

Fire in the Eastern United States: Influence on Wildlife Habitat

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Abstract.—Fire is a major influence shaping wildlife habitats in the eastern United States. Lightning- and Indian-ignited fires burned frequently and extensively over the pre-Columbian landscape and shaped the character of numerous ecosystems. Depending upon the frequency, intensity, and severity of the fires, various assemblages of plants developed along environmental gradients, creating a shifting mosaic of habitats for wildlife. For millennia, fire was a major ecological process, mostly burning as frequent, light to moderate intensity surface fires in some ecosystems and as intense, stand-replacing fires in others. Within the past 100 years, fire has been excluded from most of the East and fire-maintained habitats have dramatically declined. In many cases, wildlife species dependent on these habitats are in decline or experiencing dangerously low numbers. Unfortunately, the trend toward a relaxation of bans on burning may soon be reversed due to the adverse publicity from recent disastrous fire in the West.

Wildfires and escaped prescribed fires frequently have been in the news in recent years, e.g., those in Yellowstone National Park in 1988, Florida in 1998, and throughout the West in 2000. Usually, only catastrophic wildfires or escaped prescribed fires are deemed newsworthy. Media coverage often concludes that forests have been destroyed by these wildfires and imply that wildlife habitat has been destroyed as well. But has wildlife habitat really been destroyed? Does fire so damage ecosystems that they are gone forever? Of course not, especially in the eastern United States where vegetative recovery is relatively rapid following disturbance. From an ecological perspective, ecosystems and their associated wildlife habitats are not destroyed, only changed to an earlier stage of succession.

Fire should be considered in the context of its role as a natural ecological process that has shaped vegetative patterns in most eastern ecosystems for millennia. Even ecosystems burned with high intensity fires generally have mechanisms in place to recapture solar energy and recycle nutrients, allowing rapid ecosystem renewal. All over the world, early man used fire for his benefit. Properly used, it remains an important tool in both forest and wildlife management.

The earth has been described as a fire planet, a planet whose terrain is covered with combustible organic fuels which continually accumulate over time, an oxygenated

atmosphere that supports combustion, and two potent ignition sources—lightning and man (Pyne et al. 1996). Most ecosystems on earth have burned in the past and will burn again in the future—creating, changing, or maintaining habitats for a wide variety of wildlife. Because fire was historically so prevalent and frequent across the eastern landscape, wildlife evolved adaptations to fire in order to survive (Komarek 1974, Brennan et al. 1998).

Fire History in the Eastern United States

Approximately 12,000 years ago, man first made his way into North America (Williams 1989, Bonnicksen 2000). Within a relatively short period of less than 1000 years, these early Americans had occupied nearly all of the western hemisphere. They used fire in many ways because it helped them survive. Over thousands of years, the American Indian became expert in using fire for various purposes, e.g., for hunting, to concentrate prey species in convenient areas, to encourage fruit and berry production, to keep the woods open along major corridors of travel, to fire-proof their villages, and other uses (Williams 1989, Pyne et al. 1996, Bonnicksen 2000). Through trial and error over millennia, the Indian learned to make fire his servant and not his master. Thus, controlled, or prescribed, burning is nothing new (Komarek 1974).

The Indian population of North America at the time of Columbus was estimated by Dobyns (1983) at about 18 million. This figure has been widely quoted, although Stannard (1992) more recently suggested that there may have been as many as 100 million Indians in North America. Regardless of the accuracy of these and other estimates of the Indian population, there can be no doubt that, at the time of Columbus, there were millions of Indians modifying the “natural” forests. Their influence on the eastern forest was widespread because of their use of fire and extensive land clearing for agriculture (Hudson 1976, Williams 1989). Because of their farming and burning activities, Indians ensured that much of the eastern forests was in early successional habitats.

Indians often burned as frequently as twice a year, complementing lightning as an ignition source. Their burning extended the fire season beyond the “natural” lightning-fire season of summer. These frequent and often extensive fires, along with the wildlife foraging that fire encouraged, created and maintained open woodlands, savannahs, and prairies throughout the eastern United States (Williams 1989, McCleery 1993, Kay 2000). In fact, much of the eastern forests at the time of Columbus could be regarded as a cultural artifact of Indian activities.

