# Chapter 6
# Subalpine-Montane Grassland

**Abstract** Stands of southwestern Subalpine-Montane Grassland occur as scattered, small to large openings within Spruce-Fir, Mixed Conifer, and Ponderosa Pine Forests. Most stands are dominated by bunchgrasses. Stands are divided into moist and mesic-dry grasslands. Natural disturbances are primarily fire, herbivory, and extreme weather. Historically, moist stands likely burned infrequently and during drought years. Mesic-dry stands likely burned more often, with fire frequency correlated with that of the surrounding forest vegetation and with the dryness of the grassland. The most important anthropogenic disturbance is livestock grazing; others are fire management, modern climate change, invasive species, recreation, and nearby land use. Vegetation dynamics are dominated by three processes: rapid regrowth by resprouting from below-ground structures, succession, and tree encroachment. Where tree encroachment occurs, it appears related to increased precipitation, warmer temperatures, reduced fire, and effects of ungulate herbivory. Specifics of historical conditions are poorly known. Past livestock grazing reduced vegetation cover, altered species composition, and increased invasive plants. Vegetation dynamics are illustrated in a nested, three-tiered set of conceptual models. Key conclusions and challenges for researchers and land managers are summarized.

## 6.1 Introduction

Subalpine-Montane Grassland on the mountains and plateaus of the American Southwest is dominated by herbaceous plants of various heights; shrubs are also present. Stands generally occur as openings scattered within Spruce-Fir (*Picea-Abies*), Mixed Conifer, and Ponderosa Pine (*Pinus ponderosa*) Forests (Figs. 6.1 and 6.2), making Subalpine-Montane Grassland the most naturally fragmented of the vegetation types covered in this book (cf. Fletcher and Robbie 2004). Stands are also referred to as meadows or parks. Stands are in the range of small openings under 1 ha (2.5 acres) to large expanses of more than 1,000 ha (2,500 acres). With its patchy distribution, Subalpine-Montane Grassland occupies only a small percentage

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**Fig. 6.1** Subalpine-Montane Grassland on the San Francisco Peaks in north-central Arizona. Note other stands of Subalpine-Montane Grassland in the area, including a large stand partially obscured by the tree in the middle of the photograph (Photograph by Betty J. Huffman)

**Fig. 6.2** Subalpine-Montane Grassland in a valley in the North Rim region of Grand Canyon National Park, north-central Arizona (Photograph by Betty J. Huffman)

**Table 6.1** Common and scientific names of species in this chapter. Primary source: Integrated Taxonomic Information System (2012)

| | |
|---|---|
| *Plants* | |
| Arizona fescue | *Festuca arizonica* Vasey |
| Douglas-fir | *Pseudotsuga menziesii* (Mirbel) Franco |
| Engelmann spruce | *Picea engelmannii* Parry ex Engelm. |
| Fescue | *Festuca* L. |
| Fir | *Abies* P. Mill. |
| Intermediate wheatgrass | *Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey |
| Juniper | *Juniperus* L. |
| Kentucky bluegrass | *Poa pratensis* L. |
| Mountain muhly | *Muhlenbergia montana* (Nutt.) Hitchc. |
| Oatgrass | *Danthonia* DC. |
| Orchardgrass | *Dactylis glomerata* L. |
| Pinyon | *Pinus* L. |
| Ponderosa pine | *Pinus ponderosa* Douglas ex P. Lawson & C. Lawson |
| Quaking aspen | *Populus tremuloides* Michx. |
| Screwleaf muhly | *Muhlenbergia virescens* (Kunth) Trin. |
| Sedge | *Carex* L. |
| Smooth brome | *Bromus inermis* Leyss. |
| Southwestern white pine | *Pinus strobiformis* Engelm. |
| Spruce | *Picea* A. Dietr. |
| Subalpine fir | *Abies lasiocarpa* var. *lasiocarpa* (Hook.) Nutt. |
| Thurber fescue | *Festuca thurberi* Vasey |
| Timothy | *Phleum pratense* L. |
| White fir | *Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr. |
| *Animals* | |
| Cattle | *Bos taurus* Linnaeus, 1758 |
| Deer | *Odocoileus* Rafinesque, 1832 |
| Elk | *Cervus elaphus* Linnaeus, 1758 |
| Grasshopper | suborder Caelifera |
| Northern pocket gopher | *Thomomys talpoides* Richardson, 1928 |
| Sheep | *Ovis aries* Linnaeus, 1758 |

of most landscapes, e.g., 2 % of the forested portion of the landscape of Grand Canyon National Park in north-central Arizona (Warren et al. 1982).

Subalpine-Montane Grassland covers approximately 10,400 km$^2$ (4,000 miles$^2$) of the American Southwest, which is 1.3 % of the region's area (Fig. 6.3; calculations based on Prior-Magee et al. 2007). This is the second smallest area of the vegetation types covered in this book. The maximum area of Subalpine-Montane Grassland in the region occurs in central Utah, where for example it occupies most of the subalpine zone of the Wasatch Plateau (Ellison 1954). By definition, Subalpine-Montane Grassland is below treeline. Above treeline is alpine tundra, and although many of its stands include graminoid species, its ecology is different from grasslands.

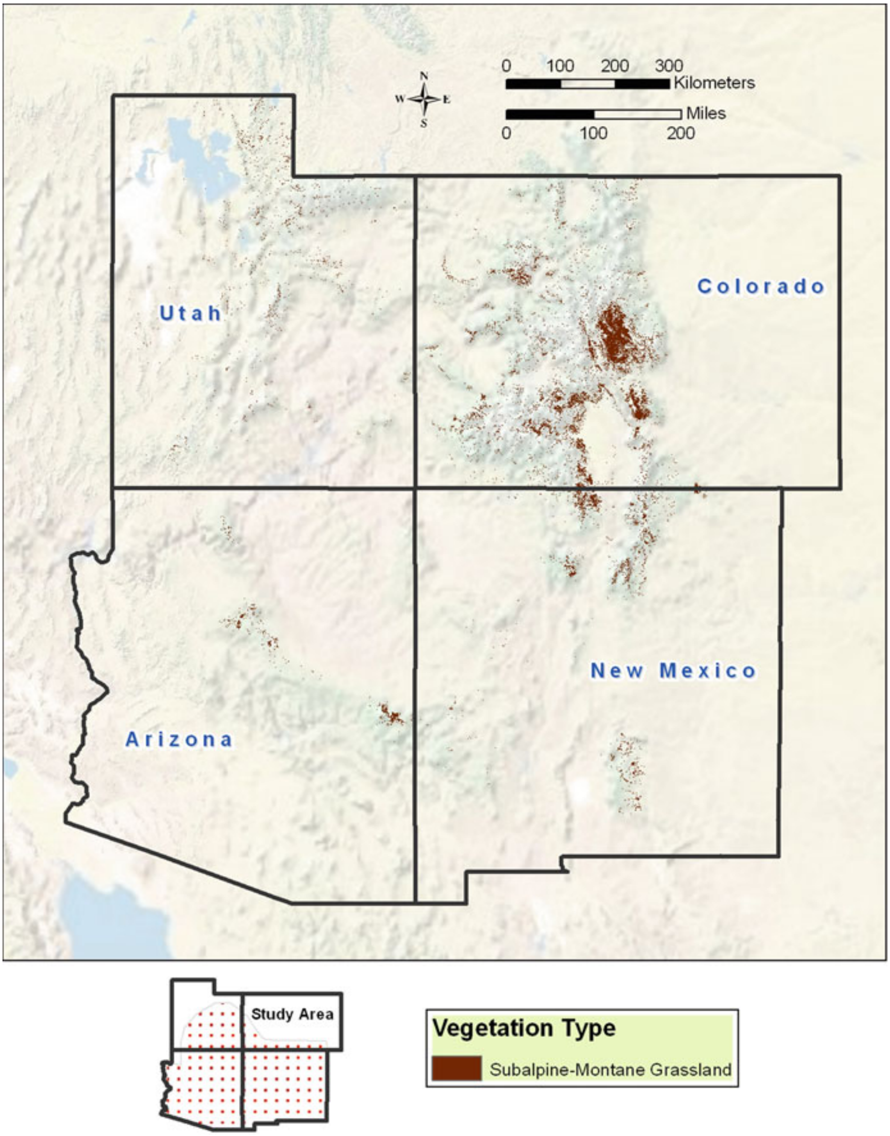


**Fig. 6.3** Distribution of Subalpine-Montane Grassland in the American Southwest. The map shows all of the states of Arizona, New Mexico, Colorado, and Utah, and the American Southwest is illustrated in *red* on the small map (Source: U.S. Geological Survey National Gap Analysis Program 2005 Southwest Regional Gap Analysis Project, RS/GIS Laboratory, College of Natural Resources, Utah State University, Logan, Utah. Map prepared by Monica Swihart)

The occurrence of Subalpine-Montane Grassland as patches within forests has led to discussions of their origin. Two hypotheses proposed early in the twentieth century continue to be applicable today: (a) site conditions limit forest trees and (b) disturbance such as stand-replacing fire replaced forest with grassland (Pearson 1913). Anecdotal evidence supporting site conditions as the cause is the association of some stands with particular habitats, including basins with microclimates involving cold air drainage and soils contrasting with those of surrounding forest (Pearson 1913). Evidence of stand-replacing fire being a causal factor is that large stands of Subalpine-Montane Grassland on mountain slopes occur on dry, expansive slopes where (a) clumps of trees are generally restricted to the upslope and lee side of topographic breaks, (b) ridgetops are often sites of abrupt transition from grassland on drier slopes to forests on mesic slopes, and (c) fire-scarred trees are present in grassland-forest ecotones (Allen 1984). In addition, some twentieth and twenty-first century forest fires have produced stands of grasses and other herbs with little or no evidence of tree invasion decades later (Savage and Mast 2005). Other disturbances, such as interaction of drought with insect and disease outbreaks, also can create some patches of Subalpine-Montane Grassland (Fletcher and Robbie 2004).

