A dendrochronological analysis of a disturbance–succession model for oak–pine forests of the Appalachian Mountains, USA

Patrick H. Brose and Thomas A. Waldrop

Abstract: Disturbance–succession models describe the relationship between the disturbance regime and the dominant tree species of a forest type. Such models are useful tools in ecosystem management and restoration, provided they are accurate. We tested a disturbance–succession model for the oak–pine (*Quercus* spp. – *Pinus* spp.) forests of the Appalachian Mountains region using dendrochronological techniques. In this model, fire promotes pines, while fire suppression, bark beetle outbreaks, and ice storms encourage oaks. We analyzed nine Appalachian oak–pine stands for species establishment dates and the occurrence of fires and canopy disturbances. We found no evidence that fire preferentially promoted the establishment of pine more than oak, nor did we find any evidence that canopy disturbances or periods of no disturbance facilitated the establishment of oak more than pine. Rather, we found that both species groups originated primarily after combined canopy and fire disturbances, and reduction of fire frequency and scope coincided with the cessation of successful oak and pine regeneration. Currently, heath shrubs are slowly dominating these stands, so we present a revised disturbance–succession model for land managers struggling to manage or restore oak–pine forests containing a dense ericaceous understory.

Résumé : Les modèles de succession engendrée par des perturbations décrivent la relation entre le régime de perturbations et l'espèce d'arbre dominante dans un type de peuplement. Ces modèles sont des outils utiles pour l'aménagement et la restauration des écosystèmes à condition d'être fidèles à la réalité. Nous avons testé un modèle de succession engendrée par des perturbations pour les forêts de chênes (*Quercus* spp.) et de pins (*Pinus* spp.) de la région des Appalaches à l'aide de techniques dendrochronologiques. Dans ce modèle, le feu favorise les pins tandis que la suppression des feux, les épidémies de scolytes et le verglas favorisent les chênes. Nous avons analysé la date d'établissement des espèces et l'occurrence des feux et des perturbations du couvert dans neuf peuplements de chênes et de pins des Appalaches. Nous n'avons trouvé aucune preuve que le feu ait favorisé l'établissement du pin plus que celui du chêne ni que les perturbations du couvert ou que les périodes exemptes de perturbations aient favorisé l'établissement du chêne plus que celui du pin. Au contraire, nous avons observé que les deux groupes d'espèces se sont établis principalement après des perturbations du couvert combinées à des perturbations causées par le feu et que la réduction de la fréquence et de l'ampleur des feux a coïncidé avec l'insuccès de la régénération du chêne et du pin. Présentement, les éricacées arbustives sont lentement en train de dominer ces peuplements de telle sorte que nous présentons un modèle révisé de succession engendrée par les perturbations à l'intention des aménagistes qui s'efforcent d'aménager ou de restaurer des forêts de chênes et de pins avec un sous-étage dense d'éricacées.

[Traduit par la Rédaction]

Introduction

The oak–pine (*Quercus* spp. – *Pinus* spp.) forest type is defined as forests that contain between 25% and 50% stocking of softwoods with oaks and other hardwoods comprising the balance (Braun 1950; Eyre 1980). This forest type is widespread, occupying more than 13 million ha of the eastern United States in a broad swath from eastern Texas and Oklahoma to northern Florida to southern New York (Smith et al. 2001). Within that range, oak–pine forests are diverse, consisting of a multitude of species mixes depending on climate, soil, topography, and disturbance history. Oak–pine forests provide an array of benefits: timber production, wildlife habitat, watershed protection, recreational opportunities, and biodiversity conservation. Consequently, land managers are interested in sustaining this forest type and that entails understanding how the two principal species groups respond to disturbance. For the oak–pine forests of the Appalachian Mountains, Williams (1998) provided a synopsis of this forest type and a model explaining the relationship between these two species groups in regards to their responses to the common disturbances of this region.

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P.H. Brose.[1] US Forest Service, Northern Research Station, Forestry Sciences Laboratory, 335 National Forge Road, Irvine, PA 16329, USA.
T.A. Waldrop. US Forest Service, Southern Research Station, 233 Lehotsky Hall, Clemson University, Clemson, SC 29634, USA.

[1]Corresponding author (e-mail: pbrose@fs.fed.us).

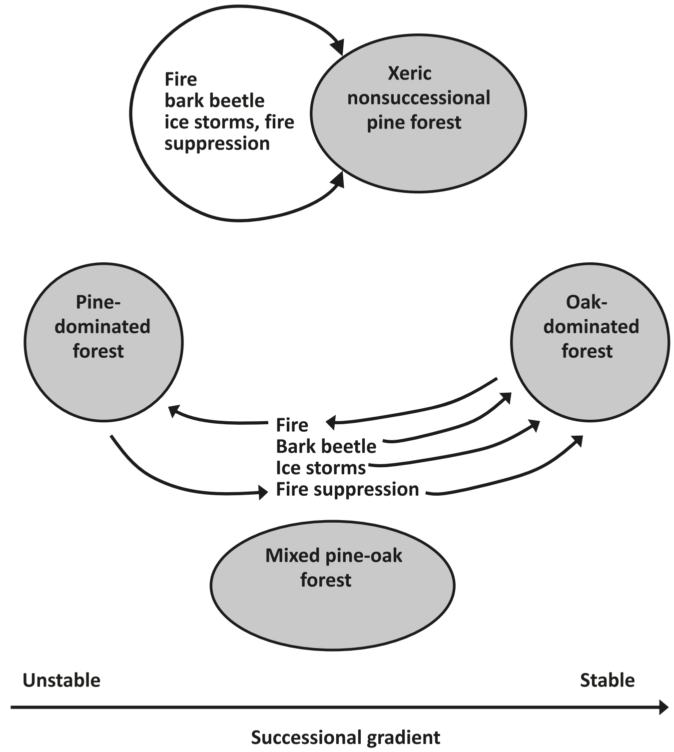
The pine component of Appalachian oak–pine forests consists of one to five species (pitch pine (*Pinus rigida* Mill.), shortleaf pine (*Pinus echinata* P. Mill.), Table Mountain pine (*Pinus pungens* Lamb.), Virginia pine (*Pinus virginiana* P. Mill.), and eastern white pine (*Pinus strobus* L.)) depending on elevation, topography, and disturbance history (Williams 1998). Of these five pines, Table Mountain pine is frequently the most common species and such stands are often called Table Mountain pine or TMP stands (Zobel 1969; Williams 1998). Chestnut oak (*Quercus montana* Willd.) is the principal oak species and there is a mix of other oaks and associated hardwoods (Zobel 1969; Williams 1998). TMP stands are small (<20 ha), widely scattered (from central Pennsylvania to northern Georgia), and restricted to dry, thin soils on south- and west-facing ridges at elevations between 300 and 1200 m. Recurring fire is generally regarded as the key factor in creating and maintaining TMP stands in an otherwise mixed-hardwood landscape (Williams and Johnson 1990, 1992; Brose and Waldrop 2006).

However, fire is not the only disturbance impacting TMP ecosystems. The occurrence of these ecosystems on southerly ridges exposes them to winds from hurricanes, tropical storms, and strong thunderstorms during the growing season. Also, ridges are prone to ice accretion and snow accumulation during winter storms. All of the pine species of TMP stands are susceptible to attack by the southern pine bark beetle (*Dendroctonus frontalis* Zimmermann, 1868). Potential human-caused disturbances, in addition to fire, include timber harvesting and livestock grazing. Finally, loss of American chestnut (*Castanea dentata* (Marsh.) Borkh.) to blight in the 1920s affected many ridge top forests in the southern Appalachian Mountains (Keever 1953).

