SCOTT H. MARKWITH
Regenerative Response of a Southern Appalachian Forest to Surface Wildfire and
        Canopy Gap Disturbances
(Under the Direction of DR. KATHLEEN C. PARKER)

Tree regenerative response after surface wildfire and within canopy gaps was examined in second-growth stands on sub-mesic slopes along the Blue Ridge in northeast Georgia. The understory was sampled in ten burned and ten unburned plots consisting of nested quadrats in gaps and non-gaps. Understory diversity, density, mean size, and species composition differed significantly between burned and unburned plots. Diversity and mean size were lower in burned plots, although density was higher in burned plots relative to unburned plots. Shade-intolerant species, *Liriodendron tulipifera* L. and *Robinia pseudo-acacia* L., had much greater abundance in burned plots, although *Acer rubrum* L. maintained dominance in both the burned and unburned understory. The evidence collected for this research supported neither the gap partitioning or density hypotheses.

INDEX WORDS: Surface wildfire, Canopy gaps, Tree regeneration, Gap partitioning
                hypothesis, Density hypothesis, Southern Appalachian Mountains,
                Georgia, Blood Mountain Wilderness

REGENERATIVE RESPONSE OF A SOUTHERN APPALACHIAN FOREST TO

SURFACE WILDFIRE AND CANOPY GAP DISTURBANCES

by

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DEDICATION

To *Ursus americanus*, who so graciously shared his morning, but not my lunch, on June 11, 2001. Your presence is etched in my memory, and may your existence never be removed from the Appalachians. There is still credence to the term wild in Blood Mountain Wilderness, and I am grateful to all of the flora and fauna that made my research experience exceptional.

ACKNOWLEDGEMENTS

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CHAPTER 1

INTRODUCTION

<u>Canopy Gaps</u>

Canopy gaps are characteristically small-scale disturbances evident in mature forests. Death of canopy trees by senescence, disease, fire, or infestation creates a gap once the tree(s) permanently lose their foliage and branches in situ, known as standing dead snags, or are uprooted or broken and toppled, called tree-fall gaps. The significance of canopy gaps as important sites for tree regeneration is a result of the resource availability differences relative to the non-gap understory. Canopy gaps may allow greater amounts of light to reach the forest floor, change temperature regimes and water availability, and alter nutrient availability and add organic material to the soil, which in turn affects tree germination, and growth of seedlings and saplings.

A number of hypotheses have been formulated to detail how canopy gap disturbance maintains species diversity in mature forests. Ricklefs (1977) proposed the gap partitioning hypothesis, which explains that a gradient exists between the center of a canopy gap and the shaded non-gap understory, and along this gradient different tree species utilize the various niches for regeneration. The hypothesis was initially proposed for tropical forests, but its significance in that environment has been questioned (Denslow, 1995). However, evidence of resource partitioning along the gap/non-gap understory gradient has been found in a New England forest (Sipe and Bazzaz, 1995). The gap partitioning hypothesis has been metamorphosed since its proposal to focus on a

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resource gradient between gaps of different sizes, and is referred to as the gap-size

partitioning hypothesis (Busing and White, 1997). The evidence for this hypothesis is

also mixed, although shade-intolerant species do appear to have advantages in large gaps

(Brokaw, 1985; Runkle and Yetter, 1987; Clebsch and Busing, 1989; Lertzman, 1992;

Runkle, 1998). Denslow (1995) has presented a third hypothesis that does not involve a

partitioning component. The density hypothesis states that the high diversity in gaps is

due primarily to the high stem density found in gaps.

In the southern Appalachians empirical research into the applicability of these

hypotheses for explaining species diversity and composition has been conducted,

although the results are mixed (Runkle and Yetter, 1987; Clebsch and Busing, 1989;

Busing and White, 1997; Runkle, 1998). Three investigations performed in the Great

Smoky Mountain National Park (GSMNP) region concluded that gap size does play a

role in vegetation dynamics and assists in the maintenance of canopy species diversity in

old growth forests (Runkle and Yetter, 1987; Clebsch and Busing, 1989; Runkle, 1998).

Busing and White's (1997) research in GSMNP yields results that attribute species

richness levels to stem density; they conclude that gap partitioning hypotheses apply only

to some intolerant species. This current research effort directly assesses the relevance of

the gap partitioning and density hypotheses in the Southern Appalachians; however, the

gap-size partitioning hypothesis was not analyzed.

Other investigations concerning canopy gaps in the southern Appalachians have

focused on gap dynamics in relation to topographic and evergreen understory influences

(Clinton et al., 1994; Waterman et al., 1995; Busing, 1996). Two of these studies have

suggested that mountain laurel (*Kalmia latifolia* L.) and rhododendron (*Rhododendron*

maximum L.) thickets limit tree regeneration in canopy gaps because the dense shrub layer hinders establishment, growth, and survival of some tree species (Clinton et al., 1994; Waterman et al., 1995). Both studies suggest that surface fires might remove enough mountain laurel and rhododendron biomass and litter to allow for the establishment of tree species sensitive to their presence. Although these authors suggest that surface fire could be potentially important to the composition and regeneration of tree species within gaps in the southern Appalachians, an investigation of these statements has not been conducted.

Southern Appalachian Fire Research

The occurrence of fire may make resources available to new tree growth by removing overabundant competitors, moving nutrients stored in dead and senescing trees into the soil, and reducing foliage that may shade species which require more light. Fire as a disturbance agent in the southern Appalachian Mountains is recognized as an intermittent component of the broader ecosystem processes that regulate forest productivity and species diversity throughout the region. The dominance of the oaks in general, and of the oak-chestnut forest type in the region, is attributed to the importance of Native American use of fire (Abrams, 1992; Delcourt and Delcourt, 1998). Human-caused wildfires are relatively frequent and overall are believed to have remained nearly consistent from Native American habitation until the mid twentieth century, when widespread suppression was implemented (Harmon, 1982; Abrams et al., 1995). Records obtained from historical accounts, local news publications, and various resource management agencies indicate that in the Chattooga watershed, which borders northeast

Georgia, North Carolina and South Carolina, anthropogenic fires have fluctuated significantly over the past century and a half due to changing land use patterns, management strategies, and social conditions. Additionally, the last couple of decades have resulted in a lowering of human-caused ignitions from high arson-related levels of the 1970's, to those equal to the low suppression-related levels of the 1940's and 1950's. Throughout this period natural ignitions have remained consistently rare, and usually occur only on xeric ridge tops (Bratton and Meier, 1998).

In this region, the application of prescribed burning techniques for regeneration of xeric pine-hardwood forests on federal land is fairly common (Danielovich et al., 1987; Clinton et al., 1993; Arthur et al., 1998; Elliott et al., 1999; Vose et al., 1999). Several studies have specifically examined effects of prescribed burning on the southern Appalachian endemic species table mountain pine (*Pinus pungens* Lambert) in stand mixtures with pitch pine (*Pinus rigida* Miller) (Waldrop and Brose, 1999; Welch et al., 2000). Research on the effects of wildfire has similarly concentrated on tree regeneration within pine-hardwood stands and table mountain-pitch pine stands (Barden and Woods, 1976; Groeschl et al., 1992). Fire and canopy gap disturbances are commonly investigated separately in relation to their effects on tree regeneration in the southern Appalachians. This study examines the independent and combined effects of canopy gaps and a fire in north Georgia that occurred in the fall of 1999 on tree regeneration in southern Appalachia.

Research Questions

A surface wildfire may increase light and nutrient availability and decrease competitive stress, which may create favorable conditions for regeneration of species uncommon within unburned forests. Shade-intolerant trees, such as some early successional hardwoods (e.g. tulip poplar [*Liriodendron tulipifera* L.]), may benefit from low intensity fire.   To assess the effects of surface wildfire disturbance on vegetation of sub-mesic southern Appalachian slopes, burned and unburned sites are compared in terms of tree species diversity, richness, and composition, and the potential affects of the burn on forest dynamics are assessed.

Similar to fire, canopy gaps may increase light and nutrient availability, and change water and temperature regimes, which may create favorable conditions for regeneration of species uncommon within the non-gap forest. Two of the canopy gap hypotheses described previously, the gap partitioning and density hypotheses, are tested for their applicability in southern Appalachian forests affected by surface wildfire. For acceptance of the gap partitioning hypothesis, it is expected that variation in understory species diversity, richness, and/or composition must be evident between the center of gaps and a point in the non-gap forest a short distance from the border of the gaps. Additionally, for the density hypothesis to be accepted, variation in density between gaps and the non-gap understory and a positive correlation between density and diversity and/or density and species richness must be found. Furthermore, burning could potentially alter conditions that have bearing on the applicability of the two gap hypotheses tested. The effect of burning is examined in order to determine whether this compounded disturbance modifies the results of the analysis.

CHAPTER 2

METHODS

Study Area

The study sites are located in and adjacent to two low-severity surface-wildfire areas in Chattahoochee National Forest in northern Georgia that burned between November 16 to19, 1999. The burned areas extend south from Blood Mountain itself and are almost entirely inside Blood Mountain Wilderness, a mixed hardwood-pine forest located within the Blue Ridge physiographic province (Figure 2.1).

Pre-sampling Methods

Actual study plots, canopy gaps located only on mesic slopes, within the burned areas and adjacent unburned areas were initially located by 6x magnification stereoscope interpretation of 1:40,000 color infrared aerial photographs taken in March of 1999, prior to the fires, by the U. S. Geological Survey (USGS) for the National Aerial Photography Program. The canopy gaps were identified on the aerial photographs for the purpose of easing the plot location process, and assure that all gaps predated the fires (see Appendix, Example of canopy gaps found on the aerial photographs). The aerial photographs were scanned with a high quality digital scanner at 600 dpi and CADImage/Scan+Feature version 1.1 software. I registered the photos to the USGS Digital Raster Graphics (DRG) 7.5 Minute Quadrangle of Neels Gap (UTM zone 17, North American Datum 1983) using Digital Mapping Software (DMS) and orthorectified them using the USGS Digital Elevation Model (DEM) for Neels Gap (National Geodetic Vertical Datum 1929).

