
Modeling the Effects of Fire on the Long-Term Dynamics and Restoration of Yellow Pine and Oak Forests in the Southern Appalachian Mountains

Charles W. Lafon,^{1,2} John D. Waldron,³ David M. Cairns,¹ Maria D. Tchakerian,⁴ Robert N. Coulson,⁴ and Kier D. Klepzig⁵

Abstract

We used LANDIS, a model of forest disturbance and succession, to simulate successional dynamics of forests in the southern Appalachian Mountains. The simulated environments are based on the Great Smoky Mountains landscapes studied by Whittaker. We focused on the consequences of two contrasting disturbance regimes—fire exclusion versus frequent burning—for the Yellow pine (*Pinus* L., subgenus *Diploxylon* Koehne) and oak (*Quercus* L.) forests that occupy dry mountain slopes and ridgetops. These ecosystems are a conservation priority, and declines in their abundance have stimulated considerable interest in the use of fire for ecosystem restoration. Under fire exclusion, the abundance of Yellow pines is projected to decrease, even on the driest sites (ridgetops, south- and west-facing slopes). Hardwoods and White pine (*P. strobus* L.) replace the Yellow pines. In contrast, frequent

burning promotes high levels of Table Mountain pine (*P. pungens* Lamb.) and Pitch pine (*P. rigida* Mill.) on the driest sites and reduces the abundance of less fire-tolerant species. Our simulations also imply that fire maintains open woodland conditions, rather than closed-canopy forest. For oaks, fire exclusion is beneficial on the driest sites because it permits oaks to replace the pines. On moister sites (north- and east-facing slopes), however, fire exclusion leads to a diverse mix of oaks and other species, whereas frequent burning favors Chestnut oak (*Q. montana* Willd.) and White oak (*Q. alba* L.) dominance. Our results suggest that reintroducing fire may help restore decadent pine and oak stands in the southern Appalachian Mountains.

Key words: disturbance, fire, forest restoration, simulation, succession.

Introduction

Historic changes in disturbance regimes of eastern North American landscapes have modified the composition and structure of forest ecosystems. Cultural disturbances associated with forestry, agriculture, and urbanization have created forest landscapes that differ strongly from pre-settlement conditions (Foster et al. 1998; Abrams 2003). Moreover, suppression activities have reduced the frequency of fire, which formerly was a pervasive disturbance integral to the functioning of many ecosystems (Pyne 1982; Abrams 1992). Removing fire permitted the successional replacement of fire-dependent vegetation by fire-intolerant species and also favored the development of dense stands of stressed trees that are vulnerable to insect infestation and disease (Schowalter et al. 1981; Coulson &

Wunneburger 2000). The impacts (ecological, economic, and social) of these changes have stimulated research on forest restoration approaches that foster conditions in which disturbances operate within the historical range of amplitude, frequency, and duration (Frelich 2002; Mitchell et al. 2002; Palik et al. 2002).

Of particular interest to many resource managers is the use of fire as a restoration tool, especially in forests dominated by Yellow pine (*Pinus* L., subgenus *Diploxylon* Koehne) and oak (*Quercus* L.) (Pyne 1982; Haines & Busby 2001; Palik et al. 2002; Van Lear & Brose 2002). These forests are hypothesized to require periodic burning for their long-term maintenance (Abrams 1992; Agee 1998; Williams 1998; Wade et al. 2000; Abrams 2003). Most pines and oaks are intolerant of shade and appear to thrive best in open, fire-maintained stands. They also are more fire tolerant than their associates and were favored by the frequent surface fires that historically characterized many landscapes in eastern North America. Fire exclusion, in concert with insects, disease, and other natural disturbances, has contributed to recent widespread declines in the abundance of Yellow pine and oak. The declines have prompted concern about the long-term maintenance of these species, because they are among the most valuable trees in North America for wildlife habitat, timber

¹ Department of Geography, Texas A&M University, 3147 TAMU, College Station, TX 77843, U.S.A.

² Address correspondence to C. W. Lafon, email clafon@geog.tamu.edu

³ Department of Environmental Studies, University of West Florida, Fort Walton Beach, FL 32547, U.S.A.

⁴ Knowledge Engineering Laboratory, Department of Entomology, Texas A&M University, 2475 TAMU, College Station, TX 77843, U.S.A.

⁵ USDA Forest Service, Southern Research Station, 2500 Shreveport Highway, Pineville, LA 71360, U.S.A.

production, and biodiversity conservation. Reversing these declines may require the reintroduction of frequent burning similar to the pre-suppression fire regime (SAMAB 1996; Harrod et al. 1998; Williams 1998; Dey 2002; Palik et al. 2002).

In the southern Appalachian Mountains, much land is under federal ownership, and resource managers are using fire to restore Yellow pine and oak forests on these lands (SAMAB 1996; Elliott et al. 1999; Waldrop & Brose 1999; Welch et al. 2000; Hubbard et al. 2004). Oak forests are the predominant land cover type, occupying xeric, sub-xeric, and submesic sites on ridgetops and dry slopes (Stephenson et al. 1993; SAMAB 1996). These are among the most extensive oak forests in North America (McWilliams et al. 2002). Yellow pine stands are less extensive but still comprise the second most widely distributed forest type in the region (approximately 15% of the forest cover) (SAMAB 1996). They generally are confined to ridgetops and southwest-facing slopes, the driest sites on the landscape (Whittaker 1956; Stephenson et al. 1993). One species, Table Mountain pine (*P. pungens* Lamb.), is endemic to the Appalachian Mountains and is a species of concern for land managers (SAMAB 1996; Williams 1998).

