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Ecological Effects of Prescribed Fire Season: A Literature Review and Synthesis for Managers

Eric E. Knapp, Becky L. Estes, and Carl N. Skinner

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Authors

Eric E. Knapp is a research ecologist, **Becky L. Estes** is a research ecologist, and **Carl N. Skinner** is a research geographer, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002.

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Abstract

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Prescribed burning may be conducted at times of the year when fires were infrequent historically, leading to concerns about potential adverse effects on vegetation and wildlife. Historical and prescribed fire regimes for different regions in the continental United States were compared and literature on season of prescribed burning synthesized. In regions and vegetation types where considerable differences in fuel consumption exist among burning seasons, the effects of prescribed fire season appears, for many ecological variables, to be driven more by fire-intensity differences among seasons than by phenology or growth stage of organisms at the time of fire. Where fuel consumption differs little among burning seasons, the effect of phenology or growth stage of organisms is often more apparent, presumably because it is not overwhelmed by fire-intensity differences. Most species in ecosystems that evolved with fire appear to be resilient to one or few out-of-season prescribed burn(s). However, a variable fire regime including prescribed burns at different times of the year may alleviate the potential for undesired changes and maximize biodiversity.

Keywords: Fire effects, fire intensity, fire season, fuel consumption, historical fire regime, phenology, prescribed fire, pyrodiversity.

Contents

Chapter 1: Overview

Prescribed burning is a tool for reducing fuels and restoring a disturbance process to landscapes that historically experienced fire. It is often assumed, or at least desired, that the effects of prescribed burns mimic those of natural fires. However, because of operational and liability constraints, a significant proportion of prescribed burning is, in many ecosystems, conducted at different times of the year than when the majority of the landscape burned historically. This has brought into question the extent to which prescribed fire mimics effects of the historical fire-disturbance regime, and whether there are any negative impacts of such out-of-season burning.

Most plant and animal species that exist in areas with a history of relatively frequent low- to moderate-intensity fire are resilient to its effects. However, burning season may influence the outcome in a number of ways. For example, many plant species recover quickly from fire, either through resprouting or fire-stimulated seed germination, but it is believed that the recovery can differ depending on the timing of the fire. When aboveground parts are consumed or killed by the fire, resprouting depends on stored resources, such as carbohydrates. These carbohydrates are typically at their lowest annual levels early in the growing season. Thus, plants may recover more slowly from fire that occurs during the active growing season than fire that occurs after plants have gone dormant. Animal species can often avoid the flames; however, they may be more vulnerable to fire at times of reduced mobility, such as during nesting or breeding season. The influence of fire season can also be indirect, through differences in habitat created, or competitive release of some species owing to damage to or mortality of others.

In some areas of the United States, most fires historically occurred when plants were dormant and animals had reproduced and dispersed. This includes the Western United States, where fires were historically most abundant during the months of the year with the driest fuels and after senescence of surface vegetation, and the forests of the Northeast, where fallen leaves of deciduous trees are the main carrier of fire. On the other hand, in the Southwestern United States, the main historical fire season was toward the end of the dry season (late spring/early summer), in association with the first thunderstorms, which ignited the fires but also provided moisture for plants to initiate growth. In the Southeastern United States, historical fires were once common throughout the summer and peaked in May at the transition from the dry spring period to the wet summer period, when lightning incidence was at its highest, vegetation was growing, and animals were active.

Prescribed fires may not only differ from natural fires in their timing relative to phenology (seasonal growth or life history stage) of organisms that live in the ecosystem, but may also often differ in their intensity. For example, in the Western United States, prescribed burns are increasingly conducted in the spring, when many of the larger surface fuels are still somewhat moist from the winter and spring precipitation. Because of the higher moisture, prescribed burns at this time of year tend to consume less fuel and therefore release less heat. Thus, to evaluate the effect of burn season, both the role of differences in intensity and timing between prescribed fire and natural fire need to be considered. Although burn season research results that have controlled for fire intensity have often shown an effect

Table 1—Historical and prescribed fire seasons plus potential fuel consumption differences between dormant- and growing-season prescribed burns[a]

Region	Main historical fire season	Main prescribed fire season	Typical potential fuel consumption difference between dormant and growing season burns
Western forests	Dormant	Dormant/growing	Very high
Southwestern forests	Growing/dormant[b]	Dormant	High
Central grasslands	Dormant/growing	Dormant	Low
Southeastern pine forests	Growing	Dormant/growing	Moderate
Eastern hardwood forests	Dormant	Dormant	Low to moderate

[a] Much variation in conditions at the time of burning exists within both the historical and prescribed fire regimes for each region—the listed text is simply a rough average.

[b] When multiple seasons are reported, the order indicates the most likely.

of fire timing, the latest research suggests that, in many cases, variation in fire intensity exerts a stronger influence on the ecosystem than variation in fire timing.

Given the potential importance of fire intensity to fire effects, a useful means of evaluating the outcome of prescribed burn season relative to what might have been expected under a natural fire regime would be to consider the amount of fuel consumed by prescribed burns and the intensity of those burns at different times of the year, in relation to the amount of fuel that was likely consumed by and the intensity of historical fires (both lightning ignited and anthropogenic) (table 1).

In forest ecosystems of the Western United States, prescribed burns are often conducted in areas with very heavy fuel loads resulting from decades of fire exclusion. Although spring prescribed burns typically consume less fuel than those that are ignited in other seasons, prescribed burns in any season can conceivably consume more fuel than historical burns would have under a natural fire regime. Several recent papers have shown that late summer or fall prescribed burns often lead to higher tree mortality and set back herbaceous understory vegetation more than spring burns, even though late summer and early fall fire was the historical norm. The difference in fuel consumption and fire intensity between the prescribed burn seasons apparently overwhelmed the effect of phenology of the organisms. Many coniferous forest ecosystems of the Southwest also typically have unnaturally high fuel loads, but times of the year with lower fuel moisture and higher consumption differs, owing to monsoon rains in the summer. Until fuels are reduced to historical levels, any prescribed burn under higher fuel moisture conditions may have effects more similar to historical burns, because the amount of fuel consumed, and fire intensity are closer to that noted for historical burns. A different situation exists in chaparral shrub lands of the West, where prescribed burns are usually conducted under more benign conditions in the winter or spring, and are therefore often less intense and consume less fuel than historical fires would have. With organisms in these shrub ecosystems presumably adapted to high-severity stand-replacing fire, reduced intensity over what might have been experienced historically also means that the outcomes sometimes have not met objectives. For example, several authors have noted that shrubs and herbs requiring intense heat to stimulate germination emerge in lesser numbers following spring burns.

Grasslands are composed of fine fuels that dry readily and are likely to be nearly completely consumed with prescribed fire in any season (table 1). Grass thatch also breaks down relatively rapidly, so there is not a large buildup of fuels relative to historical levels. Because the difference in total fuel consumption and fire intensity between burn seasons is relatively low, the effect of timing of the fire is generally more evident in grasslands than in other vegetation types. Numerous examples of alterations to grassland plant communities with prescribed burning in different seasons are found in the literature.

In the Southeastern United States, prescribed burns are typically conducted in late winter/early spring when many plants and other organisms are dormant, and in the late spring/early summer, during the historical peak period of lightning-ignited fire. Burning during the dormant season became standard practice in order to reduce direct impacts to nesting birds and other wildlife species. However, in many cases, the prescribed burns during the late spring/early summer growing season have been shown to better meet longer term management objectives for pine forests by reducing competition from competing hardwoods. Furthermore, concerns about negative effects to wildlife from late spring/early summer growing-season burns have generally not been supported by research.

In eastern forests, burn intensity does not generally vary predictably with season, with fuel consumption influenced more by time since previous rainfall and year-to-year climatic variability. Differences in fuel consumption among burning seasons is often much less in eastern forests (particularly deciduous forests) than in western forests, where because of a long history of fire exclusion and a slower decomposition rate, surface fuel loads are typically much higher. Therefore, differences among burn seasons related to fire intensity are expected to be considerably less in eastern forests than in western forests (table 1).

Many species show strong resilience to fire in either season, with the majority of studies reporting relatively minor differences, if any. Differences in the timing of a single or even several applications of prescribed fire do not appear likely to substantially change the plant or animal community. In most ecosystems studied, the change associated with either burning or not burning is much greater than differences in the outcome with burning in different seasons. This should not be interpreted as burning season not mattering. Burning season has been shown to affect community composition, particularly with repeated application of fire in the same time of year. Many authors have therefore stressed the importance of incorporating variability in prescribed fire timing (along with variability in other aspects of the fire regime) into long-term burn management plans. Because response to burning season differs a great deal among species, a heterogeneous fire regime is likely to maximize biodiversity.

One recurring problem in fire management and fire science is the inconsistency in terminology. Fire timing may be referred to as a spring burn, fall burn, early-season burn, late-season burn, wet-season burn, dry-season burn, growing-season burn, dormant-season burn, or lightning-season burn, each of which may have different meanings across ecosystems. Furthermore, the phenological status of target species often differs with latitude and yearly climate. This creates a serious impediment to truly understanding and synthesizing the literature on season of burning. To maximize what can be learned, we recommend that authors and practitioners should, whenever possible, provide information on exact burn dates, as well as variables such as weather conditions and year-to-year climatic variation (was it a drought year?), fuel moistures at the times of burns, fire behavior (including fire-line intensity), plus the phenological or life-history status of target species.

Key Points

Both fire intensity and burn season can influence fire effects. To evaluate the expected outcome of prescribed burning season, managers may need to ask the following questions: (1) What is the phenological or life-history stage of organisms at the time of the prescribed burn and how does this differ from our best approximation of historical conditions? (2) What are the loading, composition, and architecture of fuels at the site to be burned and how do these compare with historical conditions? (3) How different will fire intensity be for prescribed burns conducted in different seasons, and does this vary from historical fire intensity?

- Effects related to the phenology or life history stage of organisms at the time of prescribed burning are more likely to be noticed if differences in fuel consumption or fire intensity between seasons are low. If differences in consumption or intensity are substantial, these factors will likely drive fire effects.
- The burn season leading to an amount of fuel consumed and fire intensity closest to or within the historical range of variability will often have the best outcome.
- A prescribed burn timed to occur within the historical burn season will often have the best outcome.
- A single prescribed burn (or even a few prescribed burns) outside of the historical fire season appear(s) unlikely to have strong detrimental effects. Substantial shifts in community composition often require multiple cycles of prescribed burning. In many ecosystems, the importance of burning appears to outweigh the effect of burn season.
- Variation in the timing of prescribed burns will help to ensure biodiversity is maintained.

Chapter 2: Introduction

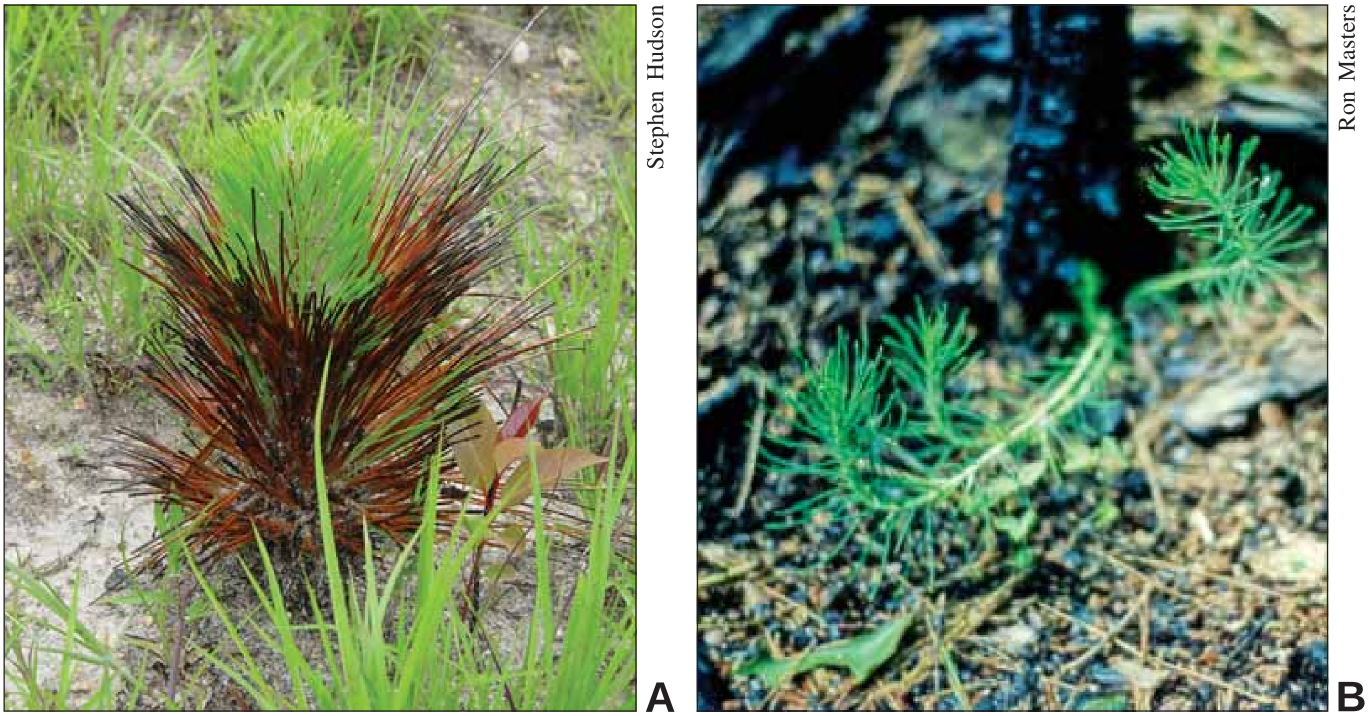
The Fire Season Issue

Fire is being reintroduced to many ecosystems that historically experienced frequent fire to reduce hazardous fuels that have accumulated and to restore important ecological functions. This reintroduction often occurs through prescribed burning, the assumption being that the disturbance produced by such fires approximates the disturbance historically produced by wildfire. However, prescribed burns are sometimes ignited outside of the historical fire season. Reasons for this include the following: (1) Safety concerns. Igniting during times of more benign weather and fuel moisture conditions lessens the chance of an escape. (2) Smoke management. Certain times of the year may be better for smoke dispersal than others. (3) Operational constraints. There may be a lack of resources during the historical fire season because personnel are being used to fight wildfires. (4) Biological management. Certain seasons may reduce the chance of injury and death of target species.

There has been concern that "out-of-season" burning might be harmful to some species because the ecosystem did not evolve with fire during these times. For example, across much of the Western United States, prescribed burns are frequently ignited in the spring and early summer, during the period of active growth of many organisms, although wildfires were historically uncommon during this time. In the Southeastern United States, the peak season for wildfires was historically during the active growth phase of trees and other vegetation, but prescribed burning is now more commonly conducted during the late winter when the majority of vegetation is dormant. Burning in the dormant season may not effectively control competing midstory vegetation, thereby reducing the establishment of fire-adapted overstory conifers.

Organisms of fire-adapted ecosystems have evolved and thrive with fire in a multitude of ways. For example, many trees have one or more of the following characteristics: thick bark; fire-stimulated sprouting, germination or seed dispersal; resistance to rotting; modified seedling structure; and thick heat-resistant buds (Abrams 1992, Bond and van Wilgen 1996, Myers 1990, Wade et al. 2000) (fig. 1). Understory herbaceous plant species survive fire through various mechanisms including resprouting from underground structures such as rhizomes or stolons that are located deeply enough in the soil to avoid the lethal heat pulse (Bond and van Wilgen 1996, Flinn and Wein 1977), or establishing from seeds that are stimulated to germinate by heat (Kauffman and Martin 1991, Keeley 1987). Other organisms survive in microenvironments where fire is less frequent as a result of lower fuel accumulation or where fuels have higher moisture levels. Among animals, less mobile species may use stump holes, cracks, or burrows as refuges when fire passes through, whereas more mobile species can flee, returning when the danger has passed. The type of adaptations depends on the fire regime, with, for example, frequent low-severity regimes requiring a different suite of characteristics than high-severity regimes such as lodgepole pine (*Pinus contorta* Dougl. ex Loud.) forest or chaparral shrublands, where the aboveground stems typically do not survive.

Fire adaptations may interact with burning season in several ways. In plants, carbohydrate reserves necessary to sustain growth are often at their lowest levels shortly after breaking dormancy (de Groot and Wein 2004, Harrington 1989). Stored carbohydrates help fuel this rapid burst of growth, and these reserves are generally replenished by products of photosynthesis during the growing season. It is thought that plants may have a harder time recovering from tissue loss to fire during the period when carbohydrate reserves are low than at other times of the year (Garrison 1972, Hough 1968, Volland and Dell 1981). In addition, tender early-season tissues may be more sensitive to heat (Bond and van Wilgen 1996, DeBano et al. 1998). Fire in the early season can also kill aboveground flowering parts prior to seed production and seed fall, limiting reproductive capacity. With animals, vulnerability to



Stephen Hudson

Ron Masters

Figure 1—Adaptations to fire in two pine species of the Southern United States. (a) Young longleaf pine seedlings in the “grass” stage resemble a tuft of grass, with height growth suppressed and the apical growing points protected from the frequent surface fires. As shown in the photograph, seedlings can recover from needle scorch during this stage. After development of the tap root, the seedling enters the candle stage where rapid height growth occurs, moving the terminal bud above average flame height. (b) Shortleaf pine can resprout from the base following disturbance, increasing resilience to fire. The ability of shortleaf pine to resprout is dependent on tree age and intensity of the fire.

prescribed fire can differ depending on the time of year. For example, birds are potentially more strongly impacted by spring and early summer burns because this coincides with the nesting season (Reinking 2005). Reptiles and amphibians may be more active or more likely to be at the surface at certain times of the year where they are less able to survive flaming combustion (Griffiths and Christian 1996, Pilliod et al. 2003). Both plant and animal species may depend on unburned patches to persist (Martin and Sapsis 1992), and creation of these refugia often differs among seasons, varying with fuel moisture levels and fuel continuity.

The response of organisms to prescribed fire depends on complex interactions between factors such as the timing of prescribed burning relative to the historical fire season, phenological stage of the organisms at the time of fire, differences in fire severity among burn seasons, and variation in climate within and among burn seasons. Many studies on the timing of prescribed fire only broadly describe the season of burning (i.e., spring burn), which allows for some variation with respect to the growth stage of plants and other organisms (Svejcar 1990). For example, a prescribed burn very early in the spring, prior to bud break, may have entirely different effects on vegetation than a prescribed burn later in the spring after leaves have flushed. In addition, no two prescribed burns are the same, even those conducted within the same season. Among the limitations of studies comparing different seasons of burning is that the timing of treatment is often confounded with other factors that affect fire intensity and severity at different times of the year. To best understand the effect of burn season, we present associated data on fire severity, phenology of vegetation, and activity level/vulnerability of the fauna of interest at the time of the burns, whenever available.

Because of differences in historical and prescribed fire regime (timing, intensity, vegetation type, spatial scale), research findings from studies conducted in one area or vegetation type may not apply to others. In this synthesis, we therefore cover three broad regions of the continental United States, adapted roughly from groupings of eco-regional divisions outlined by Bailey (1983), which are based on both climatic zones and potential natural vegetation. Our regions consider differences in vegetation with the strongest influence on fuel loading and the fire regime (fig. 2). The Western region is everything west of the central grasslands, and consists of both a humid temperate division along the Pacific Coast as well as the non-grassland portions of the dry interior division. The Central region is composed of both dry temperate to subtropical steppe (shortgrass prairie) and humid temperate prairie (tallgrass). The Eastern region consists of mainly a warm continental and a hot continental division (boreal and deciduous forest, respectively), plus a subtropical division (Bailey 1983), dominated by pine and mixed pine-oak forests, and a savanna division in south Florida. Alaska and Hawaii are not covered, as little or no information on seasonal differences of prescribed fire is available for either of these two areas.

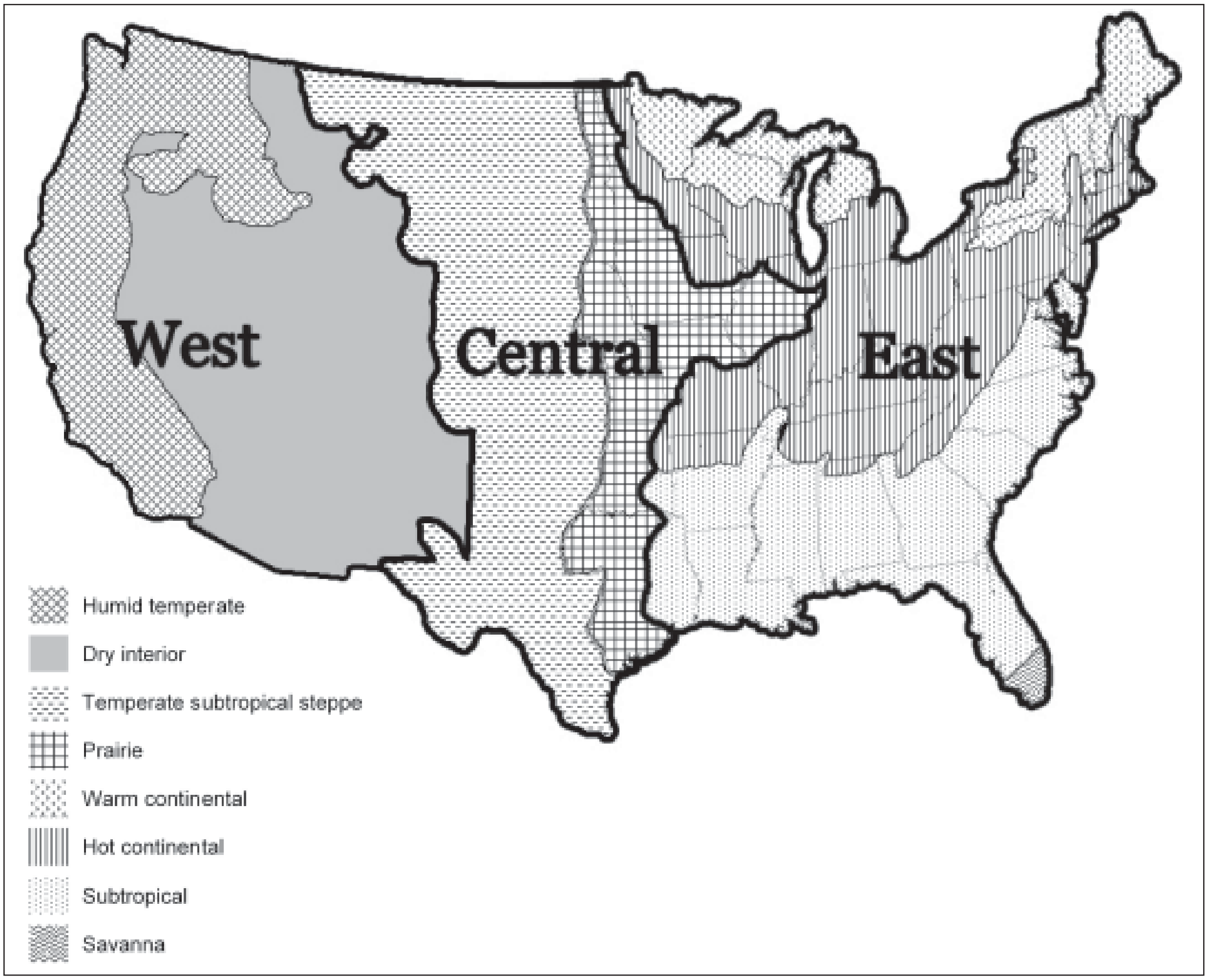


Figure 2—Three broad fire regions of the continental United States roughly adapted from ecosystem divisions outlined by Bailey (1980).

Chapter 3: Western Region

Climate, Vegetation, and Fire

Large differences in topography and climate in the Western region naturally lead to a great deal of variation in fire regime. For the purpose of this synthesis, the Western region was split into two zones–the Humid Temperate zone with maritime influence from the Pacific Ocean lying mainly closer to the coast, and the Dry Interior zone to the east, with the crest of the Cascade Range and the Sierra Nevada forming the approximate boundary.

Humid Temperate

This zone is characterized by seasonality in precipitation, with a distinct wet period between approximately October and April and dry summers (fig. 3 a, c). Because the warmest months of the year also have the least amount of precipitation, surface fuels do not decompose as readily as in some other regions. In the north, average yearly rainfall is high, with the moisture and moderate temperatures resulting in very productive coniferous forest ecosystems with heavy fuel accumulation (Schroeder and Buck 1970). Some summer rains reduce fire hazard in all but the driest years. The average yearly rainfall generally declines and temperatures increase as one moves south through this zone (fig. 3). From approximately Roseburg, Oregon, south, the climate becomes increasingly mediterranean, with a defined cool winter rainy season followed by hot, dry summers. In California, summer rainfall is rare, and fire hazard is correspondingly higher.

Vegetation within the Humid Temperate zone is highly complex, varying from mesic hemlock (*Tsuga* Endl. Carr.), western redcedar (*Thuja plicata* Donn ex D. Don), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in the north to drier mixed-conifer forests and shrublands in the south.

Historical fire regime—
Prior to fire exclusion, the historical fire-return interval averaged across all forest types in Washington was 71 years, whereas the fire-return interval in Oregon forests was estimated to be 42 years (Agee 1993). A great deal of variability existed among forest types, with mesic cedar/spruce/hemlock forests burning in mixed to stand-replacing fire every 400 to 500+ years (Agee 1993, Brown 2000), whereas drier ponderosa pine forests burned in low- to mixed-severity fires every 15 or so years (Agee 1993). Many forested regions in California burned even more frequently in low- to mixed-severity fires at approximately 8- to 30-year intervals, depending on forest type (Skinner and Chang 1996). In general, the shorter the interval, the less fuel accumulated between fires, and the lower severity the average fire. This gradient in fire regime from north to south is a function of precipitation and temperature patterns. Chaparral shrublands found in central and southern California typically burned in high-severity stand-replacing events at moderate intervals (Keeley 2006). Owing to the lack of historical records, actual number of years between fires in chaparral shrub ecosystems is somewhat uncertain, but estimated to have typically ranged from 30 to 100 years.[1]

The wildfire season generally lasts from June until September in the north, with this period expanding as one moves south (Schroeder and Buck 1970). Although wildfires in southern California are most common from May through November, they can occur in nearly every month of the year when conditions are dry. In forested

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[1] Keeley, J.E. 2008. Personal communication. Research ecologist, U.S. Geological Survey, Sequoia and Kings Canyon Field Station, 47050 Generals Highway, Three Rivers, CA 93271-9651.

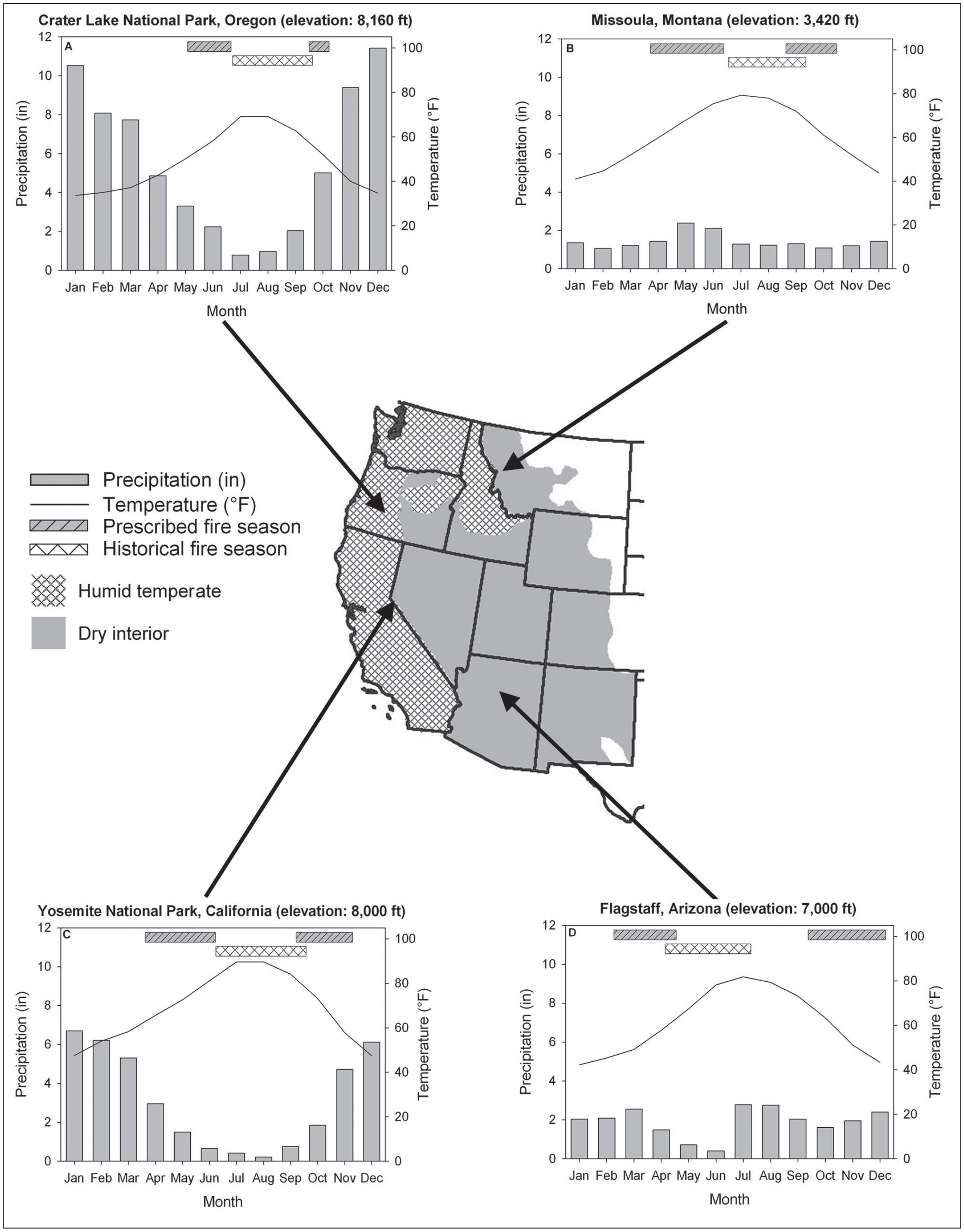

Figure 3—Climographs (monthly average temperature and precipitation) and the average time of the year of the peak historical and prescribed fire seasons from four representative locations within the Western region: (a) Crater Lake National Park, Oregon; (b) Missoula, Montana; (c) Yosemite National Park, California; and (d) Flagstaff, Arizona.

regions throughout the Humid Temperate zone, growth ring records from fire-scarred trees indicate that the majority of acres historically burned late in the growing season or after trees had ceased growth for the year and were dormant (table 2). Late growing season would correspond approximately to late July through August, whereas dormancy typically occurs by September in most years (Fowells 1941). Early to mid growing-season fires (approximately May through July) also occurred, but mainly in unusually dry years (Norman and Taylor 2003). It is believed that Native Americans made use of spring burns to manage vegetation (Lewis 1973), but such fires were likely less extensive than later lightning-ignited fires under drier conditions.

Prescribed fire regime—

Prescribed burns are typically conducted in two seasons either before or after the main period of summer drought (fig. 3). Early season burns are ignited after the cessation of winter and spring precipitation or snowmelt, as soon as the fuels have dried enough to burn (typically mid April until about July 1), until conditions become too dry and wildfire season begins in the summer (fig. 3). At lower elevations below the snowline, prescribed burning can sometimes also be successfully done during dry periods within the winter and early spring rainy season (McCandliss 2002). In black oak (*Quercus kelloggii* Newb.)-dominated forests below the snowline, periods during tree dormancy when the leafless canopy allows sunlight to dry the leaf litter on the forest floor are often ideal for burning.[2] Spring or early summer prescribed burning can be problematic because surface fuels are drying and temperatures warming. Thus, fires may continue to creep and smolder, sometimes for months. The second prescribed fire season typically occurs in the fall, after temperatures have cooled and often after the fuels have moistened with the first rains. In many areas of the West, the fall prescribed fire season coincides with inversions and poor air quality (McCandliss 2002). The spring and early summer prescribed burning period is generally earlier than the main historical fire season, and the fall prescribed burning period is often later than the historical fire season (fig. 3). Few prescribed burns are conducted in mid to late summer, the main historical fire season, because of fire control concerns that can result from the heavy fuels that characterize many contemporary forest landscapes. In addition, the summer wildfire season uses a significant proportion of available firefighting resources, meaning that fire crews are often unavailable for prescribed burns at this time of year.

The range of ecological conditions under which prescribed burns occur is quite broad. In the coniferous forest zone, early spring prescribed burns (prior to May) usually happen prior to active tree and plant growth as well as other significant biological activity. Burns conducted in late spring (May to June) occur during the main period of seasonal growth of vegetation and significant wildlife activity such as bird nesting (fig. 4a). Late summer and fall prescribed burns (September to October) typically occur during the dormant season after biological activity has slowed or ceased for the year (fig. 4b). Because of the nearly precipitation-free summers, soils are typically drier in the late summer and early fall than in the spring or early summer. However, this is not always the case, and much depends upon rainfall patterns for that year in relation to the prescribed burning period. Concerns about prescribed burning conducted outside of the historical season include (1) less-than-desired fuel consumption owing to high fuel moisture levels, and (2) potentially detrimental impacts to organisms if burns coincide with periods of peak growth/activity.

