



Fire in the American South: Vegetation Impacts, History, and Climatic Relations

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Abstract

Fire plays a key role in many ecosystems of the southeastern U.S. Longleaf pine (*Pinus palustris*) and Table Mountain pine–pitch pine (*P. pungens*–*P. rigida*) forests along with other ecosystems – including oak (*Quercus*) forests, grasslands, and spruce–fir (*Picea*–*Abies*) forests – illustrate the range of fire effects and plant persistence strategies in the American South. Fire history research reveals that fires and fire-associated vegetation were common before the fire exclusion of the past century. Both lightning and anthropogenic ignitions (caused by American Indians or European settlers) contributed to burning, but their relative importance is debated. The humid climate constrains burning, especially by lightning-ignited fires, which often occur during moist conditions. Studies of fire climatology indicate the importance of dry conditions (e.g. drought years and relatively dry areas) for widespread burning in this humid region. Landscape fragmentation also influences burning. In the past some fires also likely grew much larger than today because they were unimpeded by roads, farms, and other barriers.

Introduction

The American South (hereafter, ‘the South’) has long occupied a central place in debates about fire. By the early 1900s, widespread logging, grazing, and burning had ravaged the longleaf pine (*Pinus palustris*) stands of the Coastal Plain (Schiff 1962), and disagreements ensued about how to promote longleaf reestablishment (e.g. Cary 1932; Chapman 1932; Demmon 1929; Howell 1932).

The controversy centered on fire. Frequent light burning of grass and forest litter was used for range improvement and other purposes (Pyne 1982). Many foresters suspected the fires would impede reforestation of the logged stands and suffocate the region’s timber industry, and the U.S. Forest Service sought to guard longleaf pine seedlings from fire so the species could reclaim cutover lands (Schiff 1962). Demmon’s (1929) statements typify the Forest Service view:

The general opinion seems to be that these fires do little or no damage to the forest. Such an erroneous idea fits in well with the common practice of winter burning which has been nearly everywhere prevalent in the South since settlement took place about 100 years ago. It is true that fires rarely kill large trees outright, but they do take an immense toll from the forest tree seedlings. (Demmon 274)

He argued that ‘[t]here is adequate evidence that if fires could be eradicated new crops of trees would soon appear...’ (Demmon 273).

Chapman (1932) and others, however, contended that fire was vital to prevent the encroachment of shrubs and inferior hardwood timber species. Consider Greene’s (1931) article, ‘The forest that fire made’:

Where seed trees are available all that is necessary to get a pure stand of longleaf without a hardwood undergrowth is to have frequent grass fires. Indians and lightning could and did set fire to the dead grass and straw fall and the material was ready to burn over expanses hundreds of miles in extent ... if it had not burned the previous year. (Greene 618)

The debate stimulated research that confirmed the benefits of fire for longleaf pine and its associated wildlife habitat and livestock pasture (e.g. Chapman 1932; Greene 1931; Heyward 1939; Siggers 1932; Stoddard 1931). This work formed an early foundation for fire ecology, eventually contributing to Forest Service endorsement of prescribed fire (Chapman 1950; Schiff 1962).

The global interest in fire ecology today emerged partly from this work. Here I review the role of fire in the South, but space will not permit an exhaustive treatment of the various Southern environments. My intent is to portray the range of fire effects on vegetation – longleaf pine and selected other ecosystems – and to convey how humans and climate influence fire activity.

The Setting

The Coastal Plains cover about half the South (Figure 1), while rougher terrain occupies northern and interior areas. The humid subtropical/temperate conditions support needle-leaf evergreen and broadleaf deciduous forests. The South has higher annual precipitation than any equally large region in North America – over 1000 mm across virtually the entire region and much higher amounts in many locations (NCDC 2002). The South as defined here corresponds largely with Braun's (1950) Southeastern Evergreen, Oak-Pine, Oak-Chestnut, Mixed Mesophytic, Western Mesophytic, and Oak-Hickory Forest Regions. Some of these forest regions extend beyond the South, but because fire is both a cultural and physical phenomenon I confine my discussion to areas within the Upland and Lowland South culture regions (cf. Jordan-Bychkov 2003).



Fig. 1. The American South, noting major physiographic regions mentioned in the text. Green shading indicates the region of interest, the largely forested areas within the Upland and Lowland South.

Effects of Fire on Vegetation

The crowded plantations of spindly loblolly pines (*Pinus taeda*) that cover much of the Coastal Plain today scantily resemble the open longleaf pine woodlands and savannahs that once cloaked the uplands from Texas to Virginia (Figure 2; Frost et al. 1986; Platt et al. 1988a,b). These longleaf stands apparently developed under a surface fire regime (Frost 1998; Heyward 1939). The term 'fire regime' refers to the characteristic fire frequency, severity, seasonality, and size that emerge over time (Frelich 2002). The fires consumed the fine surface fuels and possibly recurred as often as one to three years (Frost 1998).