In the past, burning by Native Americans, European settlers, and lightning-set fires was widespread in the Appalachian Mountains and likely promoted oak and pine regeneration (Harmon et al. 1983; Van Lear & Waldrop 1989; Delcourt & Delcourt 1997, 1998). Paleocological analyses of sediment charcoal and pollen reveal that fires were common on southern Appalachian landscapes during the last 3,000–4,000 years and that oak, Chestnut (*Castanea dentata* (Marsh.) Borkh.), and pine were the dominant tree species (Delcourt & Delcourt 1997, 1998). Delcourt and Delcourt (1997, 1998, 2000) argued that burning, particularly on dry upper slopes and ridgetops, was a major factor contributing to the dominance of these species.

Dendroecological techniques have been used to construct more detailed records of fire history over the past 150–400 years in pine and oak forests of the southern and central Appalachians (Harmon 1982; Sutherland et al. 1995; Shumway et al. 2001; Armbrister 2002; Shuler & McClain 2003). These studies suggest that low-severity surface fires burned at intervals of about 5–15 years until the mid-1900s, when state and federal agencies implemented fire control efforts. Occasionally, more severe, stand-replacing fires also occurred (Sutherland et al. 1995). Other canopy-opening disturbances (e.g., storms, insect outbreaks) may have enhanced pine regeneration when combined with frequent burning (Lafon & Kutac 2003; Brose & Waldrop 2006).

Recent work demonstrates that the abundance of more shade-tolerant, and less fire-tolerant, species has increased in xerophytic pine- and oak-dominated stands of the Appalachians during the era of fire exclusion and suggests that successional replacement of pine and oak may be occurring (Harmon 1984; Williams & Johnson 1990;

Abrams 1992; Harrod et al. 1998; Williams 1998; Harrod et al. 2000; Shumway et al. 2001; Lafon & Kutac 2003). Red maple (*Acer rubrum* L.), Black gum (*Nyssa sylvatica* Marsh.), Eastern white pine (*P. strobus* L., a subgenus *Haploxyton* Koehne pine), and Eastern hemlock (*Tsuga canadensis* (L.) Carr.) are among the species becoming more abundant on xeric sites. Concomitantly, regeneration of Yellow pine and oak appears to be declining. These trends suggest that pine and oak stands will be replaced by more mesophytic vegetation under continued fire exclusion, although the rates and specific directions of change will vary spatially and temporally. Oaks themselves are among the potential replacing species in the more xerophytic Yellow pine forests (Williams & Johnson 1990; Williams 1998; Welch et al. 2000). Storms, droughts, and native and exotic insects and diseases likely will accelerate these successional trends (Schowalter et al. 1981; McGee 1984; Fajvan & Wood 1996; Williams 1998; Lafon & Kutac 2003; Waldron et al. 2006).

Assessing the potential consequences of different disturbance regimes, such as burning versus fire exclusion, for long-term forest dynamics is difficult because of the long life span of the trees. Simulation modeling provides a useful tool for exploring forest change over periods of decades to centuries—timescales relevant to successional change and of interest in restoration ecology (cf Young 2000; Callicott 2002; Urban 2006). In this paper, we apply LANDIS, a computer model of disturbance and succession on forested landscapes (He et al. 1996; Mladenoff et al. 1996; He & Mladenoff 1999a, 1999b; He et al. 1999a, 1999b; Mladenoff & He 1999), to simulate forest dynamics in the southern Appalachian Mountains, United States. LANDIS originally was developed for the Great Lakes region of North America (Mladenoff 2004), but has been adapted for use in other locations, including the Ozark Plateau (Shifley et al. 1998, 2000), the southern California foothills (Franklin et al. 2001; Franklin 2002; Sphard & Franklin 2004), northeastern China (He et al. 2002; Xu et al. 2004), Fennoscandia (Pennanen & Kuuluvainen 2002), Quebec (Pennanen et al. 2004), and the Georgia Piedmont (Wimberly 2004). Our work extends the application of LANDIS to the floristically diverse and environmentally heterogeneous landscape of the southern Appalachian Mountains.

Southern Appalachian forests are affected by various agents of natural and anthropogenic disturbance, in addition to fire. LANDIS is able to simulate multiple disturbances. However, this study focuses solely on fire because it is thought to be the key disturbance process in pine- and oak-dominated forests (SAMAB 1996; Williams 1998; Dey 2002; Lafon & Kutac 2003; Brose & Waldrop 2006) and because of the widespread interest in using fire for ecosystem restoration. Simulation modeling is employed frequently to evaluate the role of a specific disturbance process independent of the influences of other disturbances (e.g., Le Guerrier et al. 2003; Hickler et al. 2004; Lafon 2004; Sturtevant et al. 2004). Simulating the role of

fire will establish the template onto which other disturbances can be imposed. The work reported in this paper is a step within a larger effort that will use LANDIS to assess the influences of fire, Southern pine beetle (*Dendroctonus frontalis* Zimmermann) and other disturbances (e.g., Hemlock woolly adelgid [*Adelges tsugae* Annand], Balsam woolly adelgid [*A. piceae* Ratzeburg], Sudden oak death disease [*Phytophthora ramorum* Werres, de Cock & Man in't Veld.]) on the spatial and temporal dynamics of forests on southern Appalachian landscapes and to investigate the implications of restoration efforts.

The landscape simulated here is an idealized landscape capturing the predominant physical gradients (elevation and moisture) that influence vegetation distribution in the southern Appalachian Mountains (Whittaker 1956). Idealized landscapes commonly are used in simulation modeling studies to facilitate the straightforward interpretation of model projections (e.g., Mladenoff & He 1999; Pennanen et al. 2004; Syphard & Franklin 2004; Waldron et al. 2006). An idealized landscape is useful for this initial application of LANDIS to our study area, because we seek to elucidate successional dynamics on the individual site types (called "landtypes" in LANDIS), without the influences of spatial complexities. Understanding projected successional patterns on this simple landscape will inform our interpretation of subsequent modeling investigations using the same landtypes in more complex arrangements. The subsequent analyses will explore specifically the implications of landscape structure for vegetation patterns and for disturbance dynamics such as Southern pine beetle infestations and the spread of fires.

