Tree Encroachment in Forest Openings: a Case Study From Buffalo Mountain, Virginia

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ABSTRACT

In eastern forests, openings dominated by grasses, forbs, or shrubs are areas of conservation concern because they typically contain endemic, threatened, and rare plants. Understanding the ecology and mechanisms of tree encroachment would be valuable for conservation managers and would add to a substantial body of literature on forest openings. In this study, we worked in grass-dominated forest openings on Buffalo Mountain, Virginia using a method that combined dendrochronology and belt transects to assess tree encroachment. We discovered both stable ecotones and areas where trees were invading the formerly grass-dominated openings. Both gradual and episodic patterns of tree encroachment were identified; however, successful tree establishment always initiated from the edge of the forest-grass ecotone and progressed towards the center of the opening rather than occurring across the entire forest opening. This spatial pattern of recruitment implies that successional facilitation is necessary for tree encroachment in forested openings at Buffalo Mountain.

INTRODUCTION

Forests of eastern North America have a number of naturally occurring, treeless openings that are dominated by vegetation consisting of grass, forbs, or shrubs. The eight forest openings commonly discussed in the literature include: balds, barrens, flat rocks, frost pockets, glades, rock outcrops, xeric limestone prairies, and scrub gaps (Table 1). The semantics associated with these terms are full of dissention because many of the definitions differ only slightly and there exist many variations of each term (Baskin et al. 1997). For example, the term "glade" encompasses cedar glades (Baskin and Baskin 2003), diabase glades (LeGrand 1988), dolomitic glades (Erickson et al. 1942), limestone glades (Baskin et al. 1995), and sandstone glades (Jeffries 1985) depending on their specific environmental or vegetative characteristics. Regardless of semantic disagreements, research has identified that the invasion of trees into these openings has increased during the past half-century (the major exception being some of the openings described as edaphic climaxes [i.e., Baskin and Baskin 1988, 2003; Baskin et al. 1995]). The closure of these openings has caused concern among conservationists because openings frequently serve as habitat for endemic, rare, or threatened plants and insects (Platt 1951, Wyatt 1977, Bartgis 1993, Ludwig 1999). As part of the conservation of forest openings, researchers have attempted to identify the origins of these openings and discuss management options for maintaining them. The historical development of forest openings has been attributed to grazing by wild herbivores (Billings and Mark 1957), warmer temperatures and increased aridity during the hypisthermal period (Baskin, Chester, and Baskin 1997), a post-hypsithermal cooling period (Mark 1958), clearing by European settlers followed by cattle grazing (Lindsay 1976), Native American burning (Baskin et al. 1994), natural fire regimes coupled with xeric soils (Batek et al. 1999), and/or extreme radiational cooling (Motzkin et al. 2002). The proposed

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Table 1. Nomenclature of various forest openings in eastern forests

Name of Opening	Description	Citations
Balds	Treeless, grassy or heath covered areas at high elevations in the southern Appalachians	Billings and Mark 1957 Whittaker 1963 Lindsay and Bratton 1980 Knoepp et al. 1998
Barrens	Canopy openings in oak-pine forests dominated by mid and tall grasses or sparse scrubby growth of trees, shrubs, and grasses	Platt 1951 DeSelm et al. 1969 Bartgis 1993 Ludwig 1999
Flat rocks	Treeless openings in pine and oak forests with limited vegetation growing on bare rock and in small depressions	McVaugh 1943
Frost pockets	Canopy openings in pitch pine forests dominated by shrubby vegetation	Motzkin et al. 2002
Glades	Open areas with rocky substrate or shallow soil that support grassy and herbaceous edaphic climax plant communities	Erickson et al. 1942 Quarterman 1950 Kucera and Martin 1957 Baskin and Baskin 2003
Rock outcrops	Edaphically-controlled herbaceous plant communities on exposed bedrock or shallow soil	Phillips 1982 Wiser et al. 1996 Baskin and Baskin 1988
Xeric limestone prairies	Human- or disturbance-maintained openings dominated by grasses and forbs	Baskin et al. 1994
Scrub gaps	Openings in the scrubby, shrub-dominated canopy of larger than 1 m^2	Petrů and Menges 2003

conservation management plans generally involve some type of anthropogenic disturbance such as controlled burns, herbiciding unwanted saplings, bushhogging, or implementing grazing programs to prevent tree invasion (Baskin et al. 1994). The conservation maintenance of forest openings can be expensive in terms of workforce, equipment, and liability (especially if controlled burns are implemented). Therefore, an understanding of the ecology and mechanisms of tree encroachment into these forested openings would benefit conservation managers and potentially allow them to differentiate quickly, easily, and inexpensively between forest openings that are edaphic climaxes and those that are at risk of converting to forest.