Longleaf pine has thick bark that protects the cambium inside from heat (Hare 1965). Its unusual seedling development also enables it to thrive in frequently burned areas. The seedlings occupy a 'grass stage' for several years, growing deep roots but not elongating their stems (Figure 3; Keeley and Zedler 1998). Their terminal buds are protected, so they survive if burned. After 5–20 years the stems 'bolt' rapidly (Figure 2), thrusting their crowns above the reach of flames. Vulnerability to fire increases during the bolt stage, but even small stems have relatively thick, protective bark (Figure 4; Garren 1943). After one or two years the tree is virtually immune from surface fires (Agee 1998), which destroy seedlings and saplings of competing species. Frequent burning in the past would have maintained open, nearly monospecific (single-species) stands of longleaf pine with grassy understories (Heyward 1939; Platt et al. 1988a,b). Hurricanes, insect infestations, or other disturbances periodically killed some adult pines, benefiting the seedlings through reduced shading (Figure 5; Gillam et al. 2006; Myers and van Lear 1998; Platt et al. 1988a,b).

A debate in fire ecology concerns whether plant species can adapt to a fire regime (Bond and Keeley 2005). Some traits, like the grass stage in longleaf pine, seem clearly linked to fire (Keeley and Zedler 1998). Three Southern pine species – pond pine (*Pinus serotina*), shortleaf pine (*P. echinata*), and pitch pine (*P. rigida*) – may resprout following



Fig. 2. Longleaf pine woodland, Francis Marion National Forest, South Carolina. Frequent prescribed fires maintain the open, sunny conditions. The dead foliage on the foreground saplings resulted from fire.



Fig. 3. Longleaf pine seedling in the grass stage, Francis Marion National Forest, South Carolina.

stem mortality (Keeley and Zedler 1998). Sprouting is unusual in pines and is considered an adaptation to moderate or severe fires.

Some pines exhibit cone serotiny, wherein cones remain unopened on the plant for years until heated (Lamont et al. 1991). Keeley and Zedler (1998) hypothesized that serotiny adapts plants to thrive on infertile sites visited periodically by intense fires. The poor soils restrict tree height growth; their short stature exposes the entire plants to flames. Serotiny protects seeds and releases them after fire, when seedlings can root into the exposed mineral soil and grow uninhibited in the open conditions. Serotiny is common in sand pine (*Pinus clausa*) stands that inhabit infertile soils of the Florida peninsula (Brendemuehl 1990; Parker et al. 1997, 2001). Serotiny occurs in scattered populations of pitch pine (Williams 1998), typically on infertile ridgetops with stunted trees (personal observation). It is ubiquitous in an associated species, Table Mountain pine (*Pinus pungens*), which is endemic to the Appalachian Mountains (Figures 6 and 7; Williams 1998).

Table Mountain pine–pitch pine stands cloak dry ridgetops and south- or west-facing slopes. Hardwood forests surround these small patches (Figure 8). Recent dendroecological (tree-ring) work reveals that the stands burned frequently in the past (Aldrich et al. 2010; Harmon 1982; Sutherland et al. 1995). Apparently the pines thrive in a ‘polycyclic’ fire regime of frequent surface fires and occasional more severe fires (Aldrich et al. 2010; Frost 1998). Surface fires at short intervals (2–10 years) impeded the encroachment of fire-intolerant competitors from surrounding hardwood stands. They likely maintained open understories beneficial to shade-intolerant (light-demanding) herbs and small shrubs, e.g. blueberries (*Vaccinium* spp.), which recover rapidly through sprouting (Figure 9; Elliott et al. 1999; Harrod et al. 2000). More severe burns at longer intervals (50–100 years) exposed mineral soil and generated large canopy gaps that enabled the highly shade-intolerant pine seedlings to become established and grow (Aldrich et al. 2010; Sutherland et al. 1995; Waldrop and Brose 1999; Welch et al. 2000). Storms and insect outbreaks



Fig. 4. Small longleaf pine sapling, Big Thicket National Preserve, Texas. Despite its small size the sapling already has a large stem with thick bark.

occasionally disturbed the forests (Figure 9), creating gaps amenable to pine colonization (Brose and Waldrop 2006; Lafon and Kutac 2003; White 1987).

Fires do not necessarily stop at the edge of pine stands. According to the 'fire-oak hypothesis' (Abrams 1992, 2003; Brose et al. 2001; Lorimer et al. 1994) many oak (*Quercus*) forests, which have moderately flammable leaf litter, developed under centuries of frequent burning (Figure 10). Fire benefits oaks by inhibiting the establishment of fire-sensitive competitors. Many oaks have relatively thick, protective bark and an ability to 'compartmentalize' fire-damaged wood to prevent decay from spreading (Smith and Sutherland 1999). Extensive roots and a strong sprouting capacity (Figure 11) enable oak seedlings to persist through frequent burning until a longer fire-free window occurs, permitting their growth to a more fire-resistant size (Brose and van Lear 1998; Petersen and Drewa 2006). Growing-season fires seem particularly to benefit oaks by weakening the post-fire resprouting ability of competitors.