Methods

Study Area

The southern Appalachian Mountains have a humid continental climate (Bailey 1978). Temperature and precipitation exhibit pronounced fine-scale spatial patterns because of the mountainous terrain. Oak forests are the predominant land cover type, occupying xeric, subxeric, and submesic sites (Stephenson et al. 1993; SAMAB 1996). Because of their topographic complexity, however, Appalachian landscapes contain a variety of community types. These range from mesophytic hemlock-hardwood forests on the moist valley floors to Yellow pine woodlands on ridgetops and from temperate deciduous forests in the low elevations to Spruce-Fir (*Picea* Dietr.-*Abies* Mill.) stands on the high summits (Whittaker 1956; Stephenson et al. 1993). The landscape we simulate is based on Great Smoky Mountains National Park (lat 35°35'N, long 83°25'W), in which most major ecosystems of the southern Appalachians are represented and for which the general topographic distribution of communities and tree species has been described (Whittaker 1956). For this paper, we focus our discussion on the dry, pine- and oak-covered sites only.

Model Description

LANDIS 4.0 operates on a raster-based landscape in which the presence or absence of 10-year age classes of each tree species is simulated for each cell. Succession on each cell is influenced by dispersal, shade tolerance, and habitat suitability for each species. Respecting habitat suitability, the landscape can be divided into a series of landtypes, each representing different conditions of topography, elevation, soil, and/or climate. For each landtype, an establishment coefficient between 0 and 1 is assigned to each species to govern the relative growth capability of the species on that site (He & Mladenoff 1999b).

LANDIS 4.0 can simulate disturbance by fire, wind, harvesting, and biological agents such as insects and disease (Sturtevant et al. 2004). Fire ignition, initiation, and spread are stochastic processes (Yang et al. 2004). The probability of fire initiation and spread becomes higher as time since last fire increases. Fire spreads until it reaches a pre-defined maximum possible size or encounters a fire-break (e.g., a recently burned patch) (Yang et al. 2004). Different fire regimes can be defined within a single landscape by assigning different fire parameters (e.g., ignition density, frequency, severity) to different landtypes. Low-severity fires kill only the most fire-sensitive trees (young trees and/or fire-intolerant species), whereas fires of higher severity kill larger trees and more fire-tolerant species (He & Mladenoff 1999b). Because burning is simulated as a stochastic process, fire intervals vary temporally, fluctuating around the mean for each landtype. These variations in fire intervals also lead to temporal variability in fire severity, which is greater after a long fire-free interval than after a shorter interval with minimal time for fuel to accumulate. In the absence of disturbance, mortality occurs only when a tree cohort approaches the maximum age for the species.

Detailed sensitivity analyses of LANDIS have been conducted (Mladenoff & He 1999; Syphard & Franklin 2004; Wimberly 2004; Xu et al. 2004) and indicate that model projections are relatively insensitive to differences in fire size, species establishment coefficient, habitat (landtype) heterogeneity, and initial forest conditions. Model results are moderately sensitive to variations in the fire return interval and the level of spatial aggregation (i.e., model performance declines with increasing cell size) and are especially sensitive to differences in seed dispersal.

Model Application

We used LANDIS 4.0 to simulate forest dynamics over a 500-year period on a 120-ha idealized landscape. The landscape was a 100 × 120-cell grid with a cell size of 10 × 10 m, the smallest cell size permitted. Using this cell size allowed us to operate at approximately the scale of the individual canopy tree, following the logic of gap models (cf Botkin 1993). The landscape was divided into 18 rectangles, each representing an individual landtype. The arrangement of the 18 landtypes follows the mosaic

chart used by Whittaker (1956) to depict the elevation and moisture gradients on the Great Smoky Mountains landscape. The landtypes are arranged in three rows of six rectangles. The three rows represent different elevation zones, with elevation increasing from bottom to top. The elevation zones are low (400–915 m), middle (916–1,370 m), and high (1,371–2,025 m). The six rectangles in each row represent different topographic moisture classes. Moisture availability increases from right to left as follows: (1) ridges and peaks (hereafter “ridgetops”); (2) slopes facing southeast, south, southwest, or west (“south- and west-facing slopes”); (3) slopes facing northwest, north, northeast, or east (“north- and east-facing slopes”); (4) sheltered slopes; (5) flats, draws, and ravines; and (6) coves and canyons. Elevation also influences moisture availability; hence, for example, a low-elevation ridgetop would have drier conditions than a mid-elevation ridgetop. Although the simulated landscape incorporates the full range of environments in the Great Smoky Mountains, our interest in this paper is only on the successional patterns for ridgetops (first column), south- and west-facing slopes (second column), and north- and east-facing slopes (third column) at low and middle elevations, for a total of six rectangles.

Thirty tree species (the maximum allowable in LANDIS 4.0) were simulated (Table 1). We selected these species based on their importance in Whittaker’s (1956) study of vegetation in the Great Smoky Mountains. The 30-species limit necessitated the exclusion of some minor species from the simulations but did not constrain our ability to characterize the general successional dynamics of the major species. Also, because of the focus on montane vegetation, some of the species that are common on the nearby lowlands (e.g., Shortleaf pine [*Pinus echinata* Mill.]) were absent from Whittaker’s dataset and were not represented in our simulations. Species nomenclature follows Wofford (1989).

We based the species parameters listed in Table 1 on Burns & Honkala (1990), which contains an extensive array of life history data for North American trees and which has served as the basis for a number of previous forest modeling studies (e.g., Lafon 2004; Sturtevant et al. 2004; Wimberly 2004). Identical dispersal capabilities were assigned to all species (a likelihood of 0.95 that seeds will disperse within 30 m, and a likelihood of 0.05 that seeds will disperse between 30 and 50 m) (Waldron et al. 2006). The assignment of identical dispersal attributes

Table 1. Species abbreviations and life history parameters.