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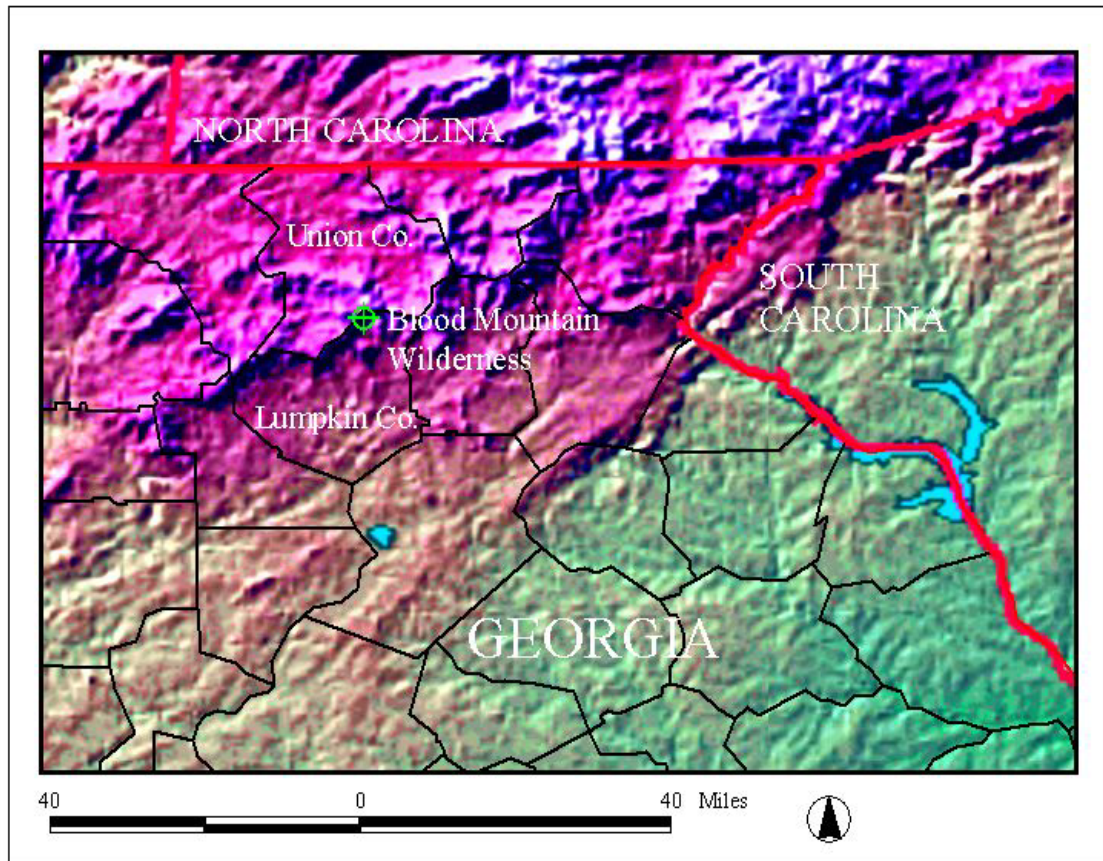
Figure 2.1: Southern Appalachians and location of Blood Mountain Wilderness.

The error per pixel for the only orthorectified photo used in the vectorization process is

5.91 meters. The gaps located with the stereoscope were transferred to the digital photos

and vectorized in a point feature coverage with ESRI ArcView GIS version 3.2 software.

Overlays were performed with the DEM for Neels Gap to obtain initial elevation data,

and the DEM was converted to a Triangular Irregular Network (TIN) to obtain initial

aspect and slope data. The DRG of Neels Gap was used to assess the proximity of sites

to human disturbed areas (e.g. roads, trails, and structures). With the use of the point

feature coverage, gaps that correspond to established criteria for slope, aspect, elevation,

and a distant position from human impact were selected for field verification. The entire

pre-field verification process resulted in 72 gaps located on the photos with acceptable slope, aspect, elevation, and human impact variables.

During the initial field check the selected canopy gaps were located with the aid of a Global Positioning System (GPS); the actual size of each gap, aspect, and slope were measured; and site quality was assessed. Site quality assessment was based on the occurrence of conditions precluding sampling, which could not be discerned on the aerial photos or through analysis of the ancillary data. Selective criteria that disqualified plots included the existence of streams, large boulders covering a majority of the gap, and discontinuous canopy coverage around the gap. Of the 72 gaps found on the photos, 51 were actually located on the ground, 5 could not be located at all, and the remaining 16 were not examined due to great difficulty of access. Only 17 of the 51 located on the ground were determined to be useful, most that were not useful were too large. Additional gaps were located in the field so that each of two size classes (small gaps = 0.0100 - 0.0290 ha and large gaps = 0.0300 - 0.0500 ha) were represented by 10 burned and 10 unburned gaps. All gaps located in the field, a total of 23 of a useable nature, that were not found on the first aerial photo examination were later verified on the photos to ensure consistency of age relative to the burn event. Due to considerations concerning the amount of time needed to sample each study plot, only the gaps within the larger size class were sampled for this study. A total of 20 plots in stands with known ages dating from 1874 to 1932 were sampled (Figure 2.2) (communication, James M. Wentworth, Central Zone Biologist, U.S.D.A. Forest Service, June 29, 2001). Each plot was sampled with a gap sub-plot and a non-gap forest sub-plot, with two quadrats per sub-plot. Field sampling was conducted between May 9 and June 11, 2001.

