

Post-fire vegetation dynamics and
the invasion of *Paulownia tomentosa*
in the southern Appalachians

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ABSTRACT

Dane Mitchell Kuppinger
Post-fire vegetation dynamics and the invasion of
Paulownia tomentosa in the southern Appalachians
(Under the direction of Peter S. White)

The last two decades have seen an increased awareness of fire's importance in xeric southern Appalachian forest communities and an increase in its use as a management tool. In the last ten years, managers have also witnessed the invasion of *Paulownia tomentosa* (hereafter *Paulownia*) following some of these fires, and apparently as a consequence of the fires. If the pattern of *Paulownia* invasion is to be understood and the species targeted for control, it is essential to determine the variables that favor the spread of this exotic species into natural areas following fire and determine if it is impacting native communities or species.

This work found that fire increases similarity between locations as measured by species composition and that the strength of this effect increases with fire severity. This is counter to Ryan's Fire Severity Matrix which predicts that similarity will be negatively correlated with fire intensity. Although similarity between study sites increased after burning, each remained distinctive in ordination space and those differences increased over time as species reestablished themselves and environmental gradients shifted towards their pre-fire distributions in response to site-specific differences.

This thesis also documents *Paulownia* seed dispersal up to 3.5 kilometers from mature individuals; distances which are orders of magnitude greater than those over which

dispersal is generally measured. It also demonstrates that although *Paulownia* seeds may enter the seed-bank under appropriate conditions, they are killed by all but the least severe fires unless protected by burial. These buried seeds, even when only under 2cm of soil in the absence of litter, exhibit very limited germination. Together this demonstrates that invasion is controlled by the yearly seed rain rather than an accumulation of seeds within the seed-bank. Habitat models document *Paulownia*'s range restriction over time as the initially prevalent high light and low competition conditions disappear with increasing native vegetation cover. *Paulownia* habitat is however maintained along cliff margins and narrow, shallow soiled benches suggesting that *Paulownia* will persist where these land forms are present. Although no significant correlation was found between *Paulownia*'s presence or cover and native species cover or diversity, this may not continue as *Paulownia*'s cover increases with stem maturity.

To my parents for starting me on the path,

To the teachers who have shown me the way,

And most of all

To my wife Ellen and children Sorrel and Quetzal who give me inspiration

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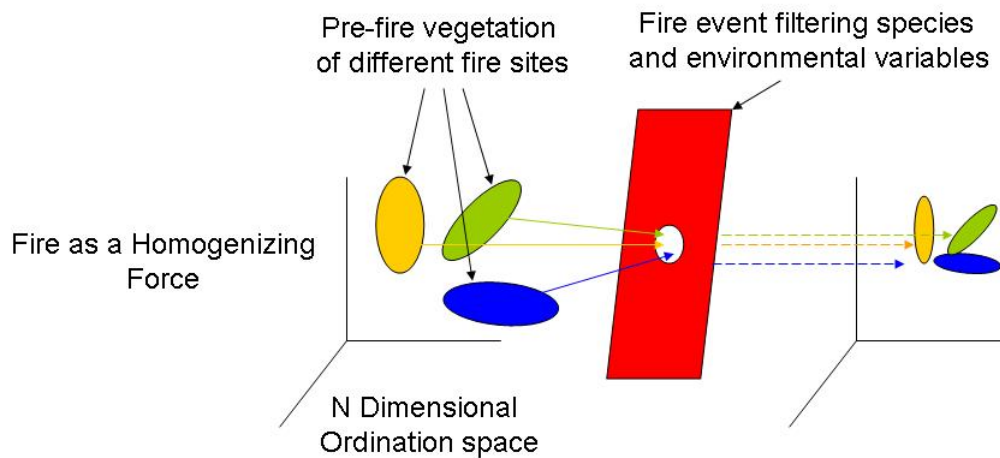
CHAPTER I: Introduction

INTRODUCTION

The invasion of exotics is often facilitated by disturbance because disturbances generally increase resources, including space, and/or decrease competition. However, disturbances vary considerably in severity and therefore on their effect on invasion patterns. In addition to disturbance, the availability and character traits of both native and exotic species, and the underlying habitat characteristics are important to understand patterns of invasion (Hobbs 1992, With 2002) and post-disturbance recovery patterns. This thesis examines these interactions in documenting the role of fire in the invasion of *Paulownia tomentosa* (hereafter *Paulownia*) in the southern Appalachians and assesses the interactions between *Paulownia* and native plants in a community's response to fire. In doing so, it increases our general knowledge about post-fire vegetation dynamics and our understanding of this exotic species. There is also a strong applied rationale for this work; land managers seek to reintroduce fire as a natural process in the southern Appalachians, but do not want to simultaneously encourage the establishment of exotic species, nor decrease the abundance of native fire dependent species through increased competition with exotics. Two conceptual models organize the questions addressed in this work. The first is a model of fire's effects

upon vegetation community distinctiveness and the second is a model of *Paulownia*'s life cycle

Conceptual model of fire effects

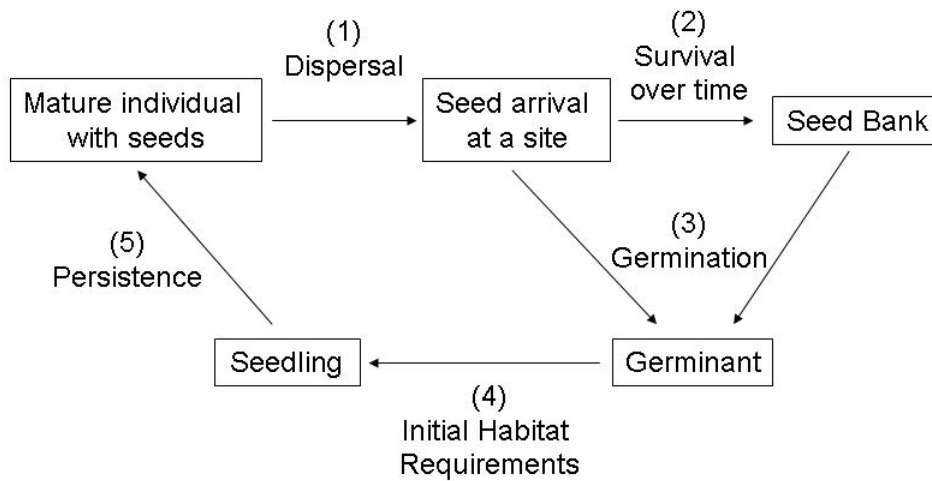


Under this model, fire acts as a homogenizing force, decreasing species diversity and cover and increasing similarity between communities. The degree to which this occurs, the size of the holes in the “fire filter”, is a function of fire severity. Under the model fire has a homogenizing effect because only particular species survive and environmental variable distributions are consistently skewed in the same direction, thus bringing individual landscapes (different burned areas) closer together in ordination space. The more intense the fire, the smaller the holes in the “fire filter”, and the closer sites are clustered in ordination space. Over time, the space occupied by different burned areas increases and they move apart in ordination space as species reestablish and the similarity of environmental variable gradients decreases in response to site specific differences.

I tested this model by analyzing how the fire severity experienced at each plot relates to its position within ordination space relative to other plots within the same fire and between

fires and how these positions change with time since the fire. I hypothesized that plots which experienced high severity fires would be closer to each other than those experiencing low severity fires and that plots and sites would become less clustered over time. Although the pre-fire configuration of sampled sites within each location studied in this dissertation is not known, the post-fire change within and between locations over time, and the environmental gradients which differentiate locations are analyzed in Chapter II.

Conceptual model of Paulownia's life history



Under this model of *Paulownia*'s life history, there are five transitions of importance to its invasion dynamics: (1) Seed dispersal, (2) Seed survival over time through incorporation into the seed-bank, (3) Seed germination, (4) Initial habitat requirements, and (5) Seedling persistence to maturity. The factors controlling each of these transitions is poorly understood and is the focus of individual chapters; dispersal in Chapter III, germination and survival over time in Chapter IV, initial habitat requirements in Chapter V, and persistence in Chapter VI. Specific questions addressed in each of these chapters are given below.

BACKGROUND

Fires produce a great range of conditions due to the interactions of weather, vegetation structure and topography, the three components of the “fire environment” (Ryan 2002). The fire environment in turn interacts with position within the fire (Backfire, Flankfire, or Headfire) to produce the fire behavior and fire effects at each point. The fire effects at each point and the spatial pattern of fire effects then determine the pattern of community recovery. Fire effects on regeneration modes were described by Ryan (2002) through the development of a Fire Severity Matrix (Figure 1.1). The matrix’s two axes (above and below ground fire effects) enclose a domain in which Ryan placed recovery strategies (resprouting, dispersal, etc) described as “first vital processes” by Nobel and Slayter (1980).

This matrix indicates that surface fire intensity and depth of soil heating act independently to influence the mode of regeneration favored in a given spot and that over the majority of the domain no single regeneration mode is in effect. Ryan’s model predicts that low levels of soil heating and low above ground fire intensities will produce a more predictable species response because of the dominance of ‘persistence’ (resprouting and fire resistance) modes of regeneration and of the seed-bank which integrates multiple years of seed rain to produce a more even suite of species across the landscape. In contrast, species’ responses to higher levels of soil heating and above ground fire intensity will be less predictable as spatially and temporally variable post-fire dispersal and recolonization will more heavily influence vegetation patterns. These predictions from Ryan’s Fire Matrix are in line with the recovery patterns observed by Turner *et al.* (1997, 1998) after the Yellowstone

fires though they do not incorporate the temporal and spatial scale patterns found to be significant in the Turner *et al.* (1989, 1997, 1998) studies. In contrast to the predictions of Ryan's model, the model presented here suggests that similarity between fires will be positively correlated with fire severity.

Although southern Appalachian xeric forests have not received as much attention as other fire prone communities, fire played a significant role in determining stand composition and structure prior to widespread suppression efforts initiated ca. 1930 (Harmon 1982, Harrod *et al.* 1998). Past work by Frost (1998), Frantz and Sutter (1987), Harmon (1982), Harrod *et al.* (1998), and Sutherland (1995) has indicated that these communities experienced low severity fires at a mean Fire Return Interval (FRI) of 12 years which maintained open woodlands with high severity fires, at ~100 yr FRI, giving rise to the majority of pine regeneration. It is believed that historically the source of these fires was a mixture of natural (lightning) and anthropogenic (Native Americans and settlers) intentional and accidentally set fires (Barden and Woods 1973, Bratton and Meier 1998, Harrod *et al.* 1998, Harmon *et al.* 1983).

The essential nature of fire in these ecosystems is evidenced by the southern Appalachian endemic *Pinus pungens* (Table Mountain Pine), which is limited to the following xeric forest and woodland Alliances: *Pinus virginiana* Forest Alliance, *Tsuga caroliniana* Forest Alliance, *Pinus pungens* – (*Pinus rigida*) Woodland Alliance, *Pinus (rigida, pungens, virginiana)* – *Quercus prinus* Woodland Alliance (NatureServe, September 4th, 2007). *P. pungens* has serotinous cones and experiences the highest recruitment rates with either a single medium-high severity fire (Waldrop and Brose 1999) or multiple low severity fires (Waldrop *et al.* 2002). Its range is entirely contained within the ranges of *P.*

rigida and *P. virginiana* and of the three it is the rarest and is generally confined to the most xeric sites (Zobel 1969). While the abundance and distribution of this species may have shifted over time in response to fire frequency and rainfall levels, increasing during periods of drought and high ignition rates, this species would not have evolved or persisted without regular fires (but see Barden 1977, 1988).

Unlike the *Pinus palustris* forests of the southeastern Coastal Plain, these mountain pine forests are highly spatially fragmented. Due to the high rainfall received by most areas of the southern Appalachians, xeric forests are limited to dry, rapidly drained ridges and crests below 1,000 m in elevation (Whittaker 1956). In addition to the Alliances listed above, the following forest and woodland Alliances are found in these areas (hereafter referred to collectively as xeric forests): *Pinus echinata* Forest Alliance, *Pinus virginiana* Forest Alliance, *Pinus echinata* - *Quercus* (*alba*, *falcata*, *stellata*, *velutina*) Forest Alliance, *Pinus echinata* – *Quercus* (*coccinea*, *prinus*) Forest Alliance, *Pinus echinata* Woodland Alliance, *Pinus echinata* - *Quercus stellata* – *Quercus marilandica* Woodland Alliance, *Pinus virginiana* Forest Alliance, *Quercus prinus* – *Quercus* (*alba*, *falcata*, *rubra*, *velutina*) Forest Alliance, *Pinus* (*rigida*, *pungens*, *virginiana*) - *Quercus prinus* Woodland Alliance, *Pinus rigida* – *Quercus* (*alba*, *stellata*) Woodland Alliance, *Pinus rigida* Woodland Alliance, NatureServe, September 4th, 2007). The fragmented nature of these communities means that historically, individual fires rarely burned across the majority of the habitat patches within a landscape. As a consequence, stand maintenance required higher ignition frequency and density than necessary in a more contiguous habitat like the Long Leaf Pine ecosystem.

The cover of these forest communities has been significantly reduced over the last ~70 years largely as a result of fire suppression policies (Harmon 1982). Fire suppression

has lead to an increase in the density and diameter at breast height (dbh) of fire sensitive species like maple and white pine. As a result of their increased size and bark thickness, a greater proportion of these hardwoods are now resistant to fire. This, combined with the buildup of litter and duff, dead woody debris, and ladder fuels, has resulted in forests that exhibit fire dynamics and recovery patterns that differ from their historic dynamics (Harmon 1984).

Although there is an increased understanding of fire's role in these ecosystems (Harrod *et al.* 2000, Harmon *et al.* 1998, Welch *et al.* 2000, Welch and Waldrop 2001, Wimberly and Reilly 2007), the potential for high severity fires within these communities has limited managers' ability to allow naturally occurring fires to burn without control. This has given rise to an increased use of prescribed fire, but these have not always effectively restored the historic state of the ecosystem (Waldrop *et al.* 2002).

Paulownia tomentosa

In the 1990's researchers and land managers began to see *Paulownia* establishment after burning in native xeric plant communities in the southern Appalachians. Although *Paulownia* had been a common invader along roadways and other areas significantly impacted by human activity for years (first recorded in the Great Smoky Mountains National Park (GSMNP) in 1975 in association with major road cuts, Baron *et al.* 1975), and occasionally a few individuals had been seen in native plant communities following hurricanes (Williams 1993), these post-fire invasions marked the first time that the species had been seen in significant numbers in native plant dominated communities following

disturbance. To date, *Paulownia* is the only exotic species that has been observed with any regularity in these xeric communities following fire.

Paulownia tomentosa, first recorded in the United States in 1844 (Hu 1961), is native to Southeast Asia (China and Japan) and was first brought over for horticultural purposes. It is a member of the Scrophulariaceae family and there are 6 species within the genus (*P. tomentosa*, *P. glabrata*, *P. elongata*, *P. fortunei*, *P. kawakamii*, and *P. fargesii*, Hu 1959). Three of these (*P. tomentosa*, *P. elongata*, and *P. fortunei*) have been grown in the United States for various purposes including horticulture (Hu 1961), goat browse (Mueller *et al.* 2001), strip mine reclamation (Tang *et al.* 1980), lumber (non-structural), pulp (Hu 1961), and as an intercrop tree (Wang and Shogren 1992).

P. tomentosa possesses many characteristics often associated with invasive behavior: rapid growth, high seed output (~2 million seeds/tree/year), vigorous re-sprouting, and a short juvenile period (7-10 yrs), yet until the recent post-fire invasions the species had not exhibited invasive behavior. Of the six *Paulownia* species mentioned above, only *P. tomentosa* has demonstrated invasive tendencies although *P. elongata* has the potential for faster growth (Mueller *et al.* 2001).

In China and Japan *Paulownia* species are a minor component of deciduous mesophytic forests. There, as in the United States, it is most commonly associated with human and natural (landslides, active river banks) disturbances and it germinates primarily on tip-up mounds due to its weak primary root and limited seed energy reserves (insufficient to penetrate litter). Although it matures rapidly, by the time an individual reaches maturity, the growth of more shade tolerant species beneath it usually precludes the establishment of further individuals in the absence of additional disturbance. In China, *Paulownia* species

also have a long history as intercrop trees (Wang and Shogren 1992), uses in traditional medicine (Hu 1961), as a source of lumber (non-structural), and fuel (Hu 1959).

QUESTIONS ADDRESSED

In studying the systems discussed above, the chapters of this dissertation address the following questions:

Chapter II

This chapter tested the hypothesis that, counter to Ryan's model, vegetation composition will become increasingly predictable with increasing fire severity. Specifically, this chapter addressed whether the sampled variables were correlated with increases in species diversity; whether sampled locations (individual fires) formed distinct groups within ordination space and the variables responsible for their differences; the effect of fire severity upon plot and site position within ordination space; and the changes in plot location over time in ordination space.

Chapter III

This chapter identifies the degree to which dispersal limitation plays a role in *Paulownia* invasion following fire. Specifically this chapter addresses how far *Paulownia* seeds disperse from mature trees, and whether similar dispersal distances and densities are predicted by seed-bank and seedling data.

Chapter IV

Chapter IV addresses the Germination and Survival over Time transitions through three experiments. Experiment #1 addressed the Survival over Time transition and asks whether germination varied between populations; how storage type (dry, field, cold storage) affected germination; and at what rate did seed viability decrease over time? Experiment #2 addressed the Germination transition by analyzing how a 50% reduction in light, the presence (or absence) of litter, and seed position (seeds buried at 2cm, on the soil surface, or on the litter surface) affected the rate of germination? Experiment #3 addressed the Survival over Time transition by investigating the ability of *Paulownia* seeds to survive fire. Specifically it addressed how seed position (buried at 2cm, at the soil surface, or on the litter surface) and fire intensity (measured by maximum temperature, duration of heating, duration or occurrence of temperatures about a certain threshold) affected seed survival as measured by germination,

Chapter V

Chapter V addresses the Initial Habitat Requirements life history transition by identifying the environmental, spatial, and fire-mediated biotic variables which correlate with *Paulownia* invasion as measured by its presence-absence and the number of seedlings?

Chapter VI

Chapter VI tests the utility of the *Paulownia* habitat model developed in Chapter V by asking whether it gives meaningful predictions of habitat in Linville Gorge. This chapter also addressed the Persistence transition of the life history model by analyzing the conditions

under which *Paulownia* persisted over the sampled time period? Finally, this chapter addresses *Paulownia* impact by asking whether its presence/absence, cover, or abundance were negatively correlated with native species.

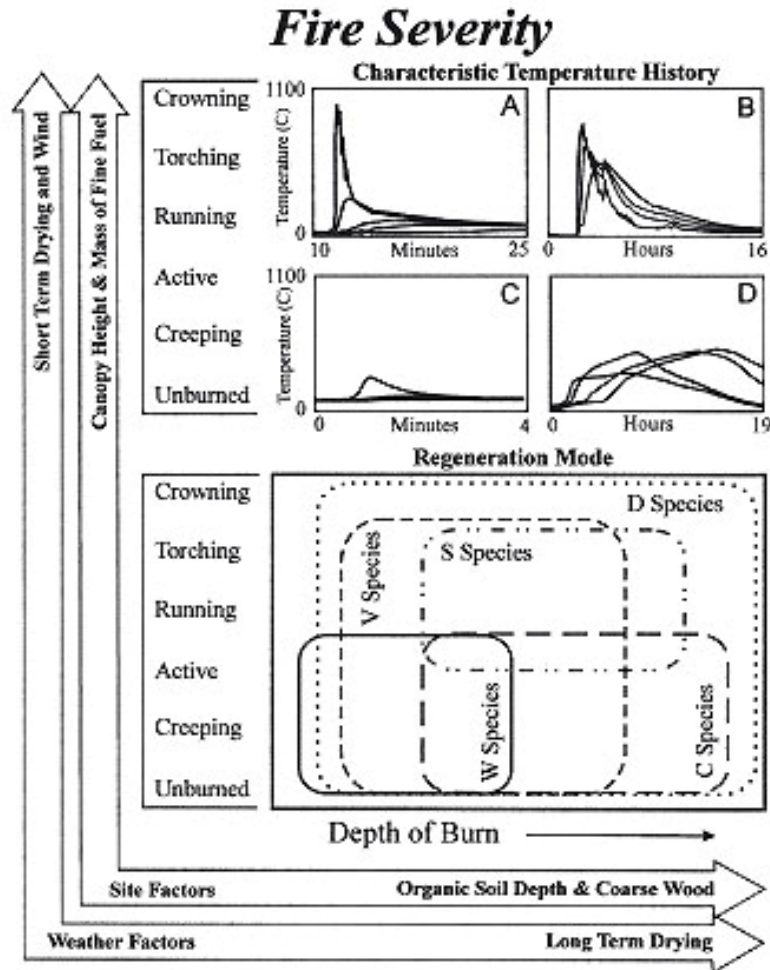
Chapter VII

Chapter VII examines the seed-bank composition of xeric forests of the GSMNP and asks what species were present and how were they distributed. It also compares the composition of the seed-bank with the extant vegetation of these communities as recorded in vegetation plots.

TABLES AND FIGURES

Figure 1.1: Fire Severity Matrix from Ryan 2002. Within the matrix, the difference in conditions is illustrated in two ways. The Characteristic Temperature History diagrams show the temperatures experienced at different heights above and below ground and the Regeneration Mode diagram maps the mode(s) of reproduction and survival at play across the matrix.

Figure 1.1: Fire Severity Matrix from Ryan 2002. Within the matrix, the difference in conditions is illustrated in two ways. The Characteristic Temperature History diagrams show the temperatures experienced at different heights above and below ground and the Regeneration Mode diagram maps the mode(s) of reproduction and survival at play across the matrix.



Changes in site variables, including terrain and vegetative structure and weather, lead to fires of different peak temperatures and duration. Arrows indicate increasing site and weather potential. Both site and weather conditions must be met to affect fire intensity.

Characteristic Temperature History: Representative temperature histories for fires of varying severities

- A: Crownfire / low depth of burn (DOB) B: Crownfire / moderate DOB
- C: Active surface fire / low DOB D: Creeping surface fire / moderate DOB

Regeneration Mode: Modes of regeneration and reproduction, Noble and Slatyer's first vital processes (1980)

Vegetative-based

- V species - able to resprout if burned in the juvenile stage
- W species - able to resist fire in the adult stage and to continue extension growth after fire (although fire kills juveniles).

Disseminule-based

- D species - with highly dispersed propagules
- S species - storing long-lived propagules in the soil
- C species - storing propagules in the canopy

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CHAPTER II:

Effects of fire severity and site conditions on post-fire vegetation patterns in the southern Appalachians

ABSTRACT

Although fire is recognized as essential for the maintenance of southern Appalachian xeric forest communities, many questions about this dynamic remain unanswered. Vegetation and environmental differences between communities are not fully understood and it is unclear whether fire acts to accentuate or minimize these differences. This chapter addresses these questions through the use of vegetation survey data collected across five fires in western North Carolina and eastern Tennessee. Although fire acted as a homogenizing force across sampling locations, decreasing the distance between them in ordination space, each site still occupied a distinct area within that space. Plots which experienced higher severity fire were more tightly clustered in ordination space than those which experienced lower severity fires. Important environmental variables which distinguish plots and sites included: soil copper concentration (Cu ppm), soil manganese (Mn ppm), % sand, slope, elevation, calcium saturation (Ca %), pH, and the amount of remaining vegetation cover. Immediately after the fire, plots were tightly clustered within and between sites, but this decreased with time as species sorting reemerged, presumably as a result of underlying environmental differences between plots.

INTRODUCTION

Whittaker's classic study of the GSMNP vegetation (Whittaker 1956), provides a template for understanding the dominant environmental gradients determining community composition. In his diagrams, moisture and elevation are the two primary axes which determine community type, and though there have been subsequent minor revisions of these diagrams (Baron and Matthews 1977, Eager 1978, Johnson 1977), they remain essentially unchanged in their application. Although Whittaker's diagrams are not dependent upon disturbance per se, Harmon *et al.* (1983) demonstrated that those species distributions cannot be completely understood without understanding the disturbance regimes at play in each community.

The xeric forests of the southern Appalachians are dependent upon recurrent fires to maintain their composition and structure (Harmon 1982, Williams 1998). Conservationists often seek to restore fire as a natural process in ecosystem management, yet the effects of fire upon these ecosystems is not yet fully understood. The fire effects model developed by Ryan (2002) for western forests focuses on the single event, multi-patch scale and suggests that fire effects will vary with severity such that low severity fires (low levels of soil heating and low above ground fire intensities) will produce a more predictable species response because of the dominance of 'persistence' (resprouting and fire resistance) modes of regeneration and of the seed-bank. High severity fires (higher levels of soil heating and above ground fire intensity) will be less predictable as spatially and temporally variable post-fire seed-rain will more heavily influence vegetation patterns. Other work (Turner *et al.* 1998) has focused on the multi-patch multi-event scale and incorporated the spatial pattern

and scale of fire severity and extent. This work suggests that fire size and severity relative to the distance to and size of refugia will determine the importance and pattern of post-fire recolonization. Other work by Turner (1993) further suggests that the stability of the vegetation community over time is determined by the disturbance interval to recovery interval and fire extent to landscape extent ratios.

The work presented here tested the hypothesis that, counter to Ryan's model, vegetation composition became increasingly predictable with increasing fire severity. Due to the increasingly fine grain of the fire effects filter as severity increases, fewer species were able to survive and species overlap between plots and sites increased. Specifically, this chapter addressed whether the sampled variables were correlated with increases in species diversity; did sampled locations (individual fires) form distinct groups within ordination space and what variables were responsible for their differences; what effect did fire severity have upon plot and site position within ordination space; and how did plot location change over time in ordination space.

STUDY AREAS

Plots were located across five fires in western North Carolina and eastern Tennessee (Figure 1.1, Table 1.1). These fires were selected following a thorough survey of recent fires in the southern Appalachians on National Park (GSMNP) and Forest Service (Pisgah, Cherokee, and Nantahala National Forests) properties which burned in 2000 or 2001. All fire names follow those given by the responsible agency and are named after the mountain, ridge,

or gorge that they are centered on with the exception of “Firebug”. Firebug was so named because there is no named feature at the site and because it was an arson fire. All plots were located within the boundaries of their respective fire.

Linville Gorge

The Linville Gorge wilderness area is located in the Pisgah National Forest and is split between 4 quadrangle maps: Linville Falls, Chestnut Mountain, Ashford, and Oak Hill. It is north of Lake James and the town of Morganton and south-southeast of the town of Linville Falls, in west-central North Carolina. Located on the Blue Ridge Escarpment, yet separated from the rest of the Appalachian Mountains, the Linville Gorge wilderness area encompasses 12,002 acres and is bounded by the Kister Memorial Highway to the west and the rim of the Gorge to the east. As the Linville River carved the gorge, it cut through the Blue Ridge overthrust to expose Late Precambrian layers beneath (Hatcher and Goldberg 1991). Most notable and striking of these are the Lower Quartzite layers which make up the steep bluff and cliff areas of the Gorge. For a full description of the geology and vegetation of Linville Gorge see Newell and Peet (1998).

The majority of the Gorge burned in November of 2000. In that fire, severity ranged from low severity ground fire to high severity crown fire. The plots in this study ranged in elevation from 645 to 1,185m, in slope from 2 to 38°, in aspect from 11 to 346°, and captured three rock types: lower quartzite, Wilson Creek gneiss, and Grandfather Mountain Formation meta-arkose. Of the 6 major vegetation communities types and 22 sub-types contained within the Gorge, 4 major vegetation types and 11 sub-types were sampled (Table 2.1). Like the xeric communities of GSMNP, the xeric communities of Linville Gorge have also experienced almost a century of fire suppression. Unlike the park, there is no prescribed fire

program for Linville Gorge. During the suppression interval these communities experienced shifts in composition, dominance, and structure from which they have not recovered (Harrod *et al.* 2000).

Green Mountain

Green Mountain is located in Tennessee in the Cherokee National Forest on the Hartford quadrangle. The mountain (and fire) forms a rough triangle bordered on the northeast by Interstate 40, on the northwest by the Foothills Parkway, and by private land on the south. Roughly the entire mountain burned during the 2001 fire which encompassed 2,262 acres. Fire severity ranged from low severity ground fire to high severity crown fire. The samples taken in this study ranged in elevation from 454 to 815m, in slope from 7 to 43°, and in aspect from 0 to 351°. No vegetation classification has been done for Green Mountain, but the overstory in sampled plots was dominated by *Pinus pungens*, *P. echinata*, and *P. virginiana* on drier sites, and *Quercus montana*, *Q. velutina*, and *Carya alba* on more sheltered sites.

Mill Ridge

Mill Ridge is located in North Carolina in the Pisgah National Forest west of the town of Hot Springs and south of Highway 25/70s. The Ridge is located on the Hot Springs quadrangle and the Appalachian train runs just east of it. The ridge and the fire which burned across all of it are fairly small, ~270 acres. An old logging road rings the majority of the ridge and another runs up one side of the ridge and along its top. Plots ranged in elevation from 759 to 839m, in slope from 7 to 17°, and in aspect from 112 to 218°. No vegetation classification has been done for Mill Ridge, but the overstory of sampled plots was dominated by *Quercus montana*, *Acer rubrum*, *Pinus echinata* and *Pinus strobus* in the

overstory, *Acer rubrum* and *Oxydendron arboreum* in the understory, and *Kalmia latifolia* and *Rhododendron maximum* in the shrub layer.

Daus Mountain

The Daus Mountain fire occurred in Tennessee on the edge of the Cumberland Plateau, south of Dunlap, North of Whitwell, and west of Highway 28. It burned the east face of Daus Mountain, including the northern part of Cartwright Gulf (also known as Lane Cove) on the Daus quadrangle. The fire burned ~1,000 acres and vegetation plots were located on private land owned by the Sequatchie Valley Institute near the mouth of Cartwright Gulch. Plots ranged in elevation from 399 to 424m, in slope from 12 to 43°, and in aspect from 58 to 264°. No vegetation classification has been done for Daus Mountain, but the the overstory of sampled plots was dominated by *Pinus virginiana* and *Quercus montana* and *Carya alba* in the overstory with *Oxydendron arboreum*, *Acer rubrum*, *Nyssa sylvatica*, *Pinus virginiana*, and *Quercus montana* in the understory.

Firebug

Firebug was located in the Cherokee National Forest, on the Tennessee-North Carolina border, and upriver from the Waterville dam on the Waterville quadrangle. The fire was south of Interstate 40 and the Pigeon River and Northeast of the GSMNP. Two of the fire boundaries were Road 1397 running along the park boundary towards Cosby and Road 1332 where it follows the river. Fire lines provided the other boundaries. The fire covered ~130 acres, and severity ranged from low severity ground fire to high severity crown fire. Plots ranged in elevation from 513 to 623m, in slope from 8 to 22°, and in aspect from 43 to 290°. The entire fire occurred on Siliciclastic metasiltstone. The plots captured the following vegetation communities: *Quercus montana*-*Acer rubrum*-*Oxydendron arboreum*

forest with sub-dominant *Pinus sp.* (yellow pine) and *Quercus montana* hardwood forest (Madden 2004).

METHODS

10x10m plots were spaced at 50m intervals along transects running across the slope. Transect length was determined by topography and transect locations were chosen to maximize the range of fire severities and landscape positions sampled within a burn. Geo-coordinates were recorded for each plot. Species were identified using the taxonomic standards of Weakley (2007). All plots were surveyed according to the North Carolina Vegetation Survey (CVS) protocol described in Peet *et al.* (1998) with the following variations and additions:

1. Plots were divided into 5x5m subplots rather than nested subplots.
2. Ground, herb, shrub, and tree coverage and dbh's were recorded at the subplot level.
3. The exact dbh of all stems >1cm was recorded. The dbh for stems that were not clearly dead prior to the fire but were dead at the time of sampling was recorded along with a species ID. In data analyses these were assumed to be fire killed.
4. Species cover was estimated for all shrubs that appeared to have been fire killed.
5. Estimates were made of the pre-fire cover by strata.
6. A spherical densiometer was used to record canopy cover from plot center.

7. Ground cover was estimated for: litter, boulder, cobble, humus, organic soil, and mineral soil. Minimum and maximum litter depth were measured along with a total humus cover measurement including the cover of exposed humus and that which was covered by litter. All measurements were taken at the plot and sub-plot level.
8. The number and height of all *Paulownia* stems within each sub-plot was recorded.
9. Fire severity within each plot was visually estimated on a 1-5 scale from percent dieback of each strata(shrub, understory, etc), scorch height, and resprouting frequency.
10. The spatial variables Hillshade and Topographic Convergence Index (TCI) were derived from the plot geo-coordinates. Hillshade measures the level of sunlight reaching a point and TCI is a measure of site moisture obtained by calculating the area of land which drains to a given point.

ANALYSES

Due to the circular nature of aspect, with each approach two transforms of the variable were tested for explanatory power in addition to the raw values. The first transform, the Beers transform, transforms aspect to a continuous scaled variable (0-2), set to maximum (2) for NE slopes and a minimum (0) for SW slopes (NW/SE=1) (Beers *et al.* 1966). The second transform split aspect into two variables, one measuring E-W orientation and the other N-S orientation (Lasting Forests 2008). The effect of environmental (slope, aspect,

ground cover, soil chemistry and texture) and spatial (hillshade, elevation, topographic position, TCI) variables upon native species diversity was tested in three ways.

The first analysis used a regression model with a negative binomial distribution to identify variables correlated with native diversity patterns (Dewdney 2000). The best fit model was determined on the basis of AIC values and the ratio of residual deviance to degrees of freedom. The fit of this model and a null model (specifying only the y intercept and dispersion parameters) was tested against the observed distribution by calculating the Pearson Statistic for a null hypothesis that the models provide an adequate fit to the observed richness distribution.

In the second analysis, a regression tree was developed to predict plot richness as a function of recorded environmental and spatial variables (Andersen *et al.* 2000). As there were no a priori assumptions as to the variables which controlled diversity, all recorded variables were tested in the model. The tree was pruned using the `cv.tree` and `prune.tree` functions in S-Plus to prevent over-fitting the data. The `prune.tree` function measures the deviance remaining in trees of different sizes. The `cv.tree` function measures the deviance of a random subset of 10% of the data (process repeated for all subsets) from values predicted by a tree built using the remaining 90% of the data. The regression tree was pruned to minimize both of these values.

Finally, species richness and the recorded environmental variables were analyzed using a Non-metric Multidimensional Scaling (NMS) ordination within PC-ORD (McCune and Grace 2002). Before importation into PC-ORD, plots with missing data were culled and species varieties were lumped to species. Within each plot, the greatest of the four subplot covers were used for each species' cover. Outlier plots were identified and removed via

outlier analysis and species coverages were smoothed using Beal's Smoothing technique. The NMS was conducted using Sorensen Distance measures, specifying a 2 axis ordination, and using the Varimax rotation (Mather 1976, Krustal 1964a, b). Output from the ordination was examined for trends in species richness and degree of clustering between sites, at different fire intensities, and over time.

RESULTS

Neither the linear regression nor the regression tree models provided a good fit of the observed richness distribution. In the linear regression model, this was demonstrated through the significantly poor fit of the predictive model ($p=.002$, Figure 2.2). A null regression model (specifying only the y intercept and dispersion parameters) also failed to produce a significant fit to the data ($p=0.00$, Figure 2.2). In the regression tree, lack of fit was seen in the high summed squared deviance values in the tree leaves (Figure 2.3).

In ordination space, richness was positively correlated with Mn ppm., Cu ppm., and vegetation cover overall (as measured with a densiometer). Richness was negatively correlated with elevation, maximum humus depth and the number of *Paulownia* stems (Figure 2.4). The most important driver of diversity was site with significantly higher species richness recorded at Daus Mountain than at any of the other sampled locations (Figure 2.5).

Sites did form distinct groups within ordination space though Mill Ridge and Daus Mountain had a high degree of overlap along the first ordination axis (Figure 2.4). Linville

Gorge and Daus Mountain. separated out along the second axis on the basis of Elevation and species richness with richness high and elevation low at Daus Mountain. and the opposite true for Linville Gorge. Green Mountain., Firebug, and Mill Ridge separated out on the second axis on the basis of soil nutrient variables (Figures 2.4).

Clustering decreased with time such that plots collected 1-2 years after a fire were more similar to each other than plots collected 3-4 years after the fire (Figure 2.6). This was due to the same, few species present immediately after the fire in most communities. As species recolonized the area and environmental gradients returned to their previous distributions, plot similarity decreased within and between fires. A similar, less pronounced, pattern was present when plots were grouped by fire severity with higher severity plots more closely clustered than lower severity fires (Figure 2.7).

DISCUSSION

The results of this study support my hypothesis that the predictability of species response immediately after fire (as measured by degree of clustering in ordination space) increases with increasing fire severity. Immediately after the fire, plots within and between sites were tightly clustered as a result of the limited suite of species able to survive; however sites remained distinct from each other. In terms of the conceptual model, the more severe the fire, the finer the fire-filter, and thus fewer species were able to pass through it, resulting in a smaller and more predictable suite of species. Over time, as species recolonized the landscape and environmental gradients played an increasing role in determining species

composition, within and between plots differences increased and clustering decreased correspondingly.

If Ryan's model is seen as an explanation of immediate post-fire species response, these results run counter to those predicted by his model. However, it may be more appropriate to see Ryan's model as predicting the subsequent paths within ordination space in the years following fire with sites that experienced low severity fire following more predictable paths back to their former positions. These paths would also be relatively shorter as these sites would have moved the least due to higher survival rates and the dominance of persistence modes of regeneration. Sites that experienced high severity fires would be less predictable in their path as the more variable process of dispersal plays a larger role in determining the path taken and potentially the future "climax" state as well.

Although there was a trend towards increasing richness with time, this was partially, obscured by richness differences between fires. Such a trend would however be expected as immediately after the fire many species have been locally extirpated. As time passes, species recolonize habitats and diversity increases till competition begins to push richness levels back down. Verification of this trend would however require different data from that in hand.

That linear regression and regression trees failed to predict species richness with any great degree of accuracy is not surprising for the reasons illustrated by the ordination. As it demonstrates, the environmental variables do not all impact plot richness in the same manner and many of the variables act orthogonally to plot richness. Consequently the richness of each plot is determined by a unique combination of variables and as such said variables do a poor job of predicting richness in a linear regression. Of those variables that are correlated

with richness in the ordination, the importance of elevation is largely a consequence of Daus Mountain's lower elevation and higher richness.

The positive correlation between vegetation cover and species richness in the ordination was not surprising as increased richness will to some extent inherently increase cover because of the increased number of individuals. Vegetation cover was also related to increased richness as a measure of fire severity. Less severely burned sites had more individuals (and species) that survived and so generally had higher vegetation cover and species richness levels than more severely burned areas with lower survival rates. Less intensively burned areas also had a greater probability of being wetter and more protected areas which likely supported greater species richness before the fire as well.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This study illustrates that southern Appalachian fire dynamics are not yet fully understood. Ryan's Fire Severity Matrix is shown to poorly predict immediate post-fire species response and a new model is presented to explain these dynamics. Ryan's model however provides a potential explanation of vegetation dynamics in the years following fire. The implication for land managers is that restoration projects seeking to return a community to a particular state through fire must consider fire severity and extent, the spatial/temporal context of previous and interacting disturbances, and species availability for recolonization.

TABLES AND FIGURES

Figure 2.1: Locations of sampled fires.

Table 2.1: Name, location, and ownership of the sampled fires along with the number of plots located at each, the date of the fire and the date of sampling.

Figure 2.2: Observed and predicted species richness distributions from generalized linear models with negative binomial distributions. The best fit model is shown in red and the null model is shown in blue.

Figure 2.3: Regression tree of environmental variables predicting subplot diversity. Values within the circles and squares are the mean diversity of that node. Values below them are the sum of the squared deviations from that mean. Analysis utilized data from all fires and plots. In the unlabeled version, branch length indicates the amount of variance explained by that division.

Figure 2.4: NMS ordination with all suitable plots (no missing data). Plots grouped by location (site) and overlaid by environmental variable regression lines. Lines point in the direction of increasing effect. Length of line indicates the strength of the relationship.

Figure 2.5: NMS ordination with all suitable plots (no missing data). Plots grouped by location (site). Side scatter plots and symbol size in the central graph show the magnitude and direction of increasing plot richness.

Figure 2.6: NMS ordination with all suitable plots (no missing data). Plots grouped by sampling date. Fires burned in 2000 (Linville and Firebug) or 2001 (Mill Ridge, Green Mountain, and Daw's Mountain).

Figure 2.7: NMS ordination with all suitable plots (no missing data). Plots grouped by Fire Severity. Severity was visually estimated on a 1-5 scale at the time of sampling.

Figure 2.1: Locations of sampled fires.