Species	Species Abbreviation	Longevity (Yr)	Maturity (Yr)	Shade Tolerance	Fire Tolerance	Vegetative Reproduction
<i>Abies fraseri</i> (Pursh) Poir.	abfr	150	70	5	1	0.0
<i>Acer rubrum</i> L.	acru	150	55	3	1	0.4
<i>A. saccharum</i> Marsh.	acsa	200	60	4	1	0.2
<i>Aesculus octandra</i> Marsh.	aeoc	200	60	4	2	0.1
<i>Betula alleghaniensis</i> Britt.	beal	300	70	2	2	0.1
<i>B. lenta</i> L.	bele	200	45	2	2	0.1
<i>Carya glabra</i> (Mill.) Sweet	cagl	300	75	2	2	0.3
<i>C. tomentosa</i> (Poir.) Nutt.	cato	200	40	2	2	0.4
<i>Fagus grandifolia</i> Ehrh.	fagr	300	60	5	1	0.3
<i>Fraxinus americana</i> L.	fram	200	55	3	1	0.3
<i>Halesia carolina</i> L.	haca	100	60	4	2	0.2
<i>Liriodendron tulipifera</i> L.	litu	300	45	2	1	0.3
<i>Magbikua acuminata</i> L.	maac	150	55	3	2	0.4
<i>M. fraseri</i> Walt.	mafr	70	55	3	1	0.2
<i>Nyssa sylvatica</i> Marsh.	nysy	200	55	3	3	0.3
<i>Oxydendrum arboreum</i> (L.) DC.	oxar	100	55	3	3	0.4
<i>Picea rubens</i> Sarg.	piru	400	70	5	1	0.0
<i>Pinus pungens</i> Lamb.	pipu	250	35	1	5	0.0
<i>Pin. rigida</i> Mill.	piri	200	35	1	5	0.2
<i>Pin. strobus</i> L.	pist	400	30	2	3	0.0
<i>Pin. virginiana</i> Mill.	pivi	100	35	1	4	0.0
<i>Pin. serotina</i> Ehrh.	prse	200	30	1	1	0.4
<i>Quercus alba</i> L.	qual	450	50	3	4	0.3
<i>Q. coccinea</i> Muenchh.	quco	130	50	1	3	0.4
<i>Q. montana</i> Willd.	qumo	350	55	3	4	0.4
<i>Q. rubra</i> L.	quru	300	50	2	3	0.4
<i>Q. velutina</i> Lam.	quve	150	40	2	3	0.3
<i>Robinia pseudoacacia</i> L.	rops	100	15	1	1	0.4
<i>Tilia heterophylla</i> Vent.	tihe	250	60	4	2	0.4
<i>Tsuga canadensis</i> (L.) Carr.	tsca	450	70	5	1	0.0

Maturity: age of sexual maturity; shade tolerance: between 1 and 5 (intolerant to tolerant); fire tolerance: between 1 and 5 (intolerant to tolerant); vegetative reproduction: probability of vegetative reproduction following mortality of a parent cohort on a cell.

minimized the effect of this parameter, which was not of primary interest for our study, in order to simplify the interpretation of successional patterns.

For the establishment coefficient parameter for each species, we consulted data about the spatial distributions of tree species along the elevation and moisture gradients in the Great Smoky Mountains (Whittaker 1956). We sought to incorporate into the establishment coefficient some of the constraints on tree growth that are hypothesized to control the spatial and temporal dynamics of vegetation along moisture gradients (Smith & Huston 1989). Specifically, lower establishment coefficients were assigned to drought- or shade-tolerant species than to less tolerant species to account for trade-offs between the ability to grow rapidly and the ability to tolerate low resource levels. Consequently, although our establishment coefficients permit drought-tolerant species to grow on moist landtypes, they are not competitive with the mesophytic species encountered there. Shade-tolerant species are not permitted to inhabit the driest landtypes, consistent with trade-offs between drought and shade tolerance (Smith & Huston 1989) and with the observed pattern of tree distribution (Whittaker 1956).

Initially, a single species was assigned to each cell on the landscape. The number of cells inhabited by each spe-

cies was based on its relative abundance in the landtype (Fig. 1), as inferred from Whittaker (1956). We distributed each species randomly to the appropriate number of cells within each landtype.

We conducted simulations for two disturbance scenarios: (1) fire exclusion (no burning) and (2) restoring fire at a frequency approximating the pre-suppression fire regime. For the burning scenario, a target fire return interval for each landtype was identified from published work on the fire regimes that characterized Appalachian landscapes prior to fire exclusion. Dendroecological data about past fire return intervals are available for xeric sites (south-, southwest-, and west-facing slopes) in the southern and central Appalachians (Harmon 1982; Sutherland et al. 1995; Shumway et al. 2001; Armbrister 2002; Shuler & McClain 2003) and are useful for guiding the selection of input parameters for LANDIS. We derived fire return intervals for mesic sites from Wade et al. (2000). We calibrated the return interval for each landtype by adjusting fire parameters until the mean return interval for ten 1,000-year simulations was within 10% of the target interval (cf Wimberly 2004). The target return interval was 10 years for ridgetops and south- and west-facing slopes and 20 years for north- and east-facing slopes. The moister landtypes had return intervals of 200–1,000 years. Rates of