Three main patterns of tree and shrub encroachment into forest openings have been observed. Several studies have found that small microenvironments within the openings favor seedling and shrub establishment which creates "islands" of woody plants within the openings that may (or may not, depending on the disturbance regime) eventually fill the entire opening (Oosting and Anderson 1939, Erickson et al. 1942, Keever et al. 1951). Other studies have identified a spatially uniform distribution of woody plants throughout the forest openings that will develop to mature trees only if environmental conditions are favorable. This pattern results in small patches of even-aged trees (Lindsay and Bratton 1980, McClenahen and Houston 1998). The third pattern involves a gradual invasion of trees from the forest-grass ecotone towards the center of the opening. This pattern often includes a change in species composition, with some species able to establish along the ecotone and encroach into the opening while others were limited to the forest interior (Matlack 1994, Arévalo 2002).

One method to assess the patterns of tree establishment within forest openings would be belt transects. Belt transects or strip transects have traditionally been used to study transitions between community types, such as the ecotone between a forested community and the grassy vegetation in a forest opening. The width of the belt transect depends on the density (#/ha) and size of the vegetation, but typically varies from 2 m to 10 m in width (Mueller-Dombois and Ellenberg 1974). Arévalo (2002) in his study of the boundary between tall grass prairie and woodland established a belt transect 100 m in length (50 m in the forest community and 50 m in the prairie community) and 10 m in width to sample the tree density and canopy cover across the prairie-woodland ecotone. Knoepp et al. (1998) sampled soil phytolith content from 1 m-wide quadrats along a belt transect to assess historical changes in the boundary between forest and grassy balds in the southern Appalachians (grasses and trees produce morphologically different phytoliths or silicaceous formations). Most studies that employ belt transect sampling quantify structural differences across an ecotone.

Another method to assess tree recruitment patterns is dendrochronology. By using tree rings to age all trees within a stand, dendrochronologists are able to identify periods of peak tree establishment and periods of limited or no establishment. However, such methods can be labor and time intensive and involve coring and dating hundreds to thousands of trees (Ågren and Zackrisson 1990). The size of plots used in dendrochronology studies varies according to forest type, but most studies use plots at least 0.5 ha in area and core all trees within each plot (Lorimer 1985). Huff (1995) used dendrochronology to identify the rates of tree invasion following fire in the Olympic Mountains in Washington. He determined that species entered the stands in phases with early successional species entering within 50 years post-fire, mid-successional species entering 150 years post-fire, and late succession species having peak recruitment periods 400 years post-fire. McClenahen and Houston (1998) in southeastern Ohio used dendrochronology in a relict prairie to determine when trees invaded historical prairie vegetation.

In this study, our primary research objective was to evaluate the risk and patterns of tree encroachment into forest openings at Buffalo Mountain Natural Area Preserve. Many areas with forest openings are owned by conservation, federal, or state organizations and these organizations frequently attempt to minimize the impact of humans (including researchers) on their lands. Therefore, a secondary objective was to complete our research with a minimal impact to the ecosystem. To meet this objective we worked closely with the Natural Heritage Program within the Virginia Department of Conservation and Recreation (the owners of the Buffalo Mountain Natural Area Preserve) because their concerns and policies would be representative of other sites where our research methods could be applied.

Buffalo Mountain Natural Area Preserve has a number of glade-like openings on the south and southeastern slopes of Buffalo Mountain. The Natural Heritage Program would like to preserve these openings and their associated rare plants; however, they are uncertain as to the current risk of tree encroachment into these glades. After discussion with the Southwest Region Steward, David Richert, we arrived at a sampling size and method that minimized the environmental impact of our research methods but had the potential to provide information about risk and patterns of tree encroachment.

