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Savannas of North America

Norma L. Fowler[1] *and Brian Beckage*[2]

[1] *Department of Integrative Biology, University of Texas at Austin, Austin, TX, USA*
[2] *Departments of Plant Biology and Computer Science, University of Vermont, Burlington, VT, USA*

5.1 Introduction

Savannas (defined below) are found in many different regions of North America, from sub-tropical south Florida to semi-arid south Texas, and from northern Mexico to south-central Canada (Figures 5.1 and 5.2). Despite their many differences in precipitation, temperature, plant and animal species, history, and dynamics, North American savannas share some important characteristics, especially the critical roles that fire plays in these ecosystems. In many regions there has been a great reduction in the extent of savanna vegetation since Europeans and Africans first arrived in North America just over 500 years ago, but what remains has supported a substantial body of research. This research has not only provided many insights into the processes that form and shape these savannas, but has also guided the management of the remaining tracts of savanna and many successful savanna restoration efforts.

This chapter can only provide a brief overview of the many different kinds of North American savannas. After clarifying some definitions and briefly describing broad climatic patterns, four factors that affect almost all North American savannas are discussed separately: fire, grazing, biodiversity, and conservation. The remainder of the chapter is a brief tour of the savanna ecosystems of North America. This is organized by the dominant woody species, rather than by the region, of each type of savanna, to draw attention to the many similarities between, for example, the longleaf pine (*Pinus palustris*) savannas of northern Florida and the ponderosa pine (*P. ponderosa*) savannas of northern New Mexico 2300 km away (see Figure 5.2 for locations of states and provinces mentioned in this chapter).

5.1.1 Definitions

We considered a savanna to be any plant community that is co-dominated by woody and herbaceous plant species and in which the woody canopy is sufficiently discontinuous to support herbaceous species that require relatively high light levels. This definition

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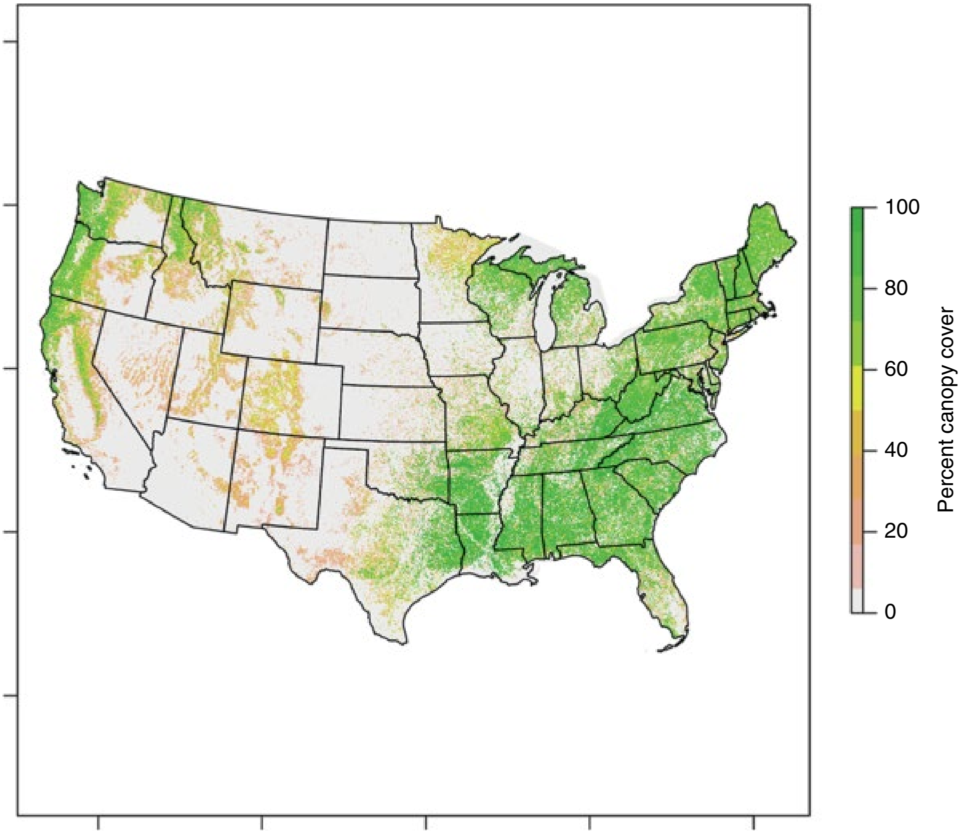

Figure 5.1 Tree canopy cover of continental United States. Percent tree canopy cover from the National Land Cover Database 2011 United States Forest Service percent tree canopy product at a 30 m spatial resolution created by the United States Department of Agriculture Forest Service Remote Sensing Applications Center. The analytic tree canopy layer was produced using a Random Forests regression algorithm. The cartographic product is a filtered version of the regression algorithm output. (*See color plate section for the color representation of this figure.*)

includes both tree savannas and shrub savannas. Authors usually did not quantify the degree of woody cover, and so we relied upon their verbal descriptions and photographs or those from other studies of the same or similar sites. However, for the map (Figure 5.1) we utilized a definition of savanna based on percent canopy cover of the landscape (e.g. Bucini et al. 2017).

In North American savannas, the woody species that form the canopy may occur as isolated individuals or in clusters. The open herbaceous component may occur as a matrix, or as patches in a woody matrix, or in any intermediate state between these. Because there is no clear division or distinction between C_3-dominated and C_4-dominated savannas in North America (see below) both have been included in this chapter. However, we excluded deserts. We included Florida and northern Mexico, where the savannas are similar to those of Georgia and southern Texas, respectively, but excluded southern Mexico and the Caribbean, whose savannas are more properly considered with those of Neotropical regions. Savannas grade into grasslands at low

Figure 5.2 Locations of US and Mexican states and Canadian provinces mentioned in the text. Numbers after state abbreviations refer to the different types of North American savannas listed in the inset legend. Abbreviations: Canadian provinces: BC, British Columbia; SK, Saskatchewan. US states: AL, Alabama; AZ, Arizona; CA, California; CO, Colorado; FL, Florida; GA, Georgia; ID, Idaho; IL, Illinois; IA, Iowa; LA, Louisiana; MI, Michigan; MN, Minnesota; MO, Missouri; MS, Mississippi; MT, Montana; NC, North Carolina; NE, Nebraska; NM, New Mexico; NV, Nevada; OK, Oklahoma; SC, South Carolina; SD, South Dakota; UT, Utah; WI, Wisconsin; WY, Wyoming. Mexican states: CH, Chihuahua; Coa, Coahuila; DU, Durango; NL, Nueva León; TM, Tamaulipas.

levels of woody cover and, at the opposite extreme, into communities with a closed canopy dominated by one or more woody species (Breshears 2006). In the North American literature, communities with closed canopies of woody species may be called forests, woodlands, or shrublands, or by a regional term (e.g. chaparral). There is some inconsistency in the use of these terms, but in general, forests are communities dominated by taller, usually single-stemmed trees, woodlands are dominated by shorter, single- or multi-stemmed trees, and shrublands are dominated by even shorter, multi-stemmed woody plants, and we have followed this usage in this chapter.

The number of monocot genera and the number of dicot genera both increase from north to south in North America (Qian 1998). The ratio of C_4 to C_3 grasses in North American savannas also increases from north to south (Ehleringer et al. 1997; Osborne et al. 2014). Perennial grass species in C_4 genera such as *Aristida*, *Bouteloua*, *Muhlenbergia*, *Paspalum*, and *Sorghastrum* usually dominate southern savannas, while perennial species in C_3 genera such as *Danthonia*, *Festuca*, *Nasella*, and *Poa* become more abundant as one goes further north. However, species in the C_4 genera *Andropogon* and *Schizachyrium* are components of almost all North American savannas and even in south Texas savannas one C_3 perennial grass, *Nasella leucotricha*, is common. Therefore North American savannas cannot readily be classified as C_4 or C_3 savannas.

North American savannas are often not called savannas. For example, some are often called forests, including the ponderosa pine (*P. ponderosa*) savannas of the southern Rocky Mountains and the longleaf pine (*P. palustris*) savannas of the south-eastern coastal plain of the United States. When travelers from eastern forested areas of North America first came to the more open vegetation of, for example, Illinois or central Texas, they called savannas "prairies" because of the new (to them) open character of the vegetation, but it does not follow that these areas were treeless (Weniger 1984). As a result, the oak savannas of the central United States and the tallgrass grasslands of the same region are often both called prairies. The aspen savannas of south-central Canada are often called parklands. Shrub savannas of the north-western United States are sometimes called steppes.

In the North American literature, savannas are sometimes called ecotones, rather than recognized as a distinct type of ecosystem (e.g. Simberloff and Gotelli 1984; Kettle et al. 2000; see also Gosz 1993). However, "ecotones" that are hundreds of kilometers wide are ecosystems in their own right, and should be treated as such. For example, Texas has savannas from approximately 95° W in east-central Texas to 102° W in west Texas (Gould 1975), a distance of ~670 km. If we include the longleaf pine savannas of east Texas, savannas (intermingled with forests in east Texas and woodlands and shrublands in central and west Texas) extend, or extended, east to 93° W, an east–west distance of ~860 km.

In North America, savannas occur in mosaic landscapes that also include grasslands, woodlands, forests, or shrublands. Woody and herbaceous vegetation are intermingled at many different scales. All of these make both the definition of savanna and estimates of the areal extent of savannas problematic. For example, if the patches of herbaceous vegetation or woody vegetation are intermingled on a scale of meters the community is unambiguously a savanna, but what of intermingling on scales of tens of meters? Hundreds of meters? Kilometers? In other words, at what scale of patchiness does the landscape cease to be a savanna and become a mosaic of savanna, woodland, and grassland? Thus, the areal extent of savanna in a region depends upon the patch scale and measurement scale used, as well as on the upper and lower bounds of woody cover in the author's definition of savanna. Figure 5.1 was constructed from 30 m resolution data, but much finer scales would be more appropriate when considering individual savanna ecosystems or study sites.

