CANOPY ACCESSION PATTERNS OF TABLE MOUNTAIN AND PITCH PINES DURING THE 19TH AND 20TH CENTURIES

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ABSTRACT

A dendrochronology study was conducted in three upland yellow pine stands in Georgia to determine whether the individual Table Mountain (*Pinus pungens*) and pitch (*P. rigida*) pines originated in sunny gaps or shaded understories, whether they grew uninterrupted into the canopy or were assisted by one or more releases, and whether these strategies changed through time. From the three stands, 169 increment cores of the two pine species were obtained and analyzed for radial growth patterns using standard dendrochronological procedures. In the 1800s, approximately 80 percent of the pitch and Table Mountain pines originated in gaps with small gaps + release being the most common strategy. After 1900, large gaps without a followup release became the most common strategy. Many of these gaps were associated with known fires, hurricanes, or chestnut blight. Approximately 20 percent of both species originated in shaded understories, but more than half of these ascended to the canopy via one or more canopy releases. These canopy ascension strategies illustrate the importance of gaps in the dual fire – canopy disturbance regime and provide insight for managers seeking to maintain this rare forest type.

INTRODUCTION

Upland Yellow Pine (UYP) stands are a rare forest type of the Appalachian Mountains. These uncommon stands consist of one to four native hard pine species of the sub-genus Diploxolon [pitch (*Pinus rigida*), shortleaf (*P. echinata*), Table Mountian (*P. pungens*), and Virginia (*P. virginiana*)] dominating the canopy while several xeric hardwood and heath shrub species, especially chestnut oak (*Quercus montana*) and mountain laurel (*Kalmia latifolia*), occupy the midstory and understory strata, respectively. UYP stands occur from central Pennsylvania to northern Georgia on thin, dry soils of south- and west-facing ridges and upper slopes between 1,000 and 4,000 feet (Williams 1998, Zobel 1969). Many of the current UYP stands are even-aged and mature because they originated during or immediately after the extensive forest clearing and wildfire era of the early 1900s (Brose and Waldrop 2006a, Lafon and Grissino-Mayer 2007). Presently, UYP stands are declining in abundance and extent (Welch and others 2000). This decline is undesirable to land managers for beta-diversity reasons beacuse UYP stands constitute an unusual conifer community in an otherwise hardwood-dominated forest landscape.

The existence of UYP stands is strongly associated with fire because the principal oak and pine species possess a variety of traits such as cone serotiny, dormant basal buds, precocious fruiting, and thick bark that allow them to survive fire and exploit the post-fire environment (Della-Bianca 1990, Little and Garrett 1990, McQuilkin 1990). Because of this relationship, the vast majority of UYP research has focused on fire. However, canopy gaps caused by storms, ice accretion, and insect/disease outbreaks are also likely important disturbances in the ecology of UYP stands. Unfortunately, not much research has been done along these lines. Whitney and Johnson (1984) and Lafon and Kutac (2003) examined the effects of ice storm and southern bark beetle (*Dendroctonus frontalis*) outbreaks in UYP stands in southwestern Virginia. The former finding increased pine regeneration after ice storms while the latter found the opposite unless fire was an accompanying disturbance.

Dendrochronology can be used to examine the role of canopy gaps in stand dynamics by determining how individual trees originated and ascended to the canopy. Rentch and others (2003) used this method in studying old-growth white oaks in Ohio, Pennsylvania, and West Virginia. They found three distinct canopy ascension patterns: gap origin with and without release and understory origin with release. In this study, we use radial growth analysis of individual Table Mountain and pitch pines found in three UYP stands in northern Georgia to determine whether they originated in gaps or understories and whether they grew uninterrupted into the canopy or experienced one or more release events. Understanding how pitch and Table Mountain pines originated and grew into the canopy will help forest managers maintain or restore this rare forest type.

METHODS

STUDY SITES

This study was conducted in three UYP stands located on the Chattahoochee National Forest in northern Georgia.

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The stands were situated on the tops and upper side slopes of south- and west-facing ridges in the vicinity of Rabun Bald. Elevations varied from 3,200 to 3,600 feet and soils were well drained sandy or silt loams formed in place by weathering of gneiss, sandstone, and schist parent material (Carson and Green 1981). Consequently, they were moderately fertile and strongly acidic. Climate was warm, humid, and continental with average monthly high temperatures ranging from 25°F in January to 85°F in July. Mean annual precipitation ranged from 53 to 73 inches distributed evenly throughout the year.