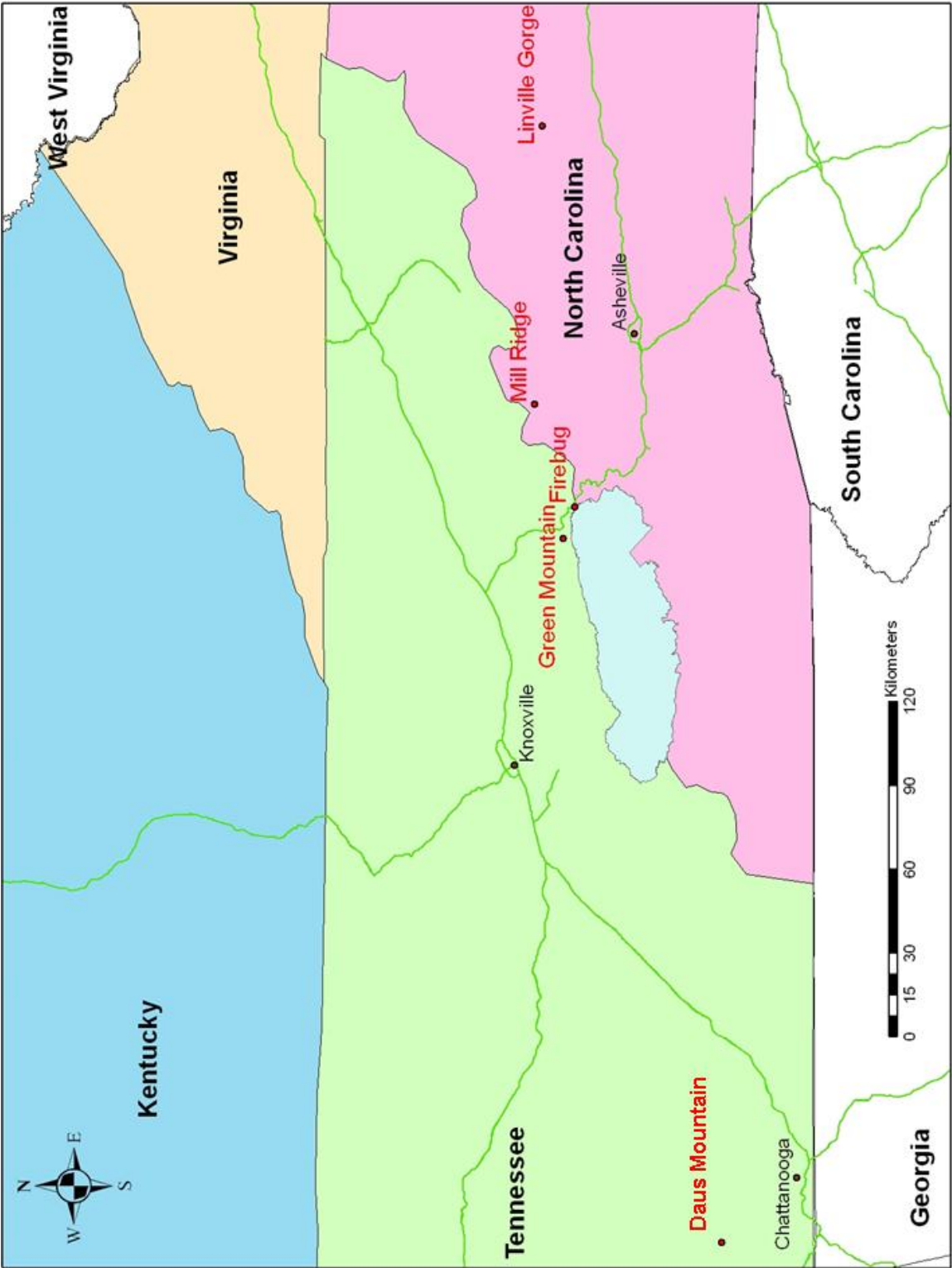


Table 2.1: Name, location, and ownership of the sampled fires along with the number of plots located at each, the date of the fire and the date of sampling.

Fire	Plot sampled by	# of Plots	Owner	State	Location	Fire Year	Fire Date	Sampling Dates
Linville Gorge	Kuppinger	45	Pisgah N.F.	NC	Linville Gorge, S. of Linville Falls	2000	Nov 10-14	June 25-30 2002, July 16-19 2002, July 9-11 2003
Linville Gorge	Reilly and Kuppinger	20	Pisgah N.F.	NC	Linville Gorge, S. of Linville Falls	2000	Nov 10-14	Summer 2003
Mill Ridge	Kuppinger	13	Pisgah N.F.	NC	Mill Ridge, S. of Hot Springs	2001	Fall	July 29-Aug 2, 2002
Green Mountain	Kuppinger	63	Cherokee N.F.	TN	Green Mtn. S. of Foothills Prkwy to Cosby	2001	Nov 11-Dec12	May 11-14 2003, June 16-28 2003, July 22-24 2004
Firebug	Kuppinger	14	Cherokee N.F.	TN	Between I40 and the GSMNP, W. of the TN/NC line	2000	Fall	July 22-25 2002, July 20-21 2004
Daus Mountain	Kuppinger	18	Private	TN	Sequatchie Valley N. of Dunlap	2001	Nov 5-7	July 29-Aug 3 2003

Figure 2.2: Observed and predicted species richness from generalized linear models with negative binomial distributions. The best fit model is shown in red and the null model is shown in blue.

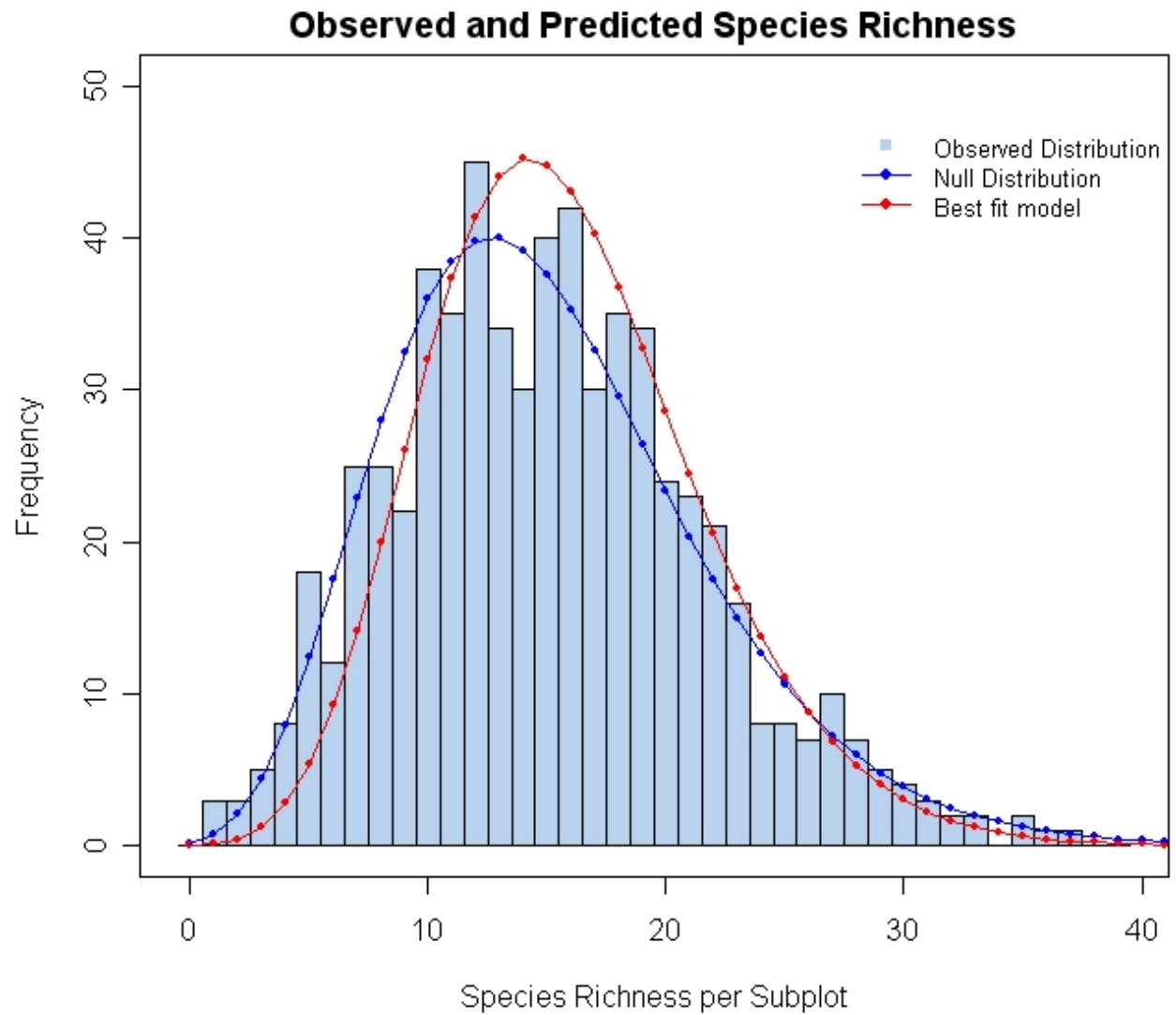


Figure 2.3: Regression tree of environmental variables predicting subplot diversity. Values within the circles and squares are the mean diversity of that node. Values below them are the sum of the squared deviations from that mean. Analysis utilized data from all fires and plots. In the unlabeled version, branch length indicates the amount of variance explained by that division.

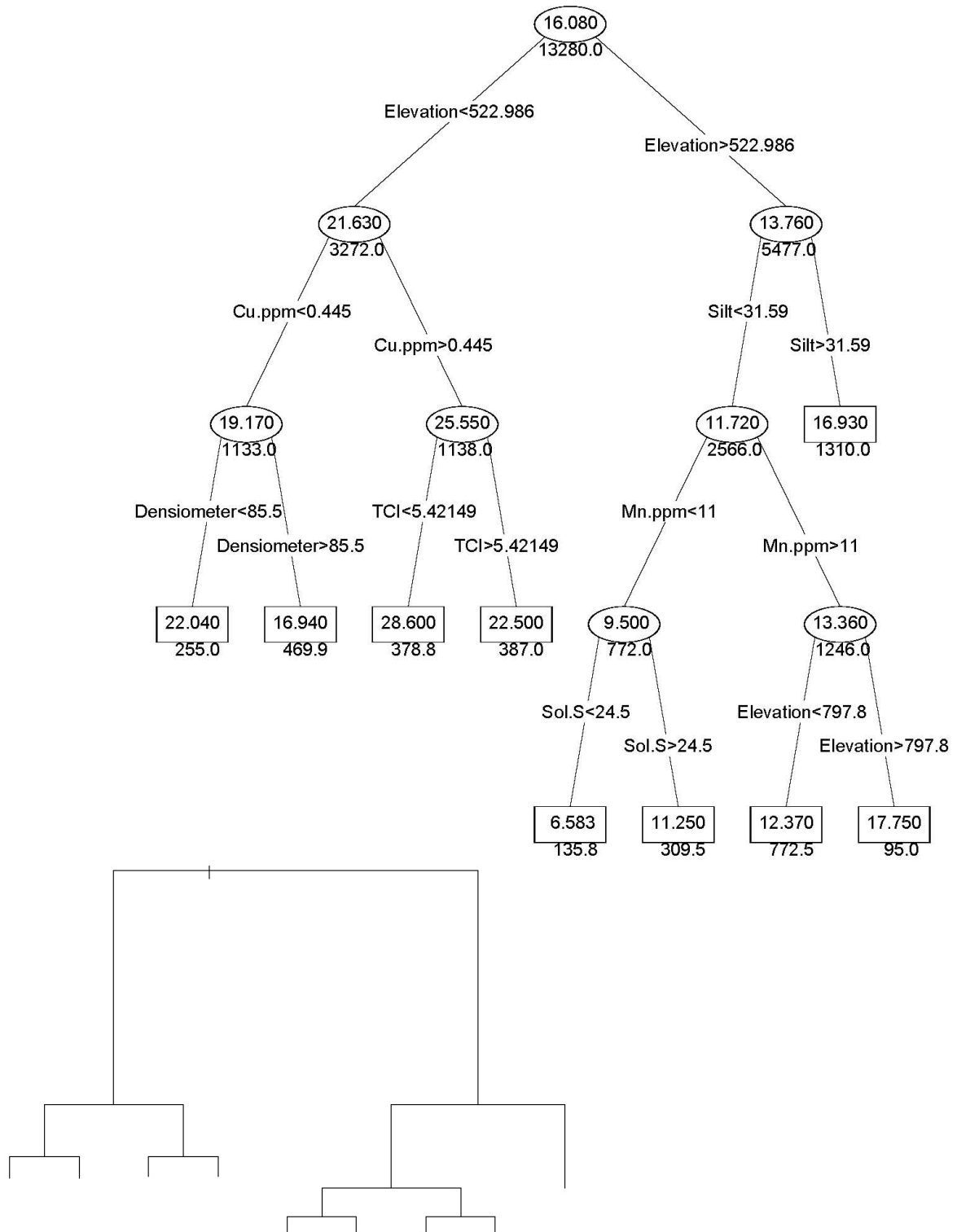


Figure 2.4: NMS ordination with all suitable plots (no missing data). Plots grouped by location (site) and overlaid by environmental variable regression lines. Lines point in the direction of increasing effect. Length of line indicates the strength of the relationship.

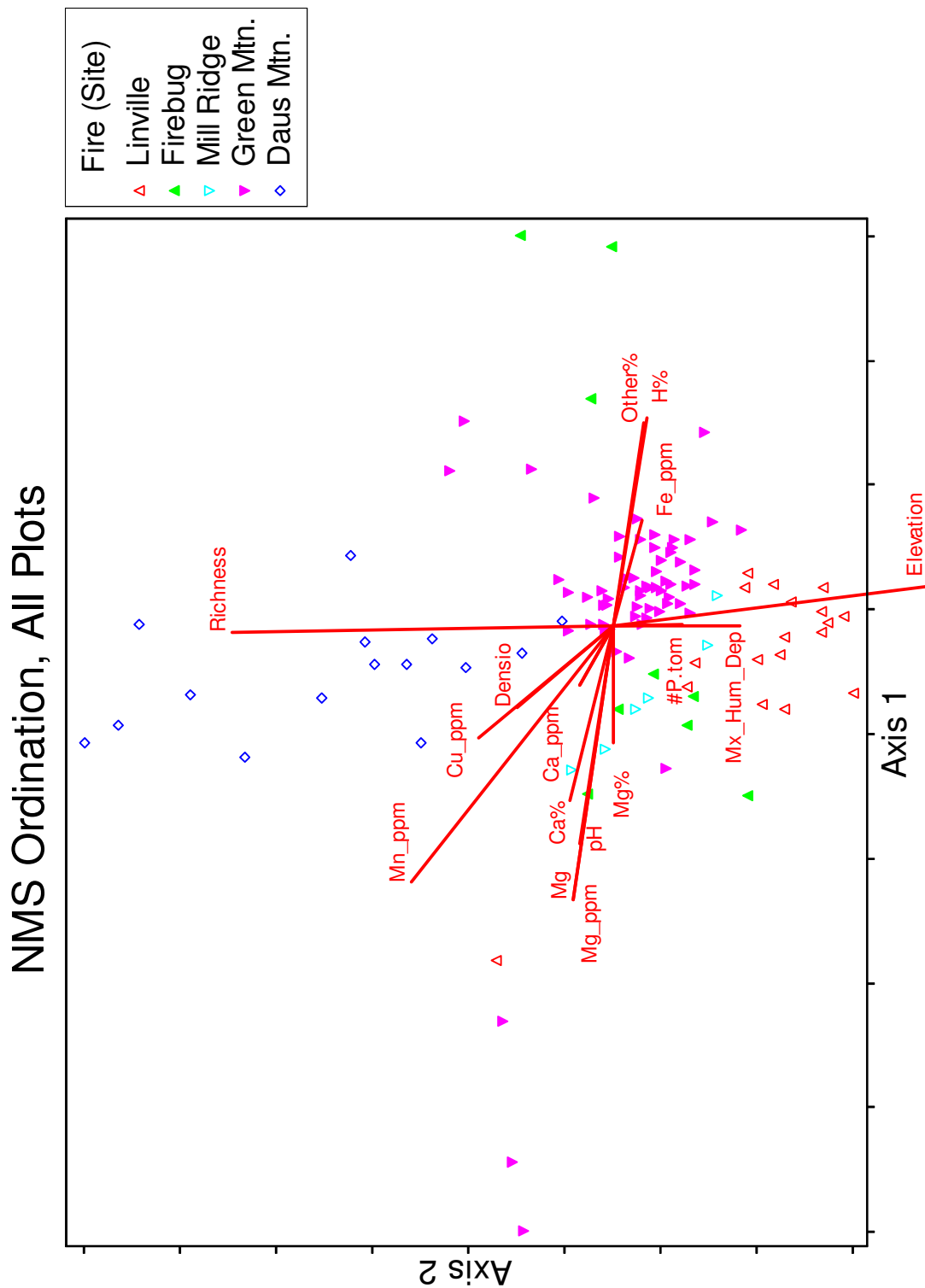


Figure 2.5: NMS ordination with all suitable plots (no missing data). Plots grouped by location (site). Side scatter plots and symbol size in the central graph show the magnitude and direction of increasing plot richness.

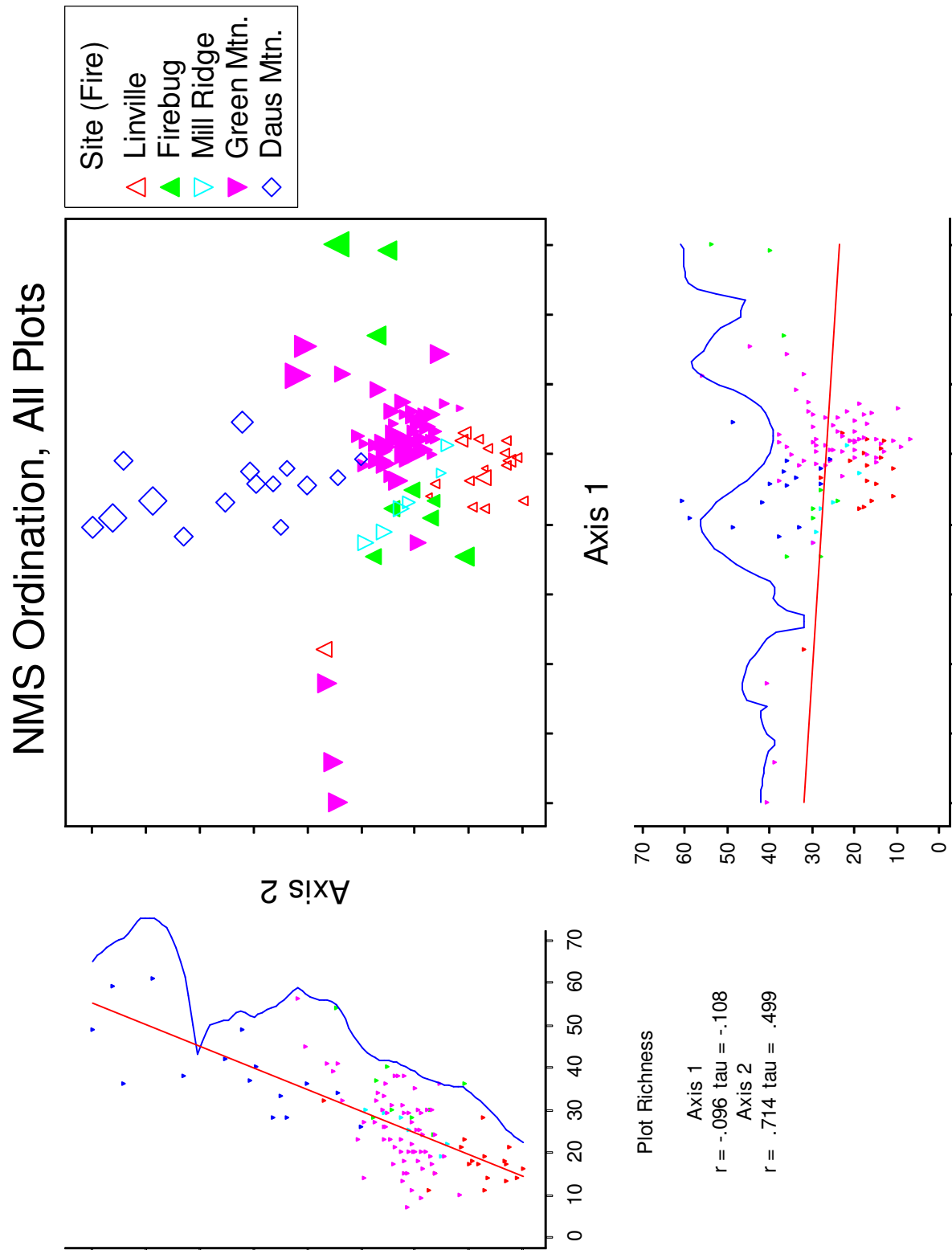


Figure 2.6: NMS ordination with all suitable plots (no missing data). Plots grouped by sampling date. Fires burned in 2000 (Linville, Firebug) or 2001 (Mill Ridge, Green Mtn., Daus Mtn.).

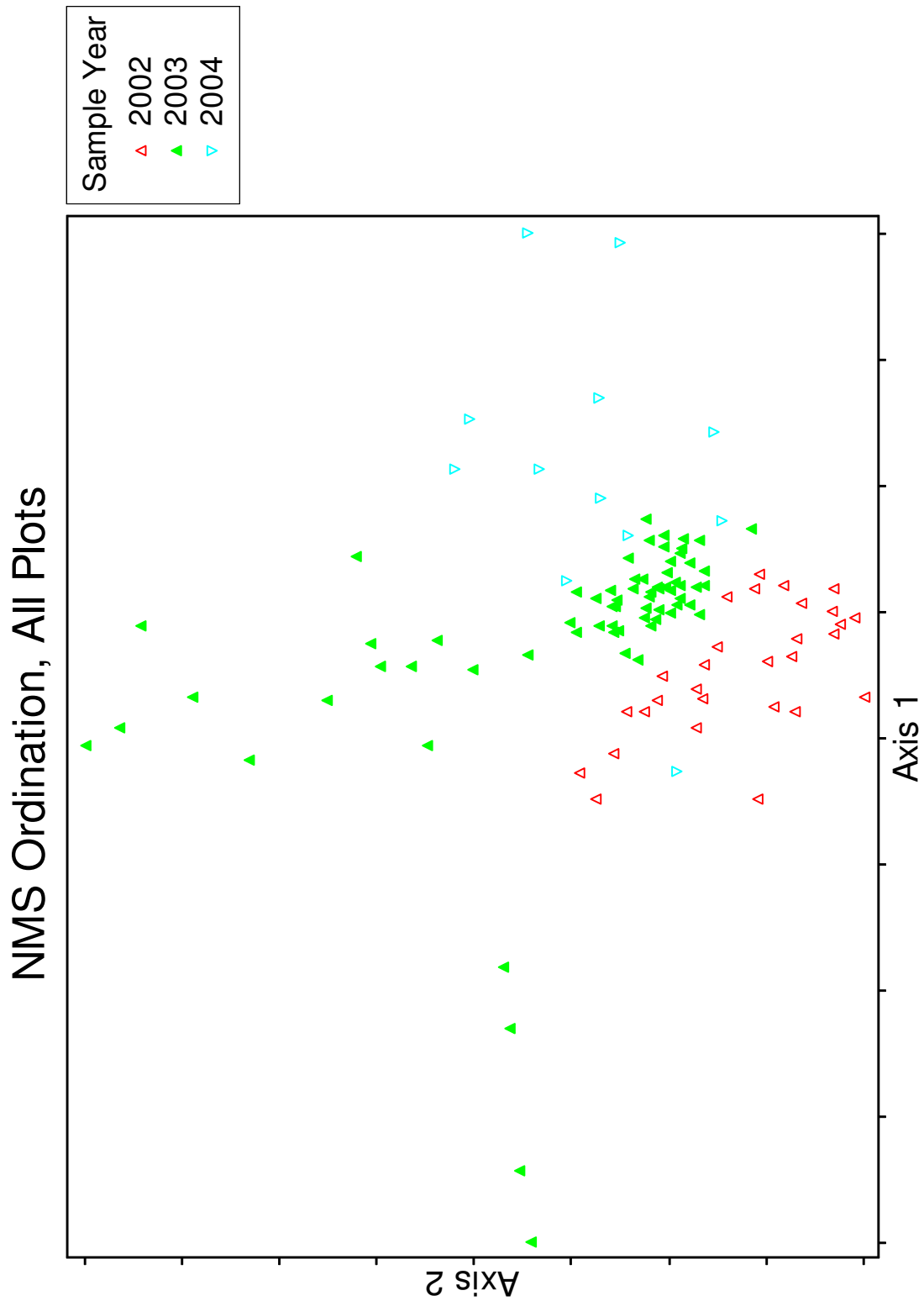
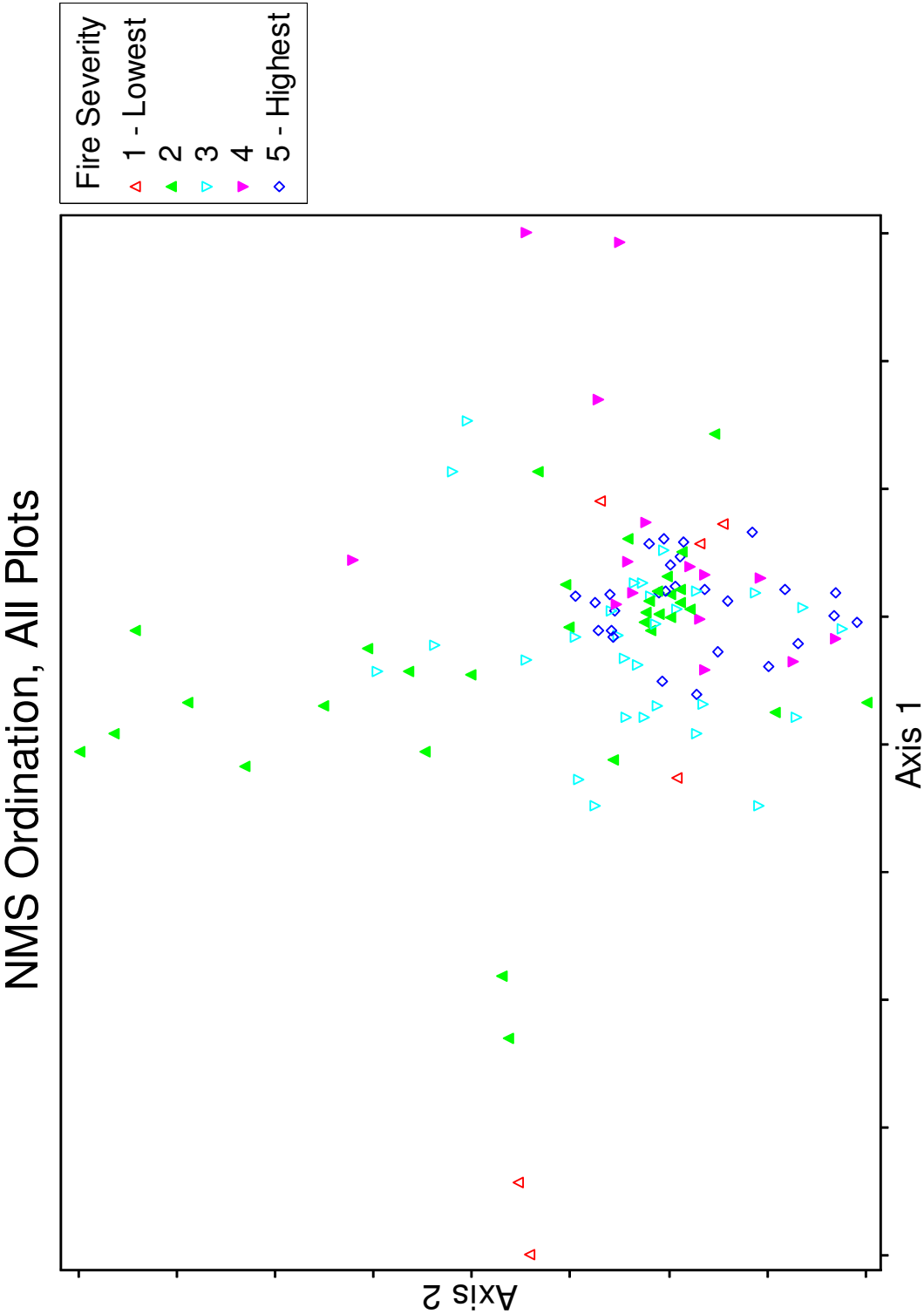


Figure 2.7: NMS ordination with all suitable plots (no missing data). Plots grouped by fire severity. Severity was visually estimated on a 1-5 scale at the time of sampling.



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CHAPTER III: Measuring the dispersal of *Paulownia tomentosa*

ABSTRACT

This chapter documents the long distance dispersal of *Paulownia tomentosa* within Great Smoky Mountains National Park via the number of seedlings germinated from soil samples and within the Linville Gorge wilderness area via the number of seedlings encountered within vegetation plots. The GSMNP study found *Paulownia* seeds dispersed over 3km from the nearest potential parent though seeds were uncommon beyond the immediate vicinity of mature trees. The observed distribution of seeds was significantly explained by a negative exponential model ($p < .001$). The results from Linville Gorge predict a much higher frequency of long distance dispersal events with high levels of invasion observed at all measured distances (maximum 3,550m). No correlation was found between Nearest Neighbor Distance and number of *Paulownia* seedlings at Linville Gorge. The proportion of invaded plots did however show a significant negative correlation with distance ($p < .005$). This trend indicates that *Paulownia* seeds will disperse up to 10km from the nearest mature individual.

INTRODUCTION

Dispersal largely determines the ability of plants to respond to changing environments from small to large spatial and temporal scales which in turn affects community processes and interactions. Ecologists have long sought to better understand and model dispersal to better predict invasive species spread (Shaw 1995, Kot 1996, Hengeveld 1994), to understand past patterns of recolonization following glacial periods (Cain *et al.* 1998, Clark 1998), and to predict how species will respond (via migration) to global climate change (Ribbens *et al.* 1994, Pitelka 1997, Clark *et al.* 1998).

Previous work has demonstrated that the majority of seeds land close to the parent (Harper 1977, Howe and Smallwood 1982, Okubo and Levin 1989, Wilson 1992, 1993) and that this short-distance dispersal dominates the response of species to small scale disturbances. However, it is the often rare Long Distance Dispersal (LDD) events which have the greatest influence on recolonization patterns after landscape-to-regional-scale disturbances (Nathan *et al.* 2002). It has also been suggested that these LDD events are the dominant factors determining the rate of invasive exotic species spread (Leonard and Fry 1986, Willson 1993). Unfortunately, while the importance of LDD is widely recognized, our ability to measure and predict it has been limited.

Numerous studies have measured seed dispersal for a variety of herbaceous (Bullock and Clarke 2000, Casper 1987, Klinkhamer *et al.* 1988, Waser *et al.* 1982), and woody (Hoppes 1988, Bond 1988, Clark *et al.* 1999) species utilizing seed trap data to fit a variety of mathematical functions (negative binomial, inverse power, and negative exponential) to describe the observed dispersal pattern. Although these functions often fit dispersal densities

well over short distances, they provide a poor fit to the tail of the dispersal curve. Fitting the tail of the curve is problematic because long distance dispersal is uncommon and thus hard to measure, and because the above equations do not provide much flexibility in the length or width of the tail. This has been addressed by utilizing two kernel components to fit the body and tail of the curve separately (Bullock and Clarke 2000, Clark *et al.* 1999, Nathan and Muller-Landau 2000) which significantly improves the fit. However, the data-intensive nature of these models makes them difficult to apply generally.

Other approaches have modeled dispersal as a function of seed morphology (Augspurger and Franson, 1987, Sheldon and Burrows 1973), climate and weather (Green and Johnson 1996), morphology and climate (Nathan *et al.* 2002, Okubo and Levin 1989), utilized genetic analysis (Dieckmann *et al.* 1999, Ouborg *et al.* 1999), or used the location of seedlings and adults (Ribbens *et al.* 1994, Clark 1998). However, direct tests of the morphology and climatic models are rare (Bullock and Clarke 2000, Nathan *et al.* 2002), genetic analyses have been criticized for confounding dispersal and establishment (Ouborg *et al.* 1999) and violating underlying assumptions (Turchin 1998), and models based on seedlings have not enabled reliable estimates of the tail of dispersal (Turchin 1998)

Except for Nathan *et al.* (2000) and Waser *et al.* (1982), the studies mentioned above share a common focus on dispersal distances less than 100 meters. Further, the majority of these studies measured dispersal over very short distances (0-35 meters), and where “long” distance dispersal was measured, distances ranged from 50 – 80m (Ruckelshaus 1996, Bullock and Clarke 2000). The difficulty of identifying potential seed sources has also lead most studies to focus on isolated individuals (Bullock and Clarke 2000) and/or seed dispersal across open terrain from a forest edge (Greene and Johnson 1996). However this approach

has been criticized because dispersal patterns are potentially quite different within a forest due to changes in wind speed and air flow (Nathan *et al.* 2002). To further complicate matters, some studies (Clark *et al.* 2003, Higgins *et al.* 2003, Aylor 2003) have suggested that the inherently stochastic nature of LDD prevents informative forecasts of spread velocity, that LDD events are usually caused by non-standard means of dispersal (ex. animal dispersal of seeds or plant parts not typically dispersed by them), that distances covered by “typical” dispersal mechanisms are irrelevant to determining the distances over which LDD events will occur, and that species spread is limited by establishment not LDD frequency.

One major hurdle to studying LDD, identifying the seed sources, is more easily overcome through a focus on a currently invading exotic. Identifying seeds sources is problematic with most species because it is extremely difficult to locate all potential seeds sources. However, with an exotic species (like *Paulownia*) which is not currently common across the landscape, that occurs in readily identifiable parts of the landscape (roadsides), and whose location can consequently be exhaustively mapped with a high degree of certainty, identifying all mature individuals is possible. In the case of *Paulownia*, it is currently invading novel habitat (burned areas), yet mature individuals are confined to roadways and other areas of intense human disturbance. These conditions make it an ideal case study for LDD and this chapter identifies the degree to which dispersal limitation plays a role in *Paulownia* invasion following fire. Specifically this chapter addresses how far *Paulownia* seeds dispersed from mature trees, and whether similar dispersal distances and densities were predicted by seed-bank and seedling data.

STUDY AREAS

Great Smoky Mountains National Park

The western portion of the GSMNP is marked by a series of ridges and valleys that run roughly in parallel from northwest to southeast. Although there is a general increase in elevation from West to East, this ridge and valley system creates the dominant elevation gradient. This area is also a transition from the high mountains in the central portion of the Park to the Tennessee Valley to the west and is markedly drier than most of the rest of the Park. Rainfall for the area averages 120cm (Busing 2005) and this is reflected in the increased cover of xeric and sub-xeric forests. Lower rainfall and drier forests also give rise to an increased fire frequency with a historic mean Fire Return Interval (FRI) of 8-12 years (Harmon 1982). These frequent fires were of low severity, sufficient to prevent to encroachment of more mesic and fire sensitive species, but stimulated only limited pine regeneration. The majority of pine regeneration occurred following less frequent (~100 year FRI), high severity fires. Fire suppression was park policy from its creation till the late 1980's. Although prescribed and wild fires are increasingly common within the park, the mean FRI remains longer than it was historically and the composition and structure of xeric vegetation communities have not yet returned to their previous state (Harrod *et al.* 1998).

Linville Gorge

The Linville Gorge wilderness area is located in the Pisgah National Forest north of Lake James and south-southeast of the town of Linville Falls, in west-central North Carolina. Located on the Blue Ridge Escarpment, yet separated from the rest of the Appalachian

mountains the Linville Gorge wilderness area encompasses 12,002 acres and is bounded by the Gorge rims. Precambrian rock layers, most notably the lower quartzite layers which make up the steep bluff and cliffs, are exposed below the Blue Ridge overthrust within the Gorge (Hatcher and Goldberg 1991). For a full description of the geology and vegetation of Linville Gorge see Newell and Peet (1998). The majority of the Gorge burned in November of 2000. Fire severity within the Gorge ranged from low severity ground fire to high severity crown fire.

METHODS

Great Smoky Mountain National Park samples

The study area was bounded by Rich Mountain Road, Cade's Cove loop Road, Rabbit Creek trail, and the Park boundary. Within this area, potential sampling sites were identified (in ArcGIS) on southwest facing ($210^{\circ} \leq \text{aspect} \leq 240^{\circ}$) slopes with xeric or sub-xeric vegetation types (Table 3.1, Madden 2006), and within 500m meters of a road or trail. Xeric sites were focused upon as these are habitats where fire and subsequent *Paulownia* invasion is a significant possibility. These potential sites were further stratified by elevation and distance from the Park boundary with each divided into three classes; 2km wide distance classes and elevation classes of 184-440m, 441-600m, and 600-800m. Elevation was so divided so that each class contained an equal area. Ten sampling sites were randomly selected from within each distance-elevation class combination where possible. Two class

combinations (Middle distance-Low elevation and Far distance-Low elevation) did not occur within the sample area. Although samples were identified using distance and elevation classes, continuous measurements of these variables were used in the analyses. Additional samples were taken from sites with appropriate habitat types as determined in the field to increase the number of collected samples.

Samples were collected in February and March of 2005 and their geo-coordinates recorded. At each location, 10 randomly located samples within a 10m diameter circle were collected using a 5cm diameter soil corer for a combined sample surface area of 196.44cm². Cores included litter and humus and were taken to a soil depth of 10cm. Samples were combined into a single composite sample for each location. Soils were refrigerated in the days between their collection and processing.

Cores were processed utilizing the approach described by Gross (1990). Soils were sieved to remove particles larger than 3cm and smaller than .25mm, the remaining mixture was spread thinly (≤ 1 cm) over a growing medium (Promix BX) in the greenhouse at UNC, and watered daily. Germination was tracked daily through November 21st, 2005 and all germinants were identified to species where possible and if not to genus or family according to the taxonomic standards of Weakly (2007).

In addition to the samples taken within the park, 9 samples were taken from a mature *Paulownia* tree located along a public roadway on the boundary of the park. These were taken at the base of this tree and at 10 and 50 meters out from the tree in each of the cardinal directions. Including these 9 samples, 84 total samples were collected.

The location of all mature *Paulownia* in the immediate vicinity of the study area was determined via an exhaustive survey of the public and private roads along the border of the

Park. The distance from the nearest mature tree (Nearest Neighbor Distance, NND) was determined for each sample using ArcGIS and this distance was regressed against the number of seedlings per sample to assess the relationship between the NND and the number of seeds germinated from a sample.

Linville Gorge samples

At Linville Gorge, *Paulownia* seedling abundance was measured within 100m² vegetation sampling plots surveyed according to the CVS protocol described in Peet *et al.* (1998) with the variations and additions explained in Chapter II. Plots were sampled in 2002, 2003, and 2004. In 2006, 17 additional locations of *Paulownia* seedlings were identified (referred to below as survey points). No plot data were collected at these survey points, simply the number of *Paulownia* within a 10x10m area and the spatial location. The location of mature *Paulownia* in the vicinity of Linville Gorge was determined through an exhaustive survey of public and private roads in the vicinity of the Gorge conducted in July of 2006. An aerial survey of *Paulownia* was also conducted on April 22nd, 2006 with the help of the non-profit SouthWings, though this failed to locate any trees not identified by ground surveys.

The NND to each plot and survey point within the Gorge was determined using ArcGIS. This distance was regressed against the number of seedlings encountered at each sampling location to assess whether there was a correlation between NND and the number of seedlings. The effect of distance upon seedling density was also assessed by looking at the proportion of invaded samples within predicted *Paulownia* habitat (Chapter V). To look at the distribution of sampling intensity across distance (Nearest Neighbor) classes, samples

were lumped into 250m distance classes and the histogram of these values compared with the histogram depicting the overall NND distribution within the fire boundary as determined by the distribution of NND's captured by 1×10^5 randomly located points within the fire boundary.

RESULTS

Great Smoky Mountain National Park

Samples ranged in aspect from 41 to 322° with an average of 211°, slopes ranged from 4 to 43°, and elevation ranged from 364m to 804m. At five of the additional locations, the observed dry forest types did not match the vegetation community identified by the vegetation map resulting in an apparently greater diversity of communities sampled (Table 3.2).

Paulownia seedlings were germinated from 14 of the 84 samples. Nine of these samples were from those collected in the immediate vicinity of a mature *Paulownia*. The remaining samples were all from the Near distance class. 17 mature *Paulownia* were found in the immediate vicinity of the Park (Figure 3.1). The most remote sample containing *Paulownia* seeds was located 1.95km (+/- 10m) from the park boundary and 3.75km (+/- 10m) from the nearest mature *Paulownia* tree. The relationship between the number of seedlings germinated and NND was described by the inverse power function:

$$S = 17.158 \times D^{-0.34467}$$

Where S is the estimated number of seedlings and D is the NND. This relationship had an R^2 of 0.6419 and a $p < .001$ (Figure 3.2). Applying this formula to the GSMNP sampling area illustrates the large distances over which *Paulownia* seeds are dispersed (Figure 3.3).

This approach does not account for the difference between the sampled soil volume and the total soil volume within the sample area. However, when this is accounted for, the resulting relationship predicts 138,143 seedlings two meters out from the parent tree and a total seedling abundance which greatly surpasses the estimated two million seeds produced annually by each tree.

Linville Gorge

The samples taken in this study ranged in elevation from 645m to 1185m, in slope from 2 to 38°, and captured three different rock types: lower quartzite, Wilson Creek gneiss, and Grandfather Mountain Formation meta-arkose. Four of the 6 major vegetation types and 11 of the 22 sub-types were captured within the vegetation plots (Table 3.3).