The Williams model provides an understanding of the relationship between disturbances and pine and oak dominance in TMP stands (Fig. 1). On extremely xeric sites, all disturbances promote pine continuance because oaks are unable to persist there. Barden (2000) describes such a TMP community in western North Carolina. On less harsh sites where hardwoods can survive and grow, TMP communities fluctuate between an unstable pine and stable oak dominance based on the occurrence of fire, insect, and storm disturbances. In this model, insect and storm disturbances favor oak regeneration and domination by creating canopy gaps without removing leaf litter. If a fire occurs, species composition shifts towards pine because of favorable regeneration conditions for pines coupled with reduced hardwood density. The prolonged absence of fire leads to an oak-dominated forest on the site.

Dendrochronology techniques can test this model by coupling tree-ring growth analysis with species recruitment patterns. Most previous dendrochronology research in TMP communities focused on fire (Brose and Waldrop 2006; Lafon and Grissino-Mayer 2007). All of these studies found that fire and pine regeneration co-occurred and both have been absent from their study sites for several decades. Unfortunately, little research has been done in TMP communities on the associated hardwood species and nonfire disturbances. Whitney and Johnson (1984) examined ice storm damage in four forest types in southwestern Virginia. In TMP communities, they found that pines sustained more

Fig. 1. Table Mountain pine (*Pinus pungens*) disturbance–succession model. Redrawn from Williams (1998).



damage than hardwoods, but pine seedling density increased after the ice storm. In this same area, Lafon and Kutac (2003) studied the interactions of ice storms, southern pine bark beetle (SPBB) infestations, and fire. They found that the two canopy disturbances without fire benefited hardwoods, but adding fire to the disturbance regime promoted TMP.

In this paper, we test the Williams disturbance–succession model for TMP communities by reanalyzing the dendrochronology data reported in our earlier paper (Brose and Waldrop 2006). We attempt to verify the model's specific predictions regarding pine and oak response to fire and canopy disturbance as well as the assertion of oak forest stability. Our hypothesis is that the model is fundamentally sound and we test these predictions: (1) more pines than oaks originated following fires and combined canopy + fire disturbances, (2) more oaks than pines originated following canopy-only disturbances and during periods of no disturbance, and (3) currently, pines have ceased to regenerate, while oaks continue to regenerate.

Understanding the relationship between different disturbances and oak and pine succession will aid land managers in maintaining and restoring these TMP communities and sustaining other pine–oak forests as well.

Methods

Study sites

Nine TMP communities located in northern Georgia, western South Carolina, and eastern Tennessee were selected for the study. Selection criteria were the following: (*i*) pines comprised 25%–50% stocking, (*ii*) the site was capable of supporting hardwoods, and (*iii*) fire scars were present. Three stands (Big Ridge, Upper Tallulah, and Lower Tallulah) were located south of Rabun Bald on the Chattahoochee National Forest in northern Georgia (Table 1). Another three stands (Upper, Middle, and Lower Gregory Ridge) were southeast of Cades Cove in the Tennessee portion of Great Smoky Mountains National Park. The remaining stands (Buzzard Roost, Poor Mountain, and Toxaway Ridge) were on the Sumter National Forest in western South Carolina, with the first two being situated northwest of Walhalla and the other west of Holly Springs.

Each stand consisted of a small (5–7 ha) TMP community on the crest and upper slopes of a south- or west-facing ridge (Table 1). The accompanying side slopes were quite steep (20%–60% slope) and rocky. Elevations varied from 400 m at Toxaway Ridge to 1100 m at Big Ridge. Soils at all the sites were well-drained sandy or silt loams formed in place by weathering of gneiss, sandstone, and schist parent material (Carson and Green 1981; Herren 1985; Davis 1993). Consequently, they were moderately fertile and strongly acidic. Climate was warm, humid, and continental with average monthly high temperatures ranging from –3 °C in January to 28 °C in July. Mean annual precipitation ranged from 135 to 185 cm distributed evenly throughout the year.

Composition and structure of the nine stands were quite similar. In general, they consisted of 10–20 woody species distributed in three distinct strata. The main canopy was 15–20 m tall, broken, and patchy and consisted almost exclusively of Table Mountain pine, one or more other pine species, and various oaks, especially chestnut oak. A ubiquitous midstory stratum (3–15 m tall) was present in all stands. It generally lacked a pine component, consisting almost exclusively of intermediate oaks and several other hardwood species such as black-gum (*Nyssa sylvatica* Marsh.), red maple (*Acer rubrum* L.), and sourwood (*Oxydendrum arboreum* (L.) DC.). Together, the main and subcanopies contained approximately 1100–1400 stems and 30–40 m^2 of basal area per hectare. The understory stratum was dominated by ericaceous (heath) shrubs (40%–75% cover) and lacked hardwood and pine seedlings as well as herbaceous plants.

Despite similarities in site characteristics, stand structure, and species composition, the TMP communities had different disturbance histories (Brose and Waldrop 2006). All had been impacted by fire, ice and wind storms, and SPBB outbreaks. The three Georgia stands had numerous sprouts of American chestnut in the understory, so the blight heavily impacted these stands. There was no visible evidence of past logging in any of these stands, and they probably had never been logged because of their remoteness and inaccessibility. All of the South Carolina stands had evidence of past logging (stumps and old skid trails), but no logging had been done in any of them for at least a decade. Also, the Toxaway Ridge stand had a moderate number of loblolly pines (*Pinus taeda* L.) in the overstory, suggesting a timber harvest decades ago. This species is outside its natural range in this part of South Carolina but was often planted on federal lands following clearcuts in the 1950s and 1960s (Paul Burris, US Forest Service silviculturist, personal communication). The Tennessee stands were in the part of Great Smoky Mountains National Park that had never been commercially logged (Mike Jenkins, National Park Service ecologist, personal communication) but had a long-term frequent fire and grazing history due to the cultural practices of the inhabitants of nearby Cades Cove (Dunn 1988).

Field procedures

At each stand in fall 1999, twelve to fifteen 0.02 hectare rectangular plots were either systematically located to ensure uniform coverage or randomly selected from an ongoing study (Waldrop and Brose 1999). Within each plot, all stems larger than 2.54 cm basal diameter were identified to species and assigned to one of four species groups (upland pines, mixed oaks, miscellaneous hardwoods, or heath shrubs). Upland pines were pitch, shortleaf, Table Mountain, and Virginia pines. Mixed oaks consisted primarily of chestnut oak and lesser amounts of scarlet oak (*Quercus coccinea* Muenchh.), black oak (*Quercus velutina* Lam.), and white oak (*Quercus alba* L.). Miscellaneous hardwoods included a wide variety of other species such as black-gum, eastern flowering dogwood (*Cornus florida* L.), hickory (*Carya* spp.), red maple, serviceberry (*Amelanchier arborea* (Michx. f.) Fern.), and sourwood. Heath shrubs were almost entirely mountain laurel (*Kalmia latifolia* L.) but also included an occasional Piedmont azalea (*Rhododendron flammeum* (Michx.) Sarg.) and rosebay rhododendron (*Rhododendron maximum* L.).

In each plot, we randomly selected up to four trees or shrubs from each species group for sampling. Trees larger than 10 cm basal diameter were cored; smaller trees and shrubs were felled and a cross section was cut from their bases at the ground line. Obtaining full or partial cross sections on the larger trees was not possible because of landowner restrictions, difficult accessibility to some sites, and safety constraints. The cores were extracted at a height of 0.3 m above ground on the uphill side. If the tree was a chestnut oak, a species with thick bark and deep fissures, the core was extracted from a fissure to intersect hidden, internal scars. Because of these bark characteristics, fire often damages the cambial tissue behind the fissures while leaving the surrounding tissue undamaged (Smith and Sutherland 1999). If a core contained a visible defect, it was kept, but more were extracted until a sound core was obtained. Usually, one core was needed from most trees, and only a few trees required more than two cores.