Composition, structure, and size of the UYP stands also were quite similar among the study sites. In general, they were 10 to 30 acres each and consisted of 10 to 20 woody species distributed in three distinct strata. The main canopy was 50 to 65 feet tall, broken and patchy, and consisted almost exclusively of Table Mountain pine, pitch pine, and chestnut oak. A ubiquitous midstory stratum (10 to 40 feet tall) was present. It generally lacked a pine component, being comprised almost exclusively of chestnut oak and several other hardwood species such as blackgum (*Nyssa sylvatica*), red maple (*Acer rubrum*), scarlet oak (*Q. coccinea*), and sourwood (*Oxydendrum arboretum*). Together, the main and sub canopies contained approximately 400 to 500 stems and 130 to 175 square feet of basal area per acre. The understory stratum (3 to 10 feet tall) varied from absent to impenetrably dense. When present, it was dominated by ericaceous shrubs, especially mountain laurel, and lacked hardwood and pine seedlings as well as herbaceous plants.

SAMPLING PROCEDURES

At each stand, twelve 0.05-acre rectangular plots were randomly selected from those of a previous study (Waldrop and Brose 1999, Welch and others 2000). In each plot, up to five pines were randomly selected and an increment core was extracted from the bole of each tree at a height of 1 foot above the ground. The cores were air-dried for several weeks, mounted, and sanded with increasingly finer sandpaper (120-, 220-, 320-, and 400-grit) to expose the annual rings (Speer 2010). The cores were skeleton plotted to identify signature years for cross-dating to recognize false or missing rings (Speer 2010). 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 System1 (Velmex Inc. Bloomfield, NY). The COFECHA 2.1 quality assurance program (Grissino-Mayer 2001, Speer 2010) in the International Tree-Ring Data Bank Program Library was used to verify the accuracy of the dating. After dating and measuring, each core was examined for major and moderate releases using the JOLTS program (Holmes 1999) in the International Tree-Ring Data Bank Program Library. A major release is defined as a ≥100 percent increase in average growth lasting at least 15 years and a moderate release as a ≥50 percent increase lasting 10 to 15 years (Lorimer and Frelich 1989). These correspond to large canopy-level disturbances that release residual trees from competition until crown closure occurs again.

Finally, each core was categorized by origin (large gap, small gap with and without release, or understory shade with and without release) using criteria established by Rentch et al. (2003). Seedlings originating in large gaps exhibit initial radial growth of 2 to 3 mm/year for 2 to 3 years until their root systems are well established. Then, growth accelerates until the gap closes from the bottom (canopy closure). At this time, the seedling has grown into a dominant sapling and subsequent radial growth slowly diminishes through time as the tree ages. Seedlings originating in small gaps show the same initial growth pattern, but this pattern is truncated because the gap quickly closes from the sides. The seedling becomes an intermediate or weak co-dominant tree with reduced radial growth relative to those growing in full sunlight. Seedlings originating in understory shade have initial radial growth rates that are less than 1 mm/year and do not exhibit any growth acceleration. They become suppressed saplings if they survive. Both small-gap and understory seedlings are susceptible to major and moderate releases. See Figure 1 for examples of these radial growth patterns. Because these criteria were developed for oaks, we verified their appropriateness for pine by comparing the oak patterns to those of pines known to have originated in gaps or understory shade. The initial growth patterns were identical for both species groups and therefore appropriate for pine.

STATISTICAL ANALYSIS

Because the sites had nearly identical age structures (Brose and others 2002), we combined the cores from all three sites to increase sample size. Then, we created a 2x5 contingency table by categorizing the cores by species (pitch or Table Mountain) and origin type (large gap, small gap with and without release, or understory with or without release). We also created a 2x5 contingency table for each species by origin type and period of origin (1800s or 1900s) because of the differences in the disturbance regimes between those two centuries (Brose and Waldrop 2006b). On each contingency table, we used Chi-square analysis (Zar 1999) to test whether the cores were distributed as expected among the different categories. Alpha was 0.05 for all comparisons.