STUDY SITE

The Buffalo Mountain Natural Area Preserve is a 400 ha preserve on the top of Buffalo Mountain (36°45′N, 80°28′W) in Floyd County, Virginia. The land is managed by the Virginia Natural Heritage Program and includes an oak-hickory forest with open, grass-dominated glade communities. Big bluestem (*Andropogon gerardii* Vitman) and little bluestem (*Schizachyrium scoparium* (Michx.) Nash) and forbs such as mountain sandwort (*Arenaria groenlandica* (Retz. Sprengel)), plains frostweed (*Helianthemum bicknellii* Fern.), Appalachian rattlesnake root (*Prenanthes roanensis* (Chick.) Chick.), purple blazing-star (*Liatris spicata* (L.) Willd.) and stiff goldenrod (*Solidago rigidum* L.) grow within the glade communities. Scattered eastern red cedar (*Juniperus virginiana* L.) are the only trees within the glade communities. The southern foot of Buffalo Mountain supports woodland seeps and provides habitat for Virginia's largest population of large-leaved grass-of-parnassus (*Parnassia grandifolia* DC.).

Buffalo Mountain is in the Blue Ridge Physiographic Province (Braun 1950). The mountain is 1,190 m above mean sea level and is the highest point in Floyd County, Virginia. Buffalo Mountain soils are classified as coarse-loamy, mixed, active, mesic Typic Dystrudepts, and contain rock outcroppings. The soils are moderately deep to deep, somewhat excessively drained and acidic with parent material of hornblende, slates, and schists (Boyd 1881; Tom Greene, Natural Resource Conservation Service, pers. comm.).

The total annual precipitation in Floyd County is 104.6 cm (based on 52 years of data), which is evenly distributed throughout the year (http://cirrus.dnr.state.sc.us/cgi-bin/sercc/cliMAIN.pl?va3071). The total annual snowfall is 47.5 cm. The average winter temperature is 1.4°C. The average summer temperature is 20.2°C. The prevailing wind is from the west-northwest with an average wind speed of 13 km/hr.

Floyd County was established in 1831 from area that had originally been designated as part of Montgomery County. The county's economy is and was historically agrarian with grain, timber, tobacco, livestock, and poultry production as the main sources of income (Boyd 1881, Davids 1970, Wood 1981). The local people have used Buffalo Mountain as a recreation area for over 100 years because the exposed rock outcrops at the top provide a beautiful view of the surrounding landscape (Davids 1970, Wood 1981). Today a hiking trail is still maintained to the top of the mountain by the Virginia Natural Heritage Program.

METHODS

Field Work

Encroachment of woody vegetation into the grassy openings was assessed using belt transects and dendrochronology. Six belt transects were established across the boundary between grassy openings and adjacent forest. The belt transects varied in length from 52 m to 17 m, depending upon the width of the ecotone. All transects originated from the edge of a grassy opening and concluded once mature forest was reached. The presence of coarse woody debris in the understory; a thick, leafy litter layer (rather than a grassy understory); and large diameter trees identified the mature forest. The location of each tree within the belt transect was measured with a tape and compass and maps of the tree locations within transects were created. Within transects, all trees were cored with an increment borer at 0.5 m in height or destructively sampled with a handsaw and a disk was removed from 0.5 m. The Natural Heritage Program wanted to limit the amount of destructive sampling. Therefore, within the transects all trees greater than 7 cm in diameter were cored in a 3 m belt and trees between 7 and 2 cm in diameter were cut from the first meter of the same 3 m belt. The direction of each transect was randomly chosen using the second-hand on a timepiece. At 2 m intervals along each transect, a soil probe was used to determine depth to bedrock. Any observations about disturbance or other competing vegetation within transects was noted.

Laboratory Work

All tree cores and disks were air dried in the laboratory. The tree cores were glued to wooden core mounts. The cores and disks were sanded with progressively finer grit sandpaper until the cellular structure was visible under a microscope. The cores and disks were sorted by species and each species was cross-dated using narrow years as indicator years (Yamaguchi 1991). The cross-dating allowed the age of the cores and disks to be determined accurately and identified any missing or false rings. For cores where the pith was missed, a graphical technique for pith estimation was used to determine the year of origin (Villalba and Veblen 1997).

Data Analysis

Relative density (# trees) and relative frequency (# of transects) were calculated from the trees sampled in the six belt transects. The relative density and relative frequency were averaged to calculate an importance value (IV) for all of the species encountered in the belt transects. Spearman correlation coefficients were calculated to identify significant correlations between tree age and distance from grassy edge. A significant positive correlation between tree age and distance from grassy edge would indicate tree encroachment into the grassy opening, because younger trees would be advancing towards the edge and older trees would only be found in the forest interior.