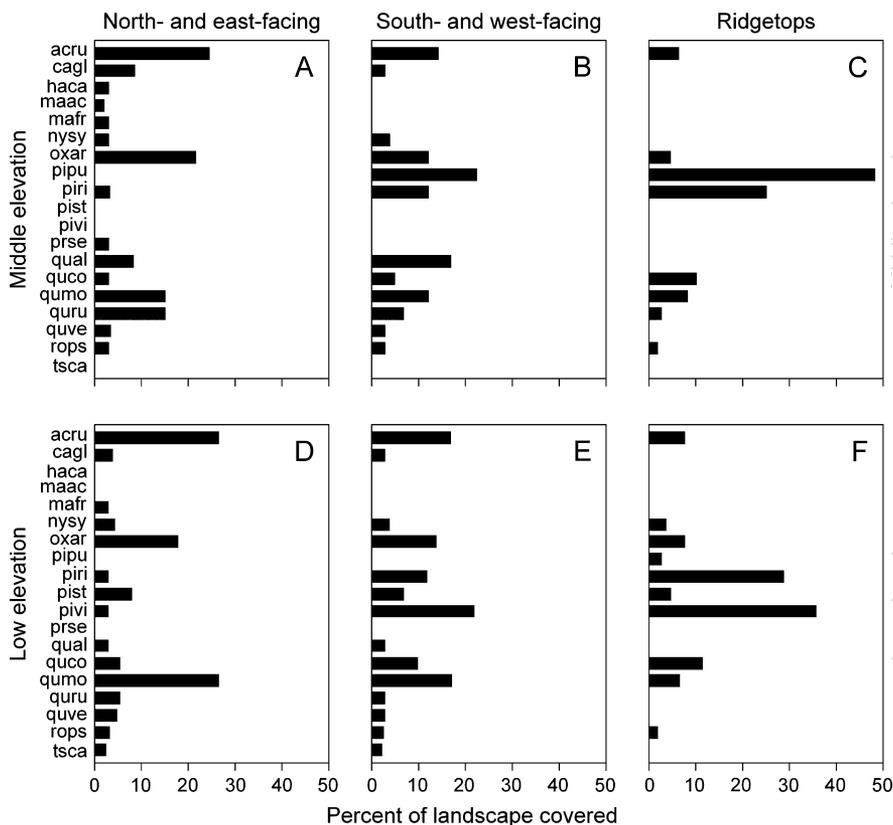


Figure 1. Number of cells initially occupied by each species as a percentage of the six landtypes. Top row = middle elevation, bottom row = low elevation. Column 1 = north- and east-facing slopes, column 2 = south- and west-facing slopes, and column 3 = ridgetops. Species abbreviations are given in Table 1.

fuel accumulation, and hence fire severity, also varied across the simulated landscape, with the highest levels on xeric sites (He & Mladenoff 1999b). The fire disturbances imposed in this study are not intended to replicate actual fire size or the patterns of fire spread with respect to landscape structure. Rather, our focus is on applying fire to each landtype at an appropriate frequency to evaluate how fire influences forest succession at individual landtypes.

Results

Under contemporary conditions, pines dominate the ridgetops at low and middle elevations (Fig. 1). LANDIS simulations in the absence of fire suggest that this is not sustainable. In middle elevation pine forests, oak species become more important over time (Fig. 2A). At low elevations, White pine and Chestnut oak (*Quercus montana* Willd.) replace Virginia pine (*Pinus virginiana* Mill.) and Pitch pine (*P. rigida* Mill.) (Fig. 2C).

When fire is simulated, Yellow pine-dominated stands persist on the ridgetops in both elevation zones (Fig. 2B & 2D). Many of the cells do not have trees (Fig. 3A & 3D). These open woodland conditions contrast with the continuous forest cover that develops under fire exclusion.

On mid-elevation south- and west-facing slopes, White oak (*Q. alba* L.), Chestnut oak, and Northern red oak (*Q. rubra* L.) dominate under conditions of fire exclusion

(Fig. 4A). Yellow pines decline, whereas Black gum increases in abundance and becomes a dominant species. On low-elevation south- and west-facing slopes, Yellow pines also decline, whereas Chestnut oak and White pine increase to become the dominant species (Fig. 4C). As in the middle elevations, Black gum expands, albeit more slowly.

When fire is simulated on mid-elevation south- and west-facing slopes, Chestnut oak, White oak, and Table Mountain pine dominate the forest (Fig. 4B). For the lower elevation sites, Pitch pine and Chestnut oak are dominant, and Virginia pine declines (Fig. 4D). Burning maintains open stands on the low-elevation site (Fig. 3E).

Forests on north- and east-facing slopes are dominated initially by Chestnut oak, Red maple, Sourwood (*Oxydendrum arboreum* (L.) DC.), and Northern red oak (Fig. 1A & 1D). High species diversity is maintained under fire exclusion (Fig. 5A & 5C). At middle elevations, White oak, Chestnut oak, and Northern red oak continue to be abundant, but some fire-intolerant mesophytic species—Eastern hemlock, White basswood (*Tilia heterophylla* Vent.), and Carolina silverbell (*Halesia carolina* L.)—steadily increase in abundance. At low elevations, Chestnut oak begins as a dominant species and increases in abundance, whereas White pine and Black gum exhibit strong, steady rises. Burning results in dominance by Chestnut oak and White oak (Fig. 5B & 5D) and maintains conditions that are slightly more open than under fire exclusion (Fig. 3C & 3F).