A total of 50 locations within Linville Gorge were identified with *Paulownia* seedlings (Figure 3.4), and 213 mature *Paulownia* were found outside the Gorge at 72 locations (Figure 3.5). There was no significant relationship between NND and the number of seedlings in any individual sampling year or for all years collectively (Figure 3.6).

Paulownia was seen at similarly remote locations at Linville and in the Park (3.55km and 3.75km respectively), but at Linville this was the most remote sample taken. At the Gorge, *Paulownia* was much more common at all distances than predicted by the seed-bank study. Sampling intensity varied between NND classes (Figure 3.7) largely, but not completely, as a reflection of the NND distribution within the Gorge (Figure 3.8).

Although there was no trend in the number of seedlings encountered as a function of distance from the nearest adult, there was a significant negative correlation between the proportion of samples within *Paulownia* habitat (Chapter V) that were invaded and NND ($p < .005$ without outliers, $p < .1$ with, Figure 3.9). This trend was fit by the equation:

$$P = 1.0271 - 0.0001 * D$$

Where P is the proportion of invaded samples and D is the distance class median (in meters). The above model excludes the 2 outlier distance classes (2,125m and 2,175m). This equation predicts *Paulownia* invasion over 10km from the point of release, though not all distance classes were represented by an equal number of samples (Table 3.4).

DISCUSSION

This study demonstrates that long distance seed dispersal on the order of kilometers is not uncommon for *Paulownia* seeds as illustrated by the number of seedlings present and the high proportion of plots invaded over 3.5km from the nearest seed source. This conclusion is backed up by two additional lines of evidence. *Paulownia* seeds have high levels of mortality when exposed to fire (Chapter IV), particularly the high severity fire that produces the best *Paulownia* habitat (Chapter V). Therefore the majority of seeds responsible for the invasion at Linville Gorge likely dispersed after the fire and hence the high rate of invasion in 2002 was likely the result of seeds dispersed in a single year (fall of 2001) as the fire occurred after seed dispersal in 2000. The second line of evidence comes from field surveys

which only rarely encountered two year old individuals in 2002 (two years after the fire), again suggesting that the invasion was the product of the 2001 seed crop. For such a significant invasion to occur after only a single year's seed rain, the density of this rain and thus the frequency of LDD must have been very high.

Only one other study has estimated dispersal at distances comparable to those studied here. Models produced by Nathan *et al.* (2002) estimated dispersal distances for *Liriodendron tuliperifera* and predicted that $\sim 10^{-3}$ of the seeds produced annually by a 35cm dbh tree travel one kilometer or more from their source. Applying this relationship to *Paulownia* would predict that $\sim 2,000$ of the 2 million *Paulownia* seeds produced annually disperse one kilometer or more. This corresponds well with the dispersal records from Linville Gorge which found significant invasion at distances greater than one kilometer.

If *Paulownia* seeds do survive for multiple years within the seed-bank as has been estimated previously (Longbrake 2001, Hyatt and Casper 2000) and the methods utilized here adequately captured that density, then the GSMNP seed-bank study should have yielded a higher abundance of *Paulownia*. The seed-bank should contain *Paulownia* seeds from multiple years, resulting in a greater seedling density than that documented at Linville Gorge where most seedlings originated from the 2001 seed crop. Instead, while the seed-bank results did show *Paulownia* seeds dispersing to distances comparable to those witnessed at Linville Gorge, it underestimated seedling density at all distances. The sample from the base of a mature tree only germinated 21 seeds while at Linville Gorge, 10 seedlings were encountered 3.18km from the nearest adult with an outlying 158 seedlings found in one plot 2.38km from the nearest adult. These results suggest that either *Paulownia* does not form a

persistent seed bank or the methods utilized in the seed-bank study significantly underestimated dispersal.

Questions remaining

Two of the sampled fires, Green Mountain and Mill Ridge, experienced very low levels of invasion despite apparently favorable environmental conditions and I hypothesize that the lack of invasion is the result of limited seed availability. At Mill Ridge, although an intensive survey was not conducted, only one mature tree was witnessed in the vicinity. At Green Mountain, a thorough survey was conducted which located 3 mature individuals in close proximity to the south flank of the mountain (where conditions seemed to be best for *Paulownia* invasion), and numerous individuals on the north-eastern side of the mountain along Interstate 40. Although these highway individuals were within 3.5 km (the most remote Linville sample) of the southern side of the mountain, no significant invasion occurred. My working hypothesis is that prevailing winds and the effect of interstate traffic on air flow blew the majority of seeds westward and that few seeds made it over the mountain to the areas of better post-fire habitat, thereby limiting invasion. This hypothesis however relies upon several untested assumptions.

It is unclear why there is a lack of agreement between the seed-bank study and the seedling study, though there are two potential reasons. First, the seed-bank sampling intensity might have been insufficient to capture the *Paulownia* seeds. Secondly, it was assumed that seeds came from the nearest adult where a more realistic approach would sum the dispersal probabilities from all adults. This might increase convergence between the

Linville and seed-bank results. These models have been created for other species (Clark *et al.* 1999), but they require more data than was available.

Finally, the approaches taken here are entirely phenomenological and provide no mechanistic explanation for the high rate of long distance dispersal. Although the morphology of *Paulownia*'s seed (small, lightweight, winged) suggests that these traits might be useful in a mechanistic model of *Paulownia*'s dispersal ability, previous studies (Nathan *et al.* 2002) have found parameters associated with wind patterns to be more important in determining dispersal distance. Determining whether this is the case for *Paulownia* is a question for future work.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This chapter demonstrates the utility of newly invading species in the development of long distance dispersal models as they offer the opportunity to locate all individuals across a landscape and track the pattern of invasion into previously uninvaded habitat. I have further demonstrated that long distance dispersal is a relatively common occurrence with *Paulownia*. Seedlings were common over 3km from the nearest adult and results suggest that seeds may disperse as far as 10km. This is particularly troubling for land managers as it suggests that only the largest blocks of uninvaded forest may have areas where invasion is precluded by distance-induced dispersal limitations. Consequently most fires that create appropriate habitat conditions should be monitored for post-fire *Paulownia* invasion.

TABLES AND FIGURES

Table 3.1: Xeric and sub-xeric vegetation associations used to identify sampling locations within the GSMNP study area. Associations identified on the basis of the GSMNP vegetation classification for the park which follows the National Vegetation Classification.

Table 3.2: Associations sampled within the GSMNP study area based on plot coordinates and the association identified for that location in the vegetation classification map of the park which follows the National Vegetation Classification.

Table 3.3: Vegetation associations sampled at Linville Gorge. Classifications identified from the Forest Service vegetation map of the Gorge and follows the National Vegetation Classification.

Figure 3.1: Sampling locations within the GSMNP. Symbol size and color indicates the number of *Paulownia* germinated from each sample. The location of mature *Paulownia* stems in the immediate vicinity of the park is also depicted.

Figure 3.2: The number of *Paulownia* seedlings germinated from soil samples plotted against the NND. Data from the GSMNP soil sample germinations. All samples are included in the figure and in the modeled relationship.

Figure 3.3: Application of the *Paulownia* dispersal model derived from the GSMNP soil sample data to the GSMNP study area. Predicted seed density indicated by the color ramp. The location of samples and mature *Paulownia* is also indicated.

Figure 3.4: Map of Linville Gorge indicating the sampled locations, fire boundary, and transportation corridors.

Figure 3.5: The location of mature *Paulownia* in the immediate vicinity of Linville Gorge. Symbol size indicates the number of mature trees at that location.

Figure 3.6: The number of *Paulownia* seedlings encountered in plots (100m²) at Linville Gorge plotted against the NND. Only samples with *Paulownia* are included. Date of sampling (2002, 2004, and 2006) is indicated by color. Only the initial plot sampling date is shown.

Figure 3.7: Histogram of the number of samples in each 250m wide NND class. All Linville Gorge samples included.

Figure 3.8: Histogram of the NND distribution within the fire boundary at Linville Gorge as measured by 1×10^5 points randomly located within that boundary. Data were grouped into 250m wide distance classes.

Figure 3.9: Proportion of samples with *Paulownia* as a function of NND. Only those samples which were present within predicted *Paulownia* habitat are included. Data were grouped into 250m distance classes.

Table 3.4: The number and proportion of plots within *Paulownia* habitat that were invaded at each distance class. Table illustrates the data behind Figure 3.9.

Table 3.1: Xeric and sub-xeric vegetation associations used to identify sampling locations within the GSMNP study area. Associations identified on the basis of the GSMNP vegetation classification for the park which follows the National Vegetation Classification.

Apriori Selected Vegetation Communities		
CEGL Code	Association	Community Name
XERIC RIDGE FORESTS		
Table Mountain Pine / Pitch Pine Woodlands		
7119	<i>Pinus virginiana</i> - <i>Pinus (rigida, echinata)</i> - (<i>Quercus prinus</i>) / <i>Vaccinium pallidum</i> Forest	Appalachian Low-Elevation Mixed Pine / Hillside Blueberry Forest
7097	<i>Pinus pungens</i> - <i>Pinus rigida</i> - (<i>Quercus prinus</i>) / <i>Kalmia latifolia</i> - <i>Vaccinium pallidum</i> Woodland	Blue Ridge Table Mountain Pine - Pitch Pine Woodland (Typic Type)
Shortleaf Pine / Shortleaf Pine-Oak Forests		
7078	<i>Pinus echinata</i> / <i>Vaccinium (pallidum, stamineum)</i> - <i>Kalmia latifolia</i> Forest	Appalachian Shortleaf Pine Forest
3560	<i>Pinus echinata</i> / <i>Schizachyrium scoparium</i> Appalachian Woodland	Shortleaf Pine/Little Bluestem Appalachian Woodland
White Pine / White Pine - Oak Forests		
7519	<i>Pinus strobus</i> - <i>Quercus Pinus strobus</i> – <i>Quercus (coccinea, prinus)</i> / (<i>Gaylussacia ursina</i> - <i>Vaccinium stamineum</i>) Forest	Appalachian White Pine - Xeric Oak Forest
7100	<i>Pinus strobus</i> / <i>Kalmia latifolia</i> - (<i>Vaccinium stamineum</i> , <i>Gaylussacia ursina</i>) Forest	Southern Appalachian White Pine Forest
7517	<i>Pinus strobus</i> - <i>Quercus alba</i> - (<i>Carya alba</i>) / <i>Gaylussacia ursina</i> Forest	Appalachian White Pine - Mesic Oak Forest
Chestnut Oak Forests		
6271	<i>Quercus (prinus, coccinea)</i> / <i>Kalmia latifolia</i> / (<i>Galax urceolata</i> , <i>Gaultheria procumbens</i>) Forest	Chestnut Oak Forest (Xeric Ridge Type)
7267	<i>Quercus prinus</i> - (<i>Quercus rubra</i>) - <i>Carya spp.</i> / <i>Oxydendrum arboreum</i> - <i>Cornus florida</i> Forest	Appalachian Montane Oak Hickory Forest (Chestnut Oak Type)

Table 3.2: Associations sampled within the GSMNP study area based on plot coordinates and the association identified for that location in the vegetation classification map of the park which follows the National Vegetation Classification.

Field Sampled Vegetation Communities				
CEGL Code	Association	Community Name	Moisture Category	# of Plots
XERIC RIDGE FORESTS				
Table Mountain Pine / Pitch Pine Woodlands				
7119	<i>Pinus virginiana</i> - <i>Pinus (rigida, echinata)</i> - (<i>Quercus prinus</i>) / <i>Vaccinium pallidum</i> Forest	Appalachian Low-Elevation Mixed Pine / Hillside Blueberry Forest	Xeric	47
7097	<i>Pinus pungens</i> - <i>Pinus rigida</i> - (<i>Quercus prinus</i>) / <i>Kalmia latifolia</i> - <i>Vaccinium pallidum</i> Woodland	Blue Ridge Table Mountain Pine - Pitch Pine Woodland (Typic Type)	Xeric	5
Shortleaf Pine / Shortleaf Pine-Oak Forests				
7078	<i>Pinus echinata</i> / <i>Vaccinium (pallidum, stamineum)</i> - <i>Kalmia latifolia</i> Forest	Appalachian Shortleaf Pine Forest	Xeric	0
3560	<i>Pinus echinata</i> / <i>Schizachyrium scoparium</i> Appalachian Woodland	Shortleaf Pine/Little Bluestem Appalachian Woodland	Xeric	0
White Pine / White Pine - Oak Forests				
7519	<i>Pinus strobus</i> - <i>Quercus Pinus strobus</i> – <i>Quercus (coccinea, prinus)</i> / (<i>Gaylussacia ursina</i> - <i>Vaccinium stamineum</i>) Forest	Appalachian White Pine - Xeric Oak Forest	Sub-xeric to xeric	4
7100	<i>Pinus strobus</i> / <i>Kalmia latifolia</i> - (<i>Vaccinium stamineum</i> , <i>Gaylussacia ursina</i>) Forest	Southern Appalachian White Pine Forest	Sub-xeric to xeric	0
7517	<i>Pinus strobus</i> - <i>Quercus alba</i> - (<i>Carya alba</i>) / <i>Gaylussacia ursina</i> Forest	Appalachian White Pine - Mesic Oak Forest	Sub-xeric to xeric	0

Table 3.2: Continued

Chestnut Oak Forests				
6271	<i>Quercus (prinus, coccinea) / Kalmia latifolia / (Galax urceolata, Gaultheria procumbens) Forest</i>	Chestnut Oak Forest (Xeric Ridge Type)	Sub-xeric to xeric	10
7267	<i>Quercus prinus - (Quercus rubra) - Carya spp. / Oxydendrum arboreum - Cornus florida Forest</i>	Appalachian Montane Oak Hickory Forest (Chestnut Oak Type)	Sub-xeric to xeric	3
LOW ELEVATION, TOPOGRAPHICALLY PROTECTED FORESTS				
Montane Cove Forests				
7710	<i>Liriodendron tulipifera – Aesculus flava - (Fraxinus americana, Tilia americana var. heterophylla) / Cimicifuga racemosa – Laportea canadensis Forest</i>	Southern Appalachian Cove Forest (Typic Montane Type)	Mesic to sub-mesic	1
7543	<i>Tsuga canadensis – Liriodendron tulipifera / Rhododendron maximum / Tiarella cordifolia Forest</i>	Southern Appalachian Acid Cove Forest (Typic Type)	Mesic to sub-mesic	3
Montane Oak-Hickory Forests				
6192	<i>Quercus rubra - Acer rubrum / Calycanthus floridus –Pyrularia pubera / Thelypteris noveboracensis Forest</i>	Appalachian Montane Oak - Hickory Forest (Red Oak Type)	Mesic to sub-mesic	1
7230	<i>Quercus alba - Quercus (rubra, prinus) / Rhododendron calendulaceum - Kalmia latifolia - (Gaylussacia ursina) Forest</i>	Appalachian Montane Oak Hickory Forest (Typic Acidic Type)	Mesic to sub-mesic	1
Hemlock Forests				
7102	<i>Pinus strobus - Tsuga canadensis / Rhododendron maximum - Leucothoe fontanesiana Forest</i>	Southern Appalachian Eastern Hemlock Forest (White Pine Type)	Mesic to sub-mesic	1
UNCLASSIFIED				
Unclassified				
N/A	Plots were located just outside the park's Vegetation Community map	None	Sub-xeric to xeric	8

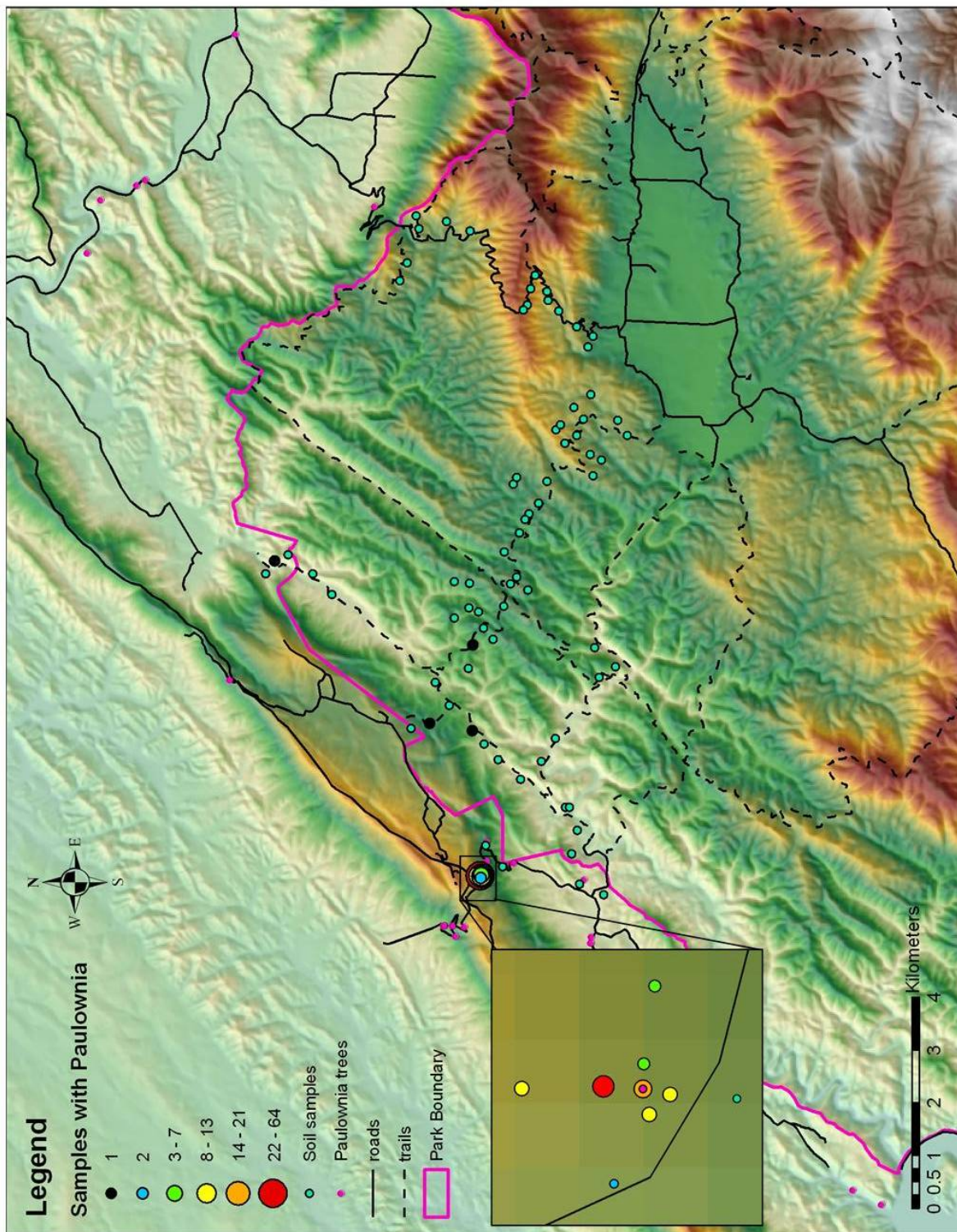
Table 3.3: Vegetation associations sampled at Linville Gorge. Classifications identified from the Forest Service vegetation map of the Gorge and follows the National Vegetation Classification.

Vegetation Communities sampled by Plots			
CEGL Code	Association	Community Name	# of Plots
ROCKY OUTCROPS AND SUMMITS			
Rocky Summits			
4283	<i>Selaginella tortipila</i> - <i>Krigia montana</i> - <i>Houstonia longifolia</i> Herbaceous Vegetation	Southern Appalachian Spike-moss Granitic Dome	2
XERIC RIDGE FORESTS			
Table Mountain Pine / Pitch Pine Woodlands			
7097	<i>Pinus pungens</i> - <i>Pinus rigida</i> - (<i>Quercus prinus</i>) / <i>Kalmia latifolia</i> - <i>Vaccinium pallidum</i> Woodland	Blue Ridge Table Mountain Pine - Pitch Pine Woodland (Typic Type)	52
7119	<i>Pinus virginiana</i> - <i>Pinus (rigida, echinata)</i> - (<i>Quercus prinus</i>) / <i>Vaccinium pallidum</i> Forest	Appalachian Low Elevation Mixed Pine Forest	26
White Pine /White Pine - Oak Forests			
7519	<i>Pinus strobus</i> - <i>Quercus (coccinea, prinus)</i> / (<i>Gaylussacia ursina</i> – <i>Vaccinium stamineum</i>) Forest	Appalachian White Pine - Xeric Oak Forest	12
Chestnut Oak Forests			
6271	<i>Quercus (prinus, coccinea)</i> / <i>Kalmia latifolia</i> / (<i>Galax urceolata, Gaultheria procumbens</i>) Forest	Chestnut Oak Forest (Xeric Ridge Type)	12
LOW ELEVATION, TOPOGRAPHICALLY PROTECTED FORESTS			
Montane Oak-Hickory Forests			
6192	<i>Quercus rubra</i> - <i>Acer rubrum</i> / <i>Calycanthus floridus</i> – <i>Pyrularia pubera</i> / <i>Thelypteris noveboracensis</i> Forest	Appalachian Montane Oak - Hickory Forest (Red Oak Type)	4
Hemlock Forests			
7136	<i>Tsuga canadensis</i> / <i>Rhododendron maximum</i> - <i>Leucothoe fontanesiana</i> Forest	Southern Appalachian Eastern Hemlock Forest (Typic Type)	4

Table 3.3: Continued

Vegetation Communities sampled by Survey Points			
ROCKY OUTCROPS AND SUMMITS			
Rock Outcrops			
4283	<i>Selaginella tortipila</i> - <i>Krigia montana</i> - <i>Houstonia longifolia</i> Herbaceous Vegetation	Southern Appalachian Spike-moss Granitic Dome	1
XERIC RIDGE FORESTS			
Table Mountain Pine / Pitch Pine Woodlands			
7097	<i>Pinus pungens</i> - <i>Pinus rigida</i> - (<i>Quercus prinus</i>) / <i>Kalmia latifolia</i> - <i>Vaccinium pallidum</i> Woodland	Blue Ridge Table Mountain Pine - Pitch Pine Woodland (Typic Type)	11
7119	<i>Pinus virginiana</i> - <i>Pinus (rigida, echinata)</i> - (<i>Quercus prinus</i>) / <i>Vaccinium pallidum</i> Forest	Appalachian Low Elevation Mixed Pine Forest	2
LOW ELEVATION, TOPOGRAPHICALLY PROTECTED FORESTS			
Hemlock Forests			
7136	<i>Tsuga canadensis</i> / <i>Rhododendron maximum</i> - <i>Leucothoe fontanesiana</i> Forest	Southern Appalachian Eastern Hemlock Forest (Typic Type)	4

Figure 3.1: Sampling locations within the GSMNP. Symbol size and color indicates the number of *Paulownia* germinated from each sample. The location of mature *Paulownia* stems in the immediate vicinity of the park is also depicted.



Scatter plot showing the relationship between the natural logarithm of the number of seedlings ($\ln(\# \text{ of Seedlings})$) and the natural logarithm of distance ($\ln(\text{Distance [m]})$).

The regression equation is $S = 17.158 \times D^{-0.34467}$.

The coefficient of determination is $R^2 = 0.6418$.

The p-value is $p < .001$.

Figure 3.3: Application of the *Paulownia* dispersal model derived from the GSMNP soil sample data to the GSMNP study area. Predicted seed density indicated by the color ramp. The location of samples and mature *Paulownia* is also indicated.

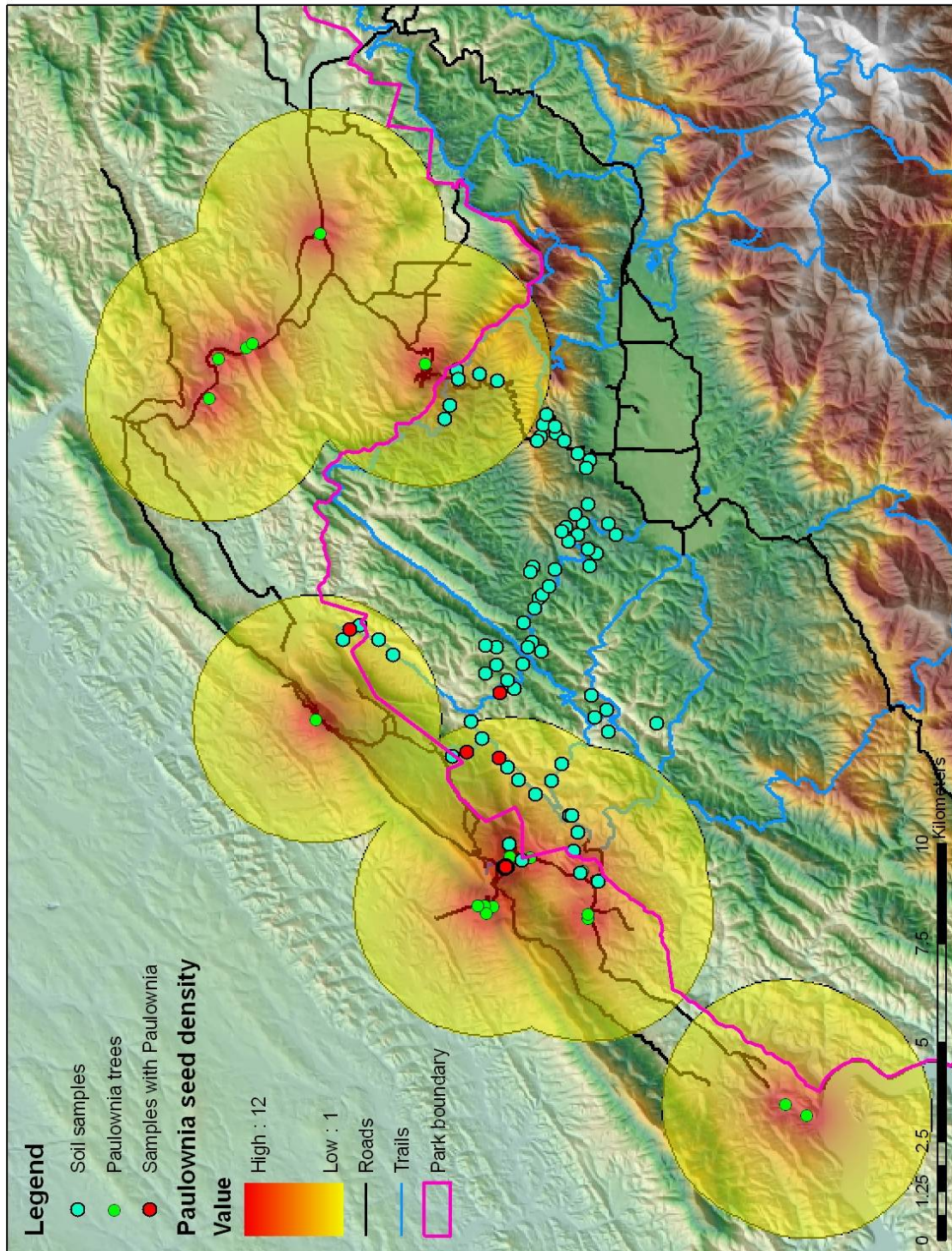


Figure 3.4: Map of Linville Gorge indicating the sampled locations, fire boundary, fire boundary, and transportation corridors.

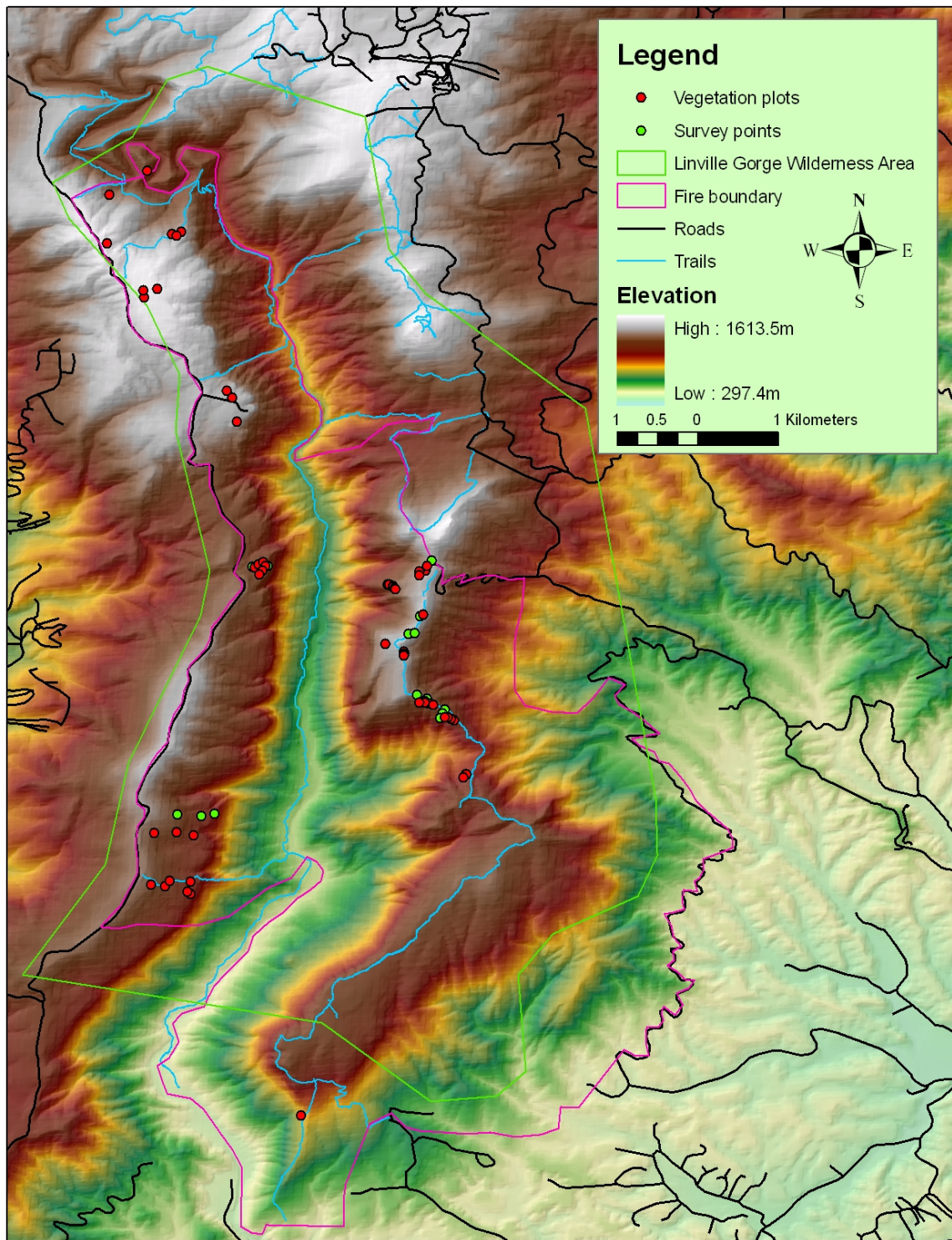


Figure 3.5: The location of mature *Paulownia* in the immediate vicinity of Linville Gorge. Symbol size indicates the number of mature trees at that location.

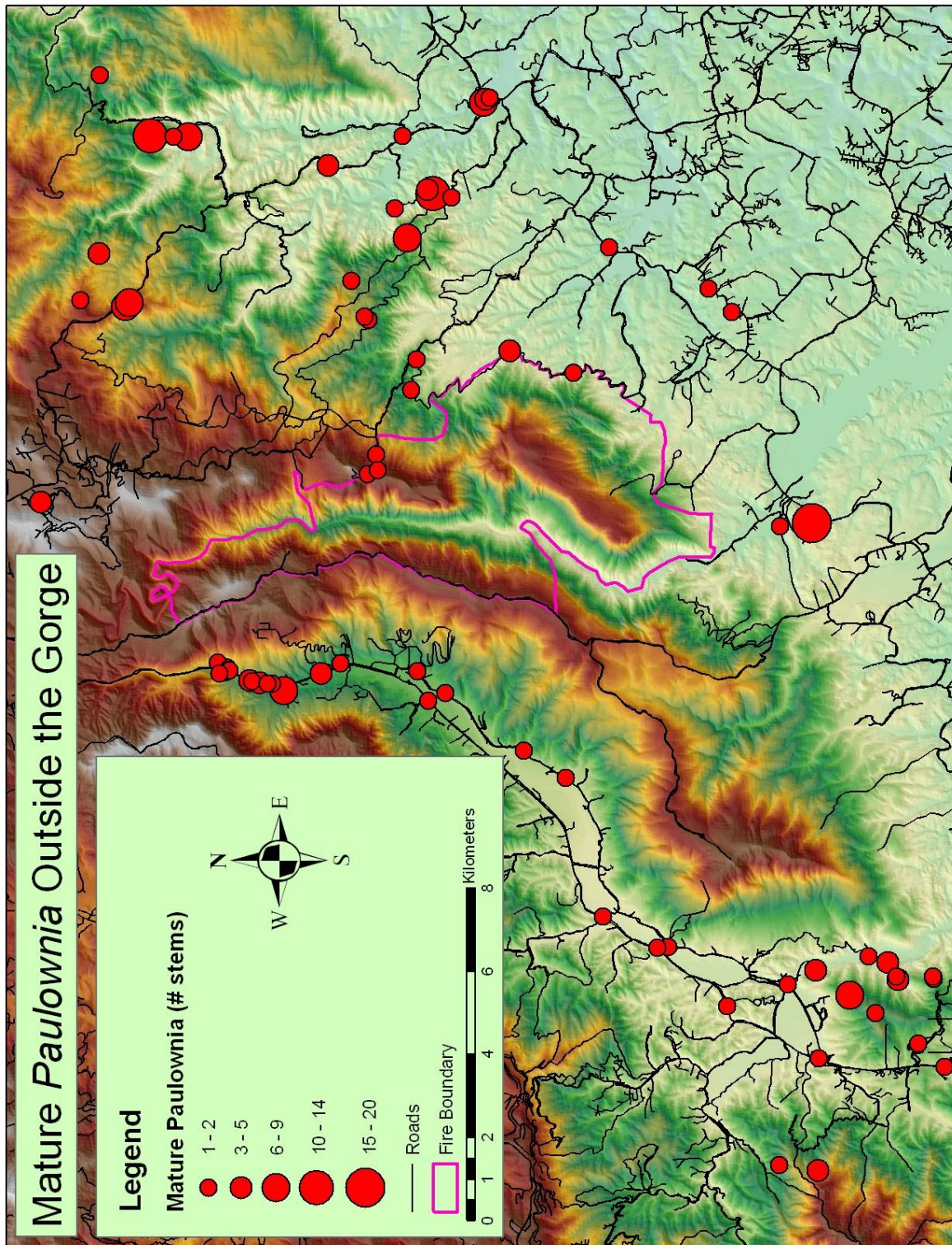


Figure 3.6: The number of *Paulownia* seedlings encountered in plots (100m²) at Linville Gorge plotted against the NND. Only samples with *Paulownia* are included. Date of sampling (2002, 2004, and 2006) is indicated by color. Only the initial plot sampling date is shown.

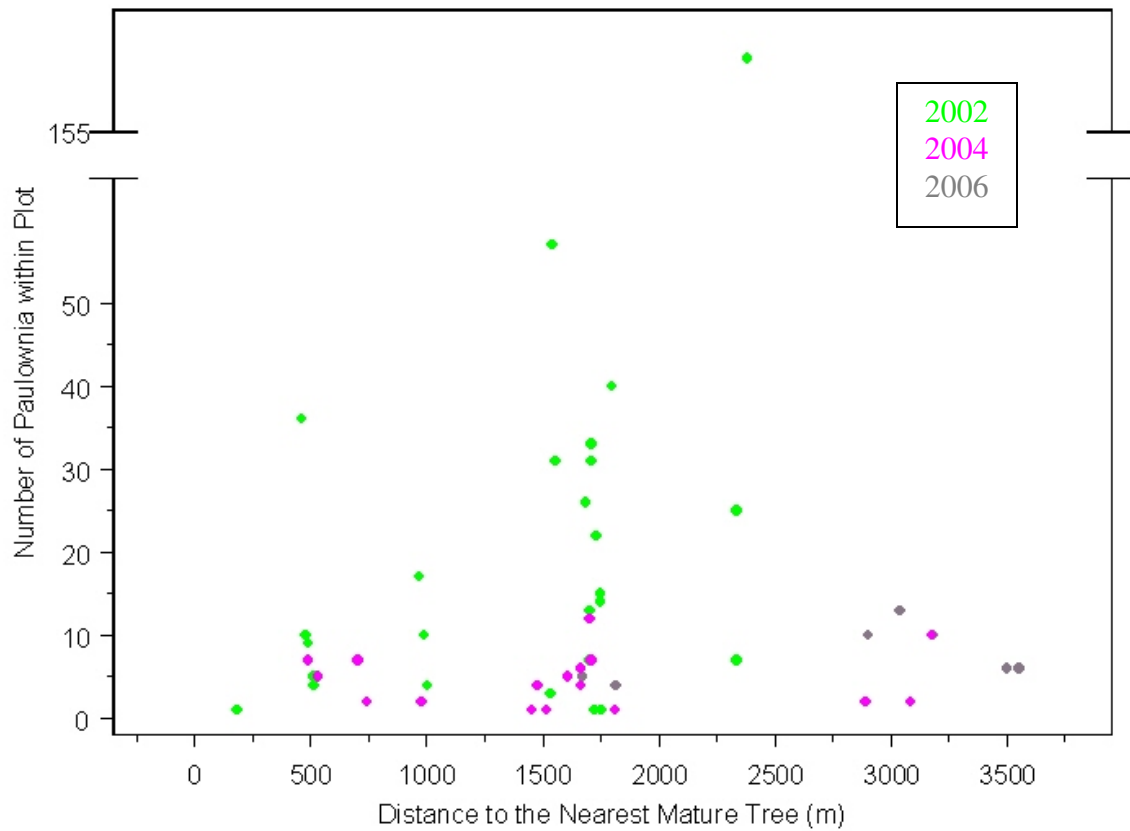


Figure 3.7: Histogram of the number of samples in each 250m wide NND class. All Linville Gorge samples included (including those without *Paulownia*).

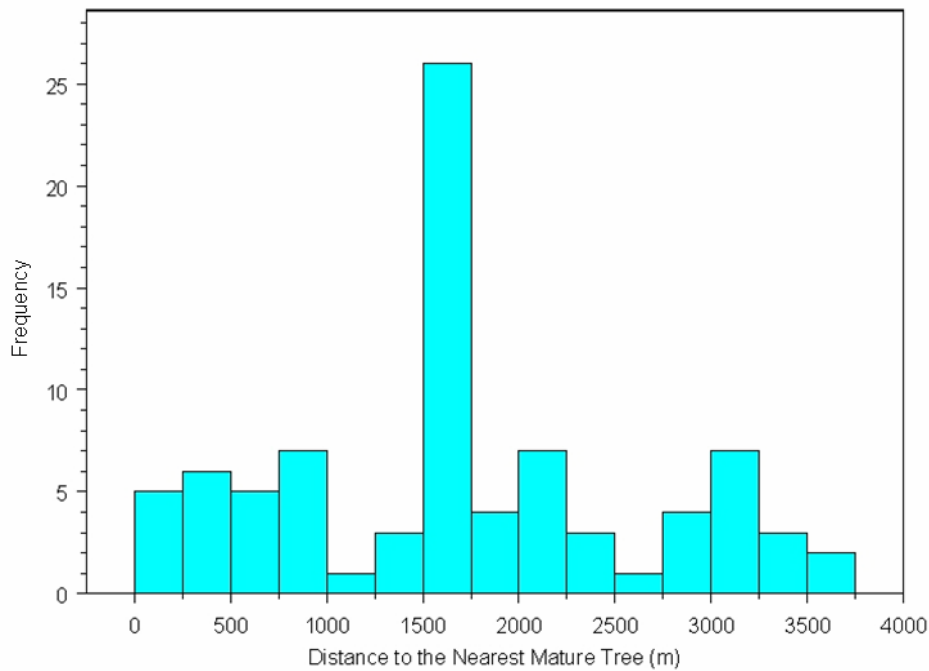


Figure 3.8: Histogram of the NND distribution within the fire boundary at Linville Gorge as measured by 1×10^5 points randomly located within that boundary. Data were grouped into 250m wide distance classes

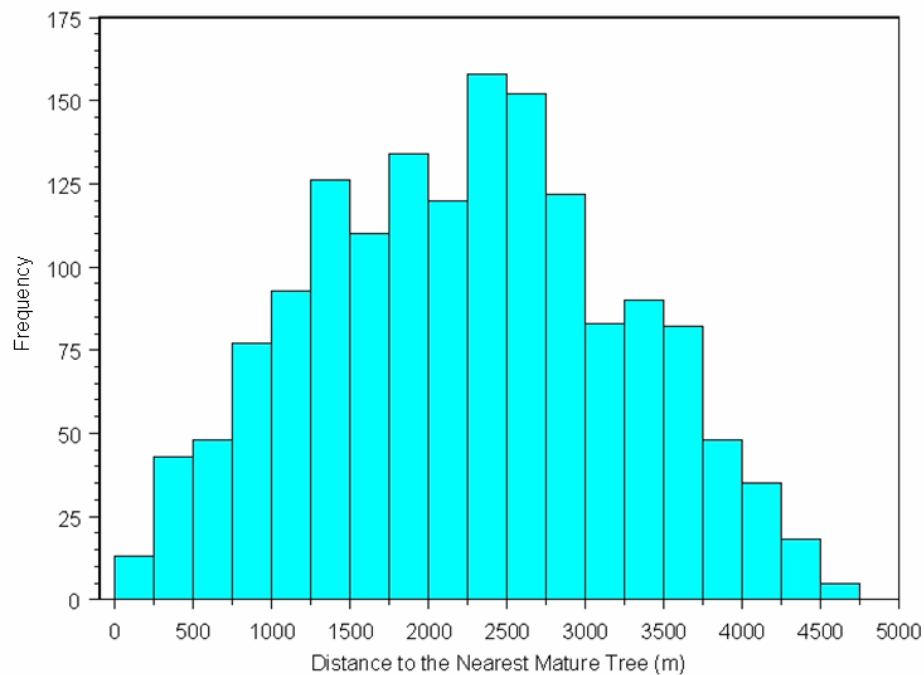


Figure 3.9: Proportion of samples with *Paulownia* as a function of NND. Only those samples which were present within predicted *Paulownia* habitat are included. Data were grouped into 250m distance classes.