It appears that both hypotheses on the origin of stands of Subalpine-Montane Grassland (i.e., limiting site conditions and forest fire) are correct and that different factors dominate on different sites. In addition, the two factors can act in combination: limiting site conditions appear to account for Subalpine-Montane Grassland in the center of some basins and drainages, whereas fire had determined the grassland-forest boundary at the perimeter.

The specific site conditions limiting to forest have been subject to much speculation. Proposed factors include (a) soil factors such as poor drainage, fine texture, less moisture, and frost heaving; (b) climate factors such as cold air drainage, severe frosts, winter desiccation, and seasonal drought/long-term precipitation patterns; and (c) biotic factors such as thick sod, allelopathy, absence of necessary mycorrhizal symbionts, competition from herbs, and herbivory (Pearson 1913, 1931; Merkle 1962; Moir 1967; Rietveld 1975; Moir and Ludwig 1979; Allen 1984, 1989; Dyer and Moffett 1999; Fletcher and Robbie 2004; Moore and Huffman 2004; Coop and Givnish 2007a, b, 2008). Few experimental data are available, but research in Subalpine-Montane Grassland of the Valles Caldera National Preserve in north-central New Mexico examined the roles of soil texture, minimum temperature, grass competition, and ungulate herbivory (Coop and Givnish 2008). It was concluded that differential establishment of ponderosa pine seedlings was driven by low minimum temperatures and that these temperatures likely had interacted with fire to determine historical grassland-forest boundaries.

Southwestern Subalpine-Montane Grassland encompasses a diverse array of stands. Species distributions appear to be influenced primarily by soil texture, soil moisture, elevation, site exposure (e.g., ridges), and disturbance (Merkle 1953; Dick-Peddie 1993; Brown 1994a). This chapter divides stands into moist and mesic-dry types, largely based on topographic position (cf. McHenry 1933; Klemmedson and Smith 1979; Chambers and Holthausen 2000).

*Moist* Subalpine-Montane Grassland (Fig. 6.4) occurs in bottoms of shallow valleys and other wet areas. They are sometimes called cienegas. Most stands are small and dominated by sedges (*Carex* spp.; e.g., Patton and Judd 1970; Dick-Peddie 1993). Stands have lower species richness than mesic-dry stands and higher herbaceous species richness than adjacent forest (Patton and Judd 1970). Moist stands generally have a discontinuous distribution and are relatively small, occupying <100 ha (250 acres; Rasmussen 1941; Dick-Peddie 1993; Brown 1994a).

*Mesic-dry* Subalpine-Montane Grassland (Fig. 6.5) occurs upslope and adjacent to moist stands, as well as on other relatively dry sites. Mesic-dry stands in most of the American Southwest are dominated by fescue (*Festuca* spp.) bunchgrasses of up to 1 m (3 ft) height. Perennial and annual forbs, sod-grasses, and sedges occur in bunchgrass interspaces. However, stands in central Utah were dominated by tall perennial forbs before extensive livestock grazing began, and grasses and sedges were also present. In general, upper-elevation stands are associated with Spruce-Fir Forest and moist-mesic Mixed Conifer Forest and are dominated by Thurber fescue (*Festuca thurberi*). Common associated species include Arizona fescue (*Festuca arizonica*), and forbs are often abundant. Lower-elevation stands cover greater total land area (Fletcher and Robbie 2004) and occur within dry-mesic Mixed Conifer Forest and Ponderosa Pine Forest. Associated species in lower-elevation stands include mountain muhly (*Muhlenbergii montanus*), screwleaf muhly (*M. virescens*), and oatgrasses (*Danthonia* spp.). Shrubs tend to be more abundant than at higher elevations. Mesic-dry stands have higher herbaceous species richness than adjacent forest (Patton and Judd 1970). Stands range in size from as small as moist stands to much larger.

Both moist and mesic-dry Subalpine-Montane Grassland exhibit seasonal variation (cf. Fletcher and Robbie 2004) and disturbance-related variation (see Sect. 6.4.2). Regional variation is also important, especially between central Utah and other regions of the Southwest, e.g., compare Ellison (1954) and Gill (2007) to Dick-Peddie (1993) and Romme et al. (2009). Species lists are available (e.g., Ellison 1954; Dick-Peddie 1993; Brown 1994a, c; White 2002). Few classifications have been published. Upper-elevation grasslands of the Apache and Sitgreaves National Forests in east-central Arizona have been divided into four community types (White 2002). Most species in all four of these types are $C_3$, perennial, and native. Grasses dominate in cover and percentage composition. Subalpine stands have higher cover of cryptogams and grasses, as well as relatively more species of perennials. Montane stands have higher cover of annuals and relatively more species of forbs, biennials, and annuals.

Although regions outside of the American Southwest also have subalpine-montane grasslands (e.g., the Rocky Mountains of central Colorado; Fig. 6.3), there are differences in climate and species composition. Therefore, this chapter is based on findings from the American Southwest, despite little quantitative information being available (cf. White 2002).

**Fig. 6.4** Moist Subalpine-Montane Grassland in central Utah (Photograph by author)

**Fig. 6.5** Mesic-Dry Subalpine-Montane Grassland near the San Francisco Peaks in north-central Arizona (Photograph by Betty J. Huffman)

## 6.2 Drivers

Key drivers of southwestern Subalpine-Montane Grassland 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. 6.5).

### *6.2.1 Landscape*

Subalpine-Montane Grassland occurs nearly throughout the elevational range of coniferous forests in the American Southwest, from approximately 1,800 to 3,500 m (6,200 to 11,500 ft) in the mid-latitudes of its distribution in the American Southwest (Fig. 6.6). As described in the previous section, elevation and topography are correlated with differences in species composition. Many stands, especially in the

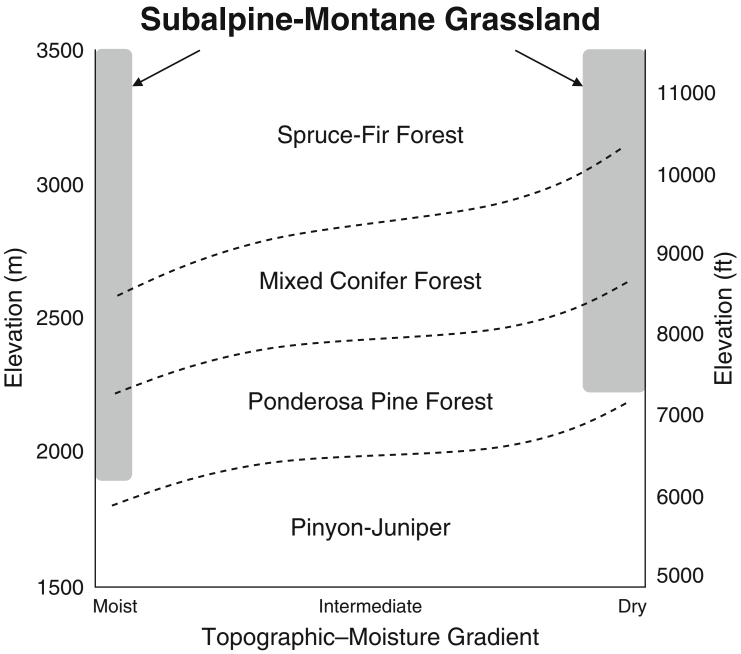


**Fig. 6.6** Ecological distribution of Subalpine-Montane Grassland (*shaded area*) on the mountains and plateaus of the American Southwest along gradients in elevation and topographic-moisture. Elevations are approximate and generally representative of mid-latitudes of the region, i.e., landscapes in northern Arizona and northern New Mexico

montane zone, occur in shallow, relatively flat depressions that are only slightly lower in elevation than forests (Pearson 1913). In deeper depressions and drainages, moist stands can be present in the bottoms and mesic-dry stands occur on slopes that lead to the surrounding forests. Mesic-dry stands also occur elsewhere on a variety of slope aspects and inclinations. For example, sites include large, little-dissected, relatively steep, south-facing mountain slopes of the Jemez Mountains in north-central New Mexico (Allen 1984, 1989). On a more local scale, topographic variations and their associated microclimates can be keys to species' distributions (e.g., Ellison 1954). For example, Kentucky bluegrass (*Poa pratensis*) occurs in narrow valley bottoms in Apache and Sitgreaves National Forests in east-central Arizona (Laing et al. 1987).

