire can return community *A2* to *A1*, and consequently *A2* decreased since circa 1970 because of management fires. Continued reduced frequency of surface fire results in the maturation of understory trees and changes community *A2* into community *A3 Denser Old Growth*. Moderate tree mortality, as for example with some insect outbreaks, changes community *A3* into *A1* or *A2*.

Transition A ↔ B changes *State A* to *State B* with crown fire or other disturbance that results in high mortality of trees. One of three *Early Successional* communities is formed: *B1* with ponderosa pine, *B2* with pinyons and junipers, or *B3* with oak shrubs or trees. Succession changes *B1*, *B2*, and *B3* into community *B4 Mid Successional* dominated by either (a) ponderosa pine, (b) ponderosa pine, pinyons, and junipers, or (c) ponderosa pine and oak. Crown fire changes *B4* into *B1*, *B2*, or *B3*. *Transition A ↔ B* can be reversed by succession.

Unusually severe or repeated crown fire can change *States A* and *B* into *State C* via *Transition AB ↔ C*. *State C* is made up of community *C1 Grassland*, which is maintained by fire. *Transition AB ↔ C* can be reversed by invasion and establishment

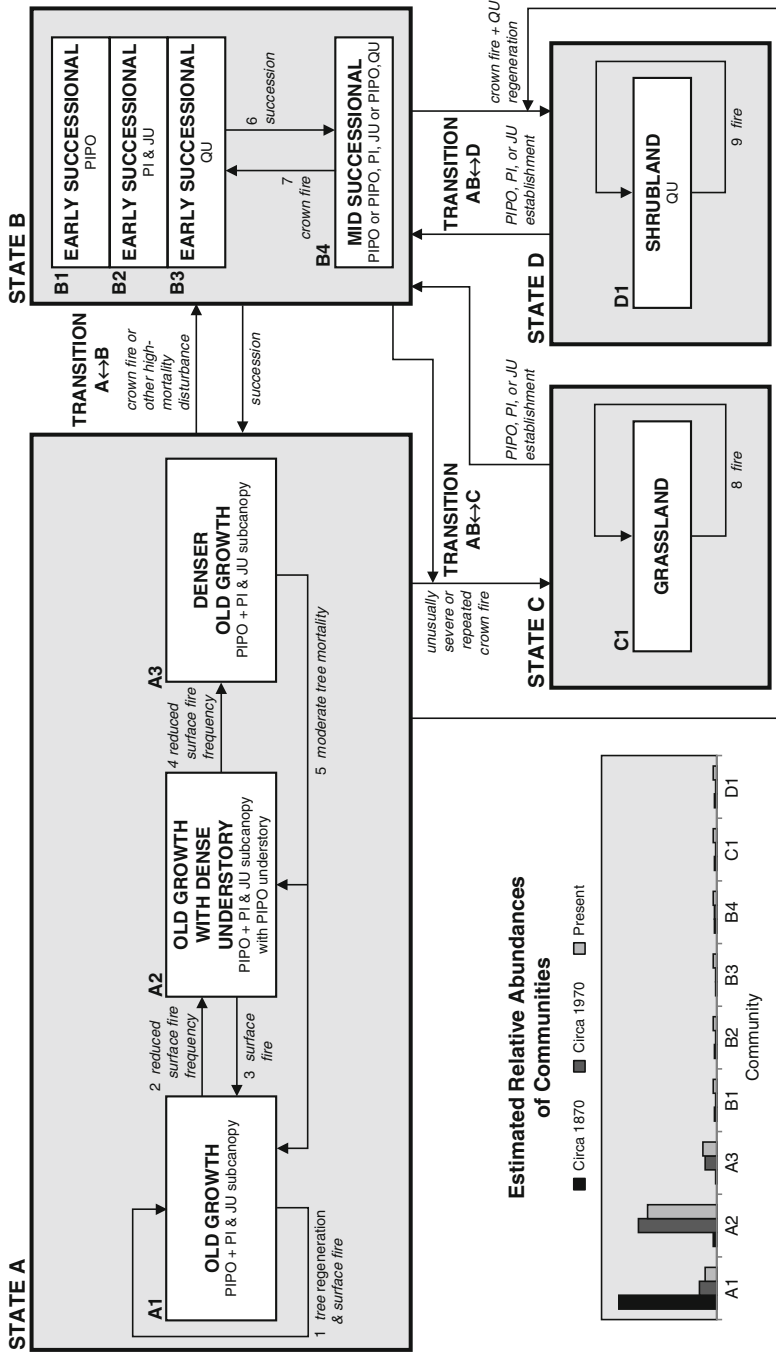


Fig. 4.30 Vegetation-dynamics model for dry Ponderosa Pine Forest. Model provides details on the vegetation-disturbance portion of the ecosystem-characterization model (Fig. 4.27a, b) by showing communities (smaller, open rectangles) within states (larger, shaded rectangles), processes that form the communities, and transitions between states. Text along arrows identifies pathways that are described in Table 4.5. Bar graph shows estimated relative shifts in abundances of the community types from circa 1870 (see Sect. 4.5.2). Species: JU junipers, PI pinyons, PIPo ponderosa pine, and QU oaks