Laboratory procedures

A total of 878 cores and 871 cross sections were collected from the nine stands. These were air-dried for several weeks, mounted, and sanded with increasingly finer sandpaper (120, 220, 320, and 400 grit) to expose the annual rings. To identify the year of origin of each sample, we aged each core and cross section to the innermost ring or pith under a 40× dissecting microscope to determine a tentative establishment date. To arrive at a final establishment date, we made two adjustments. First, if the core did not contain the pith, we adjusted the tentative establishment using a pith estimator (Villalba and Veblen 1997) to determine how many annual rings were missed. No such adjustments were made to cores containing piths or to the cross sections. Second, we moved each tentative establishment date back 5 years,

Table 1. Site characteristics of the nine Table Mountain pine (*Pinus pungens*) stands in Georgia, South Carolina, and Tennessee.

State and stand	Location	Elevation (m above sea level)	Slope (%)	Aspect (°)	Soil series	Soil family
Georgia						
Big Ridge	34°52′00″N, 83°14′45″W	975–1100	10–40	90–225	Ashe sandy loam	Typic Dystrochrept
Lower Tallulah	34°51′30″N, 83°14′15″W	850–925	10–25	90–225	Ashe sandy loam	Typic Dystrochrept
Upper Tallulah	34°51′30″N, 83°14′15″W	975–1100	20–60	90–225	Ashe sandy loam	Typic Dystrochrept
South Carolina						
Buzzard Roost	34°46′00″N, 83°08′16″W	500–600	15–30	90–225	Walhalla sandy loam	Typic Hapludult
Poor Mountain	34°46′48″N, 83°08′50″W	500–600	5–20	90–270	Walhalla sandy loam	Typic Hapludult
Toxaway Ridge	34°42′00″N, 83°15′23″W	400–450	5–35	90–270	Evard sandy load	Typic Hapludult
Tennessee						
Lower Gregory	35°32′62″N, 83°50′18″W	900–975	15–30	90–125	Ramsey silt load	Mesic Dystrochrept
Middle Gregory	35°32′57″N, 83°50′45″W	925–1000	10–20	180–270	Ramsey silt load	Mesic Dystrochrept
Upper Gregory	35°32′58″N, 83°50′51″W	975–1025	20–50	90–180	Ramsey silt load	Mesic Dystrochrept

e.g., 1910 became 1905, to account for the time needed by the stems to grow to the coring height.

All cores were visually inspected for defects, and the oak and pine cores that were free of defects and contained more than 75 annual rings were skeleton plotted to identify signature years for cross-dating to recognize false or missing rings (Stokes and Smiley 1996). After proper ages were verified for these cores, their annual rings were measured to the nearest 0.002 mm with a Unislide "TA" Tree-Ring Measurement System (Velmex Inc., Bloomfield, New York). The COFECHA 2.1 quality assurance program (Holmes 1983; Grissino-Mayer 2001) in the International Tree-Ring Data Bank Program Library (Grissino-Mayer et al. 1992) was used to verify the cross-dating.

The individual oak and pine chronologies were detrended with the ARSTAN program (Cook 1985) to remove the effects of tree age and microsite variability from the radial growth measurements and combine them into master oak and pine chronologies for each site. We analyzed each master chronology with the JOLTS program (Holmes 1999*a*) to identify when moderate and major canopy disturbances (50%–100% and more than 100% growth increases for at least 10 years, respectively) occurred throughout the site. These correspond to stand-level disturbances that release residual trees from competition until crown closure occurs again (Lorimer and Frelich 1989).

To ensure the above analysis did not miss other canopy disturbances that may be important in stand development, we also used two relatively novel dendrochronology approaches. First, we used JOLTS to examine the individual pine chronologies for a bipartite growth signal; some pines showing a strong minor release (35%–50% growth increase) while other pines showing a comparable, concurrent growth reduction. Lafon and Speer (2002) and Cseke (2003) used this approach to identify small-scale storm damage in TMP stands in Virginia and Tennessee, respectively. When we found this bipartite signal in the same or sequential years of five or more pairs of pine chronologies, we considered that to be evidence of a storm. We verified these storms using National Climatic Data Center (NCDC) historic storm data for that site and year (NCDC 2008).

Our second novel approach to identify other canopy disturbances was to use OUTBREAK (Holmes 1999*b*) to find periods of SPBB activity. This dendrochronology program finds years of insect outbreaks by comparing chronologies of host and non-host species. An outbreak is identified when the host's growth declines while the non-host's growth accelerates. OUTBREAK has never been used in the Appalachian Mountains to determine past SPBB outbreaks, but it has been successfully used elsewhere to identify mountain bark beetle (*Dendroctonus ponderosae* Hopkins, 1902) outbreaks (Lewis and Hrinkevich 2008). When we found this bipartite signal as a strong minor release in the same or sequential years of five or more pairs of pine and oak chronologies, we considered that to be evidence of SPBB. We verified the identified SPBB outbreaks with extant records (Price et al. 1997).

We examined all cross sections and the chestnut oak cores for evidence of past fires by looking for external or internal scars. Cores containing a scar were skeleton plotted and cross-dated using an unscarred core from the same tree to assign a date to the scar. Scars in cross sections were dated by comparing them to adjacent unscarred annual rings. Because scars can be caused by means other than fires, we decided that three or more scars had to occur in the same year at the same stand for them to be considered of fire origin. Fires were classified by size and seasonality. If the scars for a given year were found in more than 50% of the plots, then the fire was considered to be large or widespread. Conversely, if the scars were found in less than 50% of the plots at a site, then the fire was considered small or isolated. Fire seasonality was determined for the scars in the cross sections based on criteria by Baisan and Swetnam (1990). If the scar occurred between annual rings, then the fire was considered a dormant-season burn. A scar within an annual ring was considered caused by a growing-season fire.

Data analysis

Our previous paper indicated that these nine TMP stands could be consolidated into four TMP communities or sites based on nearly identical pine age structures and shared disturbance histories (Brose and Waldrop 2006). The four sites were the following: (*i*) GA, consisting of the three stands in Georgia; (*ii*) SC1, comprising the Buzzard Roost and Poor Mountain stands in South Carolina; (*iii*) SC2, which was a single stand, Toxaway Ridge, also in South Carolina; and (*iv*) TN, consisting of the three stands in Tennessee. Consolidating the nine stands into four communities or sites simplified data analysis and reporting, and the four site names will be used throughout the remainder of this paper.

To link species establishment dates with the disturbances, we created a history timeline for each site containing both data sets. Each timeline was from 1850 to 1990 and was divided into 5-year intervals, e.g., 1860–1864 and 1865–1869. In each interval, we tallied the number of stems originating during those 5 years by species groups. Each interval was assigned a disturbance type (canopy, fire, canopy + fire combination, or no disturbance) based on which event occurred during those 5 years. Canopy disturbances were events such as chestnut blight, logging, SPBB outbreak, or storm damage that JOLTS detected as a stand-level major, moderate, or strong minor release. Fire disturbances were all surface fires that impacted the forest floor without registering such a release in the growth chronologies. If a fire was severe enough to cause a stand-level release, we classified it as a canopy + fire disturbance. Also, if a canopy disturbance and a fire occurred within 5 years of each other, we categorized these as canopy + fire disturbances, regardless of which came first. Intervals without any disturbance were classified as no disturbance.

Occasionally, an interval was classified by the disturbance that immediately preceded it. For example, an undisturbed interval would be considered a canopy-disturbance interval if the canopy event occurred within 3 years prior to the start of the interval. This was done because there can be a lag between a disturbance and subsequent regeneration.

To test the model's predictions for oak and pine response to disturbance, we created contingency tables for each stand consisting of the species groups and the four disturbance types. We used χ^2 analysis (Zar 1999) to determine whether the numbers of sampled stems were distributed as expected among the four disturbance types and species groups. For all tests, α was 0.05.

The Williams model presents the oak component of TMP stands being stable in the absence of fire. We reasoned that stability implied ongoing or recent successful regeneration, while instability meant no recent successful regeneration. We tested this definition of stability by calculating the last establishment year (LEY) for each species group at each site by averaging the establishment years of the 10 youngest samples and then using *t* tests with unequal variances (Zar 1999) to compare these LEYs.