Basemap: USDA Forest Service, Chattahoochee-Oconee National Forests

Legend

Wildfire Area

Wilderness Boundary

Plots

1 Mile   0   1 Mile
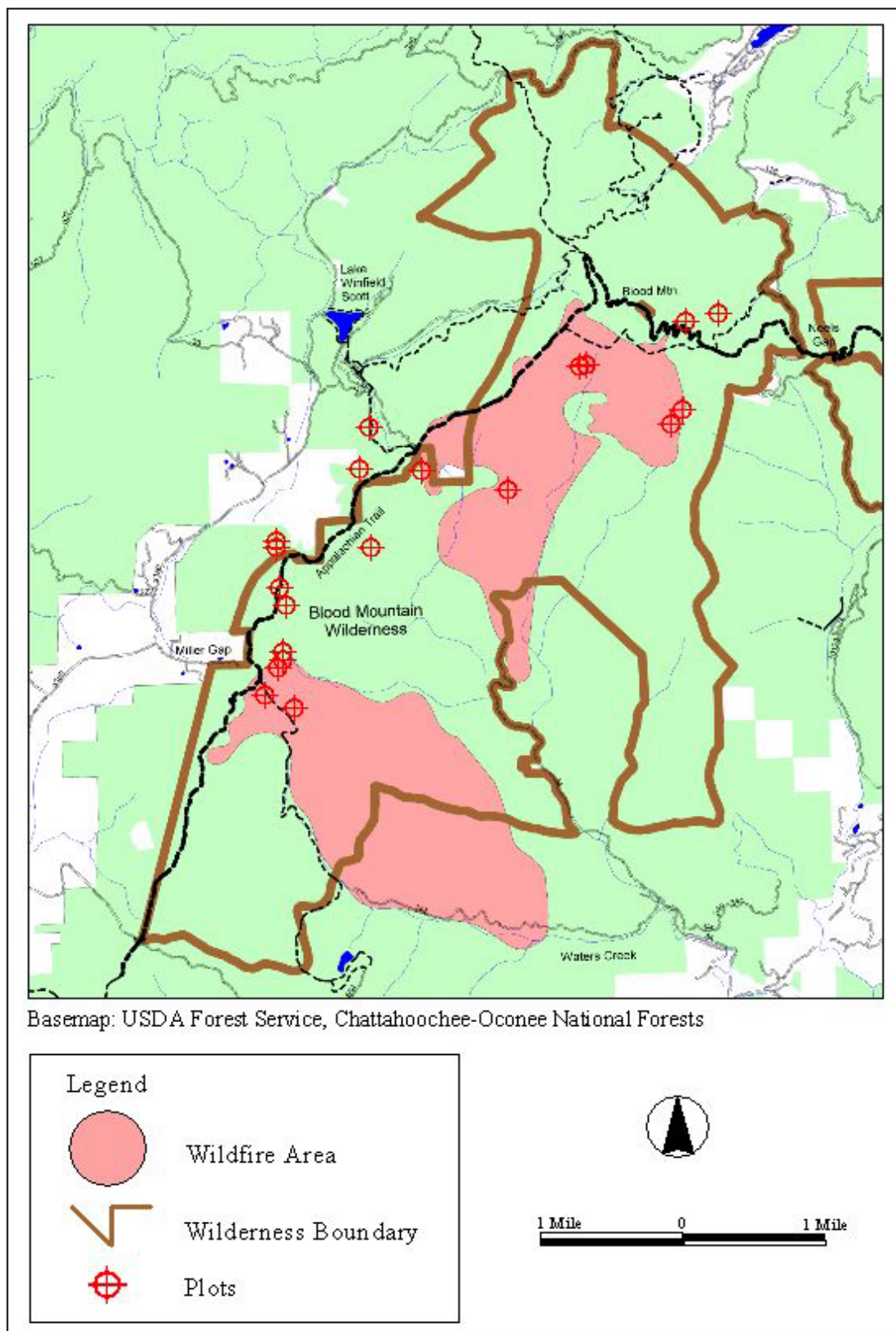
Figure 2.2: Plot locations in Blood Mountain Wilderness.

Field Sampling Methods

The sampling scheme was logically constructed to facilitate testing of both the gap partitioning and density hypotheses in unison. Since the gap partitioning hypothesis assumes a gradient exists between the middle of a gap and a point in the non-gap forest, in any direction, circular quadrats were measured concentrically in both gaps and the non-gap forest in order to capture non-overlapping portions of the hypothesized gradient (Figure 2.3).
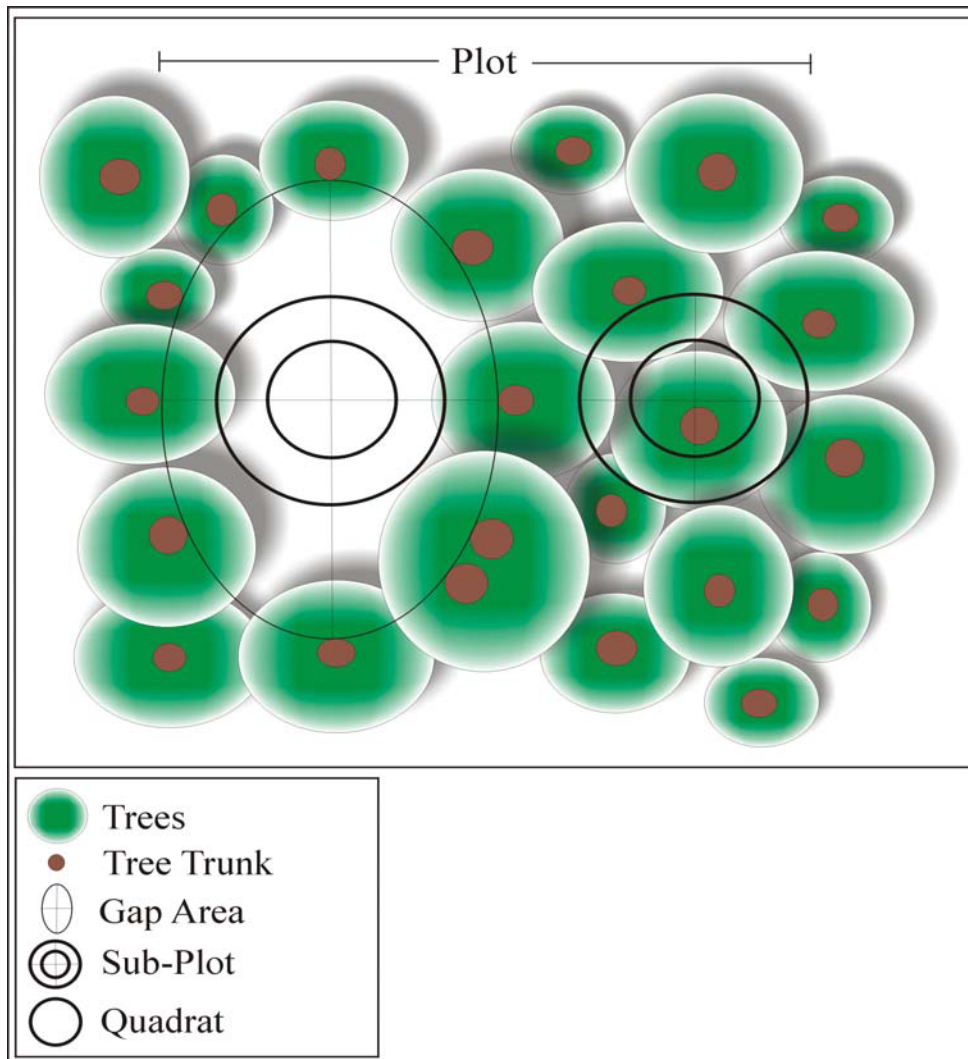
Figure 2.3: Sampling scheme.

At each study plot, the size of each gap sub-plot was determined by measuring the longest axis (length) and the first axis' longest perpendicular axis (width), to the trunk of the gap border trees; and the area of the gap was calculated based on the equation for an ellipse, in accordance with the expanded gap method (Runkle, 1990). Two concentric circular quadrats were laid out with their centers placed at the center of the gap. Circular quadrat sizes were proportional to the size of the median gap, with the area of the outer and inner quadrats each equal to 25 percent of the area of the median gap (quadrat area = 0.0093 ha). Ground cover was measured within the outer quadrat with the line-intercept method along each axis used to measure the size of the gap. Slope and aspect were measured at the center of each gap. Topographic data (aspect, degree slope, slope configuration, and topographic position) were converted into a Topographic Relative Moisture Index (TRMI) (Table 1) (Parker, 1982). Inside each quadrat all tree seedlings and saplings <2.5 cm diameter at breast height (dbh) were identified to species, and their height class was recorded (Radford et al., 1968). Height classes for seedlings and saplings consisted of five classes in 30 cm intervals up to 150 cm, and a sixth size class >150 cm. Stems >2.5 cm dbh were also identified to species, and their dbh was recorded. The gap border trees of canopy height were identified to species; their dbh was recorded; and in the burned areas, the burn scar was measured using the same size class intervals described for seedling and sapling measurement. The type of gap creation process, and the decay status of the gap maker were recorded and classified (Table 2.1). Additionally, topsoil samples were collected from multiple randomly selected points inside the quadrats, and combined to create a sub-plot sample; and the soil pH of each sub-plot sample was measured in the lab (Schofield and Taylor, 1955).

Table 2.1: Classification systems for Topographic Position, Slope Configuration, Gap Creation Type, and Decay Class of Gap Maker. (* In case of multiple gap makers with different decay classes, the most decayed class is taken to represent the gap.)

Topographic Position Classes	Slope Configuration Classes
1 – Valley bottom	**1** – Concave
2 – Lower slope	**2** – Concave/Straight
3 – Middle slope	**3** – Straight
4 – Upper slope	**4** – Convex/Straight
5 – Ridge top	**5** – Convex
Gap Creation Type Classes	
1 – Single tree snag	
2 – Multiple tree snag	
3 – Windthrow (pit and mound)	
4 – Basal shear	
5 – Combination	
Gap Maker Decay Classes*	
1 – Most or all of bark remaining, some twigs may be persistent, limbs mainly intact	
2 – More than half, but not all of bark absent, all twigs absent, numerous limbs intact	
3 – All bark absent, all twigs absent, most or all limbs absent, bole mostly intact	
4 – Bole highly decayed, wood breaking off in hand	

A non-gap forest sub-plot was sampled adjacent to every burned and unburned gap. Two concentric circular quadrats with the same size as the adjacent gap quadrats were located at approximately the same elevation, aspect, and slope angle as the adjacent gap. Quadrats were completely in the non-gap forest and outside of the influence of the gap micro-environment. The centers of the non-gap quadrats were consistently located 10 m due east of the trunk of a tree on the border of the gap, or due north of the gap if boulders, streams, or other conditions precluded sampling to the east. Data collection

followed the protocol established for the gaps except for measurement of burn scars, size

and identity of gap border trees, gap creation type class, and gap maker decay class.

<div align="center">Statistical Methods</div>

Significant results for tests involving the gapping (gaps vs. non-gaps) and burning

(burned vs. unburned) effects are only ecologically meaningful if the overstory

composition is similar across all sites. To verify that this was the case, dbh values for

overstory trees were summed by species for each gap and non-gap sub-plot, including the

gap border trees, and the relative dominance of each species was calculated for each sub-

plot. Bray-Curtis ordination was conducted with PC-ORD Version 4 to analyze

overstory species composition patterns at the sub-plot scale (McCune and Mefford,

1999). This analysis was based on the relative dominance of all species present in at least

one sub-plot. In the exploratory phase of analysis, several ordination methods were

performed, including Detrended Correspondence Analysis, with rare species

downweighted, and not downweighted. Essentially the same results were obtained with

the different ordination methods; therefore, the Bray-Curtis ordination results are the only

ordination results reported throughout due to interpretability. Bray-Curtis ordination was

also conducted to analyze understory species composition patterns at the quadrat scale.

This analysis was based on the density values of all species pulled from the sample of

individuals <2.5 cm dbh (i.e. understory stems) and present in at least one quadrat.

The Shannon-Weiner Diversity Index, simply called diversity throughout,

evenness, species richness, and density were calculated for the understory sample in each

quadrat. The mean size class for all species combined was also calculated for the

Table 2.2: Organization of statistical analysis.

Research Questions and Hypotheses	Statistical Analysis	Observational Unit	Dependent Variables	Effects/Correlation Variables
Mature Stand Analysis	Bray Curtis Ordination	Sub-plot		
	ANOVA	Sub-plot	Ordination Axis Scores	Gapping Burning Gapping x Burning
Burning Effect	Bray Curtis Ordination	Quadrat		
	ANOVA	Quadrat	Ordination Axis Scores Diversity Evenness Total Quadrat Density Species Richness Mean Size Class Dominant Species Abundances	Gapping Burning Gapping x Burning
Gap Partitioning Hypothesis	Bray Curtis Ordination	Quadrat		
	ANOVA	Quadrat	Ordination Axis Scores Diversity Evenness Species Richness	Gapping Quadrat Position Burning Gapping x Burning Gapping x Quadrat Position Quadrat Position x Buring Gapping x Quadrat Position x Burning
Density Hypothesis	ANOVA	Quadrat	Total Quadrat Density	Gapping Quadrat Position Burning Gapping x Burning Gapping x Quadrat Position Quadrat Position x Buring Gapping x Quadrat Position x Burning
Environmental Correlations	Correlation	Quadrat		Density Diversity

understory sample in each quadrat. Analysis of Variance (ANOVA) was performed with

SAS version 8.1 to determine whether tree species composition differed with gapping,

burning, quadrat position (inner vs. outer quadrat), and combinations of these effects (see

Table 2.2 for a breakdown of how individual analyses address the research hypotheses)

(SAS Institute Inc., 1999). Dependent variables for the ANOVA included axis scores

from the Bray-Curtis ordinations, diversity, evenness, species richness, density, and mean

size class. Where necessary, variables were normalized by log transformation.

Individual species having a mean number of trees per quadrat >5 were analyzed

individually with ANOVA. ANOVA was performed with abundance per quadrat for

each of these species as the dependent variable, and gapping, burning, and combinations

were effects. Correlation analysis between diversity and density was performed across

all quadrats.

CHAPTER 3

RESULTS

General Burn, Gap, and Environmental Characteristics

The severity of the wildfire was quite low, with no evidence of canopy tree
mortality due to burn damage at the time of sampling. The overall mean burn scar size
classes fell within the range of 1.00 to 3.70 (Table 3.1). The greatest burn scar size class
measurements were >150 cm; however these scars did not extend much farther up the
trunk than 150 cm, and did not appear to cause damage beyond the protective bark layer.

Gap size ranged from 0.0300 to 0.0459 ha, with no significant difference between
burned and unburned gaps (Table 3.1). Given the size of the gaps, it is not surprising that
no gaps were created by single tree snags. Additionally, it follows that the most frequent
creation type was a combination of processes in one gap, contributing to the large size.
The median decay class of the gap maker was the third class, which suggests that most of
the gaps were at least a few years older than the two-year minimum age determined by
the aerial photo date.

Measures of aspect for all sub-plots ranged from 25° to 130° azimuth (Table 3.1),
with a mean of 88°, considered the sub-mesic zone. ANOVA indicated that the aspect of
burned and unburned plots differed significantly. The mean was 98° (east-southeast) for
burned plots and 77° (east-northeast) for unburned plots. The burning effect was
significant for degree slope, elevation, and slope configuration; and degree slope was
greater in burned plots, while elevation and slope configuration were greater in unburned

plots. However, the burning effect was not significant for TRMI. Of all the

environmental variables, percent ground cover showed the greatest difference due to the

effect of burning. Burned plots contained less than half the percentage of ground cover

that unburned plots exhibited. There was not a significant difference between burned and

unburned plots for soil pH. The gapping effect was not significant for any of the

environmental variables.