5.1.2 Climatic Patterns

There is a strong gradient of precipitation across the central part of the North America, with deserts on the western end of the gradient and deciduous forests on the eastern end. At ~30° N, for example, Beaumont, Texas, receives 1536 mm year^{-1}, while El Paso, Texas, ~1200 km to the west, receives only 246 mm year^{-1}. From the Panhandle region of north Texas to southern Canada, there are large areas of true (i.e. treeless) shortgrass grasslands (e.g. Wester 2007) between the oak savannas to the east and the mountains to the west, but further south, savanna vegetation grades directly into Chihuahuan desert vegetation (Gould 1975).

There is also a strong gradient of increasing temperatures from north to south in North America. For example, in Winnipeg, southern Manitoba (~50° N), average January low temperature is −24 °C and average July high is 26 °C, while in Kingsville, Texas (~27.5° N) average January low is 6.3 °C and average July high is 35 °C.

5.2 Fire

All North American savannas owed their existence to fire: they were created and maintained by fire. Fires prevented woody species from converting savannas to closed canopy communities. Given the high degree of spatial and temporal variation typical of fire regimes, however, it is likely that many landscapes were shifting mosaics of savanna and closed canopy communities (i.e. woodland, forest, or shrubland). The spatial configuration and dynamics of such tracts would have depended on the frequency, intensity, and season of past fires, and any given site may have transitioned in and out of being a savanna multiple times. On a millennial time scale, changes in climate have also been important in determining the extent of savanna (e.g. Szeicz and MacDonald 1991; Betancourt et al. 1993; Miller and Wigand 1994; Camill et al. 2003). On evolutionary time scales, savanna vegetation may have evolved dynamically with fire regimes, developing traits not only to tolerate fire but to facilitate frequent fires, preventing conversion to forests, and thus exerting a potentially large influence on the landscape as ecosystem engineers (Beckage et al. 2009).

Savanna-maintaining fires are surface fires, that is, fires that burn biomass near the ground, but rarely consume the canopies of trees and even more rarely move directly from canopy to canopy. In contrast, crown fires consume most or all of the tree canopies as well as understory and mid-story biomass. Crown fires top-kill trees; because pines and most juniper species cannot resprout from the base, they are usually killed by crown fires. Fire suppression in a savanna allows the development of mid-story vegetation. Mid-story vegetation can act as a ladder fuel that allows a surface fire to “climb up the ladder” and ignite tree canopies. As fire suppression produces a more continuous canopy, fire can more easily move from canopy to canopy.

All of the savanna ecosystems discussed in this chapter are thought to have been present at the time of the settlement of North America by non-Indigenous peoples. In the pine savannas of the south-eastern US, where lightning strikes during ignition conditions are very common, lightning may have ignited enough fires to maintain savanna (W. Platt, personal communication), although burning by Indigenous peoples is thought to have also played a role in this region (Van Lear et al. 2005; Outcalt 2008). Elsewhere the sufficiency of lightning-ignited fires to maintain savanna is much less certain. However, with modern estimates of the population densities of Indigenous Americans (Denevan 1992; Dull et al. 2010) before 1492, and the known use of fire by Indigenous Americans to manage their land for deer, bison, nut-bearing trees, travel, and defense (Blackburn and Anderson 1993; Brose et al. 2001; Kimmerer and Lake 2001), it is not necessary to invoke lightning to account for North American savannas. However, lightning ignitions undoubtedly have played a role in many places. The consequences of

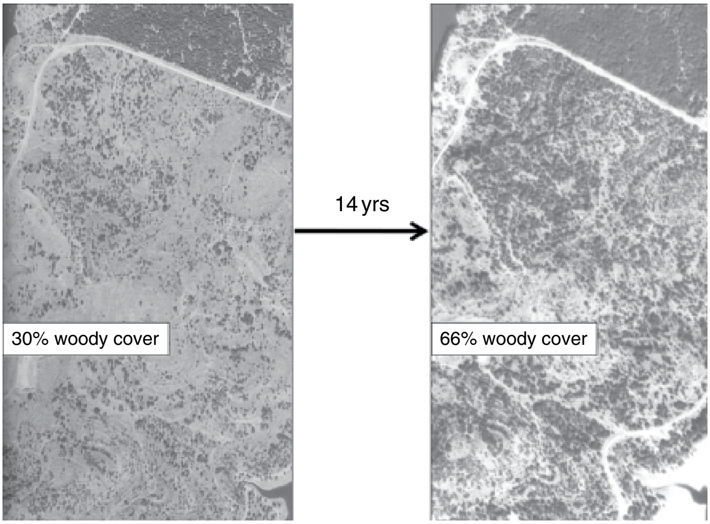

Figure 5.3 Woody plant encroachment by Ashe juniper (*Juniperus ashei*) in a central Texas juniper–live oak (*Quercus fusiformis*) savanna. The difference in canopy cover above and below the E–W road in the upper part of the image is due to different time spans since the most recent mechanical juniper removal. Sequential aerial photographs of Pace Bend Park from Texas Natural Resources Information System.

Indigenous use of fire including (i) fire timing may not have been related to the timing of lightning ignitions, and (ii) land managers using fire to restore and maintain savannas should consider past Indigenous fire use (season, frequency, etc.).

Prescribed fire is commonly recommended for the management for savannas, if safety, public acceptance, and other factors permit its use (e.g. Covington et al. 1997; McPherson 1997; Dunwiddie and Bakker 2011). However, many savannas are presently maintained by mechanical control of woody plants; herbicides may also be used for this purpose where they are effective (Hamilton 2004).

The process of woody plant encroachment (Figure 5.3) converts savannas that do not receive an appropriate fire regime and are not actively maintained by mechanical or chemical methods to forests, woodlands, or shrublands (e.g. Archer 1989; Frost 1993; Briggs et al. 2005; Hankins 2015). Overgrazing, discussed below, can increase the rate of encroachment. Increasing levels of CO_2 may increase the rate of woody plant encroachment where the grasses are primarily C_4 species, as they are in the southern US and Mexico (Polley et al. 1994; Bond and Midgley 2000; Beckage and Ellingwood 2008).

5.3 Grazing

Before settlement by non-Indigenous peoples, the savannas of the central United States and Canada were grazed by bison (*Bison bison*). While bison are mostly absent now, many North American savannas still support populations of deer (*Odocoileus virginianus*, *O. hemionus*) or elk (*Cervus canadensis*). In some cases these native herbivores may have helped maintain savannas by browsing woody species (e.g. Campbell et al. 1994).

Many of the remaining savannas in North America have survived because they occur in sites unsuitable for row crops or sown pastures, but suitable for cattle grazing. Ranchers need grass as food for their livestock (usually cattle, in North America), and so they have a financial incentive to prevent woody plant encroachment from converting these savannas to closed-canopy woody vegetation (Holechek et al. 1998). However, overgrazing by cattle, whose diet is mostly herbaceous species, can increase the rate of woody plant encroachment by reducing competition from grasses and by reducing grass biomass, which in turn reduces the amount of fine fuel available to sustain a surface fire (Scholes and Archer 1997; Van Auken 2009). The effects of overgrazing by domestic stock have been profound (Fleischner 1994). The greatest impacts occurred between the advent of barb-wire fencing in the late 1800s, which allowed ranchers to confine too many cattle in a pasture too long, and the advent of range science and its documentation of the negative effects of excessively high stocking rates in the middle of the 1900s (Holechek et al. 1998). Excessive grazing pressures are one reason why the herbaceous component of many savannas is dominated by relatively unpalatable or highly grazing-tolerant, introduced species, especially in California (Saenz and Sawyer 1986; Bossard and Randall 2007) but also elsewhere (MacDougall and Turkington 2006; Gabbard and Fowler 2007).

5.4 Biodiversity

While most North American savannas have only a few, or even a single, common woody species in the overstory, their grass, forb, and sub-shrub components can be quite diverse. The longleaf pine (*P. palustris*) savannas of the south-eastern US are especially diverse (e.g. Platt et al. 1988; Brockway and Lewis 1997). Forb diversity can also be relatively high in some oak savannas (e.g. Foster and Tilman 2003; Standiford and Purcell 2015). The woody plants add structural complexity, which provides important habitat for some animal species, especially birds (Davis et al. 2000; Zack et al. 2005; Cimprich et al. 2006; Grundel and Pavlovic 2007; Knick and Connelly 2011), while the open canopy allows enough light through to support many herbaceous plant species and their associated animals. Woody plants create low-light microhabitats suitable for more shade-tolerant plant and animal species in otherwise high-light environments and increase belowground spatial heterogeneity (Simberloff and Gotelli 1984; McPherson 1997; Meisel et al. 2002). However, woody plants may reduce the productivity of the herbaceous component and, for this reason, range managers often remove woody plants, preferring to leave only enough woody cover to provide shade and shelter for livestock (Holechek et al. 1998; Bailey 2005).

5.5 Conservation

Many North American savanna ecosystems are now quite rare, including some that once occupied very large areas. Like the tallgrass grasslands of the upper Midwest of the US, the oak (*Quercus* spp.) savannas of the same region have been replaced by row-crop agriculture (Nuzzo 1986). Their presence lives on in the names of towns, such as Oak Grove and Blue Island in Illinois. Another example of a formerly widespread but now much-reduced ecosystem is the longleaf pine (*P. palustris*) savannas of the south-east US, which were almost completely logged in the late 1800s and early 1900s (Van Lear et al. 2005). Loblolly pine (*P. taeda*) treefarms have replaced most of the former longleaf pine savannas (Zhang et al. 2010). In addition to conversion to row-crop agriculture or intensive lumber and pulp production, conversion to housing, shopping malls, and so on has reduced the extent of many savannas, especially near metropolitan areas.