### *6.2.2 Climate*

Few long-term climate data have been published for Subalpine-Montane Grassland in the American Southwest. In general, summers are warm to cool, and winters are cold. The range for mean annual temperature is 1–5 °C (34–41 °F) for subalpine grasslands and 4–8 °C (39–46 °F) for montane grasslands in the Apache and Sitgreaves National Forests (White 2002). Mean annual precipitation has been estimated as 50–100 cm (20–39 in.) for grassland in the subalpine zone (Milchunas 2006), and precipitation in the montane zone likely averages near the lower end of that range. Values in Apache and Sitgreaves National Forests are 66–78 cm (26–31 in.) with 150–170 cm (59–67 in.) of snow for subalpine grasslands and 50–62 cm (20–24 in.) with 120–150 cm (47–59 in.) of snow for montane grasslands (White 2002). In general, the percentage of precipitation falling as snow is 50–75 % in the subalpine zone, where snow commonly covers sites from October through May (Ford et al. 2004). The percentage and time of coverage by snow decrease toward lower elevations, and snow buildup is much less for stands on south aspects (Allen 1984). The growing season is short, especially in the subalpine zone where it is often <100 days (Brown 1994a), and frosts occasionally occur during the summer. The average number of frost-free days per year is 70–90 in subalpine grasslands and 90–100 in montane grasslands in the Apache and Sitgreaves National Forests (White 2002).

Subalpine-Montane Grassland in valleys, even shallow valleys, often has a microclimate different from that of adjacent forests. Data collected over a 4-year period at the Fort Valley Experimental Forest in north-central Arizona indicated maximum temperatures were similar to adjacent forested sites, with annual means of 15.1 °C in Subalpine-Montane Grassland vs. 14.6 °C in adjacent Ponderosa Pine Forest (59.2 vs. 58.3 °F; Pearson 1913). However, minimum temperatures were lower in the Subalpine-Montane Grassland throughout the year, with annual means of −5.2 °C in contrast to −1.6 °C in the Ponderosa Pine Forest (22.7 vs. 29.1 °F). Monthly mean minimum temperatures in the Subalpine-Montane Grassland were above freezing only in July–September. Except during cloudy weather, the diurnal range of temperatures was much greater in Subalpine-Montane Grassland than in Ponderosa Pine Forest, especially in winter. Subalpine-Montane Grassland also experienced more wind and had greater evaporation than adjacent forest.

Modern climate change is described in Sect. 1.6.3 and is treated as an anthropogenic disturbance in Sect. 6.2.6.3.

### *6.2.3 Soil*

Stands of southwestern Subalpine-Montane Grassland in shallow valley bottoms are on finely-textured alluvial or colluvial soils (Peet 2000). Many stands, especially in the montane zone, occur in shallow, relatively flat depressions with deep clay or clay-loam soils (Klemmedson and Smith 1979). Soils are variable, but most are deep, well-developed, and well- to poorly drained (Warren et al. 1982; Brown 1994a, c). Soil moisture regimes are udic and ustic, and soil temperature regimes are cryic and frigid (Ford et al. 2004). Soils resemble prairie soils with a deep, dark, organic A horizon (Moir 1967). Most are Mollisols, and some are Alfisols and weakly developed Entisols (Laing et al. 1987; Maker and Saugherty 1986; Miller et al. 1995). The Mollisols of mesic-dry Subalpine-Montane Grassland on slopes of the Jemez Mountains have deep profiles of >1.5 m (5 ft; Allen 1984).

Subalpine-Montane Grassland soils change upslope in shallow valleys. Soils of valley bottoms in the North Rim region of Grand Canyon National Park tend to be relatively poorly drained loams or clay loams, while slopes closer to surrounding forests are well-drained, moderately deep to deep gravelly loam to clay loam (Moore and Huffman 2004). These well-drained soils tend to be dry.

Soils of Subalpine-Montane Grassland also differ by elevation. Soils of subalpine stands with Thurber fescue have udic soil moisture regimes and cryic soil temperature regimes. Soils of montane stands with Arizona fescue have ustic soil moisture regimes and frigid soil temperature regimes (W.A. Robbie, personal communication).

Subalpine-Montane Grassland soils can be similar or different from forest soils. In Ponderosa Pine Forest, small stands are usually on the same kind of soil as the forest, but larger stands can be on different kinds of soil than forest (Klemmedson and Smith 1979). The Mollisols of mesic-dry Subalpine-Montane Grassland on slopes of the Jemez Mountains sharply differ from the Alfisols and Inceptisols of adjacent forests (Allen 1984). Subalpine-Montane Grassland soils on the Wasatch Plateau of central Utah tend to be deeper and less rocky than soils supporting Spruce-Fir Forest (Ellison 1954).

### *6.2.4 Animals*

Southwestern Subalpine-Montane Grassland is important habitat for wildlife. Common animals influencing vegetation dynamics include ungulates such as deer

(*Odocoileus* spp.) and elk (*Cervus elaphus*; Merkle 1953; Brown 1994a, b; Wolters 1996), although these species spend more time in adjacent forests (Patton and Judd 1970). Many rodent species are present (Brown 1994a, b), including northern pocket gopher (*Thomomys talpoides*), which affects plant species composition by loosening heavy soils (Ellison and Aldous 1952; Merkle 1953). Such burrowing animals also provide sites of exposed mineral soil where competition is low – sites that can be utilized by seedlings. Herbivory by grasshoppers (suborder Caelifera) also can be significant. Animals can cause substantial seedling mortality of ponderosa pines encroaching on Subalpine-Montane Grassland (Coop and Givnish 2008).

## *6.2.5 Natural Disturbance*

The natural disturbance regime of Subalpine-Montane Grassland in the American Southwest is dominated by fire, herbivory, and extreme weather. In addition, wind importantly influences the spread of fire.

### 6.2.5.1 Fire

The historical fire regime of southwestern Subalpine-Montane Grassland is poorly known. Moist stands likely burned only infrequently during drought years when plants and litter dried. Mesic-dry stands likely burned more often and fire frequency was probably correlated with that of the surrounding forest vegetation and to the dryness of the stand (Fig. 6.7a, b). Therefore, fires were less frequent in stands within Spruce-Fir Forest and moist-mesic Mixed Conifer Forest, i.e., forests that burned less frequently (Sects. 2.2.5.1 and 3.2.5.1), and more frequent in stands within dry-mesic Mixed Conifer Forest and Ponderosa Pine Forest (Sects. 3.2.5.1 and 4.2.5.1; Dick-Peddie 1993; Romme et al. 2009). Some mesic-dry stands typically do not burn during the primary fire season (Bradley et al. 1992). Indeed, larger stands can act as fire breaks during mid-summer, but can burn in late summer and early fall, as well as in early spring before vegetation green-up begins (Bradley et al. 1992). Mean fire return intervals in Subalpine-Montane Grassland dominated by Thurber fescue are thought to be 18–22 years (U.S. Forest Service 2012b). Mesic-dry Subalpine-Montane Grassland on slopes of the Jemez Mountains is estimated to have burned every 15 years or less, including both lightning- and possible human-ignited fires (Allen 1984).

Fire can alter species composition, and its effects likely depend on post-fire weather (cf. Milchunas 2006). Fire reduces litter, thereby increasing both nutrient availability and soil temperature, but reducing soil moisture. Historical fires apparently restricted encroachment of trees (e.g., Allen 1984; Moore and Huffman 2004; Romme et al. 2009; Sect. 6.3.3).

**Fig. 6.7** (**a**) Fire in mesic-dry Subalpine-Montane Grassland in Gila National Forest, west-central New Mexico (Photograph by Chris Ader/U.S. Forest Service, Gila National Forest). (**b**) Burn mosaic (*brown patches* are burned, and *green* and *tan patches* are unburned) in mesic-dry Subalpine-Montane Grassland in Fort Apache Reservation, east-central Arizona (Photograph by Kari Greer/U.S. Forest Service)

**Fig. 6.8** Elk grazing in Subalpine-Montane Grassland in Valles Caldera National Preserve, north-central New Mexico. Smoky haze is from nearby forest fire (Photograph by Jayson Coil)

#### 6.2.5.2 Herbivory

Herbivory by deer and elk (Fig. 6.8) reduces total plant cover and affects species composition by reducing palatable species and increasing less palatable ones (e.g., Wolters 1996). Secondary impacts of this herbivory likely include increased soil temperature and decreased soil moisture. Additional impacts can parallel those of livestock grazing (Sect. 6.2.6.1). Browsing by unusually large populations of deer has been a factor restricting encroachment of quaking aspen (*Populus tremuloides*) in Subalpine-Montane Grassland in the North Rim region of Grand Canyon National Park (Moore and Huffman 2004).

#### 6.2.5.3 Extreme Weather

Weather extremes can have several effects on southwestern Subalpine-Montane Grassland. These include intensive rainfall events that result in incisement (down-cutting, gullying) of drainages and lowering of water tables. Subsequent drying slowly changes moist stands into mesic-dry stands of Subalpine-Montane Grassland as species adapted to wet conditions are gradually replaced over months and years by species adapted to drier conditions. Extreme drought can similarly change stands from moist to mesic-dry. Drought also can result in mortality of encroaching trees and in overall reduction of vegetation cover. Unusually cold temperatures can combine with cold-air drainage to produce unseasonable frosts that cause tree mortality (Moore and Huffman 2004; Coop and Givnish 2007b).