Dry Interior

Although the average yearly precipitation is lower in the Dry Interior zone than in most parts of the Humid Temperate zone, distinct seasonality is also apparent. The western and northern sections are in the rain shadow of the Cascade

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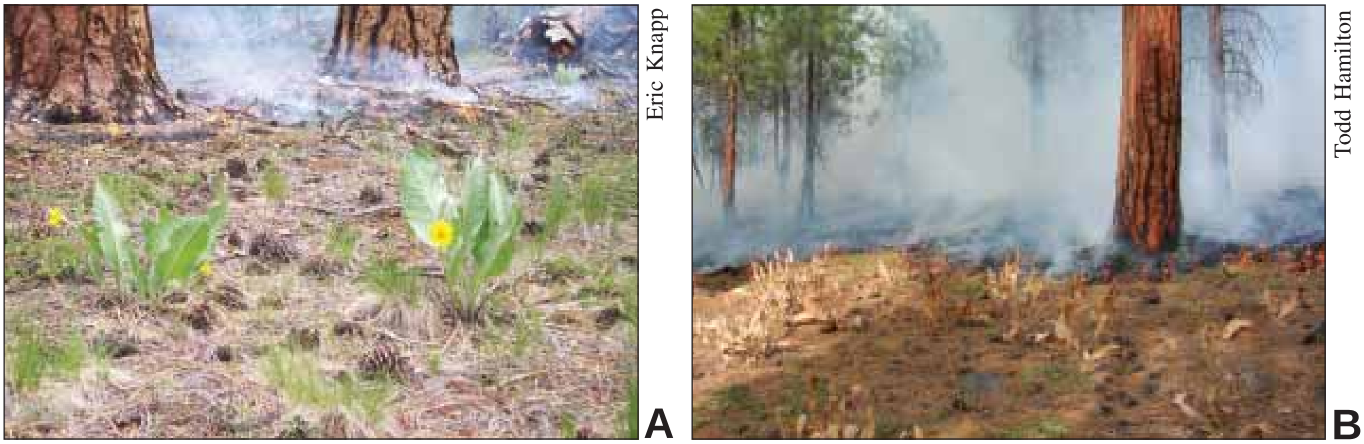
[2] Skinner, C.N. 1995. Using fire to improve wildlife habitat near Shasta Lake. 26 p. Unpublished report. On file with: USDA Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002.

Table 2—Position of fire scars within annual growth rings at different locations in the Western region (from north to south)[a]

	Approximate time						
Location	**Before May Dormant**	**May Early early**	**June Mid early**	**July Late early**	**Aug. Late**	**Sept.–Oct. Dormant**	**Author**
			Percent of all scars				
Pacific northwest:							
East Cascades, Washington	0		19		32	49	Wright and Agee 2004
southwest Montana	0			3		97	Heyerdahl et al. 2006
Blue Mtns., Washington and Oregon	0		8		20	72	Heyerdahl et al. 2001
California							
Shasta Trinity National Forest	0	1	2	4	17	76	Taylor and Skinner 2003
Whiskeytown National Recreation Area	0	0	0	7	57	36	Fry and Stephens 2006
Lassen National Forest	0	0	1	10	18	71	Bekker and Taylor 2001
Lassen National Park	0	1	7	8	1	83	Taylor 2000
Plumas National Forest	0	0	1	15	31	53	Moody et al. 2006
Southern Sierra Nevada	0	1	10	12	67	10	Swetnam et al. 1992 [b]
Sequioa National Park	0	2	3	6	89		Schwilk et al. 2006
San Jacinto Mountains	0	2	2	0	33	63	Everett 2008
Arizona, New Mexico, and Texas:							
Grand Canyon, Arizona	12	12	43	24	19	0	Fulé et al. 2003
Camp Navajo, Arizona	19	21	45	15	0	0	Fulé et al. 1997
Santa Rita Mtns. Arizona	9	30	34	25	2	0	Ortloff 1996
Rincon Mtns., Arizona	12		87		1	0	Baisan and Swetnam 1990
U.S./ Mexico border:	20	41	30	8	1	0	Swetnam et al., in press
Guadalupe Mtns., Texas	6	67	24	1	2	0	Sakulich and Taylor 2007

[a] Timing of the fire (month) is approximate and based on studies of period of radial growth in trees (Fowells 1941, Ortloff 1996, Swetnam et al., in press), which can vary with elevation, tree species, and yearly climatic differences. Giant sequoia (*Sequoiadendron giganteum* (Lindl.) J. Buchholz) is thought to have somewhat later phenology. At sites in Arizona and New Mexico, scars at the ring boundary (dormant) were assumed to have occurred in the spring, prior to tree growth, whereas at the remainder of sites, scars at the ring boundary were assumed to have occurred in the fall after tree growth was done for the year.

[b] Swetnam, T.W.; Baisan, C.H.; Caprio, A.C.; Touchan, R.; Brown, P.M. 1992. Tree ring reconstruction of giant sequoia fire regimes. 173 p. Unpublished report. On file with: National Park Service, Sequoia and Kings Canyon National Parks, 47050 Generals Highway, Three Rivers, CA 93271.



Eric Knapp

Todd Hamilton

Figure 4—(a) Late spring prescribed burn (June 3, 2008) and (b) fall prescribed burn (October 30, 2008) at Blacks Mountain Experimental Forest, Lassen National Forest, California. Note the phenological stage of the vegetation at the time of the fires. Wildfires in this area were historically uncommon in the early season, but did occur, especially in dry years. Ten-hour and 1,000-hour fuel moistures were 19 percent, and 52 percent, respectively, at the time of the June burn and 7 percent, and 8 percent, respectively, at the time of the October burn. Moisture of the top inch of soil was 24 percent in June and 4 percent in October. Both burns were halted prematurely because objectives were unlikely to be met, with high fuel moisture in June causing too little fuel to be consumed and low fuel moisture in October leading to unpredictable fire behavior.

Range and the Sierra Nevada, and as a result are characterized by lighter precipitation than the Humid Temperate zone to the west (fig. 3). The southwest and eastern portions of the Dry Interior are influenced by the summer monsoon, with two peak times of precipitation—winter and summer (fig. 3). This monsoonal rainfall is often accompanied by thunderstorms. The monsoon typically starts out with more scattered high-based storms, which start fires, whereas the later storms are often wetter (Schroeder and Buck 1970).

Vegetation is strongly associated with precipitation, usually along elevation gradients. Forests consisting of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), or ponderosa pine mixed with Douglas-fir, and white fir (*Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr.) or spruce (*Picea* A. Dietr.) at the higher elevations are found on mountain ranges, whereas the vegetation in the valleys is often composed of shrubs such as sagebrush, or even desert vegetation. Pinyon pines (*Pinus edulis* Engelm.) or junipers (*Juniperus* L.) may be found in between.

Historical fire regime—

In the western and northern areas of this zone, such as the Great Basin, the lightning fire season generally starts in June and runs through September or October (Schroeder and Buck 1970) (fig. 3b). The main fire season is somewhat earlier in areas influenced by the monsoon, with area burned historically peaking in May and June (Grissino-Mayer and Swetnam 2000) (table 2, fig. 3d). These fires are typically ignited by dry high-based thunderstorms that are common this time of year. As the summer progresses, thunderstorms begin to be accompanied by more rainfall, limiting fire spread. Although the fall may be dry enough for fire as well, thunderstorms are less common and thus sources of ignition are fewer. Native Americans also surely contributed to the historical fire regime, and may have burned at times that did not necessarily coincide with peak lightning activity.

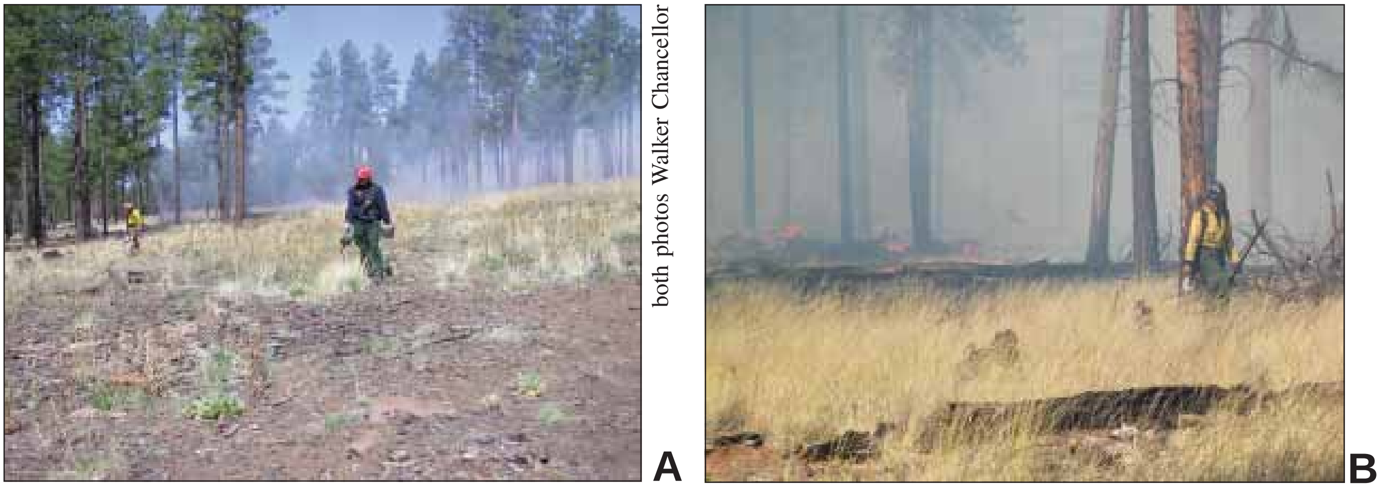
The peak of the historical fire season in parts of the Dry Interior zone not strongly affected by the summer monsoon was similar to the Humid Temperate zone to the west, with most of the fire occurring when most plants were past the peak of growth or dormant, and animals presumably less active. The peak of the historical fire season in areas strongly influenced by the summer monsoon was approximately the time at which trees begin growth for the year. Cool-season grasses in the understory are often actively growing at this time. May and June fires also coincide with bird nesting.

Prescribed fire regime—

Prescribed burns in juniper or pinyon-juniper woodlands of Nevada, as well as forested areas farther east and north, are generally conducted either in the spring or fall (fig. 3b). More days of weather and fuel conditions within the usual prescription conditions occur during the spring (Klebenow and Bruner 1977). Cool conditions in either season moderate fire behavior and reduce crown scorching. However, such prescribed burns typically occur before or well after the typical historical fire season. In areas influenced by the monsoon in the Southwest, the majority of prescribed burns are conducted in the cool conditions of fall (mid-September into December or even later in years without early snow) (Sackett et al. 1996) (fig. 3d). Fuels at this time of year are usually fairly dry, but moister conditions may also occur in some years. Prescribed burns can also be ignited when the weather is cool in early spring. Little prescribed burning is done during the peak historical fire season (late spring to early summer), because windier and drier weather make fire more difficult to control, especially when fuel loading is high (Fulé et al. 2007).

Fall is recommended for the initial prescribed burn after a long period of fire exclusion and fuel accumulation (Sackett et al. 1996). Once fuels have been reduced to near historical levels, the prescribed burning window of opportunity is a bit broader, with good results even when conditions are warmer, such as in the late spring, early fall, or even the summer (Sackett et al. 1996). Summer prescribed burns are possible depending on weather conditions, but ignition is generally limited by the availability of fire crews, which are often on assignment this time of year.

Both early spring and fall prescribed burns occur during the period of plant dormancy for many species (fig. 5). One of the main issues with prescribed burns during these times is that because of the cool conditions, they are often milder and therefore result in less ecological change than historical fires.



both photos Walker Chancellor

Figure 5—Prescribed burns during the (a) early growing season (May 3, 2007), and (b) dormant season (October 17, 2007) at Fort Valley Experimental Forest, Arizona. Understory vegetative growth in the Southwestern United States is influenced by moisture from the summer monsoon.

Fuel Consumption and Fire Intensity

Because of the seasonal nature of precipitation in the West, fuels are typically moister for prescribed burns conducted in spring/early summer or later in the fall, than for prescribed burns conducted in late summer/early fall (Kauffman and Martin 1989, Knapp et al. 2005). As a result, such burns often consume less fuel, are less intense, and are patchier (Kauffman and Martin 1989, Knapp et al. 2005, Monsanto and Agee 2008, Perrakis and Agee 2006). Kauffman and Martin (1989) reported that total fuel consumption ranged from 15 percent in early spring burns to 92 percent in early fall burns at three mixed-conifer forest sites in northern California (fig. 6). Duff moisture (as a percentage of dry weight) was 135 percent in early spring and only 15 percent in early fall.

In the Southwest, conditions at the time of fall prescribed burns are often dry, leading to nearly complete consumption of the forest floor (Covington and Sackett 1992). However, fuel consumption does not differ predictably with season and is often more of a function of time since the last rainfall event; conditions often vary substantially within both prescribed burning periods, and consumption is largely controlled by fuel moisture content.

Many prescribed burns in the Western region are conducted in forested areas where fire has been suppressed for long periods. Because of this, the amount of fuel consumed by burns in either season may be much greater than the amount of fuel typically consumed historically (Knapp et al. 2005). The elevated fuel loading also means that the difference in total fuel consumption and the resulting fire intensity among burns in different seasons may be inflated compared to what was once the case.

Ecological Effects of Burning Season in Forested Ecosystems

Trees

Differential tree mortality among burning seasons has been attributed to both phenology (seasonal growth stage) and variation in fire intensity. In a study of ponderosa pine in southwestern Colorado, Harrington (1987) reported mortality of trees in different crown scorch categories after spring (June) and summer (August) prescribed fires conducted during the active growth period, and fall prescribed fires (October) conducted when the trees were already dormant. By comparing trees that experienced similar fire intensity, the effect of phenology could be isolated. Trees with >90 percent of crown scorched were more likely to die after the spring (54 percent) and summer fires (42 percent) than after the fall fires (13 percent). Mortality in trees with crown scorch less than 90 percent was quite low in all seasons. For example, mortality of trees with 67 to 89 percent of the crown scorched was 12, 11, and 0 percent, for spring, summer, and fall burns, respectively. When crown scorch was 66 percent or less, the differences in mortality between seasons was not statistically significant. Because the goal of operational prescribed burns is generally to avoid high levels of scorching of larger trees, any difference in mortality between burning seasons may end up not being biologically meaningful. Indeed, ponderosa pines greater than 12 in diameter, which managers are most likely to want to retain, had equally low (≤ 8 percent) mortality rates after fires in all three seasons (Harrington 1993). Differential mortality among seasons was only witnessed for small size classes. Younger trees of shorter stature are more likely to have high levels of crown scorch, and as the objective of prescribed burns is often to thin the forest of younger or suppressed trees, greater mortality of this size class with early or mid-season burns may be advantageous.

In a study of interior Douglas-fir, Ryan et al. (1988) noted that overall mortality was nearly the same for spring and fall prescribed burns (53 percent vs. 47 percent, respectively), although the spring burns were more intense. Fire damage measures (proportion of cambium killed and crown scorch) were predicted to contribute much more strongly to mortality than the burning season.

Several recent prescribed fire studies (Perrakis and Agee 2006, Sala et al. 2005, Schwilk et al. 2006, Thies et al. 2005, all covered in the following paragraphs) reported at least a tendency for higher tree mortality after fall burns. Most, if not all, of the sites studied had not burned in some

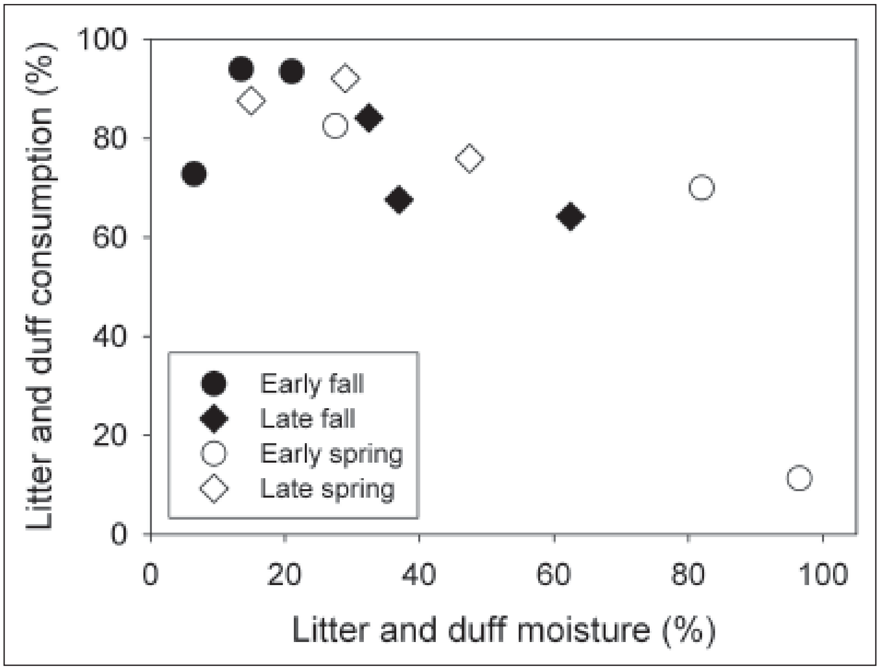


Figure 6—Average litter and duff consumption at varying litter and duff moisture levels for burns in the Sierra Nevada, California, conducted at different times of the year. Data from Kauffman and Martin (1989, 1990).

time, and common to all was greater fuel consumption in the fall. Although the spring and early summer burns were conducted during the active growth phase when loss of living material is expected to be more detrimental, it appears that when the difference in fuel consumption between spring and fall burns is substantial (such as after a period of fire exclusion and fuel buildup), the effect of fire intensity may overwhelm the effect of phenology.

Perrakis and Agee (2006) reported higher mortality after fall burns (October) than spring burns (late June) in mixed-conifer forests of Crater Lake National Park without a recent history of fire. Fall burns were conducted when fuels were drier, with burn coverage averaging 76 percent and fuel consumption averaging 52 percent, as compared to 37 percent and 18 percent, respectively, for the spring burns. The authors concluded that the higher mortality was best explained by the greater intensity of the fall burns, which may have overwhelmed seasonal vulnerabilities. Interestingly, an earlier less controlled study of prescribed burning season nearby showed the opposite result (Swezy and Agee 1991). These authors reported mortality of large ponderosa pine after prescribed fires in June, July, and September to be 38 percent, 32 percent, and 12 percent, respectively. Although the effect of burning season was significant, the relative importance of variables showed fire severity measures (scorch height and ground char) explained more of the variation in mortality than burning season. The prescribed fires in this study were conducted over a period of two decades, with all but one of the late-season burns occurring in the 1970s and most of the early-season burns occurring in the 1980s. Therefore, mortality results could have been confounded with longer term climatic patterns. It is also possible that fuel consumption differences among seasons were not as great as for the fires studied by Perrakis and Agee (2006).

In a large replicated study of burning season in mixed-conifer forests of the Southern Sierra Nevada, Schwilk et al. (2006) did not find any significant differences in tree mortality between early season (June) and late season (September to October) prescribed burns (fig. 7). The June burns were conducted shortly after trees had initiated growth (bud break), whereas the September/October burns were conducted after visual evidence suggested growth had ceased for the year. The historical fire-return interval in

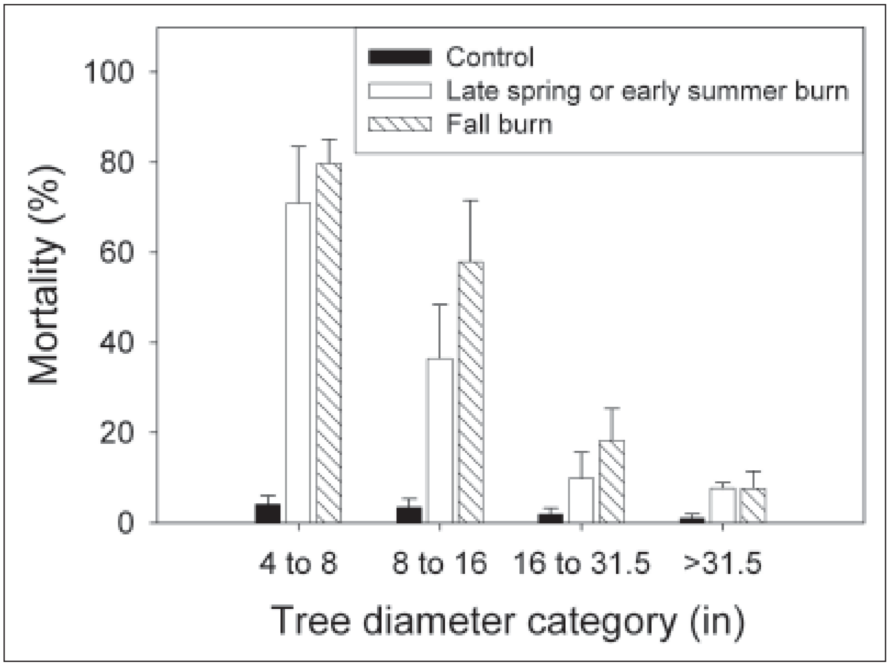


Figure 7—Mortality of fir (white fir (*Abies concolor*) and red fir (*Abies magnifica* A. Murr.)) trees in four size classes 2 years after prescribed burns in the late spring/early summer and in the fall at Sequoia National Park, California. This large-scale season-of-burning experiment was initiated in 2001 as part of the National Fire and Fire Surrogate study. Although mortality of the 4- to 8-inch and 8- to 16-inch size category trees with burning differed from background mortality in the unburned control, difference between burning-season treatments was not significant. Data based on Schwilk et al. (2006).

the study area was approximately 27 years (Schwilk et al. 2006), but as a consequence of fire exclusion, hadn't burned for over 125 years, and fuel loading was therefore very high. Because of higher moisture levels, the June burns consumed less of the available fuel; however, total amount of fuel available and consumed was likely far above historical levels for burns in both seasons. There was a tendency for higher mortality in the small tree size classes with the late-season burns (greater fuel consumption) than the early-season burns (less fuel consumption), although the differences were not statistically significant. Despite variation in fuel consumption, average crown scorch height and bole char height did not differ between seasons. For each tree size category, differences in mortality appeared to be largely a result of local variation in fire intensity, with little effect of fire season.

In a study conducted in eastern Oregon, ponderosa pine trees experienced less mortality after spring (June) burns (11 percent) than after fall (October) burns (32 percent) (Thies et al. 2005). The amount of fuel consumed was not quantified. However, the fuel at the base of the trees burned more completely, and a higher proportion of trees experienced crown scorch with the fall burns than spring burns. The apparently greater fire intensity with fall burns appeared to have a stronger impact than effects of phenology, which would have been expected to cause greater mortality with the spring burns. A tree mortality model developed using data from this study and burns in northern California did not find burn season to be a predictor variable, with approximately the same level of delayed mortality expected for a given level of fire damage, regardless of the burn timing (Thies et al. 2008).

Other studies include Sala et al. (2005), who found that physiological performance (net photosynthetic rate, stomatal conductance, and xylem water potential) and wood growth of ponderosa pine did not differ between trees in units burned in the spring or the fall. As is often the case with prescribed burns in the Western United States, the spring burns consumed less fuel than the fall burns.

Comparing the outcome of a spring wildfire (May), a summer wildfire (late June), and a fall prescribed fire (September) in Arizona, McHugh and Kolb (2003) reported that mortality in all seasons was greatest on trees most heavily damaged by fire. Total tree mortality averaged 32.4 percent, 13.9 percent, and 18.0 percent in spring, summer, and fall, respectively. Although the spring wildfire occurred prior to bud break, conditions were dry and crown scorch was also greater than for the other fires (55.3 percent) (McHugh et al. 2003). The summer fire burned during the active growth phase of trees but scorched the least canopy of the three fires (27.3 percent) (McHugh et al. 2003). Crown scorch for the fall prescribed fire was intermediate, as was the mortality. Total crown damage and bole char explained much more of the variation in tree mortality than season of the fire (McHugh and Kolb 2003).

Secondary mortality in many western conifer species is often attributed to bark beetles. Bark beetle attack probability is usually correlated to degree of tree injury, which may differ among burning seasons as a result of differences in fire intensity. The timing of fire may also influence bark beetle populations directly (Schwilk et al. 2006). Bark beetles are known to be attracted to volatiles released from tissues injured by heat (Bradley and Tueller 2001, McHugh et al. 2003). Bark beetle activity had likely already ceased for the season by the time of the fall prescribed burning period. By the time bark beetles become active again the following spring, volatiles produced by injured tissue may have already subsided. Early-season burns, on the other hand, typically coincide with increasing bark beetle flight activity (Fettig et al. 2004), and there is some concern that this could lead to a buildup of bark beetle numbers.

Schwilk et al. (2006) did not find any difference in bark beetle attack probability between June and September/October prescribed burns on pine species, but did note an increase in bark beetle attacks on smaller diameter firs with the earlier burns. Because of the overabundance of small firs in many mixed-conifer forests following logging and fire exclusion, favoring pines over firs is a management goal of many prescribed fire projects. Thus, if causing greater mortality of small firs relative to small pines is an objective, early-season burns may prove advantageous.

In a survey of bark beetle populations following fires in ponderosa pine forests in Arizona, McHugh et al. (2003) found some differences in attack probabilities among seasons, with a May wildfire leading to greater probability of attack (41 percent), compared to a June wildfire (19 percent), or a September prescribed burn (11 percent). The May wildfire also was the most intense, causing the most crown scorch, and overall attack probability was associated with degree of fire-caused damage. However, attack probability was somewhat greater for the June fire than the September prescribed burn although crown scorch was less. This suggests that the timing of fire relative to periods of bark beetle activity may play a role. Still, studies to date all point to degree of crown damage being the overriding contributing factor to bark beetle attack, regardless of season of burn.

Understory Vegetation

Steele and Beaufait (1969) found no important differences in the cover of understory vegetation between areas treated with either early- or late-season broadcast burning treatments in Montana. In southwestern ponderosa pine systems, fall prescribed burns often lead to a greater abundance of understory vegetation such as cool-season perennial grasses. Sackett and Haase (1998) suggested that burning during the natural fire season (May through early July) might lead to an even greater increase in grass production, because grasses that are growing and green are less readily consumed by such fires. In addition, seed heads are possibly less likely to be consumed with late spring/early summer burns than with fall burns (Sackett and Haase 1998). Certain species that grow later in the year, such as the warm-season grass mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc.) appear to be negatively affected by repeated fall burns (Laughlin et al. 2008).

Kauffman and Martin (1990) reported much higher shrub mortality after early fall burns (high fuel consumption), than after spring burns (low fuel consumption). Overall, the greater the consumption of fuel, the greater mortality of shrubs, regardless of burning season. Variability in mortality was also seen among sites within a burn season treatment, with lesser mortality at sites that contained the least fuel, and therefore experienced lower total heat flux upon burning. These authors hypothesized that shrub phenology at the time of fire may have also played a role, albeit a lesser one. At one site, mortality of black oak was 31 percent following early spring burns conducted prior to bud break and initiation of growth, and 55 percent following late spring burns conducted during the period of rapid growth following bud break, although fuel consumption with these two burn treatments was nearly identical (77 percent for early spring vs. 79 percent for late spring burns, respectively). Differences in plant carbohydrate storage among seasons may have been one mechanism for this observed difference (Kauffman and Martin 1990). However, variation in mortality between seasons could also be attributed to factors other than phenology. For example, soil moisture at the time of early spring burns was nearly double that of the late spring burns (Kauffman and Martin 1989, 1990), which may have also reduced the heat flux into the soil.

For fire-following species, differential response among burning seasons is also sometimes evident in the seed germination phase. Enough heat is required to scarify the seed, but not so much that the seeds are killed (Knapp et al. 2007, Weatherspoon 1988). Depth of lethal heating, which is affected by both the amount of fuel consumed and the moisture content of the soil, may determine how many seeds are available to germinate. Kauffman and Martin (1991) found that wet heat, simulating a heat pulse under moist soil conditions, was more effective for scarifying seeds of shrubs than dry heat, simulating fire in the fall when soils were dry. The dry heat actually resulted in higher seed mortality. In another study in an area with low fuel loading (10 years after a fire), Harrod and Halpern (2009) found that fall burns stimulated germination of long-sepaled globe mallow (*Iliamna longisepala* (Torr. Wiggins)), while spring burns did not. It is possible that the soil heating generated by spring burns was, in this case, insufficient.

Knapp et al. (2007) reported that understory vegetation in a mixed-conifer forest in the Sierra Nevada of California was resilient to prescribed fire conducted in either late spring/early summer (June) when plants were in the midst of active growth, or in the fall (September/ October) when most plants were nearly to fully dormant. Several years after treatment, total plant cover and species richness in the spring/early summer- and fall-burned plots did not differ significantly from each other or from an unburned control. However, there was a difference in the rate of vegetation recovery between burn season treatments. In the season immediately following the burns, cover was initially reduced relative to the control in the fall burn treatment, but not the spring/early summer burn treatment. Furthermore, certain species, particularly ones most common under the forest canopy where surface fuel loading is expected to be the highest, such as whiteveined wintergreen (*Pyrola picta* Sm.), were reduced in frequency by late-season burns but not early-season burns. Because the late-season burns were conducted when the fuels and soils were drier, the greater fuel consumption and heat penetration into the soil (see "Soils" section) may have killed more of the underground structures than the late spring/early summer burns. Late-season burns also covered a larger proportion of the forest floor, leaving fewer undisturbed patches. Vegetation change was associated with variation in fire severity, and the authors concluded that effects on vegetation suggested a greater dependency on amount of fuel consumed and fire intensity than on plant phenology.

In a longer term study of understory vegetation response to burning season in a ponderosa pine forest of eastern Oregon, Kerns et al. (2006) reported no significant difference in native perennial forb cover 5 years after early-season (June) and late-season (September/October) prescribed burns. The June burns occurred during the active growth phase of many understory plant species, whereas the September/October burns occurred when most species were dormant. Harrod and Halpern (2009) also found few effects of either spring (May) or fall (October) prescribed burns on mature individuals of two native herbaceous perennial plant species. In the Kerns et al. (2006) study, exotic species, which often thrive with disturbance, were more frequent following the higher severity (as evidenced by greater bole char and higher tree mortality) late-season burning treatments. Exotic species were also concentrated in patches within burns where local severity was the highest. This study is another example of plants responding more strongly to fire intensity and degree of environmental change than the plant phenology at the time of the fire. A similar trend, with greater numbers of exotic species in plots that burned at higher severity in the fall was noted by Knapp et al. (2007); however, in this latter study, the difference was too small to be statistically significant.

By timing prescribed burns for when plants are most vulnerable, fire can be used to control vegetation or target certain species. Harrington (1985) reported that a Gambel oak (*Quercus gambelii* Nutt.) understory of a ponderosa pine forest resprouted vigorously following single prescribed burns conducted in the spring (June), summer (August), or fall (October). The spring burns occurred 3 to 4 weeks after bud break and leaf emergence, the summer burns occurred while vegetation was still actively growing, and the fall burns occurred after plants had gone dormant and leaves had fallen. A second summer fire 2 years later significantly reduced the frequency of resprouting stems, whereas spring and fall fires did not. However, differences in sprout number among treatments were relatively small. The effect was attributed to reduced root carbohydrate reserves in the summer following a second flush of growth, which suppressed the energy available for resprouting following fire (Harrington 1989).

Several studies have been conducted to investigate whether burning in different seasons might be used to control bear clover (*Chamaebatia foliolosa* Benth.), a vigorous highly flammable shrub with rhizomatous roots that can compete strongly with conifer seedlings. Fires in May (prior to the growing season) and October (after the growing season) stimulated growth of *C. foliolosa* relative to the control, whereas prescribed burn in July (mid growing season) resulted in growth comparable to the control after 2 years (Rundel et al. 1981). Weatherspoon et al. (1991) reported that a single prescribed burn in any season (May through October) was ineffective for reducing the cover of this plant, but a second treatment during the growing season, where all tops were removed, simulating the effect of a followup prescribed burn, did slow regrowth. Studies on chamise (*Adenostoma fasciculatum* Hook. & Arn.) also have shown top removal during the growing season to slow regrowth compared to top removal during the dormant season (Jones and Laude 1960). Results suggest that carbohydrate reserves at the time of treatment may play a role in regrowth.

Burning in different seasons has been attempted as a means of controlling shrubs with seed banks stimulated to germinate by fire (such as *Ceanothus* sp. or Manzanita (*Arctostaphylos* sp.)). Hotter burns that consumed the entire duff layer under dry soil conditions in the fall killed more seeds by pushing critical temperatures deeper into the soil than burns in the spring that consumed less fuel (Weatherspoon 1988). However, so many seeds were found in the soil that sufficient seeds remained to regenerate a vigorous shrub layer no matter the burn season (Weatherspoon 1988).

Soils

Soil heating during the process of combustion can cause biological and physical changes such as root mortality or increased water repellency. The magnitude of change depends at least partially on three factors that may differ with burning season: amount of fuel consumed, duration of combustion (residence time), and soil moisture at the time of burning.

Fuel moisture largely dictates how much organic material is consumed, and therefore the residence time of combustion. Likewise, the extent to which the heat penetrates into the soil is determined by soil moisture (Campbell et al. 1995). Water has a high specific heat and therefore substantial energy is required to drive off the moisture before the temperature of that soil will exceed 212 °F, the boiling point of water. Because of this, moist soils are much less likely to heat up than dry soils. Soils are largely protected from excessive heating, even under high fuel loading conditions if they contain sufficient moisture (Busse et al. 2005, Frandsen and Ryan 1986, Hartford and Frandsen 1992). Plant roots are killed starting at soil temperatures between 118 and 129 °F, microbes are killed between 122 and 250 °F, and buried seeds have been reported to die at temperatures between 158 and 194 °F (Neary et al. 1999). Busse et al. (2005) found that the temperature at 1-inch depth in the soil below a laboratory burn that consumed a very high load of masticated wood chips (69.9 tons/ac) reached a maximum of 595 °F in dry soils and only 241 °F in moist soils.