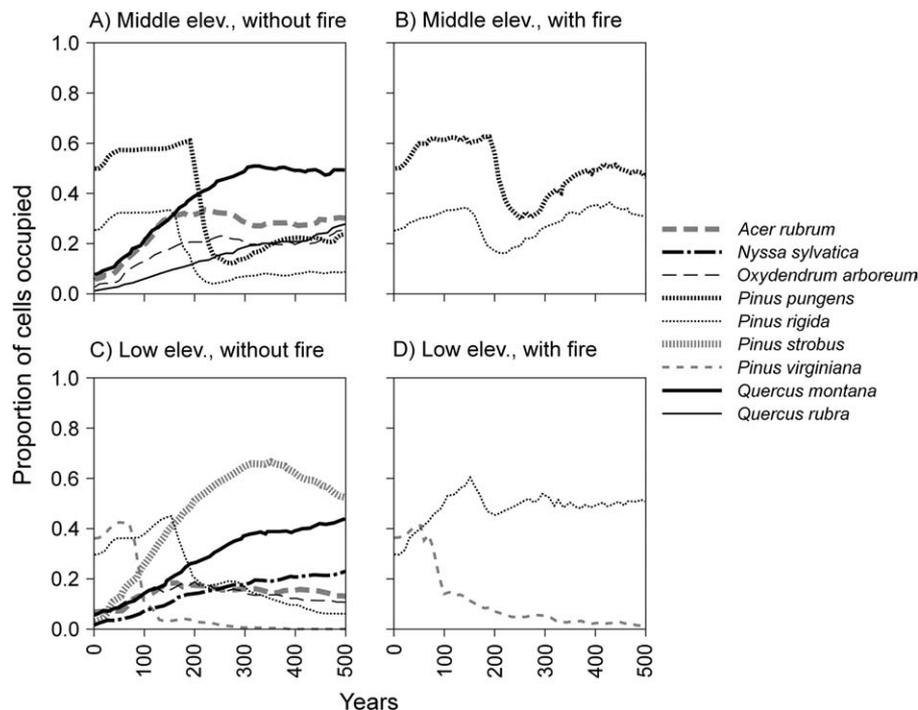


Figure 2. LANDIS simulation results for ridgetop sites at middle elevation (A & B) and low-elevation (C & D) sites. Fire exclusion conditions are shown on the left (A & C), and results from simulations with fire are shown on the right (B & D). Only species that occur on more than 15% of the landscape at any time during the simulation are shown.

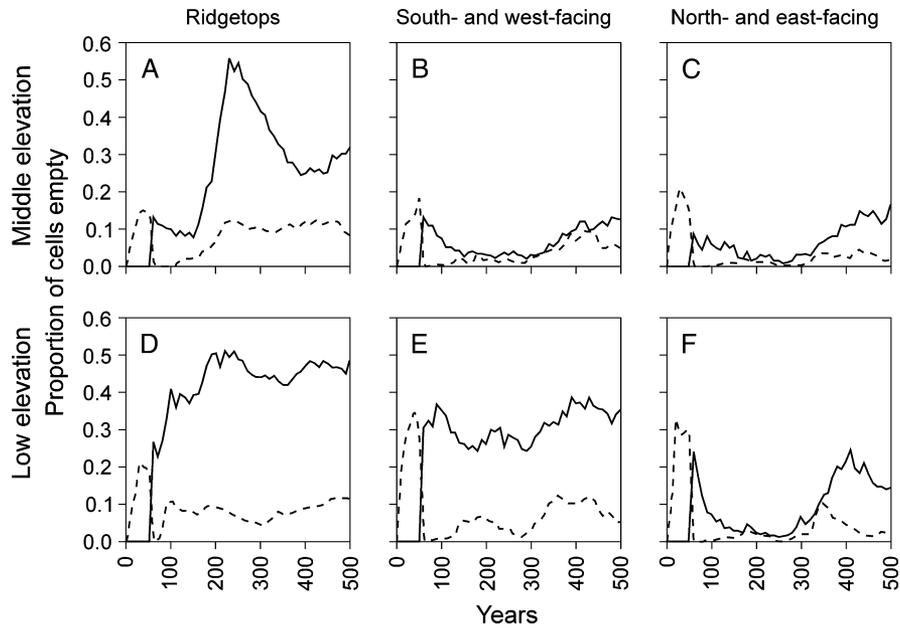


Figure 3. Proportion of empty cells over time for each simulated landscape type for simulations with (solid lines) and without (dashed lines) fire. Top row = middle elevation, bottom row = low elevation. Column 1 = ridgetops, column 2 = south- and west-facing slopes, and column 3 = north- and east-facing slopes.

Discussion

Fire promotes Yellow pine and oak dominance on ridgetops and dry slopes of the simulated landscape. The pines are especially dependent on fire, a result consistent with

field studies in the Appalachian Mountains and with the fire-pine association observed throughout the northern hemisphere (Agee 1998). Under the burning scenario, pines persist at high levels on ridgetops and south- and

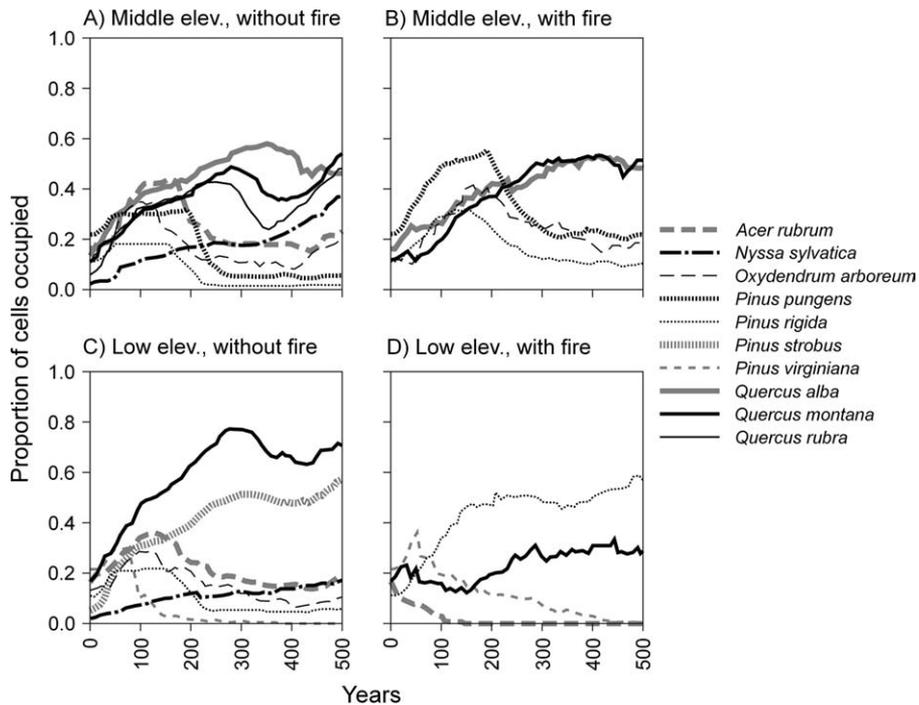


Figure 4. LANDIS simulation results for south- and west-facing slopes at middle elevation (A & B) and low-elevation (C & D) sites. Fire exclusion conditions are shown on the left (A & C), and results from simulations with fire are shown on the right (B & D). Only species that occur on more than 15% of the landscape at any time during the simulation are shown.