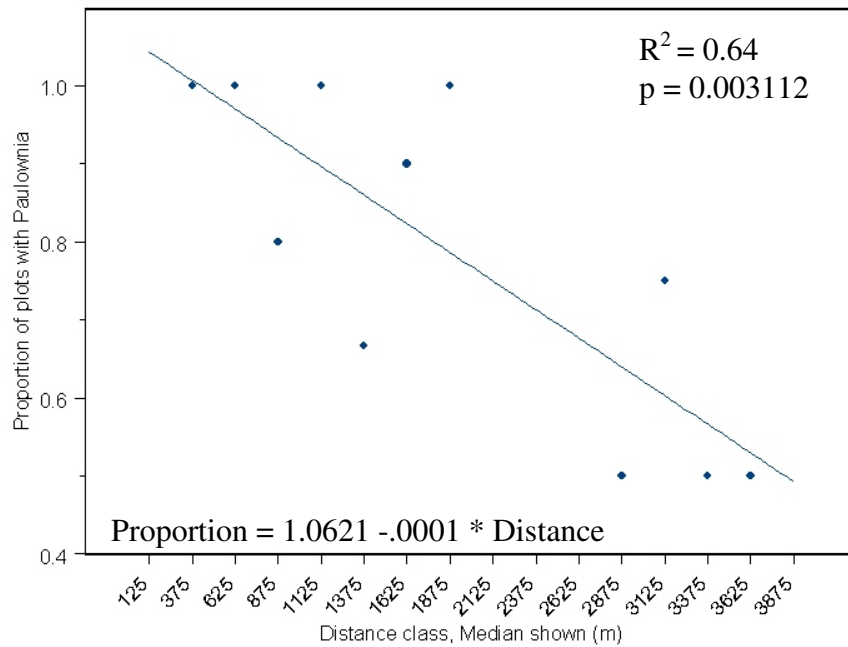


Table 3.4: The number and proportion of plots within *Paulownia* habitat that were invaded at each distance class. Table illustrates the data behind Figure 3.9.

Distance class	Total # of plots	# plots with <i>Paulownia</i>	Proportion with <i>Paulownia</i>	Distance class median
0-250	0	0	N/A	125
251-500	2	2	1	375
501-750	4	4	1	625
751-1000	5	4	0.8	875
1001-1250	1	1	1	1125
1251-1500	3	2	0.67	1375
1501-1750	20	18	0.9	1625
1751-2000	3	3	1	1875
2001-2250	2	0	0	2125
2251-2500	3	3	1	2375
2501-2750	0	0	N/A	2625
2751-3000	2	1	0.5	2875
3001-3250	4	3	0.75	3125
3251-3500	2	1	0.5	3375
3501-3750	2	1	0.5	3625
3751-4000	0	0	N/A	3875

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CHAPTER IV: Experimental Tests of *Paulownia* Seed Survival over Time and Germination Requirements

ABSTRACT

This chapter covers three experiments which tested the effect of selected variables upon *Paulownia* seed survival over time and germination. The first experiment analyzed the germination rate of seeds from two populations as a function of storage method and time since dispersal. The second experiment measured the effect of light level, litter presence, and seed position upon germination. The third measured the effect of fire intensity and duration on germination.

The first experiment, utilizing a Bayesian Hierarchical model, found no germination differences between populations or individual trees and that stratified seeds had lower germination rates than dry and field stored seeds. Time did affect germination, but this impact varied with the storage treatment; field stored seeds had decreased germination rates after a peak in the fifth month, stratified seeds exhibited very low germination rates followed by steadily increasing germination rates after the sixth month, and dry stored seeds showed no temporal trends.

The second experiment, utilizing a main effects analysis with orthogonal contrasts, found significantly higher germination rates under 50% shade than in full sun when seeds

were germinated on bare soil ($p < .001$). Germination was significantly lower ($p < .001$) when litter was present than when it was absent, and buried seeds had significantly lower ($p < .001$) germination rates than those on the soil surface. The only significant interaction was between ground cover (litter vs. bare soil) and light (sun vs. shade, $p < .001$). A second set of contrasts using a Bayesian posterior distribution found that seeds placed on the soil surface with litter present germinated at lower rates than those placed on the litter surface. It also found that buried seeds germinated at lower rates when litter was present than when it was absent.

In the third experiment, a grouped binomial model found a significant negative relationship between germination and the maximum temperature experienced by seeds. Mortality was essentially 100% when temperatures exceeded 100°C.

These results largely conform to field observations that litter cover and light levels are significant predictors of *Paulownia* presence. They also suggest that environmental conditions have a greater effect on seed survival over time than the seed source, that dormancy state is potentially variable over time, and that seeds germinate readily upon dispersal if they encounter appropriate conditions. Seeds may survive fire, but only very low intensity fires (which are unlikely to create other conditions necessary for germination) or when buried (which buffers the temperature). However, buried seeds must be brought to the surface to have more than marginal germination rates.

INTRODUCTION

Paulownia seeds are orthodox (Baskin and Baskin 1996) and germination is phytochrome controlled (Borthwick *et al.* 1964). Seeds can be induced into skotodormancy by 30 day exposure to darkness, but this can be overcome by six hours of red light or gibberellic acid (Grubisic *et al.* 1985), abscisic acid, fusaric acid, or chloro-choline (Grubisic *et al.* 1988), cold stratification (Carpenter *et al.* 1982), organic nitrate addition (Grubisic *et al.* 1992, Grubisic and Konjevic 1990), an increase in electron receptors in the soil (Giba *et al.* 1994), soaking in hypochlorite or ethanol (Ho *et al.* 1995), or diammonium phosphate addition (Cunningham and Carpenter 1980). Germination in the absence of these treatments has been reported to take longer and occur at lower rates (Grubisic *et al.* 1985, Carpenter *et al.* 1982).

Although thoroughly studied in laboratory settings, only one previous study (Longbrake 2001) has investigated the conditions under which *Paulownia* seeds germinate in the field. In these field experiments measuring germination on different substrates and across a light gradient (intact forest canopy to clear-cut), germination only occurred under full light (clear-cut) and on cobble, gravel, and bare soil treatments.

Although the work presented in this chapter was one step further removed from the “natural” conditions tested by Longbrake, it occurred under more natural conditions than previous laboratory studies and tested field-relevant variables. In doing so, it brings us closer to understanding the factors which control field germination and bridges the gap between lab experiments and the field germination reported by Longbrake.

Paulownia's adaptation to disturbed, high light environments suggests that its seeds may remain viable for extended periods of time as a strategy for colonizing a habitat that is transient but recurrent in a given location. Some studies have found evidence that there is a tradeoff between dispersal ability and seed persistence (Venable and Brown 1988), though other studies have come to contrary conclusions (Marks 1974, Thompson *et al.* 1998). Regarding *Paulownia*, Longbrake (2001) found low mortality of *Paulownia* seeds ($21 \pm 3.3\%$) after three years with higher mortality in seeds stored at the soil surface at clear-cut and edge sites than those stored buried in the intact forest. In her work, seed dormancy was variable and significantly affected by harvest date, soil profile position, and location. From this, Longbrake concluded that *Paulownia* did form a persistent seed-bank and that seeds could survive in the soil for up to 15 years. These conclusions are counter to those of Hyatt and Casper (2000) who interpreted their low germination rates ($<1.7\%$) and low seed survival rates ($<30\%$) as evidence that *Paulownia* seed longevity in the soil was limited and that it did not form a persistent seed-bank. Experiment #1 addressed the uncertainty raised by these studies by analyzing the germination rate of *Paulownia* seeds from two populations over the course of a year as a function of storage method and time since dispersal. In doing so it asked whether germination varied between populations; how storage type (dry, field, cold storage) affected germination; and at what rate seed viability decreased over time.

Although Longbrake measured the effect of *storage* position within the soil profile, no study has measured the germination rate of buried *Paulownia* seeds. However, this has potentially profound effects on post disturbance dynamics. If seeds are unable to germinate when buried, soil perturbation must accompany any disturbance that creates otherwise ideal habitat characteristics. The effect of burial upon germination is especially important due to

the often insulating effect of soil during fire. In addition to burial, germination in the field is also potentially affected by the presence of leaf litter and vegetation which increases shading and forms (in the case of leaf litter) a physical barrier to the developing seed. These unknowns regarding the effects of light level, litter cover, and seed burial upon seed germination were addressed in Experiment #2. Specifically, this experiment analyzed how a 50% reduction in light, the presence (or absence) of 2cm of leaf litter, and seed position (buried at 2cm, on the soil surface, or on the litter surface) affected the rate of *Paulownia* germination.

Finally, No other study has looked at the direct effects of fire upon *Paulownia* seed viability, though this certainly has significant impacts upon post-fire invasion. Significant fire induced mortality would enable managers to use prescribed fires to kill *Paulownia* seeds within the seed-bank, thereby increasing invasion's dependence upon seed rain and allowing native species a season's worth of growth before faced with competition from *Paulownia*. Experiment #3 addressed fire's impact upon *Paulownia* seeds present in the soil by analyzing how seed position (buried at 2cm, on the soil surface, or on top of the litter layer) and fire intensity (measured by maximum temperature, duration of heating, and duration or occurrence of temperatures above a threshold) affected seed survival as measured by germination.

EXPERIMENT #1: Effect of storage, time, and source

Methods

Seeds for Experiment #1 were collected on October 30th, 2004 from two populations. The first was located along Hwy 64 in Tennessee at UTM_N: 3888031, UTM_E: 722126 (16N, NAD83). Three trees were sampled from this population (samples #1-3). The second population, located along I40 at UTM_N:3951900, UTM_E: 315530 (17N, NAD83), was sampled (one tree) on November 14th, 2004 (sample #4). The experiment was conducted from January 20th, 2005 to January 24th, 2006.

Immediately following collection, seeds were subjected to one of three storage treatments; dry, field, or cold stratification. Seeds stored dry were kept in the dark at room temperature. Those stored under field conditions were put into mesh bags and placed outside under ~15cm of leaf litter. Those within the cold stratification treatment were taken out of dry storage 30 days prior to placement in the greenhouse and placed on the soil (Promix BX) surface on half-flats. They were then moistened and placed inside a sealed plastic bag, inside a black, light-blocking plastic bag, inside a seed storage fridge at the North Carolina Botanical Garden, and stored at 5.2° C for 30 days. This stratification method was chosen because it was consistent with methods in use by the North Carolina Botanical Garden and it did not require the transfer of seeds onto a growing medium post-stratification which raised the risk of seed loss.

Each month, January through November, 80 seeds from each population were removed from their storage treatment and moved to the greenhouse. Seeds of the dry and Field storage treatments were placed on the soil surface and seeds from the cold storage treatment were removed from their plastic bags and placed in the greenhouse. The field storage treatment only included seeds from samples #1, #2, and #4. Additionally, in the field storage treatment, only 40 seeds from sample #2 were germinated each month, and in January

only 40 seeds from sample #4 were germinated. Missing populations and seeds were due to seed bag damage by animals, experimental error, or extenuating circumstances. Seeds were kept moist and germination was checked twice weekly for two months after sowing. Germination was counted at the point of cotyledon emergence.

Analysis and Results

Data from this experiment was analyzed using a grouped binomial model with full interactions (main effects and a storage*date interaction term, McLaughlin 1999). There were no significant differences between populations or samples (looking at each sampled tree separately) so these were treated as replicates in the subsequent analyses. Because of estimation issues in some months due to smaller sample sizes or germination rates approaching zero, a Bayesian Hierarchical Model was developed using WinBUGS and R (Ellison 2004, Manly 2001). The posterior distribution of germination success by treatment and month is presented in Figure 4.1. Storage treatment did have an effect on germination rate with stratified seeds having lower germination rates than field or dry stored seeds. There were no differences between the field and dry storage treatments. Time did affect germination, but this was inconsistent in effect across storage treatments and between months. There was a trend towards decreased germination in field stored seeds after the fifth month and stratified seeds had almost no germination for the first five months followed by consistently increasing germination rates which reached over 50% by the end of the experiment (month 11).

EXPERIMENT #2: Effect of light, litter, and seed position

Methods

Seeds were collected on November 12th, 2005 from a population located off Exit 7 on I40 (Harmon's Den) at UTM_N: 3956779.5, UTM_E: 317203.94 (17N, NAD 83). The experiment was begun on August 28th, 2006 and ran until October 13th, 2006.

A randomized, block design was used to examine the effects of light level, litter cover, and seed position on *Paulownia* seed germination. The light treatment levels were full sun and 50% shade and they were arranged in blocks with 2 replicates. Shading was done by 50% shade cloth which surrounded the flats such that no unfiltered light reached them. The surface cover treatment levels were bare soil and 2cm of litter cover. Hardwood leaf litter (oak, hickory, sweet-gum, and maple) was collected from the forest at the Mason Farm Biological Station in Chapel Hill. Seed position treatments were on the litter surface, at the soil surface, and buried at 2cm beneath the soil surface. The experiment was conducted within the Coker Hall greenhouse at UNC-Chapel Hill. Seeds were germinated in half flats and Promix BX was used as the soil. Germination was counted at the point of cotyledon emergence.

Five replicates of each surface cover and burial treatment combination were randomly placed within each of the two sun and two shade enclosures (the blocks). 100 *Paulownia* seeds were added to each half-flat and the treatment combinations resulted in a total of 100 half-flats (25 per light replicate) because one treatment combination (bare soil ground cover and litter surface seed position) was not possible. Sun/Shade enclosures were oriented lengthwise along a greenhouse bench running longwise E-W with the shade enclosures in the

NW and SE corners. Enclosures were situated thus to avoid confounding the effect of shade with side of table. Although this arrangement caused some shading of the sun enclosure in the NE corner of the table, this was controlled for by switching flats between enclosures three times per week (M, W, F) such that all flats in one sun enclosure were moved to the other and the same was done for the shade enclosures. At the same time the location of each flat within the enclosures was randomized. The same process was done to both the sun and shade treatments to avoid confounding randomized/non-randomized and sun/shade effects. Germination was tracked twice weekly (M, F).

Analysis and Results

Because one treatment combination was omitted (impossible combination), a factorial randomized block analysis was not possible. Instead a main effects analysis was done through a series of orthogonal contrasts (Table 4.1, Quinn and Keough 2002). Although the third contrast (Seeds Buried and at the Soil Surface vs. at the Litter Surface) does not make intuitive sense, it allowed for the contrast to be orthogonal. These contrasts were analyzed with a grouped binomial model with random effects (Table 4.2, Figure 4.2). Random effects, added to address over-dispersion, significantly improved the model predictions, particularly for the bare soil treatments.

A second set of contrasts (Table 4.3) was used to compare treatment effects of interest not covered by the initial contrasts. The second contrast set used the results from the fitted model to obtain estimated contrast means and intervals for the appropriate treatment pairs (Table 4.4). These were obtained using a Bayesian approach with the estimated

posterior distribution of parameters obtained from Markov chain Monte Carlo sampling (Link *et al.* 2002). Random effects were again included to address data over-dispersion.

Light, ground cover and seed position all had significant effects upon germination (Table 4.2, Figure 4.2). Surprisingly, the highest germination levels were recorded under 50% shade light (with bare soil). Germination rates within the shade enclosures were significantly higher than germination rates under full sun ($p < .001$). The difference between sun and shade was greatest in the bare soil, soil surface treatment combination. Germination rates of unburied seeds were significantly lower when litter was present ($p < .001$) and buried seeds had significantly lower germination rates than seeds on the soil surface ($p < .001$). There was a significant ($p < .001$) interaction between the ground surface (bare soil vs. litter) and light (sun vs. shade) treatments. No other interactions were significant. Buried seeds had higher germination rates when litter was not present (Table 4.4), though the germination rate for both groups was very low. When litter was present, seeds placed on the litter surface did germinate at a slightly greater rate than those located on the soil surface underneath the litter (Table 4.4).

EXPERIMENT #3: Fire Survival

Methods

Seeds utilized in this experiment were collected from the same source and at the same time as those utilized in experiment #2. Experiment #3 was started on October 13th, 2006 and ran until November 28th, 2006.

For each burn event, 100 *Paulownia* seeds were enclosed in a wire mesh bag to enable retrieval and these were placed either on the litter surface, soil surface, or at 2cm depth. 2cm of litter were added to every burn. Burning was conducted using a burn tool developed by Dr. Joan Walker with the National Forest Service's Southern Research Station at Clemson University. The tool consists of an inverted propane burner attached to a tripod and lowered to the desired height above the soil surface. At each burn event, the burner was lit while at its maximum height and left stationary for one minute to simulate the heat of the approaching fire. The burner was then lowered over the next 90 seconds to 5cm above the litter surface. The burner was left there for either: 1) 30 seconds or till the temperature reached 90°C in the case of the low intensity burn category; or 2) for 60 seconds or a temperature of 150 °C in the case of the high intensity burn category. Temperature was recorded and displayed in real time through thermocouples located at the soil surface and at the seed burial depth (if different) which were attached to a computer via a data-logger. Although burns were divided into intensity categories, the continuous nature of the data enabled fire intensity variables (maximum temperature experienced by seeds, duration of heating, and duration of temperatures above different thresholds) to be analyzed as continuous variables. Burning was conducted on October 13th and 16th and soil samples were collected on both dates to measure soil moisture content. There was no rainfall in the days immediately before or between burning, soil moisture was not markedly different between the two days (12.42% and 8.34%), and it was not a significant predictor of seed survival.

The high intensity, seeds at litter surface treatment was only done once because the thermocouples placed with the seeds maxed out at 662.6°C. As no species has demonstrated survival at these temperatures and there was concern that the thermocouples might be

damaged, this treatment was not repeated. The first 5 replicates of the low and high intensity treatments were conducted with seeds and thermocouples placed at both the soil surface and at 2cm. To ensure that the seed packet at the soil surface was not affecting temperatures at 2cm, the 2cm treatment combinations were conducted twice more without seeds (but with thermocouples) at the soil surface. There was no difference in the temperature range at 2cm with or without the seed packet at the surface. A total of 30 seed packets were burned (15 in each intensity category) and 5 were left unburned. After the burn, seeds were transferred to a growing medium (Promix BX) in half-flats in the Coker Hall greenhouse at UNC-Chapel Hill for germination. Flat position was randomized three times per week (M, W, F) and germination was recorded twice weekly (M, F). Germination, counted at the point of cotyledon emergence, was tracked through November 25th.

Analysis and Results

Burial had a very significant effect on the temperature seeds experienced, particularly during high intensity burns (Figure 4.3). Germination data were analyzed with a grouped binomial model with random effects included to address over dispersion (Table 4.5, McLaughlin 1999). There was a significant negative relationship between germination and the maximum temperature experienced by seeds and the categorical variable maximum temperature $\leq 100^{\circ}\text{C}$. Only three seeds germinated when the maximum recorded temperature exceeded 100°C and as one of these germinated at 572°C , far above the maximum temperature threshold for any species, it was assumed that these seeds were protected in some fashion during the burn and that this is not reflective of *Paulownia*'s seeds true ability to survive heating. These outliers had no significant effect on the model, but as

they were outliers, they were removed prior to model development. Although soil moisture effects seed survival in fires, the slight difference in soil moisture over the two days of the experiment was not a significant factor. There were no significant interactions between model variables.

DISCUSSION

Over-dispersion was present to some extent in all three experiments. In germination experiments where the dependent variable is binary (germinated or not), this means that the assumptions of binomial data have been violated in some fashion. Since the first two assumptions of this distribution (experiment consists of a fixed number of Bernoulli trials, and only two outcomes are possible) clearly hold, the violation must occur in either the third (Bernoulli trials are identically distributed) or fourth (outcomes are independent) assumptions. Work by Crowder (1978) showed that the germination success of one seed could affect the germination success of its neighbors by altering the immediate environment to increase or decrease germination probability of as yet un-germinated neighboring seeds. The inclusion of a random effects variable accounts for this by assuming that the response probabilities are not constant but vary across replicates and treatments and are described by a normal distribution with a mean of zero.

Experiment #1

Storage treatment had a clear effect on germination with much higher germination occurring in seeds stored dry or in the field than those that were stratified. These results are counter to those of Barnhill *et al.* (1982) and Carpenter and Smith (1981) which found higher germination rates in stratified seeds than in dry stored seeds. One possible explanation for the discrepancy would be mold growth on stratified seeds and/or their medium which prevented germination, but no evidence of this was seen. Other potential explanations include: different stratification conditions, germination conditions post treatment, and how germination success was recorded. The stratification and germination methods and the way in which germination was recorded in both prior studies was significantly different from the work presented here and it is possible that this accounts for the different results. In the study reported here, stratified seeds may also have failed to mature to the point where germination was considered successful. Alternatively, an unrecorded and controlled factor may have given rise to this studies' low germination rate for stratified seeds. The over-dispersion in the data suggests that this might have occurred, however as discussed above, over-dispersion is fairly common in germination experiments so that may not be the case. The over-dispersion in this experiment was larger than in the other two experiments which suggests that either the magnitude of the over-dispersion effect was stronger here or that some other factor was at play. The almost complete absence of germination of stratified seeds through the sixth month followed by a steady increase in germination suggests some unid in this treatment.

The decreased germination of field stored seeds after the fifth month may have been caused by decreased seed viability over time, an increase in the frequency and/or strength of secondary dormancy, unobserved germination prior to removal from the storage bags, or a combination of the three. If the decreased germination was reflective of decreased viability

and the rate of viability loss does not change over time, seeds would remain viable in the soil for ~5.6 more months (~ 1.5 years since dispersal); an estimate which is significantly lower than the 15 year estimate given by Longbrake (2001). The lack of a decrease in germination rate in dry stored seeds and the increased germination rate of stratified seeds suggests that this trend may be environmental in origin and not an absolute trend. The high level of germination one year after dispersal in dry stored seeds agrees with Longbrake (2001) whose work suggested that *Paulownia* does form a persistent seed-bank. On the other hand, the results from the field stored seeds support the theory that there is a trade off between dispersal ability and seed longevity (Venable and Brown 1988).

Longbrake (2001) also found evidence of germination and seed predation prior to seed bag recovery both of which could partially account for the decreased germination over time observed in her work and that reported here. Stratification has been reported to eliminate or reduce the light requirement for germination (Carpenter *et al.* 1982) and as field-stored seeds were in place over the winter, it is possible that this had an equivalent effect and undetected germination occurred prior to seed bag collection. Finally, this experiment suggests that if secondary dormancy was induced by a thirty day absence of light (Grubisic *et al.* 1985) that it was readily broken once seeds were exposed to unfiltered full sunlight.

There was no evidence of significant variation in germination rates between the two sampled populations. Germination rates are also comparable to those reported by Longbrake (2001) suggesting low levels of variation in germination ability at the regional level and that *Paulownia* germination rates are affected more by the conditions seeds experience than the population they come from. This is in keeping with the highly dispersed nature of

Paulownia's seeds which should lead to genetically well connected populations and lower levels of trait variance including seed viability.

The best fit model for this experiment did include an interaction between storage and time. The complicated nature of that interaction is illustrated by the need to fit the full model separately for each month. The inconsistent interaction effect over time and between treatments suggests a complicated germination control mechanism that is not adequately elucidated by this study.

Experiment #2

Contrary to the predicted outcome, seed germination was significantly higher in 50% shade than in full sun. This effect was strongest when seeds were placed at the soil surface without litter and was obscured or reversed by other treatments which reduced overall germination success. These results were surprising because habitat models based on field survey data predicted that the most important variable determining invasion success was the amount of remaining vegetation cover and that cover greater than 44% prevented *Paulownia* invasion under most other environmental conditions (Chapter V). This field data agrees with work by many others who have also found that *Paulownia* was primarily or exclusively associated with high light environments (Williams 1993, Longbrake 2001, Bonner and Burton 1974, Tang *et al.* 1980). However, several factors may reconcile these results with previous work. The studies cited above did not look at the actual level of vegetation cover under which *Paulownia* occurred, leaving open the possibility that cover might have been at or just above the 50% shade used in this study. Work by Longbrake (2001) found that although *Paulownia* germinated best in clear-cut areas (across a gradient from cleared forest

to forest interior), it did germinate at the forest edge suggesting that germination was not prohibited under reduced light conditions. Also, measurements of vegetation cover presented in Chapter V may not have completely captured the degree to which light was blocked from reaching the forest floor. Those readings were taken at 1m so the actual degree of shading on the forest floor may have been greater than 50%. Another factor which covaried with the light treatment is soil moisture. All seeds were watered daily and although it has been suggested that soil moisture is not a dominant factor in determining *Paulownia* germination (Longbrake 2001), the shade cloth kept the soil moister which may have impacted germination.

Finally, the experiment only tracked germination and survival over the first two months while field surveys recorded individuals that had survived for months or years. Many species will germinate under conditions that cannot support growth till maturity and thus the environmental niche over which seedlings are encountered is often larger than that over which mature individuals are distributed (Gibson and Good 1987, Schupp 1995, Kessler 2000). Taken together these factors may explain the apparent contradiction of field observations and experimental results.

The importance of high light levels for this species and the presence of a threshold beyond which decreasing light availability reduces germination is also supported by lower (though non-significant) germination levels in the shade than in the sun when seeds were positioned at the soil surface beneath litter. This suggests that the combined shading from the shade cloth and leaves may cross a critical threshold and decrease germination. Also supportive of this is the significantly lower germination rate of buried seeds when litter was

present suggesting that burial plus litter decreases light availability further below the germination threshold.

Litter had a significant negative ($p < .001$) effect on germination rates in both the sun and shade treatments. As litter decreases light availability at the soil surface, this is further evidence in support of the negative effect of shading. This effect of litter is also in agreement with reports that *Paulownia* germinates best on bare soil (Williams 1993, Hu 1959, Hu 1961). Given the small nature of *Paulownia* seeds and the correspondingly low level of carbohydrate reserves contained within them, a seed located beneath litter may have insufficient energy resources to push its way up through it. Determining the exact mechanism at play is however beyond the scope of this experiment. Though the experiment utilized only 2cm of litter, litter on the forest floor is often much deeper. Presumably a deeper litter would further decrease the ability of a newly germinated seed to push its way through it. The intact litter of the forest floor is also often much more compacted than that used in this experiment which would also likely make it less likely in the field for a seed to get washed down to the soil surface and previous work (Hu 1961) has shown that litter presence has a significant effect on seeds located on top of it due to the seed's slender primary root and limited carbohydrate reserves. Taken together this suggests that this experiment may underestimate the negative effect of litter on *Paulownia* germination in the field.

There was a highly significant difference in the germination of seeds positioned at the litter or soil surface and those buried at 2cm ($p < .001$). Again, this is line with reports that *Paulownia* seeds germinate best at the soil surface (Williams 1993, Hu 1959, Hu 1961). These results are not surprising as *Paulownia* germination is phytochrome controlled and

buried seeds would not receive sufficient light for germination. The presence of some germination from buried seeds suggests that the seeds either responded to light they were exposed to prior to burial or that phytochrome control is not absolute even in the absence of stratification which removes phytochrome control (Carpenter *et al.* 1982).

Experiment #3

Seed position was only significant in its effect on the temperatures experienced by seeds. If seeds had been left in situ following the burning, the results and conclusions would likely be different for the reasons discussed for Experiment #2. The importance of position to seed survival is illustrated by the different temperatures experienced at the soil surface (234°C) and at 2cm. (38°C, Figure 4.4). The lack of germination in seeds which experienced temperatures greater than 100° C (with the exceptions explained in the Results) suggests that *Paulownia*'s seed's ability to survive fire is similar to the response of seeds in the *Pinus banksiana* community (mortality between 50°C and 120°C, Ryan 2002), southeastern Australian Legumes (100°C-120°C, Auld and O'Connell 1991), and seeds in an old-growth Douglas-Fir community (75-100°C degrees, Clark and Wilson 1994). That *Paulownia* shows ~100% mortality at slightly lower temperatures than some of the above species is not surprising as it is not specifically fire-dependent or adapted.

Although no data exist for the range of soil temperatures actually experienced during fires in southern Appalachian xeric forests, the range of temperatures recorded in other communities suggests that the temperature range in this experiment was appropriate. Clark and Wilson's study of slash fires in the Pacific Northwest recorded temperatures between 52 and 177 °C at the soil surface in "low" intensity fires (Clark and Wilson 1994). In Ryan's

study of the *Pinus banksiana* community, the maximum soil surface temperature ranged from ~1,000°C for ~1 minute in crown fires with no duff consumption to ~275°C for ~6 hours in a smoldering fire with deep duff (Ryan 2002). Finally, in two prescribed fires in the boreal coniferous forests of southern Finland, soil surface temperatures ranged from 401 to 809°C during a low intensity fire and from 701 to 869°C during a moderate intensity fire (Vasander and Lindholm 1985). Together these studies suggest that the temperatures in this experiment might be lower than those experienced in the field. If field temperatures are >100°C, then *Paulownia* will be largely or entirely dependent upon post-fire dispersal.

SYNTHESIS

Taken together these experiments demonstrate that if buried, *Paulownia* seeds likely survive at least 1.5 years post-dispersal and survival rate is more affected by the conditions seeds encounter than the population from which they come. If seeds are not buried and they encounter sufficient light levels and bare soil conditions- they will germinate in the first growing season following dispersal and not develop a persistent seed-bank. If there is a fire, seeds are likely to be killed unless buried or in some other protected micro-site that limits their exposure to temperatures >100°C. Seeds which survive via burial will have limited germination if not subsequently exposed through soil erosion or some other force. Germination is further diminished if litter is not consumed in the fire.

TABLES AND FIGURES

Figure 4.1: Monthly germination rates by treatment for Experiment #1. Means depicted by open symbols, smears represent the 50% (heavy, darker) and 95% (lighter, thinner) Bayesian credibility intervals.

Figure 4.2: Actual and predicted germination rates for Experiment #2. Grey dots represent observed germination rates, the * shows the predicted mean germination rates for the best model without random effects, and the open red and blue symbols are the empirical Bayes predictions of germination for the best model including random effects. The model is given in Table 4.2.

Table 4.1: Orthogonal contrasts of tested variables in Experiment #2. Variable codes are as follows: BB: Bare soil, Buried seeds; BS: Bare soil, seeds at Soil surface; LB: Litter present, Buried seeds; LS: Litter present, seeds at Soil surface; LL: Litter present, seeds on Litter surface.

Table 4.2: Model Summary utilizing the orthogonal contrasts presented in Table 4.1 for Experiment #2.

Table 4.3: Second contrast set designed to test variable effects in Experiment #2 not captured by the orthogonal contrasts laid out in Table 4.1. Variable codes are as follows: BB: Bare soil, Buried seeds; BS: Bare soil, seeds at Soil surface; LB: Litter present, Buried seeds; LS: Litter present, seeds at Soil surface; LL: Litter present, seeds on Litter surface.

Table 4.4: Model summary utilizing the contrasts presented in Table 4.3 for Experiment #2.

Figure 4.3: Data-logger output for a high intensity burn in Experiment #3.

Figure 4.4: Data-logger output for a low intensity burn in Experiment #3.

Figure 4.5: Number of *Paulownia* seeds germinated as a function of maximum temperature experienced in Experiment #3.

Table 4.5: Summary of best fit model predicting *Paulownia* germination frequency in Experiment #3.

Figure 4.1: Monthly germination rates by treatment for Experiment #1. Means depicted by open symbols, smears represent the 50% (heavy, darker) and 95% (lighter, thinner) Bayesian credibility intervals.

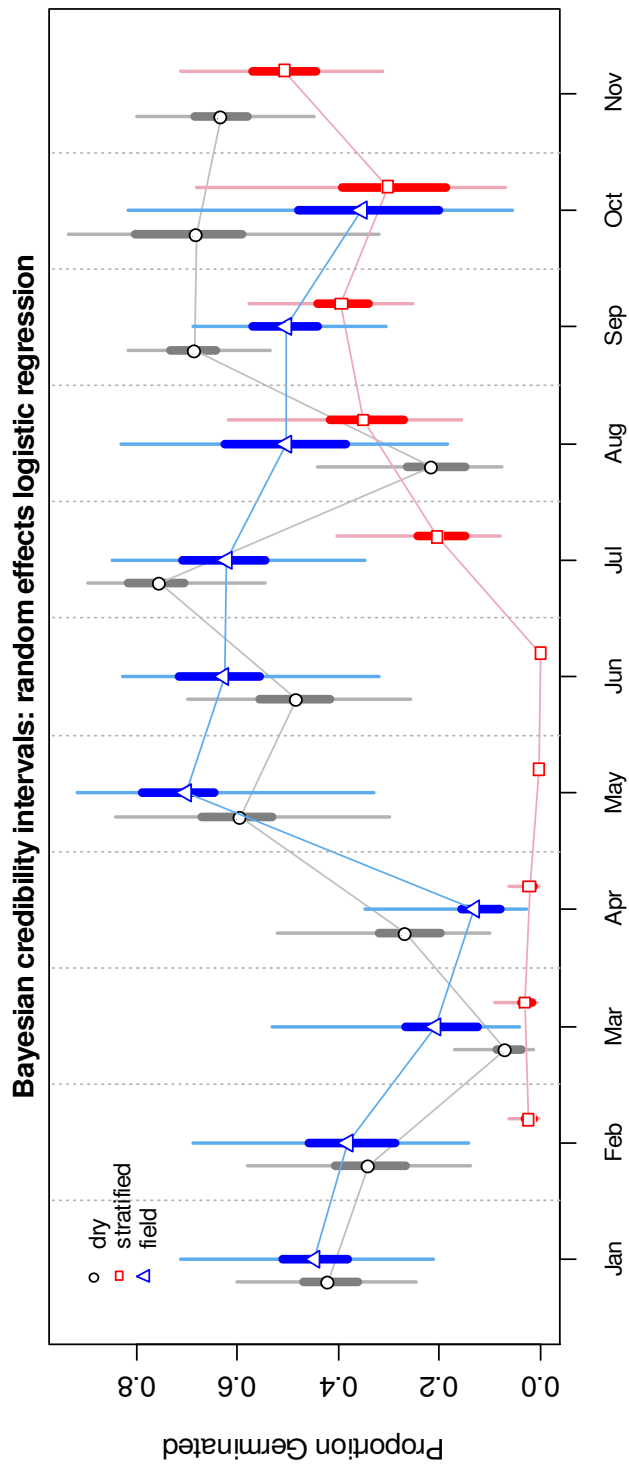


Figure 4.2: Actual and predicted germination rates for Experiment #2. Grey dots represent observed germination rates, the * shows the predicted mean germination rates for the best model without random effects, and the open red and blue symbols are the empirical Bayes predictions of germination for the best model including random effects. The model is given in Table 4.2.

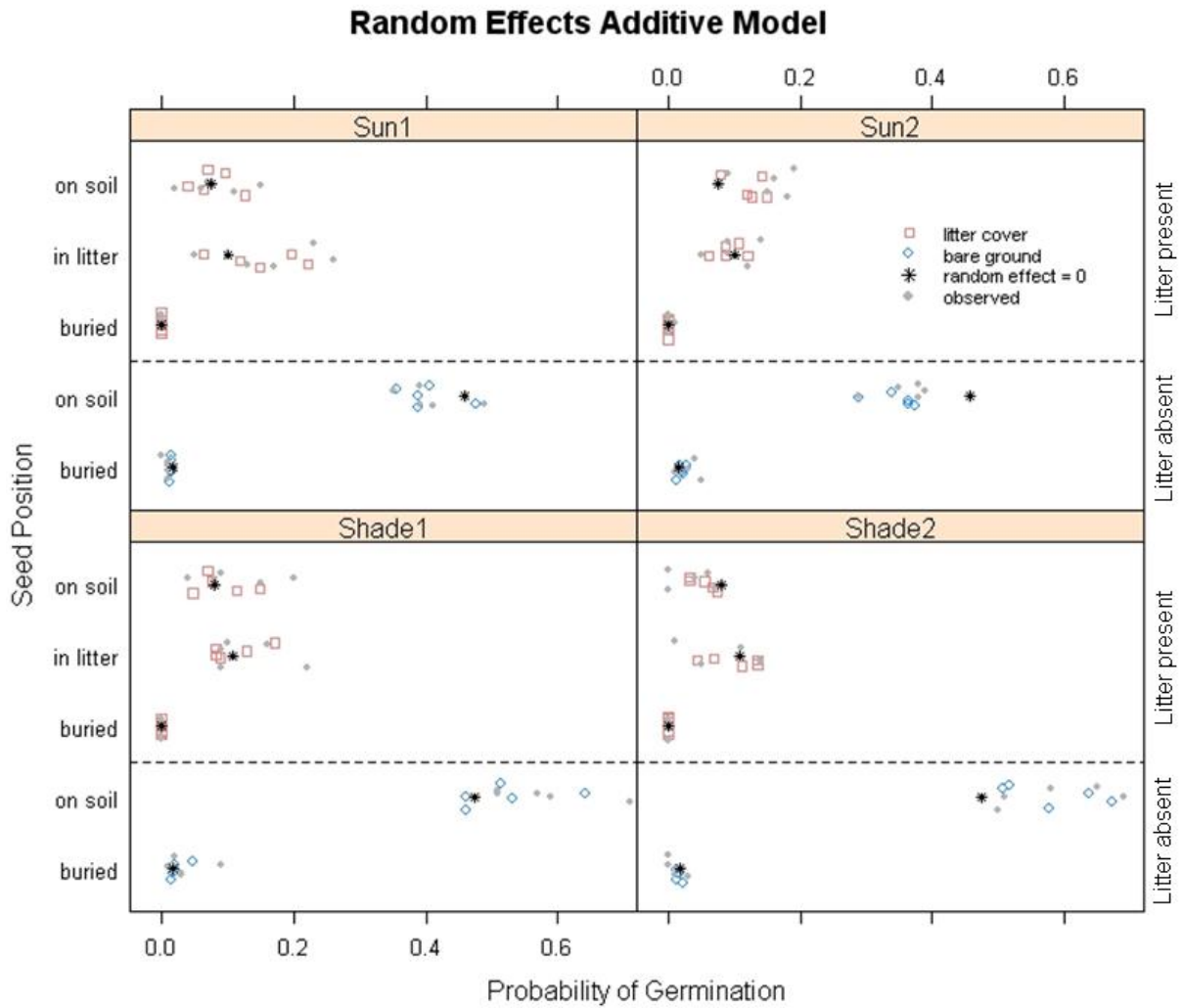


Table 4.1: Orthogonal contrasts of tested variables on Experiment #2. Variable codes are as follows: BB: Bare soil, Buried seeds; BS: Bare soil, seeds at Soil surface; LB: Litter present, Buried seeds; LS: Litter present, seeds at Soil surface; LL: Litter present, seeds on Litter surface.

Contrast	Bare		Litter		
	μ_{BB}	μ_{BS}	μ_{LB}	μ_{LL}	μ_{LS}
Ground: Bare vs. Litter	3	3	-2	-2	-2
Position 1: Buried vs. Soil	1	-1	1	0	-1
Position 2: Buried & Soil vs. Litter	0	0	1	-2	1
Interaction	1	-1	-1	0	1

Table 4.2: Model Summary utilizing the orthogonal contrasts presented in Table 4.1 for Experiment #2.

	Estimate	Std. Error	z value	pr(> z)	Sig.
(Intercept)	-3.24141	0.24969	-12.982	<2e-16	***
Ground: Bare vs. Litter (Litter baseline)	0.51703	0.07939	6.513	7.37e-11	***
Position 1: Buried vs. Soil (Soil baseline)	-2.31501	0.2744	-8.497	<2e-16	***
Position 2: Buried & Soil vs. Litter	-1.00062	0.18256	-5.481	4.23e-08	***
Interaction: Ground*Position(Buried, Soil)	0.36524	0.27244	1.341	0.180	
Light: Sun vs. Shade (Shade baseline)	-0.01752	0.19048	-0.092	0.927	
Interaction: Ground * Light (Shade base)	-0.21679	0.05225	-4.149	3.34e-05	***

Significance codes: *** < 0.001 , ** < 0.01 , • < .05

Model: Number of germinated seeds ~ Ground + Position1 + Position2 + Interaction + Light
+ Ground*Light + Block random effects + Random effects

Random Effects

Group	Name	Variance	Std. Dev.
Random effects	(Intercept)	0.200317	0.44757
Block effects	(Intercept)	0.019019	0.13791

Summary Statistics

AIC = 207

BIC = 231

logLik = -94.55

Deviance = 189.1

Degrees of freedom = 92

Table 4.3: Second contrast set designed to test variable effects in Experiment #2 not captured by the orthogonal contrasts laid out in Table 4.1. Variable codes are as follows: BB: Bare soil, Buried seeds; BS: Bare soil, seeds at Soil surface; LB: Litter present, Buried seeds; LS: Litter present, seeds at Soil surface; LL: Litter present, seeds on Litter surface.