Effects on soil physical properties and soil biota largely mirror the intensity and severity of the fire (Neary et al. 1999). In a study in mixed-conifer forest of the Southern Sierra, California, Hamman et al. (2008) reported soil temperature, moisture and pH, plus mineral soil carbon levels and microbial activity following late spring/early summer (June) prescribed burns to be generally intermediate between fall (September/October) prescribed burns and unburned controls. A similar result was reported from ponderosa pine forests in eastern Oregon, with October prescribed burns decreasing soil carbon and nitrogen, whereas June burns had little impact (Hatten et al. 2008). The magnitude of effects for both the Hamman et al. (2008) and Hatten et al. (2008) studies were in line with the greater fuel consumption and intensity of the late-season burns. In the same study plots as Hatten et al. (2008), Smith et al. (2004) found that the October prescribed burns significantly reduced fine root biomass to a depth of 4 in and depressed the number of ectomycorrhizal species, relative to units burned in June. Fine root biomass and ectomycorrhizal species richness following the June burns did not differ from the unburned control. Soil moisture values were not provided, but given the rainfall patterns, it was likely considerably higher at the time of the June burns. Other studies corroborate findings of a greater loss in soil microbes following burns when soils were dry than when soils were moist (Klopatek et al. 1988, 1990), corresponding to the amount of soil heating. Filip and Yang-Erve (1997) reported a reduction in root disease causing fungi following fall burns but not spring burns; however, soil moisture and fuel consumption were not reported.

In addition to changes within the soil, other variables that frequently differ with burning season may influence soils indirectly through erosion. Such variables include the percentage of the soil surface burned, and the depth of burn (how much of the duff layer is removed). Burns when soils and the fuels in contact with those soils are moist tend to be patchier (Knapp and Keeley 2006). These unburned patches may act as refugia from which fire-sensitive organisms such as soil ectomycorrhizae can recolonize burned areas (Smith et al. 2004), or act as barriers to soil erosion (Knapp et al. 2005). Johansen et al. (2001) reported an exponential increase in the amount of erosion once the percentage of the forest floor burned exceeded 60 to 70 percent, presumably because as the percentage increases, burned patches coalesce into larger and larger areas, leaving fewer unburned patches at a scale necessary to capture sediment. Under the high fuel loading and high fuel continuity in landscapes common today, many prescribed burns cover a greater percentage of the landscape than this, particularly ones conducted when fuel conditions are dry.

Whether changes to soils as a result of fire are beneficial or detrimental will depend on the burn objectives. Burns at times of the year when soils (and fuels) are still moist may limit the amount of soil heating and leave a greater amount of duff unconsumed, which could reduce the threat of erosion. However, burns at drier times of the year may be necessary if bare mineral soil exposure is desired to produce an adequate seedbed for species that don't germinate well through a layer of organic material, or if the objective is to heat scarify deeply buried seeds of fire-following species.

Wildlife

Wildlife populations may be affected by fire either directly by heat and flames, or indirectly through modification of the habitat. In environments where fire was historically common, there is little evidence that fires falling within the range of historical intensities cause much direct mortality of wildlife (Lyon et al. 2000b, Russell et al. 1999). Most animals have presumably developed behavioral adaptations for escaping fire that enable population persistence, and many, in fact, benefit from the habitat modifications resulting from fire.

In the Western United States, most species have already successfully produced young by peak fire season in late summer to early fall. There has been some concern that prescribed fires ignited outside of the season when historical fires were common might do harm to wildlife populations, especially for species with poor dispersal or species that raise offspring in locations that are most likely to burn. For example, small mammal young may be more vulnerable to early-season fire, because of lack of mobility prior to maturity (Lyon et al. 2000a). Many of these species have high reproductive rates, however, and recovery is likely rapid.

Ground-nesting birds could be killed prior to fledging (Reinking 2005) and forest floor arthropods in the egg or larval stages may be more vulnerable to loss (Niwa and Peck 2002). Amphibians are also likely to be more active with the moister conditions under which prescribed fires are typically conducted (Pilliod et al. 2003). On the other hand, amphibians tend to live in the moister microsites that are least likely to burn in prescribed fires, especially in the early season (Lyon et al. 2000a). In the Southwestern United States, the peak historical fire activity occurred earlier, during the spring and early summer, when effects on wildlife might be more severe. In this case, the impact of prescribed fires in the spring or fall would be expected to be less than those in the main historical fire season.

Much of the information about effects of season of prescribed fire on wildlife in the Western United States is anecdotal or has lacked a direct comparison among seasons. For example, many studies compared early-season fire with no fire, or late-season fire with no fire. What has been written generally has found very little influence of fire season on populations. Wildlife may be affected by fire both through direct mortality or habitat alteration (Lyon et al. 2000b), but the latter appears to play a larger role. In some cases, the magnitude of change in populations or communities has been associated with measures of fire severity, which may differ with burning season. For example, dark-eyed juncos (*Junco hyemalis*) often choose nest sites in unburned patches within prescribed fire units (Sperry et al. 2008), and burns in early season when fuels are moist are more likely to create such unburned islands.

One of the most rigorous evaluations of burning season to date reported similar effects of early (June)- and late (September/October)-season prescribed burns on small mammal populations in a mixed-conifer forest of the Southern Sierra Nevada (Monroe and Converse 2006). Although the June burns occurred during the small mammal breeding season, the burns consumed less fuel and were therefore less intense than later burns under dryer conditions. June burns were also patchier (Knapp and Keeley 2006), leaving more potential refuges and habitat such as coarse woody debris where animals could have escaped fire. Most of the variation in population numbers in the Monroe and Converse (2006) study was attributed to year-to-year differences in food availability tracking the yearly seed production cycles of the overstory trees. This further suggests that small mammals respond more strongly to habitat conditions, including those created by the fires, than to the burning season.

As is the case with small mammals, the effect of early season prescribed fire on forest floor arthropods might also be expected to differ with the life cycle of the organisms because of seasonal vulnerabilities. However, using the same plots as the Monroe and Converse (2006) study, Ferrenberg et al. (2006) reported no significant differences in forest arthropod community structure between the two burning season treatments. Fire influenced the arthropod community, reducing abundance but increasing diversity, but changes appeared to be mediated by habitat alteration (amount of litter and duff, coarse woody debris, vegetation), and these habitat variables differed much more strongly between the control and burn units than between the June and September/October burning treatments. Changes in the June burn treatment were generally intermediate between the control and September/October burn treatments.

Adult birds are highly mobile and easily escape prescribed burns. Early-season burns may cause some direct mortality of young, particularly for species nesting on the ground, but the ultimate impact on bird populations requires a longer term view. When nests are lost, many species will renest (Reinking 2005). In addition, like many wildlife species, bird populations are capable of responding rapidly, with population size limited by food availability and shaped by habitat changes.

Unfortunately, experimental design flaws limit the inference of many studies of the response of birds to fire (Finch et al. 1997). Published literature comparing the effects of prescribed burns in different seasons on birds are not available for the Western United States. Preliminary data from the Sequoia National Park study on burning season suggest that effects one to three seasons after the burns were minimal.[3] Population sizes of the eight most common species observed with point counts and bark foraging surveys did not differ significantly between burning season treatments. Too few nests could be located to investigate direct mortality from the June burns.

Besides direct mortality, another possible short-term impact of spring or early-summer prescribed burns is a temporary drop in food availability or cover because understory vegetation in these systems may not resprout until the following year. It is possible that lack of food could reduce reproductive success. The longer term responses of many bird species are thought to be due primarily to structural changes of vegetation or changes to food resources, as affected by fire severity (Huff and Smith 2000, Kirkpatrick et al. 2006). For example, foliage gleaners typically decline in abundance when more of the tree crowns are lost to scorch, and woodpeckers increase in abundance when fire-damaged trees are attacked by bark beetles, an important food source (Huff and Smith 2000). Variation in outcomes among prescribed burns early or late in the season would therefore mainly be expected if crown scorch or mortality of vegetation differed.

Ecological Effects of Burning Season in Chaparral and Grasslands

Chaparral

Extensive chaparral shrublands are found in nondesert areas of central and southern California and historically burned over a range of intervals, from every few decades in montane sites with more frequent lightning, to 100 years or more in areas closer to the coast. Most of the acres were burned in late summer through the fall, often in high intensity stand-replacing events (Keeley and Fotheringham 2001) (fig. 8). Because of frequent human-caused ignitions and seasonal hot and dry winds, the fire regime remains similar today, despite fire-suppression efforts. Plant species have evolved means of persisting under such burning conditions, from resprouting of lignotubers, to seeds requiring substantial heating or exposure to chemicals found in char for germination (Kauffman 1990, Keeley 1987, Odion 2000).

Prescribed burns are sometimes used to reduce fire hazard in chaparral, but such burns are controversial (Keeley 2002, Keeley and Fotheringham 2001, Parker 1987a). To avoid burning during times when the vegetation is most volatile and conditions are conducive to rapid fire spread, many prescribed burns are conducted in the winter or spring, outside of the historical fire season. Live fuel moisture is typically higher and soils considerably wetter at such times of the year, than would have been the case for historical fires (Beyers and Wakeman 2000). As a result, prescribed burns are usually considerably less intense than the wildfires that this vegetation evolved with. Observations suggest that vegetation response to such prescribed burns often differs from response to natural wildfires, with reduced germination of certain herbs and potentially altered species composition (Le Fer and Parker 2005; Parker 1987a, 1987b). For example, *Ceanothus* L. seeds require heat for germination (Keeley 1987), and abundance of seedlings has been shown to be greater following fall prescribed burns than spring burns (Biswell et al. 1952, Gibbens and Schultz 1963).

Parker (1987a) and Le Fer and Parker (2005) attributed the reduced germination of some obligate seeding chaparral species following spring prescribed burns to higher seed mortality upon heating. It was thought that seeds are particularly vulnerable when soils are moist and seeds full of water, compared to when seeds are dry. Interestingly, species producing hard seed with dormancy (such as

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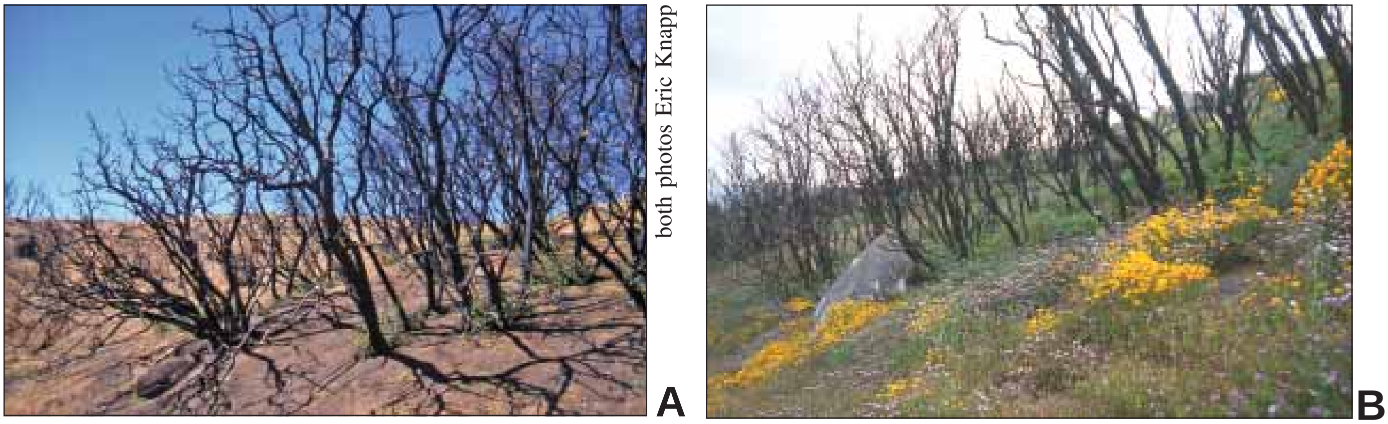
[3] Farris, K.; Zack, S. Unpublished data.



both photos Eric Knapp

Figure 8—Chaparral vegetation of the Western United States typically burns in high-intensity stand-replacing fires, and many plant species possess adaptations to persist with such a fire regime. Intensity of prescribed burns is often less than that of wildfires, which could affect the abundance of herbs and shrubs with seeds that are stimulated to germinate by heat. Recovery of chaparral and herbaceous species after the McNally Fire, southern Sierra Nevada, California, (a) March 2003, 7 months after the fire, and (b) late May 2003, 9 months after the fire.

Ceanothus spp.) that do not imbibe water until dormancy is broken, were not differentially affected by heating under moist or dry conditions (Le Fer and Parker 2005). Given that heat penetration is limited when soils are moist (Busse et al. 2005, Frandsen and Ryan 1986), it is also possible that the soil heating under prescribed burning conditions typical for this vegetation type may be insufficient to scarify seeds of hard-seeded species (Beyers and Wakeman 2000). However, Beyers and Wakeman (2000) reported no decline in numbers of shrub seedlings or herbaceous species germinating from seed following late spring prescribed burns (May) as compared to fall (October) wildfire. Although this result might seem contrary to the work of Parker (1987b), the late spring prescribed burns in the Beyers and Wakeman (2000) report were likely of higher intensity, closer to the fire intensity expected with historical wildfires. Soil moisture was likely also less.

Out-of-season burns have the potential to reduce the length of the growing season, and this could also potentially influence seedling survival.[4] Chaparral shrubs are typically actively growing throughout the winter rainy season—a seedling might have 6 months to grow after germination following a typical fall wildfire, whereas a winter or spring burn would considerably shorten the time to establish prior to the summer dry period. With less time to grow and put down deep roots, smaller seedlings may be less likely to survive.

Reported responses of mature shrubs to burning season have been variable. Shoot growth for resprouting chamise (*Adenostoma fasciculatum* Hook. & Arn.) was not found to be affected by prescribed burn season (Radosevich and Conard 1980). Beyers and Wakeman (2000) also did not note differences in mortality of resprouting shrubs with spring or fall burns. Conversely, Parker (1987) found that more than 70 percent of chamise plants had died one or two years after spring burns, while nearly all plants successfully resprouted after early fall burns. Higher mortality with spring burns was thought to have been due to the timing of fire in relation to periods during which carbohydrate storage is lowest (Jones and Laude 1960).

The bottom line is that the potential for shifts in the plant community exists when the heat generated by prescribed burning is dissimilar to what would have been experienced with the fire regime that species evolved with. Seeds of species requiring heat to germinate are dependent on receiving enough to break dormancy, but not so much that they are killed. Seeds of species requiring chemical (charate) cues rather than heat to germinate should not be

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[4] Keeley, J.E. 2008. Personal communication.

as strongly affected by fire season, unless they are killed by excess heat. Excess heat is likely to be less in the winter or spring, when soils are moist. Thus, winter or spring burning might be expected to favor species with charate-stimulated seeds, whereas late summer or early fall burning may create opportunities for a greater mix of species with different strategies. Biswell et al. (1952) suggested that some fall management burns, during the natural fire season, may be necessary to perpetuate *Ceanothus*, the seeds of which require heat to germinate.

Western Grasslands

Many western grasslands are highly altered as a result of nonnative species invasion. Rather than fuel reduction, the objective of prescribed burning is frequently to reduce the cover of nonnative species so that more desirable native species may flourish. Such burns are usually timed for periods where the nonnative species targeted may be more vulnerable to fire than the native species (DiTomaso et al. 2006, Meyer and Schiffman 1999, Pollak and Kan 1998). Prescribed burns are likely to be most effective at reducing a target species if the seeds of that species are still immature and on the plant, whereas seeds of desirable species have dispersed to the ground where they may more readily escape the heat of fire (DiTomaso et al. 2006). For example, early summer prescribed burns have been effective for controlling yellow star-thistle (*Centaurea solstitialis* L.) (DiTomaso et al. 1999)—burns occurred when this late-flowering annual still contained immature seeds, but much of the associated vegetation had senesced. Controlling target herbaceous species with fire is likely to be more effective in grasslands than many other vegetation types found in the West, because of the relatively high importance of annuals in this vegetation type. Herbaceous perennial species that emerge from underground structures are typically more difficult to kill with fire.

Parsons and Stohlgren (1989) followed vegetation in grasslands dominated by nonnative species that had been burned one, two, and three times in successive years in the spring (mid June, when grass had dried enough to burn, but prior to the period when such grasslands would have normally burned historically), and in the fall (late October or early November, at the very end of the historical fire season). Although fire in both seasons reduced the number of nonnative grass species and increased the number of forb species, fire in the fall favored nonnative forbs, whereas fire in the spring favored native and nonnative forbs equally. Meyer and Schiffman (1999) compared late spring (June), fall (September), and winter (February) burns, and reported that late spring fires suppressed non native annual grasses more so than fall burns, presumably because grass seeds were not completely mature at the time of the late spring burns and therefore more vulnerable to being killed by fire. Winter burns were less intense and much less effective at altering nonnative grass cover than either spring or fall burns. Therefore, both phenology and intensity differences among burning seasons appeared to have played a role in how grassland vegetation was affected.

Owing to the presence of nonnative species, the amount of fuel consumed and the nature of the fire may differ from historical fires in some cases. However, because grassland fuels are fine and dry quickly, the difference in moisture and therefore consumption and aboveground fire intensity between different burning seasons may not often be as substantial as in forested ecosystems. Thus, with the confounding effect of fire intensity lessened, differences among seasons may more readily be attributed to timing of the fire in relation to plant phenology.

Much more has been written about ecological effects of burning season in grasslands from the Great Plains, which may apply as well. This information is contained in chapter 4—the Central region.

Key Points–Western region

- The effect of prescribed burning season appears to be relatively minor for many of the species that have been studied.
- Although stage of plant growth (phenology) at the time of prescribed fire may have some influence on the community trajectory in forested vegetation types, it appears that the intensity and resulting severity of the fire often has a greater impact. This is likely to be especially the case in forests that contain heavy surface fuel loads, where fuel moisture differences among seasons can lead to substantial differences in consumption.
- In chaparral vegetation, prescribed burns conducted at times of the year with higher soil and fuel moistures are often considerably less intense and may not stimulate the germination and growth of some species that are adapted to the historical regime of high-severity fire.
- In predicting outcomes of prescribed burning, it may be useful to compare the prescribed fire intensity and severity to historical intensity and severity. Burning prescriptions for producing historical or near-historical intensity and severity could then be developed.
- Until heavy fuels are reduced to historical levels, out-of-season burns that consume less fuel may be useful for reintroducing fire without causing severe effects.
- A single prescribed burn outside of the historical fire season appears unlikely to have major detrimental impacts. However, the effect of multiple sequential out-of-season burns remains poorly understood.
- Variation in the timing of prescribed burns will reduce chances of selecting for certain species, thereby helping to maintain biodiversity.

Implications for Managers

The published literature on season of burning in western ecosystems indicates that most species are quite resilient to fire in any season. The majority of plants in forested vegetation types here are perennial; loss of one season's growing structures in long-lived or readily resprouting herbaceous species appears to have limited effects over the long term. In wildlife studies, the large amount of year-to-year variability in population sizes caused by non-fire factors makes detecting seasonal effects particularly difficult.

All else being equal (fuel consumption, fire intensity, etc.), evidence suggests that certain organisms might be somewhat more affected by burns during times of peak growth or during the breeding season. However, all else is rarely equal. In many areas of the Western United States, fall prescribed burns are generally conducted when fuels and soils are drier, more fuel is consumed, and resulting fire intensity is greater than at the time of spring or early summer burns. Thus phenology or life history stage and fire intensity can be seriously confounded. When the difference in fuel consumption between burns in different seasons is substantial, response of many ecological variables appears to be influenced more by fire-intensity differences than by phenology or life history stage at the time of the fire. When differences in fuel consumption between fires in varying seasons are small or nonexistent, the influence of phenology or life history stage may become more apparent. Another factor that needs to be considered is the fire intensity in relation to likely historical intensity. Most prescribed fire studies in western forest ecosystems have been conducted in areas where fire has long been suppressed and surface fuel loading is uncharacteristically high. Therefore, prescribed burns in many cases consume more fuel than wildfires burning every 10 to 15 years once did. As a result, fire intensity and resulting severity may be somewhat unnatural. In addition, when the total amount of fuel consumed is large, the magnitude of potential differences in fuel consumption among seasons as a result of fuel moisture variation, is also substantial.

If fire effects are driven by differences in intensity among seasons, burning when fuels are moister may be one means of limiting consumption and producing fire effects more similar to those found historically. Higher fuel moisture is more common in the spring or early summer. Limiting consumption may be especially advantageous under conditions of unnaturally high fuel loading. Once fuels have been reduced to closer to historical levels, burning at times of the year with higher fuel moisture may lead to less fuel consumed than was historically the norm (fig. 9a). In this case, prescribed burning may result in less ecological change than desired. Also, once fuels are reduced, the difference in consumption between seasons will likely not be as high, and the effect of phenology or life history stage may become more apparent.

In contrast to forested ecosystems that historically experienced frequent low- to moderate-intensity fire, vegetation types where high-severity stand-replacing fire was the historical norm (chaparral shrublands, for example) may require hotter prescribed burns than is currently common. Prescribed burns conducted under benign weather conditions of the late fall, winter, or spring likely consume less fuel and are less intense than historical fires were (fig. 9b). In addition, soils at the time of many of these burns are generally moist, and heat penetration into moist soils could possibly be insufficient to trigger germination of heat-stimulated seeds of certain hard-seeded fire-following species.

The take-home message is that early-season burns may be a valuable tool for more gradually reducing high fuel loads, especially for the first restoration burn(s) after a period of fire exclusion. Once fuels are reduced to historical levels, early-season burns might then be followed by late-season or a mix of late- and early-season burns. To mimic the historical highly variable fire regime, timing of prescribed burns should ideally also be variable. Shifting the fire regime to entirely spring/early summer growing season prescribed burning when the historical regime consisted of predominantly late summer/early fall dormant season fire (much of the Western United States), or shifting the fire regime to entirely fall dormant-season burning, when the historical regime consisted of late spring/early summer growing-season fire (as in areas of the Southwestern United States influenced by a monsoonal climate), may eventually lead to demonstratable ecological change, even if such change is not apparent today. Areas of the Western United States have generally seen at most three cycles of prescribed burning, and data from other parts of the United States with a longer history of prescribed fire show that numerous burn cycles may be required to dramatically shift community composition. Some of the heterogeneity in the prescribed fire regime will be produced from year-to-year variation in climate alone. A prescribed burn in one year may have entirely different effects than a fire on the same date in another year, as climatic differences can influence the phenology or life history stage.

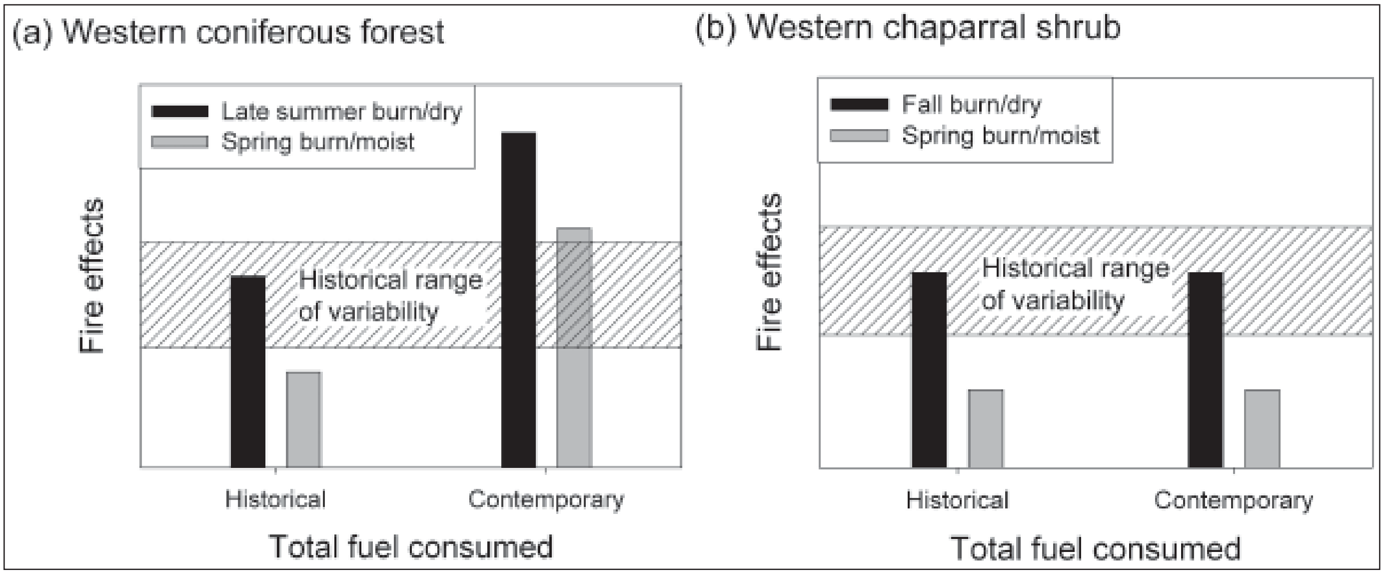


Figure 9—Conceptual diagram showing expected fire effects under typical historical and contemporary fuel loading (dead and live) conditions with prescribed burning in different seasons. Fire effects could include variables such as amount of crown loss, percentage of ground surface burned, or depth of soil heating. (a) In a western coniferous forest where fire has been excluded and fuel loading is unnaturally high, spring burns under moist conditions may consume an amount of fuel and produce fire effects closer to the historical norm than a late summer (or early fall) burn under drier conditions. Once fuels are reduced/restored to historical levels, it is possible that the opposite may occur, with late summer burns resulting in fuel consumption closer to the historical norm and early-season burns resulting in fuel consumption (and fire effects) outside of the historical range of variability. (b) In western chaparral ecosystems, spring burns under moist conditions might be expected to lead to fire effects below the historical range under both historical and contemporary fuel loading conditions. This ecosystem historically most commonly burned in high-severity stand-replacing fires in the late summer or fall, and fuel loading is today, in many areas, not greatly different from historical levels.

Chapter 4: Central Region

The Central region encompasses the major grasslands of the United States from the Rocky Mountains east to the Great Lakes, and from eastern Montana, North Dakota, and western Minnesota in the north, to the Mexican border in Texas in the south (fig. 10). Over much of the area, native grasslands have been replaced by agriculture, degraded by overgrazing, or lost through hardwood encroachment and now cover only a small portion of their former range. Many are so fragmented that the fire regime has been seriously disrupted. Reduction in fine fuels from grazing as well as fire exclusion has limited the role of fire in the maintenance of grasslands.

Climate, Vegetation, and Fire

The Central region vegetation is composed of four major grassland types: shortgrass prairie, northern mixed-grass prairie, tallgrass prairie, and southern mixed-grass prairie, with vegetation influenced by climate, topography, and soil type. Precipitation is light to moderate and generally ranges from 10 to 20 inches in the north and west to 20 to 40 inches in the south and east (Bailey 1980). Airmasses from the Gulf and the Pacific trigger precipitation, but the Pacific airmass is usually dry after passing over several mountain ranges; thus the temperate steppe and substropical steppe grasslands directly east of the Rocky Mountains receive less precipitation and are of shorter stature (northern mixed-grass and shortgrass prairie, respectively) (fig. 10a). The Gulf airmass originates in the Gulf of Mexico, producing higher humidity and greater precipitation, limiting the periods of drought in the mixed and tallgrass prairie (Anderson 1990) (fig. 10c). Stature of the grassland vegetation follows this moisture gradient, with the shortgrass prairie transitioning to the southern mixed-grass prairie and finally into the tallgrass prairie from west to east. Gradients also exist from north to south, with the polar airmass exerting a greater influence to the north. This can result in more continuous snow cover, which reduces periods of flammability.

The dominant grasses in all of the four grassland types are generally perennial with annuals becoming more abundant after disturbance (table 3). Grass composition varies within the three main grassland types. Tallgrass prairies are mainly composed of warm-season grasses (C_4 photosynthetic pathway), whereas mixed and shortgrass prairies are composed of varying quantities of cool-season (C_3 photosynthetic pathway) and warm-season grasses. Many perennial grasses have underground rhizomes or growing points at or below the soil surface, protecting them from fire, drought, and grazing. Forb abundance is dynamic with patches affected by disturbances such as fire and grazing. Hardwood pockets and scattered oak savannas are also found, especially in areas with higher precipitation, along riparian corridors, and where fire has been excluded for long periods. Another vegetation type covered in this chapter is the mesquite savannah found from southeastern Arizona through western Texas (fig. 10b). This system contains more shrubs, which have invaded an arid grassland composed of a mix of cool- and warm-season species. The growth period for many plants here is earlier than in grasslands farther north.

Historically, fire played an integral role in maintaining North American grasslands by stimulating native grass production and impeding succession to woody vegetation (Axelrod 1985; Collins and Wallace 1990; Hulbert 1969, 1988). Unless accumulated litter is periodically removed by fire, grazing, or haying, productivity and plant diversity decline (Anderson 1990, Kansas Natural Heritage Inventory 2007).

Historical Fire Regime

The central grasslands have developed and flourished in an environment with recurrent fire from lightning ignitions and Native American activity (Abrams 1992, Axelrod 1985, Baker et al. 1996, Komarek 1967). Without physical evidence such as fire scars, understanding how often grasslands burned historically is mostly anecdotal. Rate of fuel

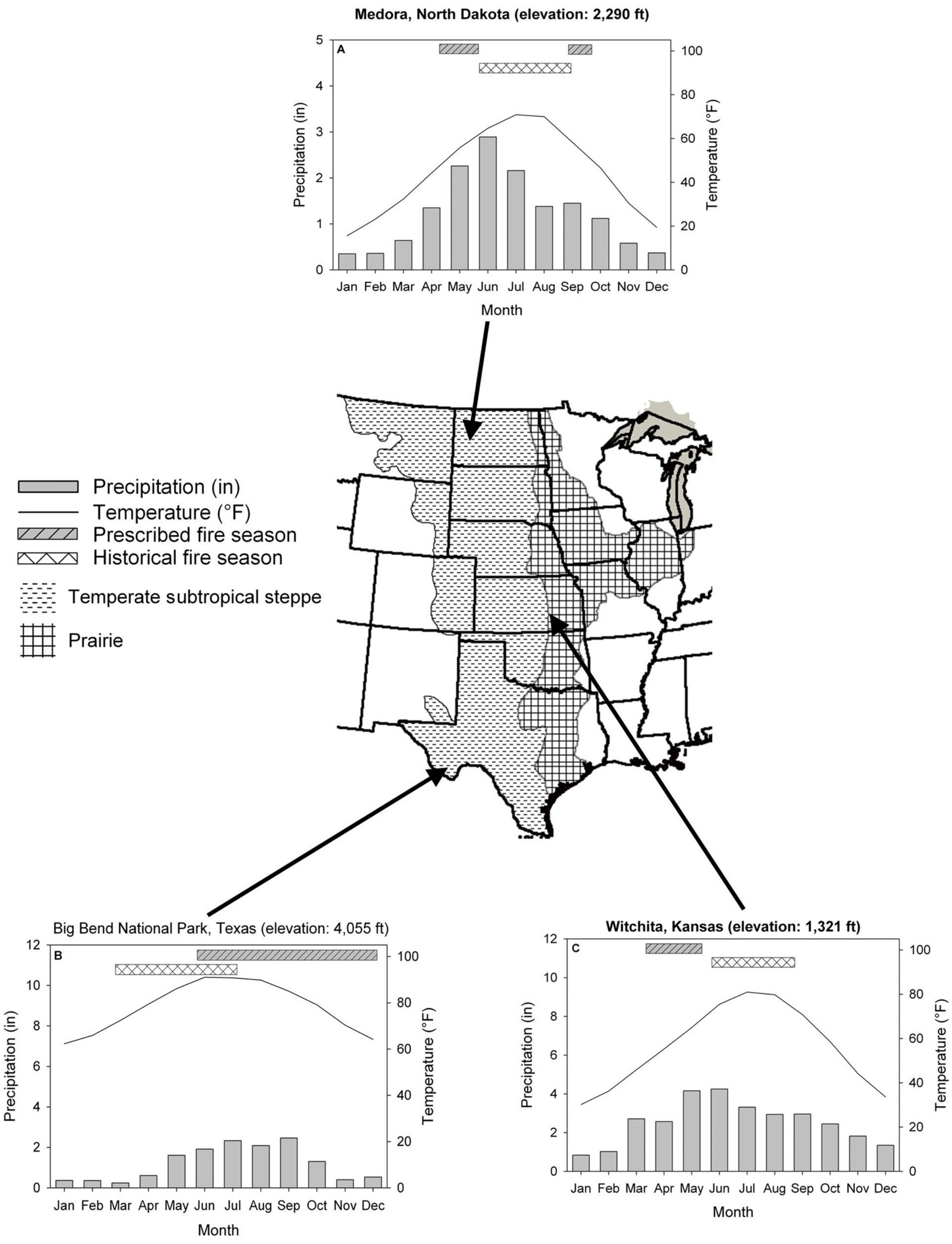


Figure 10—Climographs (monthly average temperature and precipitation) and the average time of the year of the peak historical and prescribed fire seasons from three representative locations within the Central region: (a) Medora, North Dakota; (b) Big Bend National Park, Texas; and (c) Wichita, Kansas. Note that because the timing of anthropogenic fire is poorly understood, the historical fire season reflects mainly lightning-ignited fires. Historical anthropogenic fires likely extended farther into the dormant season.

Table 3—Cool-season (C_3 photosynthetic pathway) and warm-season (C_4 photosynthetic pathway) grasses and forbs commonly found in tallgrass prairies (Howe 1994b)[a]

Cool-season grasses	Warm-season grasses	Cool-season forbs	Warm-season forbs
Texas wintergrass (*Nassella leucotricha* [Trin. & Rupr.] Pohl)	Buffalograss *(Buchloe dactyloides* (Nutt.) J.T. Columbus)	Tall goldenrod (*Solidago altissima* L.)	Richardson's alumroot (*Heuchera richardsonii* R. Br.)
Scribner panicum (*Dichanthelium oligosanthes* (Schult.) Gould)	Indiangrass (*Sorghastrum nutans* (L.) Nash)	Spotted trumpetweed *Eupatoriadelphus maculatus* (L.) King & H. Rob. var. *maculatus)*	Candle anemone (*Anemone cylindrica* A. Gray)
Porcupine grass (*Hesperostipa spartea* (Trin.) Barkworth)	Switchgrass (*Panicum virgatum* L.)	Flowering spurge (*Euphorbia corollata* L.)	Old man's whiskers (*Geum triflorum* Pursh)
Kentucky bluegrass (*Poa pratensis* L.)	Big bluestem (*Andropogon gerardii* Vitman)	Canadian hawkweed (*Hieracium canadense* Michx.)	Purple meadow-rue (*Thalictrum dasycarpum* Fisch. & Ave-Lall.)
Sweetgrass (*Hierochloe odorata* (L.) P. Beauv.)	Sideoats gramma (*Bouteloua curtipendula* (Michx.) Torr.)	Roundhead lespedeza (*Lespedeza capitata* Michx.)	Bluejacket (*Tradescanta ohiensis* Raf.)
Bluejoint (*Calamagrostis canadensis* (Michx.) P. Beauv.)	Witchgrass (*Panicum capillare* L. var. *agreste* Gattinger)	Prairie blazing star (*Liatris pycnostachya* Michx.)	
Reed canarygrass (*Phalaris arundinacea* L.)	Little bluestem (*Schizachyrium scoparium* (Michx.) Nash)	Wild bergamot (*Monarda fistulosa* L.)	
Quackgrass (*Elymus repens* (L.) Gould)	Canada wildrye (*Elymus canadensis* L.)		
	Dropseed (*Sporobolus* R. Br.)		