Results

A total of 1749 trees and shrubs were sampled from the four sites. Among sites, sample totals were 433 from GA, 464 from SC1, 438 from SC2, 414 and from TN. The species group totals were 442 upland pines, 413 mixed oak, 430 miscellaneous hardwoods, and 464 heath shrubs or about 100 samples per species group per site. The upland pine, mixed oak, and heath shrub groups were each dominated by a single species. Table Mountain pine constituted 86% of the upland pines, while chestnut oak accounted for 83% of the mixed oaks. Mountain laurel comprised more than 95% of the heath shrub group. The miscellaneous hardwood group contained 11 species; black-gum and red maple each accounted for approximately 37% of the total.

GA site

At this site, the pines were uneven-aged with no distinct cohorts (Fig. 2). They successfully regenerated in every decade from the 1850s to the 1950s. Oaks were quite similar. They originated in every decade from the 1870s to the 1940s with most dating to the early 1900s. The pine LEY was 1952 ± 4 years and for oak it was 1946 ± 4 years. The oldest miscellaneous hardwoods and heath shrubs dated to the 1910s, with the vast majority of both species groups starting between the 1930s and the 1960s. Regeneration of miscellaneous hardwoods ceased in the early 1960s, LEY was 1960 ± 3 years, while heath shrubs continued establishing new individuals into the 1980s (LEY was 1977 ± 5 years).

Since 1850, fires and canopy disturbances have been common occurrences at the GA site (Fig. 2). Scars indicated that large fires burned through all or much of the site in 1872, 1898, 1905, 1912, and 1925 and small fires occurred in 1944, 1963, and 1972. All were dormant-season burns except the 1963 fire, which occurred during the growing season. Twelve stand-level major, moderate, or strong minor canopy releases were detected between 1870 and 1990. The major and moderate releases happened before 1925, while the minor releases occurred throughout the timeline. Several of the early 1900 releases, e.g., 1902, 1911, 1916, coincide with the passage of hurricanes through the southern Appalachian Mountains, while the 1926 release matches the arrival of the chestnut blight. The fairly regular minor releases from the 1930s to the 1980s fit with SPBB outbreaks.

Pines and oaks were distributed among the four disturbance types as expected with χ^2 = 0.79 and the critical value = 7.815 (Table 2). Not only did their observed numbers not differ from the expected numbers, they differed little from each other. Both species groups had 27 and 32 stems in the fire and canopy disturbance types, respectively. When pine and oak were combined and tested with miscellaneous hardwoods and heath shrubs, significant differences were detected; χ^2 = 51.61, critical value = 12.592. This difference was driven by more pines and oaks and fewer heath shrubs originating after canopy + fire disturbances than expected and more heath shrubs and fewer pines and oaks starting after canopy-only disturbances than expected. Miscellaneous hardwoods showed no trends in stem distribution among the four disturbance types.

SC1 site

Like the GA site, pines at SC1 were uneven-aged with periodic regeneration in the mid-1800s and continuous regeneration from the late 1800s to the 1960s (Fig. 3). However, SC1 pines displayed four distinct cohorts that formed in the early 1900s, early 1920s, early 1930s, and early 1950s. Pine LEY was 1958 ± 5 years. Oaks originated from the late 1850s to the 1960s with two distinct cohorts (1915–1930 and 1945–1960). Their LEY was 1956 ± 3 years. Miscella-

Fig. 2. Age structures and temporal relationships of upland pines, mixed oaks, miscellaneous hardwoods, and heath shrubs and disturbances of the Table Mountain pine (*Pinus pungens*) community located at the GA site in northern Georgia. Disturbance abbreviations: F, large fire; f, small fire; C, major or moderate canopy release; c, minor canopy release.

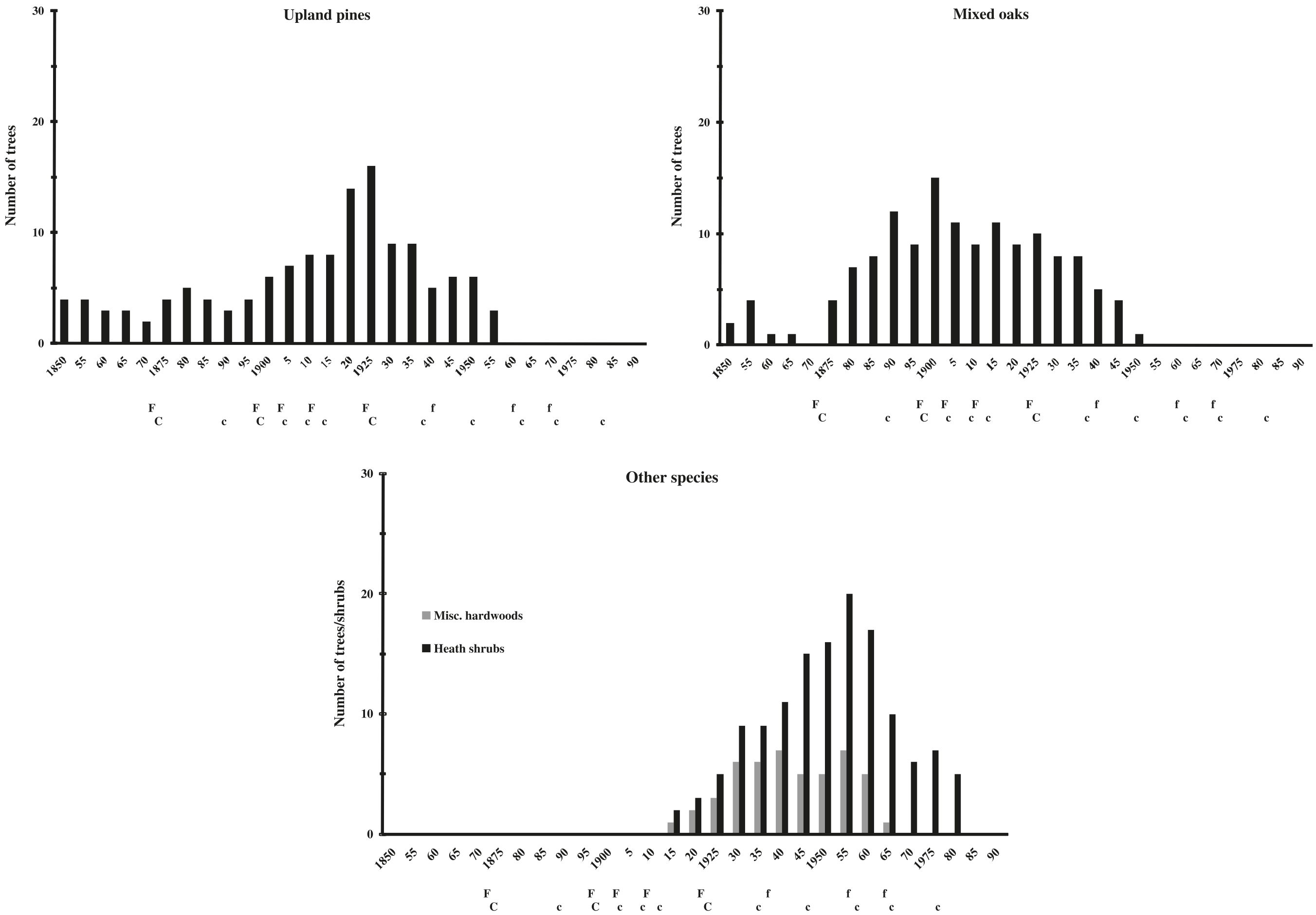


Table 2. Distribution of the 433 sampled trees and shrubs of the GA site by disturbance type and species group.