Fire does not benefit all vegetation, however. It can devastate certain forests, including high-elevation spruce-fir (*Picea-Abies*) forests on cool, moist sites rarely visited by fire (Figure 12; Delcourt and Delcourt 2000). As on mesic sites worldwide (e.g. Huston



Fig. 5. Pines snapped by Hurricane Rita, Big Thicket National Preserve, Texas. This is a mixed pine stand that the National Park Service is attempting to restore to longleaf pine woodland through thinning and fire.

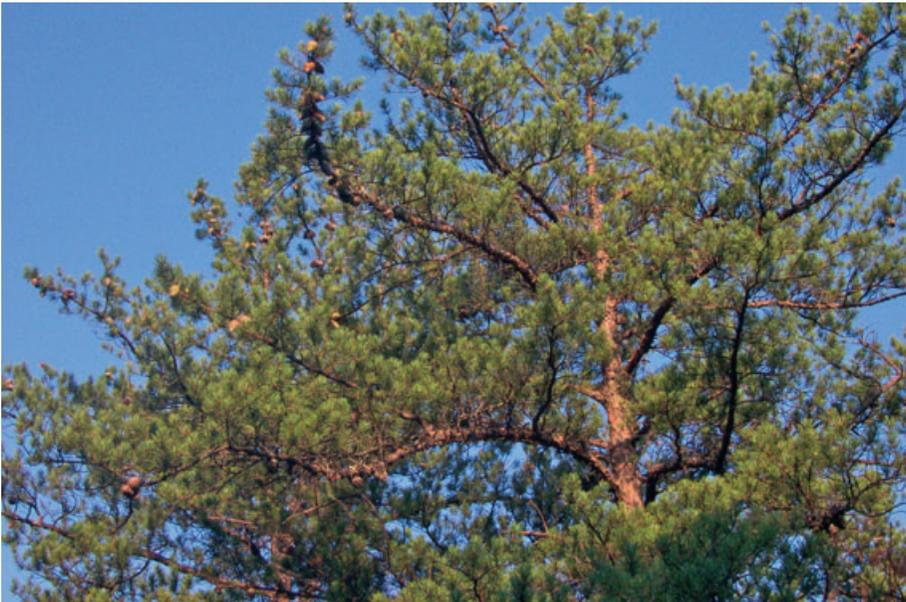


Fig. 6. Table Mountain pines, George Washington National Forest, Virginia. The numerous large, serotinous cones clustered along stout branches are typical features of the species.

1994), stands of long-lived, slow-growing, shade-tolerant species develop over long fire-free intervals. These species have low fire-resistance and slow post-fire recovery (Korstian 1937; White et al. 1993). A different suite of species typically colonizes after fire. These



Fig. 7. Old Table Mountain pine cones, still mostly unopened, and heavily armored to protect the seeds from predation.



Fig. 8. View toward the northeast from Reddish Knob, George Washington National Forest, Virginia. In this leaf-off photograph the dark green pine stands are distinguishable from the extensive deciduous forests. The pine stands occupy dry, west-facing slopes and ridgetops. Clearings in the background are farms in the Shenandoah Valley. Some writers (e.g. Maxell 1910) have suggested that before European settlement frequent fire maintained extensive grasslands in the Shenandoah Valley.



Fig. 9. Table Mountain pine stand photographed in summer 2002 one year after a wildfire, Jefferson National Forest, Virginia. Most of the understory plants are blueberry shrubs that reouted after the fire. The stand had many small Table Mountain pine seedlings but they are inconspicuous in this photograph. In addition to the fire, two other recent disturbance events had affected the forest – ice storms in 1994 and a southern pine beetle outbreak in 2001–2002. The ice storms were responsible for the downed pine trees strewn over the ground.



Fig. 10. Oak litter in a second-growth oak stand, Jefferson National Forest, Virginia. The curly nature of dead oak leaves permit more rapid drying and greater flammability than most other hardwood litter.



Fig. 11. Post-fire resprouting of chestnut oak (*Quercus montana*), Jefferson National Forest, Virginia.

include ‘weedy’ species, like pin cherry (*Prunus pensylvanica*), with widely dispersed seeds, shade-intolerant seedlings, rapid growth, and short life-spans. The original dominants eventually might recolonize, but the recovery could take centuries (Figure 13).

Despite its extensive forests the South has many herbaceous plants that thrive when burned. Best known are the bluestem (*Andropogon*)- and wiregrass (*Aristida*)-dominated understories of longleaf pine stands (Frost et al. 1986), which reportedly have greater plant diversity than any other U.S. ecosystem. Frequent burning enhances diversity by eliminating shrubs and trees that would exclude herbaceous associates – especially on fertile or mesic sites where they rapidly outgrow the herbs (Kirkman et al. 2001, 2004; Platt et al. 2006). The high-diversity understory/low-diversity overstory paradox in longleaf stands reflects tree versus herb longevity (Huston 1994). Only the fire-resistant trees (longleaf pine) persist between successive fires to become mature individuals, while numerous herbaceous species colonize and mature between fires, especially in productive ecosystems with rapid recovery. And burning enhances productivity by releasing nutrients bound in plants (Christensen 1977). Lengthening fire intervals, e.g. through fire protection, allows tree diversity to rise (Heyward 1939) but suppresses herbaceous diversity (Kirkman et al. 2004).