[a] Cool-season species typically initiate growth and flower before warm-season species.

accumulation in some grasslands is sufficient to carry fire every year, but in others at least 1 year between fires may be necessary for dead fuels to build up (Bragg 1982), particularly if the grassland is grazed.

Historical timing of fire in the central grasslands was dictated by phenology of the vegetation, sources of ignition, and other weather events such as precipitation and wind. Grassland vegetation typically starts growing in spring (March/April), senescing in late summer and fall, or earlier if summer moisture is not available. In the dormant season (fall and winter through early to mid spring), the grassland consists of a higher dry component as thatch. This thatch is more flammable than actively growing vegetation, at least at times without recent precipitation. In northern climates, snow cover limits drying of thatch, and thus the duration of the fire season. In the more mesic grasslands, fuels may also be too moist to burn during the summer growing season, especially during wet years, because of the low ratio of dead to live fuels (Engle and Bidwell 2001). However, Bragg (1982) reported that grasslands with 1 year of accumulated thatch could burn anytime during a March-to-November study of flammability and consumption.

The majority of thunderstorms occur from April to October, and the months in between comprise the typical fire season. Of lightning-ignited fires in grasslands of the Northern Great Plains from 1940 to 1981, nearly all occurred during the growing season from May through September, with 73 percent occurring in July and August alone (Higgins 1984) (fig. 11). Bragg (1982) noted that over two-thirds of lightning fires in grasslands of Nebraska during the years 1971 to 1975 occurred in July and August (fig. 11). Lightning strikes may have ignited fires in advance of precipitation during thunderstorms, but could also have occurred in conjunction with precipitation in areas of higher fuel loading and thatch buildup (Bragg 1982). Native Americans also set fire to grasslands to clear vegetation and to aid with hunting (Anderson 1990, Axelrod 1985, Stewart 2002), and may have done so anytime the vegetation was dry enough to burn—i.e., during both the growing season and the dormant season for vegetation (Reinking 2005). Higgins (1986b) wrote that Native Americans “did not pattern their use of fire with the seasonal patterns of lightning fires,” burning both in the spring and fall dormant seasons, when lightning ignitions were infrequent. In Illinois, the preferred time for igniting grassland fires for hunting purposes was apparently during warm dry spells in the fall, following the first killing frosts (McClain and Elzinga 1994).

Prescribed Fire Regime

Recognition that fire plays an important role in maintaining grasslands has led to widespread use of prescribed fire, initially to promote livestock forage and later for restoration goals such as reduction of woody vegetation. The season of prescribed burning differs, but for operational ease, the majority of burns are typically conducted when vegetation is dormant in the early spring or late fall (Bragg 1982, Ehrenreich and Aikman 1963, Howe 1994b). Spring burning (often late April) is the norm in tallgrass prairie remnants such as the Flint Hills (Seastedt and Ramundo 1990) (fig. 12a and b), which extends from Kansas into northeastern Oklahoma. Fire at this time of year is thought to be most beneficial to warm-season perennial grass species that

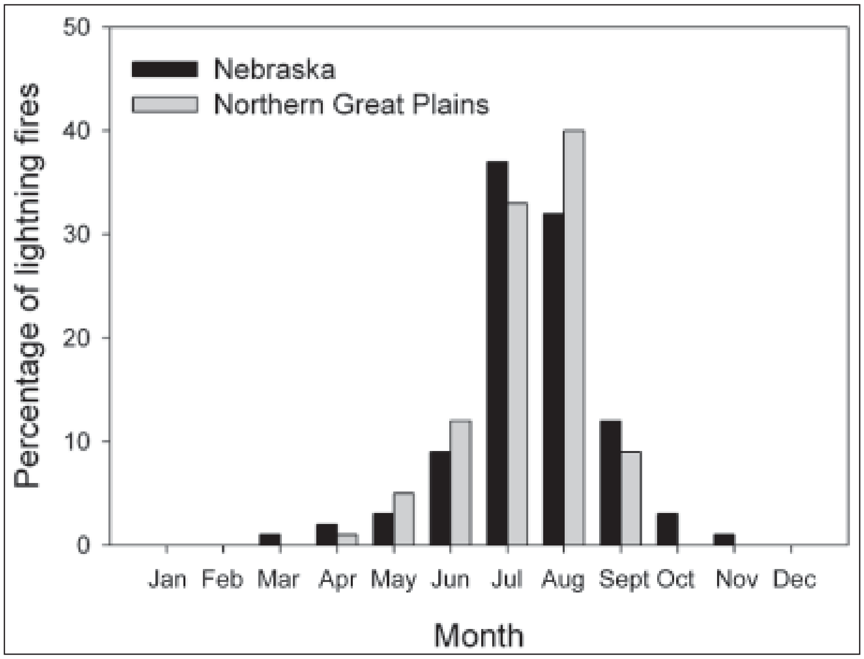
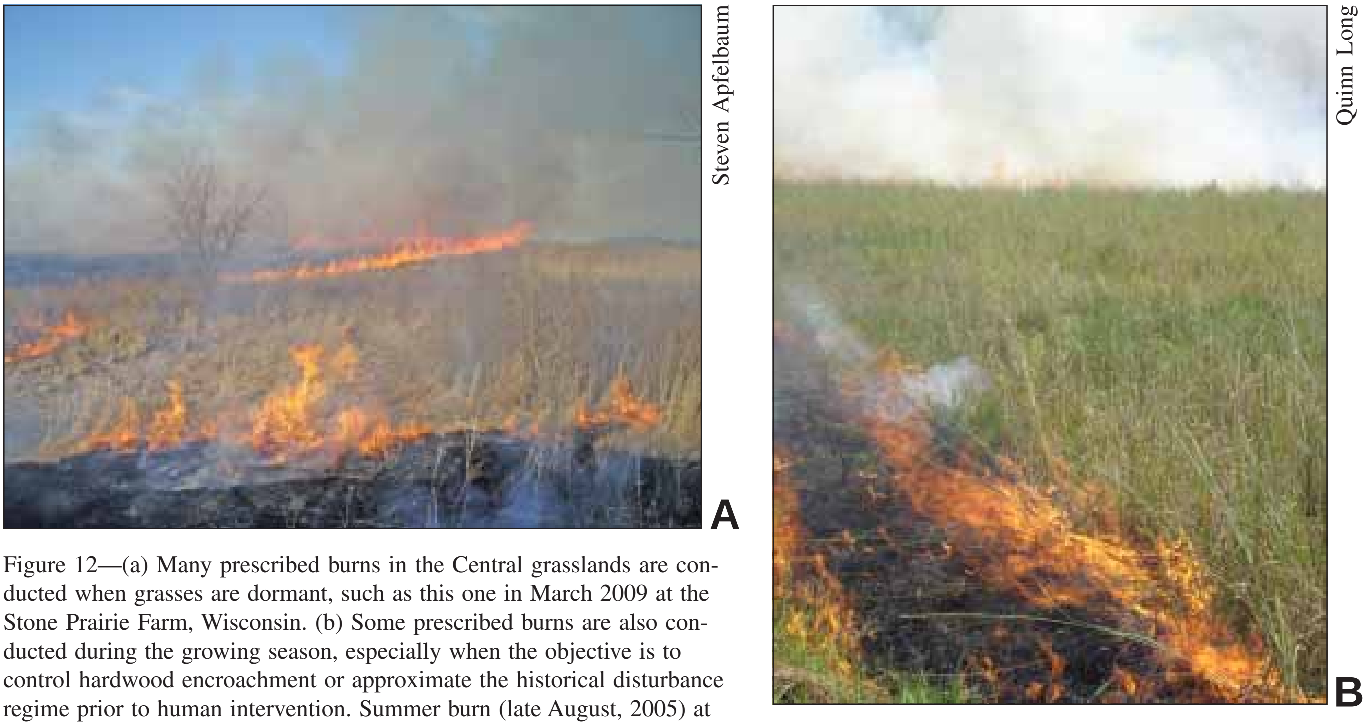


Figure 11—Percentage of lightning-ignited wildfires by month for grasslands of Nebraska, compiled for the period from 1971 to 1975 (data from Bragg 1982), and for four grassland areas in the Northern Great Plains, compiled for the period from 1940 to 1981 (data from Higgins 1984).



Steven Apfelbaum

Quinn Long

Figure 12—(a) Many prescribed burns in the Central grasslands are conducted when grasses are dormant, such as this one in March 2009 at the Stone Prairie Farm, Wisconsin. (b) Some prescribed burns are also conducted during the growing season, especially when the objective is to control hardwood encroachment or approximate the historical disturbance regime prior to human intervention. Summer burn (late August, 2005) at the University of Kansas Nelson Environmental Studies Area, near Lawrence, Kansas).

are important for grazing (Towne and Kemp 2003). Prescribed burning of grasslands farther south may be conducted earlier (January to March) (fig. 13). Overall, the majority of prescribed burns occur either earlier or later in the season, and at a time of greater plant dormancy than the majority of natural lightning-ignited fires. Greater use of growing-season burns has been advocated in order to mimic historical timing of lightning ignitions (Howe 1994a). However, there is some debate whether the goal with grassland burning should be to re-create grassland conditions representative of 30 million years of grassland evolution (predominantly growing-season lightning fires), or whether the goal should be to re-create conditions as they existed immediately prior to Euro-American settlement, which is thought to have been a mixture of growing-season lightning fires augmented by growing- and dormant-season fires, ignited by Native Americans (Howe 1994a).

Fuel Consumption and Fire Intensity

The total amount of fuel consumed is generally considerably less for grassland burns than for burns in forested ecosystems. In addition, because much of the fuel in grassland ecosystems is fine and dries rapidly, the amount of fuel consumed by burns in different seasons does not typically differ much, relative to other vegetation types. For example, Howe (1994b) noted that growing-season burns in the middle of the summer (July 15) consumed an average of 96 percent of aboveground biomass, whereas dormant-season burns conducted on March 31 consumed 100 percent of the aboveground biomass. In another study, consumption ranged from 84 percent in growing-season (mid-June) burns to >99 percent in dormant-season (April) burns (Bragg 1982). Copeland et al. (2002) reported that late-growing-season burns (Sept. 3) consumed 91 percent of the litter, whereas dormant-season burns (April 23) consumed 100 percent of the litter. In dry mesquite-savanna

Laura Calabrese

Figure 13—Spring (March) prescribed burn at Sevilleta National Wildlife Refuge on the western edge of the shortgrass prairie. Prescribed burns in south-central grasslands are often ignited earlier in the spring than burns in grasslands farther north, where frost and snowfall limit drying of fuels.

grassland in south Texas, both winter (December-February) and summer (August) burns covered 100 percent of the ground surface (Ruthven et al. 2008).

When actively growing, plant tissue contains moisture that needs to be vaporized for complete consumption to occur. Grasslands may still burn when they appear green because accumulated thatch and litter underneath can provide ample fuel. Owing to the green component, growing-season fire is often of lesser intensity, with reduced flame lengths and rates of spread, compared to dormant-season fire (Copeland et al. 2002, Ford and Johnson 2006, Steuter 1987). Also potentially playing a role are weather differences. Although air temperature (and the initial heat of the fuel) is typically higher during the growing season, relative humidity is also often higher at this time of year, particularly for tallgrass prairie ecosystems. Therefore, the suppressing effect of live fuels (and higher relative humidity) on fire behavior is apparently usually greater than the enhancing effect of higher air temperature. Growing-season burns can also result in greater variation in intensity (Howe 1999) and more burn patchiness compared to dormant-season burns (Komarek 1965, Steuter and McPherson 1995). This patchiness may be important for the persistence of many grassland species with fire. Historically, large ungulates like bison (*Bison bison*) likely reduced the amount of thatch and broke up the fuel complex by preferentially grazing some areas over others, leading to patchy burns (Fuhlendorf et al. 2006). Without historical grazing patterns, burns today (especially in the dormant season) may be more uniform in coverage.

In a mesquite savannah ecosystem in southern Texas, Ansley and Castellano (2007a) reported that summer burns (September 1) were higher intensity than winter burns (February/early March). However, because this location is farther south and warmer than the sites of other comparable grassland studies, some grass species were actively growing at the time of both winter and summer burns (cool-season species during the winter, and warm-season species during the summer). With fire-behavior suppressing live fuels present in both seasons, the higher air temperatures apparently contributed to the greater intensity of summer burns. In another mesquite savannah study, Drewa (2003) did not find any difference in fire intensity between burns in January or August. However, in this case, the January burns occurred when both cool- and warm-season grass species were dormant, whereas the warm-season grasses were still actively growing in August. Overall, less variability in intensity is generally found within and among grassland fires than among fires in plant community types that contain woody fuels (Bond and van Wilgen 1996).

Ecological Effects of Burning Season

Grassland Vegetation

In a review of the literature, Engle and Bidwell (2001) concluded that prairies are far more resilient to burning in any season than previously thought. For example, Johnson et al. (2008) noted that most prairie forbs are resilient to burning in any season, with 75 of 92 species studied unaffected by burns in different seasons. However, timing of fire can alter certain grassland species directly through injury or mortality, especially during vulnerable phenological stages. Fire during the period of most active growth is thought to be most damaging, because new plant tissues are more sensitive to heat (Bond and van Wilgen 1996) and because carbohydrate reserves are lower this time of year (Wright and Klemmedson 1965). Wright and Klemmedson (1965) compared fire in June, July, and August on four bunchgrass species and found plants to be most resistant to fire later in the season, presumably when carbohydrate reserves were again replenished. Needle and thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth) was damaged most by June fires, when plants were greenest. Squirreltail (*Elymus elymoides* (Raf.) Swezey), which was still green to partially green in both June and July was damaged most by July fires, when outside temperatures were the hottest. Data from this study demonstrated that depending on the species, both timing in relation to plant phenology, as well as the total heat experienced (from fire plus starting air temperature) may play a role in the response. In a different grassland type—mesquite savannah—the yield of Texas wintergrass (*Nassella leucotricha* (Trin. & Rupr.) Pohl) was reported to be nearly twice as high after summer fires than after winter fires (Ansley and Castellano 2007a). This cool-season grass species grows in the early season (February to June). The winter fires (February/early March) therefore coincided with growth, whereas the summer fires (September) were ignited after the species had finished growth. In a study of burning season on a rare forb, either spring (mid April) or fall burns (mid September) increased the germination of Spalding's catchfly (*Silene spaldingii* S. Watson), which grows from May through September (flowering in July and setting seed in August), but response was greater after spring burns (Lesica 1999). Benning and Bragg (1993) noted significant differences in response of big bluestem (*Andropogon gerardii* Vitman) to burns just 4 days apart, with fires shortly after initiation of spring growth increasing subsequent stem height and numbers of flowering culms compared to fires prior to initiation of spring growth. All of these studies highlight the importance of evaluating the effect on individual species in context of the timing of fire in relation to phenology of the plant at the time of the fire.

Much of the research on season of burning in grasslands has looked at the impact on the plant community. In addition to direct effects of fire on certain species, grassland vegetation can also be altered indirectly through changes in competitive relationships that occur when injury or mortality to some species is greater than to others. Prairies are typically composed of varying amounts of two groups of grass species: the cool-season grasses (C_3 photosynthetic pathway) that experience peak growth from approximately March through May and the warm-season grasses (C_4 photosynthetic pathway) that have peak growth from approximately April through October (table 3). Prescribed burns in the spring can kill, damage, or inhibit growth of early cool-season species that are active at this time of year, thereby favoring later warm-season species that have not yet started to grow (Howe 1994a, 1994b). Conversely, prescribed fire during the middle of the summer at the peak of lightning and historical fire frequency are more detrimental to the dominant warm-season grass species, thereby favoring early-flowering cool-season species, many of which have already finished growth and dropped seed by this time (Howe 1994a, 1994b, 1995; Steuter 1987). For example, population size of the early perennial forb Golden zizia (*Zizia aurea* (L.) W.D. Koch), a species that sets seed in early summer, was greater following August burns than May burns (Howe 1999). The summer burns more effectively suppressed the canopy of the taller dominant warm-season grasses, creating an environment free from shading by thatch.

Altering the fire regime of the Central and Northern Great Plains from lightning-ignited summer wildfire to spring prescribed fire has possibly shifted species composition toward a greater proportion of warm-season grasses (Anderson et al. 1970; Howe 1994a, 1994b). The warm-season grasses favored by spring (dormant season) prescribed fire are generally taller and outcompete other species for light; burning at this time of year is therefore thought to have contributed to rarity of formerly abundant species, and reduced overall diversity (Copeland et al. 2002, Howe 1994b). Conversely, summer burns, by reducing competition by dominant warm-season grasses, have been shown to favor early-flowering cool-season grasses and forbs (Howe 1995, 1999). In a study comparing mid-summer (July 15) and early spring (March 31) burns, Howe (1994b) reported that early cool-season flowering species such as black-eyed Susan (*Rudbeckia hirta* L.) and quackgrass (*Agropyron repens* (L.) Gould) increased in abundance after the mid-summer burns, whereas the spring burns caused both to decline or disappear. One census of unburned prairies found that the guild of early-flowering species covered only 2 to 15 percent of the ground; after a single mid-July burn, the cover of early-flowering species rose to 46 percent (Howe 1994b). Because lightning fires historically occurred most often during the summer, it is believed that such early-flowering species were once more abundant. With more early-flowering species in place of a few dominant warm-season grasses, tallgrass prairies managed with summer (growing season) burns have higher species diversity than prairies managed with spring or fall (dormant season) burns (Biondini et al. 1989, Howe 2000). The greater heterogeneity in intensity and effects with growing-season burns may be another reason for higher plant diversity (Howe 1999). If biodiversity management in tallgrass prairies is the goal, burning during the summer active phase of the dominant grasses may be preferred (Towne and Kemp 2008). Howe (1994b) suggested that greater biodiversity can be maintained with a “chaotic array” of burn seasons, such as what might have occurred historically.

Extent of community shifts caused by different burning seasons is largely dependent upon the mix of species present. For example, major changes in the plant community have not been noted for tallgrass prairies dominated by warm-season species. In a study of burning at Konza prairie in Kansas where cool-season species are only a minor component, Towne and Kemp (2003, 2008) noted a high degree of resilience to fire in any season. Canopy cover of warm-season grasses increased with burning in the fall, winter, or spring (Towne and Kemp 2003). Whereas some cool-season grasses did decline with repeated spring burning, low initial abundance apparently did not lead to differences in the competitive relationships between cool- and warm-season species among burning season treatments. Even repeated growing season (summer) burning, which was expected to suppress warm-season grasses and increase cool-season species, had few strong effects, possibly because watershed-scale burns in this season were patchy and incomplete (Towne and Kemp 2008). That repeated burning in different seasons led to few and slow changes of most species suggests that in this grassland type, the impact of one or a few out-of-season burns is likely to be relatively minor.

Studies in shortgrass prairies have also not demonstrated dramatic shifts in species composition with burning season. Owens et al. (2002) found that grass population size and forb composition in a shortgrass savanna did not differ after fires in the growing season (July through August) or dormant season (January through February). Based on data showing few changes in species composition, but large reductions in grass cover and biomass production, dormant-season burning (April) was deemed less likely to put the shortgrass prairie at risk than growing-season (September) burning (Brockway et al. 2002).

Another common goal of burning in grasslands is to increase forage for livestock (Engle and Bidwell 2001). In one study, forage production of a tallgrass prairie was greater after late-spring burning (May 1) than after early-spring burning (March 20), with mid-spring burning (April 10) intermediate (Anderson et al. 1970). Late-spring burns were timed for the start of growth of dominant warm-season grasses and preferentially killed or reduced cool-season species that initiated growth earlier. Similar results were reported by Towne and Owensby (1984) from the same site 20 years later, with greater forage production after late spring burns (May 1), than after winter (December 1), early-spring burns (March 20) or mid-spring burns (April 10). These plots had been burned annually since 1928. It was thought that the earlier fires led to greater duration of bare mineral soil exposure, with evaporation drying out the soil and reducing plant growth. In some grasslands, higher productivity with late-spring burns is likely partially the result of species shifts. The dominant warm-season grasses that are favored by such a fire regime are generally more robust and taller than the subdominant forbs and cool-season grasses favored by summer burns (Howe 2000).

In shortgrass prairies, biomass production following growing-season (July) burning was shown to be substantially less than following dormant-season (April) burning (Brockway et al. 2002, Ford and Johnson 2006). Grass cover was also significantly reduced after growing-season burns, owing primarily to a drop in cover of buffalograss (*Buchloe dactyloides* (Nutt.) J.T. Columbus), a late warm-season species (Brockway et al. 2002). Another study in a similar grassland type showed that spring burns enhanced forage production more than fall burns (White and Currie 1983). In a marsh plant community, summer (August) burning decreased the biomass of common reed (*Phragmites australis* (Cav.) Trin. ex Steud.), whereas spring (May) burns increased biomass, and fall (October) burns resulted in no change in biomass (Thompson and Shay 1989).

Nonnative vegetation—

Prescribed fire is sometimes used to control nonnative species in grasslands. Shifting the plant community by timing burns to coincide with the most vulnerable stage of the target nonnative species while favoring native species, is seen as key to success (Emery and Gross 2005, MacDonald et al. 2007, Simmons et al. 2007). Emery and Gross (2005) found summer (July) burning at the time of flowering reduced population growth rates of spotted knapweed (*Centaurea maculosa* L. ssp. *micranthos* (Gugler) Hayek), whereas spring (April) and fall (October) burns had no significant effect. Summer burns killed the flowering stalk, but not the adult plant. Spring burns allowed surviving plants to flower, whereas fall burns occurred after seeds had dropped. Summer burning is, however, not the best time for native late-season grasses that can keep spotted knapweed at bay through competition. In another study, mid-spring burning (late April to late May), timed to kill newly germinating seedlings, increased the dominance of native warm-season grasses and reduced spotted knapweed abundance (MacDonald et al. 2007). Because many of the nonnative species in grasslands dominated by native warm-season grasses germinate early, numbers can often be suppressed more effectively with spring burning, which also tends to be beneficial for the native grasses (Smith and Knapp 1999).

Unfortunately, because many nonnative species thrive with disturbance, populations are also often enhanced by fire (D’Antonio 2000). Hotter fall burns (September) were found to increase numbers of the nonnative sulphur cinquefoil (*Potentilla recta* L.) more than spring (April) burns (Lesica and Martin 2003).

Trees and other woody vegetation—

The presence of trees and shrubs in grasslands is often limited to areas that have experienced a break in the fire regime. This is evident in oak savannas that occur along the transition zone between the tallgrass prairie and the deciduous eastern forests. It is thought that fire may have once kept grasslands free of fire-sensitive tree species (Axelrod 1985). For example, absence of fire in Texas grasslands has contributed to an influx of mesquite and scrub oak. Although growing-season burns in mesquite savannas are sometimes higher intensity than dormant-season burns with greater flame length and faster rates of spread, Ruthven et al. (2003) reported that either dormant- or growing-season burns reduced the cover of mesquite and other shrubs. However, these shrubs also resprout, and Owens et al. (2002) found that neither growing-season nor dormant-season burns were intense enough to kill them. Intensity differences among burning seasons (higher intensity with summer burns) were associated with mortality of prickly pear cactus (*Opuntia* spp.), a grassland invader (Ansley and Castellano 2007b). Drewa (2003) manipulated fire intensity by adding fuels around the base of some mesquite shrubs prior to growing- and dormant-season burns, and noted that although resprouting was on average less vigorous after growing-season burns, resprouting was reduced in higher intensity patches within burns in both seasons. Both intensity and fire season apparently play a role, influencing the outcome by different mechanisms; intensity by damage to growing parts, and season through changes in rate of recovery as a result of seasonal differences in carbohydrate storage (Drewa 2003).

Soils

Grass fires move rapidly, and because the amount of fuel consumed and heat produced when grasslands are burned is relatively low, heating below the immediate soil surface is generally minimal (Anderson 1990, Vogl 1979). However, burning is thought to influence soil heating in other ways. Growth in the spring, especially in areas with cooler winters, is limited by soil temperature (Ehrenreich and Aikman 1963). Clearing the ground of litter and thatch, whether through spring burning or other means, allows sunlight to reach and heat the soil surface (Ehrenreich and Aikman 1963, Knapp 1984, Seastedt and Ramundo 1990), thereby promoting earlier growth of the warm-season grasses (Howe 1994b, Vogl 1979). Earlier initiation of growth and a longer growing season may be one reason why spring prescribed fire has frequently been found to increase vegetative production; however, Ehrenreich and Aikman (1963) found that plants in burned areas also senesced earlier without significantly greater production.

Burning in the early spring can lower soil moisture compared to burning in late spring, because the ground is exposed for a longer period of time, allowing more evaporation to occur (Anderson et al. 1970). Excess evaporation may be detrimental to herbage production, especially in low rainfall years when moisture is already limited. The presence of litter and thatch is also thought to increase snow accumulation, time required for snow to melt, and rate of moisture infiltration into the soil (Ehrenreich and Aikman 1963). Therefore, any burning regime that leaves the soil uncovered during the winter and spring could potentially reduce soil moisture.

Burning during the growing season minimized the impact on biological soil crusts compared to burning during the dormant season, presumably because of lower fire severity (Ford and Johnson 2006). However, recovery of soil crusts was rapid, regardless of the burn season (Ford and Johnson 2006).

Wildlife

Wildlife is impacted by fire in two main ways: direct mortality and indirect changes through alteration of their habitat. However, few data on the effect of prescribed fire season on wildlife in grasslands have been published. Most studies have looked at either the difference between growing-season fire and no fire or the difference between dormant-season fire and no fire, without comparing among burning seasons.

Birds and small mammals—

Some mortality of birds and small mammals is expected with fire, especially those that nest above the ground. Burns, stress, and asphyxiation are possible mechanisms (Kaufman et al. 1990). However, prairie vegetation is composed of fine fuels that burn rapidly in a narrow band of flame; this makes heating relatively transient and allows animals to more easily escape (Vogl 1979).

Because of their mobility, adult grassland birds rarely experience direct mortality with fire. Young birds still in the nest are more vulnerable, and as a result, spring burning during the nesting season may cause greater mortality than burning in the summer or fall (Reinking 2005). Erwin and Stasiak (1979) and Higgins (1986a) observed that nests of ducks and other bird species were destroyed by spring prescribed burns. However, if the nest is lost, many prairie species will renest (Reinking 2005). In the Nebraska grassland, harvest mouse mortality was noted with a dormant-season burn occurring during the nesting season (Erwin and Stasiak 1979). Even so, the high reproductive capability of rodents generally compensates for any impact of different seasons of fire (Kaufman et al. 1988).

As in other vegetation types, longer term changes in animal numbers owing to fire are thought to be caused mainly by effects on habitat. Burning-season-mediated shifts in grassland species composition can affect animal populations, but lack of cover likely plays a stronger role (Kaufman et al. 1990). In grasslands, fire removes all or nearly all of the aboveground biomass, and it is thought that amount of time without cover can affect wildlife (either positively or negatively, depending on the species). Because vegetative growth typically starts with warm weather and precipitation in the spring, cover is generally reduced for a longer period after a fall burn than a spring burn (Kaufman et al. 1990). In a study comparing duck nesting in plots burned in the spring (June) during the May 1 through July 31 nesting season, and plots burned in the late summer (August-September), after the nesting season, Higgins (1986a) noted that far fewer ducks initiated nests the following spring in the sparse cover after late-summer burns. In the following year, number of nests was the same between treatments, but nest success was greater in the late-summer burning treatment compared to the spring burning treatment. This difference equalized over time, and by year 4, no difference between burning seasons was found. Westmeier (1973) found that nest densities of the greater prairie chicken (*Tympanuchus cupido* L.) increased after burns in either the late summer (August) or spring (March).

Losses or gains in food sources may lead animals to migrate, and loss of cover could increase predation rates during migration. When managing for key animal species, burning has sometimes been done to manipulate the abundance of plant food sources, but as pointed out by Sparks and Masters (1996), the optimal time of the year differs, with no time best for all species. For example, growing-season prescribed fire, which favors grasses over forbs, may benefit species that feed on grass seeds but not be ideal for species that eat seeds of legumes and other forbs. If the goal is to increase the abundance of forb food sources, dormant-season burns may be preferred.

A variable fire regime with burns in multiple seasons may be necessary to maximize grassland biodiversity. Fuhlendorf et al. (2006) and Reinking (2005) argued for less uniform burn management and greater patchiness to promote multiple grassland habitats and greater diversity of birds.

Amphibians and reptiles—

In a mesquite savanna grassland in Texas, dormant-season burns had no effect on the diversity and abundance of amphibians and reptiles, whereas diversity and abundance tended to be slightly greater in plots managed with growing-season burns (Ruthven et al. 2008). One species of lizard was 10 times more abundant in plots burned in the growing season than in the unburned control; however, burning season overall had few short-term effects on the community. These authors recommended a varied fire regime to maximize diversity of this group of species.

Arthropods—

Burning in different seasons has been used in attempts to control arthropod pests, such as ticks, but results from studies to date have been mixed because of differences in fire intensity and timing in relation to periods of aboveground activity (Warren et al. 1987). For winged arthopods that can escape the main heat pulse, a fire will tend to favor those species that are mature at the time of the burn. In a Kansas prairie, grasshoppers (Acrididae), which overwinter as eggs in the soil, were reduced by burns timed to occur after the nonflying nymphs emerged (Knutson and Campbell 1976). In another study, Vermeire et al. (2004) found that the response to burning season differed among grasshopper species, with two unaffected by prescribed fire in any season, one reduced by both spring and fall burns, and one reduced more by fall than spring burns. The latter species lays eggs near the soil surface, where they are presumably killed by fall burns. Developing burning prescriptions to target vulnerabilities of each species was suggested (Vermeire et al. 2004). Mortality of other arthopods, such as centipedes and millipeds that live in crevices in the soil, is likely minor with flaming combustion, varying more with habitat modifications (Warren et al. 1987) that may differ among burning seasons. Conditions as vegetation recovers following a fire are beneficial to many arthopods. Total weight of insects in a Texas grassland was greater in burned than unburned areas one season after fire, with more insect biomass following spring burns than winter or fall burns (Chamrad and Dodd 1973), presumably owing to attributes of the postfire vegetation. In another study of a Texas grassland burned three times in either the winter (dormant season) or summer (growing season), and sampled 3 years after the final burn, Johnson et al. (2008) found 170 percent more individual insects in the summer burn plots. Although species richness was also 60 percent higher in the summer burn plots, the difference between burn-season treatments was only marginally significant.

Spring prescribed burning was shown to suppress arthropod diversity in an Illinois tallgrass prairie (Harper et al. 2000). Because of low survival in place, recovery of burned landscapes may depend upon recolonization from adjacent unburned areas. These authors suggested that to avoid negative impacts to arthropods, managing for burn patchiness and leaving unburned refuges would be beneficial. Burn seasons were not compared experimentally; therefore the magnitude of potential burn season effects is unknown.

Implications for Managers

Reviews of the literature on burning season in prairies of North America highlight the wide range of outcomes that are possible, making broad generalizations a challenge. How fire interacts with the ecosystem depends on the frequency of fire, time since previous fire or successional stage of the grassland, grassland type (shortgrass, mixedgrass, or tallgrass), the evenness of cool-season and warm-season species within grassland type, herbivory, and climatic conditions, most of which differ among the many studies that have been done. Timing of fire in relation to seasonal growth is key to understanding response in grassland species. For example, a greater increase in production with spring than summer burns might be expected in areas where warm-season grasses currently predominate (i.e., the more mesic grasslands in the eastern portion of the Central region), than in areas where cool-season grasses predominate, such as the more xeric western grasslands.

In many studies, the descriptions of when the fires were conducted is vague (i.e., spring burn, early-season burn, fall burn, late-season burn, etc.) and slight variation in timing of fire in relation to plant phenology can produce different results. Significant variation in outcomes has been reported for burns conducted as little as 4 days to 3 weeks apart. Effect of prescribed burning also depends on year-to-year variation in rainfall, with greater expected plant mortality from burning in drought years. Year-to-year variation in precipitation or temperature can also alter the onset of seasonal activity and growth. Thus lack of detail on the exact phenological stage of organisms at the time of burning, inadequate description of burn timing, and climatic variability limit syntheses and generalization of results. Each year and each burn is potentially unique.