	Disturbance type				
Species group	None	Canopy	Fire	Canopy + fire	Total
Comparison of pines and oaks (test statistics: χ^2 = 0.79, critical value = 7.815, α = 0.05, df = 3)					
Upland pine	26 (26)	32 (30)	27 (26)	34 (37)	119
Mixed oak	28 (28)	32 (34)	27 (28)	44 (41)	131
Total	54	64	54	78	250
Comparison of all species (test statistics: χ^2 = 51.61, critical value = 12.592, α = 0.05, df = 6)					
Pine and oak combined	54 (63)	**–64** (88)	54 (41)	**+78** (57)	250
Miscellaneous hardwood	13 (12)	21 (17)	3 (8)	11 (11)	48
Heath shrub	43 (34)	**+68** (48)	14 (22)	**–10** (31)	135
Total	110	153	71	99	433

Note: Numbers in parentheses are the expected values for each disturbance type andspecies group combination. Bold numbers indicate the four largest positive or negative departures contributing to a significant χ^2 value.

neous hardwoods and heath shrubs originated between 1925 and 1985 with both groups having discrete cohorts at 10- to 15-year intervals from the 1940s to the 1980s. LEYs for miscellaneous hardwoods and heath shrubs were 1978 ± 2 years and 1983 ± 1 year, respectively.

Large fires impacted most of or all of SC1 in 1894, 1904, 1914, 1925, and 1944 (Fig. 3). Small fires occurred in 1933, 1951, 1962, and 1981. All fires were dormant-season burns. Major, moderate, and strong minor canopy disturbances were common from 1870 to 1985 and generally occurred at 10- to 15-year intervals. Major and moderate disturbances were most prevalent in the early 1900s, while minor disturbances were most common after 1950. Like the GA site, several of the canopy releases in the early 1900s correspond to hurricanes passing through the region, and later ones match with outbreaks of SPBB.

Fig. 3. Age structures and temporal relationships of upland pines, mixed oaks, miscellaneous hardwoods, and heath shrubs and disturbances of the Table Mountain pine community located at the SC1 site in western South Carolina. Disturbance abbreviations: F, large fire; f, small fire; C, major or moderate canopy release; c, minor canopy release.

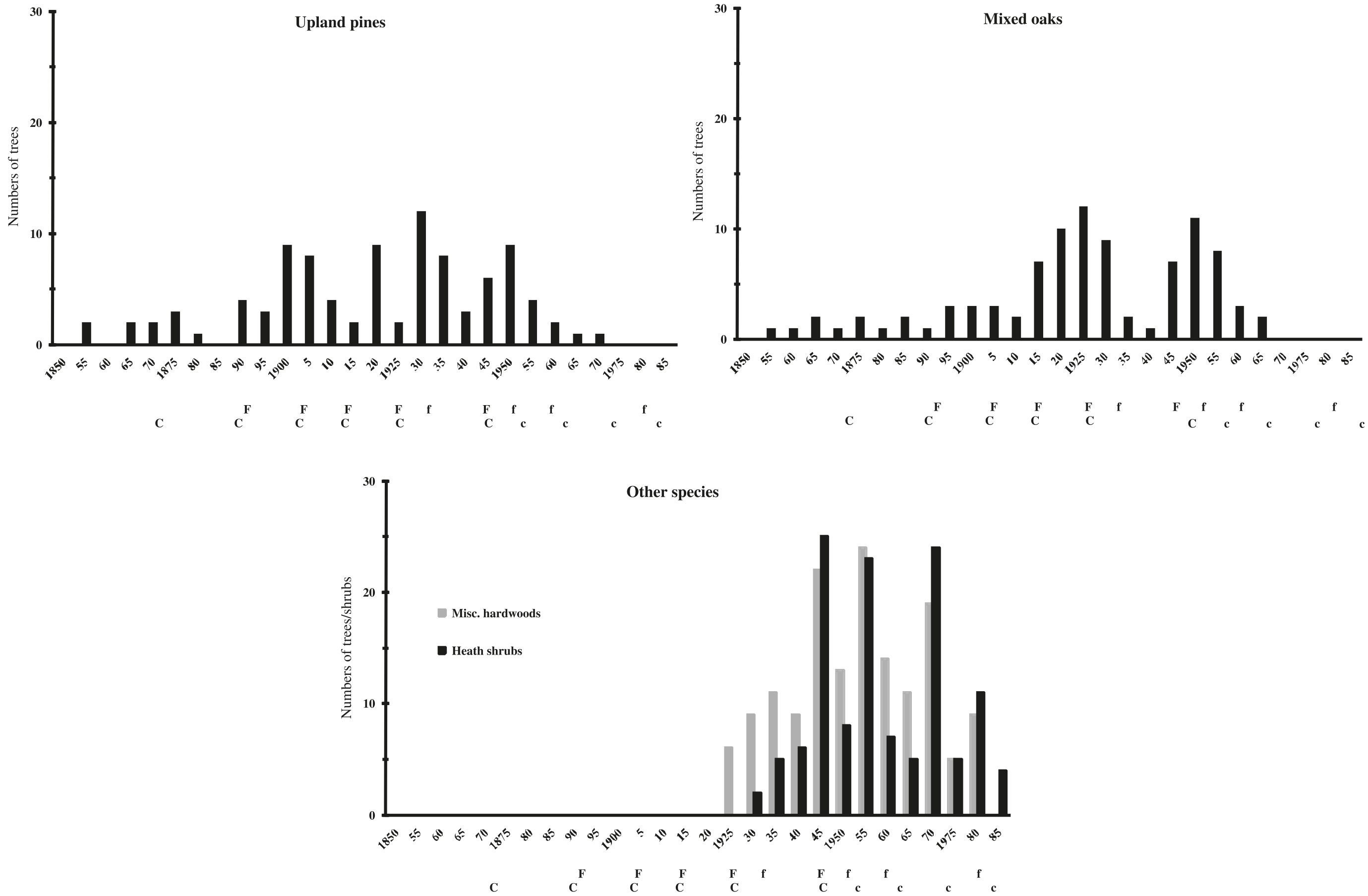


Table 3. Distribution of the 464 sampled trees and shrubs of the SC1 site by disturbance type and species group.

	Disturbance type				
Species group	None	Canopy	Fire	Canopy + fire	Total
Comparison of pines and oaks (test statistics: χ^2 = 3.71, critical value = 7.815, α = 0.05, df = 3)					
Upland pine	12 (17)	16 (15)	27 (25)	40 (38)	95
Mixed oak	21 (16)	13 (14)	23 (25)	35 (37)	92
Total	33	29	50	75	187
Comparison of all species (test statistics: χ^2 = 39.97, critical value = 12.592, α = 0.05, df = 6)					
Pine and oak combined	**–33** (47)	29 (40)	50 (39)	75 (61)	187
Miscellaneous hardwood	34 (39)	35 (32)	34 (32)	49 (49)	152
Heath shrub	**+51** (32)	35 (27)	**–12** (26)	**–27** (41)	125
Total	118	99	96	151	464

Note: Numbers in parentheses are the expected values for each disturbance type andspecies group combination. Bold numbers indicate the four largest positive or negative departures contributing to a significant χ^2 value.

The χ^2 value for pines and oaks at the SC1 site was 3.71, indicating the sampled stems were distributed as expected among the four disturbance types (Table 3). When pines and oaks were combined and tested against heath shrubs and miscellaneous hardwoods, the observed distribution of stems differed from what was expected (χ^2 = 39.97, critical value = 12.592). Fewer pines and oaks and more heath shrubs originated during periods of no disturbance than was expected. Conversely, fewer heath shrubs started after fires and canopy + fire disturbances than was expected. Miscellaneous hardwoods showed no trends in stem distribution among the four disturbance types.

SC2 site

SC2 was an even-aged TMP community with the vast majority of all tree species originating between 1950 and 1970

Fig. 4. Age structures and temporal relationships of upland pines, mixed oaks, miscellaneous hardwoods, and heath shrubs and disturbances of the Table Mountain pine (*Pinus pungens*) community located at the SC2 site in western South Carolina. Disturbance abbreviations: F, large fire; f, small fire; C, major or moderate canopy release; c, minor canopy release.