An additional threat to North American savannas is woody plant encroachment, the process by which woody cover increases until former savannas become forests, woodlands, or shrublands (Van Auken 2000). For example, encroachment by species of *Juniperus* converts oak savannas (and grasslands) in Texas and Oklahoma into woodlands (Briggs et al. 2002, 2005; Fowler and Simmons 2009). A reduction in fire frequency and intensity is the usual cause of woody plant encroachment. However, in at least one case (sagebrush savanna, discussed below), an increase in fire frequency is the threat. Fortunately there are many serious efforts to preserve and to restore savannas, and many studies of methods of management necessary to do so.

5.6 Oak Savannas

Many North American oak (*Quercus*) species have features that make them savanna species. These include leaves that, after being shed, do not flatten, and hence form excellent fuel for surface fires; thick, fire-resistant bark; the ability to resprout repeatedly from the base; and the need of their seedlings for high-light environments (Peterson and Reich 2001). It is therefore not surprising that oaks were, and are, the dominant woody species in many North American savannas. Depending on the species, they may be majestic trees (e.g. *Q. macrocarpa*, bur oak), shrubs (e.g. *Q. havardii*, shin oak), or anything in between.

5.6.1 Central US, South-Central Canada, Northern Sierra Madre (Mexico) Oak Savannas

Perhaps the best-studied of the oak savannas are the oak savannas of the north-central US (Figure 5.4). They once formed a wide belt from northern Minnesota and southern Wisconsin, Iowa, Illinois, northern and central Missouri, through eastern Kansas, and are often dominated by bur oak (*Q. macrocarpa*) (Curtis 1959). There are also isolated pockets of oak savanna to the north-east, around the Great Lakes, including some in the province of Ontario in Canada; some of these may once have been dominated by jack pine (*Pinus banksiana*) rather than oaks (Szeicz and MacDonald 1991; Will-Wolf and Stearns 1999). A changing climate may shift the zone suitable for these northern savannas northward and eastward (Frelich and Reich 2010).

The oak savanna belt continues to the south, through central Oklahoma and north and central Texas, including the Cross Timbers and the Post Oak Savanna (Gould 1975). In these southern savannas, post oak (*Q. stellata*) or blackjack oak (*Q. marilandica*) are often the dominant species (e.g. Clark and Hallgren 2003; Volder et al. 2010). However, in the savannas of the Edwards Plateau of central Texas, Plateau live oak (*Q. fusiformis*) is the dominant oak species. Oak savannas reappear at intermediate elevations in the

Figure 5.4 Oak savanna, Lulu Lake Preserve, Wisconsin. Note the abundant herbaceous vegetation, an indication that the canopy is sparse enough to allow ample light to reach the understory. *Source:* Photos by: N. Fowler.

mountains of north-eastern Mexico; one or more of many different oak species may be dominant (Muller 1939, 1947; Rzedowski 1978).

The herbaceous layer of each of these oak savannas is generally dominated by the C_4 grass species that now dominate grasslands in the same region. Little bluestem (*Schizachyrium scoparium*) is still common throughout. Before non-Indigenous settlement in the early 1800s, big bluestem (*Andropogon gerardii*) was a common dominant in the northern savannas, as was Indiangrass (*Sorghastrum nutans*) further south. However, edaphic and topographic factors and the local fire regime also have strong effects on plant community composition and stand structure (Peterson and Reich 2001; Meisel et al. 2002). In addition to the many grass species found in all of these oak savannas, forb diversity is also high (Foster and Tilman 2003). They also provide, or provided, important habitat for many animal species (Davis et al. 2000; Grundel and Pavlovic 2007).

Nuzzo (1986) estimated that, of the original 110 000–130 000 km^2 of oak savanna present before 1800 in US states north of Oklahoma, only 26 km^2 remained in 1985. In many parts of this region, almost all of the former oak savannas have been lost due to conversion of the land to row crops (Nuzzo 1986). Elsewhere fire suppression has caused many oak savannas to become forests (Leach and Givnish 1996; Peterson and Reich 2001). As canopy cover increases, oak recruitment declines and more shade-tolerant trees replace the oaks (Abrams 1992; Brudvig and Asbjornsen 2009). Savannas have also been lost to urbanization, especially around Chicago and other cities. Second only to tallgrass prairies, and for the same reasons, oak savanna is the most threatened and fragmented plant community in the Midwest (Wolf 2006). However, many of the savannas around the Great Lakes are on very sandy soil unsuitable for row crops, which has helped preserve them, as has the fact that they are habitat for the endangered Karner blue butterfly (*Lycaeides melissa samuelis*) (USFWS 2012). The calcareous soils of the Edwards Plateau of central Texas are too shallow for row crops, and a substantial amount of Edwards Plateau oak savanna has been preserved due to its value as rangeland.

5.6.2 California Oak Savannas

There are large areas of oak savanna in the interior of California, primarily in the foothills of the Coast Ranges and the Sierra Nevada (Allen-Diaz et al. 2007). The dominant species of oaks in these savannas include blue oak (*Q. douglasii*), valley oak (*Q. lobata*), interior live oak (*Q. wislizenii*), and coast live oak (*Q. agrifolia*). The herbaceous layer is often dominated by introduced European C_3 annual grass species (Saenz and Sawyer 1986). The high biodiversity of these savannas makes them a conservation priority (e.g. Zack et al. 2005; Standiford and Purcell 2015).

The oak savannas of California owe their existence in large part to fires used by Native Americans to facilitate acorn production and collection (Mensing 2006; Hankins 2015). Soon after non-Indigenous settlement in the mid-1800s and the consequent decrease in fire frequency, tree density increased, in some cases converting former oak savannas to coniferous forest. Much of the area occupied by California oak savannas is rangeland, which has helped to preserve them, but much has been lost to conversion to cropland and to urbanization (Allen-Diaz et al. 2007). More recently, reduced fire frequencies, higher oak densities, and livestock grazing have caused oak recruitment to fail in many sites, although the degree of recruitment failure and its causes in different areas are both debated (Mensing 1992; Tyler et al. 2006). The non-native disease *Phytophthora ramorum* (sudden oak death) has recently become an additional threat (Rizzo and Garbelotto 2003), and the effects of climate change are also of concern (McLaughlin and Zavaleta 2012).

5.6.3 South-West (Arizona, New Mexico, Northern Mexico) Oak Savannas

Some oak savannas are found at mid-elevations in the mountains of Arizona, New Mexico, and northern Mexico (Rzedowski 1978; Weltzin and McPherson 1999). They may be interspersed with oak woodland. In Mexico, any of a large number of oak species may be dominant, dependent on latitude, elevation, and other environmental factors (Rzedowski 1978; Návar 2009).

5.6.4 Pacific Northwest Oak Savannas

The Willamette Valley of western Oregon once had extensive oak woodlands and oak savannas, often dominated by Oregon white oak (*Q. garryanna*), and maintained by Native American burning (Vesely and Tucker 2004). Similar savannas occurred in western Washington and in south-western British Columbia (Vellend et al. 2008). These oak savannas are habitat for many rare and threatened species, including the endangered Fender's blue butterfly (*Icaricia icarioides fenderi*) (USFWS 2006). Habitat loss to row-crop agriculture, planted pasture, and urbanization, woody plant encroachment, invasive species, and climate change are ongoing threats to the remnants of these savannas, but conservation efforts are being made (Dunwiddie and Bakker 2011).

5.6.5 East-Central US: Glades, Barrens, and Other Forest Openings

East of the main oak savanna belt in the central US, the forest was not unbroken. Openings (variously called glades, brakes, balds, barrens, etc.) occurred, often in oak forest on drier sites. Anderson et al. (1999) provide detailed descriptions of these special communities. They are often of high conservation importance and have therefore been studied for purposes of conservation (e.g. Skinner et al. 1983; Albrecht et al. 2016). Prescribed fire, to prevent woody plant encroachment into these openings, is an important management tool (e.g. Brisson et al. 2003).

5.6.6 Oak-Dominated Shrub Savannas

Oak-dominated shrub savannas and shrublands may be maintained by fire, with the oaks resprouting from their bases after each fire. The degree of woody cover, and therefore whether the site is a savanna or shrubland, is strongly affected by the time since the last fire. Gambel oak (*Q. gambelii*) dominated such communities in the southern Rocky Mountains (Brown 1958, Floyd et al. 2000). A now-rare shrub savanna community of this type in Oklahoma and Texas, co-dominated by Durand (shin) oak (*Q. sinuata*) and sumac (*Rhus* spp.), is the nesting habitat of the endangered black-capped vireo (*Vireo atricapillus*; Grzybowski 1991; Cimprich et al. 2006).

Some shrub savannas and associated shrublands occur on deep sands. The sand shinnery of north-west Texas, dominated by sand shinnery oak (*Q. havardii*) is an example (Dhillion 1999; Dhillion and Mills 1999). Florida scrub can be included here, as oak species may dominate it, although in some areas other woody species such as Florida rosemary (*Ceratiola ericoides*) dominate (Menges and Hawkes 1998).

5.7 Pine Savannas

Like oaks, many pines (*Pinus* spp.) have many adaptations to life in savannas. These include needles that form a highly flammable litter, fire-resistant bark, and seedlings that require high light levels. While some North American pines (e.g. *P. contorta*, lodgepole pine; Schoennagel et al. 2004) typically grow in closed canopy forests that experience crown fires that kill the trees, several pine species form, or did form, extensive savannas (Moore et al. 1999; Frost 2006). Almost all sites that once supported pine savanna have been clearcut at least once for lumber, and lumbering remains an important activity. Fire suppression is an important threat to pine savannas, because it allows the development of mid-story ladder fuels and the closure of the canopy, making the site unsuitable for light-demanding herbaceous species and increasing the risk of crown fires that, unlike surface fires, usually kill pines.