<div align="center">General Vegetation</div>

Thirty six different species of trees were located over the entire sampling area

(Table 3.2). The most abundant species overall were northern red oak (*Quercus rubra*

L.), white oak (*Quercus alba* L.), chestnut oak (*Quercus prinus* L.), red maple (*Acer*

rubrum L.), pignut hickory (*Carya glabra* (Miller) Sweet), and tulip poplar. American

chestnut (*Castanea dentata* (Marshall) Borkh.), black locust (*Robinia pseudo-acacia* L.),

and sassafras (*Sassafras albidum* (Nuttall) Nees.) also exhibited strong abundances in the

understory. Of the 36 species, only five had no individuals <2.5 cm dbh. Additionally,

seven species were only found in the unburned forest. White basswood (*Tilia*

heterophylla Vent.) and shagbark hickory (*Carya ovata* (Miller) K. Koch) were the only

two species found only in the non-gap forest.

<div align="center">Composition of the Forest Canopy</div>

In the composition of canopy trees, chestnut oak and northern red oak clearly

dominated (Table 3.3). Only six of the 36 overstory species had a mean relative

dominance >0.05. Near-normal diameter class distributions were evident for

Table 3.1: General burn, gap, and environmental data.

	Range	Mean (±Standard Deviation)	Median	ANOVA of Burning Effect				ANOVA of Gapping Effect			
				F value	Pr>F	Burned Mean	Unburned Mean	F value	Pr>F	Gap Mean	Non-Gap Mean
Mean Burn Scar Size Class *	1.00 - 3.70	2.10 ±0.80	2.0	-	-	-	-	-	-	-	-
Gap Size (ha)	0.0300 - 0.0459	0.0380 ±0.01	0.0371	1.13	0.30	0.0368	0.0391	-	-	-	-
Gap Creation Type Class **	2 - 5	4.00 ±1.03	4	3.43	0.08	3.60	4.40	-	-	-	-
Gap Maker Decay Class **	1 - 4	2.70 ±0.80	3	3.12	0.10	3.00	2.40	-	-	-	-
Aspect (° azimuth)	25 - 130	88 ±28.0	84	6.71	0.01	98	77	0.01	0.92	87	88
Degree Slope	11 - 29	22 ±4.00	23	5.10	0.03	23.45	20.75	0.03	0.58	22.45	21.75
Slope Configuration **	2-5	3.43 ±0.81	3	7.45	0.01	3.10	3.75	0.04	0.85	3.45	3.40
Topographic Position **	2-5	2.80 ±0.69	3	0.84	0.36	2.70	2.90	0.00	1.00	2.80	2.80
TRMI ***	17 - 44	31 ±5.80	30	0.12	0.73	30	31	0.02	0.89	30	31
Elevation (meters)	801 - 1140	934 ±91.62	946	4.26	0.04	913	954	0.00	0.96	934	933
Percent Ground Cover	3.90 - 95.00	36.70 ±22.40	33.20	18.37	0.00	24.10	49.40	0.30	0.59	38.70	34.80
Soil pH	3.27 - 5.90	4.20 ±0.50	4.20	0.08	0.79	4.21	4.16	2.24	0.14	4.30	4.07

* Size Classes: $1 = 0 - 29.9$ cm, $2 = 30 - 59.9$ cm, $3 = 60 - 89.9$ cm, $4 = 90 - 119.9$ cm,
    $5 = 120 - 149.9$ cm, $6 = 150$ cm and greater.

** See Table 2.1 for definition of variable values.

*** Topographic Relative Moisture Index (TRMI).

Table 3.2: List of species encountered in the study plots. (*Species with dbh greater than 2.5 cm. † Species only in unburned forest. ‡ Species only in non-gap forest.)

Alternate Leaf Dogwood, *Cornus alternifolia* L. f.	Mockernut Hickory, *Carya tomentosa* Nuttall
American Chestnut, *Castanea dentata* Borkh.	Mountain Winterberry, *Ilex ambigua* Torrey. †
American Holly, *Ilex opaca* Aiton	Northern Red Oak, *Quercus rubra* L.
Basswood, *Tilia heterophylla* Vent. *†‡	Pale Hickory, *Carya pallida* Engler & Graebner
Black Cherry, *Prunus serotina* Ehrhart	Pignut Hickory, *Carya glabra* Sweet
Black Locust, *Robinia pseudo-acacia* L.	Red Maple, *Acer rubrum* L.
Black Oak, *Quercus velutina* Lam.	Sassafras, *Sassafras albidum* Nees.
Blackgum, *Nyssa sylvatica* Marshall	Scarlet Oak, *Quercus coccinea* Muenchh.
Carolina Silverbell, *Halesia carolina* L.	Shagbark Hickory, *Carya ovata* K. Koch *†‡
Cherry Birch, *Betula lenta* L.	Sourwood, *Oxydendrum arboreum* DC.
Chestnut Oak, *Quercus prinus* L.	Striped Maple, *Acer pensylvanicum* L.
Chinkapin Oak, *Quercus muehlenbergii* Engelm.	Tulip Poplar, *Liriodendron tulipifera* L.
Cucumber Magnolia, *Magnolia acuminata* L.	Virginia Pine, *Pinus virginiana* Miller *
Downy Serviceberry, *Amelanchier arborea* Fernald.	White Ash, *Fraxinus americana* L.
Earleaf Magnolia, *Magnolia fraseri* Walter *†	White Oak, *Quercus alba* L.
Fan-Leaf Hawthorne, *Crataegus Flabellata* K. Koch †	White Pine, *Pinus strobus* L.
Flowering Dogwood, *Cornus florida* L.	Witch Hazel, *Hamamelis virginiana* L.
Hemlock, *Tsuga canadensis* Carr. *†	Yellow Birch, *Betula lutea* Michaux f. †

northern red oak and white oak, with the majority of individuals in the middle to larger range of size classes (Figure 3.1). Chestnut oak displayed a more skewed distribution, with a greater representation of smaller trees than for either previous oak species. The bimodal distribution of tulip poplar, the third most dominant species, denoted current importance in the canopy, and indicated that a continuing presence in the canopy could be expected for this shade intolerant species. Red maple had a pronounced negative exponential distribution, indicating a very young population with an increasing potential towards canopy prominence, while pignut hickory's negative skew was slightly less pronounced.

Table 3.3: Mean overstory relative dominance (± Standard deviation) and Relative Density for the most abundant species in All Sub-Plots (Mean relative dominance > 0.05).

	Relative Dominance	**Relative Density**
N. Red Oak	0.22 ±0.24	.06
White Oak	0.08 ±0.14	.02
Chestnut Oak	0.24 ±0.28	.10
Red Maple	0.05 ±0.07	.05
Pignut Hickory	0.05 ±0.10	.04
Tulip Poplar	0.17 ±0.27	.08

Assessment of the Research Hypotheses

Ordination Results

The Bray-Curtis ordination of sub-plots based on the relative dominance of established trees indicated that the overstory composition was uniform throughout the study sites. Specifically, there were not two clearly discernable groupings on the ordination between gaps and non-gaps (Figure 3.2). Similarly, there were not two distinct groups of species between burned and unburned plots. The ANOVA indicated that axis scores for the overstory ordination did not differ significantly with respect to gapping, burning, or the combination of the two effects (Table 3.4). These findings suggested that the existing population of potentially reproducing individuals was not concentrated disproportionately around any of the sampled plot types. This provided a statistically even baseline of species distribution in which to analyze the reproductive responses of these species to gap formation and/or burning.