Clearly the South has numerous habitats, varied fire regimes, and diverse plant responses to fire. General order can be discovered by considering the ecological topic of species’ persistence ‘strategies’ (e.g. Buhk et al. 2007; Vesik 2006), the set of traits governing how plants respond to disturbances. Rowe (1983) identified two general persistence modes relevant to fire.

The first is disseminule-based persistence wherein post-fire population growth follows seed dispersal into a burned site. Some species, ‘invaders,’ produce numerous, readily dispersed seeds that enable rapid colonization. Pin cherry is a good example. Other species, ‘evaders,’ store seeds in the soil or canopy, where they are protected until released from



Fig. 12. Spruce-fir forest on Mt. Rogers, Jefferson National Forest, Virginia.

dormancy after fire. The serotinous pines provide examples. ‘Avoiders’ are the least adapted to fire. Most are slow-growing, shade-tolerant species like spruce, which recapture burned sites over a long fire-free period.

The second persistence mode is vegetative-based. The vegetative components of ‘resisters’ withstand low- to moderate-severity fires and occupy the site under repeated burning. Most pines, especially longleaf, show this strategy. ‘Endurers,’ e.g. many hardwood trees and shrubs, persist by resprouting after stem mortality.

Rowe’s persistence modes are neither mutually exclusive nor binary (e.g. resistant versus non-resistant). Table Mountain pine, for example, resists light or moderate fires (Williams 1998). It recolonizes rapidly after severe fire via serotiny. Many oak species persist via moderate fire-resistance, a moderate number of widely dispersed seeds, and sprouting (Abrams 1992; Larsen and Johnson 1998).

An important consideration is that every species cannot resist fire, resprout prolifically, and produce abundant seeds. Resource limitations preclude carbon allocation to all these responses, thus requiring tradeoffs (e.g. Huston 1994; Tilman 1990). Prolific sprouters, for example, often produce fewer seeds than non-sprouters and differ in other factors of life history (Bellingham and Sparrow 2000; Bond and Midgley 2001; Midgley 1996).



Fig. 13. The Dolly Sods area atop the Appalachian Plateau, Monongahela National Forest, West Virginia. Red spruce (*Picea rubens*) forest once cloaked the plateau, but logging and severe fires destroyed most of the soil. A century later, much of the harsh landscape remains deforested, colonized only by shrubs, grasses, and ferns.

Such tradeoffs generate biogeographic patterns by sorting species along environmental and disturbance gradients (e.g. Harmon et al. 1983; Ojeda et al. 2005); and because temporal changes in fire regime can alter these patterns, understanding plant geography requires us to consider fire history.

Fire History

Large-scale industrial logging ravaged the South ca. 1880–1930 (Clarkson 1964; Pyne 1982; Sarvis 1993). Loggers built railroads into the wildlands, cutting adjacent forests and leaving deforested landscapes strewn with woody debris that fueled catastrophic wildfires. Ignitions were pervasive. Locomotives belched sparks and cattlemen fired the cutover lands to encourage pasture. The U.S. Forest Service and state foresters launched a campaign to deter the incessant burning. Often their interventions provoked local resentment, prompting incendiarism. But they were determined to eradicate fire and rebuild the nation's timber wealth, which was considered vital to American industrial progress. Success came through fire prevention campaigns (Figure 14) and expensive technological assaults to suppress fires. Controlled burning emerged later as a tool for managing commercial timber and wildlands.

The preceding synopsis of the past century's fire history is well understood, at least qualitatively. Less certain is the role of fire before the great logging episode. Forest fires generally seem to be common during periods of extensive land use, e.g. agricultural expansion, and to decline with shifts to industrial forestry and sedentary agriculture (Pyne 1982). Some writers have argued that American Indians burned widely and frequently – annually in places – to support their agricultural/hunting/gathering economies (e.g. Abrams and Nowacki 2008; Denevan 1992; Fowler and Konopik 2007; Greene 1932;



Fig. 14. Smokey Bear posters at a work center on the Jefferson National Forest, Virginia.

Kay 2007; Mann 2005; Maxwell 1910; Rostlund 1957; Sauer 1950). European settlers apparently adopted similar burning practices, especially in the agrarian South (Otto and Anderson 1982; Prunty 1965; Pyne 1982). This portrayal contrasts with the popular view of the forest primeval (e.g. Shetler 1991). Some scholars have articulated a middle ground in which American Indians burned frequently near settlements but rarely in remote areas (e.g. Allen 2002; Baker 2002; Russell 1983; Vale 2002; Whitney 1994; Williams 1998). These diverging possibilities connect with broader debates over aboriginal impacts on the environment, but I limit the following brief discussion to evidence about fire history specifically.