5.7.1 South-Eastern US Pine Savannas

Longleaf pine (*P. palustris*) savannas once occupied ~300 000–370 000 km^2 of the south-eastern US coastal plain, including northern Florida (Frost 1993, 2006). They were extensively logged, reducing longleaf pine savanna to a small remnant of its former extent (~2700 km^2 in 1993), as longleaf pine stands do not regenerate readily (Frost 1993, 2006). Remnant longleaf pine stands are also at risk from fire suppression, which allows hardwoods to reach high densities and prevents pine recruitment (Gilliam and Platt 1999). In many places, former longleaf pine savannas have been replaced by dense stands of loblolly pine (*P. taeda*) grown for lumber or pulp. Sometimes these stands are so intensively managed that they would be better called tree farms, resulting in very low biodiversity. Many of the remaining stands of longleaf pine being actively preserved are protected as habitat for two endangered species, the red-cockaded woodpecker (*Picoides borealis*) and the gopher tortoise (*Gopherus polyphemus*) (e.g. USFS 1996, 1999; SAIC 2010), although many other species are at risk due to the loss of these pine savannas (Van Lear et al. 2005).

Longleaf pine savannas have been comparatively well-studied, especially the role of fire. Longleaf pine is famous for its adaptations to fire. In particular, it remains in the "grass stage," with its apical meristem close to the ground and therefore less susceptible to fire damage, until it has the reserves to grow very rapidly past the height at which it is vulnerable to a surface fire (Haywood 2000). In addition it has the usual pine fire adaptations, including thick bark. The grasses (mostly C_4) found in these savannas are also fire-adapted. Wiregrasses (*Aristida stricta*, *Aristida beyrichiana*) often dominate the understory; their upright, sclerophyllous blades are exceptionally good fine fuel for surface fires. Alternatively, little bluestem grass (*S. scoparium*) may be dominant. The herbaceous layer of longleaf pine savannas can be very diverse and includes orchids and other showy wildflowers (Platt et al. 1988). These savanna communities may also include small shrubs and short, fire-suppressed individuals of *Q. laevis* or other oak species.

In southern Florida, slash pine (*P. elliotii*) replaces longleaf pine and palmetto (*Seranoa repens*) becomes common. Hurricanes can be a major disturbance in these savannas. Hurricane-related pine mortality can be high, especially of larger trees (Platt et al. 2000, 2002). Non-native grasses are a threat in southern Florida because they increase fuel load, which increases fire intensity and may therefore increase pine mortality (Platt and Gottschalk 2001).

Some south-eastern pine savannas occupy sites with relatively high soil moisture, although fire is still necessary for their persistence (Brockway and Lewis 1997; Hinman and Brewer 2007). The dominant pine species may be *P. palustris*, *P. elliotii*, or *P. serotina* (pond pine). Their herbaceous layer includes wetland genera such as *Sarracenia* (pitcher plants) (Brewer 1998). These wet pine savannas have been described as transitional between the upland pine savannas and the wetland forests and shrublands of this region (variously called Carolina bays, baygalls, pocosins, etc.) (Walker and Peet 1984; Christensen 1988). There are also a few wetland savannas in which the dominant tree is *Taxodium ascendens* (cypress) rather than a pine species (Platt 1999; Kirkman et al. 2000).

There are also small areas of shortleaf pine (*P. echinata*) savanna in the south-eastern US (Sparks et al. 1998). West of the westernmost extent of longleaf pine, in central Texas, loblolly pine (*P. taeda*) may have once formed savannas in the Lost Pines area, although after it was cut in the 1930s it regrew as a closed canopy forest (until the crown fires of 2011 and 2015). Elsewhere, however, loblolly pine is usually an early-succession forest species (Glitzenstein et al. 1986; De Steven 1991).

5.7.2 Rocky Mountains Pine Savannas

At mid-elevations in the western US, stands of ponderosa pine (*P. ponderosa*) are common, especially in the southern Rocky Mountains and on the eastern slopes of the Cascade Mountains. If the canopy is sufficiently open to have a well-developed herbaceous layer, common native grasses include species in the genera *Festuca* (C_3), *Pseudoroegneria* (C_3), and *Bouteloua* (C_4). While many of these stands now have closed canopies, evidence suggests that their condition before non-Indigenous settlement was savannas maintained by surface fires (Madany and West 1983; Schoennagel et al. 2004; Stephens and Fulé 2005). Restoring these stands to savannas can substantially reduce fire danger to people and houses, a growing concern as more people choose to live in the suburbs and exurbs of American towns and cities (the wildland–urban interface; Cohen 2008). However, where substantial mid-story ladder fuels have developed, or the canopy has closed, it may not be possible to use prescribed surface fires without unacceptable rates of adult tree mortality (Covington et al. 1997). For example, the Cerro Grande fire in 2000 that burned parts of the city of Los Alamos, New Mexico, began as a prescribed fire to reduce fuel load in ponderosa pine stands (USNPS 2001). Expensive mechanical thinning may therefore be required before prescribed fire can safely be used (Moore et al. 1999). Substantial progress has been made on reintroducing fire to ponderosa pine stands after thinning them (e.g. Hughes 2008; Margolis et al. 2009; Figure 5.5). An unwanted side effect of thinning and burning is that these disturbances can promote the colonization and spread of the non-native, invasive, cheatgrass (*Bromus tectorum*, a Eurasian annual C_3 grass) in place of native forbs and grasses (McGlone et al. 2009). Below the elevation of ponderosa pine, woodlands, and savannas co-dominated by various piñon pine and juniper species occur; these are discussed below as juniper savannas.

In addition to crown fires, many western pine species (including both ponderosa pine and piñon pines) are experiencing bark beetle outbreaks. In part, at least, this is due to warming temperatures (Hicke et al. 2006). Bark beetle mortality changes fuel load and fuel structure over time in important ways, which in turn affects fire likelihood and fire severity (Hicke et al. 2012; Hoffman et al. 2012). The future of the pine forests and savannas of the western US and Canada is therefore unclear as warming temperatures, changing precipitation, fire, and bark beetles interact (Jenkins et al. 2014).

5.8 Juniper Savannas

5.8.1 Juniper Savannas in the Western Mountains

In the foothills of the mountains of western North America (Rocky Mountains, the Basin and Range region, Cascade Mountains, Sierra Nevada, and Sierra Madre Occidental of Mexico) at elevations below ponderosa pine (if present) and above desert grassland (if present) or desert, sites dominated by juniper species (*Juniperus* spp.) are common (Miller and Wigand 1994; Gottfried et al. 2008; West 1999). The particular juniper species present differ among sites and regions; important species include *Juniper osteosperma*, *J. monosperma*, *J. occidentalis*, *J. deppeana*, *J. scopulorum*, and *J. californica*. All of these juniper species usually have a shrub-like appearance due to branching at the base, but the height of small trees (Figure 5.6). In the south-western mountains, stands may be co-dominated by a species of piñon pine (*Pinus edulis*, *P. monophylla*, *P. cembroides*). Common native grasses include species of *Aristida*, *Bouteloua*, *Sporobolus*, and other C_4 shortgrass genera. These savannas may now be expanding upslope due to warming (Allen and Breshears 1998). They have also expanded

Figure 5.5 Ponderosa pine (*Pinus ponderosa*) savanna near Santa Fe, New Mexico. Top: immediately after mechanical thinning and prescribed fire. Bottom: a different site, several years after similar treatment. *Source:* Photos by: N. Fowler.

Figure 5.6 Juniper savannas. Top: *Juniperus monosperma*, Kasha-Katuwe Tent Rocks National Monument, New Mexico. Bottom: *J. ashei*, Pedernales Falls State Park, Texas. *Source:* Photos by: N. Fowler.

downslope into former grasslands and sagebrush savanna, likely as a result of overgrazing, fire suppression, and perhaps increasing CO_2 levels (Blackburn and Tueller 1970; Brockway et al. 2002; Johnson and Miller 2006; Bradley and Fleishman 2008). Because junipers replace grasses, there has been extensive mechanical removal of junipers by range managers.

Under present conditions of active fire suppression, together with reduced fine fuel loads caused by grazing, many juniper stands are now woodlands (Brockway et al. 2002). However, juniper savannas still exist in many sites due to mechanical clearing, aridity, rocky thin soils, or past fires. Converting juniper woodlands back to savannas is desirable, not only to provide forage for cattle, but also to preserve archeological sites, reduce soil erosion rates, and reduce fire danger (USNPS 2007). Mechanical clearing is commonly used (Brockway et al. 2002; Gottfried 2008). As in ponderosa pine stands, it can be difficult to safely reintroduce surface fire in juniper woodlands without mechanical clearing first.

5.8.2 Eastern Red Cedar Savannas

Unlike the western juniper species, eastern red cedar (*Juniperus virginiana*) usually grows as a tree with a single trunk. It is now an important encroacher into grasslands of the central US, from South Dakota to Texas, changing soil properties, nutrient cycles, light availability, and herbaceous species composition (Briggs et al. 2002; Horncastle et al. 2004; Ganguli et al. 2008; Pierce and Reich 2010; Meneguzzo and Liknes 2015). If eastern red cedar encroachment is not checked by mechanical means or by fire, it eventually forms woodlands. Eastern red cedar is not the only woody encroacher of these grasslands; for example, in some sites the rough-leaved dogwood (*Cornus drummondii*) is a primary woody encroacher (Lett and Knapp 2003).

5.8.3 South-Central US and Northern Sierra Madre Oriental Juniper Savannas

Junipers that resemble the multi-stemmed western junipers form savannas and woodlands in parts of Texas and in the states of Mexico south of Texas. On the eastern Edwards Plateau of central Texas, Ashe juniper (*J. ashei*) often shares dominance with *Q. fusiformis* or other oak species (Figure 5.6). Further northwest, Ashe juniper is replaced by redberry juniper (*J. pinchotii*), which has the unusual ability (for a conifer) of being able to resprout from the base. In the Sierra Madre Oriental, *J. deppeana* may share dominance with a piñon pine; other Sierra Madre Oriental juniper species include *J. flacida*, *J. deppeana*, and *J. angosturana*. Common grass genera include *Aristida*, *Bouteloua*, *Muhlenbergia*, *Schizachyrium*, and other mid- and shortgrass C_4 genera. In this region, both in the US and in Mexico, juniper species are often aggressive encroachers on rangeland. If encroachment is not checked or reversed, by mechanical means or by fire, a site can be transformed from very open savanna to a low diversity closed canopy woodland in half a century or less (Fowler and Simmons 2009; Figure 5.3).