Contrast	Bare		Litter		
	μ_{BB}	μ_{BS}	μ_{LB}	μ_{LL}	μ_{LS}
Contrast #1: Effect litter on buried seeds	1	0	-1	0	0
Contrast #2: Diff. in seeds on litter vs. soil	0	0	0	1	-1

Table 4.4: Model summary utilizing the contrasts presented in Table 4.3 for Experiment #2.

Contrast	Est. contrast (mean)	2.5% Quantile	97.5% Quantile
Contrast #1: Effect litter on buried seeds	0.484041	0.186781	0.908738
Contrast #2: Diff. in seeds on litter vs. soil	-0.187470	-0.311469	-0.078140

Figure 4.3: Data-logger output for a high intensity burn in Experiment #3.

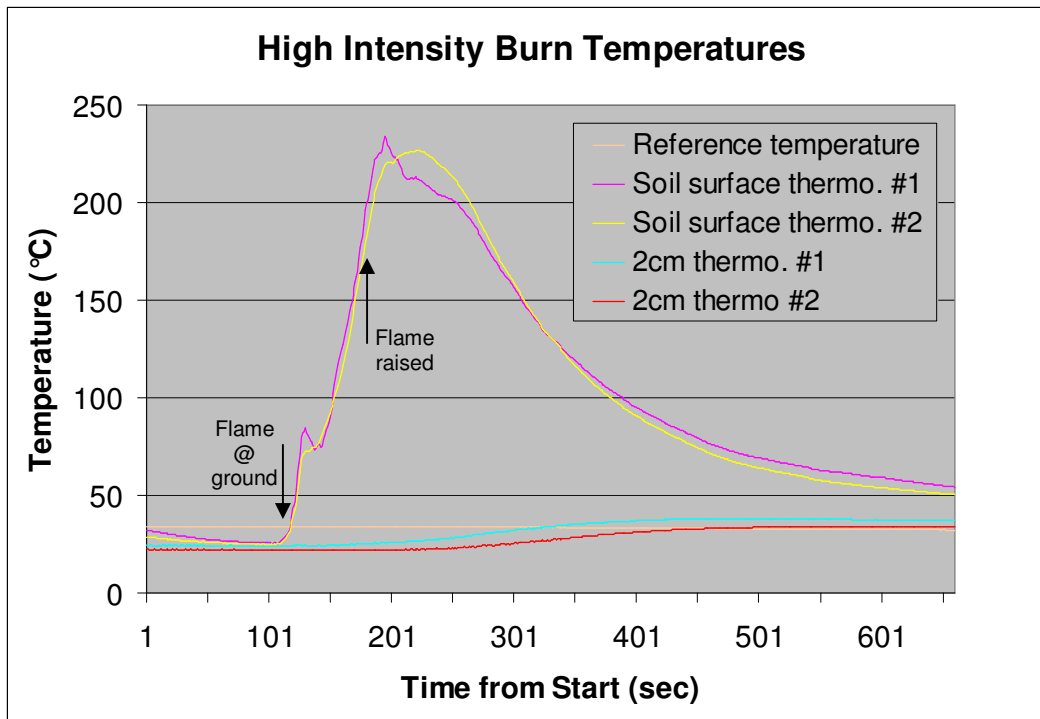


Figure 4.4: Data-logger output for a low intensity burn in Experiment #3.

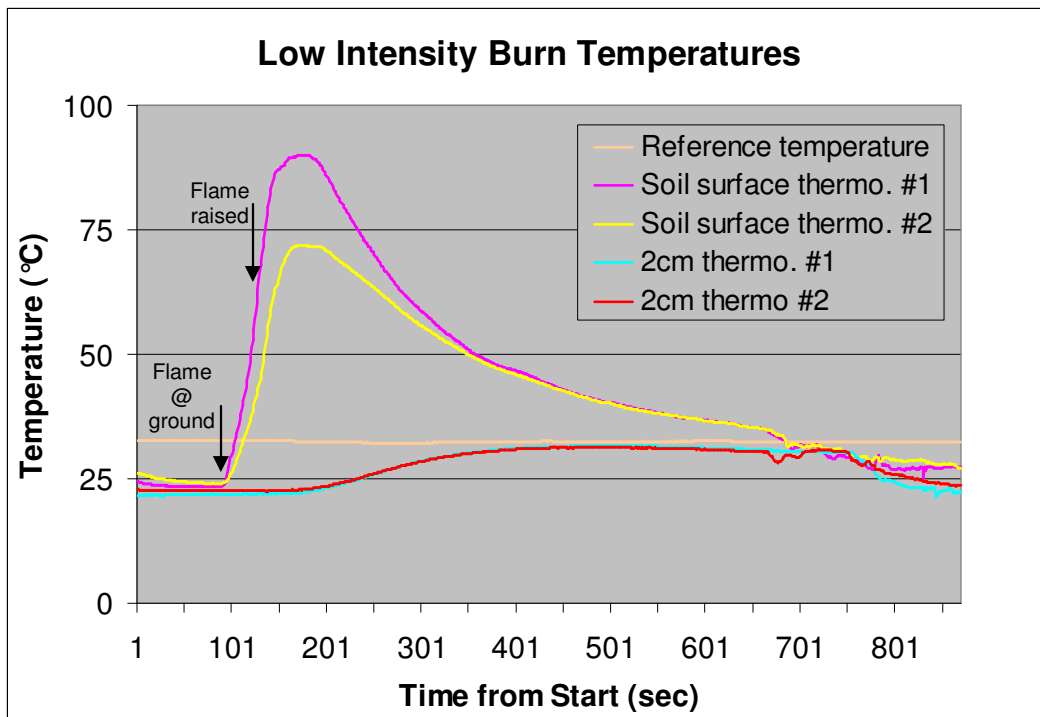


Figure 4.5: Number of *Paulownia* seeds germinated as a function of maximum temperature experienced in Experiment #3.

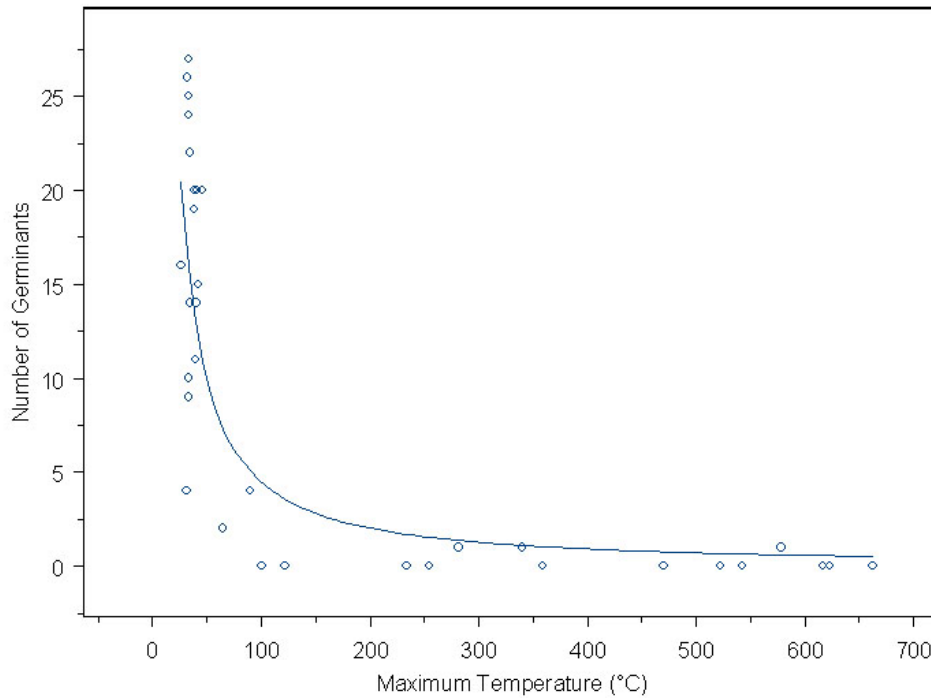


Table 4.5: Summary of best fit model predicting *Paulownia* germination frequency in Experiment #3.

	Estimate	Std. Error	z value	pr(> z)	Sig.
(Intercept)	2.4253	1.6880	1.437	0.1508	
Log (Maximum Temperature)	-1.1504	0.4641	-2.479	0.0132	*
Max. temp. >100°C (vs. <100°C, Categorical)	-2.1599	1.0703	-2.018	0.0436	*

Significance codes: *** = 0.001 , ** = 0.01 , * = .05

Model: Log (Number of germinated seeds) ~ Log (Maximum temperature) +
(Max. temp </> 100°C) + Random Effects

Summary Statistics:

AIC = 152.4368

logLik = -72.21841

Residual Deviance = 57.47933

Degrees of freedom = 29

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CHAPTER V:

Variables determining the post-fire invasion of *Paulownia tomentosa* in the southern Appalachians

ABSTRACT

The post-fire invasion by *Paulownia* in xeric forests of the southern Appalachians has, till now, only been documented anecdotally and the variables which determine invasion success have remained unexamined. In this chapter, the variables which determine the pattern of invasion are investigated through the analysis of vegetation plot data from five fires across the southern Appalachians. Analysis of this data via multiple approaches found that the most significant variable determining invasion success was the amount of remaining vegetation cover. Classification tree models predicting *Paulownia* presence-absence found elevation, topographic convergence (moisture availability), slope, and hillshade to be important predictors in addition to vegetation cover.

Similar, though slightly different results were found with a logistic regression analysis predicting *Paulownia* presence-absence. In this model, the significant variables were: vegetation cover ($p < .001$), aspect ($p = .324$), litter cover ($p < .05$), topographic position ($p < .001$), and slope ($p = .756$). Although aspect and slope were not individually significant, they decreased the model's AIC value and increased the significance of the Goodness of Fit test. A negative binomial model predicting *Paulownia* stem abundance found that it did n

deviate significantly from that predicted by a null model with only the y intercept and dispersion parameter specified.

Finally, when the plots were ordinated using Non-metric Multidimensional Scaling ordination, *Paulownia* abundance decreased with increasing species richness and vegetation cover, increased with elevation, and the maximum humus depth, and was orthogonal (or nearly so) to soil nutrient variables (Ca ppm, Mg ppm, pH, Fe ppm, and H⁺ concentration).

Although the invasion pattern of *Paulownia* is complex, its post-fire invasion is determined by “universal” variables such as elevation, remaining vegetation cover, and hillshade. As such each fire is the same from *Paulownia*’s perspective. Given an appropriately hot fire, available seeds, and sufficiently xeric locations, *Paulownia* demonstrated the ability to invade any landscape.

INTRODUCTION

The xeric forests of the southern Appalachians are dependent upon recurrent fires to maintain their composition and structure (Harmon 1982, Williams 1998). Conservationists often seek to restore fire as a natural process in ecosystem management, yet disturbance has also been implicated as a promoter of alien species invasions. This is problematic as land managers have increased their use of fire to encourage the maintenance and restoration of native, fire-adapted xeric communities. The post-fire invasion of *Paulownia* beginning in the 1980's moved this from a theoretical problem to a practical one for the Appalachians.

Paulownia seedlings have not been seen in all fires or uniformly across individual fires leading to questions about the factors that control *Paulownia* establishment. Patterns of invasion, indeed patterns of species occurrence generally, have been explained by two basic constraints: spatial-temporal constraints and environmental constraints (Nekola *et al.* 2002). The spatial constraints of dispersal were addressed in Chapter III. As *Paulownia* invades following fire, potential environmental constraints include conditions that are the result of fire effects in addition to inherent site environmental variables such as elevation, slope, and aspect. Identifying the variables associated with *Paulownia* invasion will increase understanding of the potential for this species to spread following future fires and enable managers to identify the where it is likely to be found within a fire should control efforts be undertaken. This chapter identifies those environmental, spatial, and fire mediated biotic variables underlying the post-fire pattern of *Paulownia* invasion as measured by its presence-absence and the number of seedlings.

METHODS

Details on sites (individual fires) sampled and the data collection methodologies were given in Chapter II and thus are not reprinted here. All plots and variables described in Chapter II were used in the following analyses unless otherwise noted.

ANALYSES

The effect of environmental (slope, aspect, ground cover, soil chemistry and texture) and spatial (hillshade, elevation, topographic position, TCI), and fire mediated biotic (percent cover of each strata and cover over all) variables upon *Paulownia* invasion was examined in four ways. The first approach utilized classification trees to analyze the environmental, spatial, and biotic variables associated with *Paulownia* presence-absence (Vayssières *et al.* 2000). Variables were chosen for use based on their individual correlations with the number of *Paulownia* stems and their distribution in plots with vs. plots without *Paulownia*. Due to the circular nature of aspect, with each approach two transforms of the variable, the Beers transform (Beers 1966) and the two variable transform (Lasting Forests 2008) described in Chapter II were tested for significance. These transforms are labeled EW.Aspect, NS.Aspect, and Beers where they appear in the models. The classification tree was pruned using the `cv.tree` and `prune.tree` functions in S-Plus. The `prune.tree` function measures the overall misclassification rate for different size (# of final groups) trees. The `cv.tree` function measures the misclassification rate of a random subset of 10% of the data (process is

repeated for all subsets). The classification tree was pruned to minimize both of these values. As site (which fire) was one of the early splits in the tree built utilizing data from all fires, a classification tree model was developed utilizing data from only three fires (Linville, Daus, and Firebug, hereafter “data subset”). As the two omitted fires experienced low rates of invasion due to limited seed availability (Chapter III), utilizing this data subset provided a clearer picture of *Paulownia*’s site requirements. The accuracy of the pruned tree built with the data sub-set was measured by the proportion of samples did or did not match their predicted state.

The second approach to determining the variables associated with *Paulownia* invasion utilized a logistic regression analysis of the afore mentioned variables’ explanatory power as related to the presence-absence of *Paulownia* (McLaughlin 1999, Quinn and Keough 2002). The best fit model was determined by a Hosmer-Lemeshow Goodness of Fit test and AIC values.

A negative binomial regression model was used to test whether the above variables enable accurate predictions of *Paulownia* stem abundance (McLaughlin 1999). To test this, the observed abundance distribution was compared to the best fit model and the ‘null’ distribution of abundances expected in the absence of predictive variables (specifying only the y intercept and dispersion parameters).

Finally, the plot ordinations developed in Chapter II were analyzed with regards to *Paulownia* abundance and presence (McCune and Grace 2002). The orientation of the *Paulownia* abundance vector relative to other environmental vectors was examined to determine which variables correlated with *Paulownia* abundance. *Paulownia* presence-

absence was also used as a grouping variable to see whether plots with (or without) the species were clustered in a particular portion of ordination space.

RESULTS

The most significant variable determining *Paulownia* invasion success (as measured by its presence) was the amount of remaining vegetation cover >1m high. This shows in the classification tree (Figure 5.1) as the first split at vegetation cover \leq 44% (as measured by a densiometer) and in the logistic regression model where this variable explains the highest level of variability in the data. Other significant variables in the classification tree were: slope, elevation, hillshade, and TCI. The classification tree predicted the probability of encountering *Paulownia* at a given site with a high degree of accuracy overall (89.94%), though absence predictions were slightly more accurate than presence predictions (91.7% vs. 86.9%, Table 5.1).

The significant variables in the logistic regression model were: Vegetation cover (densiometer, $p < .001$), aspect ($p = .324$), litter cover ($p = .042$), topographic position ($p < .001$), and slope ($p = .756$) (Table 5.2). Although aspect and slope were individually significant, their inclusion improved the fit of the model and lowered its AIC value. The model's overall Goodness of Fit was highly significant ($p = .012$). Substituting hillshade for aspect decreased the fit of the model though it remained significant ($p = 0.0237$). Substituting either of the aspect transformations for the raw aspect values decreased the fit of the logistic model to non-significance.

Although the classification tree model of *Paulownia* presence-absence was highly accurate, the regression tree modeling abundance of *Paulownia* did not yield accurate predictions. The reason is illustrated by the results of the negative binomial regression (Figure 5.2) which shows that *Paulownia*'s abundance distribution was not significantly different from what which would occur by random chance.

The ordination (Figures 5.3) shows the number of *Paulownia* stems increasing along the second axis with increasing humus depth and elevation and decreasing with species richness. *Paulownia* abundance was roughly orthogonal to, and hence independent of, Mg ppm., Mn ppm., Ca ppm., Fe ppm., H^+ concentration, and pH.

DISCUSSION

Paulownia's invasion after fire is controlled by a complex set of interactions between environmental variables and as such it is helpful to analyze its invasion pattern with multiple techniques. Remaining vegetation cover was the best single predictor of *Paulownia* presence in all the classification tree and regression models. This is in keeping with what is known about this species; that it requires high light levels and is well adapted to disturbed (high light) environments in both its native and introduced ranges (Hu 1959, 1961). Although vegetation cover was not as significant in the ordination as some variables, it did decrease with increasing number of *Paulownia* stems, and the ordination by its nature was not *Paulownia*-focused.

Another aspect of *Paulownia* invasion illustrated by the classification tree is that there were a number of other variables which influenced invasion and interactions between variables were important in determining invasion success. That the classification tree and logistic regression did not completely agree on the significant variables was not surprising given the different way that significance is determined in each model type. That they agreed on the most significant variable, vegetation cover, reinforced its importance and strengthens assertions that it was the dominant driver of invasion success. Both models also included slope and while the tree used hillshade and the regression aspect, both are measures of insolation and exposure and both models found invasion to be positively correlated with these variables. Finally, the variables elevation TCI used in the tree and topographic position used in the regression are all related to landscape position and invasion was positively correlated with the drier, upper reaches of the landscape in both models. The only variable without an analog in both models was litter cover in the regression and this variable was shown to be significant in the experiments described in Chapter IV. The overall model results support the hypothesis that invasion rates are highest in the most exposed positions in the landscape with *Paulownia* presence positively correlated with increasing topographic position (from mid-slope to crest) and decreasing hillshade.

Finally, it is worth noting that *Paulownia* invasion is not significantly associated with soil chemistry or texture. Boron ppm. was included in one of the alternate trees predicting *Paulownia* presence-absence, but as this did not improve the accuracy of the tree and as Boron has not been associated with other species or community vegetation patterns, it was excluded from the final classification tree. No other soil variable was found to be significant in the analyses of *Paulownia* invasion which is not terribly surprising given the prevalence of

this tree in parking lots edges, road cuts, and even cracks in the sidewalk. Although the invasion pattern of *Paulownia* is complex, its post-fire invasion is determined by “universal” variables such as elevation, remaining vegetation cover, and Hillshade. As such each fire is the same from *Paulownia*’s perspective. Given available seeds, an appropriately hot fire, and sufficiently xeric locations, *Paulownia* demonstrates the ability to invade any landscape.

TABLES AND FIGURES

Figure 5.1: Pruned Classification Tree model (two views) predicting *Paulownia* presence-absence utilizing the data subset. Branch length in the unlabeled view is proportional to the variance explained by that division.

Table 5.1: Accuracy of the classification tree model shown in Figure 5.1. “Actual values” are the presence-absence of *Paulownia* as recorded in the field and the “Predicted values” are the presence-absence of *Paulownia* as predicted by the classification tree model. Presence is denoted by 1 and absence by 0. Numbers within the cells are the number of 5x5m subplots within that category. Classification accuracies are given as percentages.

Table 5.2: The best fit logistic regression model predicting *Paulownia* presence-absence on the basis of environmental, spatial, and biotic variables. The model was built utilizing the data subset.

Figure 5.2: Observed *Paulownia* stem count distribution (bars) and the null distribution (line) predicted by a negative binomial regression specifying only the y-intercept and dispersion parameters. Model was built utilizing the data subset.

Figure 5.3: NMS ordination of all suitable plots (no missing data) across all sampled fires. Plots grouped by location (site) and overlaid by environmental variable regression lines. Lines point in the direction of increasing effect. Length of line indicates the strength of the effect.

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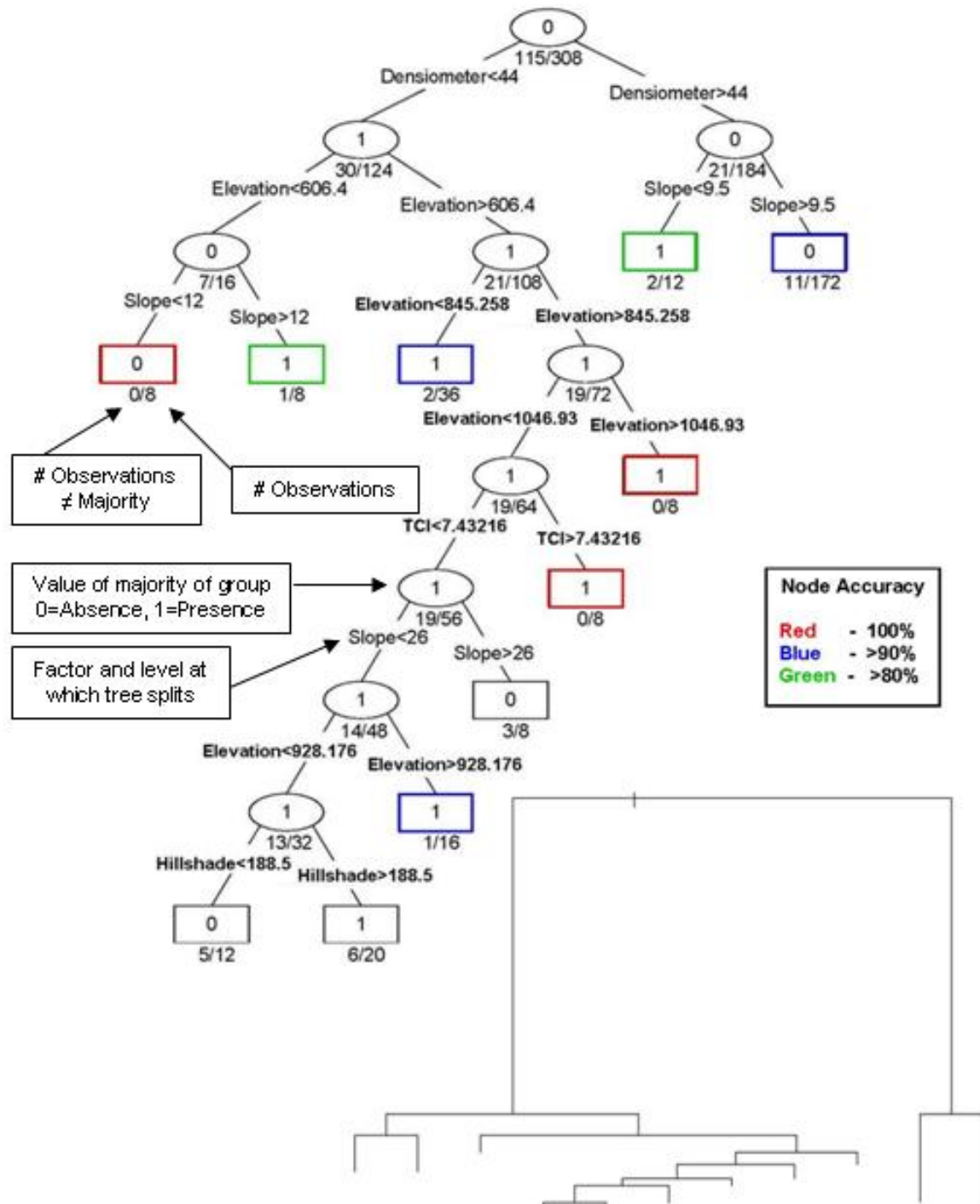


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Actual values	Predicted values	
	0	1
	0	1
	177	16
	15	100

Overall misclassification rate	10.06
Overall classification accuracy	89.94
Presence predict accuracy	86.96
Absence predict accuracy	91.71

Table 5.2: The best fit logistic regression model predicting *Paulownia* presence-absence on the basis of environmental, spatial, and biotic variables. The model was built utilizing the data subset.

	Df	Deviance	Resid. Df.	Resid. Dev.	Pr(> Chi)	Sig.
NULL			92	128.829		
Densimeter	1	33.079	91	95.749	8.85E-09	***
Aspect	1	0.971	90	94.779	0.324	
Litter cover	1	4.151	89	90.627	0.042	•
Topographic Position	3	29.676	86	60.952	1.62E-06	***
Slope	1	0.097	85	60.855	0.756	

Significance codes: *** < 0.001 , ** < 0.01 , • < .05

Model: *Paulownia* Presence-absence ~ Cover >1m in height (Densimeter) + Aspect + Litter cover (%) + Topographic Position + Slope

Goodness of fit, Hosmer-Lemeshow Test

$$\sum (O_i - E_i)^2 / E_i = 19.51689$$

$$p = 0.0123$$

Figure 5.2: Observed *Paulownia* stem count distribution (bars) and the null distribution (line) predicted by a negative binomial regression specifying only the y-intercept and dispersion parameters. Model was built utilizing the data subset.

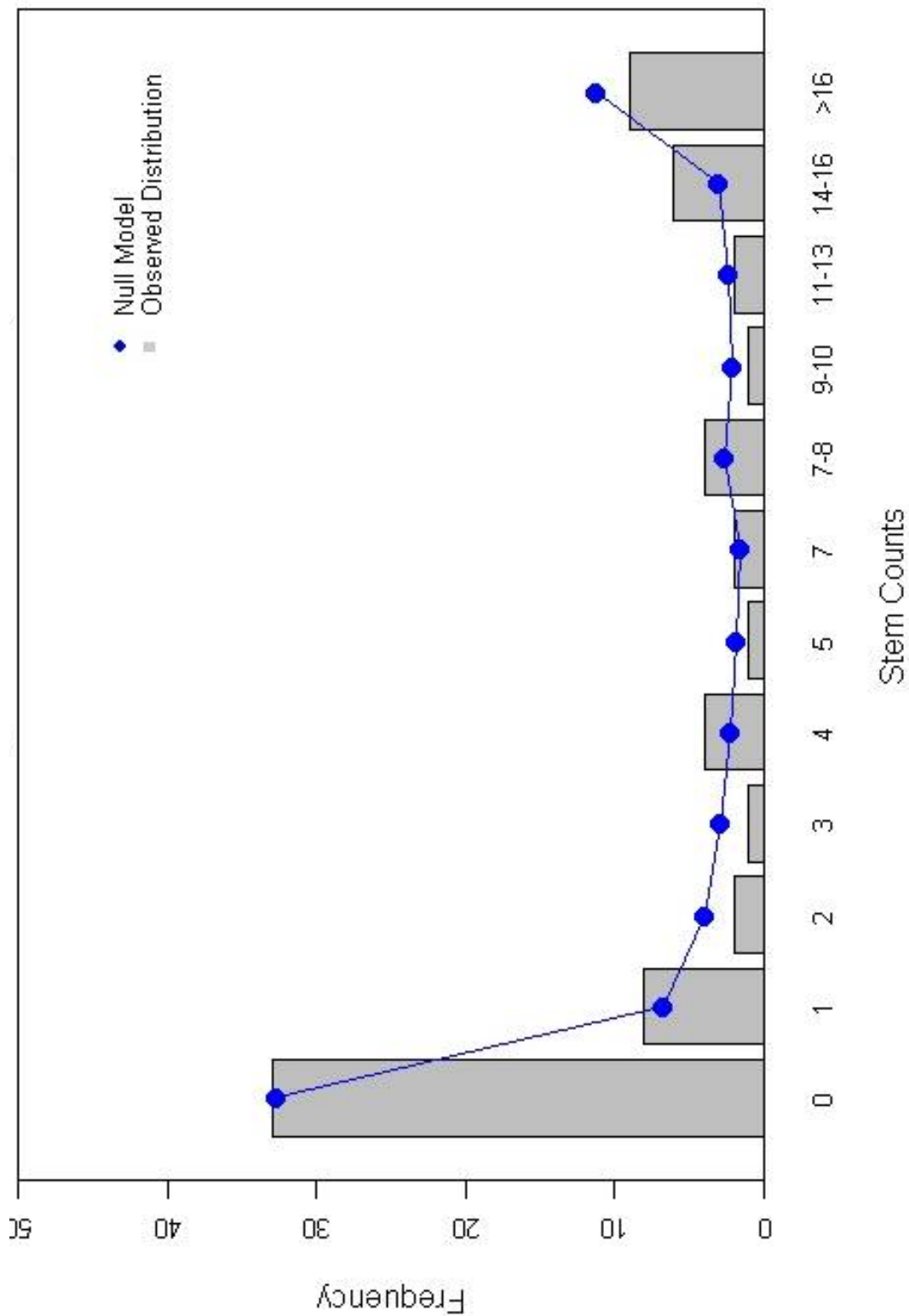
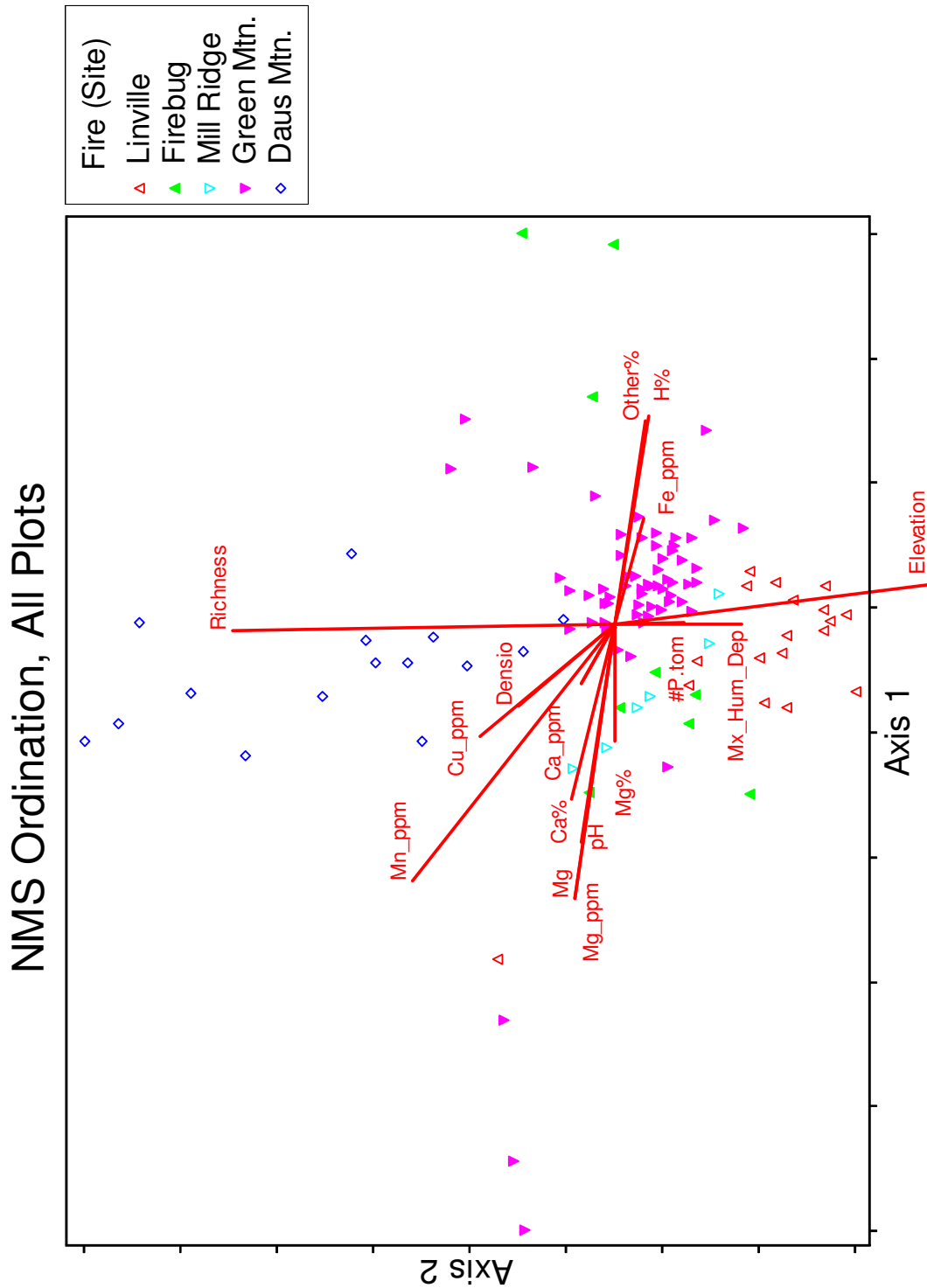


Figure 5.3: NMS Ordination of all suitable plots (no missing data) across all sampled fires. Plots grouped by location (site) and overlaid by environmental variable regression lines. Lines point in the direction of increasing effect. Length of line indicates the strength of the effect.



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CHAPTER VI: Predicting *Paulownia* Habitat, Persistence, and Impact at Linville Gorge

ABSTRACT

Although models identifying the variables correlated with invasive species are interesting from a theoretical standpoint, unless these models translate into realistic and useful habitat predictions in the field, they are of limited conservation value to land managers. Further, not all invasive exotics are equally problematic. Some species may be transient invaders following disturbance only to be excluded from the community over time due to their poor competitive ability or an inability to reproduce. Aside from their potential to impact native disturbance specialists, these species are less of a concern to managers than those that become permanent residents of the landscape.

To address these issues as they relate to *Paulownia*, this chapter applies the classification tree model developed in Chapter V (hereafter 2002 model) to Linville Gorge to test its *Paulownia* habitat predictions. Two further classification tree models were developed from resampling data in 2004 and 2006 (hereafter 2004 and 2006 models) at Linville Gorge to analyze changes in *Paulownia* habitat over time and *Paulownia*'s potential to establish self-maintaining populations within the Gorge. Finally, the potential for *Paulownia* to impact native species was analyzed by testing for correlations between *Paulownia* presence, abundance, and cover and native cover and diversity.

The 2002 model predicted 6,5709km² of *Paulownia* habitat within the fire boundary. This habitat was concentrated on dry, exposed sites that experienced high levels of fire severity in the 2000 fire, however it also predicted significant invasion in areas with low slopes and in areas which experienced fairly low severity fire. By 2004, predicted *Paulownia* habitat had shrunk to 2.43km² and this further contracted to 1.7865km² by 2006. From 2002 to 2006, habitat losses were concentrated on mesic sites, at lower elevations, and on flatter slopes. There was a complete loss of habitat where fire severity was less than 700 (median 850) and when TCI was greater than 8 (median 8.5). As a result of these changes, *Paulownia* became increasingly limited to the most xeric portions of the landscape.

Although not directly measured, these changes were probably due to *Paulownia*'s poor competitive ability. Indirect evidence of this was seen through a shift in its height distribution from left-skewed in 2002 to right-skewed in 2006; suggesting that the only surviving individuals were those that had managed to stay above the regenerating vegetation or were in a location where regeneration rates were very slow. Lack of significant habitat restriction on the steepest, driest portions of the landscape suggests that *Paulownia* is likely to persist within the Gorge. This is concerning as these areas are also habitat to two rare endangered species, *Liatris helleri* and *Hudsonia montana*.

No correlation was found between *Paulownia* presence, abundance, or cover and native species cover or diversity at any strata or spatial scale. However given that *Paulownia* cover, regardless of abundance, was still low and that competition is often a weak factor in determining the post-fire vegetation composition, the potential exists for future impacts.

INTRODUCTION

Research on rare species and exotic, invasive species overlaps in the study of suitable habitat. For rare species, the goal is often to locate new populations or potential sites for reintroduction. For invasive exotics, identifying potential habitat increases the efficiency of monitoring and control efforts. Early quantitative approaches to species distributions and habitat requirements assumed an underlying linear relationship between variables and species response. As the limitations of these assumptions became clear (Noy-Meir and Austin 1970), ordination approaches became increasingly widespread (Whittaker and Gauche 1982). However, the underlying assumptions of these approaches are frequently violated as well (Austin 1976, 1985) and they have shown a lack of robustness to these violations (Minchin 1987, van Groenewoud 1992). Recent advances in ecological statistics has provided novel tools (Bootstrap non-parametric regression, Generalized Additive Models, Classification and Regression Tree (CART) models, Boosted and Multi-CART models, and neural networks) almost faster than the ecological community has been able to make use of them.

One of these new tools, CART models, although first described in 1984 (Breiman *et al.* 1984), did not find widespread use in ecology till the 90's having first found applications in medicine (Goldman *et al.* 1988) and meteorology (Borrows 1991). One advantage of CART models is that rather than assuming the relationship between a variable and the species response has a particular form, it recursively partitions the data to minimize variation within subdivisions. By allowing different variables to determine successive divisions, variable interactions are incorporated without the interaction terms required in linear models

enabling CART models to maintain interpretability while incorporating higher orders of interaction.

The increasing availability of spatial data from satellites and GIS, has lead to tremendous advances in landscape ecology and the application of predictive models to landscapes. Here too, CART models have advantages over regression models in their easy application to landscapes. This has allowed ecologists to make testable predictions about habitat distributions and provided valuable tools for rare species management (Andersen *et al* 2000, Dettmers and Bart 1999, O'Brien *et al.* 2005), but it has not yet seen applications to invasive species research or control efforts. Although in recent years there has been an increasing interest and study in applied ecology, this has not always translated into tools and knowledge helpful to land managers (Meijaard and Sheil 2007). Regarding exotic invaders, managers need practical tools to help identify potential habitat, select effective control efforts, and identity the potential of an invading species to impact native species. This chapter assess the utility of the *Paulownia* habitat model developed in Chapter V by asking whether it gives meaningful predictions of habitat at Linville Gorge.

Another question of relevance to land managers is whether an exotic invader, in this case *Paulownia*, will persist in the community. If *Paulownia* is unable to establish a reproducing population within these burned communities, control efforts can be focused temporally on periods immediately following the fire. However, if *Paulownia* is able to establish a self-perpetuating population, then managing agencies interested in control must adopt a long-term approach, and control costs may be minimized through early identification of habitat and initiation of control. This chapter addresses this question by analyzing the conditions under which *Paulownia* persisted over the sampled time period.

Although exotic species are generally undesirable, monetary and personnel constraints often force managers to limit control efforts to those causing the biggest impacts. Consequently, it benefits agencies to know whether *Paulownia* impacts native species or has significant potential to impact species in the future. Though measurements of impact based on species composition and coverage immediately after a fire are fraught with inherent uncertainties (Turner *et al.* 1998), this chapter assesses *Paulownia* impact by asking whether its presence-absence, cover, or abundance were negatively correlated with native species diversity or cover.

METHODS AND ANALYSES

Plot resampling and survey points

At Linville Gorge, plots originally sampled in 2002 and 2003 (methods in Chapter II) were resurveyed in 2004 and in 2006 to measure the survival of *Paulownia* over time. At the time of resurvey, the number, height and dbh (where >1cm) of each *Paulownia* stem was recorded along with cover of the shrub and canopy layers, and overall vegetation cover >1m in height. Also in 2006, 17 survey points were established at Linville Gorge where *Paulownia* was present (Figure 6.1) because the loss of *Paulownia* from many of the initial plots meant an insufficient number of “positive” samples to create habitat predictions from just the 2006 plot data. At each survey location, the number, height, and dbh (where >1cm) of all *Paulownia* stems in a 10x10m area were recorded along with the geocoordinates and the shrub, canopy, and overall cover >1m in height.

Modeling Paulownia habitat

The classification tree developed in Chapter V (Figure 6.2) was used to create landscape scale predictions of initial *Paulownia* habitat within the fire boundary. Due to the circular nature of aspect, two transforms of the variable, the Beers transform (1966) and the two variable transform (Lasting Forests 2008) described in Chapter II, were tested for explanatory power in addition to the raw aspect values. These transforms are labeled EW.Aspect, NS.Aspect, and Beers where they appear in the models. Because all of the variables found to be significant in the CART algorithm, with the exception of vegetation cover, were derivable from GIS layers they were directly applied to a GIS map of Linville Gorge. In the case of vegetation cover, the relationship between these measurement and fire severity (difference in the Normalized Burn Ratio, dNBR) was described by the function:

$$S = 982.2587 - 5.8450 * D$$

Where S (Severity) is the dNBR calculated by Wimberly and Reilly (2007) and D is the measure of vegetation cover above 1m in height as recorded by a spherical densiometer. This function was developed by comparing the densiometer and fire severity values at all sampled points within Linville Gorge fire (Figure 6.3). Both a linear model and a LOESS line were fit to the data to test for non-linearity in the relationship. The LOESS method is a multivariate smoothing procedure which fits simple models to localized subsets of the data to build a function that describes a deterministic part of the variation in the data point by point without specifying a global function (Cleveland and Devlin 2008). The LOESS line fit was calculated using the default settings in R. Although the LOESS line was not completely

linear, as the linear model was highly significant, it was utilized rather than the LOESS relationship in subsequent analyses. With this relationship identified, the classification tree was applied to Linville Gorge by substituting fire severity for vegetation cover and utilizing the raster calculator within ArcGIS to predict *Paulownia* habitat from rasters of the relevant data layers.