The Bray-Curtis ordination based on understory species composition indicated that gaps and non-gaps, and inner and outer quadrats were intermingled in ecological space, without two clearly discernable groupings (Figure 3.3). However, burned and
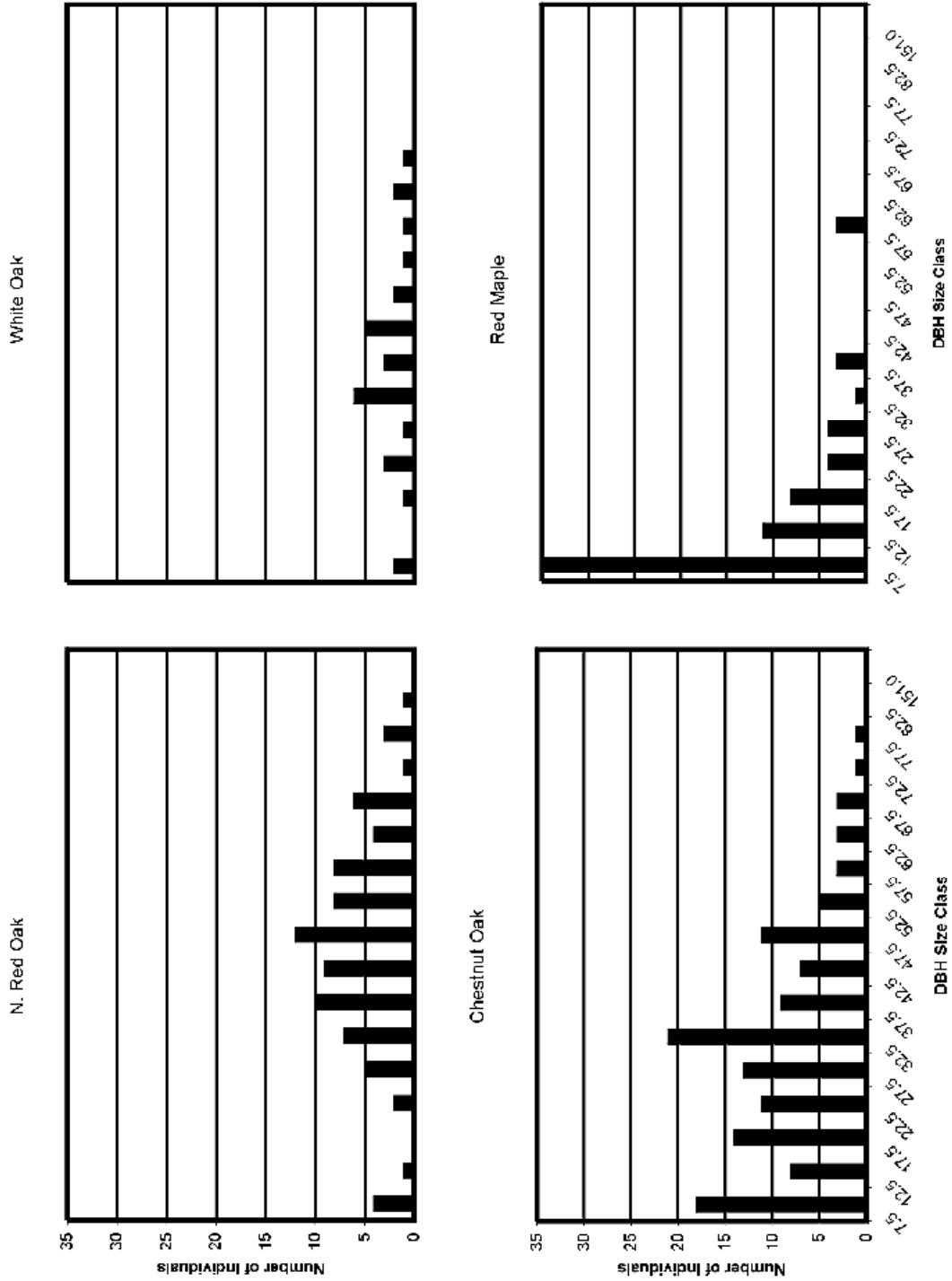
Figure 3.1: Size distribution of trees with mean relative dominance >0.05 (DBH size class indicated by value of upper limit of size class. Lowest size class begins at 2.5 cm dbh).
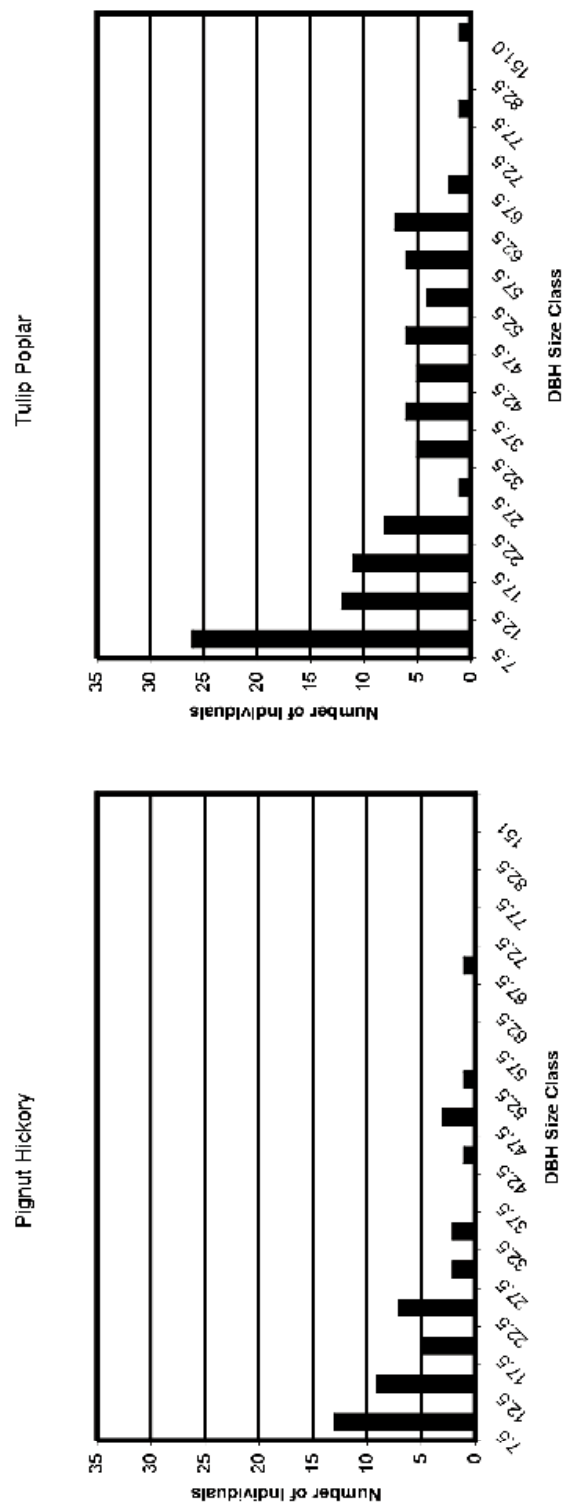
Figure 3.1 (continued): Size distribution of trees with mean relative dominance >0.05 (DBH size class indicated by value of upper limit of size class. Lowest size class begins at 2.5 cm dbh).

unburned quadrats were divided into two discernable groups. ANOVA on these axis scores confirmed that burning had a significant effect on understory species composition, while gapping, quadrat position, and combinations of these effects were not significant (Table 3.4). The relationships of these results to the research hypotheses are discussed below.

Burning Effects

Burning demonstrated a profound facility for altering the regeneration pattern characteristic of the unburned forest. The ANOVA showed that the burning effect was significant on diversity, density, mean size class, and understory ordination axis scores (Table 3.5). Diversity and mean size class were decreased in burned plots, but density was greater on burned sites. Results of the effect of burning were not significant for species richness or evenness (although in keeping with diversity, both measures were greater on unburned plots).

Analysis of the response of the most abundant species demonstrated that the shade-intolerant species had the greatest individual difference between burned and unburned plots (Table 3.6). Black locust abundance had the greatest F value for the burning effect of the nine species for which ANOVA was conducted. The density of black locust individuals was close to 100 stems per ha in unburned plots, while the number was more than 10 times as great in burned plots. Tulip poplar had greater than triple the density in burned plots, and sassafras, double the density. The more shade-tolerant species demonstrated a more mixed response to burning. Northern red oak and pignut hickory exhibited no significant response; however 200-300% greater densities
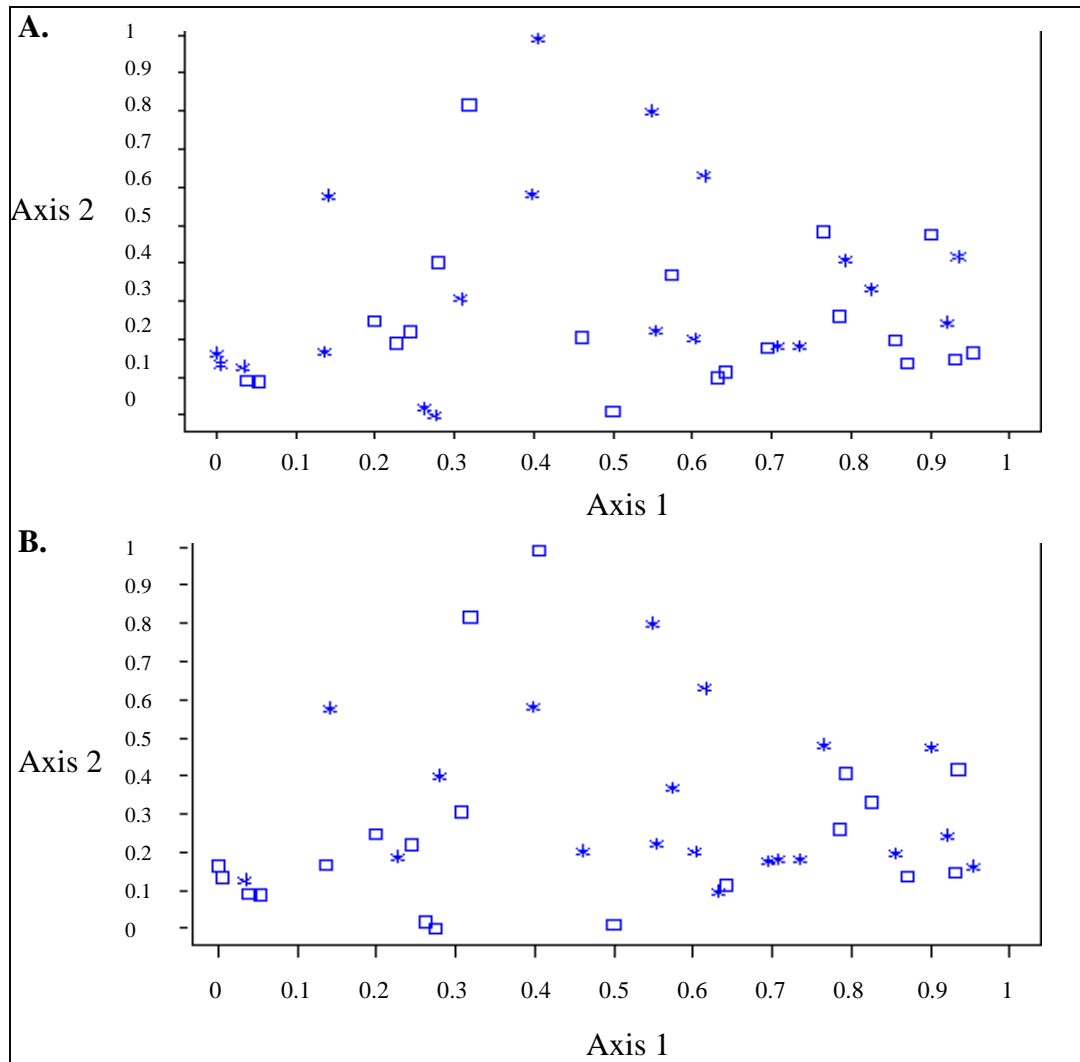
Figure 3.2: Bray-Curtis ordination based on overstory composition.
A.: □ = Gap, ∗ = Non-Gap. B.: □ = Burned, ∗ = Unburned.

were evident for white oak, chestnut oak, and red maple in burned plots. In addition to

the most abundant species, black oak (Quercus velutina Lam.) differed significantly

between burned and unburned plots (F value = 4.56, P = 0.03, burned density = 750.54,

unburned density = 215.05), and scarlet oak (Quercus coccinea Muenchh.) did not

significantly differ between plot types (F value = 0.37, P = 0.55). Although black locust

and tulip poplar exhibited the greater magnitude of difference with burning, red maple

was the most abundant species in burned plots.

Table 3.4: ANOVA results of Bray-Curtis ordination axis scores for relative dominance and species composition.