[1]The use of trade, firm, or corporation names in this paper is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture or Forest Service of any product or service to the exclusion of others that may be suitable.

RESULTS

A total of 62 pitch pines and 107 Table Mountain pines yielded sound cores that were suitable for the study (Table 1). Chi-square analysis of the species x origin type contingency table produced a value of 17.65, indicating that the samples were not distributed as expected among the five origin classes and two species. Among the five origin categories, more Table Mountain pine started in large gaps (56) than in the other four types combined. After large gaps, the other four origin classes were ranked as small gaps + release (26), small gaps with no release and understory + release (9 each), and understory with no release (7). Pitch pine distribution was more equitable among the five origin classes with the small gap + release having the most stems (20) followed by large gap (13), small gap with no release (11), understory + release (10), and understory with no release (8).

Overall, the Table Mountain pine samples were equitably distributed between the 1800s and 1900s (Table 2). However, within each period, the samples were not equitably distributed among the five origin types. Before 1900, 42 of the 52 Table Mountain pines originated in gaps and half of these started in small gaps and experienced at least one canopy release. After 1900, 47 of 55 Table Mountain pines originated in gaps, but 85 percent of these started in large gaps. These tendencies toward small gaps before 1900 and large gaps after 1900 resulted in a significant X2 value of 22.623.

The distribution of the pitch pine samples among the origin periods and origin types did not produce a significant X2 value (Table 3). Like Table Mountain pine, the 62 pitch pine samples were about evenly split between the 1800s and 1900s. Pitch pine also showed the same within-period trend of originating in small gaps before 1900 and in large gaps after 1900. However, the collective differences between observed and expected values for the origin period and origin type combinations were not large enough to produce a statistically significant X2 value at the alpha level of 0.05.

DISCUSSION

Perpetuation of any forest community requires that the keystone tree species successfully recruit to the canopy and that they successfully produce seedlings that are able to do likewise in due time. The disturbance regime is a critical part of this perpetuation process because there is an affinity between the silvics of the principal species and the characteristics of the disturbance regime. Drastic changes to the disturbance regime can promote the keystone species to become more dominant even to the point of forming natural monocultures. Or, the keystone species may fail to reproduce and recruit and the forest community changes to another forest type or vegetative association. Both scenarios are evident in the UYP stands used in this study. Understanding the relationships between the regeneration/recruitment of pitch and Table Mountain pine and gap formation via disturbances will help forest managers sustain this rare forest type throughout the Appalachian Mountains.

Before 1900, both pine species clearly preferred sunny gaps to shady understories for regeneration; about 78 percent of all stems originated in gaps. Many of these gaps were likely small in size because 70 percent of the gap-origin pines experienced extended periods of suppression beginning a few years after germination, suggesting the gap closed over them before they reached the canopy. That suppression ended for the majority of these pines; their growth chronologies show one or more moderate or major canopy releases that allowed them to grow into the canopy and become dominant or strong co-dominant trees. A few pines never experienced a canopy release and became weak co-dominant or strong intermediate stems. These releases were either direct canopy disturbances such as a storm event or caused indirectly by a surface fire that resulted in delayed tree mortality. For example, the middle graph on Figure 1 shows a Table Mountain pine that originated in the late 1800s. It was quickly suppressed, but was released in the late 1920s. This release corresponds to the arrival of the chestnut blight in the area (Keever 1953), and these stands had a sizeable component of American chestnut.

Large gaps also played an important role in these UYP stands before 1900 for Table Mountain pine, but not pitch pine. Of the 42 gap-origin Table Mountain pines, 16 germinated in gaps large enough for them to grow unaided into canopy dominants. Generally, pines using this canopy accession strategy originated after a fire. For example, the upper graph of Figure 1 is of a dominant Table Mountain pine that originated about 1875. Fire scars found in the vicinity of this tree indicate a fire occurred there in 1872. This difference in large gap utilization between the two species is understandable given their silvics. Table Mountain pine has serotinous cones so the vast majority of its seeds are released after a fire, while pitch pine cones open annually resulting in continuous rather than episodic seed fall (Williams and Johnson 1992).