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Because of burning and agriculture, the eastern United States at the time of Columbus was no “forest primeval” composed of closed canopy, old-growth forests. The oft-repeated phrase that a squirrel (*Sciurus* sp.) could travel from the Atlantic coast to the Mississippi River in pre-Columbian times without ever touching the ground is patently false (Buckner 1983, Hamel and Buckner 1998). The eastern forest at that time was a shifting mosaic of woodlands, savannahs, forests, and prairies, all in varying stages of succession. After Indian populations plummeted in the 16th century from exposure to European diseases, their level of burning declined and prairies gradually became woodlands, savannahs became dense forests, and dense undergrowth invaded open forests (McCleery 1993).

The early European settlers found that much of the East was already being fired on a frequent basis by Indians (Komarek 1974). These settlers gradually displaced the Indians, but continued their use of fire for many of the same reasons, i.e., to clear the woods of underbrush, to expose nuts, to clear agricultural fields, etc. Frequent fires occurred over large areas of the eastern landscape into the early decades of the 20th century.

Not until the early 1900s were there serious efforts to exclude fire as an ecological process in eastern North America. In 1910, an outbreak of wildfires in the western United States--concentrated in Idaho and Montana, burned millions of acres, much of which was on national forests, and killed 78 firefighters (Pyne et al. 1996). These events occurred just after the Forest Service had made fire control a top priority on the nation's national forests and caused the public to become concerned about the sustainability of the nation's natural resources. Led by the Forest Service and the state forestry commissions, the public began to see fire as an enemy to be suppressed at all costs. An era of fire suppression began that created different environments from those that had existed for millennia, often to the detriment of many wildlife species.

Habitats and Fire

Habitats are environments that provide the necessities of life for wildlife, i.e., food, water, cover, and places to rear their young, and are shaped by ecological processes acting on varying gradients of soil, topography, hydrology, and climate over time. In most of the eastern United States and in many other parts of the world, fire historically played a major role in shaping habitats. Fire, often working in combination with other disturbance factors, was the major factor determining the composition, structure, and pattern of vegetation that occupied different portions of the landscape.

Fire became a more important force in shaping habitats in the East as the climate warmed following the last glaciation because a warmer climate promoted better burning conditions. Indian populations were also

increasing, especially in the past few thousand years, as greater use of agriculture allowed them to discard their previous nomadic lifestyle. And wherever there were Indians, there was fire.

The Laurentide ice sheet, which covered the northeastern United States and extended south to the Ohio River at the peak of the Wisconsin glaciation, began to retreat about 18,000 years ago (Bonnicksen 2000). At the end of this ice age about 10,000 years ago, vegetation in the eastern United States was still migrating northward (Delcourt and Delcourt 1987). It is difficult, if not impossible, to unravel effects of a changing climate (generally warming until about 6,000 years ago, then generally cooling again--until about 1970) from the effects of Indian burning. By about 5-6,000 years ago, the vegetative associations of today were essentially in place in the South, although the structure of those forests must have been much different than today's forests. In the Northeast and Midwest, it took longer for individual species to arrive in their current locations because they had farther to travel from their southern refugia.

Burning altered the structure, composition, and pattern of vegetation. Fire regimes created types of vegetation that actually encouraged recurring fire, e.g., the longleaf pine (*Pinus palustris*)-wiregrass (*Aristida*) ecosystem, and, in so doing, shaped habitats. The habitats that developed depended upon the type of fire regime, the adaptations of plants occupying the landscape, and the length of time since the last disturbance. The magnitude of the historical role of fire is under-appreciated by the general public and even some resource managers because of almost a century of efforts to exclude it from the majority of the landscape.

Historical Fire Regimes

In the eastern United States, some areas were burned so infrequently, e.g., moist to wet areas in northern hardwood forests, that it can be said that these areas do not burn. Other areas were subject to annual fires that burned with low intensity, i.e., low flame lengths, and low severity, i.e., little damage to soil or overstory vegetation. Still other areas burned infrequently but with great intensity and killed essentially all overstory trees. Because of the many types of fires that can occur, fire scientists have devised systems for characterizing them (Table 1), using variables such as fire intensity, severity, and frequency of burning to describe fire regimes (e.g., Heinselman 1981).