5.9 Mesquite Savannas

Savannas dominated by honey mesquite (*Prosopis glandulosa*) were probably once common in south Texas and north-eastern Mexico (Johnston 1963; Archer 1989; Ansley et al. 2001). Likely, many sites had large, scattered mesquite trees in a grass matrix (Figure 5.7), plus denser stands of mesquite in narrow strips along drainages. South Texas and north-eastern Mexico also had extensive areas of Tamaulipan thorn scrub, a species-rich sub-tropical shrubland, in which *P. glandulosa* is one species among many. The relative abundance of savanna versus shrubland in south Texas and northern Mexico before non-Indigenous settlement is uncertain. Honey mesquite is rare on the Edwards Plateau of Texas due to the shallow soils there, but is common north of the Plateau (as far as Kansas), east of it, and west of it (into New Mexico), as well as south of the Plateau. *Acacia* species such as *A. berlandieri* (guajillo), *A. rigidula* (blackbrush),

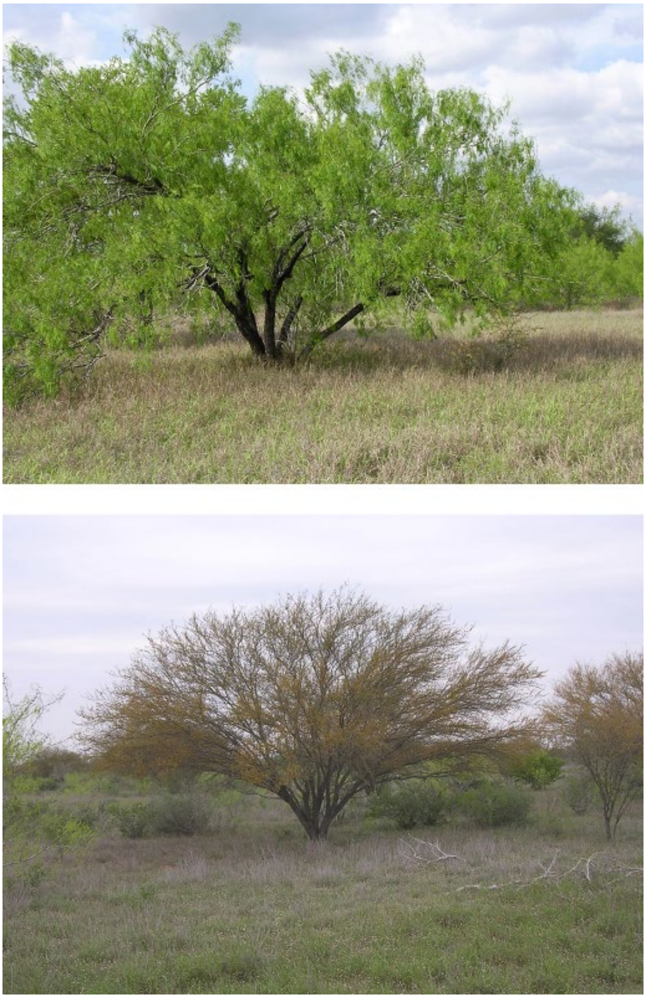

Figure 5.7 South Texas savannas. Top: Honey mesquite (*Prosopis glandulosa*) in Starr County, Texas. Bottom: Another common leguminous species in these savannas is *Acacia shaffneri* (twisted acacia, huisachillo), shown here flowering in March in Jim Hogg County, Texas. *Source:* Photos by: N. Fowler.

and *A. farnesiana* (huisache) may be important components of south Texas mesquite savannas (Figure 5.7) and Tamaulipan thorn scrub and dominate some communities in north-eastern Mexico (Muller 1947). Most of the grasses are C_4 shortgrasses: species of *Aristida*, *Bouteloua*, *Eragrostis*, *Hilaria*, *Setaria*, *Sporobolus*, etc.

Overgrazing and fire suppression have undoubtedly contributed to the increase in the density of mesquite and other woody species, and have converted some savannas into woodlands or shrublands (Archer 1990, 1995; Asner et al. 2003; Ansley et al. 2010). Extensive attempts at mechanical and chemical control have created thickets of mesquite in some areas via resprouting (Jacoby et al. 1990). In addition to savanna loss due to woody plant encroachment, mesquite savannas have also been lost, especially in south Texas and northern Mexico, to conversion to irrigated agriculture and to brush control followed by planting aggressive non-native forage grasses such as buffelgrass (*Pennisetum ciliare*) (Sands et al. 2009).

5.10 Northern and High-Elevation Savannas

At the southern edge of the boreal forest in south-central Canada (Alberta, Saskatchewan, Manitoba) are large areas of aspen (*Populus tremuloides*) savanna known as aspen parkland (Chhin and Wang 2002). Other *Populus* species and species of spruce (*Abies*) and pine may also be present. Common grass genera include *Festuca*, *Koeleria*, *Nasella*, *Poa*, and *Pseudoroegneria* (all C_3, although C_4 genera such as *Bouteloua* and *Muhlenbergia* are also present) (Archbold 1999). Surface fires, and perhaps bison grazing, maintained this savanna (Campbell et al. 1994); fire suppression and agriculture have reduced its extent (Young et al. 2006).

Fires are also thought to be responsible for the extensive areas of aspen savanna in what would otherwise be conifer forests in the Rocky Mountains and Cascade Mountains (Manier and Laven 2002). Single clones of aspen form separated clusters of aspen trees in montane grasslands. Aspen regeneration has failed in recent decades in some places (Romme et al. 1995). Both excessive elk browsing and insufficient fire have been blamed; these are, of course, not mutually exclusive and may interact in their effects (Hessl and Graumlich 2002). In some sites, aspens have been replaced by a juniper species (Miller and Rose 1995).

5.11 Shrub Savannas

Large areas of the intermontane west, primarily in the Great Basin between the Rocky Mountains to the east and the Sierra Nevada or Cascade Mountains to the west, but extending into Wyoming, are, or were, occupied by shrub savannas dominated by species of sagebrush (*Artemesia* spp., especially *A. tridentata*) and native perennial C_3 grass genera such as *Pseudoroegneria*. Overgrazing, invasion by cheatgrass (*B. tectorum*, the same Eurasian annual grass that invades *P. ponderosa* stands), and recent oil and gas development are all threats (Miller et al. 2008; Copeland et al. 2009; Walker et al. 2007). In these savannas cheatgrass replaces the native grasses and increases the fire frequency to such a degree that sagebrush can no longer persist; savanna maintenance and restoration requires reducing, not increasing, the fire frequency in this ecosystem (Baker 2006). The loss of native grasses and shrubs threatens native animal species, especially the sage grouse (Knick et al. 2003; Knick and Connelly 2011). Despite almost a century (Young et al. 1987) of research on cheatgrass, the sagebrush ecosystem, and how to manage this ecosystem, first for livestock and now for endangered species, no good general solutions to the cheatgrass problem have been found (Miller et al. 2008; Davies et al. 2011; Mack 2011).

Similar, but more mesic, shrub savannas are found to the north of the sagebrush region, such as the Okanagan shrub steppe of British Columbia (Clements et al. 2007). Shrub savannas also occur intermittently in the Mediterranean-climate regions of California, wherever the native woody species characteristic of chaparral (shrubland) occur in less dense stands. These more open shrub stands develop after fires and may persist for 50 or more years (L. Fox, personal communication); they may also be maintained permanently by fires (Keeley 2002). Oak-dominated shrub savannas are discussed above.

5.12 Conclusions

North America supports a very wide variety of savanna ecosystems. The woody components of these savannas range from tall pine trees to wide-branched oaks to sagebrush shrubs no more than a meter in height. Their herbaceous component is usually dominated by a mix of C_3 and C_4 grasses, with the ratio of C_4 to C_3 grasses increasing from north to south. North American savanna ecosystems all owed their existence to fire, although now the remaining areas of some savannas may be maintained by mechanical means rather than by fire. Many of the savanna ecosystems present when non-Indigenous peoples settled each region of the continent are now quite limited in extent, due to conversion to cropland, treefarms, planted pasture, housing, and other human uses or to fire suppression that has allowed woody plant encroachment. Because of this, and because many savanna ecosystems provide habitat for species in danger of extinction, they are of considerable conservation interest.

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References

Abrams, M.D. (1992). Fire and the development of oak forests. *BioScience* 42: 346–353.

Albrecht, M.A., Becknell, R.E., and Long, Q. (2016). Habitat change in insular grasslands: woody encroachment alters the population dynamics of a rare ecotonal plant. *Biological Conservation* 196: 93–102.

Allen, C.D. and Breshears, D.D. (1998). Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences* 95: 14839–14842.

Allen-Diaz, B., Standiford, R., and Jackson, R.D. (2007). Oak woodlands and forests. In: *Terrestrial Vegetation of California*, 3e (ed. M.G.Barbour, T.Keeler-Wolf and A.A.Schoenherr), 313–338. Berkeley, CA: University of California Press.

Anderson, R.C., Fralish, J.S., and Baskin, J.M. (eds.) (1999). *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*. Cambridge: Cambridge University Press.

Ansley, R.J., Wu, X.B., and Kramp, B.A. (2001). Observation: long-term increases in mesquite canopy cover in a north Texas savanna. *Journal of Range Management* 54: 171–176.

Ansley, R.J., Pinchak, W.E., Teague, W.R. et al. (2010). Integrated grazing and prescribed fire restoration strategies in a mesquite savanna: II. Fire behavior and mesquite landscape cover responses. *Rangeland Ecology and Management* 63: 286–297.