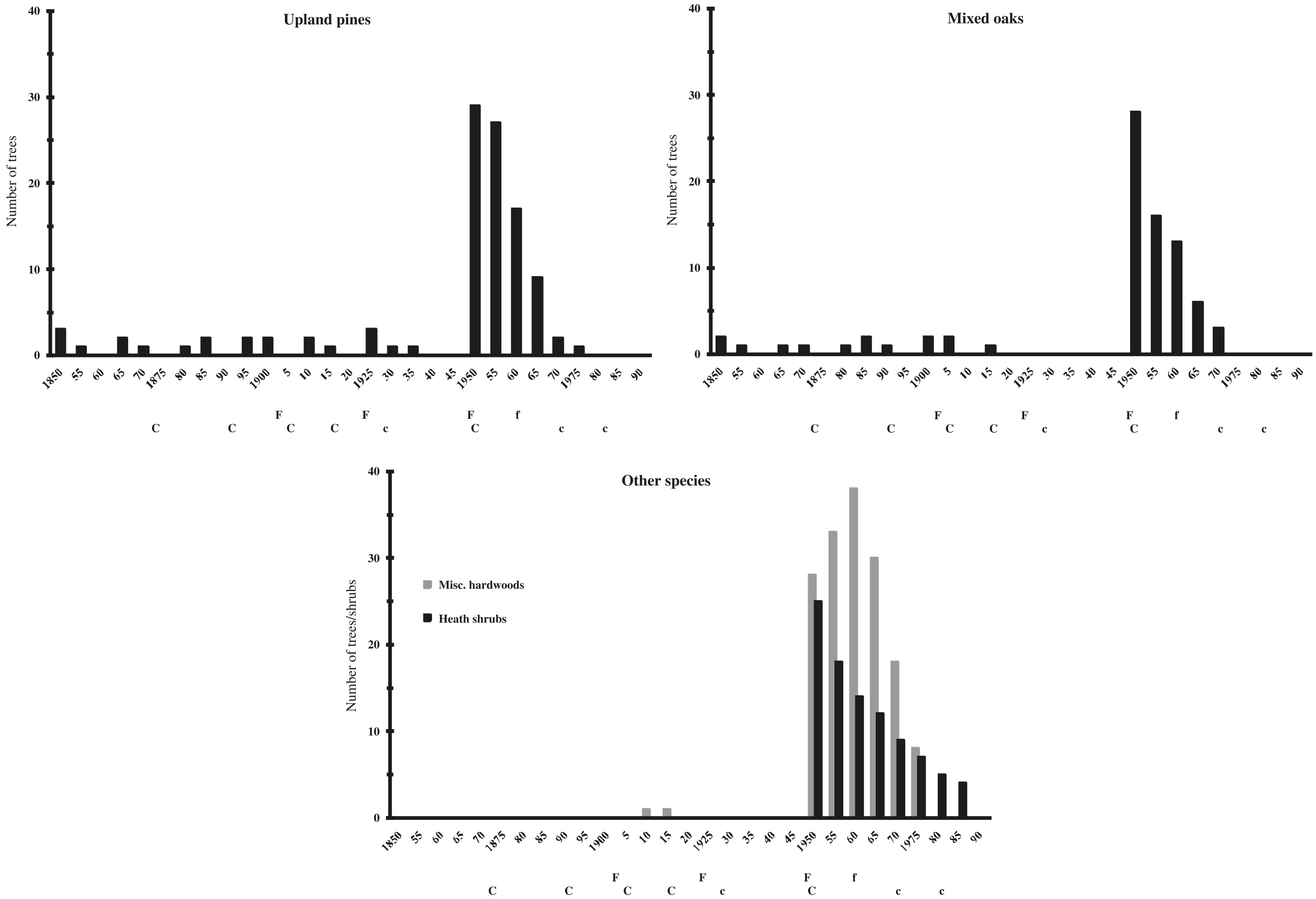


Table 4. Distribution of the 438 sampled trees and shrubs of the SC2 site by disturbance type and species group.

	Disturbance type				
Species group	None	Canopy	Fire	Canopy + fire	Total
Comparison of pines and oaks (test statistics: χ^2 = 2.95, critical value = 7.815, α = 0.05, df = 3)					
Upland pine	22 (22)	14 (18)	20 (19)	51 (47)	107
Mixed oak	17 (17)	18 (14)	14 (15)	31 (35)	80
Total	39	32	34	82	187
Comparison of all species (test statistics: χ^2 = 45.58, critical value = 12.592, α = 0.05, df = 6)					
Pine and oak combined	**–39** (54)	32 (28)	34 (32)	82 (73)	187
Miscellaneous hardwood	43 (45)	16 (24)	20 (26)	**+78** (61)	157
Heath shrub	**+45** (28)	18 (14)	20 (16)	**–11** (37)	94
Total	127	66	74	171	438

Note: Numbers in parentheses are the expected values for each disturbance type andspecies group combination. Bold numbers indicate the four largest positive or negative departures contributing to a significant χ^2 value.

(Fig. 4). There were some residual pines and oaks from the previous stand. These dated from before 1850 to 1935 and began growing in every decade during that period. Pines and oaks ceased regenerating in 1966 ± 4 years and 1967 ± 5 years, respectively. The oldest miscellaneous hardwoods and heath shrubs dated to the early 1950s, but unlike the pines and oaks they continued establishing themselves into the 1970s and 1980s. The youngest miscellaneous hardwood dated to 1973 ± 3 years, while the youngest heath shrub started in 1981 ± 4 years.

The pre-eminent disturbance at the SC2 site occurred in the early 1950s (Fig. 4). This was a timber harvest, a large fire, or both, as the stand-level oak and pine chronologies showed major and strong moderate releases for 1953. The presence of loblolly pine dating to the early 1950s suggests a timber sale, but a large fire burned all or most of the site

Fig. 5. Age structures and temporal relationships of upland pines, mixed oaks, miscellaneous hardwoods, and heath shrubs and disturbances of the Table Mountain pine (*Pinus pungens*) community located at the TN site in eastern Tennessee. Disturbance abbreviations: F, large fire; f, small fire; C, major or moderate canopy release; c, minor canopy release.