Table 4.5 Relationships and transitions in the vegetation-dynamics model of dry Ponderosa Pine Forest (Fig. 4.30)

Relationships and transitions	Circa 1870	Present
1	Periodic tree regeneration is thinned by surface fire, which maintains old growth structure and composition	Same, but surface fire is less frequent
2	Periods of reduced frequency of surface fire leave tree understory unthinned, producing old growth with dense understory	Same and surface fire is less frequent
3	Surface fire thins tree understory, changing stands into old growth without a dense understory	Same, but surface fire is less frequent
4	Periods of reduced frequency of surface fire allow understory trees to grow into the canopy, changing stands into denser old growth	Same and surface fire is less frequent
5	Moderate tree mortality, such as with some insect outbreaks, reduces density of canopy trees, changing stands into old growth or old growth with dense understory	Same and insect outbreaks are more frequent
A ↔ B	Crown fire or other high-mortality disturbance changes old growth communities of State A into early successional communities B1, B2, or B3, depending on the abundance and vigor of oak in the old growth stands and which conifers establish after fire. Reversion to State A requires succession	Same and crown fire is more common
6	Succession changes early successional stands into mid successional community	Same
7	Crown fire changes mid successional stands into early successional communities B1, B2, or B3, depending on the abundance and vigor of oak in the mid successional stands and which conifers establish after fire	Same and crown fire is more common
AB ↔ C	Unusually severe or repeated crown fire converts some stands from States A and B into State C. Reversion to State B requires invasion and establishment of ponderosa pine, pinyon, or juniper to form early successional communities B1 or B2, depending on the invading species. Reversion to State A has to be via State B	Same, but unusually severe and repeated crown fire is more common. Larger size of crown fire limits invasion of ponderosa pine, pinyon, and juniper
8	Fire maintains stand structure and composition	Same, but fire is less frequent
AB ↔ D	Crown fire followed by regeneration of oaks converts some stands from States A and B into State D. Reversion to State B requires invasion and establishment of ponderosa pine, pinyon, or juniper to form early successional community B3 transitioning into B4. Reversion to State A has to be via State B	Same, but crown fire is more common. Larger crown fire limits invasion of ponderosa pine, pinyon, and juniper
9	Fire maintains stand structure and composition	Same, but fire is less frequent