Understory fire regimes are characterized by frequent burns of relatively low intensity that do little damage to soil or overstory trees (low severity). Ecosystems subjected to frequent understory burns recover quickly as the grasses, forbs, and understory woody vegetation characteristic of this type of fire regime resprout vigorously within weeks after burning. Overstory trees

Table 1.—Heinselman’s (1981) classification of historic fire regimes, slightly modified, with selected eastern examples. (Note: Only those classes applicable to eastern conditions are given.)

Class	Characteristics of Fire Regime	Eastern Examples
0	No natural fires	Wetter regions of the eastern deciduous forest
1	Infrequent, light surface fires with more than 25-yr return intervals	Many eastern deciduous forests
2	Frequent, light to moderate surface fires with 1- to 25-yr return interval	Southern pine forests of Coastal Plain and lower Piedmont; Tall-grass prairies
3	Infrequent, severe surface fires with more than a 25-yr return interval	Dry jack pine-oak “barrens” of Minnesota, Wisconsin, and Michigan
4	Short return interval crown fires and severe surface fires in combination (25- to 100- year return intervals)	Most boreal forests in eastern Canada and United States; Sand pine

are generally little affected by these low intensity fires. Such a fire regime was typical of the longleaf pine-wiregrass ecosystem that dominated up to 90 million acres of the Coastal Plain of the Southeast at the time of Columbus, but which now occupies only about 3% of its original range (Frost 1998, Landers et al. 1995). As a result of loss of this open woodland, savannah type habitat, numerous wildlife species including the red-cockaded woodpecker (*Picoides borealis*), gopher tortoise (*Gopherus polyphemus*), and southern fox squirrel (*Sciurus niger*) are in decline.

Stand-replacement fire regimes are typified by infrequent fires of high intensity that kill most of the overstory trees and sometimes damage the soil (high severity). Such fire regimes are typical of sand pine (*Pinus clausa*) stands in Florida (Outcalt and Balmer 1983), Table Mountain (*Pinus pungens*)/pitch pine (*Pinus rigida*) stands in the southern Appalachians (Clinton et al. 1993), and jack pine (*Pinus banksiana*) stands in the boreal forests of the northern United States and Canada (Rudolph 1983, Bonnicksen 2000). Fires in these types may burn as surface fires under mild conditions but under severe weather and fuel conditions stand-replacement fires develop. In the absence of fire, especially on better sites, the species are replaced by more shade-tolerant species, i.e., scrub oaks in sand pine (Outcalt and Balmer 1983), oaks and mountain-laurel (*Kalmia latifolia*) in Table Mountain/pitch pine stands (Waldrop and Brose 1999), and red pine (*Pinus resinosa*), white pine (*Pinus strobus*), and various hardwoods in jack pine stands (Rudolph 1983). Following stand-replacement type fires, seeds from serotinous cones germinate on a fire-prepared seedbed and a new stand develops. However, ecosystem recovery may take decades before the character of the new stand recovers to that of the pre-burned stand. Burning in

these types requires intensive, experienced supervision because of the high risk of fires getting out of control.

The jack pine ecosystem is one of the most extensive in North America and exists in a variety of successional stages on many site types. Jack pine grows best on dry soils where fires are relatively frequent, i.e., every 50 - 100 years, and severe (Bonnicksen 2000). There are many wildlife species that are characteristic of these habitats, although we know of few that are threatened or endangered. Many species are cyclic in the jack pine ecosystem, including the snowshoe hare (*Lepus americanus*), Canada lynx (*Lynx canadensis*), and the snowy owl (*Nyctea scandiaca*). The Kirtland’s warbler (*Dendroica kirtlandii*), one of America’s rarest birds, nests only in pure stands of jack pine (Hunter 1990).

The Table Mountain/pitch pine ecosystem in the southern Appalachians is in decline because of fire exclusion in this type. There is some debate among fire scientists about whether the Table Mountain/pitch pine type in the southern Appalachians was maintained primarily by stand-replacement fires or periodic understory fires. Recent research by the North Carolina Wildlife Resources Commission, the U.S. Forest Service, and Clemson University suggests that periodic burning in the type creates open woodland conditions, which would enhance landscape diversity within the sea of mature, dense hardwood and pine forests that now dominate the southern Appalachian mountains.