‚able 2. **Relative density (# of trees), relative frequency (# of plots), and importance values (I.V.) of tree species sampled in the six belt transects on Buffalo Mountain, Virginia during spring 2003**

Species	Relative Density (%)	Relative Frequency (%)	I.V. (%)
Quercus alba	21	17	19
Ostrya virginiana	21	14	18
Carya ovata	17	8	13
Quercus velutina	4	14	9
Prunus serotina	4	11	8
Betula lenta	7	6	7
Crataegus sp.	5	6	6
Fraxinus americana	4	8	6
Rhododendron prinophyllum	6	3	5
Amelanchier arborea	2	3	3
Carya tomentosa	3	3	3
Carya glabra	3	3	3
Hamamelis virginiana	2	3	3
Acer pensylvanicum	1	3	2

Aerial Photographs

To verify the results found with the belt transects, we examined aerial photographs of Buffalo Mountain from 1937, 1953, and 1974 to identify changes in the area of specific forest openings over a time series chronology. The length and width of the openings were measured in each aerial photograph.

RESULTS

Fourteen tree species were identified in the belt transects on Buffalo Mountain (Table 2). The species with the highest importance values were white oak (*Quercus alba* L.) with 19%, eastern hophornbeam (*Ostrya virginiana* Lam.) with 18%, and shagbark hickory (*Carya ovata* (Mill.) K. Koch) with 13%. Only white oak was present in all belt transects and black oak and eastern hophornbeam occurred in 83% of the belt transects. A number of species had fewer than 5 individuals present in all of the plots and they were placed in the category of "minor hardwood species" for the remainder of the analysis. These species included: black cherry (*Prunus serotina* Ehrh.), azalea (*Rhododendron prinophyllum* (Small) Millais.), downy serviceberry (*Amelanchier arborea* (Michx.f.) Fern.), witch-hazel (*Hamamelis virginiana* L.), and striped maple (*Acer pensylvanicum* L.).

The six belt transects established for this study revealed different patterns of tree recruitment. Transect A (Figure 1) began at a cliff face where a few sweet birch (*Betula lenta* L.) had established during the past 35 years. The transect crossed a grassy area about 10 m in length and entered a shagbark hickory dominated hardwood stand. The trees on the very edge of this stand included a 71-year-old pignut hickory (*Carya glabra* (Mill.) Sweet). At Transect B (Figure 1) a significant correlation ($r = 0.539$; $P = 0.029$) existed between tree age and distance from the edge of the grassy opening. The tree ages demonstrated a gradual increase in tree age with progression towards the forest interior. The oldest tree in this transect was a 165-year-old white oak growing in the mature forest. Transect C (Figure 1) also had a significant correlation ($r = 0.734$; $P = 0.003$) between tree age and distance from the grassy opening. The pattern of tree encroachment was very different from the gradual encroachment identified in Transect B. In Transect C, the forest edge advanced 15 m in a period of recruitment that began 36 years ago. A historical forest edge was identified by the 143- and 152-year-old white oaks growing 20 m from the forest edge. All trees between these white oaks and the grassy opening were under 36 years of age. Transect D (Figure 1) had a gradual tree encroachment pattern similar to Transect