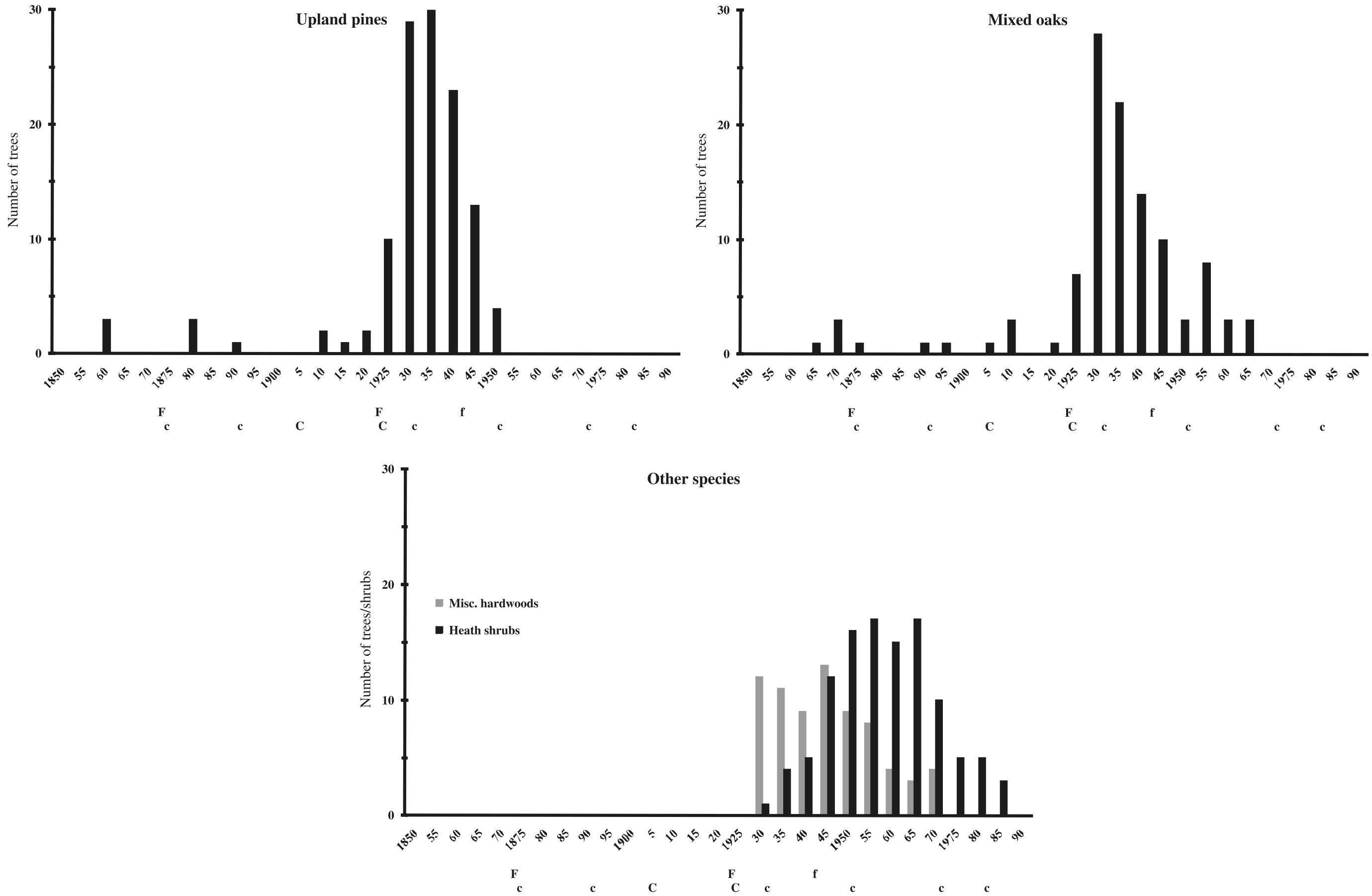


Table 5. Distribution of the 414 sampled trees and shrubs of the TN site by disturbance type and species group.

	Disturbance type				
Species group	None	Canopy	Fire	Canopy + fire	Total
Comparison of pines and oaks (test statistics: χ^2 = 1.16, critical value = 7.815, α = 0.05, df = 3)					
Upland pine	39 (41)	20 (20)	23 (20)	39 (39)	121
Mixed oak	40 (38)	19 (19)	15 (18)	36 (36)	110
Total	79	39	38	75	231
Comparison of all species (test statistics: χ^2 = 35.75, critical value = 12.592, α = 0.05, df = 6)					
Pine and oak combined	79 (83)	**–39** (55)	38 (34)	**+75** (58)	231
Miscellaneous hardwood	23 (26)	21 (18)	13 (11)	16 (19)	73
Heath shrub	46 (39)	**+40** (27)	–10 (16)	**–14** (28)	110
Total	148	100	61	105	414

Note: Numbers in parentheses are the expected values for each disturbance type andspecies group combination. Bold numbers indicate the four largest positive or negative departures contributing to a significant χ^2 value.

in 1951. The pines may have been planted in response to the fire. Other large fires also burned throughout the site in 1904 and 1925, and a small fire burned a portion of the site in 1962. All fires were in the dormant season. Aside the major or moderate release in 1953, comparable canopy disturbances occurred periodically in the early 1900s, while minor releases occurred in the 1930s, late 1960s, and late 1980s.

The χ^2 and critical values for pines and oaks at the SC2 site were 2.95 and 7.815, respectively, indicating that the stems were distributed as expected among the four disturbance types (Table 4). When pines and oaks were combined and tested against heath shrubs and miscellaneous hardwoods, χ^2 and critical values were 45.58 and 12.592, respectively, indicating the stems were not distributed as expected among the disturbance types. Specifically, more heath shrubs and fewer pines and oaks originated during periods of no disturbance than expected. Canopy + fire disturbances resulted in more miscellaneous hardwoods and fewer heath shrubs than expected.

TN site

The TN site was even-aged with the vast majority of pines and oaks originating between 1925 and 1945 (Fig. 5). Before that period, some pines and a few oaks had become established in every decade since 1850. Pines ceased regenerating in the early 1950s (LEY was 1947 ± 3 years), and oaks did likewise in the 1960s (LEY was 1959 ± 4 years). Miscellaneous hardwoods dated from 1930 to 1970, while the heath shrubs dated from 1930 to the 1980s. Miscellaneous hardwood LEY was 1965 ± 4 years, while the heath shrub LEY was 1982 ± 3 years.

Like SC1, the TN site was closely tied to a major event in the mid-1920s (Fig. 5). At that time, a large dormant-season fire burned through the stand, and a major canopy release occurred. This coincides with the beginning of the abandonment of Cades Cove and the subsequent formation of GSMNP (Dunn 1988). Besides the 1926 fire, the only other large dormant-season fire occurred in 1872. A small, growing-season fire occurred in summer 1941. The only other major canopy release disturbance was in 1905. Minor releases occurred in the late 1800s, and at 15- to 20-year intervals from 1930 to 1985.

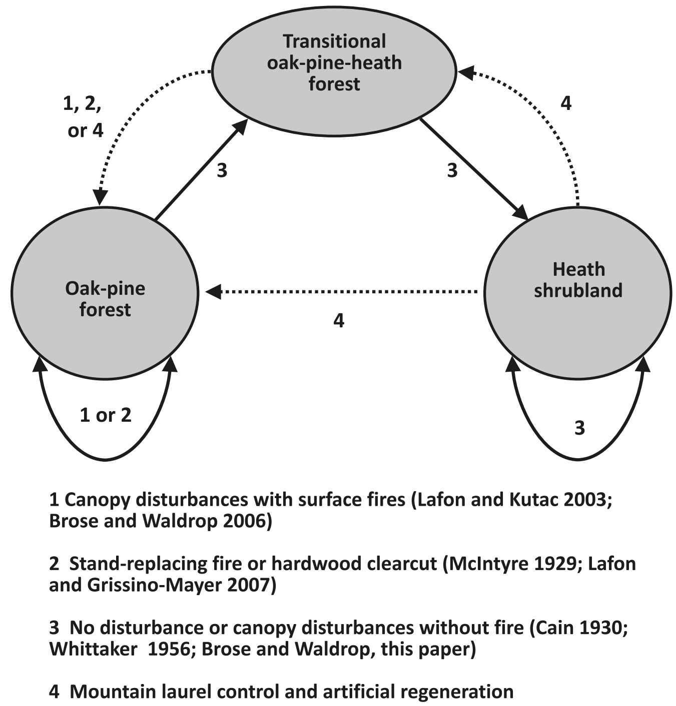
Like the other three sites, no differences were found in the distribution of sampled oak and pine stems among the four disturbance types at the TN site (Table 5). The χ^2 value was 1.16, while the critical value was 7.815. But, combining oak and pine and testing them against heath shrubs and miscellaneous hardwoods yielded a χ^2 of 35.75, indicating that the stems were not distributed as expected among the four disturbance types. Specifically, more pines and oaks and fewer heath shrubs originated after canopy + fire events than expected, and the reverse was true for these two species groups following canopy-only disturbances. Miscellaneous hardwoods showed no trends in stem distribution among the four disturbance types.

Discussion

For disturbance ecology models to be useful, they need to accurately portray successional relationships among the principal plant species groups for a wide range of conditions. The Williams disturbance–succession model presents TMP communities with two principal species groups, upland pines and oaks (Fig. 1). These two groups are portrayed as ecological antagonists; either one or the other is favored, depending on the disturbance. If a fire occurs, it promotes pines more than oaks. Conversely, canopy disturbances and no disturbance favor oaks more than pines. Also, succession is from pine to oak, and once oak dominates the site, the ecosystem becomes stable, meaning that oak is able to regenerate and persist. We tested these three premises via a dendrochronology study conducted in four TMP communities scattered throughout the southern Appalachian Mountains. Based on our data, we found little support for the model.