The existence of the fire-dependent vegetation discussed above demonstrates that fire has inhabited the South a long time. But was such vegetation common? Early travelers' accounts provide a useful source of evidence (e.g. Baskin et al. 1994; Day 1953; Rostlund 1957). Rostlund (1957) compiled such accounts to argue that grasslands – many of them probably fire-maintained – were scattered liberally over the South before European settlement. Bartram (1791), for example, described many scenes like the 'sublime forests, almost endless grassy fields, detached groves and green lawns for the distance of nine or ten miles' (Bartram 386), which he encountered near the Chattahoochee River. Some accounts describe trees, including oak and pine, growing in open forests devoid of thick understory. Maxwell (1910) noted that some travelers reported aboriginal burning over large areas. Such anecdotes seem to suggest that fire was widespread. But they do not permit quantitative estimates of fire frequency or grassland/pine/oak extent; hence a wide range of interpretations has resulted (e.g. Fowler and Konopik 2007; Maxwell 1910; Nelson 1957; Russell 1983).

Original land surveys, which record witness trees along property boundaries, help clarify the abundance of fire-dependent trees before major European influence (Wang 2005). Despite potential biases, witness trees provide quantitative, spatially explicit portrayals unavailable from travelers' accounts. The handful of such studies conducted in the South

implies that fire-associated trees, especially pine and oak, were common when European settlers arrived (Abrams and McCay 1996; Black et al. 2002; Cowell 1995; Schwartz 1994, 2007). These findings strengthen the case for widespread burning. For example, fire likely played an important role on the Georgia Piedmont (Cowell 1995). In northern Florida, pine forests overwhelmingly dominated the landscape (Schwartz 1994). Schwartz (1994) hypothesized they were mostly longleaf pine stands maintained by fire. This finding matches Chapman's (1932) statement that longleaf occupied roughly half the Coastal Plain, and reveals that fire-associated vegetation was not restricted to scattered dry sites. Instead the fire-intolerant, mesophytic (moisture-demanding) hardwoods were confined to small fire-sheltered locations.

Fire appears to have remained common after European settlement. The earliest settlers likely migrated into grasslands maintained previously by aboriginal and/or lightning-ignited fires (Prunty 1965; Pyne 1982). They continued to burn to perpetuate and expand the openings. Conceptual models of Appalachian fire history suggest that fires occurred frequently during presettlement and post-settlement times (Brose et al. 2001) or, alternatively, that fire frequency was low at first but increased gradually following European settlement (Williams 1998). Fire was necessary for shifting agriculture on marginal soils (Otto and Anderson 1982; Pyne 1982) and for the extensive 'woods ranch' settlement pattern that developed across the South (Prunty 1965). The wildlife biologist Stoddard (1962) recalled frequent – even annual – burning during his boyhood days in Florida, where woodland pasturing was practiced during the 1890s as it had been for generations. At that time, before large timbering operations, the pines were of limited value. The cattlemen burned the woodlands to encourage palatable understory herbs, control understory shrubs, facilitate travel, stimulate berry production, and reduce the habitat of 'varmints' such as chiggers and snakes.

Trees that survive mild/moderate fires often sustain injuries (Figures 15 and 16) that can be dated from tree rings, providing unequivocal evidence of fire at specific times and places. The South permits limited opportunities for dendroecological research on fire history because of rapid wood decay and past forest clearing. However, fire-scarred pines and oaks discovered in the Appalachian and Ozark-Ouachita Highlands record fires back to the 1600s and 1700s (Aldrich et al. 2010; Cutter and Guyette 1994; Guyette and Spetich 2003; Guyette et al. 2002, 2006; Hoss et al. 2008; Shumway et al. 2001). The resultant fire chronologies largely support the historical sketch above – fire abounded amid extensive land uses but virtually ceased under fire protection. Fire-scarred trees from the Ozark-Ouachita Highlands extend back to the period of aboriginal depopulation. They suggest that fire frequency was low at that time but increased as displaced eastern tribes and then white settlers arrived (Guyette and Spetich 2003; Guyette et al. 2002, 2006). The Appalachian fire chronologies have similar length, but they indicate that fires occurred frequently, and at similar levels, before and after European settlement, and during more intensive land use phases such as iron mining and logging (Aldrich et al. 2010; Hoss et al. 2008; Shumway et al. 2001).

Dendroecological data on tree establishment dates indicate that fire-resistant pines and oaks thrive under the historic fire regime (Abrams and Copenheaver 1999; Abrams et al. 1995; Aldrich et al. 2010; Hoss et al. 2008; Shumway et al. 2001; Sutherland et al. 1995), and that less fire-resistant trees encroached rapidly when frequent burning ceased (Figures 17 and 18). These findings corroborate evidence from forest plots (Harrod et al. 1998) and computer simulations (Lafon et al. 2007; Shang et al. 2007). Nowacki and Abrams (2008) argue that mesophytic tree species have expanded throughout eastern North America because of fire exclusion, while fire-associated vegetation has contracted.



Fig. 15. Fire-scarred pine near Reddish Knob, George Washington National Forest, Virginia. The 'catface' on the uphill side resulted from multiple fires that injured the tree over the course of its life. Each ridge within the catface formed as the wood grew over a new fire scar.