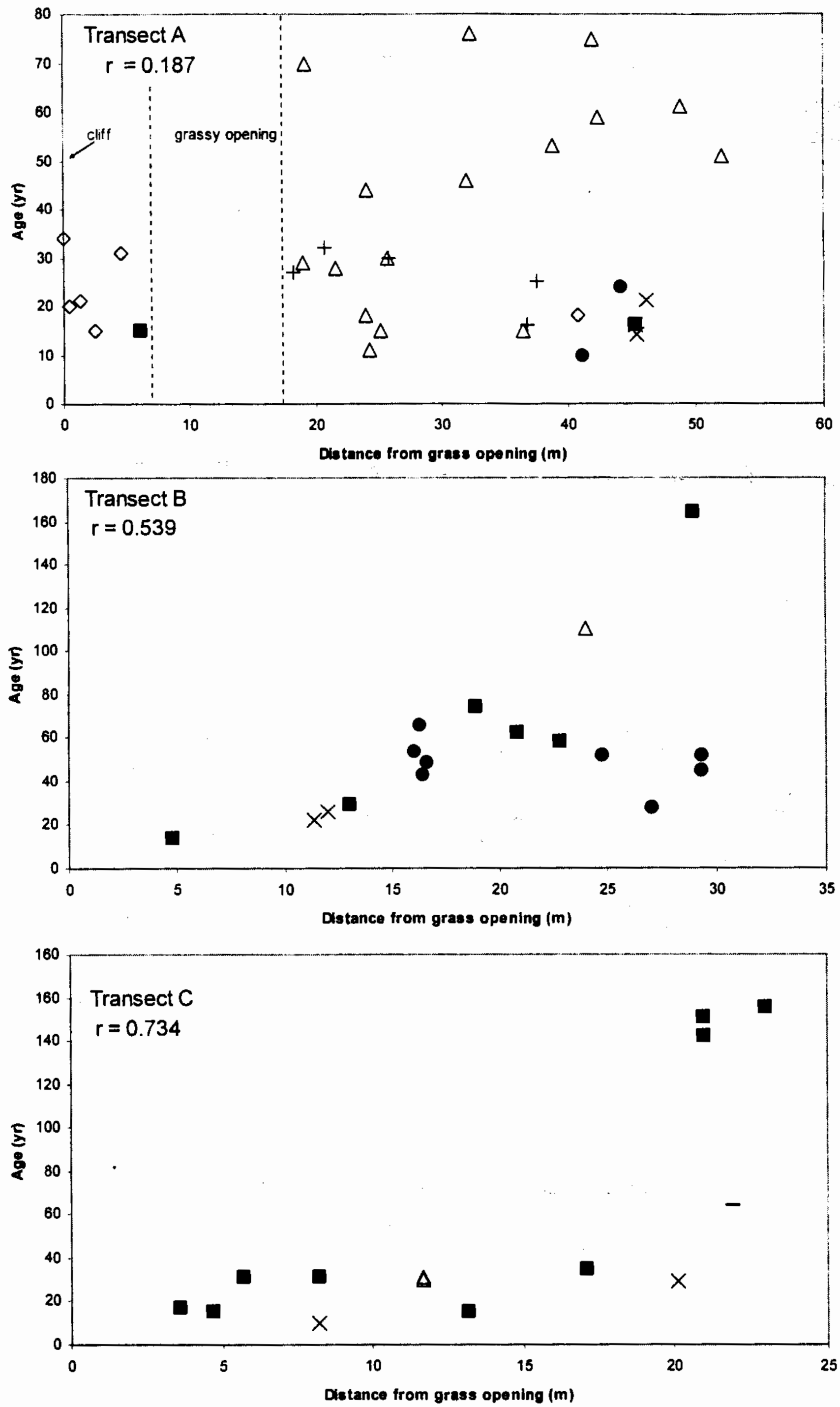

Figure 1. Ages and distances from belt transects A, B, and C from Buffalo Mountain, Virginia. Solid boxes = *Quercus* sp.; △ = *Carya* sp.; + = *Crataegus* sp.; ◇ = *Betula lenta*; • = *Ostrya virginiana*; – = *Fraxinus americana*; and × = minor hardwood species which had fewer than five individuals.