Not all stand-replacement fires occur in forests. The tallgrass prairie was dominated by fire-tolerant tall grasses, including big bluestem (*Andropogon* sp.), little bluestem (*Schizachyrium scoparium*), and Indiangrass (*Sorghastrum nutans*), but also contained forbs, shrubs, and trees. This ecosystem, which existed in pure form in

Table 2.—Plant adaptations to fire in different stages of development.

Stage of Development	Adaptation	Plant Examples
Vegetative	Sprouting from root collar buds	Most hardwoods; certain pines
	Sprouting from adventitious or latent axillary buds	Most southern pines
	Thick bark	Most oaks; southern yellow pines; numerous others
	Protected buds on boles and limbs	Pitch pine and pond pine
	Protected buds below ground	Oaks
Reproductive	Precocious flowering	Table Mountain pine; Sand pine; jack pine
	Stimulation of flowering	Wire grass
	Serotinous cones	Table Mountain pine; pitch pine; jack pine; sand pine
Germination	Heat-enhanced seed germination	Some legumes; fire cherry; yellow-poplar
	Germination on fire-prepared seedbeds	Many pines; fireweed; many other species
Other Adaptations	Increased inflammability	Longleaf pine, wiregrass, jack pine

eastern Nebraska, Illinois, Iowa, and eastern Kansas, graded into a forest-prairie complex to the east, and has been almost totally converted to agriculture (Telfer 2000). Only about 1% of the tallgrass prairie remains. It was a fire-maintained ecosystem that was burned primarily by man at intervals of 1-3 years (Pyne et al. 1996). When fires became less frequent, the eastern portions of the prairie succeeded to shrubs and trees. When burned annually, shrub species were eliminated. Wildlife species in decline because of this vanishing habitat include the greater prairie chicken (*Tympanuchus cupido*), badger (*Taxidea taxus*), and false map turtle (*Graptemys pseudogeographica*).

Some fire regimes may include both surface fires and stand-replacement fires. There are mixed severity fire regimes where fires alternate between understory burns and stand replacement burns, either within the same fire or in different fires. Such burns cause selective mortality in the overstory, especially when certain species are better adapted than others to withstand the effects of high intensity fires. Burns of this type occur, for example, in mixed pine/hardwood stands in the southern Appalachians where fuel loadings have accumulated primarily in the form of dense understories of mountain-laurel (Elliott et al. 1998, Waldrop and Brose 1998). Fires in this type are intense enough to

topkill many of the hardwoods and shrub understory but the thick bark, high crowns, and ability to quickly regenerate new needles allows many of the mature pines to survive.

Fire Adaptations

Fire is only one of many evolutionary forces that shape plants and plant communities. However, fire has been so ubiquitous on the planet and exerts such profound influences on the environment that it is reasonable to assume that fire regimes selected for individuals in populations that could best survive fire (Pyne et al. 1996). Plant species that evolved with fire adapted by developing characteristics that increase their chances of survival in various types of fire regimes (Table 2). Such adaptations occur in various stages of a plant's development, from regeneration to maturity (Kimmins 1987).

The ability to resprout from root collar buds following topkill by fire is probably a fire adaptation in some species, even though this characteristic occurs in other taxa where fire is alien (Bond and van Wilgen 1996). Many species replace scorched foliage by sprouting from adventitious or latent axillary buds on branches or boles of trees. Where fire is frequent, sprouting adaptations

such as these improve the survival potential of plants because it allows those plants to continually occupy the same growing space. Non-sprouters would be favored by longer return intervals between fires because they could allocate more of their energy to top growth, allowing them to more completely occupy the growing space in the absence of fire for long periods.

Some species have developed thick bark apparently to insulate the living cambium from the heat of surface fires. Other species have thin bark when young and are quite susceptible to fire damage or mortality, but develop very thick bark as they mature and become resistant to surface fires. The protection offered by bark is dependent upon not only its thickness but, at least for some species, by its thermal properties (Hare 1965).

Certain fire-adaptations are even more species specific. Cone serotiny, where seed accumulates in unopened cones that open after being heated by fire, is characteristic of relatively few species in the East. Species with serotinous cones normally exist in environments where high intensity, stand-replacing fires are the norm (Pyne et al. 1996, Bond and van Wilgen 1996). Another species-specific adaptation is the grass stage of longleaf pine, where their fire-sensitive buds are protected from overheating by a dense sheath of moisture-rich needles (Walhenberg 1964). This characteristic is unique among the pines.