Given the importance of oak, pine, and grasslands for numerous wildlife species (Lorimer 2001; McShea and Healy 2002), the influences of fire – and fire exclusion – ripple across multiple trophic levels.

Reconstructing a longer history of fire and vegetation involves radiometric dating of charcoal and fossil pollen buried in soils or pond/bog sediments. At a well known site in Kentucky fire occurred to varying extents over the last 9500 years (Delcourt et al. 1998). Evidence from this and other locations (Delcourt and Delcourt 1997, 1998) was inferred to imply that aboriginal burning, particularly during the last 3000 years, promoted open forests of oak, pine, and chestnut in the Appalachian uplands. Lynch and Clark (2002) also discovered charcoal evidence of fire in the Appalachian Mountains, but it was not ubiquitous among their several study sites. Continuous accumulation of pine pollen and charcoal in Coastal Plain sediments over the last 5000 years potentially evidences frequent fire in longleaf pine forests (Watts 1971). At other sites on the Coastal Plain charcoal has accumulated for the last several hundred years (Foster and Cohen 2007), with an eighteenth-century rise interpreted to indicate American Indian burning associated with the deerskin trade.



Fig. 16. Close-up view of a fire-scarred cross-section cut from a pine tree on the George Washington National Forest. After cutting the section we sanded it and then used the tree rings to date the year of each fire scar. Eight fire scars are visible in this photograph, which reveals the structure of the ridges (cf. Figure 15) that formed as the wood curled over each scar. Photo credit: Jean Wulfson, Division of Research and Graduate Studies, Texas A&M University.



Fig. 17. In the absence of fire, a dense understory of shrubs and trees has developed in this Table Mountain pine-dominated stand on the Jefferson National Forest, Virginia. The stand is located near the one shown in Figure 9. The small pine in the foreground is a white pine (*Pinus strobus*), which is less fire-tolerant than the overstory Table Mountain and pitch pines. Young white pines are common in upland forests throughout the Appalachian Mountains today, but mature white pines are uncommon except along streams.



Fig. 18. Old-growth oak forest in the Great Smoky Mountains National Park, Tennessee. Numerous fire-scarred pines in the vicinity evidence a history of frequent burning in the past, when the oak trees established. Most of the young trees that established during the recent period of fire exclusion are less fire-resistant species such as red maple (*Acer rubrum*). Photo credit: Amanda Young, Mount Allison Dendrochronology Lab, Department of Geography, Mount Allison University.

The available evidence, then, suggests that fire was common for a long time in some locations, promoting grasslands and pine/oak/chestnut forests. However, the spatial extent of fire and fire-associated ecosystems needs clarification. We probably can rule out vast, uninterrupted mesophytic forests. But did fire occur mostly near American Indian – and later European – settlements, largely sparing remote locations until industrial logging? Or did fire pervade Southern landscapes long before European settlement, maintaining vast pine/oak woodlands and grasslands that attracted settlers who perpetuated fire for a time? Increasing evidence of fire bolsters the latter view, but some inferences have been stated quite strongly given the limited, sometimes ambiguous information. Amassing firm evidence from charcoal, witness trees, and fire scars will help mitigate data limitations and enable more certain conclusions.

The existence of fire-dependent vegetation and the history of frequent fire, at least in some areas, lead to another question: given the high humidity and precipitation, what climatic conditions permit fires to ignite and spread on Southern landscapes?

Fire Climatology

The climate system influences three ingredients necessary for fire (Bond and van Wilgen 1996). First, fuel must exist and be sufficiently continuous for fire to spread. Second, fuel must be dry enough to burn. Third, an ignition source must exist. One source, lightning, originates within the climate system.

A long-recognized generalization about fire climatology (Sauer 1952), and one that has been articulated recently, is that moderately wet climates are the most fire-prone (Meyn et al. 2007; van der Werf et al. 2008). These include, for example, tropical savannas, Mediterranean shrublands, temperate grasslands, and many temperate forests – ecosystems with enough precipitation for heavy fuel production but with periodic dry spells that permit burning. High fuel moisture usually precludes fire in extremely wet locations, e.g. tropical rainforests, while insufficient fuel accumulation prevents arid lands from burning. Moderate environments, then, are the most fire-prone, but climatic influences on fire differ across the broad range of intermediate environments. In moderately dry ecosystems, e.g. low-elevation forests in the southwestern U.S., anomalous wetness promotes fuel production and subsequent fire (Brown et al. 2001; Grissino-Mayer and Swetnam 2000). Conversely, drought favors fire in more humid environments like subalpine forests (Schoennagel et al. 2004).

The South would seem to occupy the humid side of the moisture gradient where fuel moisture restricts fire. Limited fire climatology research has been conducted in the region, but records of recent fires reveal elevated burning in dry years (Beckage et al. 2003; Brenner 1991; Dixon et al. 2008; Harrison 2004; Lafon et al. 2005; Mitchener and Parker 2005). Some of this work suggests that global ocean–atmosphere teleconnections, e.g. El Niño–Southern Oscillation, contribute to fire activity by influencing interannual precipitation variability. Dendroecological research reveals limited influence of climate on fire (McEwan et al. 2007; Schuler and McClain 2003), possibly because of widespread anthropogenic burning historically, even during wet years. Most dendroecological work in the South focuses on land use–fire relationships, so historic climate–fire linkages warrant more research.