Although prairies are generally fairly resilient to burning in any season, it is clear from the literature that prescribed burns in different seasons can sometimes lead to

Key Points—Central Region

- Grasslands exhibit resiliency to fire in any season, but substantial changes in community composition can result from altering the burn season.
- Shifts in the plant community are caused by variation in phenology and susceptibility to fire among species. Prairies with a mix of cool-season and warm-season species having different periods of growth appear to be most susceptible to community shifts, whereas prairies dominated by one or the other appear to be more resistant to change.
- Phenology of the vegetation at the time of burning appears to play a more important role in grasslands than most other vegetation types, presumably because fuel consumption and fire intensity do not differ substantially among burn seasons (assuming the same firing strategy: backing or heading). When intensity is similar, the influence of phenology is more likely to be seen.
- Low fuel loading and rapid fire passage allows most mobile animal species to escape the flames in any season. Although fire during periods of vulnerability, such as the nesting season, can cause short-term losses, the effect on populations in the longer term is unclear.
- A burn program that promotes heterogeneity, including burning in multiple seasons within the historical range of variability will likely benefit the greatest number of grassland species.

substantial ecological change. Population sizes of certain species can shift from a single burn, but such changes are usually ephemeral. The role of vegetation phenology on response is perhaps stronger in grasslands than in any other ecosystem. As with other ecosystems, response is tied to both the phenology of organisms and intensity of the fire. Because grassland fires consume much, if not all, of the aboveground vegetation regardless of fire season, differences in intensity among seasons are likely of lesser magnitude than in many other vegetation types. (Note, however, that intensity does differ depending on whether heading fires or backing fires are used, and this too can affect the vegetation response [Bidwell et al. 1990]). Without strong differences in intensity, the role of phenology becomes increasingly important.

Rather than managing fire intensity through prescribed burning under different conditions or time of year, or using different firing strategies, the issue for the fire manager is mainly one of timing burning to achieve different goals. The optimal burn season depends on the objective: Is the goal to improve forage biomass, or to enhance native biodiversity? If the latter, is the goal to restore conditions/processes to the time immediately prior to Euro-American settlement, taking into account the impact that Native American burning likely had, or is the goal to mimic processes in place prior to anthropogenic manipulation of vegetation?

Fine-tuning the timing of burns will depend on many other factors including a complete understanding of the phenology or periods of greatest vulnerability of key species, the role of climatic variation, and the interaction between phenology and climate. It is also important to recognize that repeated burning in any one time of year over large land areas may have the effect of simplifying the system. With grassland species differing in response to timing of fire, heterogeneity in the prescribed burning regime, including a mix of fire seasons, may be necessary to maintain prairie diversity.

Chapter 5: Eastern Region

The Eastern region includes everything east of the Central grasslands to the Atlantic coast. Much of this area has the potential to support forest vegetation. Forests have been cleared and converted to farmland in many areas, with major disruptions of the historical fire regime. Precipitation is generally higher here than in the Central grasslands to the west. Like the grasslands, much of the Eastern region is characterized by fuels that respond quickly to fluctuations in moisture (Wade et al. 2000).

Climate, Vegetation, and Fire

Past landform shifts, latitudinal temperature and precipitation gradients, as well as the presence of disturbances such as fire have all shaped forest cover types of the Eastern United States. For this synthesis, we divide the Eastern region into two zones with distinct fire regimes. The Subtropical zone in the south consists of forests historically dominated by a mix of overstory pine species along the Coastal Plain grading into pine-oak forests in other areas (fig. 14). The Hot Continental/Warm Continental zone is dominated primarily by hardwoods in the central Eastern United States, and a mix of coniferous and deciduous species farther north.

Subtropical

The Subtropical region averages approximately 50 in of precipitation a year. Much of the rainfall occurs with the passing of maritime tropical air masses that arise from the Gulf of Mexico, as well as continental polar airmasses. These same air masses bring warm temperatures and high humidity in the summer months and cold temperatures in the winter. In south Florida, rainfall peaks in the summer, with drier weather in the fall, winter, and spring (Bailey 1980, Beckage et al. 2003) (fig. 14e). Along the gulf coast, two distinct wet periods occur: one during the summer lightning storms (June-August) and a second during the winter (January-March) with the arrival of cold fronts when transpiration rates of the vegetation are low (Chen and Gerber 1990) (fig. 14c). The Ouchita Mountains of western Arkansas and eastern Oklahoma also have two distinct wet periods, with rainfall peaking around May and November (fig. 14d). Farther east, rainfall generally becomes more evenly distributed throughout the year (fig. 14b).

Forests of the Subtropical region are dominated by overstory pines and scrub oaks closer to the coast, bottomland hardwoods along waterways, and a mixture of pines and upland hardwoods farther inland from the coast. The longleaf pine (*Pinus palustris* Mill.) forest once covered the majority of the Coastal Plain, but has been reduced owing to a variety of past land management activities (Frost 1993). Shortleaf pine (*Pinus echinata* Mill.) was at one time the most widespread pine species across the East, occupying a variety of soil types and environmental conditions, but has been reduced because of fire exclusion (Komarek 1968), logging, and replanting with other species. Slash pine (*Pinus elliottii* Engelm.) and loblolly pine (*Pinus taeda* L.) were historically restricted to wetter areas but are now found throughout the pine zone (Komarek 1968). Forest composition in the pine-oak forests has shifted to a greater percentage of mesophytic hardwoods and planted species such as loblolly pine (Nowacki and Abrams 2008).

Historical fire regime—

Based on fire scars in the tree ring record, it is believed that prior to Euro-American settlement, many forests in the south had an average fire-return interval of less than 15 years (Henderson 2006, Huffman et al. 2004, Huffman 2006, Wade et al. 2000) (table 4). The mean fire-return interval increased along a moisture gradient with more mesic sites having less frequent fire. The southernmost longleaf pine forests grow in areas with longer dry periods, and these forests burned with the highest frequency. Oak-pine forests in the highlands of eastern Okahoma burned every 2 to 12 years (Masters et al. 1995). Fires ranged from

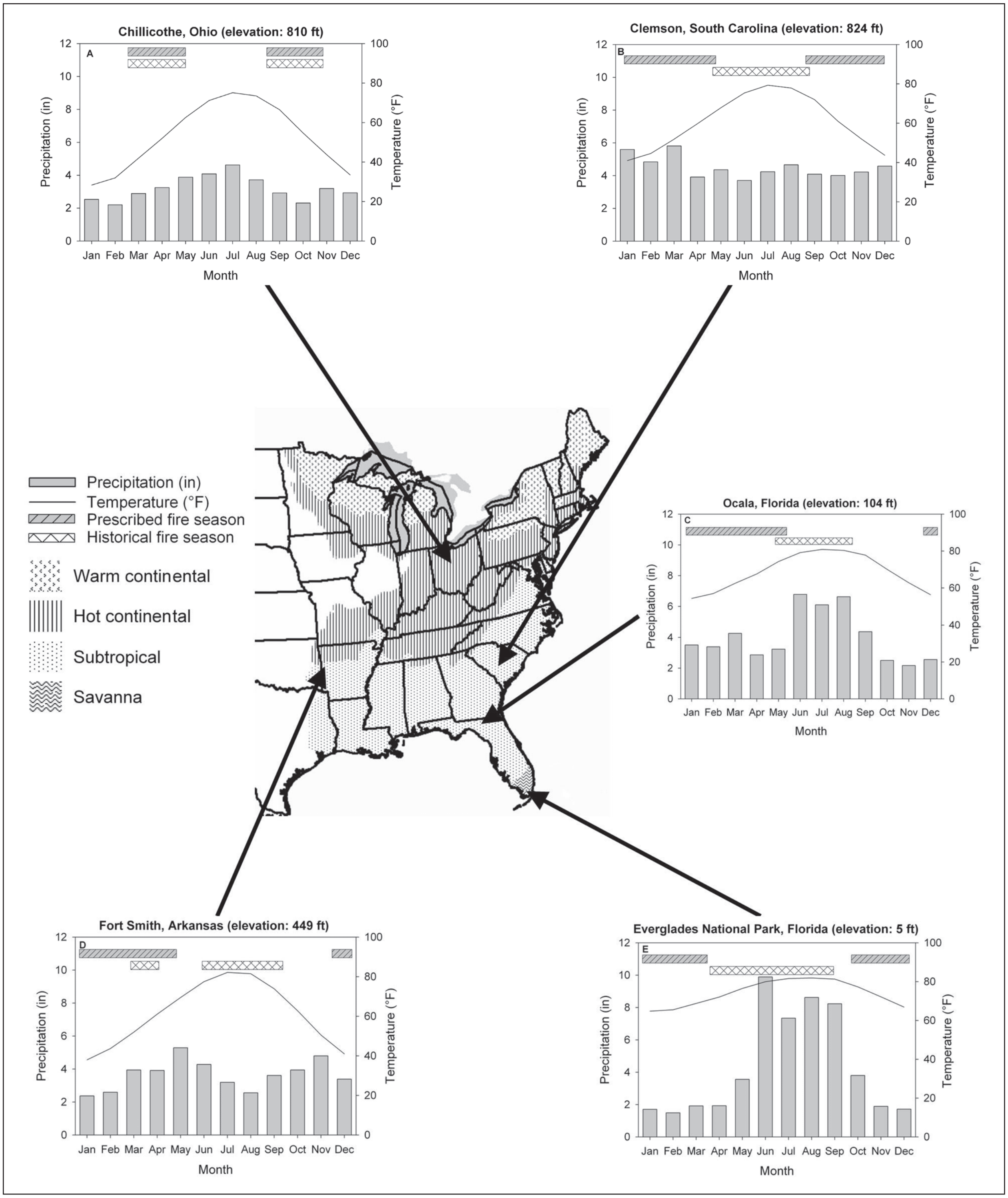


Figure 14—Climographs (monthly average temperature and precipitation) and the average time of the year of peak historical and prescribed fire seasons from five representative locations within the Eastern region: (a) Chillicothe, Ohio; (b) Clemson, South Carolina; (c) Ocala, Florida; (d) Fort Smith, Arkansas; and (e) Everglades National Park, Florida. Note that because the timing of anthropogenic fire is poorly understood, the historical fire season reflects mainly lightning-ignited fires. Historical anthropogenic fires were likely ignited during the dormant season (early spring and fall) as well.

Table 4—Estimated fire-return interval and approximate season of fire in the Eastern and Southern United States, determined from fire scars

Location	Forest type	Dates	Fire-return interval	Season of fire[a]	Author(s)
			Years	*Percent in category*	
Garrett County, Maryland	Oak forest	1615–1958	7.6	D (>90)	(Shumway et al. 2001)
Jefferson National Forest, Virginia	Southern Appalachian pine forest	1694–2004	3.3	D (80) G (20)	(DeWeese 2007)
Southeastern Ohio	Mixed oak	1871–1997	5.4	D (69) S (25)	(Sutherland 1997)
Pope County, Arkansas	Oak—shortleaf pine	1680–1910	2.8-11.2	D	(Guyette and Spetich 2003)
Choccolocco Mt., NE Alabama	Montane longleaf pine	1589–2006	3.2-11.5	D	(Bale et al. 2008)
Big Thicket, Texas	Longleaf pine forest	1668–1984	10.6	D (75) E (9) A (11)	(Henderson 2006)
Sandy Island, South Carolina	Longleaf pine forest	1580–2004	15.6	D (72) E (9) M (12) A (2)	(Henderson 2006)
Eglin Air Force Base, Florida	Longleaf pine forest	1517–2004	6.4	D (28) E (25) M (9) A (30)	(Henderson 2006)
Gulf County, Florida	Mainland pine savanna	1592–1883	2–3	D (5) LS(10) M (80)	(Huffman 2006)
Little Saint George Island, Franklin County, Florida	Coastal slash pine	1864–2000	4–9	D (14) M (67)	(Huffman et al. 2004)

[a] D = dormant (September—March), G = growing season (March—October), E = early spring (March—April), S = spring (March—May), LS = late spring/summer (April—May), M = mid-season (May—August), A = late season (August—September).

low-severity surface fires in longleaf pine forests to mixed-severity fires in oak-pine forests (Wade et al. 2000). Drought conditions sometimes led to higher fire intensity and greater damage to trees, even in areas that typically experienced low-severity fire.

The Coastal Plain pine zone is characterized by flammable understory fuels (both live and dead) that respond quickly to fluctuations in moisture, and will burn nearly year round. Moisture content of live vegetation is often lowest from April through June, prior to the onset of the summer rains and as temperatures are warming (Hough 1973, Hough and Albini 1978). Understory shrubs such as saw palmetto (*Serenoa repens* Bartram (Small)), gallberry (*Ilex glabra* (L.) A. Gray), and wax myrtle (*Morella cerifera* (L.) Small) that contain volatile oils are common (Van Lear et al. 2005). These oils allow combustion at high moisture levels, and fire is therefore not dependent upon longer periods of drying. Burns can be conducted just days after rainfall (Schroeder and Buck 1970).

Location of fire scars within annual tree rings suggest that slash and longleaf pine communities adjacent to the Gulf of Mexico were most likely to burn in the middle of the growing season (April—August) (Henderson 2006, Huffman 2006, Huffman et al. 2004) (table 4). In contrast, fire scars from other parts of the longleaf pine range showed evidence of a higher proportion of dormant season fire (September—March) (table 4).

The Southeast has the highest lightning strike frequency in the United States. Ten to 21 strikes per square mile per year are common, with a peak of 22 to over 41 strikes per square mile per year found throughout much of Florida (National Oceanic and Atmospheric Administration 2009). Most convective activity occurs between May and September, with the number of lightning-ignited fires peaking in July (Myers 2000) (fig. 15). Lighting-ignited fires burn more acres in May and June, at the transition between the dry season and the onset of the summer rains (Barden and Woods 1973, Komarek 1964, Myers and White 1987, Outcalt 2008, Petersen and Drewa 2006). Thus, the peak fire season occurs prior to the peak convective season (fig. 15). Precipitation increases with the summer convective storms (Komarek 1964, 1968), and although fires do occur during the summer, they are typically less intense and smaller as a result of higher moisture levels. During drought years, fire season tends to expand into the warm summer months, and fires are often larger and more intense (Glitzenstein et al. 1995b). In the Ouachita highlands of eastern Oklahoma, the majority of lightning fires occur in August and September, with drying following an early summer peak in thunderstorm activity and rainfall (Foti and Glenn 1991).

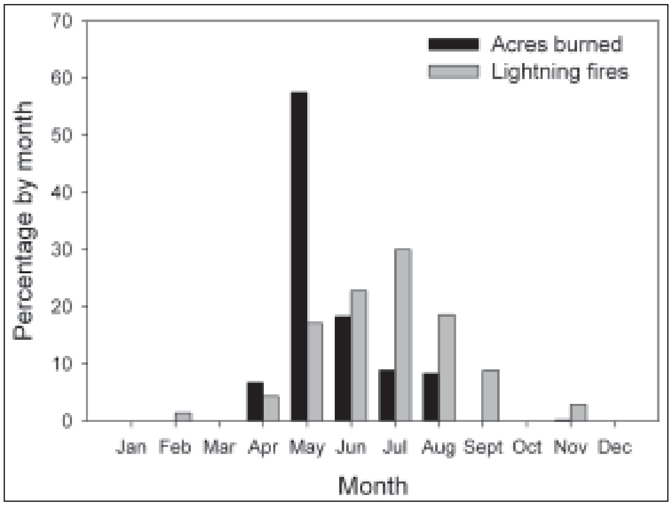
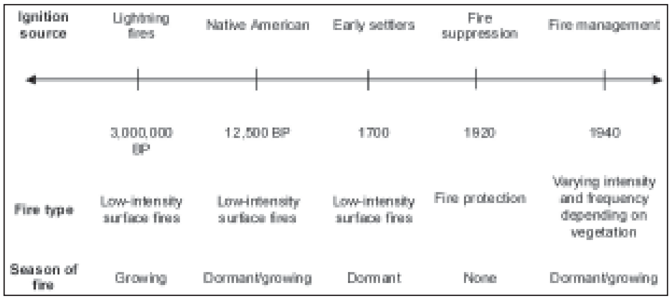


Figure 15—Percentage of lightning-ignited fires and acreage burned by month within the St. Marks National Wildlife Refuge, Florida, between 1980 and 2006 (compiled from incident records in FAMWEB).

There is some question as to the temporal and spatial extent of burning by Native Americans and its effects on native species in the East, leading to controversy as to what constitutes the historical fire regime (Henderson 2006, Myers 2000, Robbins and Myers 1992). Native Americans used fire for a number of reasons, including propagating native plants, hunting, clearing of land, defense, and communication (Fowler and Konopik 2007). It is thought that Native Americans would not have restricted their burning to a particular season, but rather used fire in a variety of seasons to meet their needs (Johnson 1992, Stewart 2002). Ignitions in the fall or late winter to early spring would have coincided with hunting season and preparation of agricultural fields, respectively (Fowler and Konopik 2007, Henderson 2006). The prevalence of



Ignition source	Lightning fires	Native American	Early settlers	Fire suppression	Fire management
	3,000,000 BP	12,500 BP	1700	1920	1940
Fire type	Low-intensity surface fires	Low-intensity surface fires	Low-intensity surface fires	Fire protection	Varying intensity and frequency depending on vegetation
Season of fire	Growing	Dormant/growing	Dormant	None	Dormant/growing

Figure 16—Summary of ignition source, fire type, and season of fire attributed to natural and human causes in the Eastern region during different time periods (based on Komarek 1964, Robbins and Myers 1992, Frost 1998, and Fowler and Konopik 2007).

dormant season scars, despite the relative lack of lightning during this time suggests a contribution of Native American ignitions to the fire regime (Henderson 2006) (table 4).

Prescribed fire regime—

Active prescribed fire management was preceded by a period of fire exclusion that began in the 1920s (fig. 16). However, the practice of fire suppression was not widely embraced in the East. Passage of the Weeks and Clarke-McNary Act, which established significant fire control organizations, sparked a debate concerning the importance of fire to the Eastern ecosystems (Chapman 1932). Managers quickly realized the importance of fire to this region and continued to use prescribed burning to maintain forested ecosystems. A substantial proportion of the prescribed burning in the southeastern coastal plain is conducted during the fall, winter, and spring (October—April) (fig. 17). Burning at this time of year is/was based on the belief that such burns would be less likely to impact nesting birds or harm growing trees (Cox and Widener 2008). Operational issues also favor burning at this time of year, with lower temperatures and more predictable winds making prescribed burns easier to conduct (Wade and Lunsford 1989). Gusty and unpredictable winds associated with thunderstorms are common during the late spring and summer.

The main prescribed burning season occurs during the dormant phase of many plant species and at a time of reduced biological activity, whereas the historical fire regime consisted of a higher proportion of spring and summer fire, when vegetation was actively growing and birds were nesting. Because these dormant-season burns

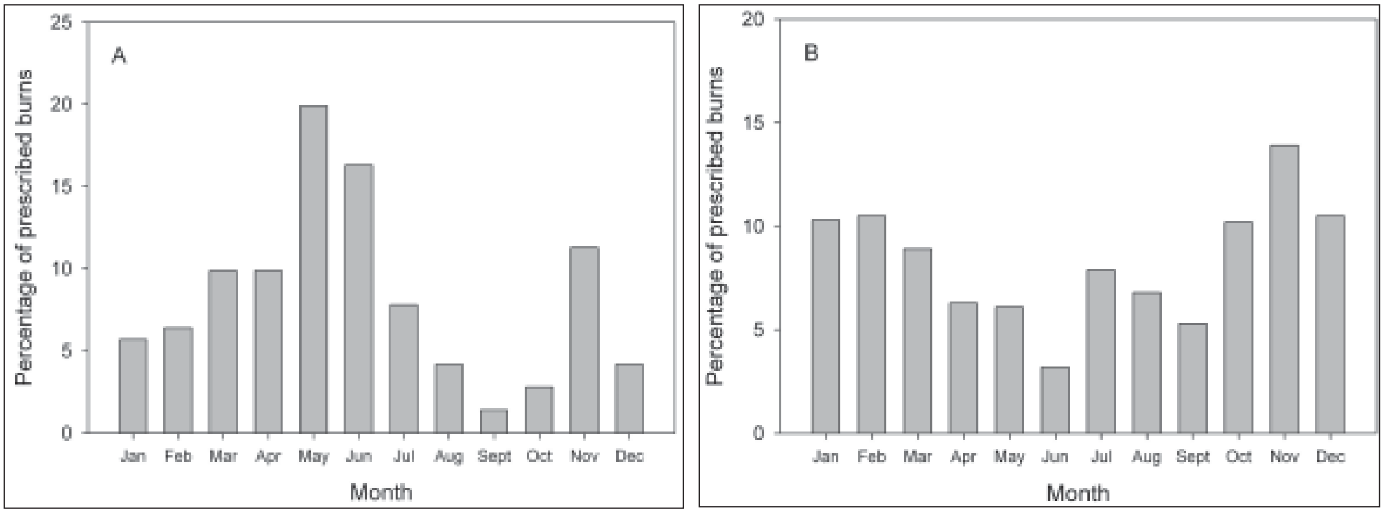


Figure 17— Percentage of prescribed burns by month at (a) St. Marks National Wildlife Refuge, Florida for the period from 1980 to 2006 (compiled from incident records in FAMWEB), and (b) Everglades National Park, Florida for the period from 1948 to 1997 (data from Myers 2000).

are outside of the typical historical period of lightning-ignited fire, there is some concern that repeated burning at this time of year may result in undesirable ecological changes.

On lands where the objective of prescribed burning is to restore historical processes, such as Everglades National Park, considerable burning is also often done during the growing season (May—August), the peak of the lightning season (fig. 17b). In Everglades National Park, South Florida slash pine (*Pinus elliottii* Engalm. var. densa Little & Dorman) has been burned every 2 to 3 years during the months of May and June since 1989 (Slocum et al. 2003). However, such burns are considered risky because of the chance for escape. Specific resource conflicts, such as game bird management and concern about nest destruction, can also make managers reluctant to use growing-season prescribed fire (Cox and Widener 2008).

Two excellent reviews and syntheses by Robbins and Myers (1992) and Streng et al. (1993) cover the issues of prescribed burning in southern pine forests at times of the year different from the historical lightning fire regime, and we draw heavily on their conclusions for this synthesis.

Hot Continental and Warm Continental

The fire climate in the Hot/Warm Continental regions of the Central, Great Lakes, and North Atlantic States is generally driven by airmasses bringing moist humid tropical air in the spring and summer and polar continental air in the late fall and winter. The annual precipitation averages between 20 to 45 inches in the Central States and about 30 inches in the Great Lakes States (Bailey 1980). Although precipitation is fairly well distributed throughout the year, somewhat more rainfall occurs during the summer, coinciding with the highest temperatures of the year (fig. 14a).

Forests of the warmer areas from the middle-Atlantic States through the Appalachian Mountains and into the Northeast are mostly dominated by oaks and hickories. The main carrier of fire is leaf litter, which differs in flammability with site and time of year (Wade et al. 2000). Recurring fire has maintained oak dominance in these forests at the expense of mesophytic tree species (Abrams 1992, Elliott et al. 2004). On xeric sites, lack of fire has increased the presence of ericaceous shrubs such as rhododendron (*Rhododendron* L.) and mountain laurel (*Kalmia latifolia* L.). When fire does occur, these shrubs can burn at high intensity, potentially leading to stand replacement (Wade et al. 2000).

Farther north, in the Great Lakes region, spruce (*Picea* A. dietr.), fir (*Abies* Mill.), eastern white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Aiton), jack pine (*Pinus banksiana* Lamb.), and aspen (*Populus* L.) dominate as a fire-maintained stage or as a climax forest (Duchesne and Hawkes 2000). Fires in pure aspen stands are typically of low intensity, but fire can still cause significant mortality of aboveground stems (Duchesne and Hawkes 2000). Areas with higher fuel loads in mature aspen stands may sometimes experience high-intensity stand-replacing fires (Jones and DeByle 1985). Red and eastern white pines occupied pure stands or were found in association with aspen, jack pine, and a variety of hardwoods, and experienced similar mixed-severity fire regimes as aspen stands (Duchesne and Hawkes 2000, Johnson 1992).

Historical fire regime—

The fire regime of the mixed-oak forests consisted of primarily low-severity events occurring approximately every 3 to 13 years (Guyette et al. 2006, Shumway et al. 2001) (table 4). Farther north, in the Great Lakes and Atlantic regions, typical fire-return intervals ranged from 35 to over 200 years (Duchesne and Hawkes 2000).

Location of fire scars within growth rings suggests that most fires occurred during the dormant season (Bale et al. 2008, DeWeese 2007, Guyette and Spetich 2003, Shumway et al. 2001) (table 4). The dormant season lasts from approximately late September to April. When hardwoods are not in leaf, litter is exposed to sunlight, making it susceptible to fast drying. Aboveground portions of understory herbaceous vegetation are also mostly dead at these times of the year, increasing the likelihood of fire spread (Wade et al. 2000). When leaves are on the trees, the microclimate on the forest floor is often shady and moist, which generally results in poor conditions for burning. The exception occurs during periods of drought. Convective activity is still high during this time (Petersen and Drewa 2006), and drought overrides the typically moist understory microclimate.

Lightning is fairly common and mostly associated with summer convective storms that also typically include precipitation. However, because of the lack of dry fuels, the peak fire season is frequently driven more by the surface fuel conditions than the times of peak lightning frequency (Barden and Woods 1973, Johnson 1992, Petersen and Drewa 2006). The relative lack of lightning during times of the year when leaves are on the ground and most flammable, and tree ring data indicating predominantly dormant-season burns, suggests the role of another ignition source in many areas. Paleoecological evidence that fire-resistant tree species were more abundant during periods of Native American settlement also hints at a link between forest composition, fire, and human activity (Henderson 2006, Shumway et al. 2001).

Prescribed fire regime—
Most prescribed burning in eastern hardwood forests is conducted during the dormant season, prior to leaf emergence in the spring or after leaf drop in the fall (Johnson 1992). The period of time that the litter fuel bed is receptive to fire depends on the latitude and year-to-year weather variation. In southern hardwood forests, prescribed burning may be conducted any time the litter layer is dry, whereas farther north, persistent snow cover limits application of fire to a narrower period in the spring and fall.

The prescribed fire season appears not to differ greatly from the historical fire season, at least for the period of Native American settlement. However, in areas where late summer burning was historically part of the fire regime, a higher proportion of the landscape is now possibly being treated in the dormant season (fig. 18). Because vegetation is dormant and wildlife species are less likely to be active during the dormant season, concerns about direct fire effects are minimized. The extent to which prescribed fire effects differ from historical fire effects may be due primarily to differences in fire intensity, if any. One concern may be the lack of heterogeneity in the fire regime when a strictly dormant-season prescribed burning program is employed.

Stephen Hudson

Figure 18—Most prescribed burns in oak and mixed oak and pine forests are conducted in the dormant season after leaf fall and prior to leaf expansion in the spring. During this time, exposure of the litter to sunlight hastens drying and ignition.

Fuel Consumption and Fire Intensity

Fuel consumption and fire intensity do not appear to differ consistently with season in eastern forests. In eastern pine forests west of the Mississippi River, dormant-season prescribed burns are sometimes described as more intense than growing-season burns (Sparks et al. 1998). Sparks et al. (2002) reported dormant-season (March—April) fuel beds in Arkansas shortleaf pine stands to consist of a reduced proportion of live fuels, more fine (1 hour) fuels, and a greater total fuel load than fuel beds in the growing season (September—October), all of which led to greater fire-line intensity and total fuel consumption when burned. In different fuel types of southern pine forests, growing-season burns were described as more intense than dormant-season burns (Komarek 1965, Liu and Menges 2005). Boyer (1993) measured greater tree crown scorch with summer burns than spring or winter burns, most likely as a result of higher air temperatures. Within the growing season, early fires (May) have been reported as generally more intense than late fires (September) (Slocum et al. 2003). Still other studies have not found differences in fire intensity among seasons. Boring et al. (2004) noted approximately the same peak temperature and flaming duration with dormant-season (March—April) burns and early growing-season (June) burns. Glitzenstein et al. (1995a) found that burns conducted at eight different times of the year consumed approximately the same amount of fuel (43 to 62 percent), but differed in fire-line intensity by a factor of four owing to variable rates of spread. This variation was not consistently associated with any time of the year. In another study of fuel moisture and consumption, burns in February, March, April, and September under conditions that started out as wet and progressed to very dry, consumed approximately the same amount of litter, but burns in May and September (the two driest times) resulted in greater duff consumption (Ferguson et al. 2002).

Growing-season burns in southeastern pine forests can be patchier than dormant-season burns because of higher moisture conditions and spatial variation in rate of green up (Slocum et al. 2003, Wade et al. 2000). However, Glitzenstein et al. (1995a) found that burns conducted at eight different times of the year all burned across much of the forest floor (96 to 100 percent).

In hardwood forests, prescribed burns typically reduce the fine woody material, but leave the duff layer intact. A fall (November) burn in southern Ohio was found to be hotter than a spring (March) burn, presumably because the leaf litter had freshly fallen and was less degraded/decomposed (Schwemlein and Williams 2007). The opposite, with spring (April) prescribed burns having greater intensity than winter (February) or summer (August) burns has also been reported (Brose and Van Lear 1998, Brose et al. 1999). In the latter study, relative humidity was the lowest during the spring burns.

Differences among studies and among season-of-burning treatments within the same study may be due to weather at the time of burning, timing relative to recent precipitation events, or just year-to-year climatic variability. Variation among studies is also possible because of differences in vegetation type and fuel bed composition. One common trend is that air temperatures are often higher at the time of growing-season burns, and higher initial vegetation temperature means that less heating may be necessary to reach the threshold for tissue damage (Byram 1948). In the Southeastern United States, greater intensity often reported with growing-season burns may also be due to the tendency to use heading fires (burning with the wind or upslope) at this time of year. Higher relative humidity and more fine fuel moisture can make backing fires (burning into the wind or downslope) slow moving or ineffective, leading to a greater use of heading fire to speed the rate of burnout (Robbins and Myers 1992).

Ecological Effects of Burning Season

Trees

Pines—

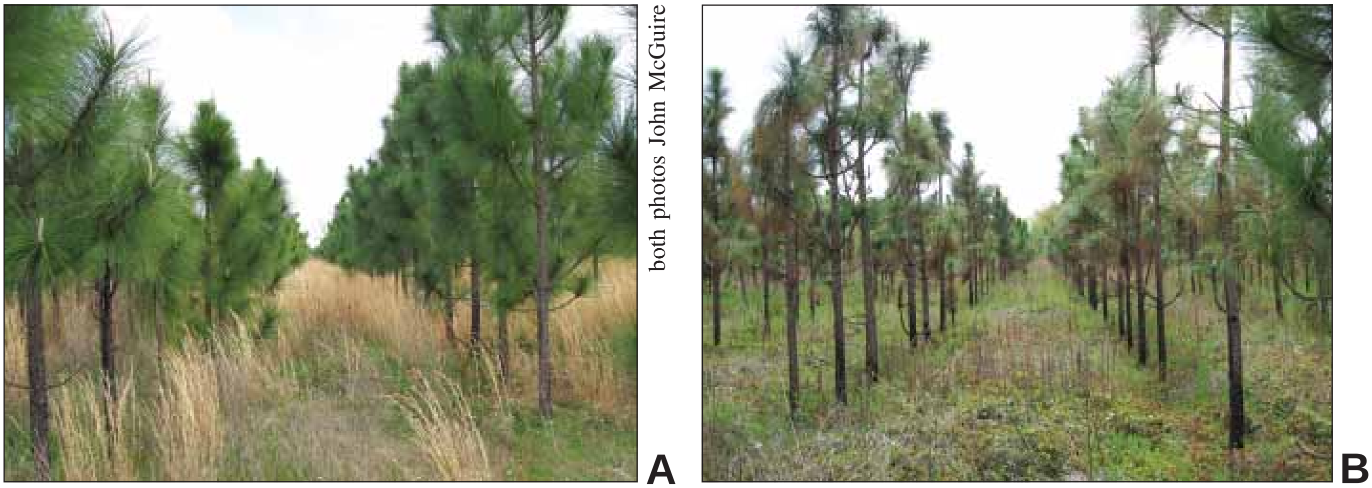
Fire is a vital tool in the management of pine forests in the Southeastern United States. Early research guided managers who were focused on timber production to avoid burning during the growing season (May—August) because of concern that damage to the tree crop would reduce profits (Bruce 1954).

Tree mortality can result from excessive root loss, damage to bole cambium, or crown scorch/photosynthetic material loss, some or all of which can differ among seasons. Duff consumption, which is considerably greater when moisture levels are low, has been linked to increased longleaf pine mortality in long unburned forests where substantial duff had accumulated (Varner et al. 2007). Lowest duff moisture levels are often found from late in the dormant season to early in the growing season (March—April) (Varner et al. 2007). Mechanisms of tree mortality were not determined, but could be the result of root death or cambium damage. However, fine roots are less likely to grow into the duff layer when it is dry. Thus greater duff consumption may not necessarily translate into greater fine root mortality. There is some evidence that root growth may be reduced more following summer (July) burns than dormant- (March) and early-growing-season burns (May) (Sword Sayer et al. 2006). However, this later study occurred during a drought year and results may be most applicable to these drought conditions.

Early research showed that pine crowns were more severely scorched by spring or summer (May—August) burns than by fall and winter (October—March) burns, owing to higher ambient temperature, which reduced the time to reach lethal heating and cause foliage mortality (Byram 1948). It was assumed that greater crown loss would mean higher mortality or slower growth. To test the effect of crown loss in different seasons, Weise et al. (1989) experimentally defoliated loblolly and slash pines to varying levels in January, April, July, and October, and found substantial mortality only after October defoliation. Southern pines form new buds and flush multiple times during the growing season and can therefore recover better from defoliation if it occurs prior to the last flush of the season. In the fall, when no additional growth is expected until the following spring, the time between tissue loss and regrowth of photosynthetic structures is greater, which apparently causes more stress on the tree.

In one of the most robust long-term studies of burning season (St. Marks study, St. Marks National Wildlife Refuge, Florida), mortality of mature longleaf pines with burns conducted at eight different times of the year did not vary in any predictable way (Glitzenstein et al. 1995a). Much of the other literature on postfire mortality or growth rates of pines has also reported no effect or mixed results of burning season (Boyer 1987, 1993, 2000; Waldrop et al. 1987, 1992). Magnitude of any burning-season effect may be a function of tree age, with the seedling stage of some species being more sensitive. Greater mortality was noted in longleaf pine saplings following summer (August) than following winter (January) or spring (May) burns (Boyer 1982, 1987) (fig. 19). Seedlings appear to benefit more from growing season (May) burns, presumably at least in part because fire at this time of year reduces the incidence of fungal infections such as brown spot needle blight (*Scirrhia acicola* (Dearn.) Siggers) (Bruce and Bickford 1950; Glitzenstein et al. 1995a; Grelen 1978, 1983; Wade and Johansen 1986).