Paulownia persistence over time

Additional classification tree based habitat models were developed from the 2004 and 2006 resampling data. In these models, severity was used instead of the densiometer readings because the densiometer readings taken in 2004 and 2006 were impacted by regrowth. Severity was not used in the initial classification tree model because the trees utilizing densiometer provided better predictions of *Paulownia* presence-absence. Data from the survey points was used in the creation of habitat models for 2004 and 2006; *Paulownia* present in 2006 was assumed to have been present in 2004 because the trees were the same age as those persisting within plots originally sampled in 2002. Because the 2004 and 2006 habitat models also utilized variables derivable from GIS layers, they were applied to the Linville Gorge landscape via ArcGIS in the manner described above. The habitat predictions for 2004 were clipped to the boundaries of the 2002 habitat and the 2006 habitat was clipped to the boundaries of the 2004 habitat.

To measure changes in variable distribution within predicted habitat from 2002 to 2006, 1,600 points were randomly placed within the fire boundary. Values at these points were extracted along with the point's presence (or not) within *Paulownia* habitat in 2002 and

in 2006. Variable distributions within 2002 and 2006 *Paulownia* habitat were compared via histograms in S-Plus.

Impacts of Paulownia

The potential impact of *Paulownia* upon native species diversity was analyzed in two ways. First, by testing for a significant relationship between *Paulownia* (cover, number of stems, average height, and total height) and native species overall richness, herbaceous layer richness, and the cover of pines at the whole plot and sub-plot levels. Potential relationships were assessed with a linear regression model and by analyzing the shape of a loess line fit between *Paulownia* and native species variables. The second approach utilized the ordination developed in Chapter II and used *Paulownia* presence-absence as a grouping variable to test for patterns relative to species richness.

RESULTS

Modeling Paulownia habitat

The habitat predictions for 2002 suggest that initial *Paulownia* habitat is widespread across the fire boundary with 7,301 cells (6,5709km²) of predicted *Paulownia* habitat (Figure 6.6). The first split in the classification tree (vegetation cover \leq 44%) accounted for over half of the predicted habitat (4,603 of 7,301 cells). Overall, this initial habitat was concentrated on dry, exposed sites that experienced high severity fire in 2000; however the

model also predicted significant invasion in areas with low slopes and in areas which experienced fairly low severity fire.

Paulownia persistence over time

Paulownia habitat shrank to 2,700 cells (2.43km²) in 2004 and further to 1,985 cells (1.7865km²) in 2006 (Figure .66). Between 2002 and 2006, habitat was particularly lost at lower elevations (Figure 6.7) and on flatter slopes (Figure 6.8). There was a complete loss of habitat where fire severity was less than 700 (median 850, Figure 6.9) and when TCI was greater than 8 (median 8.5, Figure 6.10). Finally, the distribution of Hillshade values within predicted habitat flattened out due to the higher rate of habitat loss where Hillshade ranged from 150-180 but there was no preferential loss at either tails of the distribution (Figure 6.11). In 2002, the height distribution of *Paulownia* at Linville Gorge was significantly left-skewed. By 2006, the height distribution was significantly right-skewed (Figure 6.12). In 2004, the distribution was non-skewed.

Impacts of Paulownia

None of the regression analyses identified any correlation between *Paulownia* presence, abundance, or cover and decreased native species richness or cover (Figures 6.13). *Paulownia* variables did not increase the predictive success of the regression tree predicting native species richness (Figure 2.3), nor the fit of the negative binomial model predicting native species richness (Figure 2.2), though neither of these models significantly fit the observed richness distribution. *Paulownia* abundance was a factor in the ordination identifying differences between plots and fires, but it acted almost orthogonally to species

richness (Figure 2.4). Using *Paulownia* presence-absence as a grouping variable in the ordination showed that the presence of this species did not correlate with decreased native species richness (Figure 6.14).

DISCUSSION

Although other work utilizing Classification and Regression Tree models has successfully predicted habitat requirements for rare plants (Englers *et al.* 2004) and animals (Andersen *et al.* 2000, Dettmers and Bart 1999), species' response to climate change (Iverson and Prasad 1998), coral distributions (De'ath and Fabricius 2000), and the distribution of California oak species (Vayssieres *et al.* 2000), this is the first study to utilize these models to predict exotic species habitat. Just as the above studies have shown the utility of CART models for native species management and research, this work demonstrates the same potential for invasive species. In both instances knowing where to locate a species is very helpful for management and research and the CART derived habitat models are tractable to application across a landscape in ways that linear regression analyses are not. The agreement of CART derived habitat model with field observations demonstrates that it provides an accurate picture of the areas within Linville Gorge susceptible to *Paulownia* invasion.

The change in habitat over time illustrates the difference between *Paulownia*'s recruitment niche and its persistence niche. Like many species, *Paulownia* is able to germinate and survive for a year or two across a much larger range of habitat conditions than will enable it to survive to maturity. For disturbance specialists like *Paulownia*, their

persistence niche is often further limited by changing environmental conditions associated with regenerating vegetation. Although *Paulownia*'s habitat shrank significantly over time within the Gorge, the lack of significant reductions in some locations suggests that *Paulownia* is not going to be extirpated from the Gorge through succession and competition alone.

Locations where *Paulownia* lost the greatest area of habitat appear to be locations which saw the highest level of regeneration by the native plant community (Photo 6.1). In these areas, the *Paulownia* that survived (Photo 6.2), apparently did so by staying above the regenerating native vegetation. Locations within the Gorge where *Paulownia* habitat showed the least restriction are steep, exposed areas where native regeneration was limited and thus *Paulownia* apparently experienced limited direct competition for light or space (Photo 6.3). Competition's impact was also suggested by *Paulownia*'s shifting height distribution from left to right skewed, indicative of the preferential survival of the tallest individuals. Although this occurs with most species over time, the rapidity of the shift (4 yrs) suggests that competition was a driving force determining *Paulownia* persistence at a site. *Paulownia*, a poor competitor for light, only survived where it remained above the other vegetation resulting in the preferential survival of the tallest individuals.

Paulownia's increasing restriction to the most exposed portions of the landscape over time was also captured through the increased fire severity value at which the first split occurs in the 2006 model, and the changing distributions of TCI, fire severity, and slope variables within *Paulownia* habitat. *Paulownia*'s ability to succeed in the most xeric portions of the landscape is likely attributable, at least in part, to its deep root system. Although it has been suggested that *Paulownia* does not possess a tap root (Hu 1959), in the field the plant

produces a significant main root (~30-100cm) in the first two years. Possession of this deep root system potentially enables *Paulownia* to access deeper water sources than the surrounding vegetation, especially since the majority of the trees (who would possess deeper roots) are killed in the high severity fire associated with these landscape positions.

Although the absence of a correlation between *Paulownia* and native species diversity is encouraging from a management perspective, it does not eliminate the potential for future impact. The highest recorded *Paulownia* cover class was 6 (10-25%), but the median was 2 (0-1%) illustrating that the majority of plots had only limited *Paulownia* cover regardless of how many stems were present (due to their size), thus limiting the potential for competitive effects. Given that *Paulownia* is predicted to persist within the Gorge and that its cover and the number of individuals are likely to increase, the potential for future impact still exists. The landscape positions where *Paulownia* habitat was maintained are also areas associated with *Liatrix helleri*, Heller's Blazing Star, and *Hudsonia montana*, Mountain Golden-Heather. These endangered species are limited to dry outcrops in North Carolina, their largest remaining populations occur at Linville Gorge (USFWS 1989 and NatureServe 2007 respectively), and they are dependent upon fire to maintain appropriate habitat conditions. Although this work found no impact of *Paulownia* presence or abundance upon native species richness, neither of these two rare species were captured by the field data so the potential impact of *Paulownia* upon these species remains unknown.

In situations where there is interest and resources for control efforts, the habitat models developed here indicate that control may be unnecessary over large portions of the landscape initially invaded by *Paulownia*. In these areas, it is likely that regeneration of native vegetation will eventually exclude *Paulownia* as it is apparently a poor competitor for

space and light. Because of this, control efforts should be focused on the most xeric and exposed portions of the landscape where habitat models predict *Paulownia* will persist and a high-light, low-competition environment will be maintained.

Questions remaining

Although the habitat models applied here make reasonable predictions of *Paulownia* habitat at Linville Gorge, the models' ability to predict invasion patterns at other fires remains untested. The occurrence of wildfires in the Pisgah National Forest in 2007, presents an opportunity to apply the model to new areas and to see whether habitat predictions match with the observed pattern of post-fire invasion.

After *Paulownia*'s initial invasions at Linville Gorge in 2002 following the 2000 wildfire, no new seedlings were encountered during the course of field surveys. Presumably this was because changing environmental conditions limited germination of seeds arriving after fall of 2001. Consequently, habitat models only showed a loss of habitat as individuals succumbed to competition. It is likely however that the current environmental conditions do not categorically preclude seed germination and seedling growth, but simply decrease its probability. The first post-fire invaders in the Gorge reached sexual maturity in 2006 and it remains to be seen what effect the increased propagule pressure will have upon *Paulownia*'s population trends within the Gorge, especially in light of further habitat creation by recent (summer 2007) and future fires.

TABLES AND FIGURES

Figure 6.1: Vegetation plots and survey points at Linville Gorge from which *Paulownia* habitat models were developed for 2004 and 2006.

Figure 6.2: Pruned classification tree predicting *Paulownia* habitat in 2002 based on the presence-absence of *Paulownia* in vegetation plots within the data subset (two views). In the unlabeled version, branch length indicates the amount of variance explained by that division.

Figure 6.3: Relationship between densiometer readings and fire severity as measured by the change in the Normalized Burn Index (dNBR). Both the linear and LOESS relationships between the variables are indicated in the figure. Model constants and statistics are for the linear relationship. The linear relationship was used in subsequent analyses.

Figure 6.4: Pruned classification tree predicting *Paulownia* habitat in 2004. Tree is based on the presence-absence of *Paulownia* in vegetation plots and survey points at Linville Gorge in 2004.

Figure 6.5: Pruned classification tree predicting *Paulownia* habitat in 2006. Tree is based on the presence-absence of *Paulownia* in vegetation plots and survey points at Linville Gorge in 2006.

Figure 6.6: Predicted reduction in *Paulownia* habitat over time at Linville Gorge. Habitat predictions for each year are derived from the corresponding Classification Tree models (Figures 6.3, 6.4, 6.5). Each successive year's habitat is a subset of the previous year.

Figure 6.7: Histogram comparing the distribution of elevation values within predicted *Paulownia* habitat in 2002 (blue) and 2006 (pink).

Figure 6.8: Histogram comparing the distribution of slope values within predicted *Paulownia* habitat in 2002 (blue) and 2006 (pink).

Figure 6.9: Histogram comparing the distribution of fire severity values within predicted *Paulownia* habitat in 2002 (blue) and 2006 (pink).

Figure 6.10: Histogram comparing the distribution of TCI values within predicted *Paulownia* habitat in 2002 (blue) and 2006 (pink).

Figure 6.11: Histogram comparing the distribution of Hillshade values within predicted *Paulownia* habitat in 2002 (blue) and 2006 (pink).

Figure 6.12: Histogram comparing the distribution of *Paulownia* seedling heights in 2002 (blue) and 2006 (pink) at Linville Gorge.

Figure 6.13: Herbaceous layer species richness at the subplot level (5x5m) plotted against the number of *Paulownia* stems. LOESS line fit (shown) indicates no relationship between the two variables.

Figure 6.14: NMS ordination of all suitable plots (no missing data). Plots grouped by *Paulownia* presence-absence. Side scatter plots show the trend in species richness along the axes. Symbols in the central graph increase in size with plot richness.

Photo 6.1: Areas where *Paulownia* habitat has decreased significantly have high regeneration rates giving rise to a very dense and tall shrub and herbaceous layer.

Photo 6.2: *Paulownia* that do persist where significant regeneration has occurred are taller than the regenerating native vegetation.

Photo 6.3: *Paulownia* habitat is largely maintained on steep, exposed areas where regeneration is slow and sparse and *Paulownia* has limited competition for light and space.

Figure 6.1: Vegetation plots and survey points at Linville Gorge from which *Paulownia* habitat models were developed for 2004 and 2006.

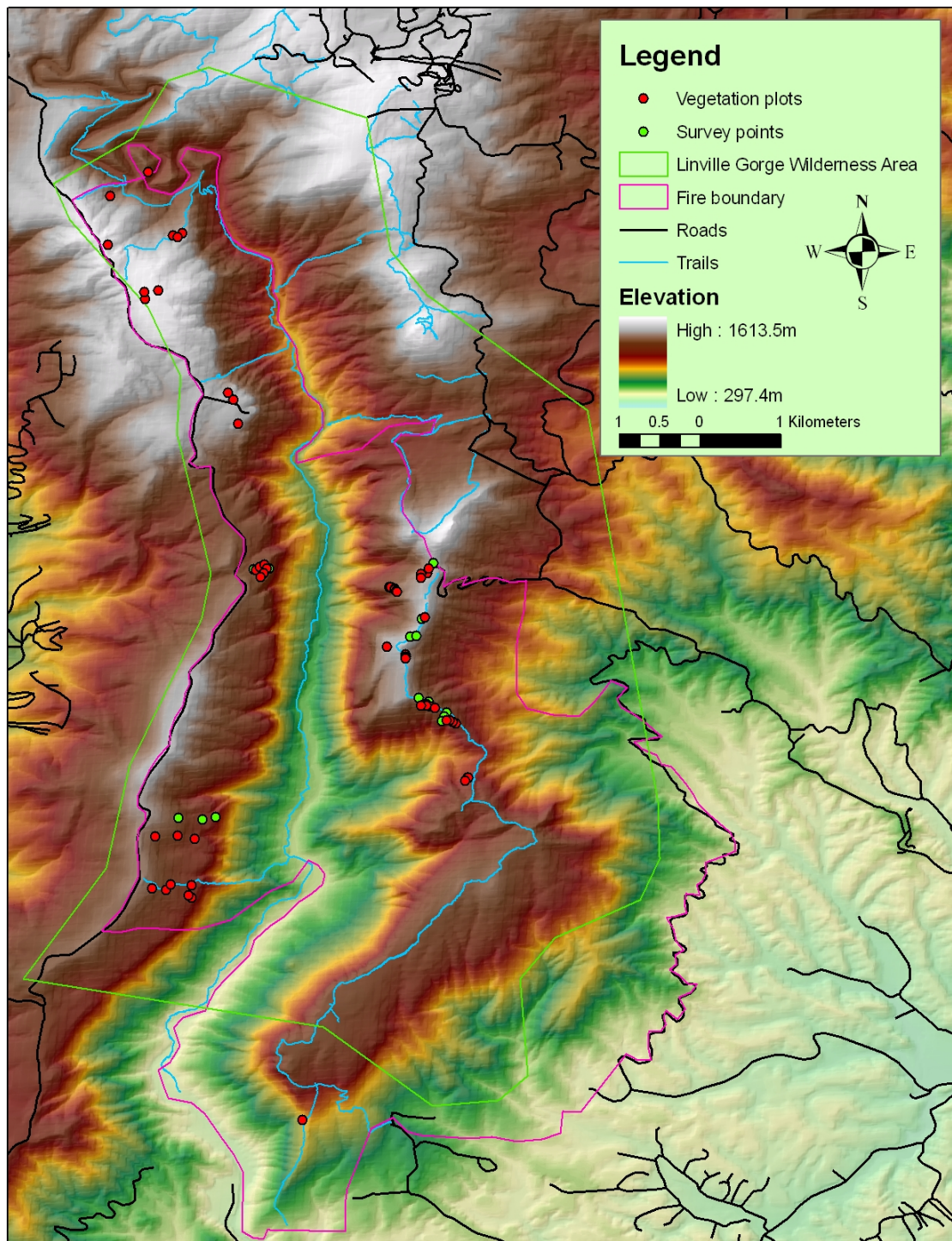


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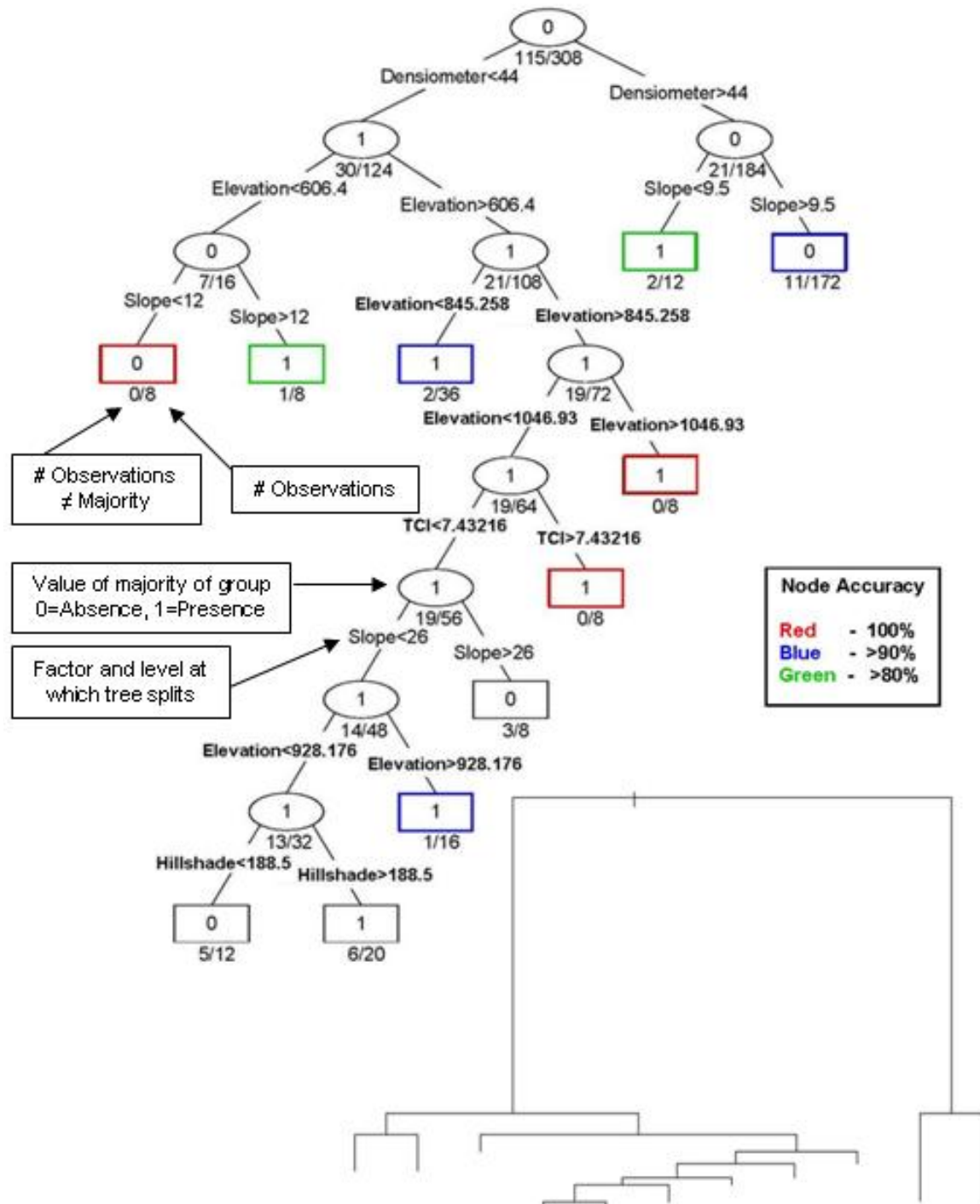
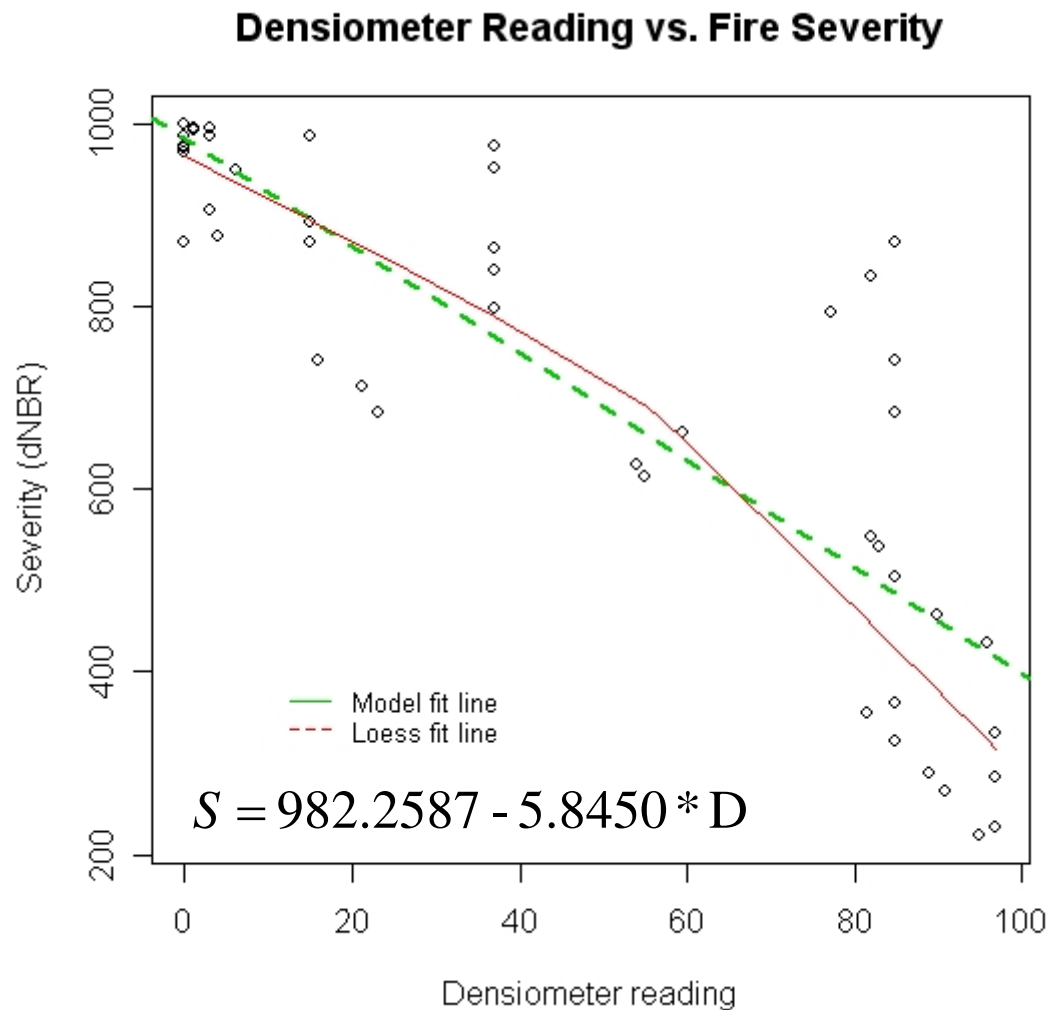


Figure 6.3: Relationship between densiometer readings and fire severity as measured by the change in the Normalized Burn Index (dNBR). Both the linear and LOESS relationships between the variables are indicated in the figure. Model constants and statistics are for the linear relationship. The linear relationship was used in subsequent analyses.



	Estimate	Std. Error	T value	Pr (< t)	Sig.
(Intercept)	982.2587	30.4748	32.23	<2e-16	***
Densiometer	-5.845	0.5102	-11.46	3.34e-15	***

Significance codes: *** < 0.001, ** < 0.01, • < .05

Model: Severity ~ Densiometer

Summary Statistics

$R^2 = 0.7307$

Residual SE = 136.9

Degrees of freedom = 47

F-statistic = 131.2

p-value = 3.337e-15

Figure 6.4: Pruned classification tree predicting *Paulownia* habitat in 2004. Tree is based on the presence-absence of *Paulownia* in vegetation plots and survey points at Linville Gorge in 2004.

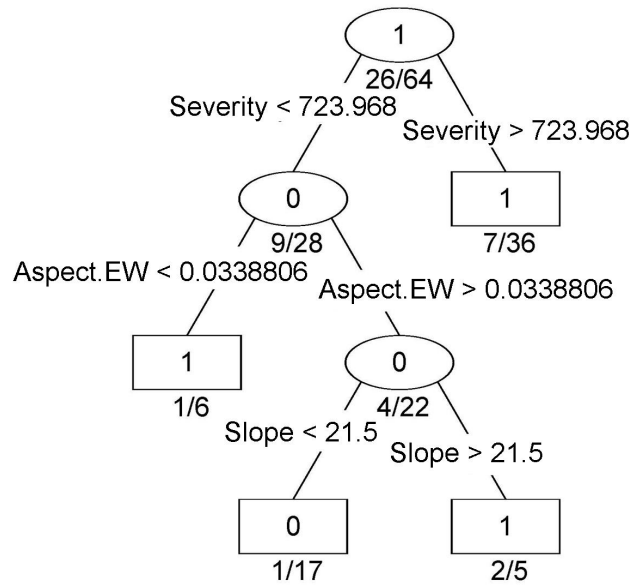


Figure 6.5: Pruned classification tree predicting *Paulownia* habitat in 2006. Tree is based on the presence-absence of *Paulownia* in vegetation plots and survey points at Linville Gorge in 2006.

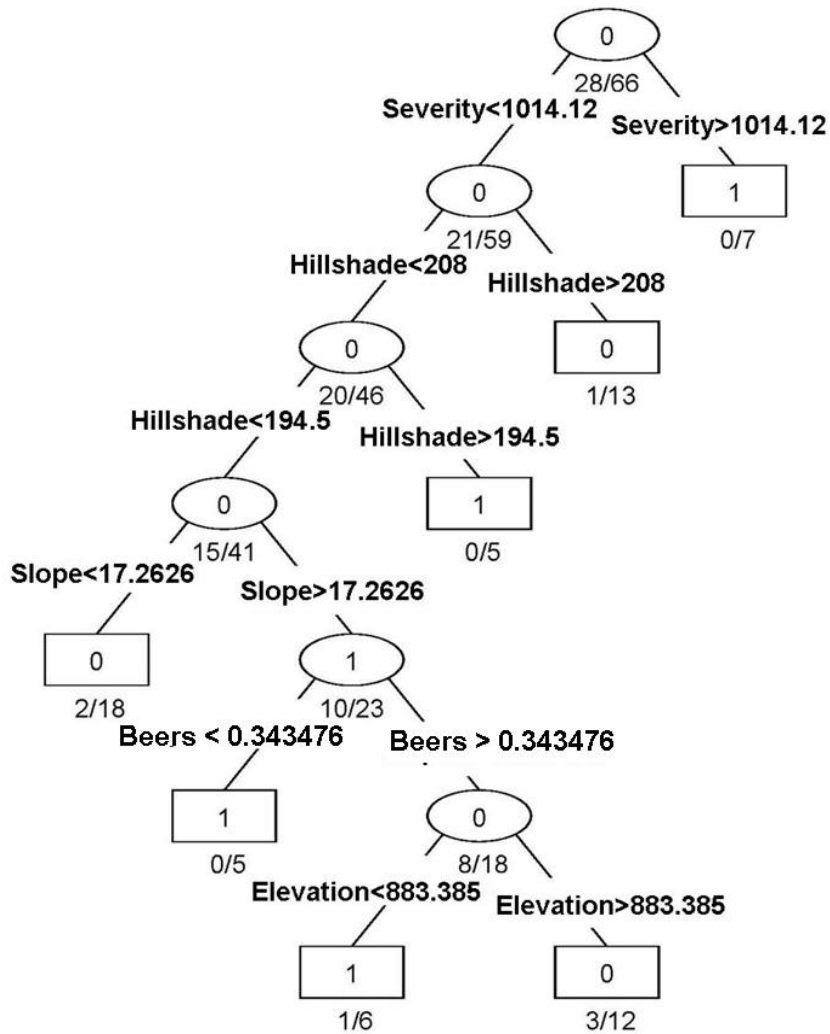


Figure 6.6: Predicted reduction in *Paulownia* habitat over time at Linville Gorge. Habitat predictions for each year are derived from the corresponding Classification Tree models (Figures 6.3, 6.4, 6.5). Each successive years' habitat is a subset of the previous year.

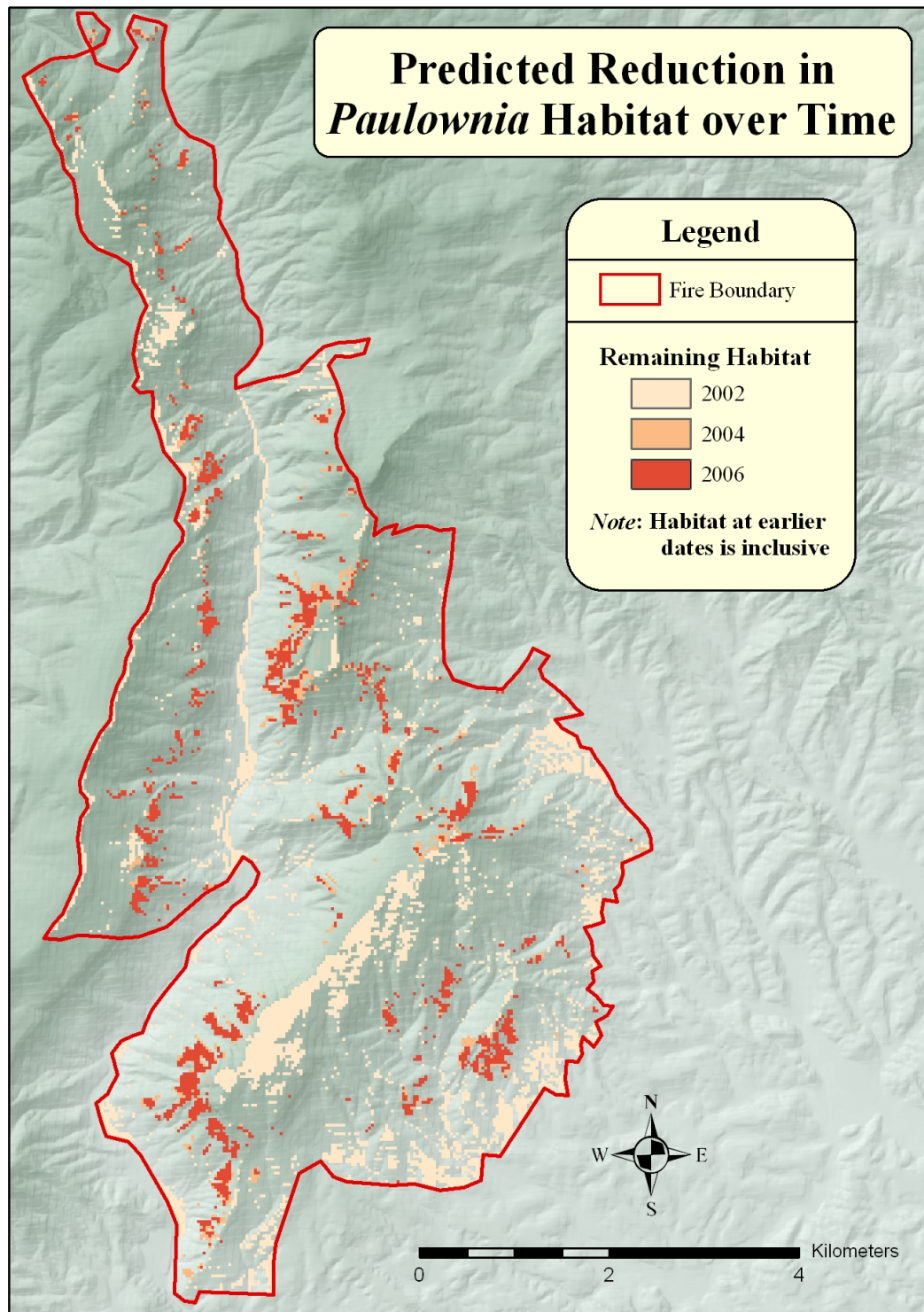


Figure 6.7: Histogram comparing the distribution of elevation values within predicted *Paulownia* habitat in 2002 (blue) and 2006 (pink).

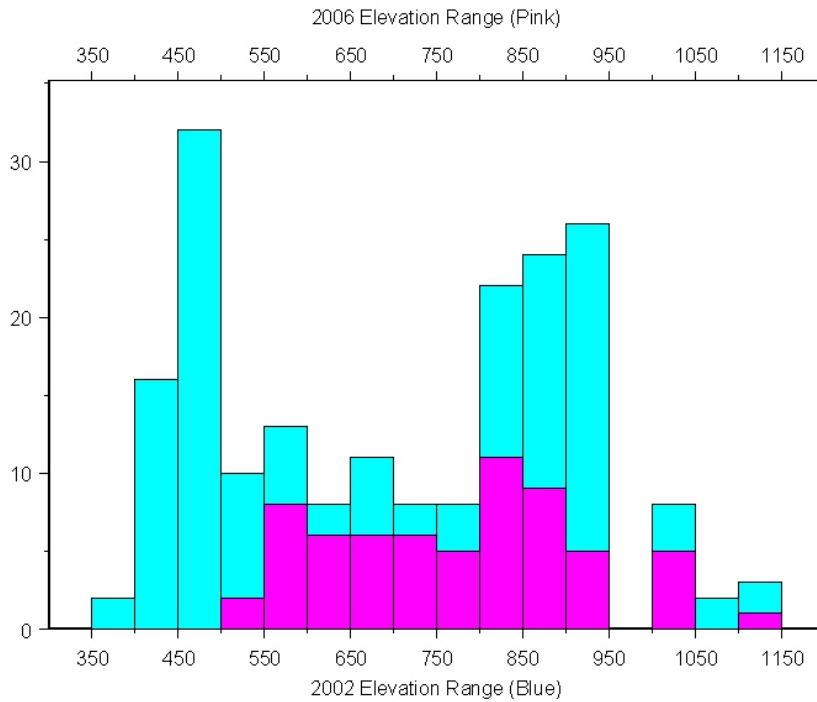


Figure 6.8: Histogram comparing the distribution of slope values within predicted *Paulownia* habitat in 2002 (blue) and 2006 (pink).

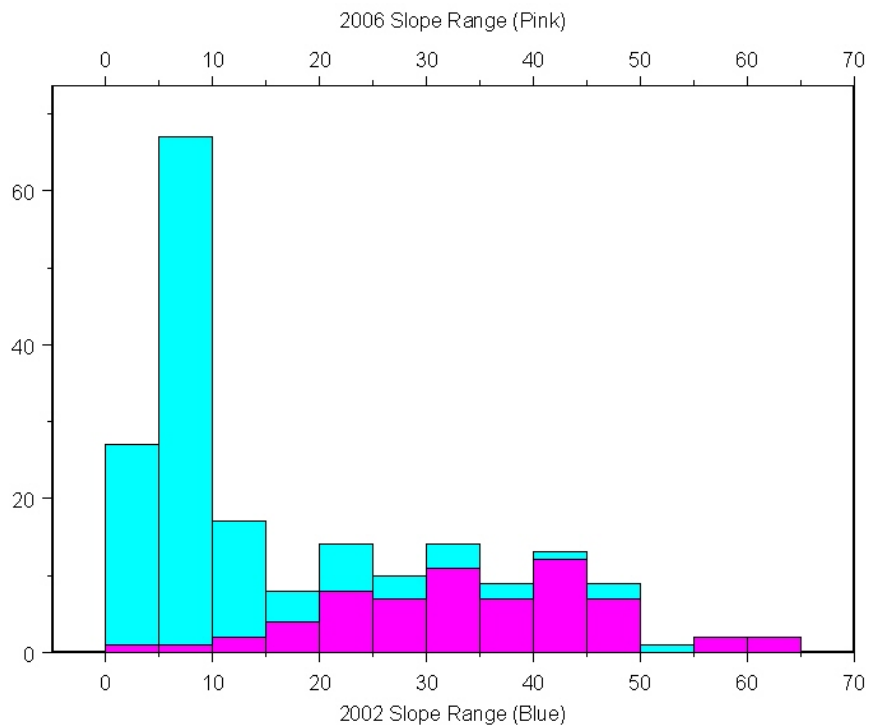


Figure 6.9: Histogram comparing the distribution of fire severity values within predicted *Paulownia* habitat in 2002 (blue) and 2006 (pink).

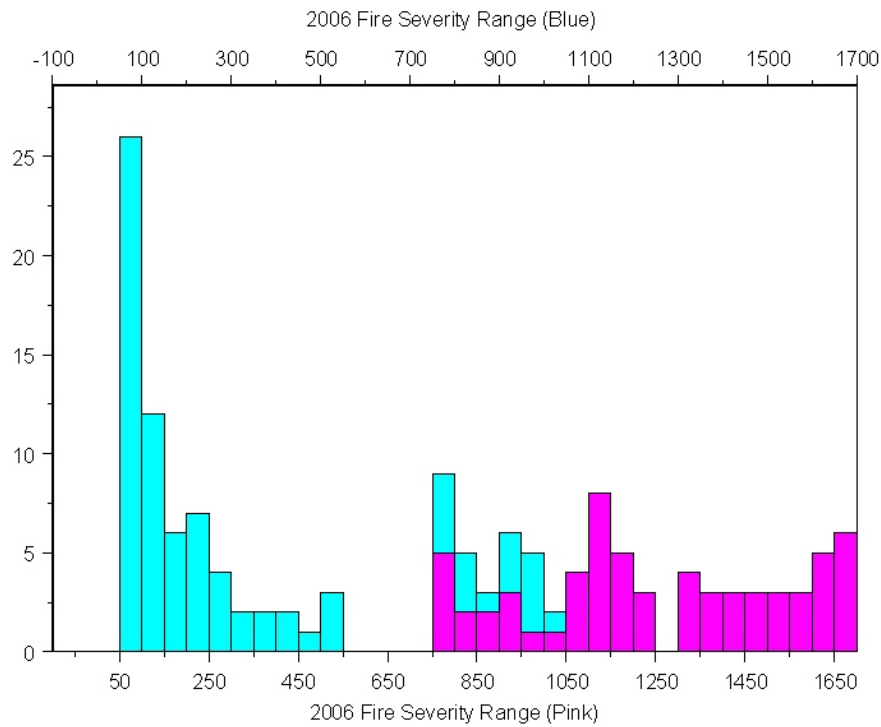


Figure 6.10: Histogram comparing the distribution of TCI values within predicted *Paulownia* habitat in 2002 (blue) and 2006 (pink).

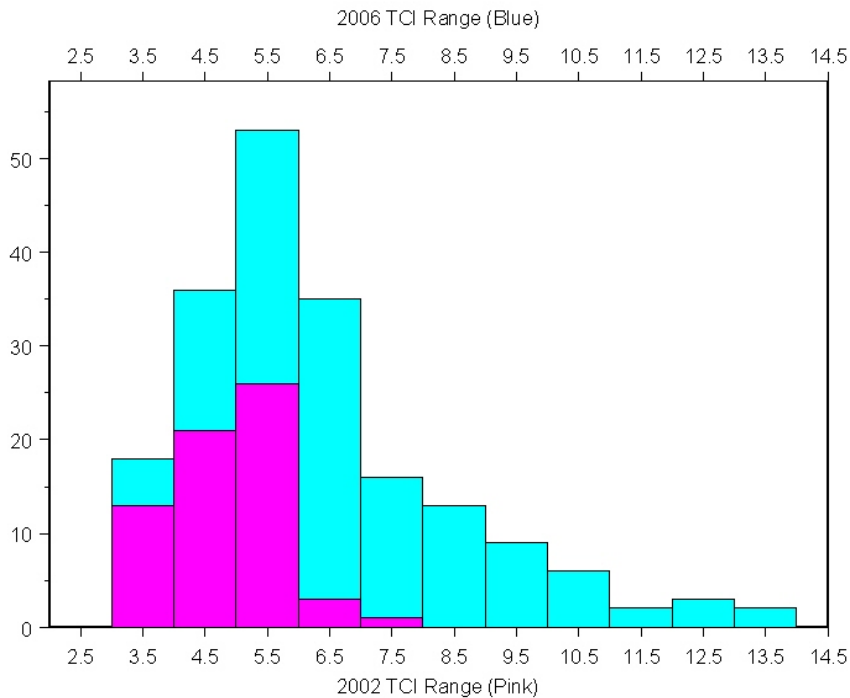


Figure 6.11: Histogram comparing the distribution of Hillshade values within predicted *Paulownia* habitat in 2002 (blue) and 2006 (pink).

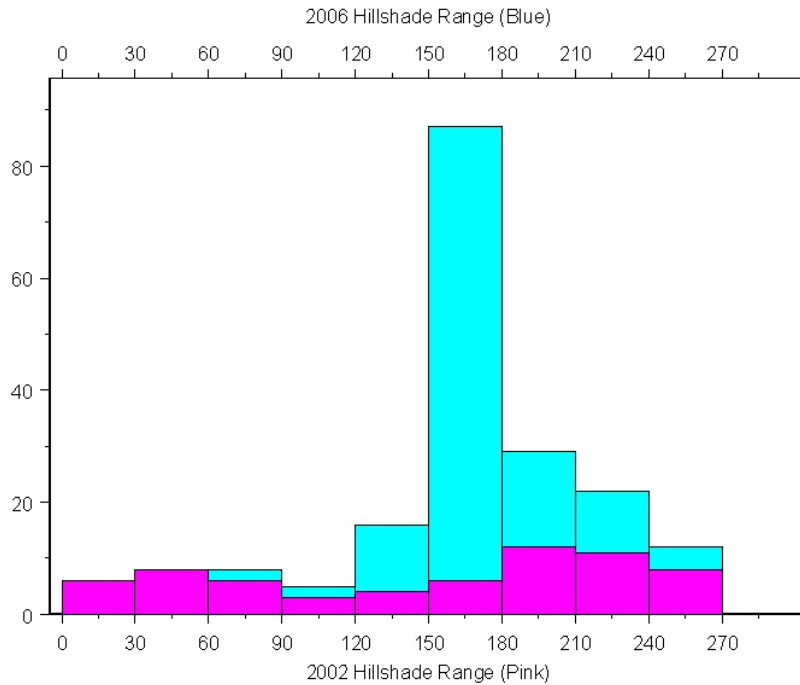


Figure 6.12: Histogram comparing the distribution of *Paulownia* seedling heights in 2002 (blue) and 2006 (pink) at Linville Gorge.