		Understory		Overstory	
		All Quadrats		*Sub-Plots*	
		Axis 1	**Axis 2**	**Axis 1**	**Axis 2**
Burning	F value	**21.00**	**4.71**	2.59	0.98
	Pr>F	**0.00**	**0.03**	0.12	0.33
Gapping	F value	0.15	2.01	0.82	1.54
	Pr>F	0.70	0.16	0.37	0.23
Quadrat Position	F value	0.01	0.01		
	Pr>F	0.92	0.93		
Gapping*Burning	F value	0.35	1.09	0.06	0.02
	Pr>F	0.55	0.30	0.82	0.90
Quadrat Position*Burning	F value	0.00	0.02		
	Pr>F	0.96	0.88		
Gapping*Quadrat Position	F value	0.48	0.00		
	Pr>F	0.49	1.00		
Gapping*Quadrat Position *Burning	F value	0.06	0.02		
	Pr>F	0.81	0.90		
% Extracted from matrix		21.79	16.46	34.83	19.49

Gap Partitioning Hypothesis

ANOVA was conducted to determine whether the gap partitioning hypothesis accounted for variation in diversity, evenness, and species richness. The effects of gapping and burning were found to be significant for diversity, with greater diversity in non-gaps and unburned plots; however quadrat position and combinations of effects were not significant (Tables 3.7 and 3.8). None of the effects was significant for evenness and species richness. Additionally, the ANOVA of understory ordination axis scores showed a significant effect of only burning alone on understory composition patterns; gapping, quadrat position, and combinations of these effects had no significant influence (Table 3.4). Analysis of the response of the most abundant species indicated that gapping only had a significant effect on northern red oak and chestnut oak (Table 3.6).
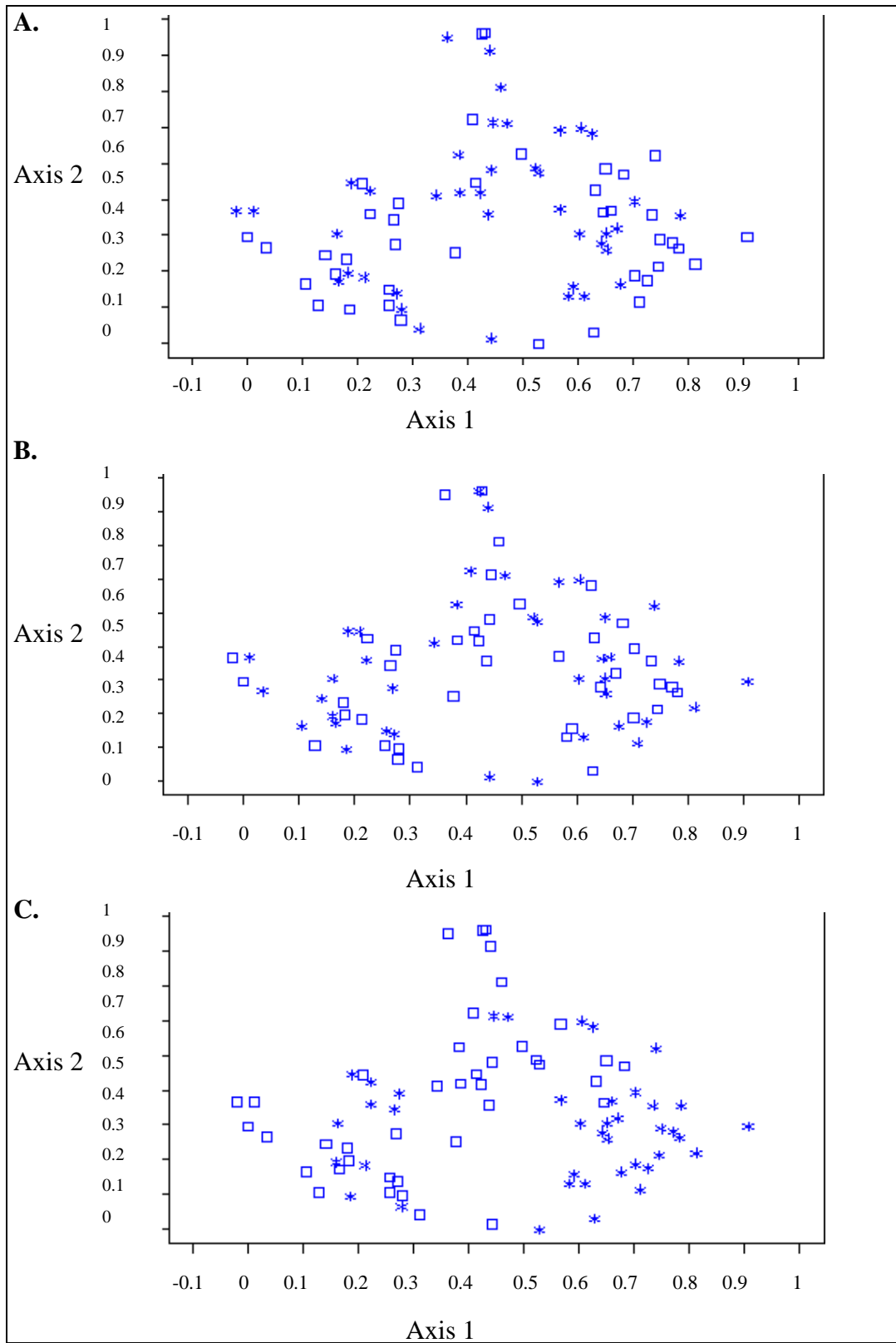
Figure 3.3: Understory Bray-Curtis ordination, all quadrats. A.: □ = Gap, * = Non-Gap.
B.: □ = Outer Quadrats, * = Inner Quadrats. C.: □ = Burned, * = Unburned.

Table 3.5: Effect of burning on Shannon-Weiner diversity index, evenness, species richness, density, mean size class, and species composition ordination axis scores.

	F value	Pr > F
Shannon-Weiner Diversity Index burn mean: 1.66, unburned mean: 1.78	4.59	0.04
Evenness burn mean: 0.69, unburned mean: 0.73	3.76	0.06
Species Richness burn mean: 11.55, unburned mean: 12.08	0.74	0.39
Density (Log Transformed Analysis) burn mean: 28223.72, unburned mean: 14547.17	23.58	<0.0001
Mean Size Class burn mean: 1.56, unburned mean: 2.82	110.30	<0.0001
Understory Bray-Curtis Ordination **Axis 1** burn mean: 0.34, unburned mean: 0.56	22.42	<0.0001
Axis 2 burn mean: 0.29, unburned mean: 0.39	4.89	0.03

Density Hypothesis

ANOVA was executed to test for variation in density due to gapping, quadrat position, burning, and combinations of these effects. With the exception of burning alone, none of the effects or combined effects was significant (Table 3.9). Additionally, density and diversity were negatively correlated (-0.29, P = 0.02), however density and species richness were positively correlated (0.51, P = <0.0001). Although density and species richness are positively correlated, the density hypothesis fails the test for acceptance due to the absence of significant differences between gaps and non-gaps for density.

Table 3.6: Burning and gapping effect on the most abundant understory species (Abundance >5 per quadrat.)
*Does not reach canopy due to Chestnut Blight.

	ANOVA of Burning Effect				Relative Density		ANOVA of Gapping Effect			
	F value	Pr > F	Burned Density	Unburned Density	Burned	Unburned	F value	Pr > F	Gap Density	Non-Gap Density
N. Red Oak	0.04	0.84	2819.89	2935.48	10	20	5.13	0.03	3518.82	2236.56
White Oak	6.59	0.01	1416.67	419.35	5	3	0.03	0.86	892.47	943.55
Chestnut Oak	7.32	0.01	2239.25	811.83	8	6	3.87	0.05	991.94	2059.14
Red Maple	6.93	0.01	8225.81	4252.69	29	29	0.03	0.85	6379.03	6099.46
Am. Chestnut*	3.67	0.06	798.39	478.49	3	3	0.01	0.93	634.41	642.47
Pignut Hickory	0.30	0.59	537.63	610.22	2	4	0.00	0.97	594.09	553.76
Tulip Poplar	9.21	0.00	6905.91	1879.03	25	13	1.13	0.29	5336.02	3448.93
Black Locust	17.53	0.00	1169.36	99.46	4	1	0.40	0.53	717.74	551.08
Sassafras	5.56	0.02	1099.46	489.25	4	3	0.45	0.50	704.30	884.41

Table 3.7: Effect of burning, gapping, and quadrat position on diversity, evenness, and species richness of the understory.

	Shannon-Weiner Diversity Index		Evenness		Species Richness	
	F value	Pr > F	F value	Pr > F	F value	Pr > F
Burning	**4.46**	**0.04**	3.65	0.06	0.71	0.40
Gapping	**6.93**	**0.01**	2.85	0.10	2.21	0.14
Quadrat Position	1.35	0.25	0.44	0.51	0.36	0.55
Gapping*Quadrat Position	0.05	0.82	0.03	0.87	0.13	0.72
Gapping*Burning	0.12	0.73	0.44	0.51	0.01	0.90
Quadrat Position*Burning	0.05	0.82	0.00	0.99	0.20	0.66
Gapping*Quadrat Position*Burning	0.38	0.54	0.01	0.93	0.47	0.50

Table 3.8: Means (± Standard Deviation) of diversity, evenness, species richness, and density for gaps, non-gaps, and inner and outer quadrats.

	Shannon-Weiner Diversity Index	Evenness	Species Richness	Density
Gaps	1.64 ±0.29	0.69 ±0.12	11.35 ±2.67	22390.84 ±15661.54
Non-Gaps	1.80 ±0.22	0.73 ±0.10	12.28 ±2.75	20380.05 ±14021.63
Inner Quadrat	1.69 ±0.26	0.70 ±0.11	11.63 ±2.76	22266.85 ±16065.76
Outer Quadrat	1.75 ±0.27	0.72 ±0.11	12.00 ±2.72	20504.04 ±13574.28

Table 3.9: Effect of burning, gapping, and quadrat position on density of the understory.

	Density	
	F value	Pr > F
Burning	**23.23**	**0.00**
Gapping	0.11	0.74
Quadrat Position	0.10	0.75
Gapping*Quadrat Position	0.50	0.48
Gapping*Burning	0.17	0.68
Quadrat Position*Burning	0.08	0.78
Gapping*Quadrat Position*Burning	0.04	0.84

CHAPTER 4

DISCUSSION

General Environmental Issues

Drought

The approximately two and a half year period preceding the field sampling for this research encompassed an episode of severe drought that was well outside the norm in yearly precipitation. The climatological normal from 1961-1990, calculated by the Southeast Regional Climate Center using data from the Blairsville Experimental Station, Georgia (Sta. #090969), was 144.60 cm average annual precipitation. The U. S. Department of Commerce, National Oceanic and Atmospheric Administration's precipitation records show that in 1999, precipitation was 25.20 cm below normal; in 2000, precipitation was 36.78 cm below normal; and through the first four months of 2001, precipitation was 11.28 cm below normal.