Fire intensity and season are confounded in many burning studies. In south Florida, slash pine was found to experience higher mortality with fall burns (September—November) compared to burns in other seasons (Menges and Deyrup 2001). However, char heights were also greatest for the fall burns. Measures associated with fire intensity (i.e., percentage of green canopy and bark char) were most strongly associated with tree mortality within burns in the same season as well. Glitzenstein et al. (1995a) reported fall (October) burns to be the most intense in one treatment cycle, and found that pine mortality in the 2 to 3.5 in diameter at breast height (dbh) size class appeared to be correlated with amount of fuel consumed (and total heat released), whereas mortality of pines greater than 3.5 in dbh was correlated with fireline intensity. Menges and Deyrup (2001) noted that mortality was less when low-intensity backing fires were used, rather than heading fires.



both photos John McGuire

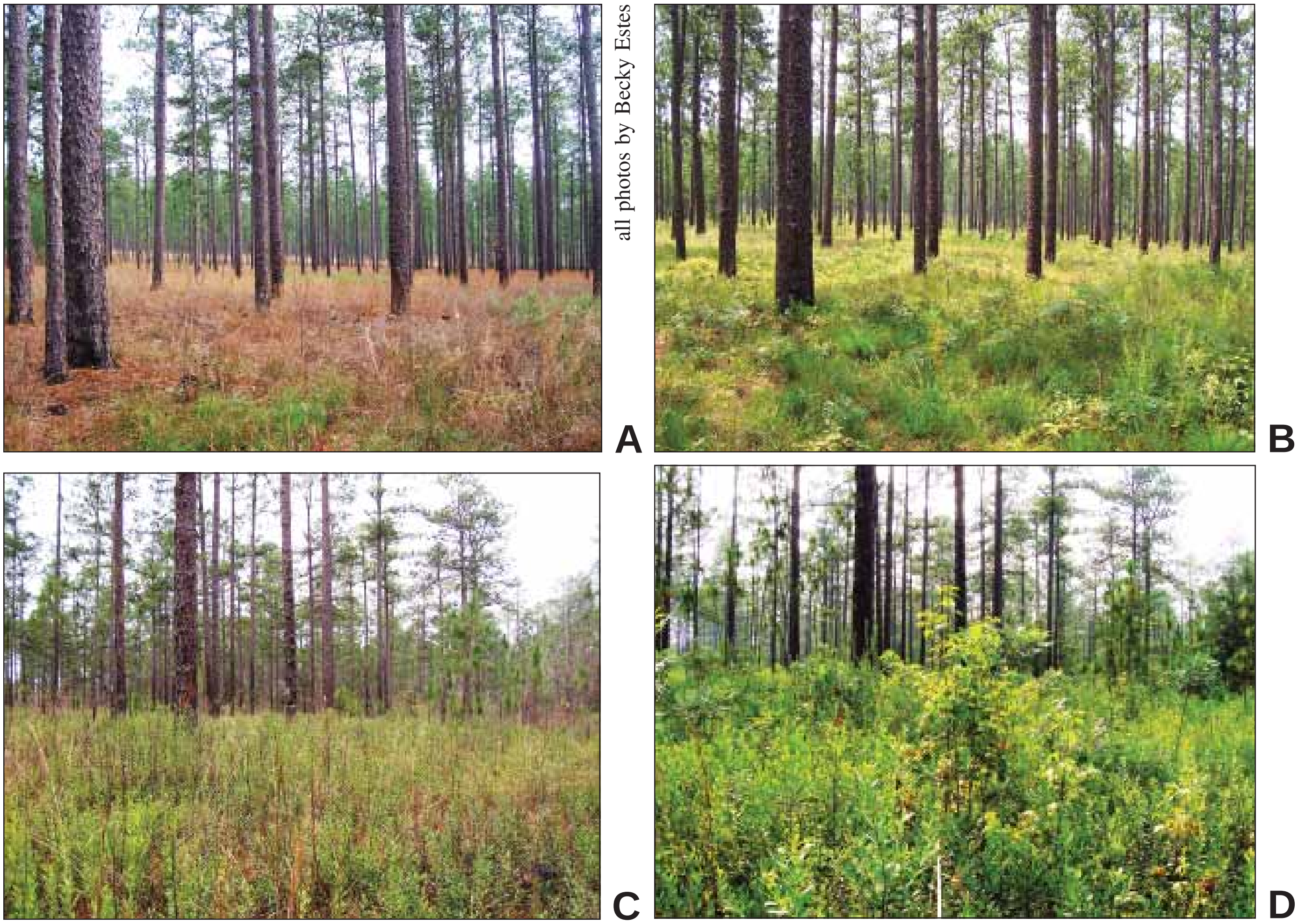
Figure 19—Comparison of the effects of prescribed burns conducted in a 6-year-old longleaf pine plantation established on old agricultural fields at the Monroeville Experiment Station, Alabama burned in (a) February 2007 and (b) August 2007. Photos were taken in March of 2008. Fire intensity was greater in the August burns, causing more crown scorch. However, little mortality was noted with fires in either season. Trees burned in the February fire dropped their scorched needles during the summer, but trees burned in the August fire retained scorched needles throughout the winter.

Reviewing the literature, Robbins and Myers (1992) concluded that burning season appears to have little effect on the growth rate of mature pines, but mortality is often somewhat more following fires late in the growing season, which corroborates the previously mentioned defoliation study of Weise et al. (1989). However, considerable variation in results have been reported, which probably has to do with differences in fuel consumption and resulting fire intensity among seasons, as well as the time of year burns were conducted relative to tree phenology (Glitzenstein et al. 1995a, Robbins and Myers 1992) (fig. 20). Glitzenstein et al. (1995a) suggested that fire intensity may explain much more of the variation in effects to longleaf pine than either the ambient temperature at the time of burning or the phenology/burning season.

Overstory hardwoods—

A frequent goal in restoring fire to eastern hardwood forests is to improve growing conditions for a variety of oak (*Quercus* L.) species. In the absence of fire, hardwoods such as maples (*Acer* L. sp.) and yellow poplar (*Liriodendron tulipifera* L.) that would normally be restricted to wetter sites have gradually moved into the uplands, outcompeting and eventually replacing the oaks (Nowacki and Abrams 2008). Because the majority of prescribed burning in this forest type is done in the dormant season when litter is the most flammable (similar to the main historical fire season), season of burning is less of an issue. As a result, few burning-season studies have been done in hardwood stands.

Of fires conducted in February, April, and August, the April fires were, on average, the most intense and did the most to favor oaks over yellow poplar (Brose and Van Lear 1998, 1999; Brose et al. 1999). Variation within burns was exploited to investigate regeneration differences with burn intensity and burn season. High-intensity fire was the most effective at reducing yellow poplar and favoring oak in each burn season. Although summer burns were predominantly low intensity owing to shading and higher relative humidity, moderate- and high-intensity patches within the fires at this time of year produced the strongest differences in regeneration success between species. It therefore appears that both fire intensity and phenology play a role.



all photos by Becky Estes

Figure 20—Longleaf pine stands on the Escambia Experimental Forest, near Brewton, Alabama, that have been managed with prescribed fire for multiple decades, showing both the phenology of vegetation at different times of the year and vegetation changes owing to timing of the fire treatments. The top two photos are from a unit managed with a mix of growing- and dormant-season burns, with photos taken in (a) March—dormant season and (b) July—growing season. The bottom two photos are from a unit managed with primarily dormant-season burns, with photos taken in (c) March—dormant season and (d) July—growing season. Note that the growing season burns appear to have more effectively reduced shrubby understory vegetation. The mechanisms of burning-season effects are often difficult to isolate because fire frequency, fuel loading, and canopy cover can confound the role season may play in determining the outcome.

Understory Vegetation

Shrubs and hardwoods—

Maintaining adequate regeneration of overstory trees is a common goal in the management of pine forests. To reduce competition for light, fire is used to selectively top-kill the hardwood midstory and shrub understory, while minimizing the impact to overstory pines. Numerous research results have suggested that burning during the peak of the historical fire season (May) reduces stem density of understory hardwoods more so than burns at other times of the year (Boyer 1993, Drewa et al. 2006, Glitzenstein et al. 1995b, Streng et al. 1993, Waldrop et al. 1987, White et al. 1991). This is particularly true if burns are repeated at annual or biennial intervals. A single burn in any season will not kill enough plants to control hardwood resprouting (Boyer 1990). However, following 43 years of burning on the Santee Experimental Forest in

South Carolina, fewer hardwood sprouts survived with a fire regime of annual late spring/early summer (June) burns than annual winter (December) burns (Waldrop and Lloyd 1991). With late spring/early summer burns, the woody vegetation was gradually replaced by an understory dominated by forbs and grasses (Waldrop et al. 1987) (fig. 20). In contrast, more oaks and other hardwoods were maintained with repeated burns during the fall/winter dormant season (October—January) (Jacqmain et al. 1999). In another study in shortleaf pine—grassland ecosystems of Arkansas, late-growing-season (September—October) burns were found to be less effective for reducing understory hardwoods than late-dormant-season (March—April) burns (Sparks et al. 1999).

It is important to note that the regime of annual growing-season burning that most successfully reduced competing hardwoods and shrubs in two of the most widely cited studies (Santee Experimental Forest study (Waldrop et al. 1987, Waldrop and Lloyd 1991), and St. Mark's National Wildlife Refuge study (Glitzenstein et al. 1995a, 1995b; Streng et al. 1993) was considerably more frequent and invariant than was likely the case historically and therefore may not be the most beneficial for other components of the ecosystem. Although fires as frequent as 1 to 2 years apart have been recorded in the tree ring record of eastern pine forests, the overall historical fire-return interval averaged 3 to 7 years (Henderson 2006). Annual prescribed burning may not even be possible in some stands, if fuel accumulation rates are slower. For pines to regenerate naturally, longer fire-free periods may be necessary so that seedlings can establish and grow above the zone of lethal heat. Depending on the management objective, a prescribed burning regime of variable frequency and seasonality (within the historical ranges) may be preferred.

There are several explanations relating both to the physiological status of the plant and to fire intensity for the difference in midstory hardwood and shrub mortality following burns in different seasons. Physiological status appears to play a role in the greater shrub and hardwood reductions noted with growing-season burns in many studies. During the dormant season, shrubs store more of their carbohydrates underground, and these carbohydrates enable resprouting when the aboveground portion is killed by fire (Drewa et al. 2002). During the growing season, more of the carbohydrates are allocated aboveground, and are lost with topkill, leaving fewer reserves for resprouting. Drewa et al. (2002) evaluated shrub response to fires of different temperatures in different seasons and found changes were not associated with fire intensity, suggesting that the physiological status of the shrub at the time of burning may be playing a greater role. Studies of defoliation of evergreen shrub species in different seasons also point to a physiological influence, with one study reporting complete kill following leaf removal in October, but a much reduced effect in April (Kramer and Wetmore 1943). Other studies suggest an effect of fire intensity differences among burn seasons (Drewa et al. 2006, Glitzenstein et al. 2003). Shorter statured vegetation, such as midstory hardwoods and shrubs, is more likely to be affected by seasonal differences in scorch height (Robbins and Myers 1992). In the Sparks et al. (1999) study, the dormant-season burns (March—April) were both more intense and more effective at thinning the midstory hardwoods than the late-growing-season burns (September—October), suggesting that differential intensity may have overwhelmed effects of phenology. Indeed, some burning-season studies have reported fire intensity to be just as important as phenology in shaping the outcome (Glitzenstein et al. 1995b, Sparks and Masters 1996).

Less is known about effects of burning season on understory shrubs in areas north of the southeastern pine zone. In one of the few studies on the topic, Schwartz and Heim (1996) noted that 95 percent of small saplings and shrubs in an Illinois forest were top-killed by either a single dormant-season (March) burn or a single growing-season (May) burn. In another study of understory response in mixed-hardwood and pine forests of Minnesota, both spring dormant-season and summer growing-season burns completely top killed hazel (*Corylus* L.), but resprouting was enhanced by repeated spring burning and reduced by repeated summer burning (Buckman 1964). Because humus was combustible during dry summer conditions, fires at this time of year were more likely to kill the roots. Carbohydrate reserves were also more likely to be exhausted following repeated summer burning.

Herbaceous understory—
Burning during the historical fire season has been hypothesized as important because organisms are presumably best adapted to disturbance at this time of year. Studies show that this may indeed be the case for some understory plant species of southern pine forests. At the St. Marks National Wildlife Refuge in Florida, greater increases in shoot number and flowering of narrowleaf goldenaster (*Pityopsis graminifolia* (Michx.) Nutt.) were observed following burns in May than burns in January or August (Brewer and Platt 1994a, 1994b; Brewer et al. 1996). The increases in shoot numbers did not lead to long-term increases in stem densities, however, suggesting that there may be some cost to using resources for reproduction (Brewer 2006). Although the flowering response indicates an adaptation to and dependence on growing-season fire, Brewer (2006) hypothesized that this species would likely benefit from "modest variability in fire frequency and fire season." Numerous grass species, including the commonly studied wiregrass (*Aristida beyrichiana* Trin. & Rupr.), also flower more vigorously after growing-season burns (Main and Barry 2002, Outcalt 1994, Streng et al. 1993). Saw palmetto produced more flowers and fruits with periodic growing-season (April—July) burns than with dormant-season (November—February) burns (Carrington and Mullahey 2006). Growing-season burns have also been shown to increase flowering synchrony of forbs and shrubs by decreasing the flowering duration (Platt et al. 1988). Flowering synchrony may lead to a higher probability of cross pollination. In another study, no difference in the density of reproductive American chaffseed (*Schwalbea americana* L.) plants was noted between burning-season treatments (Kirkman et al. 1998). Numbers increased following burning in either the growing or dormant season. However, burning season did influence the timing of flowering, with plants flowering earlier after dormant-season burns than after growing-season burns.

The positive response of some species to growing-season burning provides evidence for fire at this time of year being an important part of the natural disturbance regime. However, what is best for one species may not be for all, with some species also responding more strongly to dormant-season burns (Hiers et al. 2000, Liu and Menges 2005, Sparks et al. 1998). Many species do not appear to be influenced by burning season at all. For example, of the more than 150 plant species evaluated for response to late growing-season (September—October) and late dormant-season (March—April) burns in a shortleaf pine-grassland community in Arkansas, fewer than 10 percent were differentially affected by burning season (Sparks et al. 1998). The variable response of understory species to fire season suggests that a heterogeneous fire regime (including variation in the seasonal timing of fire) may help conserve biodiversity (Hiers et al. 2000, Liu et al. 2005).

For species with growth or flowering influenced by burning season, response has sometimes been shown to differ at fine temporal scales—i.e., for fires within the same growing season (Negron-Ortiz and Gorchov 2000, Rideout et al. 2003), or among plant growth stages (Spier and Snyder 1998). Negron-Ortiz and Gorchov (2000) reported that early wet-season (May—June) fires were beneficial and late wet season (July—September) fires detrimental to the cycad species *Zamia pumila* L. The variation in response of herbs and woody plants observed among burns within the growing season by Rideout et al. (2003) was attributed mainly to climatic differences. Liu and Menges (2005) noted that slight differences in burn timing within the wet (growing) season had substantial effects on survival and growth of big pine partridge pea (*Chamaecrista lineata* (Sw.) var. *keyensis* (Pennell) Irwin & Barneby), and concluded that comparing fires by seasons may be too broad and not useful to managers.

In a study of response of multiple growth stages, small plants of the forest herb pineland Jacquemontia (*Jacquemontia curtisii* Peter ex Hallier f.) suffered greater mortality with growing-season (June) prescribed burns than dormant-season (January) burns, even though the latter burns were hotter (Spier and Snyder 1998). However, the plants surviving the growing-season burns produced more flowers. Therefore, different parts of the plant lifecycle were variably affected by burning season. Similar findings have been reported for wiregrass, where growing-season burns promote flowering, but also cause higher mortality of established seedlings than dormant-season burns (Mulligan et al. 2002, Streng et al. 1993), and big pine partridge pea, where stem growth was greater but plant survival lower following growing-season (summer) burns (Liu and Menges 2005). These results all highlight the importance of variability in the fire regime.

At the plant community level, repeated growing-season burning generally increases the cover of grasses and diversity of herbaceous species (Drewa et al. 2002, 2006; Lewis and Harshbarger 1976; Waldrop et al. 1987; White et al. 1991). This shift is likely because of release from shrub competition (shrubs are selected against by growing-season burns) and removal of the litter layer (Lewis et al. 1982). The robustness of the understory herbaceous layer is not only important for biodiversity conservation, but also for grazing animals. Studies focused on livestock management have reported grass productivity gains with early growing-season burns (Grelen and Epps 1967, Lewis and Harshbarger 1976), which is likely also tied to reduced shrub competition. However, overall productivity (herbs and shrubs) was found to be greater following fall burns than spring burns (Schneider 1988). Other studies that have followed productivity over several years have been unable to document any increase in biomass and cover of grasses and forbs with burns in different seasons (Streng et al. 1993).

Sparks et al. (1998) suggested that understory composition was, in part, influenced by fire intensity through its effect on litter consumption and woody shrub removal. However, fire intensity did not appear to play much of a role in another study. Hierro and Menges (2002) burned plots containing between 2.6 and 7.1 tons/ac of surface fuel with and without 54.0 tons/ac of additional fuel, and found little effect on understory shrub species richness or density although the fuel addition treatment significantly increased fire temperatures and soil heating. The authors suggested that species are well adapted to variation in fire intensity. In another study, plant mortality did not differ with fuel consumption differences, suggesting that seasonal timing may be more important than fire intensity (Liu and Menges 2005). However, a big picture view suggests that the effect of season of burning is less critical to maintaining understory biodiversity in the longleaf pine system, than frequency of burning (Palik et al. 2002).

One cautionary note on repeated burning: despite the many benefits of growing-season burning that have been reported in the literature, a recent publication from the St. Marks study in Florida indicates that growing-season burns, if applied annually, may over time actually reduce the cover of plants such as wiregrass that are stimulated to flower by fire (Glitzenstein et al. 2008). These results warrant closer scrutiny to determine whether invariable and frequent growing-season burns cause the grasses to invest an excessive amount of carbohydrate reserves into reproduction, thereby reducing the plants’ ability to grow vegetatively over the long term (Brewer et al. 2009).

Much less literature is available for the understory of eastern hardwood ecosystems than southern pine-dominated ecosystems. Perennial herbs in oak forests generally emerge from rhizomes and are dormant during the typical spring and fall burning periods. Because heat penetration into the soil with the burning of leaf litter is generally minimal, resprouting from dormant rhizomes is likely little affected by burning at either time. Any change in the understory as a result of burning season is expected to result more from indirect effects, such as reduced competition with top kill of midstory shrubs, or consumption of the litter layer (Keyser et al. 2004). Keyser et al. (2004) found that plant cover and species richness in an oak-dominated forest increased following fire regardless of whether burning occurred in February, April, or August, but the more intense spring and summer burns led to a shift toward herbaceous species, whereas the winter burn resulted in dominance by shrubs. In a degraded Illinois woodland, growing-season (May) burns were more effective than dormant-season (March) burns at controlling an exotic species (Schwartz and Heim 1996). However, May burns also caused different and longer lasting effects to the native herbaceous understory than March burns, with composition in the March (dormant season) burn plots appearing more similar to the unburned control.

Soils

Consumption of surface and live fuels releases nutrients, some of which may be leached from the system unless they are taken back up by micro-organisms or growing vegetation. It is therefore believed that prescribed fire close to the onset of growth or during the active season when growing tissue is accumulating nutrients might lead to less leaching from the system (Robbins and Myers 1992). Another possibility is that more nutrients could be volatilized when actively growing tissues are burned than when tissues are burned during the dormant season. By the time of the dormant season, at least some of the nutrients from aboveground structures have already been translocated to underground storage structures and therefore escape being volatilized (Robbins and Myers 1992). However, as Robbins and Myers (1992) noted, very little data are available to back up either the leaching or volatilization theories. In longleaf pine forests, Boring et al. (2004) documented greater nitrogen loss with growing-season (June) burns than dormant-season (March—April) burns, presumably as a result of live fuels being volatilized. However, nitrogen fixation and atmospheric deposition were believed sufficient to compensate for this loss if the fire regime is not exclusively growing season—i.e., including a mix of seasons. There was no difference in phosphorous with burning-season treatments (Boring et al. 2004). Temperatures were apparently not high enough for any of the burns to volatilize this nutrient. Another recent study reported very little effect of burning season on soil variables in an oak-pine forest in Massachusetts (Neill et al. 2007). The organic horizon (duff layer) was reduced more by summer burns than by spring burns, and replacement with mineral soil caused the bulk density to also be higher. All other variables including pH, acidity, base saturation, total exchangeable cations, carbon, and nitrogen did not differ between burn seasons.

Some other potential impacts of fire in different seasons on soils are likely associated with variation in fire intensity or extent of soil exposure. Soil is exposed for a longer period after burns in fall and winter (dormant season), and this could alter the rate of erosion. In their literature review, Robbins and Myers (1992) found only a single study addressing erosion and season of burning. Dobrowolski et al. (1987) reported greater sediment yields after winter burns than spring and summer burns, attributing this to direct exposure of the soil to raindrops for a longer period with winter burns. Summer burning produced the least erosion, possibly because these burns were patchier. The lack of studies on erosion with prescribed fire in the Eastern region may be due, in part, to the relative lack of topography in many areas with active prescribed burning programs.

Wildlife

Early forest managers generally avoided burning southeastern pine forests during the late spring and early summer, because of concerns about harming wildlife species. However, with this time of year being the peak historical fire season, others concluded that wildlife must have evolved means to survive (Komarek 1965). Direct effects to wildlife are perhaps less of a concern in the eastern hardwood forest ecosystems because especially in the north, fire historically occurred primarily during the dormant season when many species are less active.

Birds—

Timing of early prescribed burning in the Southeastern United States was strongly influenced by concerns about game birds and other ground-nesting species (Stoddard 1931). Late winter to early spring burning became popular because this period occurred after the end of hunting season but prior to nesting season for quail and other species (Brennan et al. 1998). To reduce the feared catastrophic effect on clutch success of ground-nesting species, burning at this time of year became “ingrained in the culture of the Southeast" (Brennan et al. 1998). However, the majority of studies have since shown few strong effects of burn season on direct mortality, breeding success, or survival of birds (Cox and Widener 2008; Engstrom et al. 1996; Tucker et al. 2004, 2006). In fact, overwinter survival of Henslow's sparrow (*Ammodramus henslowii*) was found to be greater in areas previously burned in the growing season than in areas previously burned in the dormant season (Thatcher et al. 2006). In another study, abundance of wintering bird communities did not differ one year after burns conducted in the growing season (April—August) or the dormant season (January—March) (King et al. 1998).

Many bird species prefer to nest in stands that have been burned within 1 or 2 years (Cox and Widener 2008). For example, the majority of Bachman's sparrow (*Aimophila aestivalis*) nests (>85 percent) were found in areas that were recently burned during the growing season, and the majority of wild turkey nests (62 percent) were found in forest that had experienced a growing-season burn within the past 2 years (Cox and Widener 2008, Sisson et al. 1990). Management using a regime of growing-season burns 3 or more years apart, but within a patchy landscape with units varying in time since last fire, would therefore likely impact relatively few ground nests.

Changes in vegetation brought about by burning in different seasons can indirectly influence bird populations (Engstrom 1993). Dormant-season burning in longleaf pine forests can impact the structure and composition preferred by different bird species by promoting hardwoods over grasses and forbs (Abrahamson and Hartnett 1990). Red-cockaded woodpecker (*Picoides borealis*) and other bird species are generally less abundant in forests where understory hardwoods have encroached (Provencher et al. 2002, Sparks et al. 1999). Although lengthening of fire intervals is believed to be the main cause of red-cockaded woodpecker decline, growing-season burns have been shown to more effectively suppress midstory hardwoods and promote a ground cover composition favorable for arthropod food sources for these birds (James et al. 1997). In a study of bird community response to fire, Fitzgerald and Tanner (1992) found that neither January nor June prescribed burns in a dry prairie in south Florida altered bird species richness, compared with the unburned control. Both of the burning-season treatments reduced shrub cover.

Ground cover is beneficial to some overwintering migratory birds such as Henslow's sparrow—burns in the winter (February—March) eliminate this ground cover, and research shows that growing-season burns improve survival over dormant-season winter burns (Thatcher et al. 2006). Spatial patchiness is another characteristic of fires potentially important for birds and other wildlife (Sparks et al. 1999), and spatial patchiness can differ among burning seasons because of variation in fuel moisture.

Overall, reviews of the limited literature show few if any effects of burning season on bird populations. Although growing-season burns may cause some direct mortality by destroying nests and killing young birds, many bird species renest, and the indirect benefits of habitat alteration are usually far more important and likely compensate or more than compensate for losses (Engstrom et al. 2005, Robbins and Myers 1992).

Small mammals—

The effect of different prescribed burning seasons on small mammal populations remains poorly studied. Both historical fires and prescribed burns in eastern forests may be of sufficiently low intensity and patchy enough that the variable needs of small mammal populations are met, regardless of burn season (Keyser and Ford 2006). A study in oak stands in Virginia that compared effects of winter, spring, and summer prescribed burns reported no detectable short-term losses of ground-dwelling species such as shrews (*Sorex* and *Blarina*) and white-footed mice (*Peromyscus leucopus*) (Keyser et al. 1996, 2001). Longer term habitat changes, such as differences in hardwood midstory cover or ground exposure owing to variation in the burning season, could potentially affect small mammal populations. Fires conducted in March or August annually for 3 years in Florida longleaf pine sandhill forests resulted in no difference in pocket gopher (*Geomys pinetis*) mounding or body size (Gates and Tanner 1988). Although a minor increase in herbaceous biomass was noted following March burns, this apparently did not influence gopher behavior (Gates and Tanner 1988). Overall, consistent trends in small mammal response to habitat changes with burning season have not emerged (Ahlgren 1966, Brose and Van Lear 1999, Kirkland et al. 1996).

Amphibians and reptiles—

Direct effects of fire are not expected to be strong for amphibian species occupying moist habitats that are less flammable than the surrounding landscape. Prescribed burns during cool weather in the winter, or any time of the year when moisture is high, have a lower probability of passing through and consuming fuels in wetter areas. However, burns at these times of year may also coincide with winter mating migrations when individuals can be more vulnerable. Varying the burn season to include growing-season burns as well as dormant-season burns has been suggested as one means of reducing the potential impact of fire (Schurbon and Fauth 2003).

It is possible that amphibian and reptile species are indirectly influenced by burning season through differential effects on habitat structure. For example, certain species of longleaf pine forests require bare sandy habitats and are thus benefited most by relatively intense and spatially variable burns (Russell et al. 1999), which are more likely in some seasons than others. Growing-season burns have been reported to be more intense and more likely to clear overgrown vegetation surrounding wetlands; some amphibians apparently prefer the higher light levels and warmer temperatures that result (Bishop and Haas 2005). In a study by Yager et al. (2007), reduction of midstory cover of longleaf pine forests through application of a mixture of dormant-season and growing-season burns increased habitat usage by gopher tortoises (*Gopherus polyphemus*). Burn seasons most effective at reducing the height of understory vegetation are likely to favor not only the gopher tortoise but other species that utilize gopher tortoise burrows such as the Florida pine snake (*Pituophis melanoleucus mugatis*) and Florida gopher frog (*Rana capito aesopus*).

Several studies have compared amphibian and reptile populations after dormant- and growing-season prescribed burns and none have found a significant difference in numbers (Floyd et al. 2002, Keyser et al. 2004). The lack of an effect can be attributed to incomplete consumption of coarse woody debris and duff, the existence of moist environments such as tunnels and cracks in the soil or under rocks that escape heating, mobility of the organisms, relatively few changes to the overstory canopy, and generally quick regrowth of understory vegetation (Renken 2006).

Arthropods—

Hall and Schweitzer 1992 (cited in Hermann et al. 1998) hypothesized that burning during the growing season may have fewer detrimental effects on arthropods than burning during the dormant season because a greater number of individuals have wings and are mobile at this time of year. Arthropod abundance was found to be equal or greater following growing-season burns than following dormant-season burns (Hermann et al. 1998). However, a fall survey in Florida oak scrub found that garden orbweaver spider (*Argiope* sp.) numbers were not affected by burns in February, but were substantially reduced by burns in July and August (Carrel 2008). Spiderlings disperse in April and May through ballooning, so the low numbers immediately following summer fires may simply be due to lack of dispersal opportunities between the time of the fire and the time of sampling. In a hardwood stand in Kentucky, a single March prescribed fire reduced the invertebrate mass by 36 percent, with the majority of this loss occurring among species associated with the forest floor (Kalisz and Powell 2000).

Neither burns in July nor November altered the population size of the Karner Blue butterfly (*Lycaeides melissa samuelis*) 1 to 3 years later, compared with unburned controls (King 2003). The July burns were during the period of the second flight of the summer, whereas the November burns occurred after activity had ceased for the year. Burns in both seasons were described as “cool” (i.e., not at times of the year when flame lengths are greatest), which may have allowed some of the eggs on vegetation in this oak savanna system to survive.

Overall, it is apparent that how fire affects arthropods will differ greatly by species and functional group, with burning potentially most detrimental if the timing coincides with a particularly vulnerable life history stage (Robbins and Myers 1992). Several authors have recommended that prescribed burning be done in such a way as to maximize patchiness so that invertebrates are able to survive in refugia and recolonize the burned areas (Kalisz and Powell 2000, Knight and Holt 2005).

Implications for Managers

The majority of studies on burning-season effects in eastern forest ecosystems have been conducted in pine- and pine-oak-dominated forests of the Southeast. In this forest type, the literature provides compelling evidence that growing-season fire can lead to shifts in the plant community, relative to a regime of dormant-season fire. Repeated burns during the growing season (especially in May, early in the growing season) curtail resprouting and eventually suppress the less fire-resistant midstory hardwood vegetation more so than burns at other times of the year. On the other hand, the pine overstory appears to be minimally affected by burns in any season. This is particularly true for longleaf pine, a strongly fire-adapted species. The end result is that repeated growing-season burning leads to greater grass and herbaceous species abundance and diversity under the pine canopy, whereas more shrubs may be maintained with a regime of dormant-season burning.

Key Points—Eastern Region

- There is little evidence that mortality or growth of southern pines differs after growing- or dormant-season prescribed burns.
- Phenology does influence the response of midstory hardwoods in pine forests, with early-growing-season (May) burns (coupled with short fire-return intervals) more likely to control or kill these species than dormant-season burns. The result of early-growing-season burns is often an understory with greater cover of grasses and forbs.
- Burning season has little effect on growth and mortality of overstory oak species, but higher intensity fire (in whatever season fuels are sufficiently dry to burn at higher intensity) likely favors oaks over the long term, by killing competing mesophytic species such as yellow poplar or maple.
- Although some understory plant species respond positively to fire in the growing season and others respond positively to fire in the dormant season, the majority do not appear to be significantly affected by burning season.
- Few strong direct impacts to wildlife from prescribed fire in any season have been documented; effects, both positive and negative, appear to be mostly indirect, and primarily the result of fire-season-specific habitat changes.
- Whether the ecosystem is burned or not (fire frequency) appears to play a stronger role in the response of most species than the relatively minor effect caused by different burning seasons.
- Differences in fire effects among species suggests that a variable fire regime, including a mix of growing- and dormant-season burns and different burn intensities may maximize biodiversity.

Early prescribed burning was often done during the dormant season to avoid conflicts with wildlife reproduction, including bird nesting. However, recent research generally does not show that burns in the growing season affect bird populations more than burns at other times of the year. In the few cases where differences in animal communities with varying burning seasons have been reported, the mechanism is usually indirect, involving some alteration of understory structure. Understory vegetation of the Southern United States grows so rapidly in the absence of fire that the effect of burning or not (fire frequency) is generally much greater than the effect of burning season.

Both phenology and fire intensity appear to play a role in determining fire effects in forests of the Eastern region, with the outcome depending on the species and the differences in intensity between burn seasons. As with fire in the Western and Central regions, phenology and intensity are often confounded, making their relative contributions a challenge to determine. Several of the more robust studies of burning season concluded that for many species, fire intensity plays a significant role in determining the outcome. Differences in intensity, if any, are often due to higher ambient temperatures and greater use of heading fires during the growing season. However, lower fuel moisture levels can also sometimes result in dormant-season burns being more intense, particularly in hardwood forests that lack the pyrogenic vegetation of the southeastern pine zone.

The importance of phenology relative to fire intensity in the Eastern region appears to be intermediate between the Western region and the Central grasslands; this goes along with apparent differences in the amount of fuel consumed between seasons, which are in most cases less than differences among burning seasons in the Western region, but greater than differences among burning seasons in the Central grasslands. For some species, fire intensity may override the effects of phenology at the time of the burn, especially if the difference in fire intensity among seasons is substantial.

Data from the many long-term burning studies conducted in the Southeastern United States indicate that substantial changes likely require many burn cycles to achieve. A single burn in any season generally does little to alter plant or animal communities. Therefore one burn or a few burns outside of normal season is/are unlikely to have a major impact. In addition, the importance of burning generally outweighs any effect of season of burning. Because prescribed burns are usually easier to conduct during the dormant season than during the growing season/lightning season, more acres may ultimately be treated by employing a regime of both dormant- and growing-season burns.