## *6.2.6 Anthropogenic Disturbance*

Land Use by Native Americans in the American Southwest was concentrated in Pinyon-Juniper vegetation (*Pinus-Juniperus*; Sects. 1.5.1.1 and 5.2.6), but Subalpine-Montane Grassland was likely used for hunting and possibly other purposes such as agriculture, especially at low elevations. Little information is available on anthropogenic drivers affecting southwestern Subalpine-Montane Grassland, except for livestock grazing. Other anthropogenic drivers related primarily to Euro-American land use are fire management, modern climate change, invasive species, recreation, and nearby land use. Each of these can be important in vegetation dynamics, and therefore all are incorporated in the conceptual models (Sect. 6.5).

### 6.2.6.1 Livestock Grazing

Southwestern Subalpine-Montane Grassland has been grazed by cattle (*Bos taurus*) and sheep (*Ovis aries*) since at least the mid nineteenth century (Fig. 6.9). Although herbivory by deer and elk is natural, historical livestock grazing was different because of the large numbers of livestock. Livestock grazing was especially intensive from approximately 1880 to the early twentieth century:

> …between 1888 and 1905, the Wasatch [Plateau] was a vast dust bed, grazed, trampled, and burned to the utmost. The timber cover was reduced, the brush thinned, the weeds and grass cropped to the roots, and such sod as existed was broken and worn. (Reynolds 1911)

Livestock grazing affected the understories of adjacent forests (Sects. 2.2.6.1, 3.2.6.1, and 4.2.6.1), but livestock utilized meadows proportionately more than forests because of greater accessibility, more forage, and abundant palatable species (Patton and Judd 1970). Livestock grazing continues in many stands today (Fig. 6.10), but levels are much reduced from the early twentieth century.

Livestock grazing has increased invasive species, because invasives are spread attached to animal coats and in their feces. Moreover, grazing that reduces vegetation cover can facilitate colonization by invasives. Although invasives can decline within a few years after grazing is reduced, recovery is incomplete (Dick-Peddie 1993; Wolters 1996). Land managers have seeded invasives such as Kentucky bluegrass, intermediate wheatgrass (*Thinopyrum intermedium*), orchardgrass (*Dactylis glomerata*), smooth brome (*Bromus inermis*), and timothy (*Phleum pratense*) as forage for livestock and for revegetation of disturbed areas (Merkle 1953; Romme et al. 2009).

See Sect. 6.4.2 for more on impacts of livestock grazing.

**Fig. 6.9** Cattle grazing in Subalpine-Montane Grassland circa 1910 in Fort Valley, north-central Arizona (Photograph by A.G. Varela, courtesy of Fort Valley Experimental Forest Historic Images, U.S. Forest Service)

**Fig. 6.10** Sheep grazing in mesic-dry Subalpine-Montane Grassland in southwestern Utah (Photograph by Betty J. Huffman)

#### 6.2.6.2 Fire Management

The history of fire management in southwestern Subalpine-Montane Grassland parallels that of fire management in adjacent forests (Sects. 2.2.6.2, 3.2.6.2, and 4.2.6.2), except prescribed fires rarely have been intended for grassland. Fire management likely has had little effect on moist Subalpine-Montane Grassland; however, fire suppression focused on adjacent forests likely contributed to tree encroachment into some mesic-dry stands (Allen 1984; Merola-Zwartjes 2004; Moore and Huffman 2004; see Sect. 6.4.2).

#### 6.2.6.3 Modern Climate Change

Effects of modern climate change on southwestern Subalpine-Montane Grassland have been little studied. Climate change likely has contributed to tree encroachment into mesic-dry stands (Dyer and Moffett 1999; Merola-Zwartjes 2004; Zier and Baker 2006; Sect. 6.3.3). One aspect of modern climate change is increased frequency of extreme events (Sect. 1.6.3), and these can have a variety of effects on Subalpine-Montane Grassland (see Sect. 6.2.5.3).

#### 6.2.6.4 Invasive Species

Invasive plants are abundant in Subalpine-Montane Grassland of the American Southwest, so much so that they dominate many moist stands in the Jemez Mountains (Allen 1989) and elsewhere. For example, the invasive Kentucky bluegrass characterizes one of the three major Subalpine-Montane Grassland communities described by Romme et al. (2009) for north-central New Mexico and southwestern Colorado. This community occurs across subalpine and montane zones, and includes other invasives as associated species. The community persists because of grazing, either by livestock (Fletcher and Robbie 2004; Romme et al. 2009) or native ungulates (Wolters 1996). Compaction of moist Subalpine-Montane Grassland by livestock trampling inhibits water infiltration, which results in drier soil on the site, changes the area from moist to mesic-dry Subalpine-Montane Grassland, and favors expansion by Kentucky bluegrass (Fletcher and Robbie 2004). Other invasive plants such as intermediate wheatgrass, orchardgrass, smooth brome, and timothy also dominate some sites (Romme et al. 2009). Floristic study of Subalpine-Montane Grassland in the Apache and Sitgreaves National Forests determined that 28 of 199 species (14 %) were non-native (White 2002).

#### 6.2.6.5 Recreation

No studies have explicitly addressed effects of recreation on southwestern Subalpine-Montane Grassland, but the presence of invasive species in recreational areas suggests recreation facilitates their spread and establishment (cf. Romme et al. 2009). Recreation is also a source of fires. Moreover, recreation that reduces vegetation cover, such as off-highway vehicle use, can increase erosion.

#### 6.2.6.6 Nearby Land Use

Land use in Mixed Conifer and Ponderosa Pine Forests is considered to be an anthropogenic driver of southwestern Subalpine-Montane Grassland (Romme et al. 2009). This nearby land use is a source of fires and invasive plants. Land use in Spruce-Fir Forest is less extensive and intensive; therefore, it is less of a driver of Subalpine-Montane Grassland.

## 6.3 Processes

Important processes in southwestern Subalpine-Montane Grassland are rapid regrowth following light to moderate disturbance, succession following more severe disturbance, and tree encroachment with shifts in the environment. These three processes play key roles in the conceptual models (Sect. 6.5).

### *6.3.1 Rapid Regrowth*

The primary process of vegetation dynamics in southwestern Subalpine-Montane Grassland is rapid regrowth, which occurs within weeks to months following disturbances such as fire and herbivory (Fig. 6.11). The key to rapid regrowth is that grasses and sedges sprout and regrow from meristems (zones of dividing cells) at or below the soil surface where they are little damaged by fire or herbivory. Moreover, many herbs have storage structures at shallow soil depth, where they are protected from disturbance and provide carbohydrates for rapid regrowth. Also, grassland species are relatively small in stature and therefore individuals rapidly regrow to full size.

Little is known about the fire ecology of the dominant bunchgrasses, Thurber fescue and Arizona fescue. Root crowns of Thurber fescue appear to be able to survive fire (Bradley et al. 1992), and plants likely recover 2–3 years after fire (U.S. Forest Service 2012b). Arizona fescue has meristems in the soil where they are protected from heat produced by fires, and thereby plants survive and rapidly recover following most fires (U.S. Forest Service 2012a).

Other species also rapidly recover following fire by sprouting from below-ground structures such as roots, rhizomes, and bulbs The greater the depth of these structures in the soil, the more likely the species will be undamaged by fire and regenerate (Antos et al. 1983). Other species can regenerate from soil seed banks or by dispersal of seeds from outside the burned area. Therefore, the rate and degree of post-fire

**Fig. 6.11** Rapid regrowth of small stand of mesic-dry Subalpine-Montane Grassland following crown fire in the North Rim region of Grand Canyon National Park, north-central Arizona (Photograph by Fire and Aviation Management, Grand Canyon National Park)

recovery are influenced by species composition (reflecting different modes and rates of regeneration). Additional factors likely to influence recovery include severity of fire, time since previous fire (accumulation of litter influences fuel loadings), season of fire (species dormant at the time of fire are more likely to survive and regenerate), and patchiness of fire (unburned patches facilitate more rapid recovery of the stand; Antos et al. 1983; Baker 2009).

The other common disturbance, herbivory, occurs annually, but herbivory by deer and elk is typically a less-severe disturbance than fire. Rapid recovery from light to moderate herbivory largely parallels that described above for fire, but can be more complete. Intensive, repeated herbivory, such as with livestock grazing from the late nineteenth century into the twentieth century, has greater impacts. For example, Thurber fescue and Arizona fescue can resprout following light to moderate herbivory by utilizing carbohydrates stored in roots, but intensive repeated herbivory can exhaust carbohydrate reserves and result in mortality. Neither of these common native bunchgrasses produces and spreads by rhizomes (underground stems). Therefore, self-replacement following mortality requires regrowth from seed, a slow process that additional herbivory can prevent. Consequently, Thurber fescue and Arizona fescue are often replaced by species spreading below-ground by rhizomes. There are no common, native rhizomatous grasses in Southwestern Subalpine-Montane Grassland, so replacement is often by invasive rhizomatous species such as Kentucky bluegrass and smooth brome (Paulson and Baker 2006).