Archbold, O.W. (1999). The aspen parkland of Canada. In: *Savannas, Barrens, and Rock Outcrop Plant Communities of North America* (ed. R.C.Anderson, J.S.Fralish and J.M.Baskin), 406–420. Cambridge: Cambridge University Press.

Archer, S. (1989). Have southern Texas savannas been converted to woodlands in recent history?*American Naturalist* 134: 545–561.

Archer, S. (1990). Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, USA. *Journal of Biogeography* 17: 453–462.

Archer, S. (1995). Tree-grass dynamics in a *Prosopis*–thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* 2: 83–99.

Asner, G.P., Archer, S., Hughes, R.F. et al. (2003). Net changes in regional woody vegetation cover and carbon storage in Texas drylands, 1937–1999. *Global Change Biology* 9: 316–335.

Bailey, D.W. (2005). Identification and creation of optimum habitat conditions for livestock. *Rangeland Ecology and Management* 58: 109–118.

Baker, W.L. (2006). Fire and restoration of sagebrush ecosystems. *Wildlife Society Bulletin* 34: 177–185.

Beckage, B. and Ellingwood, C. (2008). Fire feedbacks with vegetation and alternative stable states. *Complex Systems* 18: 159–173.

Beckage, B., Platt, W.J., and Gross, L.J. (2009). Vegetation, fire, and feedbacks: a disturbance-mediated model of savannas. *American Naturalist* 174: 805–818.

Betancourt, J.L., Pierson, E.A., Rylander, K.A. et al. (1993). Influence of history and climate on New Mexico piñon–juniper woodlands. In: *Managing Piñon–Juniper Ecosystems for Sustainability and Social Needs; Proceedings of the Symposium 1993 April 26–30; Sante Fe, New Mexico. Gen. Tech. Rep. RM-236* (ed. E.F.Aldon and D.W.Shaw), 42–62. Fort Collins, CO: US Forest Service, Rocky Mountain Forest and Range Experiment Station.

Blackburn, T.C. and Anderson, K. (eds.) (1993). *Before the Wilderness: Environmental Management by Native Californians*. Menlo Park, CA: Ballena Press.

Blackburn, W.H. and Tueller, P.T. (1970). Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. *Ecology* 51: 841–848.

Bond, W.J. and Midgley, G.F. (2000). A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* 6: 865–869.

Bossard, C.C. and Randall, J.M. (2007). Non-native plants of California. In: *Terrestrial Vegetation of California* (ed. M.G.Barbour, T.Keeler-Wolf and A.A.Schoenherr), 107–123. Berkeley, CA: University of California Press.

Bradley, B.A. and Fleishman, E. (2008). Relationships between expanding pinyon–juniper cover and topography in the central Great Basin, Nevada. *Journal of Biogeography* 35: 951–964.

Breshears, D.D. (2006). The grassland–forest continuum: trends in ecosystem properties for woody plant mosaics?*Frontiers in Ecology and the Environment* 4: 96–104.

Brewer, J.S. (1998). Patterns of plant species richness in a wet slash-pine (*Pinus elliottii*) savanna. *Journal of the Torrey Botanical Society* 125: 216–224.

Briggs, J.M., Hoch, G.A., and Johnson, L.C. (2002). Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* 5: 578–586.

Briggs, J.M., Knapp, A.K., Blair, J.M. et al. (2005). An ecosystem in transition: causes and consequences of the conversion of Mesic grassland to shrubland. *BioScience* 55: 243–254.

Brisson, J.A., Strasburg, J.L., and Templeton, A.R. (2003). Impact of fire management on the ecology of collared lizard (*Crotaphytus collaris*) populations living on the Ozark Plateau. *Animal Conservation* 6: 247–254.

Brockway, D.G. and Lewis, C.E. (1997). Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. *Forest Ecology and Management* 96: 167–183.

Brockway, D.G., Gatewood, R.G., and Paris, R.B. (2002). Restoring grassland savannas from degraded pinyon–juniper woodlands: effects of mechanical overstory reduction and slash treatment alternatives. *Journal of Environmental Management* 64: 179–197.

Brose, P., Schuler, T., van Lear, D., and Berst, J. (2001). Bringing fire back: the changing regimes of the Appalachian mixed-oak forests. *Journal of Forestry* 99: 30–35.

Brown, H.E. (1958). Gambel oak in west-central Colorado. *Ecology* 39: 317–327.

Brudvig, L.A. and Asbjornsen, H. (2009). Dynamics and determinants of *Quercus alba* seedling success following savanna encroachment and restoration. *Forest Ecology and Management* 257: 876–884.

Bucini, G., Beckage, B., and Gross, L.J. (2017). Climate seasonality, fire and global patterns of tree cover. *Frontiers of Biogeography* 9: e33610.

Camill, P., Umbanhowar, C.E., Teed, R. et al. (2003). Late-glacial and Holocene climatic effects on fire and vegetation dynamics at the prairie–forest ecotone in south-central Minnesota. *Journal of Ecology* 91: 822–836.

Campbell, C., Campbell, I.D., Blyth, C.B., and McAndrews, J.H. (1994). Bison extirpation may have caused aspen expansion in western Canada. *Ecography* 17: 360–362.

Chhin, S. and Wang, G.G. (2002). Spatial and temporal pattern of white spruce regeneration within mixed-grass prairie in the Spruce Woods Provincial Park of Manitoba. *Journal of Biogeography* 29: 903–912.

Christensen, N.L. (1988). Vegetation of the southeastern coastal plain. In: *North American Terrestrial Vegetation* (ed. M.G.Barbour and W.D.Billings), 317–363. Cambridge: Cambridge University Press.

Cimprich, D.A., Kostecke, R.M., and Brush, T. (2006). Distribution of the black-capped vireo at Fort Hood, Texas. *Southwestern Naturalist* 51: 99–102.

Clark, S.L. and Hallgren, S.W. (2003). Dynamics of oak (*Quercus marilandica* and *Q. stellata*) reproduction in an old-growth cross timbers forest. *Southeastern Naturalist* 2: 559–574.

Clements, D.R., Krannitz, P.G., and Gillespie, S.M. (2007). Seed bank responses to grazing history by invasive and native plant species in a semi-desert shrub-steppe environment. *Northwest Science* 81: 37–49.

Cohen, J. (2008). The wildland–urban interface fire problem. *Forest History Today* Fall: 20–26.

Copeland, H.E., Doherty, K.E., Naugle, D.E. et al. (2009). Mapping oil and gas development potential in the US Intermountain West and estimating impacts to species. *PLoS One* 4: e7400.

Covington, W.W., Fule, P.Z., Moore, M.M. et al. (1997). Restoring ecosystem health in ponderosa pine forests of the southwest. *Journal of Forestry* 95: 23.

Curtis, J.T. (1959). *The Vegetation of Wisconsin: An Ordination of Plant Communities.* Madison, WI: University of Wisconsin Press.

Davies, K.W., Boyd, C.S., Beck, J.L. et al. (2011). Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144: 2573–2584.

Davis, M.A., Peterson, D.W., Reich, P.B. et al. (2000). Restoring savanna using fire: impact on the breeding bird community. *Restoration Ecology* 8: 30–40.

De Steven, D. (1991). Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. *Ecology* 72: 1066–1075.

Denevan, W.M. (1992). The pristine myth: the landscape of the Americas in 1492. *Annals of the Association of American Geographers* 82: 369–385.

Dhillion, S. (1999). Environmental heterogeneity, animal disturbances, microsite characteristics, and seedling establishment in a *Quercus havardii* community. *Restoration Ecology* 7: 399–406.

Dhillion, S. and Mills, M. (1999). The sand shinnery oak (*Quercus havardii*) communities of the Llano Estacado: history, structure, ecology, and restoration. In: *Savannas, Barrens, and Rock Outcrop Plant Communities of North America* (ed. R.C.Anderson, J.S.Fralish and J.M.Baskin), 262–274. Cambridge: Cambridge University Press.

Dull, R.A., Nevle, R.J., Woods, W.I. et al. (2010). The Columbian encounter and the little ice age: abrupt land use change, fire, and greenhouse forcing. *Annals of the Association of American Geographers* 100: 755–771.

Dunwiddie, P.W. and Bakker, J.D. (2011). The future of restoration and management of prairie-oak ecosystems in the Pacific Northwest. *Northwest Science* 85: 83–92.

Ehleringer, J.R., Cerling, T.E., and Helliker, B.R. (1997). C4 photosynthesis, atmospheric CO_2, and climate. *Oecologia* 112: 285–299.

Fleischner, T.L. (1994). Ecological costs of livestock grazing in western North America. *Conservation Biology* 8: 629–644.

Floyd, M.L., Romme, W.H., and Hanna, D.D. (2000). Fire history and vegetation pattern in Mesa Verde National Park, Colorado, USA. *Ecological Applications* 10: 1666–1680.

Foster, B.L. and Tilman, D. (2003). Seed limitation and the regulation of community structure in oak savanna grassland. *Journal of Ecology* 91: 999–1007.

Fowler, N.L. and Simmons, M.T. (2009). Savanna dynamics in central Texas: just succession?*Applied Vegetation Science* 12: 23–31.

Frelich, L.E. and Reich, P.B. (2010). Will environmental changes reinforce the impact of global warming on the prairie-forest border of central North America?*Frontiers in Ecology and the Environment* 8: 371–378.

Frost, C. (1993). Four centuries of changing landscape patterns in the longleaf pine ecosystem. In: *Proceedings of the Tall Timbers Fire Ecology Conference, No. 18* (ed. S.M.Hermann), 17–43. Tallahassee, FL: Tall Timbers Research Station.

Frost, C. (2006). History and future of the longleaf pine ecosystem. In: *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration* (ed. S.Jose, E.J.Jokela and D.L.Miller), 9–48. New York: Springer.