One key point mentioned repeatedly in the literature is that a frequent yet heterogeneous fire regime, including a range of fire seasons, may be necessary to sustain species diversity, or even to maximally benefit individual species where different parts of the life cycle are variably affected by burning season. To mimic the variability inherent in the historical fire regime, Robbins and Myers (1992) created a table of random fire frequencies and seasons (within specified ranges) for xeric to mesic longleaf pine habitats, with a weighting so that two growing-season (May-June) burns are conducted for each dormant-season burn. The objective of such a table is to ensure that rigid burning schedules, which would tend to favor some species over others, are avoided. Also, occasional longer (8 to 10 years) rest periods are incorporated that would allow seedlings of certain species to become established (Robbins and Myers 1992).

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Metric Equivalents

When you know:	Multiply by:	To find:
Inches (in)	2.54	Centimeters
Square miles (mi^2)	2.59	Square kilometers
Tons per acre	2.24	Tonnes or megagrams per hectare
Degrees Fahrenheit	0.55 (F-32)	Degrees Celsius

Literature Cited

Abrahamson, C.R.; Hartnett, D.C. 1990. Pine ecosystems. In: Myers, R.L.; Ewel, J.J., eds. Ecosystems of Florida. Orlando, FL: University of Central Florida Press: 103–149.

Abrams, M.D. 1992. Fire and the development of oak forest. Bioscience. 42(5): 346–353.

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Covelo, CA: Island Press. 505 p.

Ahlgren, C.E. 1966. Small mammals and reforestation following prescribed burning. Journal of Forestry. 64: 614–618.

Anderson, K.L.; Smith, E.F.; Owensby, C.L. 1970. Burning bluestem range. Journal of Range Management. 23: 81–92.

Anderson, R.C. 1990. The historic role of fire in the North American grassland. In: Collins, S.L.; Wallace, L.L., eds. Fire in North American tallgrass prairies. Norman, OK: University of Oklahoma Press: 8–18.

Ansley, R.J.; Castellano, M.J. 2007a. Texas wintergrass and buffalograss response to seasonal fires and clipping. Rangeland Ecology and Management. 60(2): 154–164.

Ansley, R.J.; Castellano, M.J. 2007b. Prickly pear cactus responses to summer and winter fires. Rangeland Ecology and Management. 60(3): 244–252.

Axelrod, D.I. 1985. Rise of the grassland biome, central North America. Botanical Review. 51(2): 163–201.

Bailey, A.D.; Mickler, R.; Frost, C.C. 2007. Presettlement fire regime and vegetation mapping in southeastern coastal plain forest ecosystems. In: Butler, B.W.; Cook, W., eds. The fire environment—innovations, management, and policy: proceedings of a conference. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 275–286.

Bailey, R.G. 1980. Description of the ecoregions of the United States. Misc. Publ. 1391. Washington, DC: U.S. Department of Agriculture, Forest Service. 77 p.

Bailey, R.G. 1983. Delineation of ecosystem regions. Environmental Management. 7(4): 365–373.

Baisan, C.H.; Swetnam, T.W. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, U.S.A. Canadian Journal of Forest Research. 20: 1559–1569.

Baker, R.G.; Bettis, E.A.I.; Schwert, D.P.; Horton, D.G.; Chumbley, C.A.; Gonzalez, L.A.; Reagan, M.K. 1996. Holocene paleoenvironments of northeast Iowa. Holocene. 66(2): 203–234.

Bale, A.M.; Guyette, R.P.; Stambaugh, M.C. 2008. Fire regime of a montane longleaf pine ecosystem, Alabama. In: Kush, J.S.; Hermann, S.M., eds. Proceedings of the third montane longleaf conference. Auburn, AL: Longleaf Alliance: 54–59.

Barden, L.S.; Woods, F.W. 1973. Characteristics of lightning fires in Southern Appalachian forests. In: Proceedings, 13th Tall Timbers fire ecology conference. Tallahassee, FL: Tall Timbers Research Station: 345–361.

Beckage, B.; Platt, W.J.; Slocum, M.G.; Panko, B. 2003. Influence of the El Niño southern oscillation on fire regimes in the Florida Everglades. Ecology. 84(12): 3124–3130.

Bekker, M.F.; Taylor, A.H. 2001. Gradient analysis of fire regimes in montane forests of the southern Cascade Range, Thousand Lakes Wilderness, California, USA. Plant Ecology. 155: 15–28.

Benning, T.L.; Bragg, T.B. 1993. Response of big bluestem (*Andropogon gerardii* Vitman) to timing of spring burns. American Midland Naturalist. 130(1): 127–132.

Beyers, J.L.; Wakeman, C.D. 2000. Season of burn effects in southern California chaparral. In: Second interface between ecology and land development in California. Open-File Report 00-62. Sacramento, CA: U.S. Department of the Interior, Geological Survey: 45–55.

Bidwell, T.G.; Engle, D.M.; Claypool, P.L. 1990. Effects of spring headfires and backfires on tallgrass prairie. Journal of Range Management. 43(3): 209–212.

Biondini, M.E.; Steuter, A.A.; Grygiel, C.E. 1989. Seasonal fire effects on the diversity patterns, spatial distribution, and community structure of forbs in the northern mixed prairie. Vegetatio. 85: 21–31.

Bishop, D.C.; Haas, C.A. 2005. Burning trends and potential negative effects of suppressing wetland fires on flatwoods salamanders. Natural Areas Journal. 25(3): 290–294.

Biswell, H.H.; Taber, R.D.; Hedrick, D.W.; Schultz, A.M. 1952. Management of chamise brushlands for game in the north coast region of California. California Fish and Game. 38(4): 453–484.

Bond, W.J.; van Wilgen, B.W. 1996. Fire and plants. London: Chapman and Hall. 272 p.

Boring, L.R.; Hedrick, J.J.; Wilson, C.A.; Mitchell, R.J. 2004. Season of burn and nutrient losses in a longleaf pine ecosystem. International Journal of Wildand Fire. 13: 443–453.

Boyer, W.D. 1982. Growth of young longleaf pine as affected by biennial burns plus chemical or mechanical treatment of competition control. In: Proceedings, 2nd biennial southern silvicultural research conference. Gen. Tech. Rep. SE-24. Atlanta, GA: U.S. Department of Agriculture, Forest Service: 62–65.

Boyer, W.D. 1987. Volume growth loss: a hidden cost of periodic prescribed burning in longleaf pine? Southern Journal of Applied Forestry. 11(3): 154–157.

Boyer, W.D. 1990. Growing season burns for control of hardwoods in longleaf pine stands. Res. Pap. SO-256. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 7 p.

Boyer, W.D. 1993. Eighteen years of seasonal burning in longleaf pine: effects on overstory growth. In: Fire, meteorology and the landscape: 12th conference on fire and forest meteorology. Bethesda, MD: Society of American Foresters: 602–610.

Boyer, W.D. 2000. Long-term effects of biennial prescribed fires on the growth of longleaf pine. In: Moser, W.K.; Moser, C.F., eds. Proceedings, 21st Tall Timbers fire ecology conference. Fire and forest ecology: innovative silviculture and vegetation management. Tallahassee, FL: Tall Timbers Research Station: 18–21.

Bradley, T.; Tueller, P. 2001. Effects of fire on bark beetle presence on Jeffrey pine in the Lake Tahoe Basin. Forest Ecology and Management. 142(1-3): 205–214.

Bragg, T.B. 1982. Seasonal variations in fuel and fuel consumption by fires in a bluestem prairie. Ecology. 63(1): 7–11.

Brennan, L.A.; Engstrom, R.T.; Palmer, W.E.; Hermann, S.M.; Hurst, G.A.; Burger, L.W.; Hardy, C.L. 1998. Whither wildlife without fire? In: Transactions of the 63rd North American wildland and natural resources conference. Washington, DC: Wildlife Management Institute: 402–414.

Brewer, J.S. 2006. Long-term population changes of a fire-adapted plant subjected to different fire seasons. Natural Areas Journal. 26(3): 267–273.

Brewer, J.S.; Cunningham, A.L.; Moore, T.P.; Brooks, R.M.; Waldrup, J.L. 2009. A six-year study of fire-related flowering cues and coexistence of two perennial grasses in a wet longleaf pine (*Pinus palustris*) savanna. Plant Ecology. 200: 141–154.

Brewer, J.S.; Platt, W.J. 1994a. Effects of fire season and herbivory on reproductive success in a clonal forb, *Pityopsis graminifolia*. Journal of Ecology. 82: 665–675.

Brewer, J.S.; Platt, W.J. 1994b. Effects of fire season and soil fertility on clonal growth in a pyrophilic forb, *Pityopsis graminifolia* (Asteraceae). American Journal of Botany. 81(7): 805–814.

Brewer, J.S.; Platt, W.J.; Glitzenstein, J.S.; Streng, D.R. 1996. Effects of fire-generated gaps on growth and reproduction of golden aster (*Pityopsis graminifolia*). Bulletin of the Torrey Botanical Club. 123(4): 295–303.

Brockway, D.G.; Gatewood, R.G.; Paris, R.B. 2002. Restoring fire and an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. Journal of Environmental Management. 65: 135–152.

Brose, P.H.; Van Lear, D.H. 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Canadian Journal of Forest Research. 28: 331–339.

Brose, P.; Van Lear, D. 1999. Effects of seasonal prescribed fires on residual overstory trees in oak-dominated shelterwood stands. Southern Journal of Applied Forestry. 23(2): 88–93.

Brose, P.; Van Lear, D.; Cooper, R. 1999. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. Forest Ecology and Management. 113: 125–141.

Brown, J.K. 2000. Introduction and fire regimes. In: Brown, J.K.; Kapler Smith, J., eds. Wildland fire in ecosystems: effects of fire on flora. Gen. Tech. Rep. RMRS-GTR-42-vol. 2. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 1–7.

Bruce, D. 1954. Mortality of longleaf pine seedlings after a winter fire. Journal of Forestry. 52(6): 442–443.

Bruce, D.; Bickford, C.A. 1950. Use of fire in natural regeneration of longleaf pine. Journal of Forestry. 48(2): 114–117.

Buckman, R.E. 1964. Effects of prescribed burning on hazel in Minnesota. Ecology. 45(3): 626–629.

Busse, M.D.; Hubbert, K.R.; Fiddler, G.O.; Shestak, C.J.; Powers, R.F. 2005. Lethal temperatures during burning of masticated forest residues. International Journal of Wildland Fire. 14: 267–276.

Byram, G.M. 1948. Vegetation temperature and fire damage in the southern pines. Fire Control Notes. 9: 34–36.

Campbell, G.S.; Jungbauer, J.D.J.; Bristow, K.L.; Hungerford, R.D. 1995. Soil temperature and water content beneath a surface fire. Soil Science. 159(6): 363–374.

Carrel, J.E. 2008. The effect of season of fire on density of female garden orbweavers (Araneae: Araneidae: *Argiopei)* Florida scrub. Florida Entomologist. 91(2): 332–334.

Carrington, M.E.; Mullahey, J.J. 2006. Effects of burning season and frequency on saw palmetto (*Serenoa repens*) flowering and fruiting. Forest Ecology and Management. 230: 69–78.

Chamrad, A.D.; Dodd, J.D. 1973. Prescribed burning and grazing for prairie chicken habitat manipulation in the Texas coastal prairie. Proceedings of the 12th Tall Timbers fire ecology conference. Tallahassee, FL: Tall Timbers Research Station: 257–276.

Chapman, H.H. 1932. Some further relations of fire to longleaf pine. Journal of Forestry. 30: 602–604.

Chen, E.; Gerber, J.F. 1990. Climate. In: Myers, R.L.; Ewel, J.J., eds. Ecosystems of Florida. Gainesville, FL: University of Florida Press: 11–34.

Collins, S.L.; Wallace, L.L. 1990. Fire in North American tallgrass prairies. Norman, OK: University of Oklahoma Press. 176 p.

Copeland, T.E.; Sluis, W.; Howe, H.F. 2002. Fire season and dominance in an Illinois tallgrass prairie restoration. Restoration Ecology. 10(2): 315–323.

Covington, W.W.; Sackett, S.S. 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. Forest Ecology and Management. 54: 175–191.

Cox, J.; Widener, B. 2008. Lightning-season burning: friend or foe of breeding birds? Misc. Publ. 17. Tallahassee, FL: Tall Timbers Research Station. 16 p.

D'Antonio, C.M. 2000. Fire, plant invasions, and global changes. In: Mooney, H.A.; Hobbs, R.J., eds. Invasive species in a changing world. Washington, DC: Island Press: 65–93.

de Groot, W.J.; Wein, R.W. 2004. Effects of fire severity and season of burn on *Betula glandulosa* growth dynamics. International Journal of Wildland Fire. 13: 287–295.

DeBano, L.F.; Neary, D.G.; Ffolliott, P.F. 1998. Fire's effects on ecosystems. New York, NY: John Wiley & Sons. 333 p.

DeWeese, G. 2007. Past fire regimes of table mountain pine (*Pinus pungens* Lamb.) stands in the central Appalachian Mountains, Virginia, U.S.A. Knoxville, TN: University of Tennessee. 308 p. Ph.D. dissertation.

DiTomaso, J.M.; Brooks, M.L.; Allen, E.B.; Minnich, R.; Rice, P.M.; Kyser, G.B. 2006. Control of invasive weeds with prescribed burning. Weed Technology. 20(2): 535–548.

DiTomaso, J.M.; Kyser, G.B.; Hastings, M.S. 1999. Prescribed burning for control of yellow starthistle (*Centaurea solstitialis*) and enhanced native plant diversity. Weed Science. 47(2): 233–242.

Dobrowolski, J.P.; Blackburn, W.H.; Grelen, H.E. 1987. Sediment production from long-term burning of a longleaf pine-bluestem association. In: Pearson, H.A.; Smeins, F.E.; Thill, R.E., eds. Ecological, physical, and socioeconomic relationships within southern national forests. Proceedings, southern evaluation project workshop. Gen. Tech. Rep. SO-68. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Experiment Station: 251–260.

Drewa, P.B. 2003. Effects of fire season and intensity on *Prosopis glandulosa* Torr. var. *glandulosa*. International Journal of Wildland Fire. 12: 147–157.

Drewa, P.B.; Platt, W.J.; Moser, E.B. 2002. Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. Ecology. 83(3): 755–767.

Drewa, P.B.; Thaxton, J.M.; Platt, W.J. 2006. Responses of root-crown bearing shrubs to differences in fire regimes in *Pinus palustris* (longleaf pine) savannas: exploring old-growth questions in second-growth systems. Applied Vegetation Science. 9(1): 27–36.

Duchesne, L.C.; Hawkes, B.C. 2000. Fire in northern ecosystems. In: Brown, J.K.; Smith, J.K., eds. Wildland fire in ecosystems: effects of fire on flora. Gen. Tech. Rep. RMRS-GTR-42-vol. 2. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 35–51.

Ehrenreich, J.H.; Aikman, J.M. 1963. An ecological study of the effect of certain management practices on native prairie in Iowa. Ecological Monographs. 33(2): 113–130.

Elliott, K.J.; Vose, J.M.; Clinton, B.D.; Knoepp, J.D. 2004. Effects of understory burning in a mixed mesic-oak forest of the Southern Appalachians. In: Engstrom, R.T.; Galley, K.M.; de Groot, W.J., eds. Fire in temperate, boreal, and montane ecosystems: Proceedings, 22nd Tall Timbers fire ecology conference. Tallahassee, FL: Tall Timbers Research Station: 272–283.

Emery, S.M.; Gross, K.L. 2005. Effects of timing of prescribed fire on the demography of an invasive plant, spotted knapweed *Centaurea maculosa*. Journal of Applied Ecology. 42(1): 60–69.

Engle, D.M.; Bidwell, T.G. 2001. Viewpoint: the response of central North American prairies to seasonal fire. Journal of Range Management. 54: 2–10.

Engle, D.M.; Bultsma, P.M. 1984. Burning of northern mixed prairie during drought. Journal of Range Management. 37: 398–401.

Engstrom, R.T. 1993. Characteristic mammals and birds of longleaf pine forests. In: Hermann, S.M., ed. The longleaf pine ecosystem ecology, restoration, and management. Proceedings of the 18th Tall Timbers fire ecology conference. Tallahassee, FL: Tall Timbers Research Station: 127–138.

Engstrom, R.T.; McNair, D.B.; Brennan, L.A.; Hardy, C.L.; Burger, L.W. 1996. Influence on birds of dormant versus lightning-season prescribed fire in longleaf pine forests: experimental design and preliminary results. In: Wadsworth, K.G.; McCabe, R.E., eds. Transactions of the 61st North American wildlife and natural resources conference. Washington, DC: Wildlife Management Institute: 200–207.

Engstrom, R.T.; Vickery, P.D.; Perkins, D.W.; Shriver, W.G. 2005. Effects of fire regime on birds in southeastern pine savannas and native prairies. Studies in Avian Biology. 30: 147–160.

Erwin, W.J.; Stasiak, R.H. 1979. Vertebrate mortality during the burning of reestablished prairie in Nebraska. American Midland Naturalist. 101(1): 247–249.

Everett, R.G. 2008. Dendrochronology-based fire history of mixed-conifer forests in the San Jacinto Mountains, California. Forest Ecology and Management. 256(11): 1805–1814.

Ferguson, S.A.; Ruthford, J.E.; McKay, S.J.; Wright, D.; Wright, C.; Ottmar, R. 2002. Measuring moisture dynamics to predict fire severity in longleaf pine forests. International Journal of Wildland Fire. 11(4): 267–279.

Ferrenberg, S.M.; Schwilk, D.W.; Knapp, E.E.; Groth, E.; Keeley, J.E. 2006. Fire decreases arthropod abundance but increases diversity: early and late season prescribed fire effects in a Sierra Nevada mixed-conifer forest. Fire Ecology. 2(2): 79–102.

Fettig, C.; Shea, P.; Borys, R. 2004. Seasonal flight patterns of four bark beetle species (Coleoptera: Scolytidae) along a latitudinal gradient in California. Pan-Pacific Entomologist. 80(1-4): 4–17.

Filip, G.M.; Yang-Erve, L. 1997. Effects of prescribed burning on the viability of *Armillaria ostoyae* in mixed-conifer forest soils in the Blue Mountains of Oregon. Northwest Science. 71(2): 137–144.

Finch, D.M.; Ganey, J.L.; Yong, W.; Kimball, R.T.; Sallabanks, R. 1997. Effects and interactions of fire, logging, and grazing. In: Block, W.M.; Finch, D.M., tech. eds. Songbird ecology in southwestern ponderosa pine forests: a literature review. Gen. Tech. Rep. RM-GTR-292. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 103–136.

Fitzgerald, S.M.; Tanner, G.W. 1992. Avian community response to fire and mechanical shrub control in south Florida. Journal of Range Management. 45(4): 396–400.

Flinn, M.A.; Wein, R.W. 1977. Depth of underground plant organs and theoretical survival during fire. Canadian Journal of Botany. 55: 2550–2554.

Floyd, T.M.; Russell, K.R.; Moorman, C.E.; Van Lear, D.H.; Guynn, D.C., Jr.; Lanham, J.D. 2002. Effects of prescribed fire on herpetofauna within hardwood forests of the upper piedmont of South Carolina: a preliminary analysis. In: Outcalt, K.W., ed. Proceedings, 11th biennial southern silvicultural research conference. Gen. Tech. Rep. SRS-48. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 123–127.

Ford, P.L.; Johnson, G.V. 2006. Effects of dormant- vs. growing-season fire in shortgrass steppe: biological soil crust and perennial grass responses. Journal of Arid Environments. 67: 1–14.

Foti, T.L.; Glenn, S.M. 1991. The Ouachita Mountain landscape at the time of settlement. In: Henderson, D.; Hedrick, L.D., eds. Proceedings, Conference on restoring old-growth forests in the interior highlands of Arkansas and Oklahoma. Morrilton, AR: Winrock International Institute: 49–65.

Fowells, H.A. 1941. The period of seasonal growth of ponderosa pine and associated species. Journal of Forestry. 39: 601–608.

Fowler, C.; Konopik, E. 2007. The history of fire in the Southern United States. Human Ecology Review. 14(2): 165–176.

Frandsen, W.F.; Ryan, K.C. 1986. Soil moisture reduces belowground heat flux and soil temperatures under a burning fuel pile. Canadian Journal of Forest Research. 16: 244–248.

Frost, C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. In: Hermann, S.M., ed. Longleaf pine ecosystem ecology, restoration, and management. Proceedings of the 18th Tall Timbers fire ecology conference. Tallahassee, FL: Tall Timbers Research Station: 17–44.

Frost, C.C. 1998. Presettleement fire frequency regimes of the United States: a first approximation. In: Pruden, T.L.; Brennan, L.A., eds. Fire in ecosystem management: shifting the paradigm from suppression to prescription. Proceedings of the 20th Tall Timbers fire ecology conference. Tallahassee, FL: Tall Timbers Research Station: 70–81.

Fry, D.L.; Stephens, S.L. 2006. Influence of humans and climate on the fire history of a ponderosa pine-mixed conifer forest in the southeastern Klamath Mountains, California. Forest Ecology and Management. 223: 428–438.

Fuhlendorf, S.D.; Harrell, W.C.; Engle, D.M.; Hamilton, R.G.; Davis, C.A.; Leslie, D.M., Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications. 16(5): 1706–1716.

Fulé, P.Z.; Covington, W.W.; Moore, M.M. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications. 7(3): 895–908.

Fulé, P.Z.; Denton, C.; Springer, J.D.; Kalies, E.L.; Egan, D. 2007. Prescribed and wildland use fires in the Southwest: Do frequency and timing matter? Working Papers in southwestern ponderosa pine forest restoration. Flagstaff, AZ: Ecological Restoration Institute, Northern Arizona University. 8 p.

Fulé, P.Z.; Heinlein, T.A.; Covington, W.W.; Moore, M.M. 2003. Assessing fire regimes on Grand Canyon landscapes with fire-scar and fire-record data. International Journal of Wildland Fire. 12(2): 129–145.

Garrison, G.A. 1972. Carbohydrate reserves and response to use. In: McKell, C.M.; Blaisdell, J.P.; Goodin, J.R., eds. Wildland shrubs—their biology and utilization. Proceedings of a symposium. Gen. Tech. Rep. GTR-INT-1. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 271–278.

Gates, C.A.; Tanner, G.W. 1988. Effects of prescribed burning on herbaceous vegetation and pocket gophers (*Geomys pinetis*) in a sandhill community. Florida Scientist. 51(3): 129–139.

Gibbens, R.P.; Schultz, A.M. 1963. Brush manipulation on a deer winter range. California Fish and Game. 49(2): 95–118.

Glitzenstein, J.S.; Platt, W.J.; Streng, D.R. 1995a. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecological Monographs. 65(4): 441–476.

Glitzenstein, J.S.; Streng, D.R.; Masters, R.E.; Platt, W.J. 2008. Clarifying long-term impacts of fire frequency and fire season in southeastern Coastal Plain pine savannas. In: Managing an ecosystem on the edge: Proceedings, 6th eastern native grass symposium. Columbia, SC: Clemson University. 16 p.

Glitzenstein, J.S.; Streng, D.R.; Platt, W.J. 1995b. Evaluating the effects of season of burn on vegetation in longleaf pine savannas. Nongame Wildlife Project Report. Tallahassee, FL: Florida Game and Fresh Water Fish Commission. 118 p.

Glitzenstein, J.S.; Streng, D.R.; Wade, D.D. 2003. Fire frequency effects on longleaf pine vegetation in South Carolina and Northeast Florida, USA. Natural Areas Journal. 23(1): 22–37.

Grelen, H.E. 1978. May burns stimulate growth in longleaf pine seedlings. Res. Note SO-234. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 5 p.

Grelen, H.E. 1983. May burning favors survival and early height growth of longleaf pine *Pinus palustris* seedlings. Southern Journal of Applied Forestry. 7(1): 16–20.

Grelen, H.E.; Epps, E.A. 1967. Herbage responses to fire and litter removal on southern blue-stem range. Journal of Range Management. 20: 403–404.

Griffiths, A.D.; Christian, K.A. 1996. The effect of fire on the frillneck lizard (*Chlamydosaurus kingii*) in northern Australia. Australian Journal of Ecology. 21: 386–398.

Grissino-Mayer, H.D.; Swetnam, T.W. 2000. Century-scale climate forcing of fire regimes in the American Southwest. The Holocene. 10(2): 213–220.

Guyette, R.P.; Dey, D.C.; Stambaugh, M.C.; Muzika, R. 2006. Fire scars reveal variability and dynamics of eastern fire regimes. In: Dickinson, M.B., ed. Fire in eastern oak forests: delivering science to land managers. Gen. Tech. Rep. GTR-NRS-P-1. Columbus, OH: U.S. Department of Agriculture, Forest Service, Northern Research Station: 20–39.

Guyette, R.P.; Spetich, M.A. 2003. Fire history of oak-pine forests in the Lower Boston Mountains, Arkansas, USA. Forest Ecology and Management. 180: 463–474.

Hamman, S.T.; Burke, I.C.; Knapp, E.E. 2008. Soil nutrients and microbial activity after early and late season prescribed burns in a Sierra Nevada mixed conifer forest. Forest Ecology and Management. 256(3): 367–374.

Harper, M.G.; Dietrich, C.H.; Larimore, R.L.; Tessene, P.A. 2000. Effects of prescribed fire on prairie arthropods: an enclosure study. Natural Areas Journal. 20: 325–335.

Harrington, M.G. 1985. The effects of spring, summer, and fall burning on gambel oak in a southwestern ponderosa pine stand. Forest Science. 31(1): 156–163.

Harrington, M.G. 1987. Ponderosa pine mortality from spring, summer, and fall crown scorching. Western Journal of Applied Forestry. 2(1): 14–16.

Harrington, M.G. 1989. Gambel oak root carbohydrate response to spring, summer, and fall prescribed burning. Journal of Range Management. 42(6): 504–507.

Harrington, M.G. 1993. Predicting *Pinus ponderosa* mortality from dormant season and growing season fire injury. International Journal of Wildland Fire. 3(2): 65–72.

Harrod, R.J.; Halpern, C.B. 2009. Effects of experimental burning on individual performance and population structure of two rare plants of northcentral Washington. Restoration Ecology 17(2): 215–225.

Hartford, R.A.; Frandsen, W.F. 1992. When it's hot, it's hot... or maybe it's not! (Surface flaming may not portend extensive soil heating). International Journal of Wildland Fire. 2(3): 139–144.

Hatten, J.A.; Zabowski, D.; Ogden, A.; Thies, W. 2008. Soil organic matter in a ponderosa pine forest with varying seasons and intervals of prescribed burn. Forest Ecology and Management. 255: 2555–2565.

Henderson, J.P. 2006. Dendroclimatological analysis and fire history of longleaf pine (*Pinus palustris* Mill.) in the Atlantic and Gulf Coastal Plain. Knoxville, TN: University of Tennessee. 197 p. Ph.D. dissertation.

Hermann, S.M.; Van Hook, T.; Flowers, R.W.; Brennan, L.A.; Glitzenstein, J.S.; Streng, D.R.; Walker, J.L.; Myers, R.L. 1998. Fire and biodiversity: studies of vegetation and arthopods. In: Transactions of the 63rd North American wildland and natural resources conference. Washington, DC: Wildlife Management Institute: 384–401.

Heyerdahl, E.K.; Brubaker, L.B.; Agee, J.K. 2001. Spatial controls of historical fire regimes: a multiscale example from the interior West, USA. Ecology. 82(3): 660–678.

Heyerdahl, E.K.; Miller, R.F.; Parsons, R.A. 2006. History of fire and Douglas-fir establishment in a savanna and sagebrush-grassland mosaic, southwestern Montana, USA. Forest Ecology and Management. 230: 107–118.

Hierro, J.L.; Menges, E.S. 2002. Fire intensity and shrub regeneration in palmetto-dominated flatwoods of central Florida. Florida Scientist. 65(1): 51–61.

Hiers, J.K.; Wyatt, R.; Mitchell, R.J. 2000. The effects of fire regime on legume reproduction in longleaf pine savannas: Is a season selective? Oecologia. 125(4): 521–530.

Higgins, K.F. 1984. Lightning fires in North Dakota grasslands and in pine-savanna lands of South Dakota and Montana. Journal of Range Management. 37(2): 100–103.

Higgins, K.F. 1986a. A comparison of burn season effects on nesting birds in North Dakota mixed-grass prairie. Prairie Naturalist. 18(4): 219–228.

Higgins, K.F. 1986b. Interpretation and compendium of historical fire accounts in the northern Great Plains. Resource Publ. 161. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service. 39 p.

Hough, W.A. 1968. Carbohydrate reserves of saw-palmetto: seasonal variation and effects of burning. Forest Science. 14(4): 399–405.

Hough, W.A. 1973. Fuel and weather influence wildfires in sand pine forests. Res. Pap. SE-106. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeast Forest Experiment Station. 9 p.

Hough, W.A.; Albini, F.A. 1978. Predicting fire behavior in palmetto-gallberry fuel complexes. Res. Pap. SE-174. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experimental Station. 44 p.

Howe, H.F. 1994a. Managing species diversity in tallgrass prairie: assumptions and implications. Conservation Biology. 8(3): 691–704.

Howe, H.F. 1994b. Response of early- and late-flowering plants to fire season in experimental prairies. Ecological Applications. 4(1): 121–133.

Howe, H.F. 1995. Succession and fire season in experimental prairie plantings. Ecology. 76(6): 1917–1925.

Howe, H.F. 1999. Response of *Zizia aurea* to seasonal mowing and fire in a restored prairie. American Midland Naturalist. 141: 373–380.

Howe, H.F. 2000. Grass response to seasonal burns in experimental plantings. Journal of Range Management. 53: 437–441.

Huff, M.H.; Smith, J.K. 2000. Fire effects on animal communities. In: Smith, J.K., ed. Wildland fire in ecosystems: effects of fire on fauna. Gen. Tech. Rep. RMRS-GTR-42-vol. 1. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 35–42.

Huffman, J. 2006. Historical fire regimes in southeastern pine savannas. Baton Rouge, LA: Louisiana State University. 77 p. Ph.D. dissertation.

Huffman, J.M.; Platt, W.J.; Grissino-Mayer, H.; Boyce, C.J. 2004. Fire history of a barrier island slash pine (*Pinus elliottii*) savanna. Natural Areas Journal. 24(3): 258–268.

Hulbert, L.C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. Ecology. 50(5): 874–877.

Hulbert, L.C. 1988. Causes of fire effects in tallgrass prairie. Ecology. 69(1): 46–58.

Jacqmain, E.I.; Jones, R.H.; Mitchell, R.J. 1999. Influences of frequent cool-season burning across a soil moisture gradient on oak community structure in longleaf pine ecosystems. American Midland Naturalist. 141(1): 85–100.

James, F.C.; Hess, C.A.; Kufrin, D. 1997. Species-centered environmental analysis: indirect effects of fire history on red-cockaded woodpeckers. Ecological Applications. 7(1): 118–129.

Johansen, M.P.; Hakonson, T.E.; Breshears, D.D. 2001. Post-fire runoff and erosion from rainfall simulations: contrasting forests with shrublands and grasslands. Hydrological Processes. 15: 2953–2965.

Johnson, E.A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge, United Kingdom: Cambridge University Press. 144 p.

Johnson, S.D.; Horn, K.C.; Savage, A.M.; Windhager, S.; Simmons, M.T.; Rudgers, J.T. 2008. Timing of prescribed burns affects abundance and composition of arthropods in the Texas Hill Country. The Southwestern Naturalist. 53(2): 137–145.

Jones, J.R.; DeByle, N.V. 1985. Fire. In: DeByle, N.; Winokur, R.P., eds. Aspen: Ecology and management in the Western United States. Gen. Tech. Rep. RM-119. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 77–81.

Jones, M.B.; Laude, H.M. 1960. Relationship between sprouting in chamise and the physiological condition of the plant. Journal of Range Management. 13: 210–214.

Kalisz, P.J.; Powell, J.E. 2000. Effects of prescribed fire on soil invertebrates in upland forests on the Cumberland Plateau of Kentucky, USA. Natural Areas Journal. 20(1): 336–341.

Kansas Natural Heritage Inventory. 2007. Native prairie hay meadows: a landowner's management guide. Lawrence, KS: University of Kansas. 32 p.

Kauffman, J.B. 1990. Ecological relationships of vegetation and fire in Pacific Northwest forests. In: Walsted, J.D.; Radosevich, S.R.; Sandberg, D.V., eds. Natural and prescribed fire in Pacific Northwest forests. Corvallis, OR: Oregon State University Press: 39–52.

Kauffman, J.B.; Martin, R.E. 1989. Fire behavior, fuel consumption, and forest-floor changes following prescribed understory fires in Sierra Nevada mixed conifer forests. Canadian Journal of Forest Research. 19: 455–462.

Kauffman, J.B.; Martin, R.E. 1990. Sprouting shrub response to different seasons and fuel consumption levels of prescribed fire in Sierra Nevada mixed conifer ecosystems. Forest Science. 36(3): 748–764.

Kauffman, J.B.; Martin, R.E. 1991. Factors influencing the scarification and germination of three montane Sierra Nevada shrubs. Northwest Science. 65(4): 180–187.

Kaufman, D.W.; Finck, E.J.; Kaufman, G.A. 1990. Small mammals and grassland fires. In: Collins, S.L.; Wallace, L.L., eds. Fire in North American tallgrass prairies. Norman, OK: University of Oklahoma Press: 46–80.

Kaufman, D.W.; Gurtz, S.K.; Kaufman, G.A. 1988. Movements of deer mouse in response to prairie fire. Prairie Naturalist. 20(4): 225–229.

Keeley, J.E. 1987. Role of fire in seed germination of woody taxa in California chaparral. Ecology. 68(2): 434–443.

Keeley, J.E. 2002. Fire management of California shrubland landscapes. Environmental Management. 29(3): 395–408.

Keeley, J.E. 2006. South coast bioregion. In: Sugihara, N.G.; van Wagtendonk, J.W.; Shaffer, K.E.; Fites-Kaufman, J.; Thode, A.E., eds. Fire in California's ecosystems. Berkeley, CA: University of California Press: 350–414.

Keeley, J.E.; Fotheringham, C.J. 2001. History and management of crown-fire ecosystems: a summary and response. Conservation Biology. 15(6): 1561–1567.