### 6.3.2 Succession

Succession occurs in southwestern Subalpine-Montane Grassland following high-severity disturbances such as soil erosion and long, intensive herbivory. Rapid regrowth can play an important role early in succession, except where the severity of the disturbance causes substantial mortality of plants (including their below-ground structures). Chronic disturbance, such as long-term livestock grazing, can similarly limit the role of rapid regrowth in succession.

Little is known about succession in Subalpine-Montane Grassland, especially where information is unavailable on stand structure and composition before grazing began (cf. Sect. 6.4.1) and where invasive plants are present. Decadal variations in species composition in response to weather, grazing, etc. also can obscure successional patterns. Moreover, details of succession are highly species-, site-, region-, and disturbance-specific (e.g., Ellison 1954).

Succession can involve tree encroachment where encroachment is sustained (next section).

### 6.3.3 Tree Encroachment

The colonization and establishment of trees in Subalpine-Montane Grassland is termed tree encroachment (Fig. 6.12a, b). It can be followed by infill by additional trees, as well as by mortality that reduces or eliminates encroachment. Tree encroachment has been studied in a few locations.

Encroachment into Subalpine-Montane Grassland on the slopes of the Jemez Mountains was mostly by ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*), but it also included quaking aspen and Engelmann spruce (*Picea engelmannii*; Allen 1984, 1989). In the past, invading trees were likely killed by fire and winter desiccation. During the twentieth century, tree establishment was enabled by fire exclusion, and establishment occurred primarily during the period between the end of intensive sheep grazing and recovery of Subalpine-Montane Grassland vegetation.

Initial tree encroachment in the White Mountains of south-central New Mexico is by Douglas-fir, which is a nurse-plant for southwestern white pine (*Pinus strobiformis*; Dyer and Moffett 1999). The lack of evidence implicating livestock grazing or fire exclusion led to the conclusion that encroachment had resulted from increased precipitation and possibly warmer temperatures. Climate was also considered the primary driver of encroachment – mostly by quaking aspen – in small Subalpine-Montane Grassland stands within forests of the San Juan Mountains of southwestern Colorado (Zier and Baker 2006).

Most tree encroachment on the North Rim of Grand Canyon National Park has involved quaking aspen, but other trees – in decreasing order of abundance – are spruce, subalpine fir (*Abies lasiocarpa*), white fir (*Abies concolor*), and ponderosa pine (Moore and Huffman 2004). Both spruce and ponderosa pine appear to

**Fig. 6.12** (**a**, **b**) Tree encroachment in mesic-dry Subalpine-Montane Grassland at two elevations on the San Francisco Peaks in north-central Arizona: (**a**) moderately high elevation and (**b**) moderately low elevation; (note small saplings of ponderosa pine in front of *yellow-colored* quaking aspen) (Photographs by Betty J. Huffman)

progressively encroach from the grassland-forest boundary. In contrast, quaking aspen and firs infill among trees. Encroachment occurred during a period of climate change, fire exclusion, and herbivory by livestock and native ungulates, making it challenging to identify a primary driver of encroachment.

In conclusion, tree encroachment – along with infill and mortality – produces spatially dynamic grassland-forest boundaries. Encroachment can involve most tree species that are dominant in adjacent or nearby forests. It is favored by various changes in environmental factors, including increased precipitation, warmer temperatures, reduced fire, reduced ungulate herbivory, and possibly by increased ungulate herbivory that reduces competition. Tree mortality occurs with reduced precipitation, colder temperatures, and fire. Tree seedling mortality can be caused by additional factors such as herbivory (Sects. 6.2.4 and 6.2.5.2).

## 6.4 Historical Changes

### *6.4.1 Pre-Euro-American Settlement*

Little is known about southwestern Subalpine-Montane Grassland prior to Euro-American influence. Historical descriptions provide qualitative information on cover:

> …we found luxuriant bunch-grass covering the ground as thickly as it could stand. (Rothrock 1878, for south-central Colorado in 1873)

as well as quantitative information on stand size:

> These parks are of varying extent, from a mere glade of five acres up to tracts embracing 14,000 acres [2 to 5700 ha]… (Leiberg et al. 1904, for the vicinity of the San Francisco Peaks in north-central Arizona)

> Everywhere through the forest we encounter beautiful open parks, from a few acres to several square miles in area. (Rusby 1889, for north-central Arizona in 1883)

and stand height:

> …we passed successive vales and glades, filled with verdant grass knee high to our mules… (Beale 1858, for east of the San Francisco Peaks)

> …the grasses are…often nearly two yards [1.8 m] high… (Rusby 1889, for north-central Arizona in 1883)

Historical photographs (Figs. 6.13 and 6.14) also provide little information on stand composition and structure. However, they can document the expansion of Subalpine-Montane Grassland (such as caused by forest fire) as well as their contraction (by tree encroachment).

Nevertheless, it is difficult to obtain a detailed, accurate description of conditions prior to Euro-American settlement (Fletcher and Robbie 2004). Historical data are lacking, relict sites are rare and generally small, and the effects of livestock grazing were both widespread and intensive. In addition, there are few dateable, long-lived plants (i.e., trees).

**Fig. 6.13** Subalpine-Montane Grassland in 1871 at the base of the San Francisco Peaks in north-central Arizona. Note the abundance of bunchgrasses (Photograph by Timothy H. O'Sullivan, courtesy of the National Archives and Records Administration)

Intensive livestock grazing altered the vegetation of the Wasatch Plateau so thoroughly and so long ago that there are no historical accounts of it, and researchers in the mid twentieth century found no early inhabitants who remembered what it was like (Ellison 1954; Prevedel et al. 2005). Evidence pieced together from small areas that were much less-intensively grazed and from observations of changes that have occurred in grazing exclosures indicated that mesic-dry Subalpine-Montane Grassland in this region had high species richness of tall perennial forbs along with grasses and sedges; plants and litter likely combined for about 70 % cover (Ellison1954).

Conditions in mesic-dry Subalpine-Montane Grassland in north-central New Mexico and southwestern Colorado (and probably elsewhere in New Mexico and Arizona) are thought to have included high diversity and cover of herbaceous species (Romme et al. 2009). Thurber fescue and Arizona fescue dominated and likely combined for more than 50 % cover. Bunchgrass interspaces had forbs, sod-forming grasses, and sedges. Litter and plant cover combined was probably 80–90 %. Annual forbs and species that increase with disturbance were minor components of most stands. Moist Subalpine-Montane Grassland likely had been more common before Euro-American settlement.

**Fig. 6.14** Subalpine-Montane Grassland in 1867 in north-central New Mexico. Bare patches in foreground are likely from livestock grazing. Trees in background are ponderosa pine (Photograph by Alexander Gardner, courtesy of the Boston Public Library)

### *6.4.2 Post-Euro-American Settlement*

The lack of data and paucity of information on pre-Euro-American conditions in southwestern Subalpine-Montane Grassland also limit understanding of changes since then (e.g., Ellison 1954). Nevertheless, it is clear that changes have occurred, and livestock grazing has been a primary driver (Sect. 6.2.6.1). For example, comparison of data collected in the Apache and Sitgreaves National Forests for 1913–1915 to 1997–1998 determined significant decreases in vegetation cover and increases in bare ground that were more related to livestock and elk grazing than to either fire exclusion or variation in precipitation (White 2002). Greater change occurred in montane grassland types than in subalpine grassland types.

The impacts of livestock grazing depend on many variables, including site conditions, intensity and duration of grazing, and whether grazing was by sheep, cattle, or both. General effects of livestock grazing on Subalpine-Montane Grassland of the American Southwest include: (a) changed structure and composition (e.g., reduced cover, altered species composition, increased shrubs, reduced species diversity, and introduction and establishment of invasive plants); (b) changed processes of vegetation dynamics (e.g., altered succession and increased tree invasion); (c) modified site conditions (e.g., reduced likelihood of fire, reduced animal species diversity, altered populations of native animal species, increased soil exposure and compaction, reduced water infiltration, increased erosion, and reduced nutrient cycling); and (d) decreased resilience, decreased connectivity, and greater fragmentation (e.g., Ellison 1954; Fleischner 1994; Fletcher and Robbie 2004; Merola-Zwartjes 2004; Prevedel et al. 2005; Romme et al. 2009). While the general impacts of historical grazing are clear, details of the impacts are not. Even the impacts of more recent livestock grazing have been characterized as poorly known, confusing, and controversial (Merola-Zwartjes 2004).