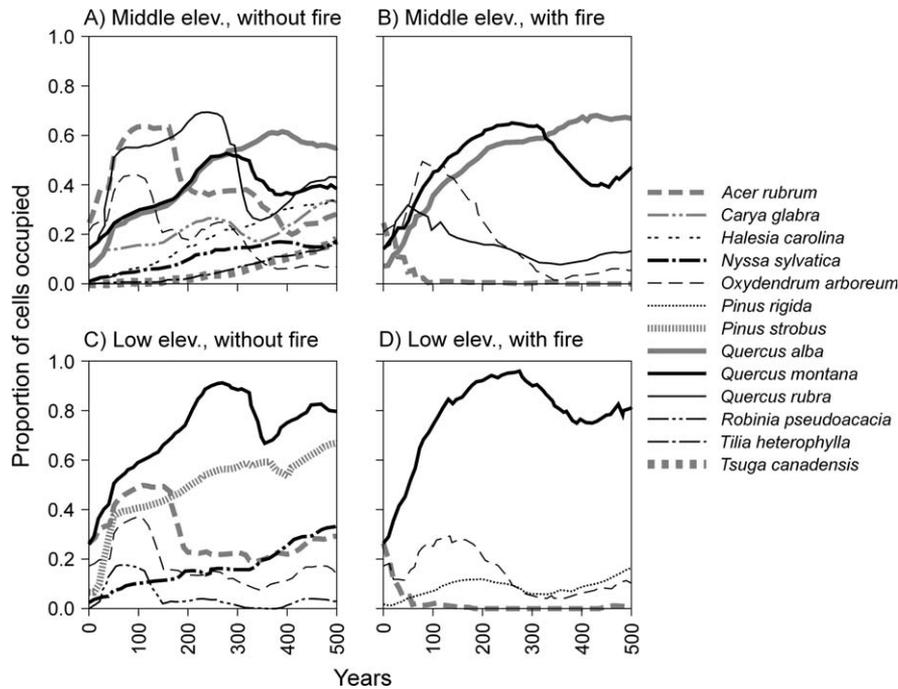


Figure 5. LANDIS simulation results for north- and east-facing slopes at middle elevation (A & B) and low-elevation (C & D) sites. Fire exclusion conditions are shown on the left (A & C), and results from simulations with fire are shown on the right (B & D). Only species that occur on more than 15% of the landscape at any time during the simulation are shown.

west-facing slopes. Without fire, pines virtually disappear from south- and west-facing slopes. They persist at low to moderate levels on ridgetops, but hardwoods increase steadily and ultimately dominate the ridgetop stands. Ridgetops could serve as pine refugia during long fire-free intervals. Williams (1998) proposed that before European settlement, pines were restricted to such dry sites during periods of low fire activity, expanding periodically onto moister sites following severe fires associated with extended drought. On extreme sites that are too dry for hardwood invasion, pine-dominated communities may be able to persist indefinitely. For example, Barden (1977, 1988, 2000) discovered a population of stunted Table Mountain pines that apparently is maintaining itself without fire; the trees occupy shallow soils in cracks and depressions on a granite dome in North Carolina. We did not simulate these extremely dry environments because they are unusual features. Relying on these rare sites for maintaining pine populations would not be a prudent management strategy.

Respecting the individual species of Yellow pine, Table Mountain pine and Pitch pine fare well under the burning regime we impose, but Virginia pine declines. This species is less fire tolerant than the other two Yellow pines, and consequently, frequent burning reduces its abundance. In fact, burning can be used to eliminate Virginia pine from mixed pine stands (Wade et al. 2000). Virginia pine is a relatively short-lived pioneer species that thrives in a regime of less frequent, but more severe, fire (Iverson et al. 1999; Wade et al. 2000). Its abundance in Whittaker's (1956)

dataset, and hence in our input file, may reflect (1) a history of severe, stand-replacing fires on some low-elevation ridgetops in the Great Smoky Mountains or (2) establishment of the species in abandoned pastures (Pyle 1988). Our study does not consider either of these disturbance regimes. Regardless, the endemic Table Mountain pine of the middle elevations is of greater management concern, and the fire regime we impose seems appropriate for maintaining it.

The consequences of burning versus fire exclusion are mixed for oaks. Fire exclusion favors oak on the driest sites, which otherwise would be dominated by Yellow pine. This result matches previous suggestions that fire exclusion in the Appalachians promotes the replacement of Yellow pines by oaks (Williams & Johnson 1990; Williams 1998; Welch et al. 2000). On moister sites, oaks benefit from burning, because it reduces the abundance of less fire-tolerant competitors. Chestnut oak and White oak are the most fire-tolerant oaks and thrive under frequent burning. These species often dominate forests on moderately dry sites in the Appalachians and did so historically as well (Whittaker 1956; Stephenson et al. 1993; Abrams 2003). Our results suggest that their importance is largely a consequence of periodic burning, without which a diverse mix of mesophytic and xerophytic species would develop. These simulations may be relevant to oak-dominated forests elsewhere, e.g., eastern Asia, where declining oak dominance associated with fire exclusion seems analogous to North America (Abrams et al. 1999).