Oaks in some ways might be considered to be the longleaf pine of the hardwoods. They have multiple adaptations to fire, including thick bark that protects them from damage by surface fires. Oaks also have hypogeal germination, i.e., their root collar buds are below the surface of the soil because their acorns are buried by squirrels and/or jays (*Sciuridae* and *Corvidae*). Because these buds are protected from the heat of surface fires (soil is a poor conductor of heat), oaks are better able to successfully sprout following fire than many of their competitors whose seeds germinate on the soil surface, such as yellow-poplar (*Liriodendron tulipifera*) (Brose and Van Lear 1998, Brose et al. 1999).

Many species in the eastern United States have seeds that are either encouraged to germinate by heating or to germinate on fire-prepared seedbeds (Pyne et al. 1996, Lyon et al. 2000). Heat from fire can crack the seedcoat and release the seed from dormancy. Some grasses, such as the wiregrasses, only flower when burned in certain seasons, with blooming following spring burns but not after winter fires (Brennan et al. 1998).

Some adaptations not only allow plants to survive fire but also play a major role in predisposing plant communities to recurrent fire (Mutch 1970). For example, the dominance of wiregrass in the herbaceous layer, with its high proportion of dead leaves and their overlapping nature, along with the resinous nature of fallen longleaf pine needles, insures that surface fires

will be frequent in this ecosystem (Landers et al. 1995). Another example would be in oak forests where the fallen leaves curl and resist decay, allowing a highly aerated fuel bed to develop, which encourages frequent surface fires. In contrast, leaves of fire-sensitive hardwoods like American beech (*Fagus grandifolia*), yellow-poplar, and red maple (*Acer rubrum*) lie flat on the ground and decay rapidly, preventing a flammable fuel bed from developing. Unless fire-adapted plant communities tend to promote recurrent fire, they are likely to be replaced by non-flammable communities (Bond and van Wilgen 1996).

These adaptations of different plant species, along with conditions for establishment and the availability of plant propagules, determine patterns of succession and the types of habitats that develop following burning.

Effects of Fire on Habitat Components

Fire affects habitat components in many ways. Periodic understory burns cause many plants to resprout and these new sprouts, whether woody or herbaceous, are more palatable and have higher protein and nutritive content than the older tissues that they replaced (Stransky and Harlow 1981, MacCracken and Viereck 1990). Enhanced palatability and higher nutrient contents in post-burn growth are relatively short lived (generally 1-2 years), but are important in areas frequently burned. Regrowth after burning is not only more palatable and nutritious than older tissue, it is also more available because most sprouting occurs at ground level (Lay 1967).

Frequent burning tends to favor herbaceous vegetation over woody vegetation, i.e., it increases the proportion of herbage to browse (Lewis and Harshbarger 1976, Pack et al. 1988). Growing season burns discriminate against woody growth more than dormant season burns. Frequent burning creates open forest conditions in both pine and hardwood forests, i.e., understory and midstory woody vegetation are replaced by herbaceous vegetation (Landers et al. 1995, Thor and Nichols 1974). Burning does not eliminate woody growth but controls its size (Waldrop et al. 1987). Annual summer burns in southern pine stands will eventually remove hardwoods from the stand but it takes numerous burns. Certain woody species, such as oaks, tend to be more tenacious sprouters than competitors and therefore persist in frequently burned ecosystems.

Seed and mast production generally increase after burning in Southern forests. Seed production by legumes, grasses and spurges is usually greater on frequently burned areas (Cushwa et al. 1970, Robbins and Myers 1992). Production of berries, drupes, and pomes normally peaks about 2 to 4 years following burning (Harlow and Van Lear 1989). However, burning too frequently, i.e., annually or biennially, reduces most mast-producing species (Robbins and Myers 1992).

Numerous hard-seeded species require their seed to be heated to 60 - 80°C to break dormancy (Auld 1986). Some shrub species (*Vaccinium*) and small trees such as dogwood (*Cornus florida*) tend to be more fruitful a few years following burning, although others do not (Harlow and Van Lear 1989). Hard mast-producing species, such as oaks and hickories (*Carya* sp.), are generally favored by fire during the regeneration period (Abrams 1992, Barnes and Van Lear 1998, Brose et al. 1999).