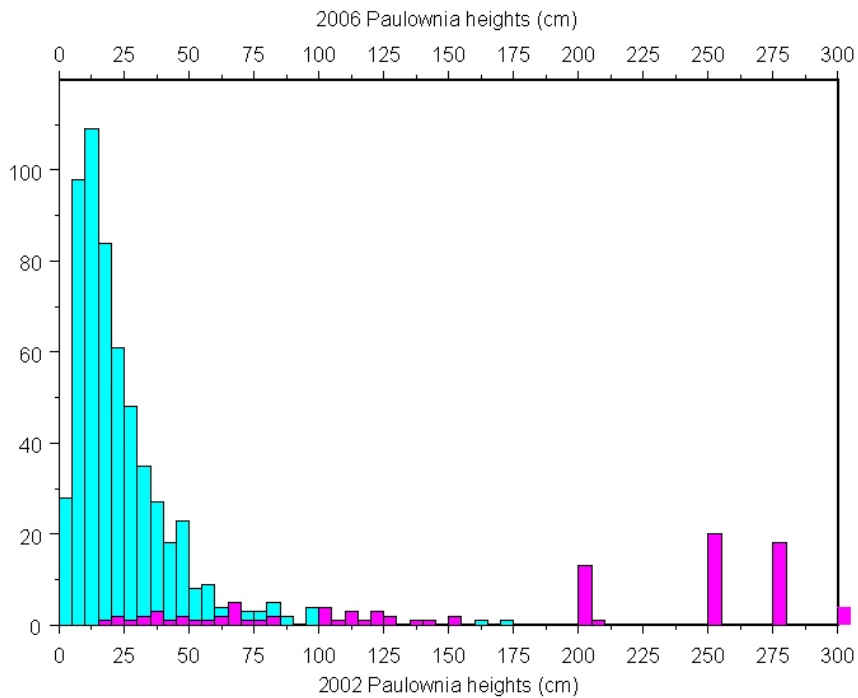


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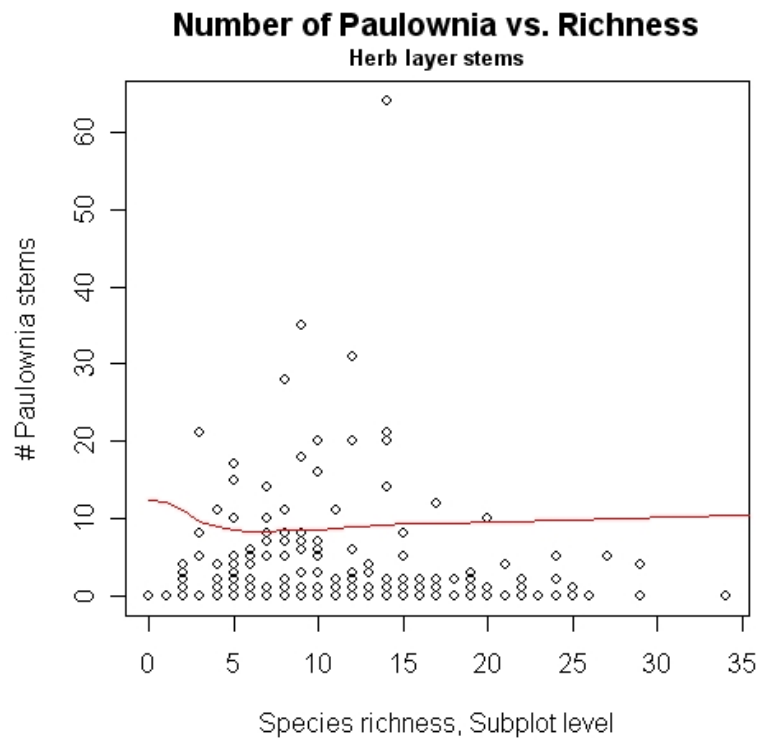


Figure 6.14: NMS ordination of all suitable plots (no missing data). Plots grouped by *Paulownia* presence-absence. Side scatter plots show the trend in species richness along the axes. Symbols in the central graph increase in size with plot richness.

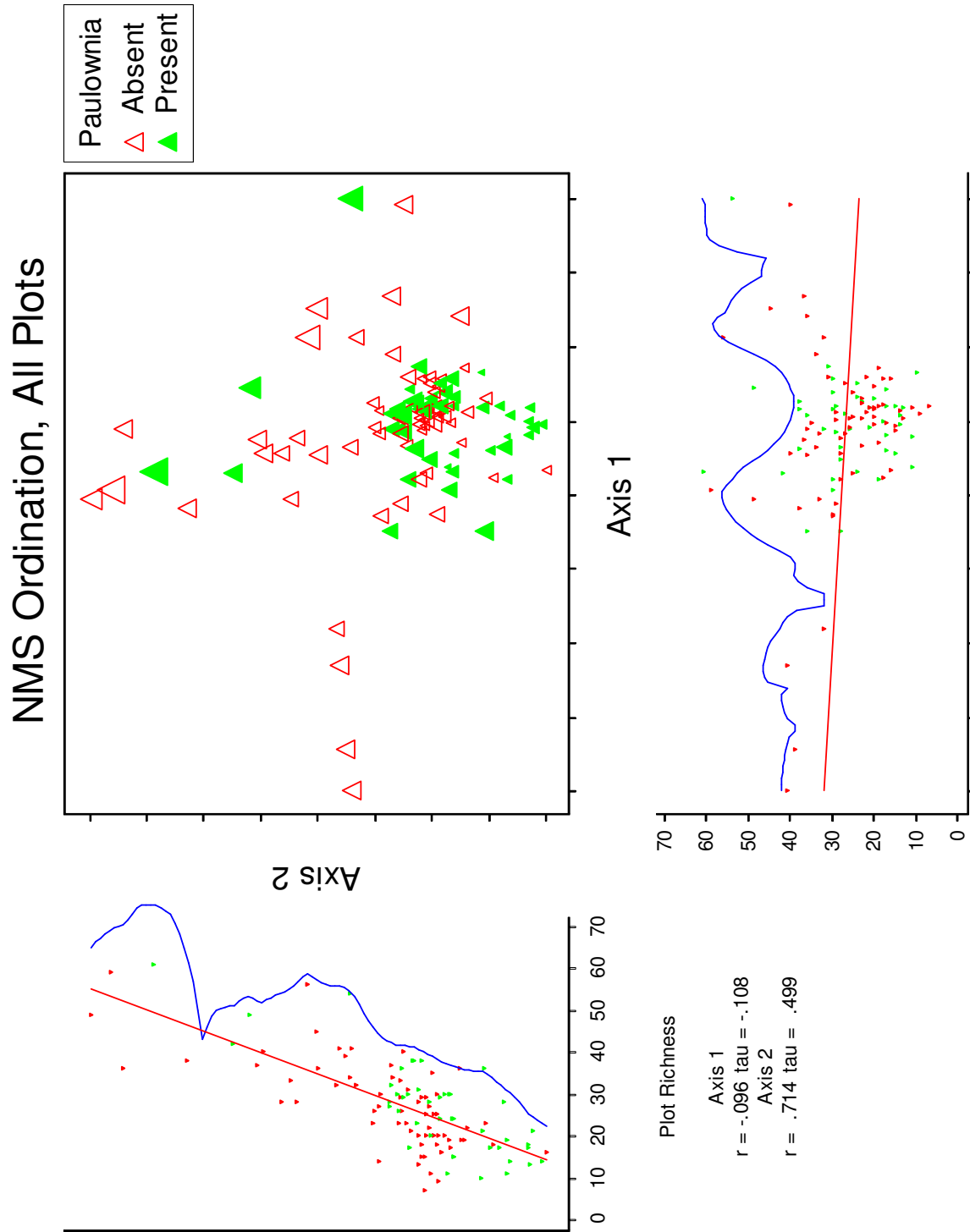


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Photo 6.2: *Paulownia* that do persist where significant regeneration has occurred are taller than the regenerating native vegetation.



Photo 6.3: *Paulownia* habitat is largely maintained on steep, exposed areas where regeneration is slow and sparse and *Paulownia* has limited competition for light and space.



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CHAPTER VII: Xeric forest seed-banks in the Great Smoky Mountains National Park

ABSTRACT

In xeric forests, many species are adapted to or dependent on fire disturbances. Although some of these species have life stages able to survive fire, many depend upon a seed-bank or post-fire seed rain for site recolonization. Unfortunately, the seed-bank composition and spatial patterns within it are unknown. This knowledge could improve predictions about post-fire recovery patterns and exotic species invasions. Utilizing 84 soil samples, this chapter investigates the composition of and spatial patterns within the seed-bank of xeric forests in the western portion of the Great Smoky Mountains National Park.

Within the seed-bank, both tree and shrub species had very low levels of recruitment (13 and 11 species respectively) from the collected soil samples. As a result no pattern was discernable in the number or identity of recruits in relation to community type or the tested spatial variables (distance to: roads, Park boundary, trails, roads outside the Park boundary, and elevation). Herbaceous species germinated with greater frequency and abundance, but none of the collected variables explained the distribution of species or species groups better than a null distribution.

Species composition and occurrence frequency was widely divergent between collected seeds and vegetation plots in these same communities for all growth forms and

fewer species were represented in the soil than in the extant vegetation. For woody plants, the most common species germinated from the seed-bank (*Ulmus alata*, *Betula alleghaniensis*) were not recorded within the plots. The most common species within the plots were either not present in the seed-bank (*Oxydendrum arboreum*) or occurred only once (*Acer rubrum*, *Nyssa sylvatica*). Forbs and grasses were much more abundant (448 occurrences, 67 species) within the seed-bank than woody species (181/40 occurrences, 15/14 species, with/without *Paulownia*), but had low levels of overlap with the extant vegetation though their overlap was higher than with the other growth forms. Unlike woody species, more graminoid species were present in the seed-bank (67) than in the extant vegetation (9) and this group had the highest level of species overlap between plots and soil samples.

INTRODUCTION

The presence of viable seeds within the soil has long been recognized as an important determinant of community composition. Many species are not consistently present in the community as growing individuals, but instead are found only when conditions match their environmental and competitive tolerances. These species typically rely upon seeds to reach new suitable habitats in time or space and have been variously identified as ruderals (Grime 1977), or existing at the r end of the r-K life history spectrum (MacArthur and Wilson 1967). This chapter identifies the species present within the seed-banks of xeric forest communities of the GSMNP and determines whether their makeup is due to chance alone or is determined by variables related to plot location.

Generally speaking, there are two groups of seeds within the soil. The first, the seed-rain, contains seeds less than a year old; this annual input of seeds is referred to as the seed rain. These seeds will either germinate in the next growing season, become unviable, or become dormant to join the second component of soil-stored seeds, the seed-bank. Seeds found within the seed-bank are dormant and require environmental cues (light/dark interval exposure, chemical cues, removal of the seed coat) for germination. While some seeds are dispersed ready to germinate, others are dormant at the time of dispersal. Those seeds that pass from being initially ready to germinate to a dormant state are said to have undergone induced dormancy or secondary dormancy. Finally, some seeds typically do not survive beyond the immediate growing season. These seeds are known as recalcitrant, are generally fleshy, and/or have high water content and are rarely components of the seed-bank.

Although seed-banks are presumed to play a role in vegetation dynamics over time, their relative importance in xeric forests is unclear. Work by Schiffman and Johnson (1992) found a sparse (.43 seeds/m²) seed-bank in a southern Appalachian oak forests of Virginia that was significantly different in composition from the extant vegetation. Forest herbs were much more common within the soil than forest trees, shrubs, or ruderals. They attributed these results to the cumulative effects of: (1) the lack of past cultivation, (2) past low-severity ground fires, (3) the scarcity of nearby sources of ruderal and early-successional seeds, and (4) the inherently short longevities of forest species' seeds. From this they concluded that succession will be highly spatially variable and greatly influenced by vegetative resprouting and post-disturbance seed dispersal and that seed-banks would have a lesser influence.

Different conclusions were reached by Lambers *et al.* (2005) in their study of southern Appalachian woody species. Although they too found that some extant species were never identified from the seed-bank, they concluded that seed-banking may play an important, and overlooked, role in successional dynamics. They argued that although the annual recruitment of many woody species into the seed-bank is low, that even low annual recruitment can form a significant buffer against environmental stochasticity and that prevailing thought to the contrary is at least in part due to the limited availability of appropriate data on long-term production and seed mortality estimates (Pickett and McDonnell 1989). This chapter utilized 84 soil samples collected from the western portion of the GSMNP to identify species present within the seed-bank of dry forest communities of the southern Appalachians and analyze the species were distributed spatially. The composition of the seed-bank was also compared with the extant vegetation recorded in plots located within the same vegetation communities.

STUDY AREA

The western portion of the GSMNP is marked by a series of ridges and valleys that run roughly in parallel from northwest to southeast. Although there is a general increase in elevation from West to East, this ridge and valley system creates the dominant elevation gradient. This area is also a transition from the high mountains in the central portion of the Park to the Tennessee Valley to the west and is markedly drier than most of the rest of the Park. Rainfall for the area averages 120cm (Busing 2005) and this is reflected in the increased cover of xeric and sub-xeric forests. Lower rainfall and drier forests also give rise to an increased fire frequency with a historic mean Fire Return Interval (FRI) of 8-12 years (Harmon 1982). These frequent fires were of low severity, sufficient to prevent to encroachment of more mesic and fire sensitive species, but stimulated only limited pine regeneration. The majority of pine regeneration occurred following less frequent (~100 year FRI), high severity fires. Fire suppression was park policy from its creation till the late 1980's. Although prescribed and wild fires are increasingly common within the park, the mean FRI remains longer than it was historically and the composition, and structure of xeric vegetation communities have not yet returned to their previous state (Harrod *et al.* 1998).

METHODS

The study area was bounded by Rich Mountain Road, Cade's Cove loop Road, Rabbit Creek trail, and the Park boundary. Within this area, potential sampling sites were identified

(in ArcGIS) on southwest facing ($210^{\circ} \leq \text{aspect} \leq 240^{\circ}$) slopes with xeric or sub-xeric vegetation types (Table 7.1, Madden 2006), and within 500m meters of a road or trail. These potential sites were further stratified by elevation and distance from the Park boundary which were each divided into three classes; three 2km wide distance classes and three elevation classes (184-440m, 441-600m, 600-800m) such that each elevation class contained an equal area. Ten sampling sites were randomly selected from within each distance-elevation class combination where possible. Two class combinations (Middle distance-Low elevation and Far distance-Low elevation) did not occur within the sample area. Although samples were identified using distance and elevation classes, continuous measurements of these variables were used in the analyses. Additional samples were taken from sites with appropriate habitat types as determined in the field to increase the number of collected samples.

Samples were collected in February and March of 2005 and their geo-coordinates recorded with a GPS. At each location, 10 randomly located samples within a 10m diameter circle were collected using a 5cm diameter soil corer for a combined sample surface area of 196.44cm^2 . Cores included litter and humus and were taken to a soil depth of 10cm. Samples were combined into a single composite sample for each location. Soils were refrigerated in the days between their collection and processing.

Cores were processed utilizing the approach described by Gross (1990). Soils were sieved at the North Carolina Botanical Garden in Chapel Hill to remove particles larger than 3cm and smaller than .25mm, the remaining mixture was spread thinly ($\leq 1\text{cm}$) over a growing medium (Promix BX) in the greenhouse at UNC, and watered daily. Germination was tracked daily through November 21st, 2005 and all germinants were identified to species

where possible and if not to genus or family according to the taxonomic standards of Weakly (2007).

Vegetation plots used to compare species composition and frequency were pulled from a Park plot database on the basis of their occurrence in or within 5m of the vegetation communities used to locate samples and within the elevation range of the collected samples. Plot species lists (Appendix 1) were derived from the herbaceous strata data (stems less than 1m) because tree (>2.5 cm. dbh) records were unavailable.

Negative Binomial regression models were fit to the data using the number of individuals in the species or vegetation group as the response variable and the following as potential predictor variables: distance to all roads, distance to roads outside the Park boundary, distance to the park boundary, distance to trails, slope, and aspect, Topographic Convergence Index, elevation, and vegetation community dryness. Best fit models were chosen on the basis of their AIC values (McLaughlin 1999, Manly 2001).

RESULTS

Samples ranged in aspect from 41 to 322° with an average of 211°, slopes ranged from 4 to 43°, and elevation ranged from 364m to 804m. At five of the additional locations, the observed dry forest types did not match the vegetation community identified by the vegetation map resulting in an apparently greater diversity of communities sampled (Table 7.2). Six different bedrock types as identified by the GSMNP bedrock map were captured by the samples: Graphitic sulfidic coarse siliciclastic rocks, Siliciclastic feldspathic

metasandstone and conglomerate, Siliciclastic metasandstone and slate, Siliciclastic metasilstone, Siliciclastic quartzite, Siliciclastic sulfidic slate. In total 13 tree, 11 shrub, 46 herbs/forb, 16 grainoids, and 1 vine species were identified from the soil samples (counting individuals identifiable only to family or genus as distinct from congeners identified to species, Table 7.3). *Paulownia tomentosa* and *Mazus pumilus* were the only exotic species which germinated from the samples.

Patterns by Growth Form

Trees

Although 13 tree species (including *Rhus copallina* and *R. glabra*) were germinated from the soil samples (Appendix 1), with the exception of *Paulownia*, the abundance of all species was exceedingly rare. After *Paulownia*, the most abundant were *Rhus copallina* and *Betula alleghaniensis* (with 6 seedlings occurring across 2 and 3 samples respectively). *Ulmus alata* was the 2nd most common species with 4 seedlings found across 4 samples. The pattern of *Paulownia* occurrence has been addressed within Chapter III and will not be addressed further here. No other individual tree species occurred with sufficient frequency to determine whether their abundance was correlated with the collected variables, nor did the pooled number of individuals or species at each site correlate with the above variables.

Six of the thirteen tree species present in the soil samples were not recorded in vegetation plots sampled within the same community types (Appendix 1). These included the most common species (# samples), *Ulmus alata*, and the 2nd most abundant species (# seedlings) within the samples, *Betula alleghaniensis*. The most abundant was *Paulownia* due to 9 samples taken in the immediate vicinity of a mature *Paulownia* (hereafter *Paulownia*

samples) to measure *Paulownia* seed dispersal (Chapter III). *Rhus copallinum* was as abundant as *Betula alleghaniensis* in the soil samples (6 germinated individuals), and occurred only once in the plots. The other three species present in the seed-bank but not the vegetation plots were: *Aralia spinosa*, *Rhus glabra*, and *Salix nigra*. The first and third most common species in the vegetation plots, *Acer rubrum* and *Nyssa sylvatica*, were represented by only one seedling in the soil samples.

Shrubs

Eleven shrub species (including *Ericaceae* sp. and *Viburnum dentatum*) were germinated from the seed-bank but no species occurred in great abundance (Appendix 1). *Rubus allegheniensis* had the greatest number of seedlings (13 in 4 samples) and *Rubus* sp. occurred in the greatest number of samples (12 seedlings in 7 samples). As with the trees, no individual species occurred with sufficient frequency to determine whether their abundance correlated with the collected variables, nor did the pooled number of individuals or species at each site correlate with these variables.

Only one shrub species was definitively also present in the vegetation plots though four seedlings were identifiable only to family or genus (*Rosaceae* sp., *Rosaceae* sp.1, *Ericaceae* sp., and *Rubus* sp.). *Rubus alleghaniensis* was the most abundant species (13 seedlings in 4 samples) within the soil samples yet only present in one vegetation plot. Three species, *Hydrangea arborescens*, *Hypericum stragulum*, and *Viburnum dentatum*, present in the soil samples were not recorded within the vegetation plots.

Herbs

46 herbs and forbs, 16 grainoides, and 1 vine species were germinated from the soil samples (Appendix 1). Of the 46 forbs, only six (*Acalypha virginica*, *Ageratina aromatica*,

Cardamine hirsute, *Chamaesyce maculate*, *Erechtites hieracifolia*, and *Oxalis grandis*) were encountered in more than ten samples. Four other species (*Oxalis sp.*, *Stelleraria media*, *Mazus pumilus*, and *Lobelia sp.*) occurred in more than five samples with the remaining species occurring only transiently. The exotic *Mazus pumila* was present in soil samples, but was potentially a greenhouse artifact as it was observed in other experimental flats where no outside seeds or soils were intentionally added. As a result of the low frequency at which each species was encountered, correlations with sampled variables were not possible for individual taxa other than *Oxalis grandis*, *Dichanthelium comutatum*, and *Cardamine hirsuta*. Correlations were also conducted for the following vegetation groups: all forbs, all *Dichantheliums*, all Poacea species, all Cyperaceae, and all herbaceous species together.

No fitted model was significantly different from the null distribution. This was true for both binned and count distributions of all species and vegetation groups (Figure 7.5-7.10). Three abundance values occurred more frequently than expected by a null distribution when all herbaceous species were considered together (Figure 7.10), but these were partially explained by the *Paulownia* samples (Figure 7.11) and due to their spatial proximity, these may not be independent samples. Removing these samples reduced the degree to which these counts were outliers but did not affect the results otherwise. Although species abundance varied with community dryness (Figure 7.12), vegetation community was not a significant predictor in the regression models when communities were considered independently or grouped by dryness (mesic to sub-xeric, sub-xeric to xeric, and xeric).

Extant vegetation in the herb layer and seed-bank composition were dramatically different with very little overlap between the two species lists. Two species (*Erechtites hieraciifolia* var. *hieraciifolia* and *Lysimachia quadrifolia*) occurred in both soil samples and

plots, and the only vine present in the seed-bank, *Vitis rotundifolia*, was also present in the extant vegetation. There were four shared graminoid species (*Dichanthelium commutatum*, *Schizachyrium scoparium*, *Dichanthelium boscii*, and *Dichanthelium dichotomum*) and this group had a higher diversity in the seed-bank than in the extant vegetation.

DISCUSSION

The observed abundance distributions of individual species and species groups were not significantly different from a null negative binomial distribution and no significant pattern was seen in relation to distance to park boundary, distance to all roads, distance to roads outside of the park, distance to trails, slope, aspect, Topographic Convergence Index, elevation, or vegetation community,. However, the ability to detect patterns was limited by the sparseness of the seed-bank.

The other notable result from this study is the limited number and abundance of species germinated from the soil samples. These results may be explainable by one or more of the following factors: (1) Seed-bank dominance by disturbance specialists, (2) Short lived seeds, (3) Unmet germination requirements, (4) Insufficient sampling volume, or (5) Species dependence upon vegetative spread.

Seed-banks may be most important for disturbance specialists (factor [#]1). These species, identified as ruderals by Grime (1977) and as r strategists by MacArthur and Wilson (1967), depend upon seed dispersal and seed-banks to colonize post-disturbance habitats which are transient in time and space. In these communities, many of these specialists are

adapted to fire, and the post-fire conditions. Although these species' seeds generally survive for many years to insure local persistence between fires, seed viability decreases with time and can lead to local extinction or decreased population density when the inevitable disturbance occurs. Fire suppression will eventually result in an increased density of fire intolerant species in both the extant vegetation and within the seed-bank, but without historic information on the seed-bank of these forests it is unknown how they have changed. However no accumulation of fire-intolerant species was observed in the seed-bank and disturbance specialists were the most abundant species group. Many of the species that germinated were disturbance specialists. *Rhus copallium*, *Rubus alleghaniensis*, and the *Solidago*'s were among the germinated disturbance specialists and these species were also absent from the vegetation plots; not surprising as plots are often chosen to capture relatively homogeneous, *undisturbed* habitat. The dominant vegetation in the interval between disturbances is typically perennial and adapted to more temporally/spatially consistent habitats. As these species are able to persist as extant vegetation within a landscape over time, they rely less heavily upon seed-banks. The contrasting importance of seed-banks for these life history strategies partially explains the contrasting composition the extant vegetation and the seed-bank.

Many forest species also have short lived seeds (factor ^{#2}, Baskin and Baskin 1989, Pickett and McDonnell 1989, Ingersoll and Wilson 1990, Shiffman and Johnson 1992), which limits the development of a significant seed-bank. For many species, although seeds do over winter, low survival rates beyond a year prevents the buildup of a significant seed-bank and results in a low seed density. Sampling in the very early spring also meant that

species whose seeds germinate in the same year that they are produced were not captured within the samples.

Although greenhouse conditions are ideal for the germination of some species, these conditions will not meet the germination requirements of all species (factor #3). High light levels may prevent or decrease germination of shade-tolerant species adapted to germinate and grow through the seedling stage in moderate to deep shade. Species requiring scarification, chemical cues, heat from fire, or exposure to smoke to break dormancy may also not germinate and thus would not be included in the seed-bank measurements of this study.

It is also possible that an insufficient soil volume was collected to capture all of the species present (factor #4). The total surface area collected by each sample was 196.44cm^2 (from a plot of 78.5 m^2), which is less than the 250cm^2 suggested by Forcella (1992); however Forcella suggests that only 11 samples need to be taken with a 10cm diameter soil corer, one more than was collected here. The research by Benoit (1989) upon whose work the soil-sampling formula is based studied a 1.35ha area and Forcella (1992), whose plots which ranged from 65.27 m^2 to 279.38m^2 , offered no comment on the effect of plot size on the necessary soil sample volume. The generally larger plots in both of these studies, suggests that the number of samples collected in this study is likely not an important factor and that the sparseness of the observed seed-bank properly reflects actual conditions.

Finally, some species within these communities, *Vacciniums* notable among them, rely more upon vegetative spread than on seed germination (factor #5). These species would not be expected to occur frequently in the seed-bank and consequently are easily missed by soil samples.

This is not the first work to find a sparse seed-bank in southern Appalachian forests. Schiffman and Johnson's (1992) work on southern Appalachian oak forests reported a limited seed-bank with an average of .43 seeds/m² though it is unclear whether they reported the number of seeds per surface area collected or per surface area of the entire plot. My study found an average of 316.95 seeds/m² using the surface area of the soil cores or .0622 seeds/m² using the surface area of the entire 78.5m² plot. Like this study, they found only a limited correspondence between the seed-bank and the extant vegetation, that the seed-bank poorly represented the relative dominance of species present in the extant vegetation, and that herbaceous species diversity was significantly greater than that of the shrubs or trees. Unlike their study however, this study did find significant densities of disturbance specialists.

My results are also consistent with work by Hanlon *et al.* (1998) on seed-banks of Allegheny Plateau riparian forests who found extant vegetation to be more diverse than seed-bank samples and a predominance of non-woody species within the seed-bank. Their study did identify a greater number of species, but their samples included a greater diversity of habitats, more species rich habitats, and riparian habitats which receive seeds from vegetation communities upstream.

Finally, recent work by Lambers *et al.* (2005) suggested that seed-banks may play an important role in woody species recruitment in temperate forests. Although many forest species are never found in the seed-bank and many species' seeds experience high mortality as they enter it, the high number of seeds produced still results in significant numbers entering the seed-bank each year. They draw evidence for this from results showing that for three species (*Acer rubrum*, *Betula sp.*, and *Liriodendron tulipifera*), a substantial portion of seeds available for germination came from seeds dispersed two or more years previously.

Additionally, in years where no seeds fell into local microsites (~ 1 in 5), seed-banks were the only source of germination. It is worth noting that the species in their study (above) were uncommon to absent from the communities sampled in this study. Finally, they conclude that seed decay may vary greatly between vegetation communities suggesting that the trends in their study and in this one may not hold true for other communities.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Results of this study indicate that the seed-bank of sub-xeric to xeric forest communities of the southern Appalachians is sparsely populated, dominated by herbaceous species, and that prevalence within the seed-bank is not reflective of dominance within the vegetative community. Successional species are more prevalent within the seed-bank than in the extant forest and seed-bank diversity overall is lower than that found in the aboveground vegetation. Although the number of studies in similar communities is limited, their results are largely consistent with results presented here.

This study also sheds light upon important management considerations for these communities. First, evidence from this study shows that the seed-bank is insufficient to regenerate these communities *de novo*. Thus the continued persistence of these communities is in large part dependent upon their vegetative presence and management should focus on preventing their loss as reestablishment from the seed-bank will be limited. The limited presence of exotics suggests that control of extant individuals will significantly impact their future abundance as there is no a large pool of seeds within the soil. In the case of

Paulownia, its presence was highly correlated with distance from mature individuals (Chapter III) suggesting that control on the Park boundary would significantly limit invasion into the interior.

TABLES AND FIGURES

Figure 7.1: Map depicting the location of soil samples (green) and vegetation plots (red) used for species comparisons.

Table 7.1: Xeric and sub-xeric vegetation associations used to identify sampling locations within the GSMNP study area. Associations identified on the basis of the GSMNP vegetation classification for the Park which follows the National Vegetation Classification.

Table 7.2: Associations sampled within the GSMNP study area based on plot coordinates and the association identified for that location in the vegetation classification map of the Park which follows the National Vegetation Classification.

Table 7.3: All species germinated from soil samples broken up by growth form.

Figure 7.2: Observed frequency counts for *Oxalis grandis* (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). The null frequency distribution is hidden by the overlapping best fit model. All samples were included in this plot.

Figure 7.3: Observed frequency counts for *Dichanthelium commutatum* (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). All samples were included in this plot.

Figure 7.4: Observed frequency counts for all forbs (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). All samples were included in this plot.

Figure 7.5: Observed frequency counts for all Poaceae (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). All samples were included in this plot.

Figure 7.6: Observed frequency counts for all Cyperaceae (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). The null frequency distribution is hidden by the overlapping best fit model. All samples were included in this plot.

Figure 7.7: Observed frequency counts for all herbaceous species (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). All samples were included in this plot.

Figure 7.8: Observed frequency counts for all herbaceous species (grey bars) plotted alongside the frequency distribution predicted by the null Negative Binomial

model (blue) and the best fit model (green). All samples included except the nine “*Paulownia* samples”.

Figure 7.9: Boxplot of the mean number of herbaceous species (± 1 s.e.) germinated from soil samples grouped by moisture availability.

APPENDICES

Appendix 1: Species germinated from soil samples and those found within the xeric vegetation community plots shown in Figure 7.1. “# Plot Occur” is the number of plots that the species occurred in and “# in Sample” is the number of individuals germinated from soil samples. Species are organized by growth form and listed in descending frequency of occurrence in the vegetation plots.

Figure 7.1: Map depicting the location of soil samples (green) and vegetation plots (red) used for species comparisons.

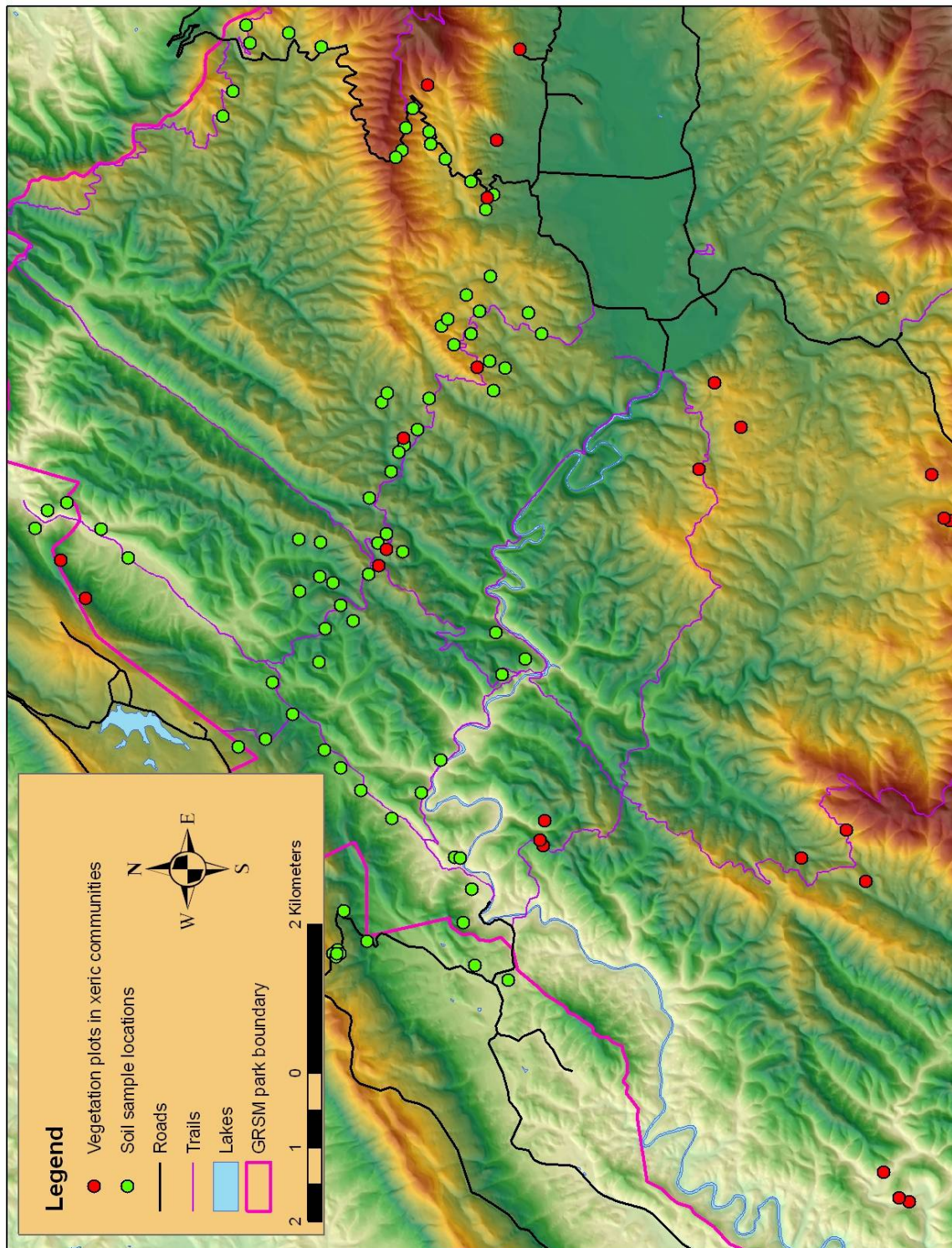


Table 7.1: Xeric and sub-xeric vegetation associations used to identify sampling locations within the GSMNP study area. Associations identified on the basis of the GSMNP vegetation classification for the park which follows the National Vegetation Classification.

Apriori Selected Vegetation Communities		
CEGL Code	Association	Community Name
XERIC RIDGE FORESTS		
Table Mountain Pine / Pitch Pine Woodlands		
7119	<i>Pinus virginiana</i> - <i>Pinus (rigida, echinata)</i> - (<i>Quercus prinus</i>) / <i>Vaccinium pallidum</i> Forest	Appalachian Low-Elevation Mixed Pine / Hillside Blueberry Forest
7097	<i>Pinus pungens</i> - <i>Pinus rigida</i> - (<i>Quercus prinus</i>) / <i>Kalmia latifolia</i> - <i>Vaccinium pallidum</i> Woodland	Blue Ridge Table Mountain Pine - Pitch Pine Woodland (Typic Type)
Shortleaf Pine / Shortleaf Pine-Oak Forests		
7078	<i>Pinus echinata</i> / <i>Vaccinium (pallidum, stamineum)</i> – <i>Kalmia latifolia</i> Forest	Appalachian Shortleaf Pine Forest
3560	<i>Pinus echinata</i> / <i>Schizachyrium scoparium</i> Appalachian Woodland	Shortleaf Pine/Little Bluestem Appalachian Woodland
White Pine / White Pine – Oak Forests		
7519	<i>Pinus strobus</i> - <i>Quercus Pinus strobus</i> – <i>Quercus (coccinea, prinus)</i> / (<i>Gaylussacia ursina</i> - <i>Vaccinium stamineum</i>) Forest	Appalachian White Pine - Xeric Oak Forest
7100	<i>Pinus strobus</i> / <i>Kalmia latifolia</i> - (<i>Vaccinium stamineum</i> , <i>Gaylussacia ursina</i>) Forest	Southern Appalachian White Pine Forest
7517	<i>Pinus strobus</i> - <i>Quercus alba</i> - (<i>Carya alba</i>) / <i>Gaylussacia ursina</i> Forest	Appalachian White Pine - Mesic Oak Forest
Chestnut Oak Forests		
6271	<i>Quercus (prinus, coccinea)</i> / <i>Kalmia latifolia</i> / (<i>Galax urceolata</i> , <i>Gaultheria procumbens</i>) Forest	Chestnut Oak Forest (Xeric Ridge Type)
7267	<i>Quercus prinus</i> - (<i>Quercus rubra</i>) - <i>Carya spp.</i> / <i>Oxydendrum arboreum</i> - <i>Cornus florida</i> Forest	Appalachian Montane Oak Hickory Forest (Chestnut Oak Type)

Table 7.2: Associations sampled within the GSMNP study area based on plot coordinates and the association identified for that location in the vegetation classification map of the park which follows the National Vegetation Classification.

Field Sampled Vegetation Communities				
CEGL Code	Association	Community Name	Moisture Category	# of Plots
XERIC RIDGE FORESTS				
Table Mountain Pine / Pitch Pine Woodlands				
7119	<i>Pinus virginiana</i> - <i>Pinus (rigida, echinata)</i> - (<i>Quercus prinus</i>) / <i>Vaccinium pallidum</i> Forest	Appalachian Low-Elevation Mixed Pine / Hillside Blueberry Forest	Xeric	47
7097	<i>Pinus pungens</i> - <i>Pinus rigida</i> - (<i>Quercus prinus</i>) / <i>Kalmia latifolia</i> - <i>Vaccinium pallidum</i> Woodland	Blue Ridge Table Mountain Pine - Pitch Pine Woodland (Typic Type)	Xeric	5
Shortleaf Pine / Shortleaf Pine-Oak Forests				
7078	<i>Pinus echinata</i> / <i>Vaccinium (pallidum, stamineum)</i> - <i>Kalmia latifolia</i> Forest	Appalachian Shortleaf Pine Forest	Xeric	0
3560	<i>Pinus echinata</i> / <i>Schizachyrium scoparium</i> Appalachian Woodland	Shortleaf Pine/Little Bluestem Appalachian Woodland	Xeric	0
White Pine / White Pine - Oak Forests				
7519	<i>Pinus strobus</i> - <i>Quercus Pinus strobus</i> – <i>Quercus (coccinea, prinus)</i> / (<i>Gaylussacia ursina</i> - <i>Vaccinium stamineum</i>) Forest	Appalachian White Pine - Xeric Oak Forest	Sub-xeric to xeric	4
7100	<i>Pinus strobus</i> / <i>Kalmia latifolia</i> - (<i>Vaccinium stamineum</i> , <i>Gaylussacia ursina</i>) Forest	Southern Appalachian White Pine Forest	Sub-xeric to xeric	0
7517	<i>Pinus strobus</i> - <i>Quercus alba</i> - (<i>Carya alba</i>) / <i>Gaylussacia ursina</i> Forest	Appalachian White Pine - Mesic Oak Forest	Sub-xeric to xeric	0

Table 7.2: Continued

Chestnut Oak Forests				
6271	<i>Quercus (prinus, coccinea) / Kalmia latifolia / (Galax urceolata, Gaultheria procumbens) Forest</i>	Chestnut Oak Forest (Xeric Ridge Type)	Sub-xeric to xeric	10
7267	<i>Quercus prinus - (Quercus rubra) - Carya spp. / Oxydendrum arboreum - Cornus florida Forest</i>	Appalachian Montane Oak Hickory Forest (Chestnut Oak Type)	Sub-xeric to xeric	3
LOW ELEVATION, TOPOGRAPHICALLY PROTECTED FORESTS				
Montane Cove Forests				
7710	<i>Liriodendron tulipifera – Aesculus flava - (Fraxinus americana, Tilia americana var. heterophylla) / Cimicifuga racemosa – Laportea canadensis Forest</i>	Southern Appalachian Cove Forest (Typic Montane Type)	Mesic to sub-mesic	1
7543	<i>Tsuga canadensis – Liriodendron tulipifera / Rhododendron maximum / Tiarella cordifolia Forest</i>	Southern Appalachian Acid Cove Forest (Typic Type)	Mesic to sub-mesic	3
Montane Oak-Hickory Forests				
6192	<i>Quercus rubra - Acer rubrum / Calycanthus floridus –Pyrularia pubera / Thelypteris noveboracensis Forest</i>	Appalachian Montane Oak - Hickory Forest (Red Oak Type)	Mesic to sub-mesic	1
7230	<i>Quercus alba - Quercus (rubra, prinus) / Rhododendron calendulaceum - Kalmia latifolia - (Gaylussacia ursina) Forest</i>	Appalachian Montane Oak Hickory Forest (Typic Acidic Type)	Mesic to sub-mesic	1
Hemlock Forests				
7102	<i>Pinus strobus - Tsuga canadensis / Rhododendron maximum - Leucothoe fontanesiana Forest</i>	Southern Appalachian Eastern Hemlock Forest (White Pine Type)	Mesic to sub-mesic	1
UNCLASSIFIED				
Unclassified				
N/A	Plots were located just outside the park's Vegetation Community map	None	Sub-xeric to xeric	8

Table 7.3: All species germinated from soil samples broken up by growth form.