Changes in plant species composition resulting from livestock grazing have been a focus of research. In general terms, there have been reductions in palatable species and increases in less-palatable or unpalatable species. A quantitative study of Subalpine-Montane Grassland in the Apache and Sitgreaves National Forests determined that almost 95 % of species shared by all four community types were not preferred forage species for livestock (White 2002). In general, bunchgrasses have decreased (Milchunas 2006; Zier and Baker 2006; see Sect. 6.3.1), especially Thurber fescue. Also, the tall perennial forbs that were the primary growth form in central Utah were reduced by livestock grazing (Ellison and Aldous 1952; Ellison 1954). Species that have increased with grazing include unpalatable shrubs, forbs, and uncommon grasses, as well as invasive plants, rhizomatous species, and species from drier habitats (Ellison and Aldous 1952; Ellison 1954; Merola-Zwartjes 2004; Prevedel et al. 2005; Milchunas 2006; Zier and Baker 2006). Sheep and cattle have different effects on species composition. Sheep grazing results in palatable forbs being replaced by grasses, and cattle grazing results in palatable grasses being replaced by unpalatable forbs and shrubs (Ellison 1954; Milchunas 2006). However, the impacts of livestock grazing are not always separable from grazing by deer and elk (cf. Rambo and Faeth 1999).

Overall, species changes in north-central New Mexico and southwestern Colorado (and likely elsewhere in New Mexico and Arizona) were characterized as changes from tall bunchgrass to short sod- or forb-dominated Subalpine-Montane Grassland (Romme et al. 2009). Species changes in Utah involved replacement of tall perennial forbs with shorter forbs, grasses, and shrub species (Ellison 1954; Lewis 1993 in Prevedel et al. 2005). Erosion is thought to have increased with livestock grazing and to have led to stream incisement, which lowered water tables and led to drying of some moist Subalpine-Montane Grassland (Patton and Judd 1970; Bradley et al. 1992; cf. Sect. 6.2.5.3) and replacement of sedges with species of mesic-dry stands. Changes from 1913–1915 to 1997–1998 in the Apache and Sitgreaves National Forests were characterized as negatively affecting soil and site stability, hydrologic function, and biotic community integrity (White 2002).

Changes involving trees are a special case, because of the uncommonness of that growth form in Subalpine-Montane Grassland. Not all stands have experienced encroachment by trees (Allen 1984; Dyer and Moffett 1999; Zier and Baker 2006). Evidence of long-term persistence of treeless Subalpine-Montane Grassland includes large stands on mountains in north-central New Mexico that early Spanish explorers named for having extensive grasslands (Allen 1984), e.g., Cerro Pelon ("bald peak") and Cerro Pelado ("bare peak"). Historical photographs also provide evidence of persistence of some stands (e.g., Zier and Baker 2006).

Nevertheless, other stands of Subalpine-Montane Grassland have decreased in size or have been lost since Euro-American settlement because of tree encroachment (see Sect. 6.3.3 for mechanisms). For example, mesic-dry Subalpine-Montane Grassland on the slopes of the Jemez Mountains has been invaded by trees, reducing the area of grassland by 55 % during 1935–1981 with the disappearance of some small stands and fragmentation of larger stands (Allen 1989). Decrease in size of stands has also been reported for the White Mountains of New Mexico (Dyer and Moffett 1999), the North Rim region of Grand Canyon National Park (Moore and Huffman 2004), and the San Juan Mountains (Zier and Baker 2006).

In addition, changes in adjacent forests, particularly Ponderosa Pine Forest, likely have affected Subalpine-Montane Grassland. Before Euro-American settlement, grassland species were extensive in the understory of open forest stands, resulting in connectivity among grassland patches. As fire exclusion resulted in increased tree densities, the forest understory decreased (Sect. 4.4.2) and thereby the connectivity of grassland species was reduced (Fletcher and Robbie 2004).

## 6.5 Conceptual Models

The following nested, three-tiered set of conceptual models is based on my interpretation of best-available information on Subalpine-Montane Grassland of the American Southwest. The models summarize and synthesize material on drivers (Sect. 6.2) and processes (Sect. 6.3) of vegetation dynamics, and they account for historical changes (Sect. 6.4). 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.

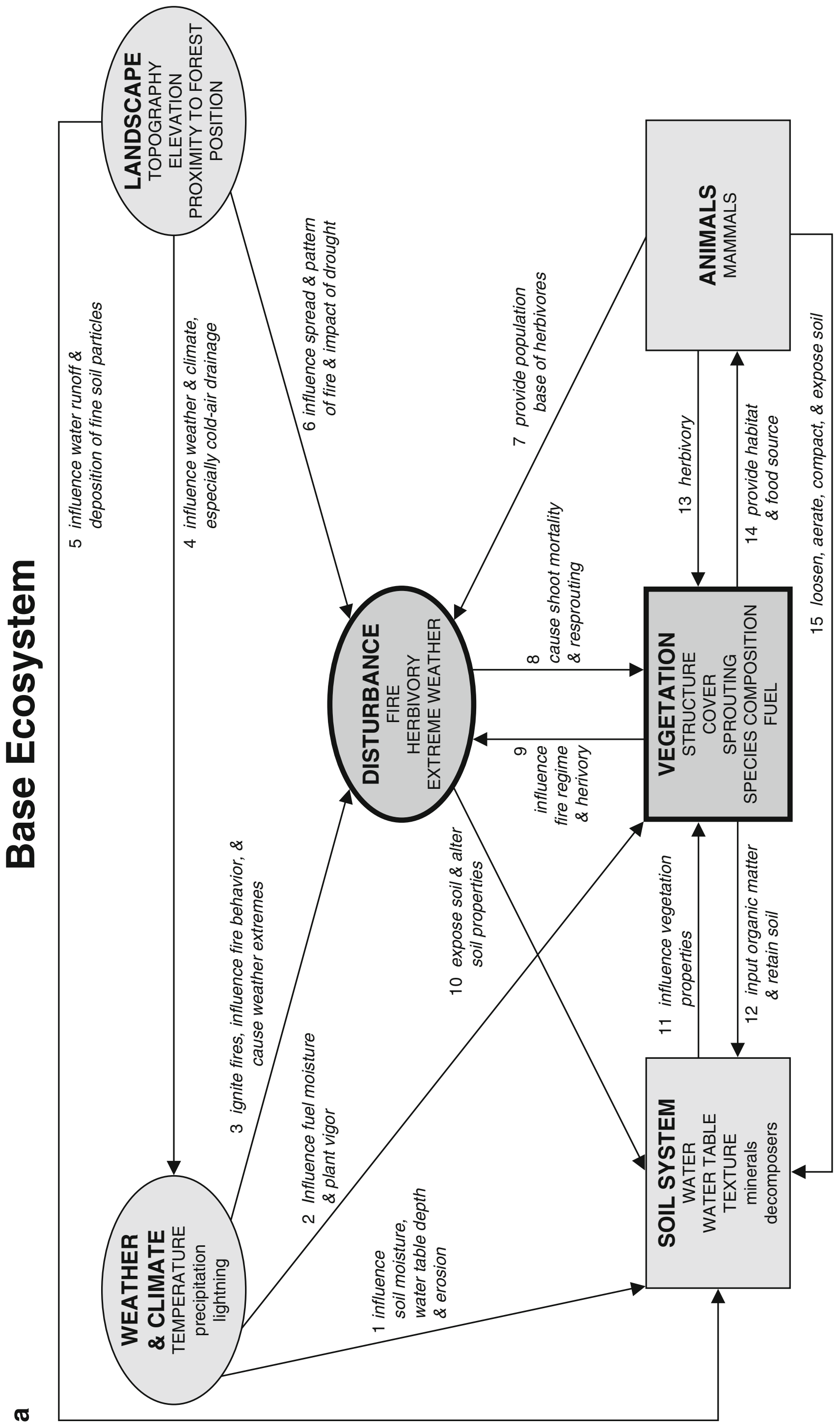
### *6.5.1 Ecosystem-Characterization Model*

The ecosystem-characterization model for southwestern Subalpine-Montane Grassland emphasizes *Vegetation* (a biotic component) and *Disturbance* (a driver; Fig. 6.15a, Table 6.2). Key aspects of *Vegetation* are structure, cover, sprouting, species composition and fuel, and these affect *Disturbance*. The primary agents of *Disturbance* are fire, herbivory, and extreme weather, and these cause shoot mortality followed by resprouting of some species. A second biotic component is *Soil System*, the key aspects of which are water, water table, and texture, all of which influence vegetation structure and composition. The third biotic component is *Animals*. They affect vegetation through herbivory, especially when animal populations increase to where herbivory is a disturbance. Animals also affect the soil system by burrowing, which loosens and aerates soils and exposures mineral soil. Larger mammals also can compact soils. A second driver is *Weather & Climate*, which ignites fires, causes weather extremes, and influences fire behavior, fuel moisture, plant vigor, soil moisture, water table depth, and erosion. The third driver is *Landscape*, with its primary features being topography, elevation, proximity to forest, and landscape position. It influences weather, climate, water runoff, deposition of fine soil particles, spread and pattern of fire, and impact of drought. Landscape position combines with the Soil System to determine differences between moist and mesic-dry Subalpine-Montane Grassland. The model also includes six anthropogenic drivers (Fig. 6.15b, Table 6.2): *Livestock Grazing*, *Fire Management*, *Modern Climate Change*, *Invasive Species*, *Recreation*, and *Nearby Land Use*.

### *6.5.2 Vegetation-Dynamics Model*

The same vegetation-dynamics model represents both moist and mesic-dry Subalpine-Montane Grassland. The 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 graph, 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 this generalized bar graph.