The negative influence of disturbance on the species diversity of dry sites is consistent with empirical observations in the southern Appalachian Mountains (Harrod et al. 1998) and elsewhere (e.g., Walker et al. 1995; Osem et al. 2002), and it agrees with ecological theory. In particular, the dynamic equilibrium model of Huston (1979, 1994) predicts that without disturbance, species diversity will be high on dry sites because of the low growth rates of vegetation (and hence, relatively low rates of competitive displacement). Frequent disturbances reduce diversity in dry environments because low growth rates prevent the populations of some species from recovering between successive disturbances. Such patterns of diversity have been simulated using individual-based gap models of forest succession (Smith & Huston 1989; Huston 1994). Our results demonstrate that LANDIS can generate similar patterns and imply that LANDIS is capable of incorporating vegetation processes (e.g., interspecific competition, life history trade-offs) in a manner sufficient to simulate diversity dynamics that agree with ecological theory pertinent to biodiversity conservation and ecosystem restoration.

In our simulations, fire exclusion favors Northern red oak, which becomes a dominant species at middle elevations without burning. This trend reflects that (1) Northern red oak is more fire sensitive than Chestnut oak and White oak and (2) it has a relatively high establishment coefficient. These results are consistent with an expansion of Northern red oak observed in oak forests throughout the eastern United States as a consequence of reduced fire activity and more frequent canopy disturbances (e.g., cutting, chestnut blight) (Stephenson et al. 1993; Abrams 2003). However, the simulations may overestimate the increase in Northern red oak on the driest, pine-dominated sites, where conditions may become too stressful for the species during periodic extreme drought events.

Our results suggest that frequent burning creates open woodland conditions on xeric sites, rather than continuous closed-canopy forest. Such open-canopy woodlands may have occupied xeric sites in the southern Appalachian Mountains prior to fire exclusion (Delcourt & Delcourt 1998; Harrod et al. 2000). Currently, these open conditions are a restoration target for decadent woodland/savanna ecosystems throughout central and eastern North America (Davis et al. 2000), including the Appalachian Mountains (e.g., U.S. Forest Service 2004a, 2004b). Under fire exclusion, our simulations imply that denser forests with a more continuous canopy develop. Indeed, such conditions have arisen on southern Appalachian landscapes. Harrod et al. (1998) found that canopy tree density nearly tripled during four decades without fire or other anthropogenic disturbances on xeric sites in the Great Smoky Mountains. The recent Southern pine beetle outbreak that devastated Yellow pine stands throughout the region likely was a consequence of this change in vegetative structure and underscores the need for restoring these ecosystems to a more sustainable condition.

Other model projections also correspond with successional changes occurring because of fire exclusion in the Appalachian Mountains. In particular, White pine, Black gum, Red maple, and eastern hemlock are favored under the fire exclusion scenario, precisely the pattern observed in field studies (Williams & Johnson 1990; Harrod et al. 1998; Shumway et al. 2001; Armbrister 2002). Our results suggest that the successional trends inferred from these field studies will continue in the future and result in pronounced shifts in tree species composition, although expansion of the slow-growing, shade-tolerant hemlock may be limited by other disturbances (e.g., droughts, storms, hemlock wooly adelgid) not considered here.

Conclusions

As a spatially explicit model capable of simulating vegetation dynamics across entire landscapes, LANDIS lacks detail about mechanisms (e.g., individual tree growth, tree life history trade-offs) that help drive forest succession (Mladenoff 2004). Nonetheless, the model appears to account for such processes in a fashion that is adequate for representing successional dynamics on a southern Appalachian landscape and that is also able to generate results consistent with biodiversity theory.

The model projections in this paper underscore the critical role of fire in xerophytic forests of the Appalachian Mountains, where burning appears to be necessary for maintaining Yellow pine and oak dominance. Simulation modeling augments field studies of Appalachian fire ecology by providing a means to explore long-term vegetation dynamics and by permitting the examination of a single disturbance agent under controlled conditions. Elucidating LANDIS projections for these simple scenarios of burning versus fire exclusion is an important step in simulating Appalachian forest dynamics under multiple-disturbance scenarios, in which fire is a key process. It is also important because burning is a primary management tool for restoring xerophytic forests.

We anticipate that simulating multiple disturbance agents on more complex landscapes will yield greater realism in some respects, for example, the issue of hemlock expansion noted above. Biotic disturbances (herbivory, disease) may amplify the successional changes identified under the no burning scenario in this paper. This is because an increase in tree density under fire exclusion likely would exacerbate the extent and severity of biotic disturbances (Schowalter et al. 1981; Savage 1997), leading to more precipitous declines in the dominant pines (Paine et al. 1984, 1985; Coulson et al. 1998) and oaks and to more rapid rates of successional replacement. When combined with fire, however, such canopy disturbances may increase opportunities for pine regeneration (Lafon & Kutac 2003; Brose & Waldrop 2006). Recently, LANDIS has been extended to simulate biotic disturbances (Sturtevant et al. 2004); incorporating Southern pine beetle outbreaks and other biotic

disturbances will enable us to investigate potential consequences of disturbance interactions and restoration efforts.

A final consideration is that future climate changes may alter long-term forest dynamics. Projected increases in summer temperatures (Houghton et al. 2001; Chen et al. 2003) could permit lowland tree species to expand into the Appalachian montane forests, although competition from existing vegetation will slow these expansions (Loehle 2000). Future moisture conditions in the region seem uncertain (Houghton et al. 2001; Bachelet et al. 2003; Chen et al. 2003). However, greater drought stress and increased wildfire activity are possible (Flannigan et al. 2000; Bachelet et al. 2003) and could slow the successional replacement of oak and pine.

Implications for Practice

- Despite simplifying assumptions, LANDIS can represent ecological processes that lead to results consistent with ecological theory and field studies of vegetation change in the southern Appalachian Mountains. The simulations imply that ongoing vegetation changes linked to fire exclusion will contribute to long-term declines in pine and oak abundance.
- Reintroducing fire appears necessary for restoring and maintaining pine and oak stands in the southern Appalachian Mountains.
- Reintroducing fire likely will restore more open stand conditions similar to those thought to exist before fire exclusion.

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