Effects of fire on standing dead trees, i.e., snags, and fallen woody debris are variable (Lanham and Guynn 1993, Van Lear 1993). Surface fires burning under droughty conditions frequently kill stressed trees, creating snags. In addition, fires may scar the bases of some trees and eventually become basal cavities. However, some snags may be consumed by fire or at least brought to the ground, where they become fallen woody debris. Both forms of coarse woody debris are extremely important habitat components (McMinn and Crossley 1993). In the East, most snags do not stand for long periods of time, often falling within a decade of death (Dickenson et al. 1983, Sabin 1991). Coarse woody debris is generally not consumed by fire unless the drought index, e.g., the Keetch-Byrum drought index, is high. Only when the debris becomes dry throughout during droughty conditions will significant amounts be consumed by fire.

In the southeastern United States, long-term studies in the Coastal Plain show that periodic burning increases availability of phosphorus, as well as other nutrients in the mineral soil, probably because of increased mineralization and because soil pH is raised (McKee 1992). Most soil nutrients become more available for plant uptake as soil acidity approaches neutral. This increased availability probably accounts, at least in part, for the higher nutrient levels in regrowth following fires. Enhanced soil phosphorus levels resulting from burning may have implications in Quality Deer Management programs because phosphorus is needed for antler development (Cowan and Long 1962).

Burning historically provided a mosaic of habitat types in a variety of seral stages and fuel conditions over the landscape (Wood 1981, Williams 1989, Pyne et al. 1996). Fire did not burn uniformly across the landscape, but interacted with topographic, edaphic, vegetative, and weather conditions to produce a mix of habitats and ecotones. While fire occasionally changed mature forests to early successional habitats, i.e., jack pine ecosystems, it also maintained the structure and composition of certain ecosystems where fire was a frequent visitor, e.g., the longleaf pine-wiregrass ecosystem and the tallgrass prairie ecosystem. These varied conditions created habitats for many species of wildlife which, over millennia, came to depend on these conditions. As the role of fire has declined over the past century, so have many plant and wildlife species.

Conclusions

Fire has shaped the pattern, composition, and structure of vegetation in the eastern United States for millennia, especially since the arrival of Indians at least 12,000 years ago. Indians used fire for many purposes and often fired the woods on an annual basis. Frequent burning kept the forests more open and increased the ratio of herbaceous/woody vegetation. Fire did not burn uniformly across the landscape but created a shifting mosaic of habitats depending upon fuel, weather, and site conditions at the time of burning. In some ecosystems, fire burned frequently but with low intensity and severity and maintained the *status quo* of the ecosystem. In other cases, fires burned with high intensity and severity and completely changed the ecosystem. Plants and animals adapted to these different fire regimes in order to survive. Over time, many wildlife species became dependent upon these fire-maintained habitats.

During most of the past century, attempts have been made to exclude fire from much of the eastern landscape. Exclusion of fire, along with other factors, have resulted in major declines in fire-maintained habitats, the most notable examples being the longleaf pine-wiregrass habitat and the tallgrass prairie habitat. Fire also played a role in maintaining other habitats important to wildlife. Historically, it perpetuated the jack pine, sand pine, and Table Mountain/pitch pine ecosystems and was instrumental in maintaining oak forests on good-quality sites throughout much of the East. The exclusion of fire in fire-maintained habitat types may make catastrophic wildfires more frequent, potentially changing ecosystems and eliminating desirable habitat for some species. Burning on a regular basis prevents fuel build-up and minimizes the chances of a catastrophic wildfire occurring.

There is no question of the historical importance of fire in creating and maintaining wildlife habitats in the eastern United States. However, we now live in a different time and there are numerous restrictions on the application of fire for wildlife habitat purposes. We suggest that prescribed fire be used where feasible and where it can accomplish desired objectives, because it has unique habitat effects. However, in the future it will be necessary to use other management techniques, including harvesting, thinning, and herbicides, to mimic, at least partially, the effects of prescribed fire on wildlife habitat where burning is not appropriate.

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