Kerns, B.K.; Thies, W.G.; Niwa, C.G. 2006. Season and severity of prescribed burn in ponderosa pine forests: implications for understory native and exotic plants. Ecoscience. 13(1): 44–55.

Keyser, P.D.; Brose, P.H.; Van Lear, D.H. 1996. Enhancing oak regeneration with fire in shelterwood stands: preliminary trials. In: Wadsworth, K.G.; McCabe, R.E., eds. Transactions of the 61st North American wildlife and natural resources conference. Washington, DC: Wildlife Management Institute: 215–219.

Keyser, P.D.; Ford, W.M. 2006. Influence of fire on mammals in eastern oak forests. In: Dickinson, M.B., ed. Fire in eastern oak forests: delivering science to land managers. Gen. Tech. Rep. GTR-NRS-P-1. Newton Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 180–190.

Keyser, P.D.; Sausville, D.J.; Ford, W.M.; Mengak, M.J.; Brose, P.H.; Van Lear, D.H. 2001. Fire impacts to small mammals in Piedmont oak shelterwoods. In: Proceedings of the annual conference of the Southeastern Association of Fish and Wildlife Agencies. 55: 375–381.

Keyser, P.D.; Sausville, D.J.; Ford, W.M.; Schwab, D.J.; Brose, P. 2004. Prescribed fire impacts to amphibians and reptiles in shelterwood-harvested oak-dominated forests. Virginia Journal of Science. 55(4): 159–168.

King, R.S. 2003. Habitat management for the Karner blue butterfly (*Lycaeides melissa samuelis*): evaluating the short-term consequences. Ecological Restoration. 21: 101–106.

King, T.G.; Howell, M.A.; Chapman, B.R.; Miller, K.V.; Schorr, R.A. 1998. Comparisons of wintering bird communities in mature pine stands managed by prescribed burning. The Wilson Bulletin. 110(4): 570–574.

Kirkland, G.L.; Snoddy, H.W.; Amsler, T.L. 1996. Impact of fire on small mammals and amphibians in a central Appalachian deciduous forest. American Midland Naturalist. 135: 253–260.

Kirkman, L.K.; Drew, M.B.; Edwards, D. 1998. Effects of experimental fire regimes on the population dynamics of *Schwalbea americana* L. Plant Ecology. 137(1): 115–137.

Kirkpatrick, C.; Conway, C.J.; Jones, P.B. 2006. Distribution and relative abundance of forest birds in relation to burn severity in southeastern Arizona. Journal of Wildlife Management. 70(4): 1005–1012.

Klebenow, D.A.; Bruner, A.D. 1977. Determining factors necessary for prescribed burning. In: Busby, F.E.; Storey, E., eds. Use of prescribed burning in western woodland and range ecosystems: a symposium. Logan, UT: Utah Agricultural Experiment Station, Utah State University: 69–74.

Klopatek, C.C.; DeBano, L.F.; Klopatek, J.M. 1988. Effects of simulated fire on vesicular-arbuscular mycorrhizae in pinyon-juniper woodland soil. Plant and Soil. 109: 245–249.

Klopatek, J.M.; Klopatek, C.C.; DeBano, L.F. 1990. Potential variation of nitrogen transformations in pinyon-juniper ecosystems resulting from burning. Biology and Fertility of Soils. 10: 35–44.

Knapp, A.K. 1984. Post-burn differences in solar radiation, leaf temperature, and water stress influencing production in a lowland prairie. American Journal of Botany. 71(2): 220–227.

Knapp, E.E.; Keeley, J.E. 2006. Heterogeneity in fire severity within early season and late season prescribed burns in a mixed-conifer forest. International Journal of Wildland Fire. 15: 37–45.

Knapp, E.E.; Keeley, J.E.; Ballenger, E.A.; Brennan, T.J. 2005. Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fires in a Sierra Nevada mixed conifer forest. Forest Ecology and Management. 208: 383–397.

Knapp, E.E.; Schwilk, D.W.; Kane, J.M.; Keeley, J.E. 2007. Role of burning season on initial understory vegetation response to prescribed fire in a mixed conifer forest. Canadian Journal of Forest Research. 37: 11–22.

Knight, T.M.; Holt, R.D. 2005. Fire generates spatial gradients in herbivory: an example from a Florida sandhill ecosystem. Ecology. 86(3): 587–593.

Knutson, H.; Campbell, J.B. 1976. Relationships of grasshoppers (Acrididae) to burning, grazing, and range sites on native tallgrass prairie in Kansas. In: Proceedings of the Tall Timbers conference of ecology animal control by habitat management. Tallahassee, FL: Tall Timbers Research Station. 6: 107–120.

Komarek, E.V. 1964. The natural history of lightning. In: Komarek, E.V., ed. Proceedings, 3rd Tall Timbers fire ecology conference. Tallahassee, FL: Tall Timbers Research Station: 139–183.

Komarek, E.V. 1965. Fire ecology—grasslands and man. In: Komarek, E.V., ed. Proceedings, 4th Tall Timbers fire ecology conference. Tallahassee, FL: Tall Timbers Research Station: 169–220.

Komarek, E.V. 1967. The nature of lightning fire. In: Komarek, E.V., ed. Proceedings, 7th Tall Timbers fire ecology conference. Tallahassee, FL: Tall Timbers Research Station: 5–41.

Komarek, E.V. 1968. Lightning and lightning fires as ecological forces. In: Komarek, E.V., ed. Proceedings, 8th Tall Timbers fire ecology conference. Tallahassee, FL: Tall Timbers Research Station: 169–197.

Kramer, P.; Wetmore, T. 1943. Effects of defoliation on cold resistance and diameter growth of broad-leaved evergreens. American Journal of Botany. 30: 428–431.

Laughlin, D.C.; Bakker, J.D.; Daniels, M.L.; Moore, M.M.; Casey, C.A.; Springer, J.D. 2008. Restoring plant species diversity and community composition in a ponderosa pine-bunchgrass ecosystem. Plant Ecology. 197(1): 139–151.

Le Fer, D.; Parker, V.T. 2005. The effect of seasonality of burn on seed germination in chaparral: the role of soil moisture. Madroño. 52(3): 166–174.

Lesica, P. 1999. Effects of fire on the demography of the endangered, geophytic herb *Silene spaldingii* (Caryophyllaceae). American Journal of Botany. 86(7): 996–1002.

Lesica, P.; Martin, B. 2003. Effects of prescribed fire and season of burn on recruitment of the invasive exotic plant, *Potentilla recta*, in a semiarid grassland. Restoration Ecology. 11(4): 516–523.

Lewis, C.E.; Grelen, H.E.; Probasco, G.E. 1982. Prescribed burning in southern forest and rangeland improves forage and its use. Southern Journal of Applied Forestry. 6: 19–25.

Lewis, C.E.; Harshbarger, T.J. 1976. Shrub and herbaceous vegetation after 20 years of prescribed burning in the South Carolina Coastal Plain. Journal of Range Management. 29: 13–18.

Lewis, H.T. 1973. Patterns of Indian burning in California: ecology and enthnohistory. Anthropological Paper No. 1. Ramona, CA: Ballena Press. 101 p.

Liu, H.; Menges, E.S. 2005. Winter fires promote greater vital rates in the Florida Keys than summer fires. Ecology. 86(6): 1483–1495.

Liu, H.; Menges, E.S.; Quintana-Ascencio, P.F. 2005. Population viability analysis of *Chamaecrista keyensis*: effects of fire season and frequency. Ecological Applications 15(1): 210–221.

Lyon, L.J.; Huff, M.H.; Telfer, E.S.; Schreiner, D.S.; Smith, J.K. 2000a. Fire effects on animal populations. In: Smith, J.K., ed. Wildland fire in ecosystems: effects of fire on fauna. Gen. Tech. Rep. RMRS-GTR-42-vol. 1. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 25–34

Lyon, L.J.; Telfer, E.S.; Schreiner, D.S. 2000b. Direct effects of fire and animal responses. In: Smith, J.K., ed. Wildland fire in ecosystems: effects of fire on fauna. Gen. Tech. Rep. RMRS-GTR-42-vol. 1. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 17–23.

MacDonald, N.W.; Scull, B.T.; Abella, S.R. 2007. Mid-spring burning reduces spotted knapweed and increases native grasses during a Michigan experimental grassland establishment. Restoration Ecology. 15(1): 118–128.

Main, M.B.; Barry, M.J. 2002. Influence of season of fire on flowering of wet prairie grasses in south Florida, USA. Wetlands. 22(2): 430–434.

Martin, R.E.; Sapsis, D.B. 1992. Fires as agents of biodiversity: pyrodiversity promotes biodiversity. In: Kerner, H.M., ed. Proceedings, Symposium on biodiversity in northwestern California. Report 29. Santa Rosa, CA: Wildland Resources Center, University of California: 150–157.

Masters, R.E.; Skeen, J.E.; Whitehead, J. 1995. Preliminary fire history of McCurtain County Wilderness Area and implications for red-cockaded woodpecker management. In: Kulhavy, D.L.; Hooper, R.G.; Costa, R., eds. Red cockaded woodpecker species recovery, ecology, and management. Nagadoches, TX: School of Forestry, Center for Applied Studies, Stephen F. Austin State University: 240–232.

McCandliss, D.S. 2002. Prescribed burning in the Kings River Ecosystem Project Area: lessons learned. In: Verner, J., ed. Proceedings of a symposium on the Kings River sustainable forest ecosystems project: progress and current status. Gen. Tech. Rep. PSW-GTR-183. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 37–45.

McClain, W.E.; Elzinga, S.L. 1994. The occurrence of prairie and forest fires in Illinois and other Midwestern States 1679-1854. Eriginia. 13: 79–90.

McHugh, C.W.; Kolb, T.E. 2003. Ponderosa pine mortality following fire in northern Arizona. International Journal of Wildland Fire. 12: 7–22.

McHugh, C.W.; Kolb, T.E.; Wilson, J.L. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. Environmental Entomology. 32(3): 510–522.

Menges, E.S.; Deyrup, M.A. 2001. Postfire survival in south Florida slash pine: interacting effects of fire intensity, fire season, vegetation, burn size, and bark beetles. International Journal of Wildland Fire. 10: 53–63.

Meyer, M.D.; Schiffman, P.M. 1999. Fire season and mulch reduction in a California grassland: a comparison of restoration strategies. Madroño. 46(1): 25–37.

Monroe, M.E.; Converse, S.J. 2006. The effects of early season and late season prescribed fires on small mammals in a Sierra Nevada mixed conifer forest. Forest Ecology and Management. 236: 229–240.

Monsanto, P.G.; Agee, J.K. 2008. Long-term post-wildfire dynamics of coarse woody debris after salvage logging and implications for soil heating in dry forests of the eastern Cascades, Washington. Forest Ecology and Management. 255: 3952–3961.

Moody, T.J.; Fites-Kaufmann, J.; Stephens, S.L. 2006. Fire history and climate influences from forests in the northern Sierra Nevada, USA. Fire Ecology. 2(1): 115–141.

Mulligan, M.K.; Kirkman, L.K.; Mitchell, R.J. 2002. *Aristida beyrichiana* (wiregrass) establishment and recruitment: implications for restoration. Restoration Ecology. 10(1): 68–76.

Myers, R.L. 1990. Scrub and high pine. In: Myers, R.L.; Ewel, J.J., eds. Ecosystems of Florida. Orlando, FL: University of Central Florida Press: 150–193.

Myers, R.L. 2000. Fire in tropical and subtropical ecosystems. In: Brown, J.K.; Smith, J.K., eds. Wildland fire in ecosystems: effects of fire on flora. Gen. Tech. Rep. RMRS-GTR-42-vol. 2. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 161–173.

Myers, R.L.; White, D.L. 1987. Landscape history and changes in sandhill vegetation in north-central and south-central Florida. Bulletin of the Torrey Botanical Club. 114(1): 21–32.

National Oceanic and Atmospheric Administration. 2009. Data from the U.S. National Lightning Detection Network 1996–2000. http://www.crh.noaa.gov/Image/pub/ltg2/usa_ltg_fdm.gif. (June 10, 2009).

Neary, D.G.; Klopatek, C.C.; DeBano, L.F.; Ffolliott, P.F. 1999. Fire effects on belowground sustainability: a review and synthesis. Forest Ecology and Management. 122: 51–71.

Negron-Ortiz, V.; Gorchov, D.L. 2000. Effects of fire season and post-fire herbivory on the cycad *Zamia pumila* (Zamiaceae) in slash pine savanna, Everglades National Park, Florida. International Journal of Plant Science. 161: 659–669.

Neill, C.; Patterson, W.A., III; Crary, D.W., Jr. 2007. Responses of soil carbon, nitrogen and cations to the frequency and seasonality of prescribed burning in a Cape Cod oak-pine forest. Forest Ecology and Management. 250: 234–243.

Niwa, C.G.; Peck, R.W. 2002. Influence of prescribed fire on carabid beetle (Carabidae) and spider (Araneae) assemblages in forest litter in southwestern Oregon. Environmental Entomology. 31(5): 785–796.

Norman, S.P.; Taylor, A.H. 2003. Tropical and north Pacific teleconnections influence fire regimes in pine-dominated forests of north-eastern California, USA. Journal of Biogeography. 30(7): 1081–1092.

Nowacki, G.; Abrams, M.D. 2008. The demise of fire and “mesophication” of forests in the Eastern United States. Bioscience. 58(2): 123–138.

Odion, D.C. 2000. Seed banks of long-unburned stands of maritime chaparral: composition, germination behavior, and survival without fire. Madroño. 47(3): 195–203.

Ortloff, W. 1996. Wood-anatomical evidence of fire seasonality. In: Dean, J.S.; Meko, D.M.; Swetnam, T.M., eds. Tree rings, environment, and humanity. Radiocarbon. Tucson, AZ: University of Arizona: 89–93.

Outcalt, K.W. 1994. Seed production of wiregrass in central Florida following growing season prescribed burns. International Journal of Wildland Fire. 4(1): 123–125.

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

Owens, M.K.; Mackley, J.W.; Carroll, C.J. 2002. Vegetation dynamics following seasonal fires in mixed mesquite/acacia savannas. Journal of Range Management. 55: 509–516.

Palik, B.J.; Mitchell, R.J.; Hiers, J.K. 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. Forest Ecology and Management. 155(1/3): 347–356.

Parker, V.T. 1987a. Can native flora survive prescribed burns? Fremontia. 15(2): 3–6.

Parker, V.T. 1987b. Effects of wet-season management burns on chaparral vegetation: implications for rare species. In: Proceedings of a California conference on the conservation and management of rare and endangered plants. Sacramento, CA: California Native Plant Society: 233–237.

Parsons, D.J.; Stohlgren, T.J. 1989. Effects of varying fire regimes on annual grasslands in the southern Sierra Nevada of California. Madroño. 36(3): 154–168.

Perrakis, D.D.B.; Agee, J.K. 2006. Seasonal fire effects on mixed-conifer forest structure and ponderosa pine resin properties. Canadian Journal of Forest Research. 36: 238–254.

Petersen, S.M.; Drewa, P.B. 2006. Did lightning-initiated growing season fires characterize oak dominated ecosystems of southern Ohio? The Journal of the Torrey Botanical Society. 133(2): 217–224.

Pilliod, D.S.; Bury, R.B.; Hyde, E.J.; Pearl, C.A.; Corn, P.S. 2003. Fire and amphibians in North America. Forest Ecology and Management. 178: 163–181.

Platt, W.J.; Evans, G.W.; 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.; Glitzenstein, J.S.; Streng, D.R. 1991. Evaluating pyrogenicity and its effects on vegetation in longleaf pine savannas. In: Hermann, S.M., ed. High-intensity fire in wildlands: management challenges and options. Proceedings, 17th Tall Timbers Fire Ecology Conference. Tallahassee, FL: Tall Timbers Research Station: 143–162.

Pollak, O.; Kan, T. 1998. The use of prescribed fire to control invasive exotic weeds at Jepson Prairie Preserve. In: Witham, C.W.; Bauder, E.T.; Belk, D.; Ferren, W.R., Jr.; Ornduff, R., eds. Ecology, conservation, and management of vernal pool ecosystems. Sacramento, CA: California Native Plant Society: 241–249.

Provencher, L.; Gobris, N.M.; Brennan, L.A. 2002. Effects of hardwood reduction on winter birds in northwest Florida longleaf pine sandhill forests. The Auk. 119(1): 71–87.

Radosevich, S.R.; Conard, S.G. 1980. Physiological control of chamise shoot growth after fire. American Journal of Botany. 67(10): 1442–1447.

Reinking, D.L. 2005. Fire regimes and avian responses in the central tallgrass prairie. Studies in Avian Biology. 30: 116–126.

Renken, R. 2006. Does fire affect amphibians and reptiles in Eastern U.S. oak forests? In: Dickinson, M.B., ed. Proceedings, Conference on fire in eastern oak forests: delivering science to land managers. Gen. Tech. Rep. NRS-P-1. Columbus, OH: U.S. Department of Agriculture, Forest Service, Northern Research Station: 158–166.

Rideout, S.; Rickard, J.K.; Wade, D.D. 2003. Preliminary response of herbaceous plants to biennial cycles applied at different dates during the growing season. Natural Areas Journal. 23(1): 38–42.

Robbins, L.E.; Myers, R.L. 1992. Seasonal effects of prescribed burning in Florida: a review. Misc. Publ. 8. Tallahassee, FL: Tall Timbers Research Station. 97 p.

Rundel, P.W.; Baker, G.A.; Parsons, D.J. 1981. Productivity and nutritional responses of *Chamaebatia foliolosa* (Rosaceae) to seasonal burning. In: Margaris, N.S.; Mooney, H.A., eds. Components of productivity of mediterranean-climate regions—basic and applied aspects. The Hague/Boston/London: Dr. W. Junk: 191–196.

Russell, K.R.; Van Lear, D.H.; Guynn, D.C., Jr. 1999. Prescribed fire effects on herpetofauna: review and management implications. Wildlife Society Bulletin. 27(2): 374–384.

Ruthven, D.C.; Braden, A.W.; Knutson, H.J.; Gallagher, J.F.; Synatzske, D.R. 2003. Woody vegetation response to various burning regimes in South Texas. Journal of Range Management. 56: 159–166.

Ruthven, D.C., III; Kazmaier, R.T.; Janis, M.W. 2008. Short-term response of herpetofauna to various burning regimes in the south Texas plains. The Southwestern Naturalist. 53(4): 480–487.

Ryan, K.C.; Peterson, D.L.; Reinhardt, E.D. 1988. Modeling long-term fire-caused mortality of Douglas-fir. Forest Science. 34(1): 190–199.

Sackett, S.S.; Haase, S.M. 1998. Two case histories for using prescribed fire to restore ponderosa pine ecosystems in northern Arizona. In: Pruden, T.L,; Brennan, L.A., eds. Fire in ecosystem management: shifting the paradigm from suppression to prescription. Proceedings of the 20th Tall Timbers fire ecology conference, Tallahassee, FL: Tall Timbers Research Station: 380–389.

Sackett, S.S.; Haase, S.M.; Harrington, M.G. 1996. Prescribed burning in southwestern ponderosa pine. In: Ffolliott, P.F.; DeBano, L.F.; Baker, M.B., Jr.; Gottfried, G.J.; Solis-Garza, B.; Edminster, C.B.; Neary, D.G.; Allen, L.S.; Hamre, R.H., eds. Effects of fire on Madrean Province ecosystems. Gen. Tech. Rep. RM-289. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 178–186.

Sakulich, J.; Taylor, A.H. 2007. Fire regime and forest structure in a sky island mixed conifer forest, Guadalupe Mountains National Park, Texas, USA. Forest Ecology and Management. 241: 62–73.

Sala, A.; Peters, G.D.; McIntyre, L.R.; Harrington, M.G. 2005. Physiological responses of ponderosa pine in western Montana to thinning, prescribed fire and burning season. Tree Physiology. 25(3): 339–348.

Schneider, R.E. 1988. The effect of variation in season of burning on a pine-wiregrass savanna in the Green Swamp, North Carolina. Durham, NC: Duke University. 141 p. Ph.D. dissertation.

Schroeder, M.J.; Buck, C.C. 1970. Fire weather: a guide for application of meteorological information to forest fire control operations. Agric. Handb. 360. Washington, DC: U.S. Department of Agriculture, Forest Service. 229 p.

Schurbon, J.M.; Fauth, J.E. 2003. Effects of prescribed burning on amphibian diversity in a Southeastern U.S. National Forest. Conservation Biology. 17(5): 1338–1349.

Schwartz, M.W.; Heim, J.R. 1996. Effects of a prescribed fire on degraded forest vegetation. Natural Areas Journal. 16(3): 184–191

Schwemlein, D.J.; Williams, R.A. 2007. Effects of landscape position and season of burn on fire temperature in southern Ohio's mixed oak forests. In: Buckley, D.S.; Clatterbuck, W.L., eds. Proceedings, 15th central hardwood forest conference. Gen. Tech. Rep. SRS-101. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 250–257.

Schwilk, D.W.; Knapp, E.E.; Ferrenberg, S.M.; Keeley, J.E.; Caprio, A.C. 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. Forest Ecology and Management. 232: 36–45.

Seastedt, T.R.; Ramundo, R.A. 1990. The influence of fire on belowground processes of tallgrass prairie. In: Collins, S.L.; Wallace, L.L., eds. Fire in North American Tallgrass Prairies. Norman, OK: University of Oklahoma Press: 99–117.

Shumway, D.; Abrams, M.D.; Ruffner, C.M. 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, USA. Canadian Journal of Forest Research. 31(8): 1437–1443.

Simmons, M.T.; Windhager, S.; Power, P.; Lott, J.; Lyons, R.K.; Schwope, C. 2007. Selective and non-selective control of invasive plants: the short-term effects of growing-season prescribed fire, herbicide, and mowing in two Texas prairies. Restoration Ecology. 15(4): 662–669.

Sisson, D.C.; Speake, D.W.; Landers, J.L.; Buckner, J.L. 1990. Effects of prescribed burning on wild turkey habitat preference and nest site selection in south Georgia. National Wild Turkey Symposium. 6: 44–50.

Skinner, C.N.; Chang, C.-R. 1996. Fire regimes, past and present. Sierra Nevada Ecosystem Project: final report to Congress. Assessments and scientific basis for management options. Davis, CA: Centers for Water and Wildland Resources, University of California Davis: 1041–1069. Vol. 2.

Slocum, M.G.; Platt, W.J.; Cooley, H.C. 2003. Effects of differences in prescribed fire regimes on patchiness and intensity of fires in subtropical savannas of Everglades National Park, Florida. Restoration Ecology. 11(1): 91–102.

Smith, J.E.; McKay, D.; Niwa, C.G.; Thies, W.G.; Brenner, G.; Spatafora, J.W. 2004. Short-term effects of seasonal prescribed burning on ectomycorrhizal fungal community and root biomass in ponderosa pine stands in the Blue Mountains of Oregon. Canadian Journal of Forest Research. 34: 2477–2491.

Smith, M.D.; Knapp, A.K. 1999. Exotic plant species in a C4-dominated grassland: invasibility, disturbance and community structure. Oecologia. 120: 605–612.

Sparks, J.C.; Masters, R.E. 1996. Fire seasonality effects on vegetation in mixed-, tall-and southeastern pine-grassland communities. In: Wadsworth, K.G.; McCabe, R.E., eds. Transactions of the 61st North American wildlife and natural resources conference, Washington, DC: Wildlife Management Institute: 246–255.

Sparks, J.C.; Masters, R.E.; Engle, D.M.; Bukenhofer, G.A. 2002. Season of burn influences fire behavior and fuel consumption in restored shortleaf pine-grassland communities. Restoration Ecology. 10(4): 714–722.

Sparks, J.C.; Masters, R.E.; Engle, D.M.; Palmer, M.W.; Bukenhofer, G.A. 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.

Sparks, J.C.; Masters, R.E.; Engle, D.M.; Payton, M.E.; Bukenhofer, G.A. 1999. Influence of fire season and fire behavior on woody plants in red-cockaded woodpecker clusters. Wildlife Society Bulletin. 27(1): 124–133.

Sperry, J.H.; George, T.L.; Zack, S. 2008. Ecological factors affecting response of dark-eyed juncos to prescribed burning. The Wilson Journal of Ornithology. 120(1): 131–138.

Spier, L.P.; Snyder, J.R. 1998. Effects of wet- and dry-season fires on *Jacquemontia curtisii*, a south Florida pine forest endemic. Natural Areas Journal. 18(4): 350–357.

Steele, R.W.; Beaufait, W.R. 1969. Spring and autumn broadcast burning of interior Douglas-fir slash. Bulletin 36. Missoula, MT: University of Montana, School of Forestry. 12 p.

Steuter, A.A. 1987. C^3/C^4 production shift on seasonal burns—northern mixed prairie. Journal of Range Management. 40: 27–31.

Steuter, A.A.; McPherson, G.R. 1995. Fire as a physical stress. In: Bedunah, D.J.; Sosebee, R.E., eds. Wildland plants: physiological ecology and developmental morphology. Denver, CO: Society for Range Management: 550–579.

Stewart, O.C. 2002. Forgotten fires: Native Americans and the transient wilderness. Norman, OK: University of Oklahoma Press. 364 p.

Stoddard, H.L. 1931. The Bobwhite quail: its habits, preservation, and increase. New York, NY: Charles Scribner's Sons. 559 p.

Streng, D.R.; Glitzenstein, J.S.; Platt, B. 1993. Evaluating effects of season of burn in longleaf pine forests: a critical literature review and some results from an ongoing long-term study. In: Hermann, S.M., ed. The longleaf pine ecosystem ecology, restoration, and management. Proceedings of the 18th Tall Timbers fire ecology conference. Tallahassee, FL: Tall Timbers Research Station: 227–264.

Sutherland, E.K. 1997. History of fire in a southern Ohio second-growth mixed-oak forest. In: Pallardy, S.G.; Cecich, R.A.; Garrett, E.H.; Johnson, P.S., eds. Proceedings, 11th central hardwood forest conference. Gen. Tech. Rep. NC-188. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 172–183.

Svejcar, T.J. 1990. Response of *Andropogon gerardii* to fire in the tallgrass prairie. In: Collins, S.L.; Wallace, L.L., eds. Fire in North American tallgrass prairies. Norman, OK: University of Oklahoma Press: 19–27.

Swetnam, T.W.; Baisan, C.H.; Kaib, J.M. [In press]. Forest fire histories of La Frontera: fire scar reconstructions of fire regimes in the United States/Mexico borderlands. In: Webster, G.L.; Bahre, C.J., eds. Vegetation and flora of La Frontera: historic vegetation change along the United States/ Mexico boundary. Albuquerque, NM: University of New Mexico Press.

Swezy, D.M.; Agee, J.K. 1991. Prescribed fire effects on fine-root and tree mortality in old-growth ponderosa pine. Canadian Journal of Forest Research. 21: 626–634.

Sword Sayer, M.A.; Goelz, J.C.G.; Haywood, J.D. 2006. Effects of prescribed fire on production of foliage by sapling longleaf pine. In: Connor, K.F., ed. Proceedings, 13th biennial southern silvicultural research conference. Gen. Tech. Rep. SRS-92. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 478–485.

Taylor, A.H. 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, U.S.A. Journal of Biogeography. 27: 87–104.

Taylor, A.H.; Skinner, C.N. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications. 13(3): 704–719.

Thatcher, B.S.; Krementz, D.G.; Woodrey, M.S. 2006. Henslow's sparrow winter-survival estimates and response to prescribed burning. Journal of Wildlife Management. 70(1): 198–206.

Thies, W.G.; Westlind, D.J.; Loewen, M. 2005. Season of prescribed burn in ponderosa pine forests of eastern Oregon: impact on pine mortality. International Journal of Wildland Fire. 14(3): 223–231.

Thies, W.G.; Westlind, D.J.; Loewen, M.; Brenner, G. 2008. A field guide to predict delayed mortality of fire-damaged ponderosa pine: application and validation of the Malheur model. Gen. Tech. Rep. PNW-GTR-769. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 16 p.

Thompson, D.J.; Shay, J.M. 1989. First-year response of a *Phragmites* marsh community to seasonal burning. Canadian Journal of Botany. 67: 1448–1455.

Towne, E.G.; Kemp, K.E. 2003. Vegetation dynamics from annually burning tallgrass prairie in different seasons. Journal of Range Management. 56: 185–192.

Towne, E.G.; Kemp, K.E. 2008. Long-term response patterns of tallgrass prairie to frequent summer burning. Rangeland Ecology and Management. 61(5): 509–520.

Towne, G.; Owensby, C. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass. Journal of Range Management. 37: 392–397.

Tucker, J.W., Jr.; Robinson, W.D.; Grand, J.B. 2004. Influence of fire on Bachman's sparrow, an endemic North American songbird. Journal of Wildlife Management. 68(4): 1114–1123.

Tucker, J.W., Jr.; Robinson, W.D.; Grand, J.B. 2006. Breeding productivity of Bachman's sparrows in fire-managed longleaf pine forests. The Wilson Journal of Ornithology. 18(2): 131–280.

Van Lear, D.H.; Carroll, W.D.; Kapeluck, P.R.; Johnson, R. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. Forest Ecology and Management. 211(1-2): 150–165.

Varner, J.M.; Hiers, J.K.; Ottmar, R.; Gordon, D.R.; Putz, F.E.; Wade, D. 2007. Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: the importance of duff moisture. Canadian Journal of Forest Research. 37: 1349–1358.

Vermeire, L.T.; Mitchell, R.B.; Fuhlendorf, S.D.; Wester, D.B. 2004. Selective control of rangeland grasshoppers with prescribed fire. Journal of Range Management. 57: 29–33.

Vogl, R.J. 1979. Some basic principles of grassland fire management. Environmental Management. 3(1): 51–57.

Volland, L.A.; Dell, J.D. 1981. Fire effects on Pacific Northwest forest and range vegetation. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 23 p.

Wade, D.D.; Brock, B.L.; Brose, P.; Grace, J.B.; Hoch, G.A.; Patterson, W.A. 2000. Fire in eastern ecosystems. In: Brown, J.K.; Smith, J.K., eds. Wildland fire in ecosystems: effects of fire on flora. Gen. Tech. Rep. RMRS-GTR-42-vol. 2. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 53–96.

Wade, D.D.; Johansen, R.W. 1986. Relating wildland fire to defoliation and mortality in pine. In: Proceedings, 4th biennial southern silvicultural research conference. Gen. Tech. Rep. SE-42. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 107–110.

Wade, D.D.; Lunsford, J.D. 1989. A guide for prescribed fire in southern forests. Tech. Publ. R8-TP11. Atlanta, GA: U.S. Department of Agriculture, Forest Service, Southern Region. 56 p.

Waldrop, T.A.; Lloyd, F.T. 1991. Forty years of prescribed burning on the Santee fire plots: effects on overstory and midstory vegetation. In: Nodvin, S.C.; Waldrop, T.A., eds. Fire and the environment: ecological and cultural perspectives, Proceedings of an international symposium. Gen. Tech. Rep. SE-69. Knoxville, TN: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 45–50.

Waldrop, T.A.; Van Lear, D.H.; Lloyd, F.T.; Harms, W.R. 1987. Long-term studies of prescribed burning in loblolly pine forests of the southeastern Coastal Plain. Gen. Tech. Rep. SE-45. Asheville, NC: U.S. Department of Agriculture, Forest Service Southern Research Station. 23 p.

Waldrop, T.A.; White, D.L.; Jones, S.M. 1992. Fire regimes for pine-grassland communities in the Southeastern United States. Forest Ecology and Management. 47: 195–210.

Warren, S.D.; Scifres, C.J.; Teel, P.D. 1987. Response of grassland arthopods to burning: a review. Agriculture, Ecosystems and Environment. 19: 105–130.

Weatherspoon, C.P. 1988. Preharvest prescribed burning for vegetation management: effects on *Ceanothus velutinus* seeds in duff and soil. In: Proceedings, 9th annual vegetation management conference. Redding, CA: Forest Vegetation Management Conference: 125–141.

Weatherspoon, C.P.; Skinner, C.N.; Simpson, C.S. 1991. Reducing bearclover by repeated growing-season prescribed burns: preliminary test results. In: Proceedings, 12th annual forest vegetation management conference. Redding, CA: Shasta County Opportunity Center: 1–9.

Weise, D.R.; Wade, D.D.; Johansen, R.W. 1989. Survival and growth of young southern pine after simulated crown scorch. In: MacIver, D.C.; Auld, H.; Whitewood, R., eds. Proceedings, 10th conference on fire and forest meteorology. Bethesda, MD: Society of American Foresters: 161–168.

Westmeier, R.L. 1973. Prescribed burning in grassland management for prairie chickens in Illinois. In: Komarek, E.V., ed. Proceedings, 12th Tall Timbers fire ecology conference, Tallahassee, FL: Tall Timbers Research Station: 317–338.

White, D.L.; Waldrop, T.A.; Jones, S.M. 1991. Forty years of prescribed burning on the Santee fire plots: effects on understory vegetation. In: Nodvin, S.C.; Waldrop, T.A., eds. Fire and the environment: ecological and cultural perspectives: Proceedings of an international symposium. Gen. Tech. Rep. SE-69. Knoxville, TN: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 51–59.

White, R.S.; Currie, P.O. 1983. Prescribed burning in the northern Great Plains: yield and cover responses of three forage species in a mixed grass prairie. Journal of Range Management. 36: 179–183.

Wright, C.; Agee, J.K. 2004. Fire and vegetation history in the eastern Cascade Mountains, Washington. Ecological Applications. 14(2): 443–459.

Wright, H.A.; Klemmedson, J.O. 1965. Effect of fire on bunchgrasses of the sagebrush-grass region in southern Idaho. Ecology. 46(5): 680–688.

Yager, L.Y.; Hinderliter, M.G.; Heise, C.D.; Epperson, D.M. 2007. Gopher tortoise response to habitat management by prescribed burning. Journal of Wildlife Management. 71(2): 428–434.

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