Gabbard, B.L. and Fowler, N.L. (2007). Wide ecological amplitude of a diversity-reducing invasive grass. *Biological Invasions* 9: 149–160.

Ganguli, A.C., Engle, D.M., Mayer, P.M., and Hellgren, E.C. (2008). Plant community diversity and composition provide little resistance to *Juniperus* encroachment. *Botany* 86: 1416–1426.

Gilliam, F.S. and Platt, W.J. (1999). Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. *Plant Ecology* 140: 15–26.

Glitzenstein, J.S., Harcombe, P.A., and Streng, D.R. (1986). Disturbance, succession, and maintenance of species diversity in an East Texas forest. *Ecological Monographs* 56: 243–258.

Gosz, J.R. (1993). Ecotone hierarchies. *Ecological Applications* 3: 369–376.

Gottfried, G.J. (2008). Silviculture and multi-resource management case studies for southwestern pinyon–juniper woodlands. In: *Ecology, Management, and Restoration of Piñon-Juniper and Ponderosa Pine Ecosystems: Combined Proceedings of the 2005 St. George, Utah and 2006 Albuquerque, New Mexico Workshops. Proceedings RMRS-P-51* (ed. G.J.Gottfried, J.D.Shaw and P.L.Ford), 90–103. Fort Collins, CO: US Forest Service, Rocky Mountain Research Station.

Gottfried, G.J., Shaw, J.D., and Ford, P.L. (eds.) (2008). *Ecology, Management, and Restoration of Piñon–Juniper and Ponderosa Pine Ecosystems: Combined Proceedings of the 2005 St. George, Utah and 2006 Albuquerque, New Mexico Workshops. Proceedings RMRS-P-51*. Fort Collins, CO: US Forest Service, Rocky Mountain Research Station.

Gould, F.W. (1975). *The Grasses of Texas*. College Station, TX: Texas A&M Press.

Grundel, R. and Pavlovic, N.B. (2007). Distinctiveness, use, and value of midwestern oak savannas and woodlands as avian habitats. *Auk* 124: 969–985.

Grzybowski, J.A. (1991). *Black-Capped Vireo Recovery Plan*. Austin, TX: US Fish and Wildlife Service.

Hamilton, W.T. (2004). *Brush Management: Past, Present, Future*. College Station, TX: Texas A&M University Press.

Hankins, D.L. (2015). Restoring indigenous prescribed fires to California oak woodlands. In: *Managing Oak Woodlands in a Dynamic World. Proceedings of the Seventh California Oak Symposium. PSW-GTR-251* (ed. R.B.Standiford and K.L.Purcell), 123–129. Berkeley, CA: US Forest Service Pacific Southwest Research Station.

Haywood, J.D. (2000). Mulch and hexazinone herbicide shorten the time longleaf pine seedlings are in the grass stage and increase height growth. *New Forests* 19: 279–290.

Hessl, A.E. and Graumlich, L.J. (2002). Interactive effects of human activities, herbivory and fire on quaking aspen (*Populus tremuloides*) age structures in western Wyoming. *Journal of Biogeography* 29: 889–902.

Hicke, J.A., Logan, J.A., Powell, J., and Ojima, D.S. (2006). Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *Journal of Geophysical Research: Biogeosciences* 111: G02019.

Hicke, J.A., Johnson, M.C., Hayes, J.L., and Preisler, H.K. (2012). Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management* 271: 81–90.

Hinman, S.E. and Brewer, J.S. (2007). Responses of two frequently-burned wet pine savannas to an extended period without fire. *Journal of the Torrey Botanical Society* 134: 512–526.

Hoffman, C.M., Sieg, C.H., McMillin, J.D., and Fulé, P.Z. (2012). Fuel loadings 5 years after a bark beetle outbreak in south-western USA ponderosa pine forests. *International Journal of Wildland Fire* 21: 306–312.

Holechek, J., Pieper, R.D., and Herbel, C.H. (1998). *Range Management: Principles and Practices*, 3e. Upper Saddle River, NJ: Prentice Hall.

Horncastle, V.J., Hellgren, E.C., Mayer, P.M. et al. (2004). Differential consumption of eastern red cedar (*Juniperus virginiana*) by avian and mammalian guilds: implications for tree invasion. *American Midland Naturalist* 152: 255–267.

Hughes, L.E. (2008). Restoration of the ponderosa pine ecosystem and its understory. In: *Ecology, Management, and Restoration of Piñon–Juniper and Ponderosa Pine Ecosystems: Combined Proceedings of the 2005 St. George, Utah and 2006 Albuquerque, New Mexico Workshops. Proceedings RMRS-P-51* (ed. G.J.Gottfried, J.D.Shaw and P.L.Ford), 187–191. Fort Collins, CO: US Forest Service, Rocky Mountain Research Station.

Jacoby, P.W., Ansley, R.J., Meadors, C.H., and Cuomo, C.J. (1990). Control of honey mesquite with herbicides: influence of stem number. *Journal of Range Management* 43: 36–38.

Jenkins, M.J., Runyon, J.B., Fettig, C.J. et al. (2014). Interactions among the mountain pine beetle, fires, and fuels. *Forest Science* 60: 489–501.

Johnson, D.D. and Miller, R.F. (2006). Structure and development of expanding western juniper woodlands as influenced by two topographic variables. *Forest Ecology and Management* 229: 7–15.

Johnston, M.C. (1963). Past and present grasslands of southern Texas and northeastern Mexico. *Ecology* 44: 456–466.

Keeley, J.E. (2002). Native American impacts on fire regimes of the California coastal ranges. *Journal of Biogeography* 29: 303–320.

Kettle, W.D., Rich, P.M., Kindscher, K. et al. (2000). Land-use history in ecosystem restoration: a 40-year study in the prairie-forest ecotone. *Restoration Ecology* 8: 307–317.

Kimmerer, R.W. and Lake, F.K. (2001). The role of indigenous burning in land management. *Journal of Forestry* 99: 36–41.

Kirkman, K.L., Goebel, C.P., West, L. et al. (2000). Depressional wetland vegetation types: a question of plant community development. *Wetlands* 20: 373–385.

Knick, S. and Connelly, J.W. (eds.) (2011). *Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats*. Berkeley, CA: University of California Press.

Knick, S.T., Dobkin, D.S., Rotenberry, J.T. et al. (2003). Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105: 611–634.

Leach, M.K. and Givnish, T.J. (1996). Ecological determinants of species loss in remnant prairies. *Science* 273: 1555–1558.

Lett, M.S. and Knapp, A.K. (2003). Consequences of shrub expansion in Mesic grassland: resource alterations and graminoid responses. *Journal of Vegetation Science* 14: 487–496.

MacDougall, A.S. and Turkington, R. (2006). Dispersal, competition, and shifting patterns of diversity in a degraded oak savanna. *Ecology* 87: 1831–1843.

Mack, R.N. (2011). Fifty years of "waging war on cheatgrass": research advances, while meaningful control languishes. In: *Fifty Years of Invasion Ecology: The Legacy of Charles Elton* (ed. D.M.Richardson), 253–265. New York: Blackwell.

Madany, M.H. and West, N.E. (1983). Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. *Ecology* 64: 661–667.

Manier, D.J. and Laven, R.D. (2002). Changes in landscape patterns associated with the persistence of aspen (*Populus tremuloides* Michx.) on the western slope of the Rocky Mountains, Colorado. *Forest Ecology and Management* 167: 263–284.

Margolis, E., Lyons, D., Dupzyk, P., and McCarthy, L. (2009). *Santa Fe Municipal Watershed Plan 2010–2029*. Santa Fe, NM: Santa Fe Watershed Association.

McGlone, C.M., Springer, J.D., and Covington, W.W. (2009). Cheatgrass encroachment on a ponderosa pine forest ecological restoration project in northern Arizona. *Ecological Restoration* 27: 37–46.

McLaughlin, B.C. and Zavaleta, E.S. (2012). Predicting species responses to climate change: demography and climate microrefugia in California valley oak (*Quercus lobata*). *Global Change Biology* 18: 2301–2312.

McPherson, G.R. (1997). *Ecology and Management of North American Savannas*. Tucson, AZ: University of Arizona Press.

Meisel, J., Trushenski, N., and Weiher, E. (2002). A gradient analysis of oak savanna community composition in western Wisconsin. *Journal of the Torrey Botanical Society* 129: 115–124.

Meneguzzo, D.M. and Liknes, G.C. (2015). Status and trends of eastern red cedar (*Juniperus virginiana*) in the central United States: analyses and observations based on forest inventory and analysis data. *Journal of Forestry* 113: 325–334.

Menges, E.S. and Hawkes, C.V. (1998). Interactive effects of fire and microhabitat on plants of Florida scrub. *Ecological Applications* 8: 935–946.

Mensing, S. (1992). The impact of European settlement on blue oak (*Quercus douglasii*) regeneration and recruitment in the Tehachapi Mountains, California. *Madroño* 39: 36–46.

Mensing, S. (2006). The history of oak woodlands in California, part II: the native American and historic period. *California Geographer* 46: 1–31.

Miller, R.F., Knick, S.T., Pyke, D.A. et al. (2008). *Characteristics of Sagebrush Habitats and Limitations to Long-Term Conservation*. Reston, VA: US Geological Survey.

Miller, R.F. and Rose, J.A. (1995). Historic expansion of *Juniperus occidentalis* (western juniper) in southeastern Oregon. *Great Basin Naturalist* 55: 37–45.

Miller, R.F. and Wigand, P.E. (1994). Holocene changes in semiarid pinyon–juniper woodlands. *BioScience* 44: 465–474.

Moore, M.M., Covington, W.W., and Fulé, P.Z. (1999). Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecological Applications* 9: 1266–1277.

Muller, C.H. (1939). Relations of the vegetation and climatic types in Nuevo Leon, Mexico. *American Midland Naturalist* 21: 687–729.

Muller, C.H. (1947). Vegetation and climate of Coahuila, Mexico. *Madroño* 9: 33–57.