Clinton et al. (1993) found that the number of gaps created per year increased with drought in the Coweeta Basin of North Carolina. These drought-induced gaps were created mainly by scarlet and northern red oaks. Elliott and Swank (1994) found that red maple had lower drought mortality than oaks. The frequency of annual seed crop failures, or near failures, is higher in large seeded trees, such as oaks, than small seeded trees (Godman and Mattson, 1976). Failures may be due to direct or indirect effects of adverse weather and herbivory on reproduction and overall plant productivity, and the high energy cost of large crops of large seeds. Additionally, oaks do not compensate for year-to-year seed crop variation with a buried seed bank, (Canham and Marks, 1985). If

drought differentially affects tree species survivorship and seed production, the results for this research may differ from studies conducted in non-drought years.

Environmental Heterogeneity

The southern Appalachians are characterized by heterogeneity. Precipitation, evaporation, elevation, and slope characteristics are all highly variable throughout the region. Given this degree of variability in the region overall, differences between study plots are almost unavoidable. Due to the replacement of space for time, it was necessary to study burned plots and unburned plots with relatively large distances between them, which resulted in some environmental variation.

Four of the six variables related to topographic situation did show significant differences due to the burning effect. Three of these variables are components in the calculation of TRMI. Mean aspect was more east-southeasterly in burned plots than the unburned, east-northeast, mean aspect. The aspect ranged from 60° to 130° for burned plots and from 25° to 130° for unburned plots; thus burned and unburned plots actually overlapped in their range of aspects. Degree slope was also significantly greater in burned plots; however, the means of both burned and unburned plots fell within a range of slope steepness that received the same value for the calculation of TRMI. The slope configuration mean was convex, or drier, in unburned plots relative to burned plots. The variation in these three variables is a potential confounding factor for vegetation analysis; however the nonsignificant difference in TRMI may alleviate this concern. The greatest concern with the difference in aspect, degree slope, and slope configuration is that

moisture availability would vary between burned and unburned plots; however, TRMI does not differ, so moisture availability should be similar in both plot types.

The fourth differing variable related to topographic situation was elevation, and elevation was somewhat greater in unburned plots. Higher elevations are typically more exposed; however the topographic position variable did not differ significantly. Thus, unburned plots were not more predisposed to the highly exposed, driest sites, such as ridge tops, than burned plots.

Evidence of the effect of these variable environmental factors on species distribution should have been evident in the existing composition of the overstory if these differences were highly confounding. However, there were no discernable groups on the Bray-Curtis ordination based on canopy species relative dominance per sub-plot. ANOVA on the axis scores also resulted in no significant differences in overstory composition due to the effects of burning, gapping, or combinations of the two effects.

A hypothesized effect of surface wildfire is that burning may hasten the rate at which dead trees, woody debris, and ground litter are moved into the soil for use as nutrients for the post-burn cohort of trees. There was not a significant difference between burned and unburned sub-plots for soil pH, an indicator of variation in the topsoil stratum. The fire did not burn hot enough to consume the majority of dead trees and woody debris and release their nutrients; instead it only left them moderately charred. In keeping with these results, Thor and Nichols (1974) found that soil pH and phosphorous availability did not differ significantly in stands annually or periodically winter-burned over a 7-year period on the Highland Rim of eastern Tennessee.

<u>The Burning Effect</u>

Generalized Community Effects

Similar to other studies in the southern Appalachians, the effect of the wildfire in

Blood Mountain Wilderness was significant for a number of vegetation parameters in the

understory forest layer. Percent ground cover was significantly lower in burned plots

than in unburned plots.   Welch et al. (2000) found similar results after a prescribed fire

in table mountain and pitch pine stands in the southern Appalachians of Virginia and

North Carolina, where ground cover was reduced by 40-70%. Converse to these

findings, Arthur et al. (1998) reported a doubling of percent ground cover in both the

herb and shrub strata on sites after a single fire in the Cumberland Plateau of Kentucky.

The density of midstory trees (2.5 to 10 cm dbh) in burned plots was much lower

than in unburned plots, while the density of individuals in the burned understory was

significantly higher. The mean size class of the understory was also significantly lower

in burned plots. The fire likely reduced the ground cover and thinned tree seedlings and

saplings, providing more available light at the ground floor and less competitive stress

relative to unburned plots. This may have triggered a wave of establishment, as

evidenced by the significantly higher density in the burned understory. In a similar

manner, Welch et al. (2000) found that post-burn mean understory densities significantly

increased with a corresponding reduction in ground cover.

This combination of factors corresponding with greater density in burned plots

implies that density was higher due to the success of seed germination and seedling

growth. However, individuals in the understory were not categorized based on their

status as a true seedling or a root sprout and during field sampling it was apparent that

root sprouts were abundant for many of the species.   Whether increased success of seed germination and seedling growth, or sprouting account for higher density, or both in tandem, cannot be discerned.

Diversity was significantly lower in burned plots; evenness was similarly lower in burned plots, but the trend was not significant. Species richness had no significant difference between burned and unburned plots. The lower diversity in burned relative to unburned plots can be attributed to inordinately higher densities for a small number of species. Although a few species were nearly restricted to one type of plot (e.g., white pine (*Pinus strobus* L.) to unburned plots and black locust to burned plots), burned and unburned plots did not differ from each other in species richness, any difference in diversity was attributable to differences in evenness.

Increased species richness was found by both Welch et al. (2000) and Arthur et al. (1998) in burned plots. However, Arthur et al. (1998) included both trees and herbs in their calculation of species richness, and the richest plots overall were those that included the most herb species. After a prescribed fire on xeric slopes in the southern Appalachian Mountains of Georgia, Elliott et al. (1999) found decreased diversity, species richness, and evenness in mid-slope plots that burned moderately severely. They concluded that many infrequent species disappeared on the mid-slope plots. On the other hand, in the most severely burned ridge top plots they measured increased evenness and diversity. The decreased evenness and diversity results on mid-slope sites of Elliott et al. (1999) are in keeping with those of this research conducted predominantly on mid-slope plots.

Forest Dynamics

Surface wildfire may create favorable conditions for uncommon species in the unburned forest. These are likely shade-intolerant species that gradually become less dominant in maturing hardwood stands. Of the three environmental factors potentially changed by burning, higher light availability and reduced competition may be only temporary phenomena; and indication of higher nutrient availability was not present in burned plots. As seedlings and saplings in the higher density burned plots continue to grow, any gain in light availability at the soil surface will decrease, competition will become intense, and mortality may become extremely high in the next couple of years. Oliver (1981) suggests that where rapid regrowth occurs, colonization should reach a peak soon after disturbance. First-arriving plants enjoy greater availability of resources than later arrivals, and establishment of seedlings of many woody plants is often limited to 1-5 years post-disturbance. Additionally, the number of plants present at a site soon after a disturbance generally will far exceed the number of plants that will reach reproductive size. Thus, differential growth rates should be important in competition during the early stages of biomass recovery (Canham and Marks, 1985).

The two greatest benefactors from burning for this research were shade-intolerant species, tulip poplar and black locust. Compared to its overstory relative density, tulip poplar had a slightly greater relative density in the understory of unburned plots, but had a >300% greater relative density in the burned understory. The species had a >350% greater understory abundance in burned over unburned plots, and had almost twice the relative density in burned plots. Black locust was very poorly represented in the overstory; only two individuals were located with a dbh >10 cm. In the unburned forest

the species was only sparsely represented in the understory, but density was higher by >1150% in burned plots. If the tulip poplar and black locust seedlings and sprouts in the burned plots are able to grow more quickly than shade-tolerant species in the couple of years following the burn and avoid intense competition for decreasing light availability at the ground surface, then they potentially will have an opportunity to increase canopy representation.

The hypothesis proposed by Abrams (1992) and Delcourt and Delcourt (1998) that fire played an integral role in fostering the dominance of oak species, and oak community associations, in the southern Appalachians is intriguing. Arthur et al. (1998) and Elliott et al. (1999) proposed that reintroduction of a fire regime may help oak reproduction and sustain the classical depiction of the southern Appalachian forest. They found that *Quercus* seedling numbers increased significantly in the post-burn forest. In Blood Mountain Wilderness, white, chestnut, and black oak each differed significantly between burned and unburned plots, and each had greater understory density in burned areas. Northern red oak and scarlet oak did not significantly differ between burned and unburned plots. Chestnut oak did not have as high a relative density in the understory layer as the species had in the canopy. This could be an indication, in conjunction with the overstory size distributions of northern red oak and white oak, that despite the surface wildfire, oak may be declining in dominance on sub-mesic slopes in this study area. Harrod et al. (1998) explained that low juvenile oak survivorship might be due to competition from more shade-tolerant species, such as *Nyssa* and *Acer rubrum,* in northeastern oak forests.

Red maple, a shade-tolerant species, has likely increased in abundance in the southern Appalachians due to fire suppression (Arthur et al. 1998, Elliott et al. 1999). Some evidence suggests that the physiology of red maple may be more sensitive to fire than other hardwoods (Reich et al., 1990). In Blood Mountain Wilderness red maple had greater representation in the understory layer than in the overstory. Red maple density was greater on burned sites; however red maple's relative density was identical in burned and unburned plots. Regardless of burning, red maple was the most abundant species in the understory.

Published results pertaining to red maple abundance in post-prescribed burned plots are mixed. Lorimer (1984) examined four oak forest stands in Massachusetts and New York, and found that red maple is replacing oak in second growth stands. Burning was found to have only a minimal effect on red maple density and none on basal area. Welch et al. (2000) found numerous red maple sprouts after one burn. Contrary to a hypothesis that multiple burns would rid the understory of fire intolerant species, which supposedly includes red maple, this species increased in sprouting on a site burned twice (Arthur et al. 1998). Waldrop et al. (1992) showed that post-burn increases in red maple were difficult to control, and they persisted even after 43 years of annual winter burning on the Atlantic coastal plain. Fire did substantially reduce red maple in the understory and overstory after a prescribed burn in the north Georgia mountains, which coincided with a promotion of growth and recruitment of oak species (Elliott et al. 1999).