A few pines of both species originated in understory shade for they showed suppressed growth from the beginning. About half of these eventually experienced one or more moderate or major releases that allowed them to persist. The bottom graph in Figure 1 shows a pitch pine with this canopy accession pattern. It originated about 1840 and grew slowly for 30 years, becoming a small sapling. The sapling escaped or survived the 1872 fire, but the resultant gap released the sapling, resulting in accelerated growth. By 1900, the gap had closed, but a hurricane passed through the area in 1902 and this storm apparently formed another gap. The pine then grew into a dominant canopy position.

The other half of the understory-origin pines showed no evidence of any moderate or major releases in their growth chronologies. All of these were canopy intermediate trees. Many were as old as nearby pines, but substantially smaller.

The limited occurrence of these understory-origin pitch and Table Mountain pines suggests an important concept relative to stand conditions in the 1800s. Modern UYP stands are not regenerating and have not done so for decades due to the proliferation of mountain laurel in their understories (Brose and Waldrop 2010). The ability of pitch and Table Mountain pines to germinate and persist as suppressed seedlings in the 1800s may indicate that the forest floor was less dense and the light levels were sufficient for their survival. The periodic occurrence of surface fires in the 1800s and their absence for much of the 1900s is the most likely explanation for the presence of understory-origin pines in the past and their absence now.

In the 1900s, regeneration and recruitment in large gaps became the modus operandi for Table Mountain pine and, to a lesser degree, pitch pine. In the 20th century, nearly 73 percent of all Table Mountain pines and 41 percent of all pitch pines originated in large gaps and grew uninhibited into the canopy. The remaining pines of both species germinated in a mix of small gaps and understory environments with a majority of these attaining the canopy via one or more canopy releases. This shift in regeneration/recruitment strategy from a mix of gap types in the 1800s to primarily large gaps in the 1900s is a result of the increase in severe disturbances during the first half of the 20th century (Brose and Waldrop 2006b). Besides the chestnut blight, these stands experienced several fires and hurricanes between 1900 and 1950. Many of these disturbances were severe, creating large gaps that were ideal habitats for both pine species to regenerate and ascend into the canopy. Conversely, disturbances and gaps became scarce in the second half of the 20th century, and regeneration/recruitment of the pines diminished and then ceased altogether.

CONCLUSIONS

In the 1800s, periodic surface fires maintained open understories in UYP stands that allowed pitch and Table Mountain pines to regenerate, persist as seedlings and saplings, and eventually ascend into the main canopy through small gaps created by canopy disturbances. In the early 1900s, fires and canopy disturbances such as chestnut blight became more severe, creating large gaps. In these large gaps, Table Mountain pine was especially successful at regenerating and recruiting to the canopy without needing further releases. Since the mid-to-late 1900s, pine regeneration and canopy recruitment has virtually ceased, corresponding to the advent of fire control as well as a decline in tropical storms passing through the region. Forest managers desiring to regenerate or maintain UYP stands should strive to recreate the dual disturbance regime of the 1800s and early 1900s via prescribed burning and other management techniques.

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Table 1—Distribution of the 169 sampled trees by species and origin type. Numbers in parentheses are the expected values for each species and origin type combination

Species	Pitch pine	Table Mountain pine	Total
Large Gap	13 (25)	56 (44)	69
Small Gap	11 (7)	9 (13)	20
Small Gap + release	20 (18)	26 (28)	46
Understory	8 (5)	7 (10)	15
Understory + release	10 (7)	9 (12)	19
Total	62	107	169

Comparison of pine species by origin type (test statistic: X2 = 17.65, critical value = 9.488, α = 0.05, df = 4)

Table 2—Distribution of the 107 sampled Table Mountain pines by origin period and origin type. Numbers in parentheses are the expected values for each origin type and origin period combination