Návar, J. (2009). Allometric equations for tree species and carbon stocks for forests of northwestern Mexico. *Forest Ecology and Management* 257: 427–434.

Nuzzo, V.A. (1986). Extent and status of Midwest oak savanna: presettlement and 1985. *Natural Areas Journal* 6: 6–36.

Osborne, C.P., Salomaa, A., Kluyver, T.A. et al. (2014). A global database of C4 photosynthesis in grasses. *New Phytologist* 204: 441–446.

Outcalt, K.W. (2008). Lightning, fire and longleaf pine: using natural disturbance to guide management. *Forest Ecology and Management* 255: 3351–3359.

Peterson, D.W. and Reich, P.B. (2001). Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications* 11: 914–927.

Pierce, A.M. and Reich, P.B. (2010). The effects of eastern red cedar (*Juniperus virginiana*) invasion and removal on a dry bluff prairie ecosystem. *Biological Invasions* 12: 241–252.

Platt, W.J. (1999). Southeastern pine savannas. In: *Savannas, Barrens, and Rock Outcrop Plant Communities of North America* (ed. R.C.Anderson, J.S.Fralish and J.M.Baskin), 23–51. Cambridge: Cambridge University Press.

Platt, W.J. and Gottschalk, R.M. (2001). Effects of exotic grasses on potential fine fuel loads in the groundcover of south Florida slash pine savannas. *International Journal of Wildland Fire* 10: 155–159.

Platt, W.J., Evans, G.W., and Davis, M.M. (1988). Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. *Oecologia* 76: 353–363.

Platt, W.J., Doren, R.F., and Armentano, T.V. (2000). Effects of Hurricane Andrew on stands of slash pine (*Pinus elliottii* var. *densa*) in the Everglades region of South Florida (USA). *Plant Ecology* 146: 43–60.

Platt, W.J., Beckage, B., Doren, R.F., and Slater, H.H. (2002). Interactions of large-scale disturbances: prior fire regimes and hurricane mortality of savanna pines. *Ecology* 83: 1566–1572.

Polley, H.W., Johnson, H.B., and Mayeux, H.S. (1994). Increasing CO_2: comparative responses of the C_4 grass *Schizachyrium* and grassland invader *Prosopis*. *Ecology* 75: 976–988.

Qian, H. (1998). Large-scale biogeographic patterns of vascular plant richness in North America: an analysis at the generic level. *Journal of Biogeography* 25: 829–836.

Rizzo, D.M. and Garbelotto, M. (2003). Sudden oak death: endangering California and Oregon forest ecosystems. *Frontiers in Ecology and the Environment* 1: 197–204.

Romme, W.H., Turner, M.G., Wallace, L.L., and Walker, J.S. (1995). Aspen, elk, and fire in northern Yellowstone Park. *Ecology* 76: 2097–2106.

Rzedowski, J. (1978). *Vegetación de México*. México: Editorial Limusa.

Saenz, L. and Sawyer, J.O. (1986). Grasslands as compared to adjacent *Quercus garryana* woodland understories exposed to different grazing regimes. *Madroño* 33: 40–46.

Sands, J.P., Brennan, L.A., Hernández, F. et al. (2009). Impacts of buffelgrass (*Pennisetum ciliare*) on a forb community in south Texas. *Invasive Plant Science and Management* 2: 130–140.

Schoennagel, T., Veblen, T.T., and Romme, W.H. (2004). The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience* 54: 661–676.

Scholes, R.J. and Archer, S.R. (1997). Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517–544.

Science Applications International Corporation (SAIC) (2010). *Final Integrated Natural Resources Management Plan, Prepared for Department of the Air Force, Eglin Air Force Base, Florida*. Shalimar, FL: Science Applications International Corporation (SAIC).

Simberloff, D. and Gotelli, N. (1984). Effects of insularisation on plant species richness in the prairie-forest ecotone. *Biological Conservation* 29: 27–46.

Skinner, B., Probasco, G., and Samson, F. (1983). Environmental requirements of three threatened plants on limestone glades in southern Missouri. *Biological Conservation* 25: 63–73.

Sparks, J.C., Masters, R.E., Engle, D.M. et al. (1998). Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. *Journal of Vegetation Science* 9: 133–142.

Standiford, R.B. and Purcell, K.L. (eds.) (2015). *Managing oak woodlands in a dynamic world. Proceedings of the seventh California oak symposium. PSW-GTR-251*. Berkeley, CA: US Forest Service Pacific Southwest Research Station.

Stephens, S.L. and Fulé, P.Z. (2005). Western pine forests with continuing frequent fire regimes: possible reference sites for management. *Journal of Forestry* 103: 357–362.

Szeicz, J.M. and MacDonald, G.M. (1991). Postglacial vegetation history of oak savanna in southern Ontario. *Canadian Journal of Botany* 69: 1507–1519.

Tyler, C.M., Kuhn, B., and Davis, F.W. (2006). Demography and recruitment limitations of three oak species in California. *Quarterly Review of Biology* 81: 127–152.

US Fish and Wildlife Service (USFWS) (2006). Designation of critical habitat for the Fender's blue butterfly (*Icaricia icarioides fenderi*), *Lupinus sulphureus* ssp. *kincaidii* (Kincaid's lupine), and *Erigeron decumbens var. decumbens* (Willamette daisy); final rule. *Federal Register* 72: 63862–63977.

US Fish and Wildlife Service (USFWS) (2012). *Karner blue butterfly (Lycaeides melissa samuelis) 5-year review: summary and evaluation*. New Franken, WI: US Fish and Wildlife Service, Ecological Services Field Office.

US Forest Service (USFS) (1996). *Revised land and resource management plan: National Forests and Grasslands in Texas*. Atlanta, GA: US Forest Service.

US Forest Service (USFS) (1999). *Revised land and resource management plan for National Forests of Florida*. Atlanta, GA: US Forest Service.

US National Park Service (USNPS) (2001). *Cerro Grande prescribed fire; Board of Inquiry final report*. Washington, DC: US National Park Service.

US National Park Service (USNPS) (2007). *Bandelier National Monument final ecological restoration plan and environmental impact statement*. Washington, DC: US National Park Service.

Van Auken, O.W. (2000). Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31: 197–215.

Van Auken, O.W. (2009). Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* 90: 2931–2942.

Van Lear, D.H., Carroll, W.D., Kapeluck, P.R., and Johnson, R. (2005). History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. *Forest Ecology and Management* 211: 150–165.

Vellend, M., Bjorkman, A.D., and McConchie, A. (2008). Environmentally biased fragmentation of oak savanna habitat on southeastern Vancouver Island, Canada. *Biological Conservation* 141: 2576–2584.

Vesely, D. and Tucker, G. (2004). *A Landowner's Guide for Restoring and Managing Oregon White Oak Habitats*. Corvallis, OR: Pacific Wildlife Research, for the US Bureau of Land Management, etc.

Volder, A., Tjoelker, M.G., and Briske, D.D. (2010). Contrasting physiological responsiveness of establishing trees and a C4 grass to rainfall events, intensified summer drought, and warming in oak savanna. *Global Change Biology* 16: 3349–3362.

Walker, B.L., Naugle, D.E., and Doherty, K.E. (2007). Greater sage-grouse population response to energy development and habitat loss. *Journal of Wildlife Management* 71: 2644–2654.

Walker, J. and Peet, R.K. (1984). Composition and species diversity of pine-wiregrass savannas of the green swamp, North Carolina. *Vegetatio* 55: 163–179.

Weltzin, J.F. and McPherson, G.R. (1999). Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. *Ecological Monographs* 69: 513–534.

Weniger, D. (1984). *The Explorers' Texas: The Lands and Waters*. Austin, TX: Eakin Press.

West, N.E. (1999). Distribution, composition, and classification of current juniper-pinyon woodlands and savannas across western North America. In: *Proceedings: Ecology and Management of Pinyon–Juniper Communities within the Interior West. RMRS-P-9* (ed. S.B.Monson and R.Stevens), 20–23. Ogden, UT: Rocky Mountain Research Station, Forest Service, United States Department of Agriculture.

Wester, D.B. (2007). The Southern High Plains: a history of vegetation, 1540 to present. In: *Shrubland Dynamics – Fire and Water; Proceedings 2004 August 10–12; Lubbock, TX. RMRS-P-47* (ed. R.E.Sosebee, D.B.Wester, C.M.Britton, et al.), 24–47. Fort Collins, CO: US Forest Service, Rocky Mountain Research Station.

Will-Wolf, S. and Stearns, F. (1999). Dry soil oak savanna in the Great Lakes region. In: *Savannas, Barrens, and Rock Outcrop Plant Communities of North America* (ed. R.C.Anderson, J.S.Fralish and J.M.Baskin), 135–154. Cambridge: Cambridge University Press.

Wolf, J. (2006). Effects of disturbance frequency on canopy age structure and species composition in a managed Midwestern oak savanna. *Physical Geography* 27: 519–533.

Young, J.A., Evans, R.A., Eckert, R.E., and Burgess, L.K. (1987). Cheatgrass. *Rangelands* 9: 266–270.

Young, J.E., Sánchez-Azofeifa, G.A., Hannon, S.J., and Chapman, R. (2006). Trends in land cover change and isolation of protected areas at the interface of the southern boreal mixed wood and aspen parkland in Alberta, Canada. *Forest Ecology and Management* 230: 151–161.

Zack, S., Chase, M.K., Geupel, G.R., and Stralberg, D. (2005). The oak woodland bird conservation plan: a strategy for protecting and managing oak woodland habitats and associated birds in California. In: *Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference. 2002 March 20–24, Asilomar, California. Volume 1. PSW-GTR-191* (ed. C.J.Ralph and T.D.Rich), 174–178. Albany, CA: US Forest Service, Pacific Southwest Research Station.

Zhang, Y., Majumdar, I., and Schelhas, J. (2010). Changes in woodland use from longleaf pine to loblolly pine. *Sustainability* 2: 2734–2745.