For prediction 1, where fires favor pine more than oak, we found no demonstrable difference at any site between

Fig. 6. Disturbance–succession model for Table Mountain pine (*Pinus pungens*) communities with understories dominated by mountain laurel (*Kalmia latifolia*). Solid lines between the plant communities (shaded ovals) represent known successional pathways for that disturbance regime, while broken lines indicate hypothetical pathways and accompanying disturbance regime.



the numbers of oaks and pines that originated following a fire. Large fires and fires occurring in conjunction with canopy disturbances clearly provided more benefit to oaks and pines than small fires, but this type of disturbance did not favor pine establishment and recruitment more than that of oak. This is compatible with the growing body of literature that upland oaks are well suited to a periodic surface fire regime (Yaussy 2000; Dickinson 2006).

Prediction 2, where canopy-only disturbances and periods of no disturbance favor oak more than pine, was the opposite of prediction 1, and we found no support for it either. Oaks and pines regenerated in equal numbers at all sites, regardless whether there were canopy-only disturbances or periods of no disturbance. This result may be due to favorable understory conditions for seedling establishment and survival persisting from earlier fire disturbances, or the pines are not as restricted in their regeneration niche as previously thought. Waldrop and Brose (1999) documented the roots of new pine germinants that were able to penetrate Oa horizons several centimetres thick, and Mohr et al. (2002) demonstrated that new pine germinants had their highest survival rate in partial shade.

Closely tied to prediction 2 was prediction 3, cessation of pine regeneration and continuation of oak regeneration in the prolonged absence or reduction of fire. We found partial support for this prediction. Pine regeneration had ceased at all four sites, but so had that of oak. Generally, oaks started and stopped successfully regenerating at approximately the same times as the pines. No differences were found between their respective LEYs at any site. Apparently the circumstances that spurred successful pine regeneration in the past were the same ones needed by the oaks, and the conditions currently preventing pine establishment are likewise stopping oak regeneration. The oak component is no more stable than the pine component when it comes to successfully regenerating in a disturbance regime lacking an adequate fire component.

Why did our findings not support the Williams model? Two factors stand out as the probable reasons for these discrepancies. First, the model presents a dichotomy between pine and oak, implying that they respond differently to disturbance. That dichotomy is far more artificial than actual. Pines and oaks respond similarly to disturbance because of similarities in some of their silvical characteristics. Consider the two principal species; chestnut oak and Table Mountain pine. Both have rooting strategies and physiological traits designed to thrive on dry, nutrient-poor sites (Della-Bianca 1990; McQuilkin 1990). Chestnut oak is intermediate in shade tolerance, while Table Mountain pine is intolerant of shade (Della-Bianca 1990; McQuilkin 1990). However, Mohr et al. (2002) indicates that Table Mountain pine readily regenerates and survives for at least a few years in partial shade, so the species may be more like chestnut oak in shade tolerance than previously thought. Likewise, Waldrop and Brose (1999) and Mohr et al. (2002) showed roots of new pine germinants were capable of penetrating Oa horizons several centimetres thick, so pine seedbed requirements may not substantially differ from those of chestnut oak. Seedlings of both species grow rapidly and develop thick basal bark by the time they become saplings, giving them protection from most surface fires. Given these similarities in silvical characteristics, it is not surprising that we found no differences between the two species regarding their regeneration success after the different disturbance types. Instead of looking at the upland pines and oaks as ecological antagonists in response to disturbance, perhaps they should be considered ecological analogs.

The second major reason why our results do not support the Williams model is the presence of mountain laurel in the understories of all our sites. In the model, TMP communities in a reduced fire disturbance regime become dominated by oak via superior oak regeneration and longevity. These oaks form an edaphic climax; a stable oak forest that can regenerate itself. While oak forests can perpetuate themselves on dry, low-quality sites (Johnson et al. 2002), that does not appear to happen when mountain laurel and similar heath shrubs dominate the forest floor (Nilsen et al. 2001; Chastain and Townsend 2008). In this study, each of the sites had from 40% to 75% mountain laurel cover. The current thickets arose since the last large fire at each site and continue to successfully regenerate. At each site, the oaks ceased successfully regenerating once the heath shrubs dominated the forest floor. Mountain laurel and rhododendron have dense branching and foliage, and their leaves are evergreen. They continually cast dense shade on the forest floor, too much shade for the survival and growth of oak regeneration, and also reduce soil resources (Nilsen et al. 2001; Chastain and Townsend 2008).

Is the Williams disturbance–succession model still useful? It may well be in oak–pine forests lacking a dense heath understory. We could not test it in that setting because all our study sites had abundant mountain laurel. It would be interesting to test the model in oak–pine forests in the Ozarks or Piedmont regions where there is no interfering layer of large heath shrubs.

To make the model applicable to Appalachian oak–pine forests with a heath understory, we recommend the following revised model (Fig. 6). Oak–pine forests are maintained as uneven-aged communities via periodic canopy disturbances coupled with surface fires (Lafon and Kutac 2003; Brose and Waldrop 2006) or as even-aged communities through stand-replacing events (McIntyre 1929; Lafon and Grissino-Mayer 2007). In this environment, heath shrubs may be present in the understory, but they never become an interfering layer. The absence of disturbance or canopy disturbances without fire allows them to eventually dominate the forest floor to the point that they stop oak and pine regeneration processes. The oak–pine community becomes a transitional oak–pine–heath community and may stay in this state for many decades. Because fire is missing from the site and the heath shrubs can regenerate in their own shade, they continue occupying the forest floor. Eventually, the overstory oaks and pines succumb to various mortality agents, and the forest converts to a shrubland (Cain 1930; Whittaker 1956).

Preventing this succession from oak–pine forest to heath shrubland to ever start is the wisest course of action for land managers. Periodic surface fires and timber harvests can keep the heath understory of an oak–pine forest from becoming a problem while allowing the oaks and pines to regenerate. If the heath layer has become dominant, but the canopy is still healthy, a stand-replacing fire or clearcut will result in a new oak–pine forest (McIntyre 1929; Waldrop and Brose 1999). However, if the overstory is in decline, artificial regeneration coupled with herbicide control of the heath may be necessary. If the oak–pine forest has converted entirely to a heath shrubland, then herbicide control with artificial regeneration will be necessary, but this approach is speculative. Clearly, management to prevent heath shrub domination of the understory of oak–pine forests is a better approach than trying to restore such a community.

Finally, two unexpected results merit some discussion. First, miscellaneous hardwoods showed no clear response to any of the disturbance types, including fire. This is likely due to this group containing several species, so the gain or loss of stems of one species to a particular disturbance may have been offset by the opposite response of another. Also, most of the fires were dormant-season burns, and these types of fires cause little mortality to black-gum and red maple (the two most common non-oaks), especially at low fire intensities (Brose and Van Lear 1998; Brose et al. 1999).

The second unexpected result was that canopy + fire combination disturbances were especially conducive to regenerating pines and oaks. Of the four disturbance types, this one generally led to establishing more pines and oaks than the others, regardless of site. We do not know if these were moderately intense fires occurring closely in time with canopy disturbances or exceptionally intense fires that caused overstory mortality or both. We lean towards the first possibility, because two of the sites were uneven-aged, and several of the canopy + fire events coincided with hurricanes passing through the region. Recent research shows that hurricanes can cause substantial gaps in forest canopies as they pass through the southern Appalachian Mountains, even though this region is 400 km from the eastern and southern coasts (Greenberg and McNab 1998; McNab et al. 2004). The sequencing and interaction of hurricanes and fires in the southern Appalachian Mountains and elsewhere merits more research.

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