Trees	Shubs	Herbs and Forbs		Grasses	Vines
<i>Acer rubrum</i>	<i>Aralia spinosa</i>	<i>Acalypha virginica</i>	<i>Helianthus strumosus</i>	<i>Andropogon</i> sp.	<i>Vitis rotundifolia</i>
<i>Aralia spinosa</i>	<i>Ericaceae</i> sp.	<i>Ageratina aromatica</i>	<i>Hypericum punctatum</i>	<i>Andropogon virginicus</i>	
<i>Betula alleghaniensis</i>	<i>Hydrangea arborescens</i>	<i>Asteraceae</i> sp. 1	<i>Hypericum stragulum</i>	<i>Carex</i> sp.	
<i>Betula</i> sp.	<i>Hypericum stragulum</i>	<i>Asteraceae</i> sp. 2	<i>Lamiaceae</i> sp.	<i>Cyperus pseudovegetus</i>	
<i>Liriodendron tulipifera</i>	<i>Rosaceae</i> sp. 1	<i>Asteraceae</i> sp. 3	<i>Lechea racemulosa</i>	<i>Cyperus</i> sp. 1	
<i>Nyssa sylvatica</i>	<i>Rosaceae</i> sp. 2	<i>Asteraceae</i> sp. 4	<i>Lespedeza virginica</i>	<i>Cyperus</i> sp. 2	
<i>Paulownia tomentosa</i>	<i>Rubus allegheniensis</i>	<i>Asteraceae</i> sp. 5	<i>Lobelia inflata</i>	<i>Dichanthelium accuminatum</i> var <i>accuminatum</i>	
<i>Quercus velutina</i>	<i>Rubus</i> sp.	<i>Asteraceae</i> sp. 6	<i>Lobelia</i> sp.	<i>Dichanthelium boscii</i>	
<i>Rhus copallina</i>	<i>Viburnum dentatum</i>	<i>Asteraceae</i> sp. 7	<i>Lysimachia quadrifolia</i>	<i>Dichanthelium clandestinum</i>	
<i>Rhus glabra</i>		<i>Asteraceae</i> sp. 8	<i>Mazus pumilus</i>	<i>Dichanthelium commutatum</i>	
<i>Robinia pseudoacacia</i>		<i>Asteraceae</i> sp. 9	<i>Oenothera biennis</i>	<i>Dichanthelium commutatum</i> var. <i>commutatum</i>	
<i>Salix nigra</i>		<i>Asteraceae</i> sp. 10	<i>Oxalis grandis</i>	<i>Dichanthelium dichotomum</i> var <i>dichotomum</i>	
<i>Ulmus alata</i>		<i>Cardamine hirsute</i>	<i>Oxalis</i> sp.	<i>Dichanthelium</i> sp.	
		<i>Cardamine pensylvanica</i>	<i>Potentilla canadensis</i>	<i>Digitaria sanguinalis</i>	
		<i>Chamaesyce maculate</i>	<i>Pseudognaphalium obtusifolium</i>	<i>Digitaria</i> sp.	
		<i>Chamaesyce</i> sp.	<i>Solidago bicolor</i>	<i>Eleusine indica</i>	
		<i>Conyza Canadensis</i>	<i>Solidago erecta</i>	<i>Kyllinga pumila</i>	
		<i>Dichanthelium</i> sp.	<i>Solidago</i> sp.	<i>Muhlenbergia capillaris</i>	
		<i>Erechtites hieracifolia</i>	<i>Solidago</i> sp1	<i>Panicum gattingeri</i>	
		<i>Eupatorium serotinum</i>	<i>Sonchus asper</i>	<i>Poa annua</i>	
		<i>Eupatorium</i> sp.	<i>Stellaria media</i>	<i>Poaceae</i> sp.	
		<i>Euphorbia</i> sub gen <i>Chamaesyce</i>	Unidentifiable herb	<i>Schizachyrium scoparium</i>	
		<i>Fabaceae</i> sp. Herb	<i>Valerianella</i> sp.	<i>Schizachyrium scoparium</i>	
			<i>Viola</i> sp.		

Figure 7.2: Observed frequency counts for *Oxalis grandis* (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). The null frequency distribution is hidden by the overlapping best fit model. All samples were included in this plot.

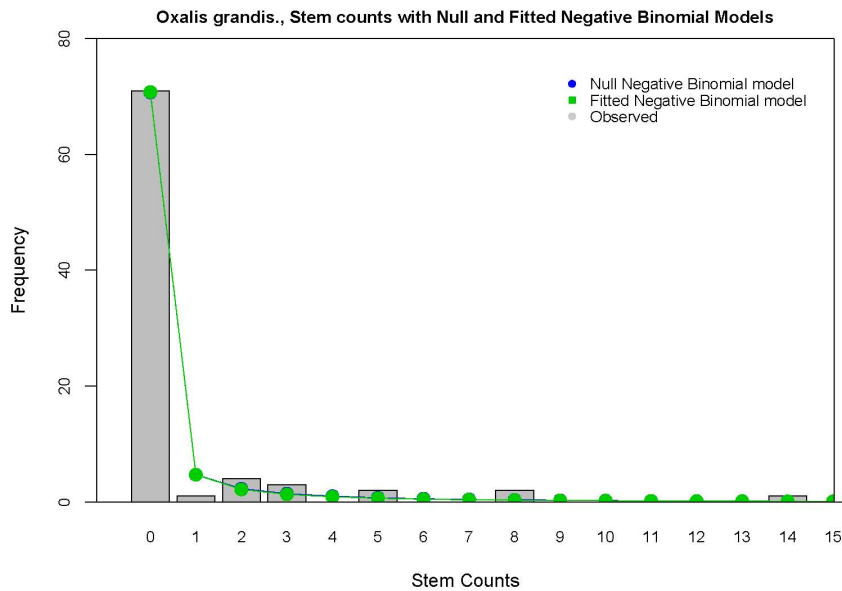


Figure 7.3: Observed frequency counts for *Dichanthelium commutatum* (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). All samples were included in this plot.

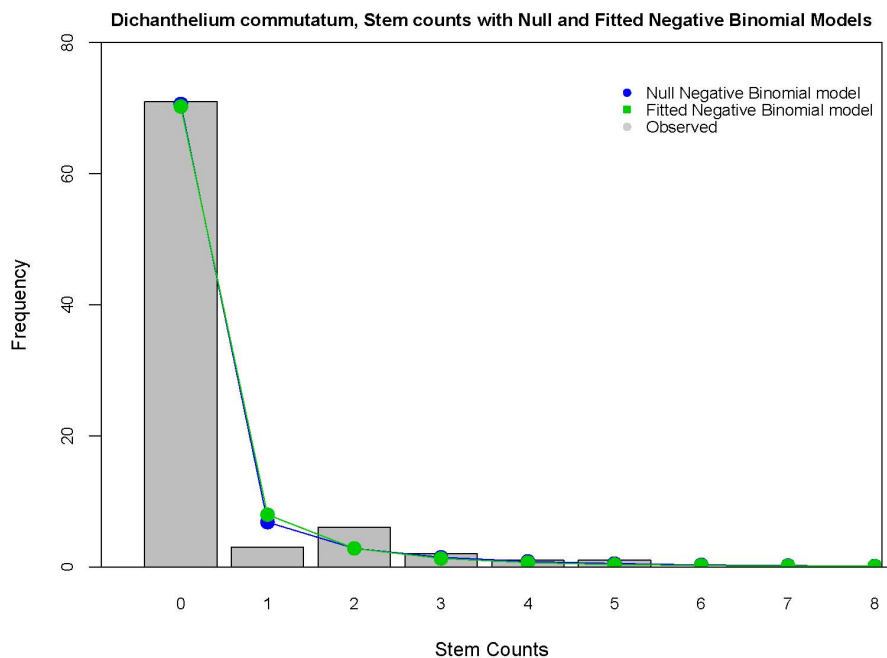


Figure 7.4: Observed frequency counts for all forbs (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). All samples were included in this plot.

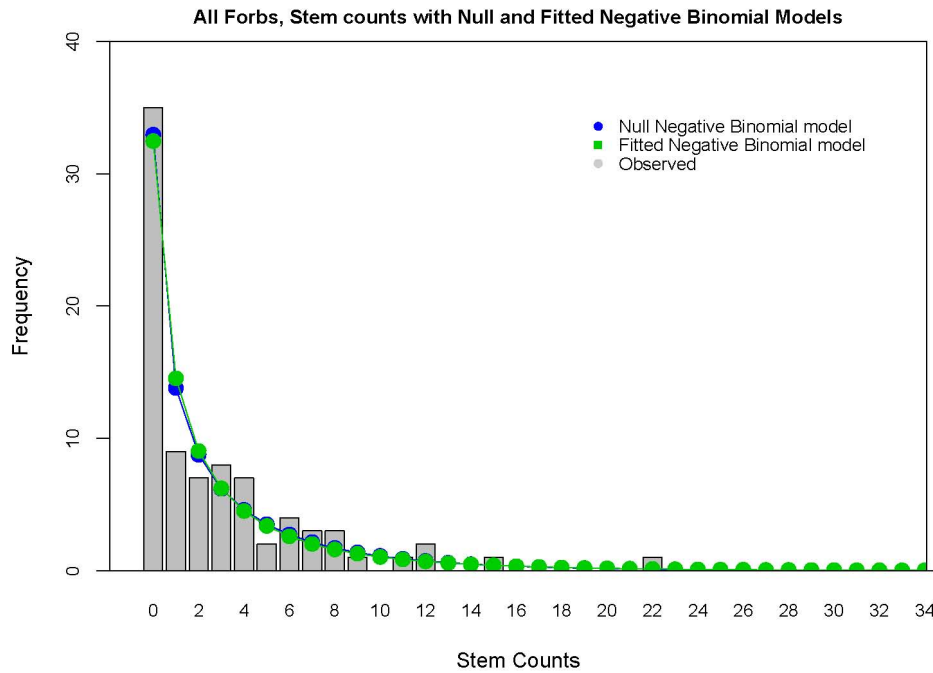


Figure 7.5: Observed frequency counts for all Poaceae (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). All samples were included in this plot.

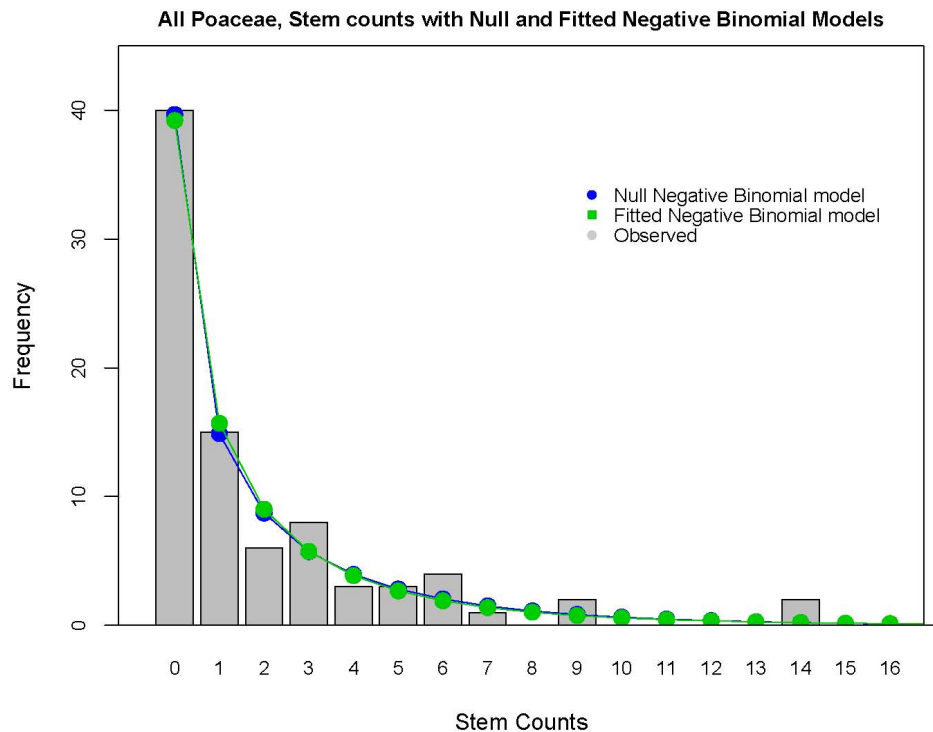


Figure 7.6: Observed frequency counts for all Cyperaceae (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). The null frequency distribution is hidden by the overlapping best fit model. All samples were included in this plot.

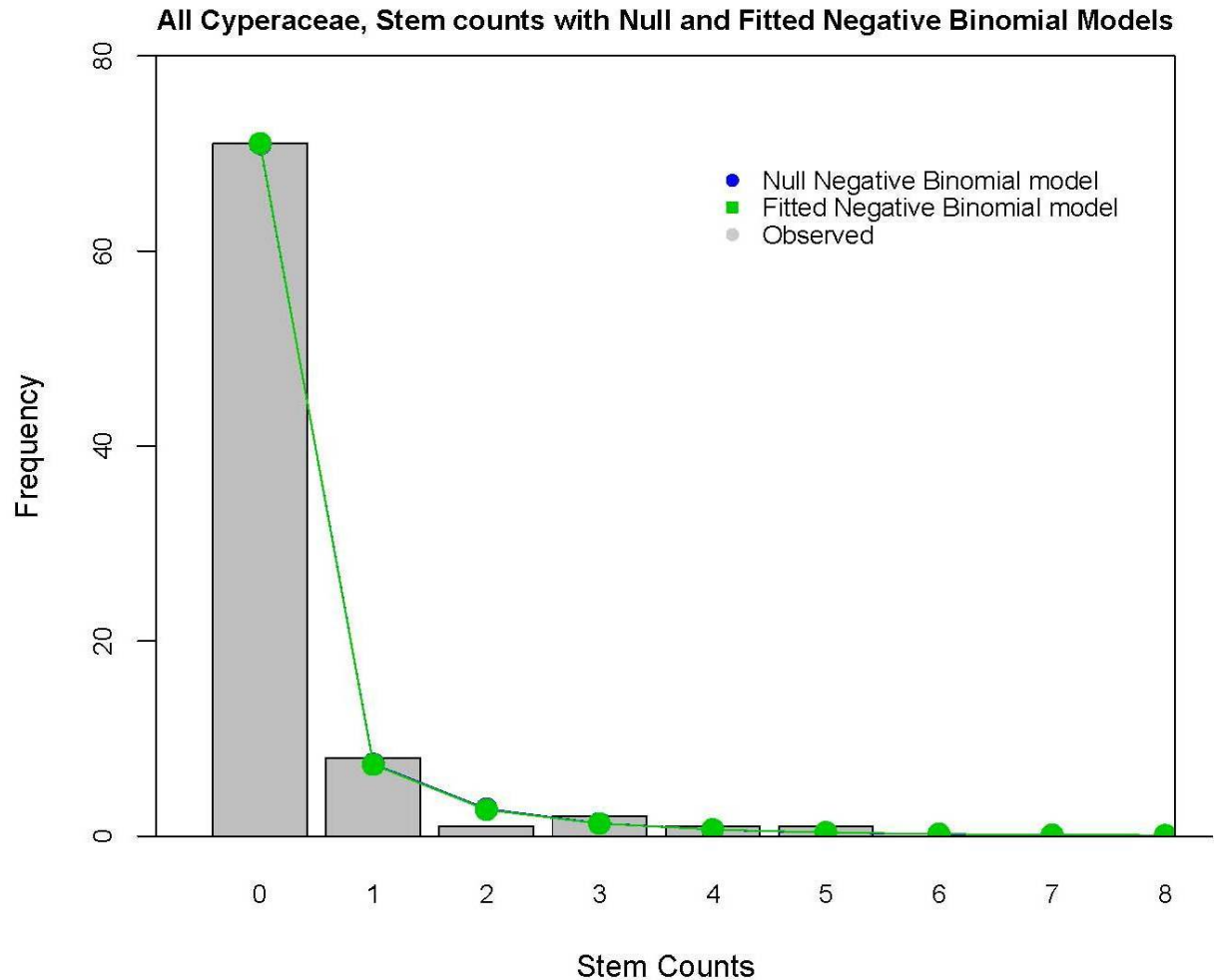


Figure 7.7: Observed frequency counts for all herbaceous species (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). All samples were included in this plot.

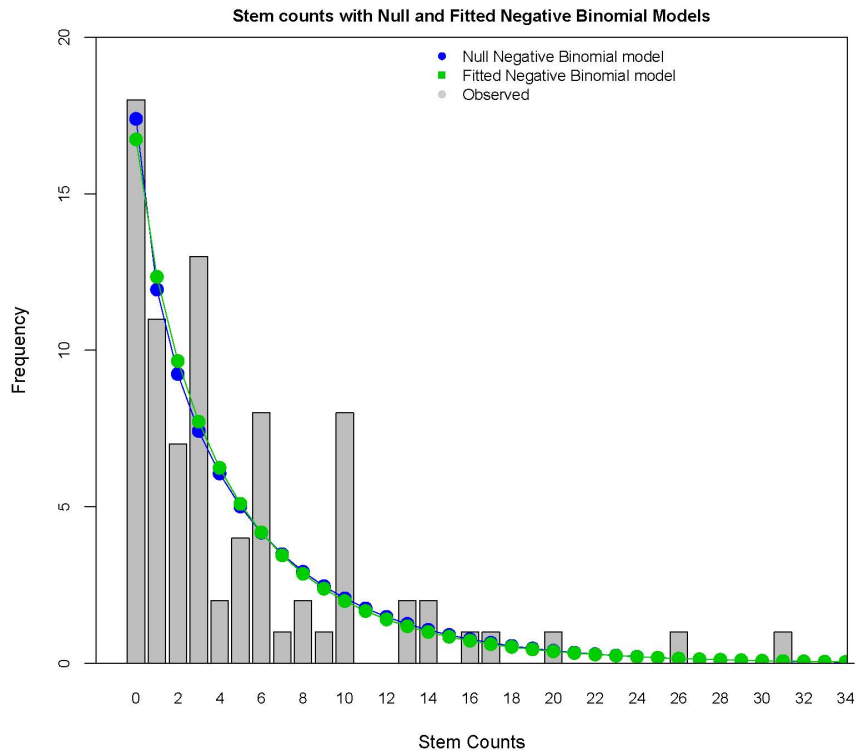


Figure 7.8: Observed frequency counts for all herbaceous species (grey bars) plotted along side the frequency distribution predicted by the null Negative Binomial model (blue) and the best fit model (green). All samples included except the nine “*Paulownia* samples”.

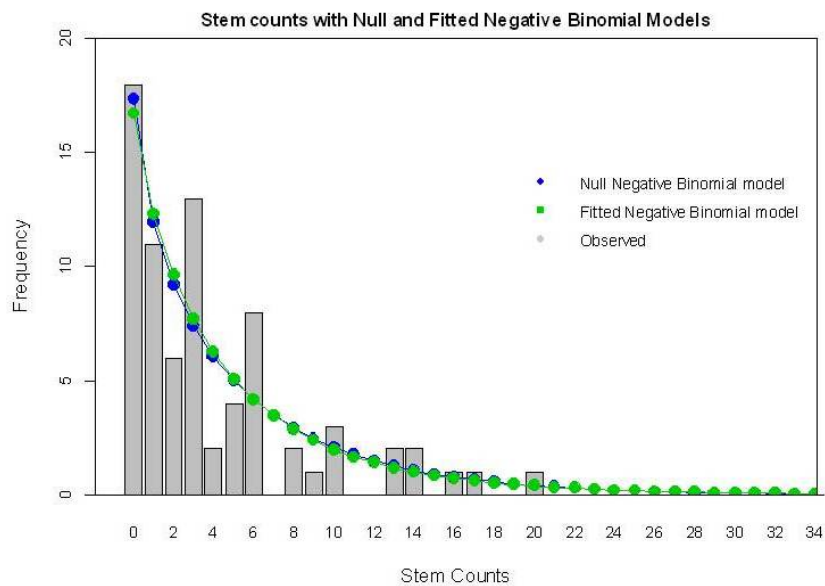
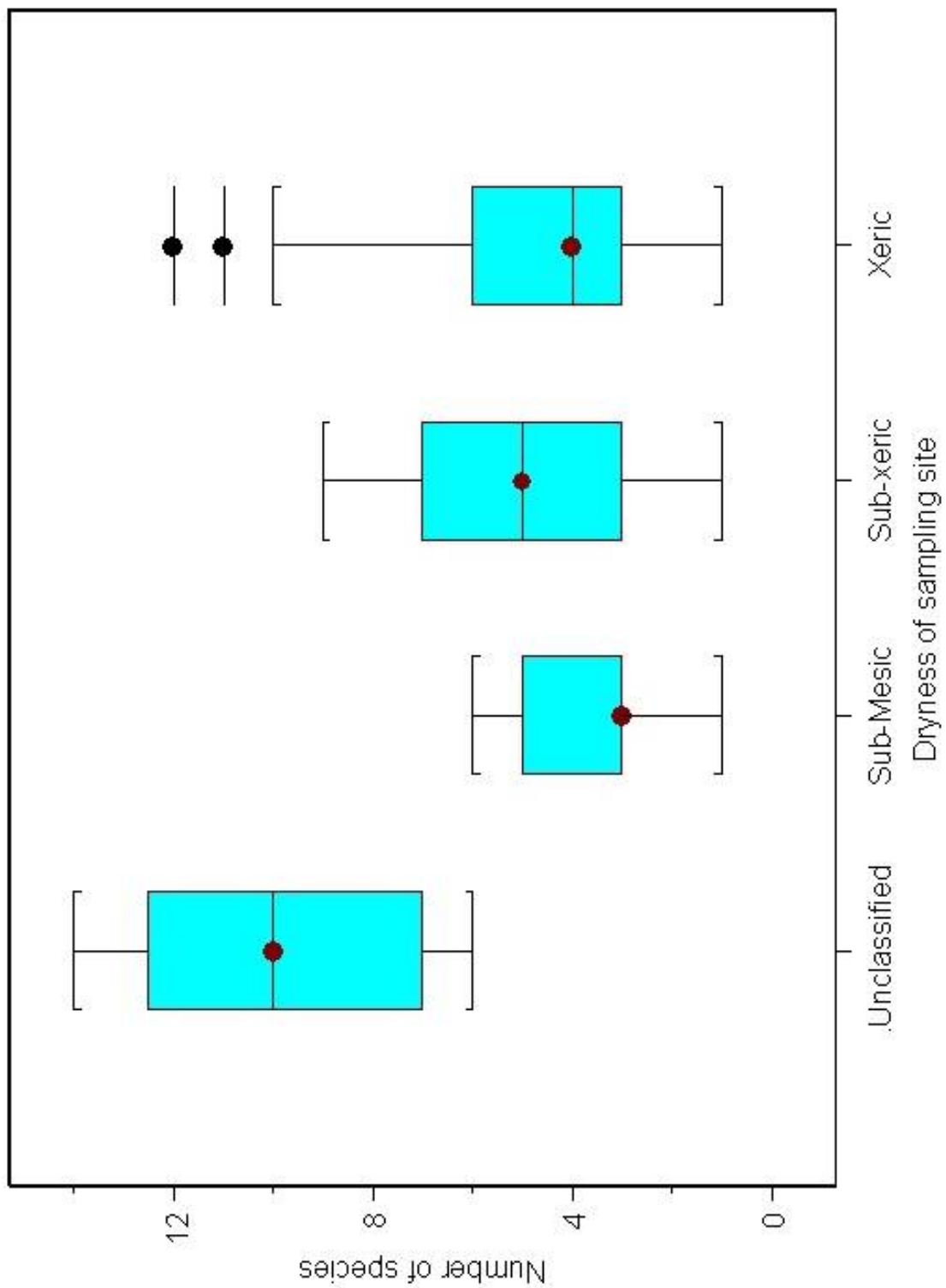


Figure 7.9: Boxplot of the mean number of herbaceous species (± 1 s.e.) germinated from soil samples grouped by moisture availability.



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CHAPTER VIII: Conclusion

FIRE IN THE SOUTHERN APPALACHIANS

Fundamental contributions

Although knowledge of fire's importance to xeric southern Appalachian forests has increased in the last few decades, this dissertation revealed that there is much still to learn. Chapter II showed that in this region, fire acts as a homogenizing force with similarity between plots increasing with fire severity; though different landscapes remain distinct within ordination space. Over time, plots became less tightly clustered within ordination space as species recolonize areas and species sorting reemerges, presumably as a result of underlying environmental gradients. As illustrated by the seed-bank study (Chapter VII), most of the species found within these xeric communities prior to fire do not depend upon the seed-bank for post-disturbance colonization and depend either upon surviving the fire or post-fire seed rain to reestablish themselves. The most common species in the seed-bank were not present in the extant vegetation and were herbaceous and ruderal species adapted for rapid post-disturbance colonization.

This work also adds to the Ryan's (2002) predictions of post-fire recovery patterns where disseminule-based modes of recovery dominate at high fire intensities and vegetative-based modes dominate at low fire intensities. I have shown here that while disseminule-

based modes may dominate at high intensities, they do not initially lead to less predictable vegetation composition as suggested by potentially highly variable seed inputs. Instead, areas that experienced the highest severity fires were the most predictable in composition as these fires had the strongest effect in limiting the species able to survive or recolonize in the extreme post-fire habitat conditions.

Questions remaining

Due to the manner in which data were collected, it was impossible to identify which stems and species were present within a plot as resprouts versus new seedlings. Collection of this data in conjunction with data on fire severity along each axis of Ryan's Fire Severity Matrix would enable a direct test of the matrix's predictions of dispersal-mode dominance and greatly further our understanding of post-fire vegetation dynamics in the southern Appalachians. It would also assist managers in their development of fire prescriptions to achieve management goals like the restoration of Table Mountain Pine or decreased maple dominance.

In this work, changes in plot clustering over time were determined from plot data collected over the course of 3 years. However, these were not the same plots sampled repeatedly. Further work with repeated samples would enable an analysis not only of the general trajectory of plots over time, but also of the trajectory of individual plots within different habitats following different fire severities. Lack of such data remains a potential weakness in the conclusions presented here.

PAULOWNIA INVASION

Fundamental contributions

Although *Paulownia* has been present in the United States since 1844, until recently its habitat has been restricted to areas heavily impacted by human land use practices and occasional individuals present after large scale natural disturbances. The recent post-fire invasion into xeric forests marks a novel expansion for *Paulownia* and may indicate a shift towards invasiveness in these community types. A number of studies have looked at specific portions of *Paulownia*'s life history, but till now none have systematically covered *Paulownia*'s dominant life-history transitions or analyzed this novel post-fire invasion.

In measuring *Paulownia* seed dispersal (Chapter III), this study found that *Paulownia* seeds disperse orders of magnitude further than the scale at which other dispersal studies have been conducted. *Paulownia* seeds and seedlings were encountered over 3.5km from the nearest mature individual. Further, the trend in number of plots invaded as a function of NND suggests that seeds may disperse as far as 10km. This suggests that preventing *Paulownia* invasion after fire will depend upon a landscape-scale control program to limit the influx of seeds.

Experiments of *Paulownia* germination rates under varying conditions (Chapter IV) found that under appropriate conditions, seed germination can be quite high. However, germination is significantly inhibited by the presence of litter and almost nonexistent when seeds are buried; underlining *Paulownia*'s dependence upon bare soil and high light levels for significant germination to occur. Although these conditions are abundant following high severity fires, seeds experience very high mortality rates when exposed to the heat of burning suggesting that invasion is dependent upon post-fire seed rain rather than a surviving seed-bank.

Models of *Paulownia*'s initial habitat requirements (Chapter V) and its persistence over time (Chapter VI) demonstrate that the most important factor determining initial invasion success is the availability of high light environments. Although *Paulownia* invasion is initially widespread and concentrated in areas that experienced high severity fire and are consequently very open, persistence occurs in a limited subset of the landscape; primarily where vegetation cover remains sparse due to exposure and water-stress. Within landscapes like Linville Gorge where these habitats are common, *Paulownia* is likely to persist in the absence of control efforts.

Perhaps the most important result from this study, particularly for land managers, is the development of a habitat model for *Paulownia* which identifies the key variables driving the pattern of *Paulownia* invasion. As this model can be applied to novel landscapes via GIS in the absence of plot data, it is a powerful tool for managers who seek to predict where *Paulownia* will invade following fire and focus their control efforts on those areas which are most likely to witness *Paulownia* persistence to maturity. Unfortunately for managers, *Paulownia* persistence is most likely in the least accessible and steepest portions of the landscape. Fortunately, no evidence of impact on native species was found by this study, but if *Paulownia* abundance and cover continues to increase in these habitats, there is no guarantee that this will continue to be the case.

Questions remaining

Although seeds and seedlings were observed at over 3.5 km from the nearest mature individual, *Paulownia* seeds were very sparse in the seed-bank and no seeds were found within the soil at greater distances. Seedlings were abundant in plots at these same distances,

but no more remote samples were taken. A study of the seed-rain at these distances would clarify the number of seeds which are dispersing this far and help assess the utility of seed-bank studies in the characterization of *Paulownia*'s dispersal capabilities.

Another question worthy of further study is *Paulownia*'s germination rate in the field. Although greenhouse experiments found high germination rates under ideal conditions, two previous iterations of these experiments in the field found very low germination rates. Clarifying the germination rate in the field will help to identify the magnitude of seed-rain associated with a given seedling stem density and may isolate factors which limit germination success.

Experimental and field survey results also differed in the importance of high light levels. Where field studies found seedlings largely restricted to areas with less than 44% remaining vegetation cover over 1m in height, the greenhouse experiments found that germination was slightly but significantly higher under 50% shade than in full sun. Although other factors varied between the field and greenhouse measurements and between sun and shade treatments in the greenhouse (most notably variance in soil moisture) which could explain this difference, this remains an uncertainty in the reported results. This uncertainty could be addressed through: a) future studies which controlled for factors like soil moisture that co-varied with the light treatment and b) studies of the actual cover experienced at seedling-height in the field coupled with experiments utilizing multiple shading treatments above and below that utilized here.

The models developed here also need to be applied to novel landscapes and fires to test whether they accurately predict the pattern of invasion elsewhere. This will assess the utility of these models to the larger region and their general applicability to managers.

Studies of older fires or the continued study of those in this dissertation would enable the assessment of *Paulownia*'s persistence over longer time periods and determine whether its range will continue to restrict over time to the point of extirpation.

Finally, although no impact on native species was documented in this study, due to its design it did not sample any areas containing the rare or endangered species found in these xeric communities on cliff margins and rock outcrops. Further work is needed to determine whether these species are indeed un-impacted by *Paulownia*. The preferential persistence of *Paulownia* in the very areas which are habitat to these rare species is cause for concern, particularly if *Paulownia* is destined to persist in the absence of management efforts.

APPENDIX 1:
Species germinated from soil samples and species found within vegetation plots

Species germinated from soil samples and those found within the xeric vegetation community plots shown in Figure 7.1. “# Plot Occur” is the number of plots that the species occurred in and “# in Sample” is the number of individuals germinated from soil samples. Species are organized by growth form and listed in descending frequency of occurrence in the vegetation plots.

Trees			Shrubs			Forbs/herbs		
Species	# Plot Occur	# in Sample	Species	# Plot Occur	# in Sample	Species	# Plot Occur	# in Sample
Acer rubrum	31	1	Calycanthus floridus var. glaucus	1	0	Adiantum pedatum	3	0
Oxydendrum arboreum	31	0	Hypericum hypericoides ssp. Multicaule	1	0	Ageratina altissima	2	0
Nyssa sylvatica	29	1	Vaccinium corymbosum	1	0	Agrimonia rostellata	1	0
Sassafras albidum	23	0	Hydrangea radiata	2	0	Anemone quinquefolia var. quinquefolia	1	0
Quercus coccinea var. coccinea	23	0	Euonymus americana	3	0	Antennaria plantaginifolia	3	0
Tsuga canadensis	24	0	Rhododendron calendulaceum	3	0	Arisaema triphyllum	1	0
Pinus strobus	29	0	Rubus canadensis	3	0	Arisaema triphyllum ssp. triphyllum	3	0
Amelanchier laevis	22	0	Calycanthus floridus	4	0	Aristolochia serpentaria	1	0
Kalmia latifolia	17	0	Gaylussacia baccata	4	0	Asplenium platyneuron	1	0
Pinus rigida	22	0	Lyonia ligustrina	4	0	Athyrium filixfemina ssp. asplenioides	2	0
Pinus virginiana	24	0	Gaultheria procumbens	5	0	Aureolaria flava	3	0
Castanea dentata	13	0	Viburnum acerifolium	5	0	Baptisia tinctoria	2	0
Quercus rubra	13	0	Pyrularia pubera	11	0	Botrychium virginianum	1	0
Quercus velutina	22	1	Vaccinium hirsutum	13	0	Campanulastrum americanum	1	0
Acer pensylvanicum	11	0	Epigaea repens	15	0	Chamaecrista nictitans ssp. nictitans	1	0
Ilex montana	12	0	Chimaphila maculata	18	0	Chrysopsis mariana	1	0
Magnolia fraseri	11	0	Gaylussacia ursina	18	0	Coreopsis major	8	0
Carya glabra	16	0	Vaccinium stamineum	21	0	Cynoglossum virginianum var. virginianum	1	0
Pinus pungens	8	0	Vaccinium pallidum	26	0	Dennstaedtia punctilobula	1	0
Cornus florida	16	0	Ericaceae sp.	0	10	Desmodium glutinosum	1	0
Robinia pseudoacacia	8	2	Hydrangea arborescens	0	1	Desmodium nudiflorum	9	0
Ilex opaca var. opaca	16	0	Hypericum stragulum	0	1	Desmodium rotundifolium	1	0
Liriodendron tulipifera	10	1	Rosaceae sp.	0	3	Dryopteris marginalis	1	0

Appendix 1: Continued

Trees			Shrubs			Forbs/herbs		
Species	# Plot Occur	# in Sample	Species	# Plot Occur	# in Sample	Species	# Plot Occur	# in Sample
Carya alba	14	0	Rosaceae sp1	0	1	Erechtites hieraciifolia var. hieraciifolia	1	16
Quercus alba	14	0	Rubus allegheniensis var. allegheniensis	0	13	Eupatorium album	3	0
Fagus grandifolia	8	0	Rubus sp.	0	12	Eupatorium altissimum	4	0
Hamamelis virginiana	3	0	Viburnum dentatum	0	1	Eupatorium purpureum	1	0
Rhododendron maximum	1	0				Eurybia divaricata	5	0
Halesia tetraptera var. monticola	5	0				Eurybia macrophylla	4	0
Quercus marilandica	6	0				Eurybia surculosa	7	0
Betula lenta	3	0				Galax urceolata	15	0
Pinus echinata	5	0				Galearis spectabilis	1	0
Prunus serotina	1	0				Galium circaezans	2	0
Stewartia ovata	4	0				Galium latifolium	1	0
Diospyros virginiana	3	0				Gamochaeta purpurea	1	0
Fraxinus americana	2	0				Goodyera pubescens	5	0
Quercus stellata	2	0				Hepatica nobilis var. acuta	1	0
Tilia americana var. heterophylla	1	0				Heuchera americana	1	0
Acer saccharum	1	0				Hexastylis arifolia var. ruthii	1	0
Carpinus caroliniana	1	0				Hieracium paniculatum	1	0
Carya ovalis	1	0				Hieracium venosum	7	0
Carya ovata	1	0				Houstonia purpurea var. purpurea	2	0
Cercis canadensis var. canadensis	1	0				Houstonia serpyllifolia	1	0
Gleditsia triacanthos	1	0				Hypoxis hirsuta	3	0
Liquidambar styraciflua	1	0				Iris cristata	1	0
Morus rubra var. rubra	1	0				Lespedeza hirta	2	0
Ostrya virginiana var. virginiana	1	0				Lespedeza repens	1	0
Quercus falcata	1	0				Lysimachia quadrifolia	8	3
Rhus copallinum	1	6				Maianthemum racemosum ssp. racemosum	8	0
Ulmus americana	1	0				Melampyrum lineare	1	0
Ulmus rubra	1	0				Melanthium parviflorum	1	0
Vaccinium arboreum	1	0				Mitchella repens	7	0
Aralia spinosa	0	2				Monotropa uniflora	2	0
Betula alleghaniensis	0	6				Osmunda claytoniana	2	0
Betula sp	0	3				Packera anonyma	1	0

Appendix 1: Continued

Trees			Forbs/herbs		
Species	# Plot Occur	# in Sample	Species	# Plot Occur	# in Sample
Paulownia tomentosa	0	142	Pellaea atropurpurea	1	0
Rhus glabra	0	1	Phegopteris hexagonoptera	1	0
Salix nigra	0	1	Pityopsis graminifolia var. latifolia	2	0
Ulmus alata	0	4	Polygala paucifolia	1	0
			Polypodium appalachianum	1	0
			Polystichum acrostichoides var. acrostichoides	8	0
			Potentilla canadensis	6	0
			Prenanthes trifoliolata	5	0
			Pteridium aquilinum	12	0
			Pteridium aquilinum var. latiusculum	1	0
			Pycnanthemum montanum	1	0
			Pyrrhopappus carolinianus	1	0
			Sanicula canadensis var. canadensis	1	0
			Sericocarpus linifolius	1	0
			Solidago odora var. odora	5	0
			Stellaria pubera	1	0
			Stylosanthes biflora	1	0
			Symphyotrichum cordifolium	3	0
			Symphyotrichum dumosum var. dumosum	2	0
			Symphyotrichum lowrieianum	1	0
			Symphyotrichum undulatum	5	0
			Taenidia integerrima	1	0
			Thalictrum thalictroides	7	0
			Thaspium barbinode	1	0
			Thelypteris noveboracensis	3	0
			Tiarella cordifolia	1	0
			Trillium undulatum	3	0
			Uvularia perfoliata	2	0
			Uvularia puberula	8	0
			Uvularia sessilifolia	5	0
			Viola blanda	2	0
			Viola canadensis	1	0
			Viola cucullata	1	0
			Viola hastata	5	0
			Viola palmata	4	0
			Viola tripartita	2	0
			Acalypha virginica	0	13
			Ageratina aromatica	0	18
			Asteraceae sp. 1	0	2
			Asteraceae sp. 2	0	3

Appendix 1: Continued

Forbs/herbs			Graminoides			Vines		
Species	# Plot Occur	# in Sample	Species	# Plot Occur	# in Sample	Species	# Plot Occur	# in Sample
Asteraceae sp. 3	0	2	Dichanthelium commutatum	14	51	Smilax glauca	30	0
Asteraceae sp. 4	0	1	Schizachyrium scoparium	13	7	Smilax rotundifolia	30	0
Asteraceae sp. 5	0	2	Sorghastrum nutans	4	0	Dioscorea quaternata	5	0
Asteraceae sp. 6	0	1	Carex albicans var. emmonsii	3	0	Vitis aestivalis	5	0
Asteraceae sp. 7	0	1	Brachyelytrum erectum	2	0	Toxicodendron radicans	3	0
Asteraceae sp. 8	0	1	Dichanthelium boscii	2	4	Clitoria mariana	2	0
Asteraceae sp. 9	0	1	Danthonia sericea	1	0	Parthenocissus quinquefolia	2	0
Asteraceae sp. 10	0	1	Danthonia spicata	1	0	Amphicarpaea bracteata	1	0
Cardamine hirsuta	0	39	Dichanthelium dichotomum	1	25	Bignonia capreolata	1	0
Cardamine pensylvanica	0	1	Andropogon sp.	0	1	Passiflora lutea	1	0
Chamaesyce maculata	0	12	Andropogon virginicus	0	2	Vitis rotundifolia	1	1
Chamaesyce sp.	0	1	Carex sp.	0	11	Vitis vulpina	1	0
Conyza canadensis	0	3	Cyperus pseudovegetus	0	6			
Eupatorium serotinum	0	2	Cyperus sp. 1	0	6			
Eupatorium sp.	0	1	Cyperus sp. 2	0	1			
Euphorbia sub gen Chamaesyce	0	1	Dichanthelium sp.	0	56			
Fabaceae sp. herb	0	1	Dichanthelium villosissimum var. villosissimum	0	2			
Helianthus strumosus	0	2	Digitaria sanguinalis	0	1			
Hypericum punctatum	0	2	Digitaria sp.	0	18			
Hypericum stragulum	0	1	Eleusine indica	0	1			
Lamiaceae sp.	0	3	Kyllinga pumila	0	1			
Lechea racemulosa	0	1	Muhlenbergia capillaris	0	1			
Lespedeza virginica	0	1	Panicum gattingeri	0	1			
Lobelia inflata	0	2	Poa annua	0	1			
Lobelia sp.	0	6	Poaceae sp.	0	9			
Mazus pumilus	0	6						
Oenothera biennis	0	3						
Oxalis grandis	0	58						
Oxalis sp.	0	6						
Potentilla canadensis	0	3						
Pseudognaphalium obtusifolium	0	1						

Appendix 1: Continued

Forbs/herbs		
Species	# Plot Occur	# in Sample
Solidago bicolor	0	1
Solidago erecta	0	2
Solidago sp. 1	0	2
Solidago sp. 2	0	3
Sonchus asper	0	1
Stellaria media	0	7
Unidentifiable herb	0	2
Valerianella sp.	0	1
Viola sp.	0	2