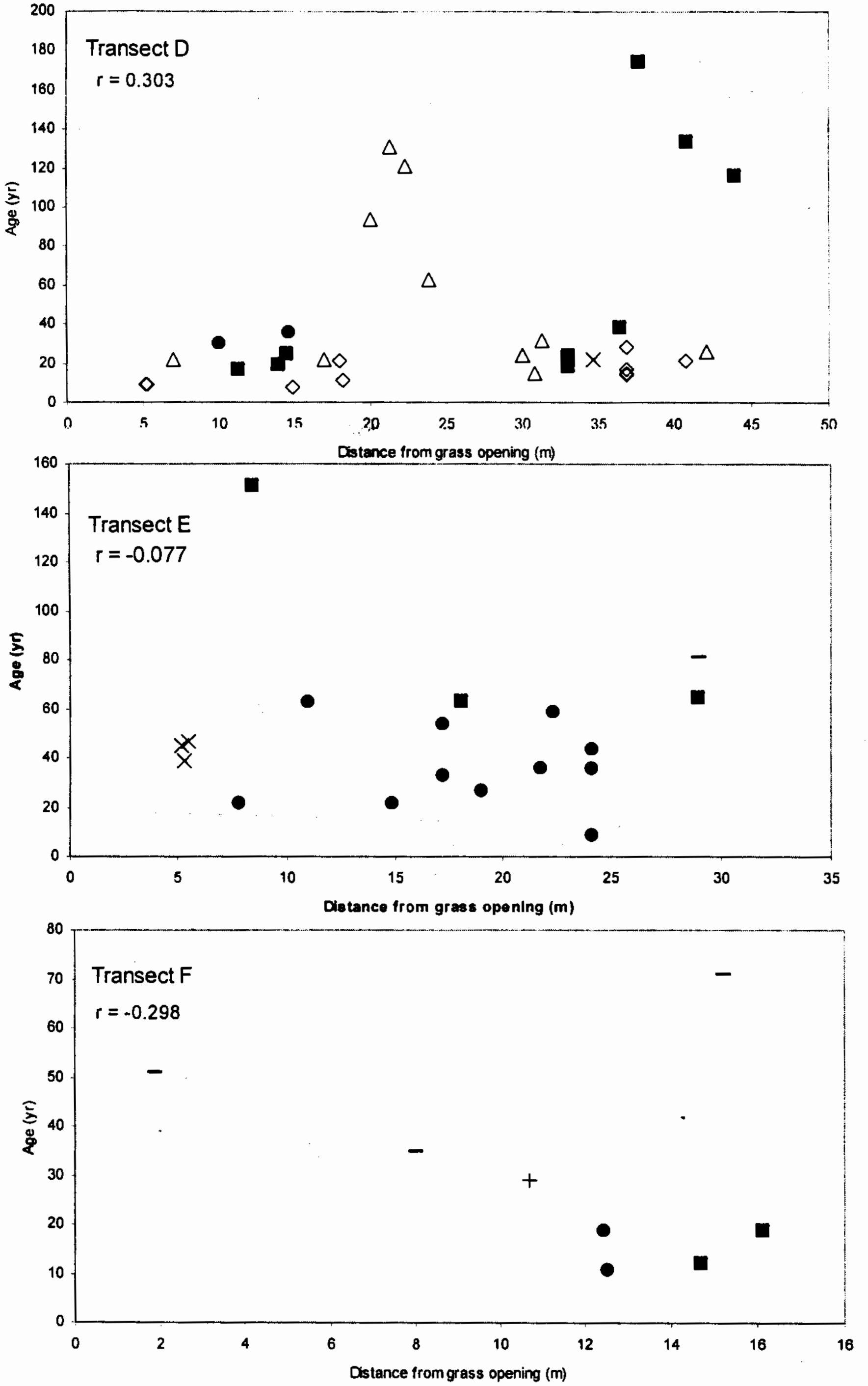

Figure 1. Continued. Ages and distances from belt transects D, E, and F at Buffalo Mountain, Virginia. Solid boxes = *Quercus* sp.; Δ = *Carya* sp.; + = *Crataegus* sp.; ◇ = *Betula lenta*; • = *Ostrya virginiana*; – = *Fraxinus americana*; and × = minor hardwood species that had fewer than five individuals.