The vegetation dynamics model of moist and mesic-dry Subalpine-Montane Grassland has three states with five communities and two transitions (Fig. 6.16, Table 6.3). All communities occurred historically. *State A* is composed of community *A1 Moist Grassland*, which is characterized by sedges, forbs, grasses, and shrubs. It rarely burns and is maintained by a high water table. *State B* includes community *B1 Mesic-Dry Grassland*, which is dominated by grasses, forbs, and shrubs. *B1* was the only common community circa 1870 (most stands of *A1 Moist Grassland* were and are small). It can be maintained by fire. Alternatively, it can form community *B2 Degraded Mesic-Dry Grassland* by disturbance such as intensive or long-lasting herbivory. *B2* has been the most common community since circa 1870. It is dominated by forbs, shrubs, and grasses, including invasive plants, and is maintained by on-going disturbance. Without disturbance, succession can change *B2* into *B1*. Alternatively, tree establishment (encroachment) can change *B2* or *B1* into *B3 Wooded Mesic-Dry Grassland*. *B3* is dominated by the same growth forms as *B1* and *B2*, with invasion and establishment of trees. Tree species are those found in adjacent or nearby forests. *B3* can revert to community *B1* of *B2* with tree mortality.


a
Base Ecosystem
LANDSCAPE
TOPOGRAPHY
ELEVATION
PROXIMITY TO FOREST
POSITION
WEATHER & CLIMATE
TEMPERATURE
precipitation
lightning
DISTURBANCE
FIRE
HERBIVORY
EXTREME WEATHER
ANIMALS
MAMMALS
VEGETATION
STRUCTURE
COVER
SPROUTING
SPECIES COMPOSITION
FUEL
SOIL SYSTEM
WATER
WATER TABLE
TEXTURE
minerals
decomposers
1 influence soil moisture, water table depth & erosion
2 Influence fuel moisture & plant vigor
3 ignite fires, influence fire behavior, & cause weather extremes
4 influence weather & climate, especially cold-air drainage
5 influence water runoff & deposition of fine soil particles
6 influence spread & pattern of fire & impact of drought
7 provide population base of herbivores
8 cause shoot mortality & resprouting
9 influence fire regime & herivory
10 expose soil & alter soil properties
11 influence vegetation properties
12 input organic matter & retain soil
13 herbivory
14 provide habitat & food source
15 loosen, aerate, compact, & expose soil

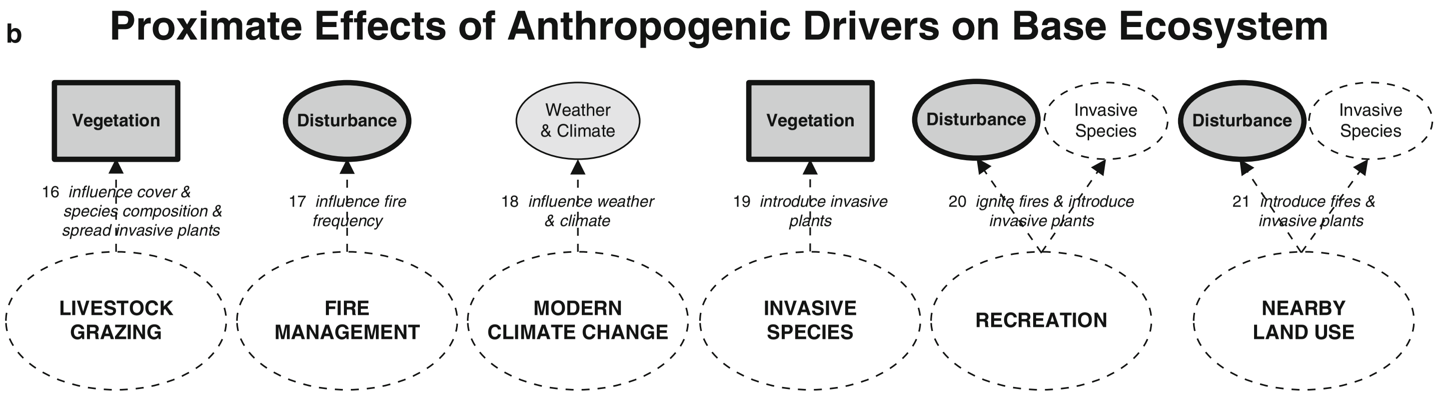


**Fig. 6.15** (**a**, **b**) Ecosystem-characterization model for Subalpine-Montane Grassland. In the base model (**a**), biotic components are shown as *rectangles* and drivers as *solid ovals*. Text within them identifies major features in *upper case* and other important features in *lower case*. Disturbance and Vegetation are *highlighted*, because they are the basis for the vegetation-dynamics model (Fig. 6.16). 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 6.2

**Table 6.2** Relationships in the ecosystem-characterization model of southwestern Subalpine-Montane Grassland (Fig. 6.15a, b)

| Relationships | Circa 1870 | Present |
|---|---|---|
| 1 | Precipitation influences soil moisture, water table depth, and erosion | Same, but climate change increases the severity and duration of drought |
| 2 | Precipitation and temperature largely determine fuel moisture and are important in plant recruitment, growth, and vigor | Same, but climate change increases the severity and duration of drought |
| 3 | Lightning ignites fires, wind influences fire behavior, and weather extremes occur | Same, but weather extremes are more common |
| 4 | Topography influences weather and climate, especially cold-air drainage | Same |
| 5 | Topography influences water runoff, deposition of fine soil particles | Same |
| 6 | Fires can spread from other areas of the landscape (especially from adjacent forests), and position in landscape and topography influence patterns of fire and drought | Same, but fires are probably less frequent |
| 7 | Increase in populations of herbivores result in increased herbivory | Same |
| 8 | Fires and herbivory cause shoot mortality and lead to resprouting | Same |
| 9 | Cover of plants and litter influence fire regime, and species composition influences herbivory | Same |
| 10 | Fires expose soil surface and alter soil properties | Same, but fires are probably less frequent |
| 11 | Water, depth of water table, etc. influence plant cover and species composition | Same |
| 12 | Plants add organic matter to soil and stabilize soil | Same |
| 13 | Herbivory influences plant cover and species composition | Same |
| 14 | Vegetation is habitat and food for animals | Same |
| 15 | Burrowing animals loosen, aerate, and expose soil, and large mammals compact soil | Same |
| 16 | Not applicable | Livestock grazing reduces plant cover, alters species composition, and spreads invasive species |

| | | |
|---|---|---|
| 17 | Not applicable | Fire suppression reduces the frequency and spread of fires |
| 18 | Not applicable | Modern climate change increases temperatures, the frequency and extent of drought, and other extreme weather |
| 19 | Not applicable | Invasive plants change species composition |
| 20 | Not applicable | Recreationists ignite fires and introduce and spread invasive plants |
| 21 | Not applicable | Nearby land use that initiates fires and colonization by invasive plants can introduce fires and invasives into Subalpine-Montane Grassland |

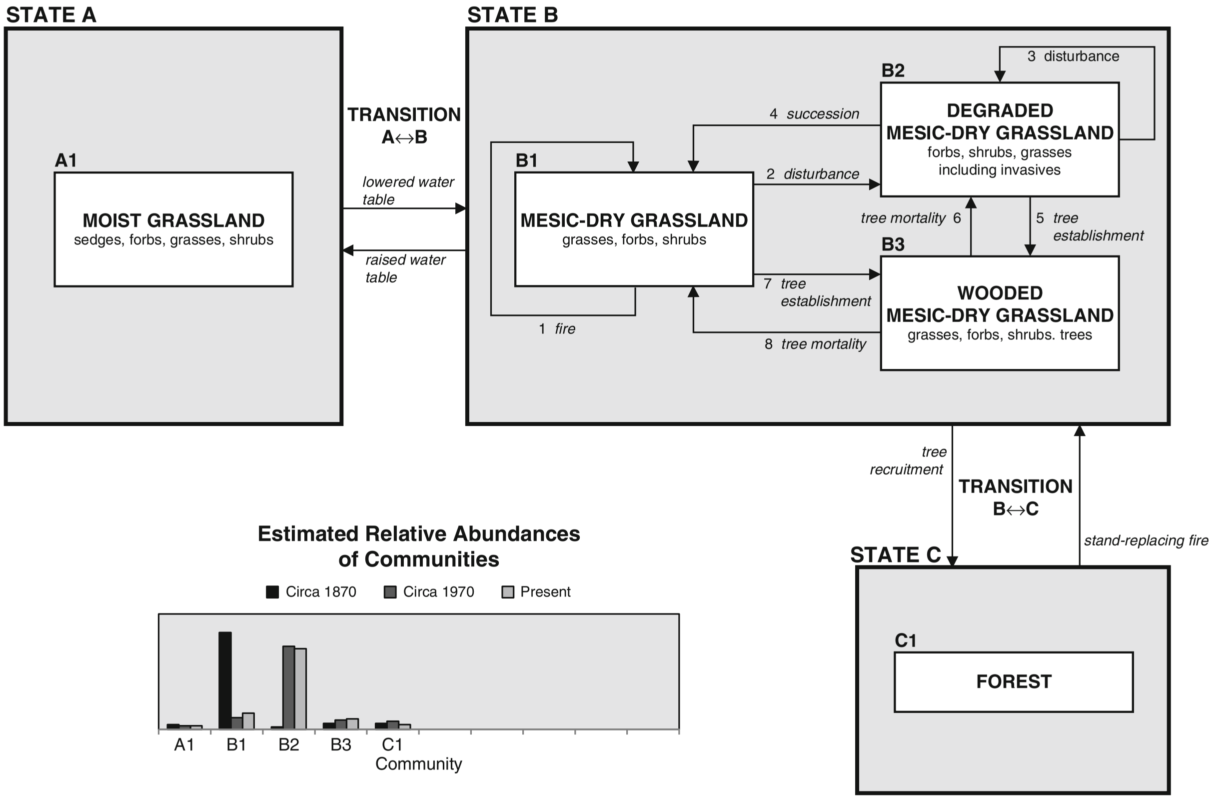


**Fig. 6.16** Vegetation-dynamics model for Subalpine-Montane Grassland (both moist and mesic-dry subtypes). Model provides details on the vegetation-disturbance portion of the ecosystem-characterization model (Fig. 6.15a, b) by showing communities (*smaller*, *open rectangles*) within states (*larger*, *shaded rectangles*), processes that form the communities, and transitions between states. Text along *arrows* identifies pathways that are described in Table 6.3. *Bar graph* shows estimated relative shifts in abundances of the community types from circa 1870 (see Sect. 6.5.2)