Within the humid South spatial patterns in burning reflect precipitation gradients. Mitchener and Parker (2005) found that relatively warm, dry environments (e.g. Florida) are more flammable than cool, moist areas (e.g. Appalachian Highlands). Within Appalachia the relatively dry Ridge and Valley province has more fire than the wetter Appalachian Plateau (Lafon and Grissino-Mayer 2007). Surprisingly, however, the Ridge and Valley experiences less burning than the Blue Ridge, which has high annual precipitation similar to the Appalachian Plateau. Lafon and Grissino-Mayer speculated that intra-annual precipitation variability might contribute to the spatial pattern – a climate with infrequent heavy precipitation (Blue Ridge) should have longer dry spells, hence more fire, than one with frequent light precipitation (Appalachian Plateau).

Seasonality is a form of intra-annual climatic variability, and seasonal burning patterns underscore the importance of dry conditions. Most of the South has bimodal fire seasonality (Schroeder and Buck 1970). Burning peaks in spring and fall (Lafon et al. 2005), when low relative humidity, high winds, and warm temperatures desiccate surface fuels. Deciduous canopies are absent, so wind and sun penetrate to the forest floor and dry the litter. Winter has less fire, apparently because cool temperatures and/or snow restrict drying. The winter curtailment is more pronounced in northern/high-elevation areas (Lafon and Grissino-Mayer 2007) than in southern parts of the region (Dixon et al. 2008). During summer, flammability is reduced by high humidity, low windspeed, succulent vegetation, partial decay of dead fuels, and presence of deciduous canopy (Lafon et al. 2005).

The seasonal fire distribution primarily reflects anthropogenic (human-ignited) fires (Abrams and Nowacki 2008; Lafon et al. 2005). People can ignite fires in dry weather, but lightning ignitions are limited to periods of thunderstorm occurrence, mostly late spring and summer. As noted, summer weather often does not favor burning, and when rain accompanies lightning it further dampens ignition. These constraints have led some

researchers to propose that lightning is an insignificant ignition source in the humid South (Schroeder and Buck 1970), a hypothesis supported by fire records from some areas (Yaussy and Sutherland 1994). Florida, however, has many lightning ignitions during the transition from winter drought to summer thunderstorms (Beckage et al. 2003; Harrison 2004). Lightning ignitions also are more important in the Appalachian Mountains than commonly recognized (Cohen et al. 2007; Lafon and Grissino-Mayer 2007). The transitional period from dry spring to humid summer seems especially favorable.

Lightning ignitions likely have ecological consequences disproportionate to their frequency (Lafon et al. 2005). Plants – especially woody species – often sustain higher mortality from summer fires than dormant-season burns (Drewa et al. 2002; Glitzenstein et al. 1995; Harrington 1993; Waldrop et al. 1992; Figures 19 and 20). Leaf-scorch during the growing season reduces photosynthetic capacity at a time when the plant is physiologically active and continues to have high respiration demands. Reduced photosynthesis inhibits the replenishment of carbohydrate reserves that were depleted



Fig. 19. Recently burned hardwood forest in the Linville Gorge along the eastern front of the Blue Ridge, Pisgah National Forest, North Carolina. This and other lightning-ignited fires during the dry spring and summer of 2007 killed trees over extensive tracts of the forest. The photograph was taken within a few weeks of the fire.



Fig. 20. Patches of forest killed by a lightning-ignited fire along the west slope of the Blue Ridge, Jefferson National Forest, Virginia. The fire occurred during the dry summer of 2001, and the photograph was taken in summer 2003. The patchiness in tree mortality apparently resulted from variations in fire intensity. Forest stands on the presumably moister north-facing slopes fared better than those on other sites. North is toward the left of the photograph.

during the spring growth flush. With diminished carbohydrate reserves the plant suffers reduced post-fire resprouting ability and has lower root and shoot growth the following spring. All these factors combine to increase the probability of mortality following a growing-season fire. A dormant-season fire, in contrast, occurs when respiration is low, carbohydrate reserves are protected in underground storage, and deciduous foliage is absent.

Periodic high-mortality episodes such as growing-season fires promote disturbance-dependent species like Table Mountain pine (Aldrich et al. 2010). Summer burns also can favor herbaceous over woody vegetation (Sparks et al. 1998; Waldrop et al. 1992) because of high mortality of the woody competitors. Summer burning synchronizes flowering and stimulates increased flower and seed production among some common herbaceous species of longleaf pine-wiregrass savannas (Brewer and Platt 1994; Outcalt 1994; Platt et al. 1988a,b). A long history of lightning-ignited fires may have selected for a mass reproductive effort timed to the season of lightning ignitions (Brewer and Platt 1994). But many legume species in wiregrass communities respond less favorably to growing-season than other fires (Hiers et al. 2000), suggesting their reproductive biology is not adapted to lightning-ignited fires. Hiers et al. argued that a seasonally varied fire regime would be more effective than a growing-season fire regime for maintaining high understory plant diversity.