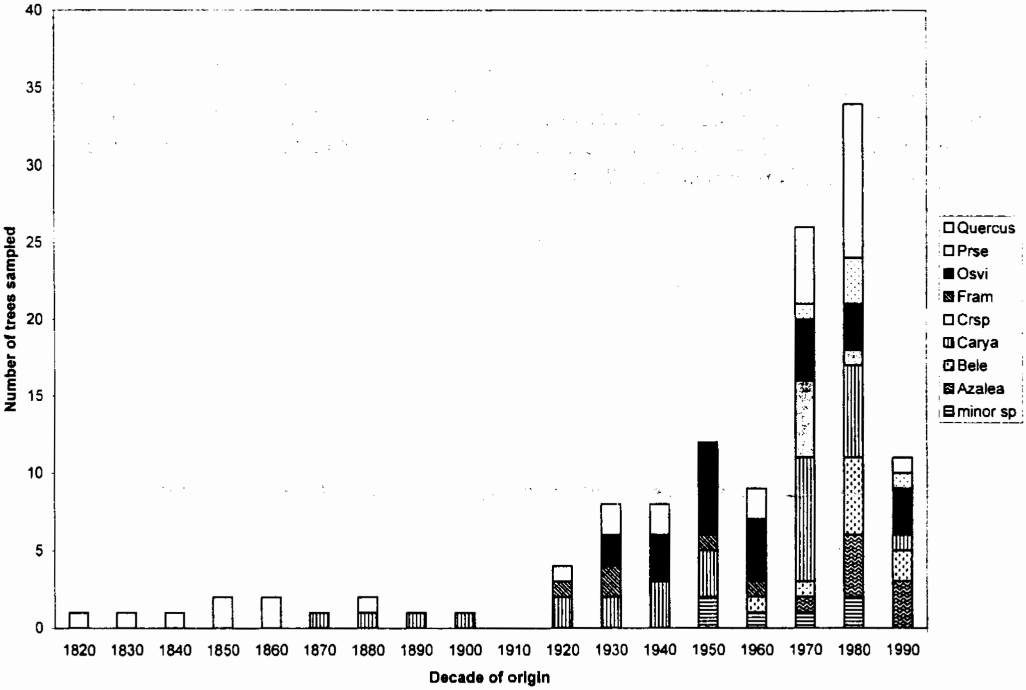

Figure 2. Age distribution from all trees and saplings sampled in six belt transects on Buffalo Mountain, Virginia in the spring of 2003. Prse = *Prunus serotina*, Osvi = *Ostrya virginiana*, Fram = *Fraxinus americana*, Crsp = *Crataegus* sp., and Bele = *Betula lenta*.

B. A significant correlation did not ($r = 0.303$; $P = 0.087$) exist between tree age and distance from grassy opening. The older white oaks (176, 135, and 117-years old) growing in the mature forest had azalea, an understory tree, in the same vicinity indicating a two-tiered canopy. At Transect E (Figure 1) the correlation between tree age and distance from grassy opening was not significant ($r = -0.077$; $P = 0.761$). The forested portion of the transect was dominated by eastern hophornbeam and most of the trees were less than 66 years of age. The one exception was a 152-year-old white oak located 8.5 m from the edge of the grassy opening. Transect F (Figure 1) was the youngest forest sampled, and it had no significant relationship between tree age and distance from the grassy opening ($r = -0.298$; $P = 0.474$). The second-oldest tree in Transect F, a 52-year-old white ash (*Fraxinus americana* L.), was located within 1.9 m of the grassy edge.

When the trees from all six transects were evaluated together to identify potential periods of peak recruitment (Figure 2) the age distribution conformed to the typical inverse-J curve of unevenaged stands. The one exception was the 1960s when the recruitment rate was lower than the adjacent decades. The steep reduction in trees during the 1990s was an artifact of our sampling regime because we did not sample saplings less than 2 cm in diameter. Many of the saplings that established in the late 1990s would have been less than 2 cm in diameter.

Aerial photographs of Buffalo Mountain were examined to compare the size of forest openings over a time-series chronology. Due to the poor quality of the earlier photographs, only two of the larger openings on Buffalo Mountain could be clearly compared across three time periods—1937, 1953, and 1974. The one opening decreased in area by 2% from 1937 to 1953 and continued to decrease by 15% from 1937 to 1974. The other opening decreased in area by 6% from 1937 to 1953 and did not decrease in size between 1953 and 1974.

Only one significant relationship existed between soil depth to bedrock and distance from grassy opening. Transect E ($r = -0.51$, $P = 0.03$) had a significant negative correlation between soil depth and distance from grassy opening which implied that the soils became shallower towards the interior of the forest as compared to the edge near the grassy opening. All other transects had no significant ($P < 0.05$) correlation between soil depth and distance from grassy opening (Transect A: $r = 0.37$, $P = 0.11$; Transect B: $r = 0.07$, $P = 0.82$; Transect C: $r = -0.33$, $P = 0.32$; Transect D: $r = 0.10$, $P = 0.71$; Transect F: $r = 0.06$, $P = 0.86$). The depth to bedrock from all sample points ranged from 0 cm to 23 cm.

DISCUSSION

Condition of Forested Openings at Buffalo Mountain

The forest openings on Buffalo Mountain demonstrated evidence of invasion by trees. The significant correlations between distance from grassy edge and tree age (Figure 1—Transects B, C, and D) and the decrease in forest opening areas from the aerial photograph series clearly demonstrated an ecotone that has shifted in the past century as trees gradually replaced grasses as the dominant vegetation along the edges of the openings. The transects without significant correlations between distance from grassy edge and tree age (Figure 1—Transects A and E) also demonstrated a recent encroachment of trees into formerly non-forested areas because most of the trees sampled were less than 70 years old. Seventy years is considerably younger than the surrounding forested areas on Buffalo Mountain where we have cored white oaks that were over 300 years old (unpubl. data). The openings on Buffalo Mountain, like many of the grassy openings in eastern deciduous forests (Lindsay and Bratton 1980), are at risk of closure unless active management is initiated by the Virginia Natural Heritage Program.