**Table 6.3** Relationships and transitions in the vegetation-dynamics model of Subalpine-Montane Grassland (Fig. 6.16)

| Relationships and transitions | Circa 1870 | Present |
|---|---|---|
| A↔B | Decrease in depth of water table can change moist grassland of State A into mesic-dry grassland of State B. Reversion to State A requires a raised water table | Same, but decreases in depth of water table are more common. Livestock grazing results in greater soil erosion that can initiate stream incisement. Also, modern climate change increases the frequency and extent of extreme weather events such as high precipitation that can result in incisement |
| 1 | Frequent fires kill trees, maintaining treeless mesic-dry grassland | Same, but fires are less frequent |
| 2 | Disturbance changes mesic-dry grassland into degraded mesic-dry grassland | Same, but disturbance is more common because of livestock grazing and invasive plant species |
| 3 | Disturbance maintains degraded mesic-dry grassland | Same, but disturbance is more common |
| 4 | Succession changes degraded mesic-dry grassland into mesic-dry grassland | Same, but is possibly affected by invasive species |
| 5 | Tree invasion and establishment convert degraded mesic-dry grassland into wooded mesic-dry grassland | Same, but tree establishment is likely more common because fires are less frequent |
| 6 | Tree mortality converts wooded mesic-dry grassland into degraded mesic-dry grassland | Same, but is likely less common because fires are less frequent |
| 7 | Tree invasion and establishment convert mesic-dry grassland into wooded mesic-dry grassland | Same, but tree establishment is likely more common because fires are less frequent |
| 8 | Tree mortality converts wooded mesic-dry grassland into mesic-dry grassland | Same, but is likely less common because fires are less frequent and invasive species are present |
| B↔C | Infill of trees changes wooded mesic-dry grassland into forest. Reversion to State B requires stand-replacing fire | Same, but transition likely occurs more frequently, because infill increases with infrequent fire and because stand-replacing fire is more common |

*Transition A↔B* changes *State A* to *State B* with lowering of the water table, which is caused by incisement or long drought. *Transition A↔B* can be reversed by rising of the water table.

*Transition B↔C* changes *State B* (community *B3*) to *State C* with tree recruitment that infills the wooded site. *State C* is composed of community *C1 Forest*. *Transition B↔C* is reversed by stand-replacing fire, forming either community *B1*, *B2*, or *B3*, depending on the colonizing species and survival of trees. See also Sects. 2.5.2, 3.5.2, and 4.5.2 for relationships between forests and Subalpine-Montane Grassland.

### *6.5.3 Mechanistic Model*

The mechanistic model (Fig. 6.17) has six biotic components on the right side of the figure (including three aspects of fuels), five drivers on the left side, and six anthropogenic factors at the bottom. In general, *Trees* influence *Fuel Type & Loading*, which influences *Fire Intensity*, which affects the density of *Trees*. *Herbs & Shrubs* affect *Fuel Continuity* and *Fuel Type & Loading*, both of which – along with *Fuel Moisture* and *Fire Frequency* in adjacent forest – affect *Fire Frequency* in grassland. *Fire Frequency* in grassland and *Weather* affect the density of *Trees*. *Weather* also affects the *Water Table* and *Fuel Moisture*. *Weather* and *Water Table* affect the cover and species composition of *Herbs & Shrubs*. *Herbs & Shrubs* and *Trees* determine the community type.

*Modern Climate Change* affects *Weather*. *Fire Management*, *Nearby Land Use*, and *Recreation* affect *Fire Frequency* in grassland. *Nearby Land Use* and *Recreation* also affect *Invasive Species*. *Invasive Species* and *Livestock Grazing* affect the cover and species composition of *Herbs & Shrubs*.

## 6.6 Conclusions and Challenges

Subalpine-Montane Grassland of the American Southwest is understudied. Consequently there are relatively few conclusions and many challenges for researchers and managers. Some research needs are basic, such as more information on site conditions, including correlations with elevation and topography. In addition, better understanding of site factors that limit tree growth is important, as is the percentage, ecological distribution, and permanence of stands formed by site conditions vs. historical crown fire. The fire regime is poorly known, and land managers need information on fire frequency. Land managers also need a better understanding of almost all aspects of anthropogenic drivers, including the effects of historical and present-day grazing, fire exclusion, prescribed burning, and modern climate change. Understanding the impacts of recreation and the need for its regulation is important

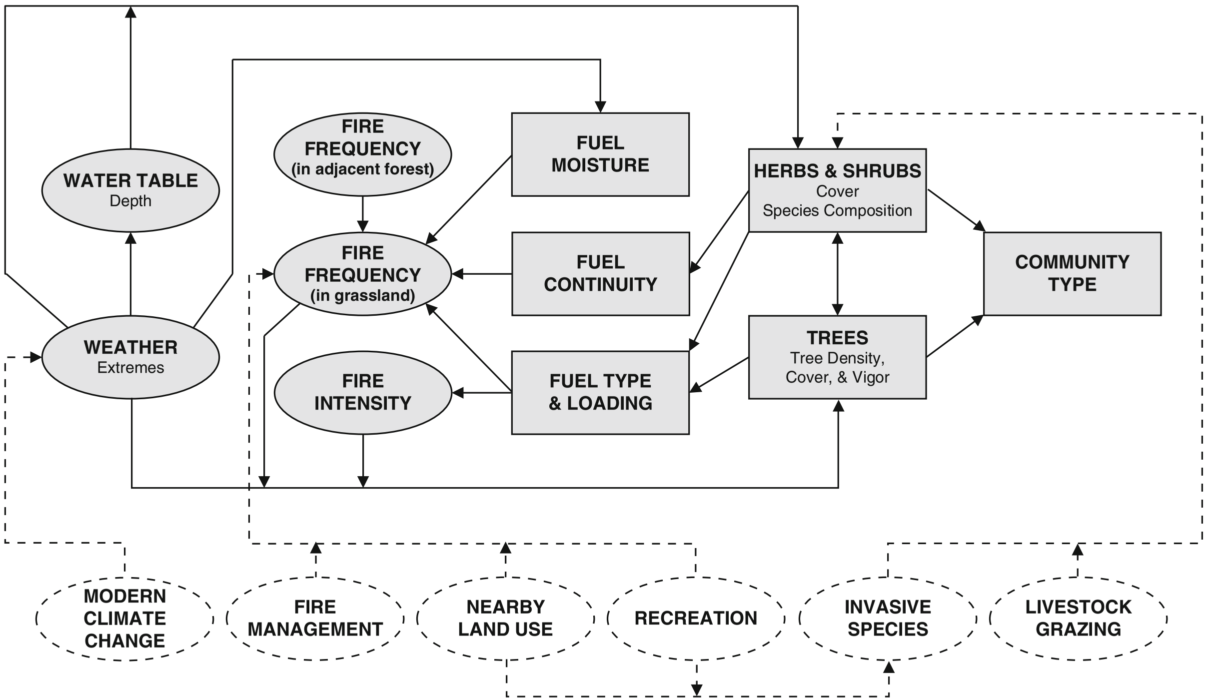


**Fig. 6.17** Mechanistic model for Subalpine-Montane Grassland. Model provides details on the mechanisms involved in the vegetation-dynamics model (Fig. 6.16). *Rectangles* are biotic components (including fuels), *ovals* are drivers, and *dashed ovals* are anthropogenic drivers

to managers, as is the effects of land use and management of adjacent forests on Subalpine-Montane Grassland. Stand dynamics involve rapid regrowth, succession, and tree encroachment, none of which are well understood. The fire ecology of species, especially the dominant bunchgrasses, needs study, as do factors influencing successional patterns. Tree encroachment has received more attention, but additional research is needed on its relationship to ungulate herbivory, including that of livestock. Little is known about conditions prior to Euro-American settlement, yet that is essential to more fully understand changes that followed.

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