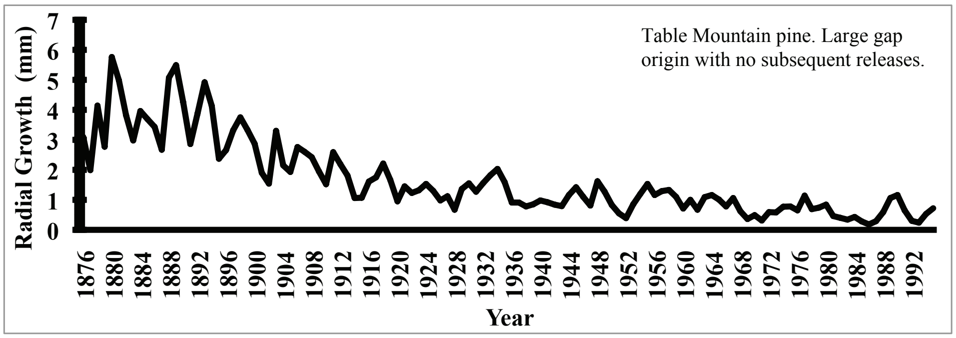
	Origin Period		
Origin Type	before 1900	after 1900	Total
Large Gap	16 (27)	40 (29)	56
Small Gap	5 (3)	2 (4)	7
Small Gap + release	21 (13)	5 (13)	26
Understory	6 (4)	3 (5)	9
Understory + release	4 (4)	5 (5)	9
Total	52	55	107

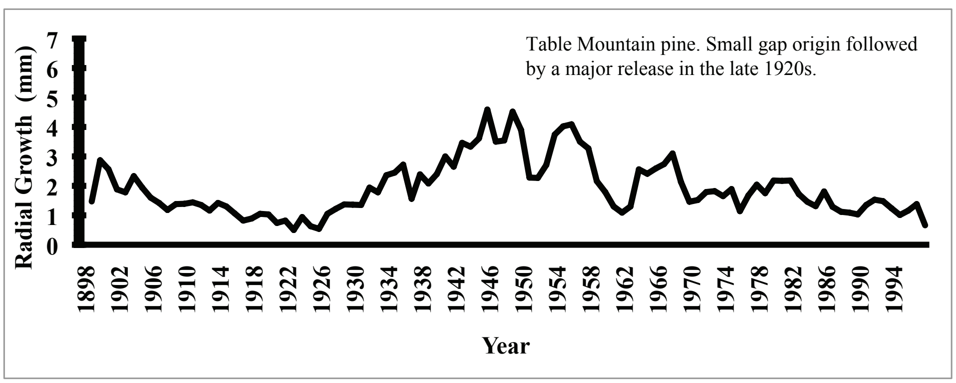
Comparison of origin type by origin period (test statistic: X2 = 22.623, critical value = 9.488, α = 0.05, df = 4)

Table 3—Distribution of the 62 sampled pitch pines by origin period and origin type. Numbers in parentheses are the expected values for each origin type and origin period combination

	Origin Period		
Origin Type	before 1900	after 1900	Total
Large Gap	4 (7)	9 (6)	13
Small Gap	6 (6)	5 (5)	11
Small Gap + release	14 (11)	6 (9)	20
Understory	4 (5)	4 (3)	8
Understory + release	7 (6)	3 (4)	10
Total	35	27	62

Comparison of origin type by origin period (test statistic: X2 = 5.55, critical value = 9.488, α = 0.05, df = 4)





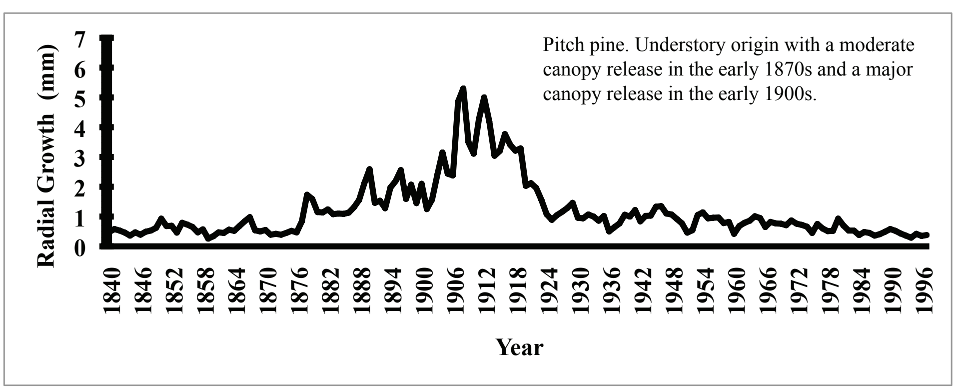


Figure 1—Examples of canopy accession patterns (large gap, small gap + release, and understory + release) of dominant pitch and Table Mountain pines growing in northern Georgia. Note that the horizontal axes are different scales for the three graphs.