The historic role of anthropogenic versus lightning ignitions in the South and elsewhere is debated (e.g. Abrams and Nowacki 2008; Barrett et al. 2005; Kay 2007; Petersen and Drewa 2006). Some (e.g. Chapman 1950; Frost 1998) have argued that fire-dependent plants demonstrate the primacy of lightning ignitions, i.e. human habitation has been too brief to explain these adaptations. One question is whether it is

conceivable for aboriginal or even early European fires to have burned vast wildlands frequently enough to maintain fire-associated vegetation without help from lightning (Barrett et al. 2005). Several authors think so (e.g. Kay 2007; Pyne 1982). Given climatic/weather constraints on lightning ignitions, and their limited role today, Kay (2007), Delcourt and Delcourt (2007), and others argue that people caused the preponderance of pre-European fires. This debate has implications for understanding aboriginal landscape manipulation (e.g. Abrams and Nowacki 2008) and for guiding fire management. Over the past decade many federal agencies have suppressed anthropogenic but not lightning-ignited fires (Zimmerman and Bunnell 1998). This policy assumes that ecosystems developed historically with minimal human influence and that lightning ignitions by themselves can maintain 'natural' conditions.

The historic fire records discussed above afford some insights about this debate but do not resolve it. Fire-scar seasonality indicates that most fires occurred in spring before stem growth began or in fall after growth ceased (e.g. Aldrich et al. 2010; Guyette et al. 2006). This pattern matches the seasonality of anthropogenic fires today. But lightning ignitions overlap the spring anthropogenic fire season; therefore some dormant-season scars could reflect lightning ignitions. Also, some growing-season scars exist.

Where temporal variations in fire frequency correspond with land use changes they may offer glimpses into ignition sources (Allen 2002). Fire history work in the Ozark-Ouachita Highlands suggests a strong land use control and minimal lightning influence (e.g. Guyette et al. 2002, 2006). But Appalachian fire chronologies show little temporal variation (Aldrich et al. 2010; Shumway et al. 2001), even during the depopulated period preceding European settlement, possibly reflecting lightning ignitions from terrain-induced thunderstorms under dry conditions.

Fire, Vegetation, and Climate on Southern Landscapes

Hidden within the lightning ignition question is the issue of landscape fragmentation. Two centuries or more of sedentary agriculture, logging, urbanization, etc. have disrupted fuel continuity. Where fires once may have spread unimpeded for miles, they now encounter obstacles. Fire suppression erects additional barriers; indeed the objective of fire suppression is to contain small fires before they expand (Pyne 1982). Lightning ignitions usually are readily contained as they smolder in moist fuels (Cohen and Dellinger 2006). How large might some have grown historically, when they could smolder several days until the fuels dried? And how large did anthropogenic fires become?

Answers are unavailable, but if some grew large, e.g. during droughts, it is easier to imagine landscapes burning frequently enough to maintain fire-dependent vegetation. Even in remote areas that may have had sparse ignitions, large fires could have sustained high fire frequency by spreading across the landscape (Aldrich et al. 2010; Ward et al. 2001). A computer simulation suggested that much larger and more frequent fires likely occurred on a Florida landscape when it was less fragmented (Duncan and Schmalzer 2004).

Fragmentation and fire spread illustrate the value in keeping real landscapes and their history in view. Vegetation, fire, and climate exist within a specific place and time that are linked inextricably to surrounding landscape and previous history (Baker 2003). Dry uplands covered with fire-resistant plants are interspersed with stream valleys occupied by shade-tolerant fire avoiders (Harmon et al. 1983). The moist valleys can inhibit fire spread between neighboring uplands, but severe droughts may erase these boundaries. Hilly terrain presents more such obstacles than flatlands, partly explaining the high fire

frequency of the Coastal Plain and the abundance of fire-avoiding plants in the Appalachian Mountains (Frost 1998). Terrain also interacts with climate, for example, by forcing thunderstorm/lightning development along the Blue Ridge and near the coast (Hodanish et al. 1997; Lafon and Grissino-Mayer 2007). Such interactions may elevate fire activity, promoting open, flammable vegetation and dry microclimatic conditions that further escalate burning (Harrod et al. 2000).

Land use changes have disrupted these feedbacks, reducing fire frequency and permitting a shift to mesophytic forests ('mesophication') with less combustible leaf litter, more shade, and cooler, moister conditions (Nowacki and Abrams 2008). Although mesophytic tree seedlings do not resist fire, some can resprout if top-killed (Welch et al. 2000), and their fire resistance increases as they mature (Harmon 1984). Today resource managers use prescribed fire to attempt to restore fire-associated ecosystems. But mesophication – and the decline of pine/oak/grassland seed sources – make it increasingly difficult to restore such vegetation (Nowacki and Abrams 2008). These alterations in vegetation and flammability also make it harder for us to envision the historic role of fire on Southern landscapes.

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Short Biography

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Note

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