The long-term effect of the wildfire on stand structure and composition may not be apparent for years to come, and very few examples of long-term sampling and analysis exist in eastern oak forests. Ward and Stephens (1989) analyzed 55 years of change in 9

adjacent strip transects established in 1926, a third of which burned in a surface fire in 1932. From 1934-1957 regeneration in burned transects was dominated by oak, while for the same period red maple dominated regeneration on unburned transects. By 1987, 55 years after the fire, burned transects had higher relative and absolute dominance of oak, birch, and hickory, while red maple dominated unburned transects. Post-fire vegetation parameters in Blood Mountain Wilderness are somewhat different. Although some oak species have higher density in burned plots, red maple clearly dominates the understory in both burned and unburned plots. The effect of this surface wildfire may actually have the counter effect to that of the stand examined by Ward and Stephens: red maple and shade-intolerant species will likely gain in future canopy dominance, while the oak species will apparently continue to decline in status.

Gap Partitioning Hypothesis

The gap partitioning hypothesis states that along an environmental gradient trending from the middle of a canopy gap to a point in the non-gap forest, different species will differentially utilize the various niches. This differential niche affinity hypothetically acts to develop and/or maintain species diversity. For acceptance of the gap partitioning hypothesis, variation in understory species diversity, richness, and/or composition should be evident between the center of gaps and a point in the non-gap forest a short distance from the border of the gaps. ANOVA showed that the effect of gapping on diversity was significant, although quadrat position and combinations of effects were not significant. Diversity was greater in the non-gap quadrats. Species

richness, evenness, and understory species composition did not differ significantly due to the effects of gapping, quadrat position, or combinations of these effects.

The effect of quadrat position and the combination of gapping and quadrat position were not significant for any of the analyses. The sampling scheme was devised to provide measurements of two contiguous portions of the gaps. Inner gap quadrats would potentially have more consistent exposure and greater variation in micro-environmental characteristics due to a completely open canopy, whereas the outer gap quadrats would be located closer to the border of gaps where canopy extension may moderate the effects of gapping somewhat while still providing a potential for increased light relative to the non-gap understory. The non-gap quadrats would then complete the measurement of the hypothesized gradient by providing samples of the areas under complete canopy cover. Thus, the fact that none of the analyses returned significant differences for quadrat position and the combination of quadrat position and gapping indicated that species were not differentially utilizing the various niches along an environmental gradient. Additionally, shade-intolerant species should theoretically find gaps more favorable environments for regeneration; however none of the shade-intolerant species significantly differed between gaps and non-gaps.

On mesic northern aspects in *Tsuga*-mixed hardwood deciduous forests in the Great Smoky Mountains National Park (GSMNP), Busing and White (1997) found no evidence of gap partitioning. They noted that few gap specialists were found, and most species occurred along the entire gap to non-gap gradient. During a controlled experiment in New England where red, striped (*Acer pensylvancium* L.), and sugar maple (*Acer saccharum* Marshall.) were transplanted, Sipe and Bazzaz (1995) did find an

environmental gradient in mean daily photosynthetic photon flux (PPF), which was paralleled to varying degrees by mean daily air and soil temperatures. Growth and survival of all three species paralleled each other along the entire PPF gradient, with striped maple showing the most pronounced response, and sugar maple the least. Little evidence of partitioning was found, although some partitioning within gaps between northern and southern parts of large gaps was apparent. In a mid-successional second growth forest in eastern Tennessee, Wilder et al. (1999) also found partitioning within gaps in the northern and southern parts for maples, but again evidence for partitioning along the gap to non-gap gradient was not apparent.

<u>Density Hypothesis</u>

The density hypothesis states that high diversity in gaps is due primarily to the high stem density found in gaps. For the density hypothesis to be accepted, variation in density between gaps and the non-gap understory and a positive correlation between density and diversity and/or density and species richness must be found. However, in Blood Mountain Wilderness density did not significantly differ between gaps and non-gaps, and a negative correlation between density and diversity was obtained. Although species richness and density were significantly positively correlated, data from Blood Mountain Wilderness fail to support the density hypothesis due to the absence of significant differences between gaps and non-gaps for density and species richness.

In *Tsuga*-mixed hardwood forests of GSMNP, Busing and White (1997) concluded that the density hypothesis was the most likely explanation for elevated species richness in gaps. They suggest that in a forest that is dominated by intolerant

species the density effect may be less important. The stands studied for this research consisted of more species that are shade-intolerant or moderately shade-tolerant than the *Tsuga*-mixed hardwood cove forests of the GSMNP, which may explain why the results of the current research are not in keeping with those of Busing and White. In tropical forests of Costa Rica, Denslow (1995) found that the combined increases of density and species richness in gaps resulted in increased diversity. High treefall frequencies on slopes provided more establishment opportunities for more species in the higher density gap communities than in the non-gap forest.

The Effect of Burning on Analysis of the Gap Hypotheses

Given that burning alone had such a profound effect on understory diversity, density, species composition, and mean size class, one may be inclined to expect that burning also affected the outcome of the gap partitioning and density hypotheses. Burning was not significant in combination with gapping and/or quadrat position on the understory Bray-Curtis ordination axis scores, diversity, evenness, species richness, and density. Thus, burning did not remove or allow the expression of a gap to non-gap environmental gradient that influenced species regeneration, nor result in higher density and diversity in gaps.

CHAPTER 5

CONCLUSION

Severity of disturbance is one attribute that determines which perturbation type results in significant differences between control and disturbed plots. The severity of most surface wildfires is undoubtedly much greater than the severity of gap creation. Burning causes a high mortality rate in the understory that tree species may respond to by sprouting or seed germination. Depending on a species' ability to respond to the disturbance in either manner, it will likely increase in importance in a plot, or be lost. Surface wildfire does remove some of the midstory and most of the sapling layer, increasing light availability at the ground surface, decreasing competition, and enhancing conditions for shade-intolerant species, such as tulip poplar and black locust. In contrast, gaps are created by the death of one or more overstory trees, and mortality in the gap understory may not be higher than in the non-gap forest. Thus, the understory and midstory that develop under full canopy are probably preserved after gap creation in a relatively unchanged state. Without burning to reduce competition from the existing cohort of saplings, seedlings of shade-intolerant species may not find environmental conditions that facilitate germination and growth at the ground surface after gap creation. However, shade-intolerant species in an advanced-regeneration layer may overtop more slowly growing species in the higher light conditions and fill the gap. In Blood Mountain Wilderness, two factors may account for the absence of understory differences between gaps and non-gaps. First, the advanced-regeneration layer in gaps was likely established under the same conditions as the non-gap forest used as the control and would, therefore,

have been similar in composition. Second, the study plots were dominated by moderately

shade-tolerant generalist species (e.g., red maple), which may have shown less sorting

according to light levels than would have been the case with a pool of species more

varied in their shade tolerance.

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APPENDIX
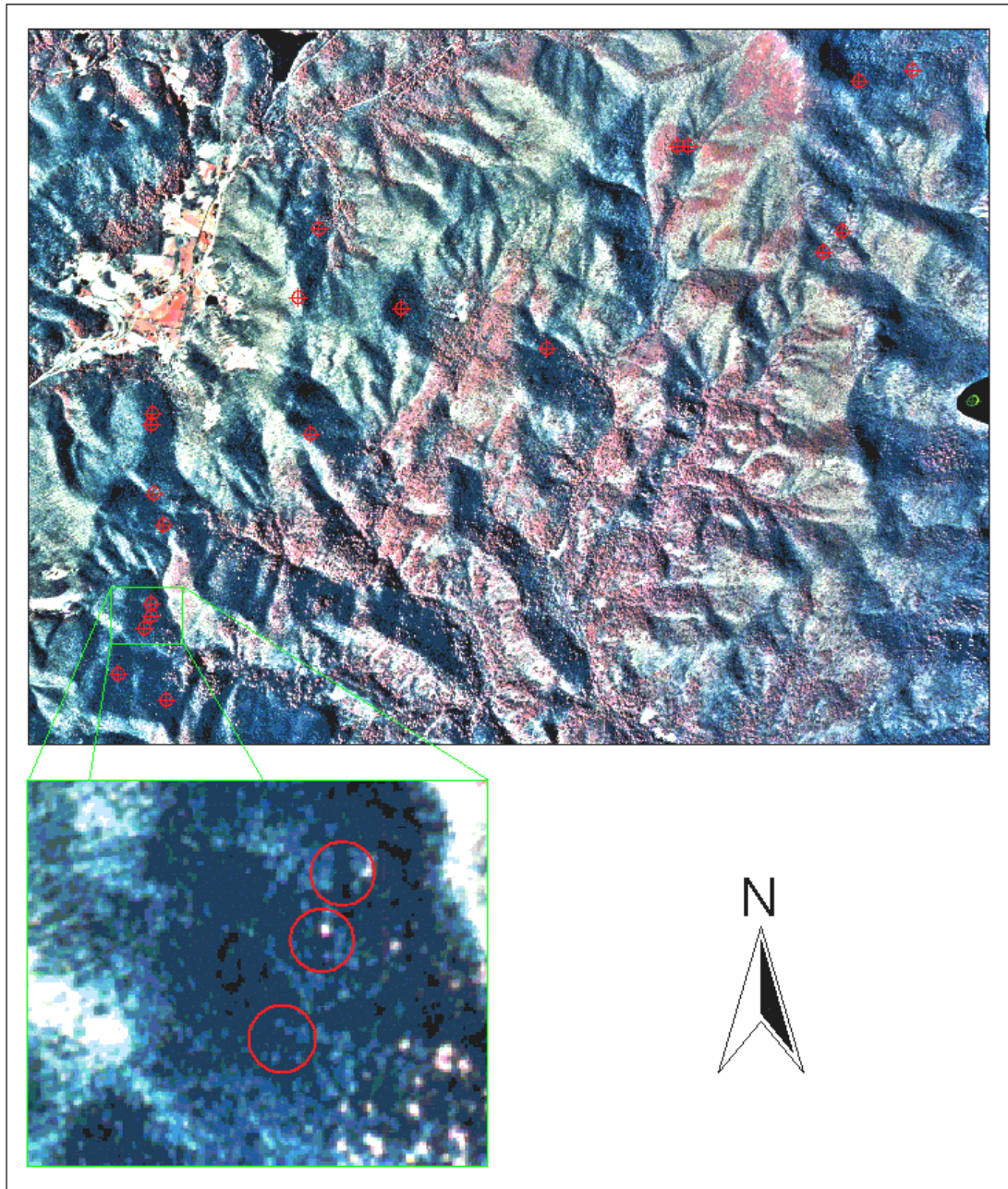
Appendix Figure: Examples of canopy gaps found on the orthorectified aerial photographs. Canopy gaps used as study plots circled in red in green inset box.