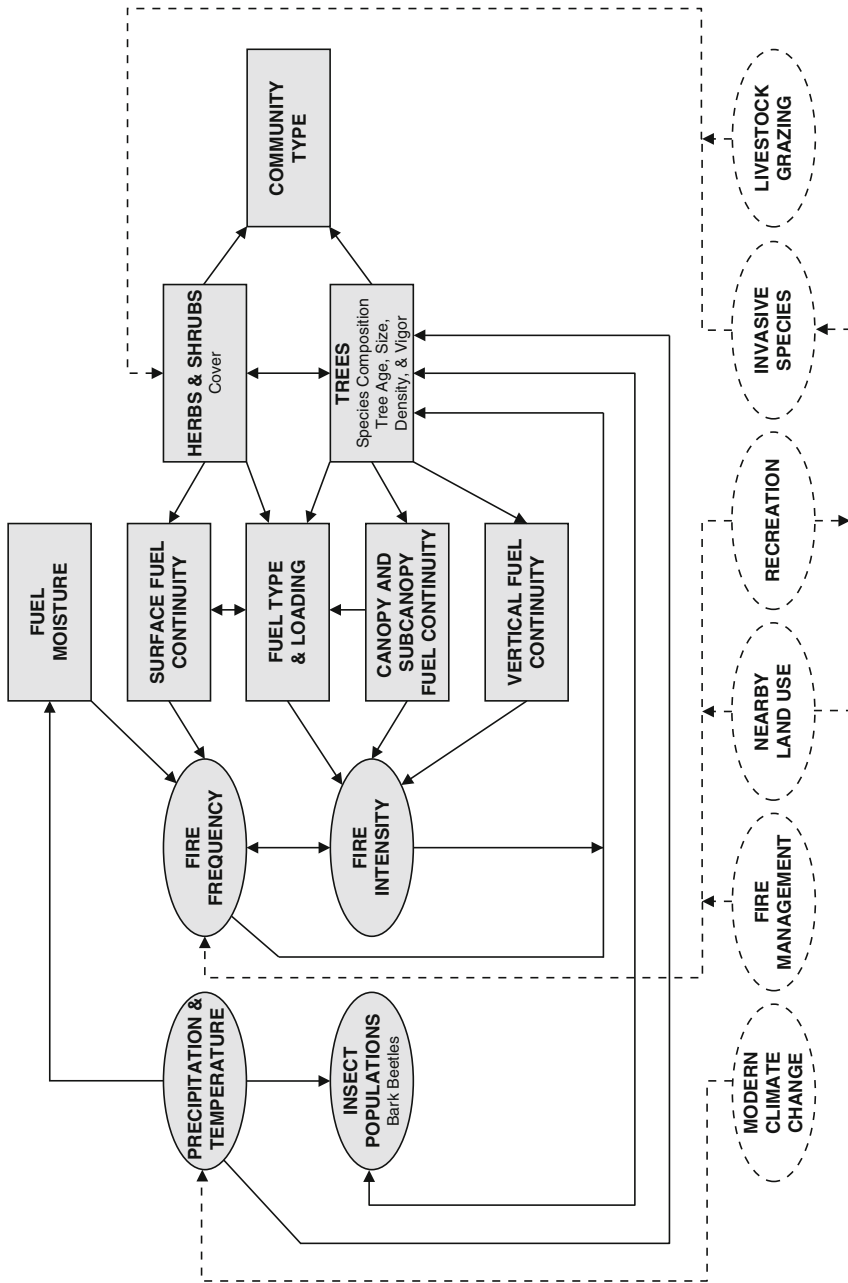


Fig. 4.31 Mechanistic model for Ponderosa Pine Forest. Model provides details on the mechanisms involved in the vegetation-dynamics models (Figs. 4.28, 4.29, and 4.30). *Rectangles* are biotic components (including fuels), *ovals* are drivers, and *dashed ovals* are anthropogenic drivers

of ponderosa pine, pinyons, and/or junipers, converting *C1* into either *B1* or *B2* depending on the invading species. Reversion to State A occurs only via State B.

Crown fire followed by regeneration of oak can change *States A and B* into *State D* via *Transition AB ↔ D*. *State D* consists of community *D1 Shrubland*, which is dominated by oak and maintained by fire. *Transition AB ↔ D* can be reversed by invasion and establishment of ponderosa pine, pinyons, and/or junipers, converting *D1* into *B3* transitioning into *B4*. Reversion to State A occurs only via State B.

4.5.3 Mechanistic Model

All three vegetation-dynamics models are explained by the same mechanistic model (Fig. 4.31). It has eight biotic components on the right side of the figure (including five aspects of fuels), four drivers on the left side, and six anthropogenic factors at the bottom. In general, *Herbs & Shrubs*, *Trees*, and *Precipitation & Temperature* affect the five fuel characteristics. The fuel characteristics combined with *Fire Intensity*, *Fire Management*, *Nearby Land Use*, and *Recreation* influence *Fire Frequency*. Also, *Fire Frequency*, *Fire Intensity*, *Precipitation & Temperature*, and *Insect Populations* influence characteristics of *Trees*, such as species composition and tree age, size, density, and vigor. *Trees* and *Herbs & Shrubs* determine *Community Type* (of the eight/nine appearing in the vegetation-dynamics models).

4.6 Conclusions and Challenges

Ponderosa Pine Forest is the most thoroughly studied vegetation on southwestern mountains and plateaus. Nevertheless, there are many challenges for researchers and managers. Historical stand structure has been characterized as generally open and park-like; however, some evidence indicates greater variation in stand structure prior to Euro-American settlement. Additional research is needed. A historical fire regime of frequent, low-severity fires is widely documented, but research has indicated that the fire regime also included mixed- and high-severity fire. This too requires additional study, with attention to identifying historical mixed- and high-severity fires, their spatial extent, and factors associated with their spatial and temporal distributions. Fire regimes have been documented mostly by mean fire intervals, but the length of fire-free periods possibly provides insight into differences in species composition among stands. Questions have been raised about methods of forest reconstruction. Comparison of reconstructions by tree rings vs. land surveys in the same landscape could provide insight into the advantages and disadvantages of both methods. Although useful information has been obtained from forest reconstructions based on tree rings, future studies need to report data for diameter distributions and for multiple twentieth century dates to enable comparison of findings with other studies. Increasing stand densities during the twentieth century are well-known, but a more detailed understanding is important. For example,

research is needed on the timing of past regeneration pulses of ponderosa pine. Were regeneration levels in late nineteenth century abnormally low, thereby biasing our perspective of historical conditions? Also, have old-growth stands reached or surpassed peak density and basal area, as reported for Grand Canyon National Park? Anthropogenic disturbances have had greater impact on Ponderosa Pine Forest than on other vegetation types on southwestern mountains and plateaus. Key factors needing study and subsequent management planning and action include the direct impacts of air pollution, the spread and control of invasive plants, and the impacts and regulation of recreation. Most importantly, the long-term viability of southwestern Ponderosa Pine Forest is threatened by the combination of climate change, human use, and landscape-scale crown fires. Is conversion to grasslands and shrublands following crown fires – especially repeated crown fires – the fate of southwestern Ponderosa Pine Forest? Well-founded, ecologically based management plans for regional restoration of Ponderosa Pine Forest must be developed and implemented. A major challenge is to develop fire-management programs that achieve forest structure and function that are sustainable during climate change.

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