The pattern of encroachment in openings at Buffalo Mountain involved trees invading from the edges and moving towards the center of openings. This matches tree encroachment identified in forest openings in Oklahoma, Pennsylvania, and Delaware (Matlack 1994, Arévalo 2002) and implies that the forest edge facilitates tree establishment while conditions in the center prevent tree establishment. Conditions in the forest opening may be similar to the state of arrested succession described by Abrams et al. (1985) who found that tree seedlings were unable to regenerate in *Carex* meadows because of the severe competition from the established sedges. Our results and Abrams et al. (1985) contrast with Berkowitz et al. (1995) who found that herbaceous plants facilitate the invasion of tree species, particularly in harsh environments similar to those found at Buffalo Mountain.

The establishment of trees appears to occur both gradually and incrementally (Figure 1). Transect C demonstrated an incremental pattern of tree encroachment compared to the more gradual encroachment patterns identified in Transects B and D. This difference may be attributed to the high density of rhododendron (*Rhododendron maximum* L.) that bordered the edge of the grassy opening (this was not the only transect where rhododendron was present, but it was the densest thicket we sampled). Rhododendron is known to reduce seedlings survival (Baker and van Lear 1998, Nilsen et al. 2001) and it was likely that the rhododendron thicket was responsible for the step-like recruitment that occurred. Unless a disturbance (such as fire) disrupts the competition caused by the rhododendron, this forest edge may be temporarily stalled. Unfortunately, we did not sample shrubs and therefore are unable to know whether the rhododendron is actively encroaching into the forested areas in lieu of tree seedlings.

In addition to competition from other vegetation, the patterns of tree establishment may also be controlled by climate. The age distribution (Figure 2) showed a decrease in the successful tree establishment in the 1960s. During this decade, Virginia experienced several severe droughts that caused significant reductions in tree ring growth (Orwig and Abrams 1997). At other locations, droughts have been shown to both decrease tree growth and increase tree mortality (Jenkins and Pallardy 1995) and it is likely that severe droughts were responsible for the reduced rate of tree establishment in the 1960s within openings at Buffalo Mountain.

Assessment of Method as a Minimum Impact Ecological Sampling Technique

Combining dendrochronology and belt transects proved to be a quick method for assessing tree encroachment. Dendrochronology studies that reconstruct the demography of entire stands are extremely labor intensive in the field and the laboratory. Standard methods include coring all trees ≥10.0 cm dbh (McClenahen and Houston 1998) or >5 cm in dbh (Bergeron and Gagnon 1987) in the entire stand. This methodology involves huge sample sizes, i.e., Ågren and Zackrisson (1990) worked with 3,393 tree cores. However, the small-scale sampling from our belt transects provided sufficient information to identify tree encroachment into grassy areas without being excessively labor intensive. However, the belt transects we used in this study were limited in their application and for regional disturbance signals, we still recommend the large sample sizes of traditional demographic studies (Lorimer 1985, Fritts and Swetnam 1989).

Though the influence of recreation, ecotourism, and military activities on natural areas has been examined, few studies have addressed the issue of environmental impacts of scientific research on natural area preserves (Kuss and Hall 1991, Westing 1992, Sekercioglu 2002, Grossberg et al. 2003). As a consequence, research methodologies on natural area preserves are often negotiated (without sufficient information) between researchers and preserve managers rather than determined by minimum sampling calculations. This is not the most scientific method for plot size selection, but it is the reality for researchers working in areas where the management objective is to minimize the impacts of humans. Sometimes these negotiated plot sizes provide useful information. For example, our belt transect width was selected because the Virginia Natural Heritage Program was concerned with the visual impacts of the destructive sampling of trees and wanted to minimize the number of trees cut. Thus, only trees less than 7 cm within a 1 m strip of the 3 m belt transect were cut. This negotiated plot size appears to have identified successfully whether trees were invading the grassy balds on Buffalo Mountain. However, Transect F is an example of inadequate sample size to meet the research objective. Eight trees were sampled in Transect F before the mature forest structure was reached (Figure 1). No conclusions about tree encroachment can be drawn safely from such a small sample size. This implies that in most southern Appalachian deciduous stands (represented by Transects A–E), a 3 m wide belt transect serves as a minimum sampling area; however, for less dense stands (such as Transect F) a wider belt transect will be necessary.

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