Predicting the invasion and survival of the exotic species *Paulownia tomentosa* following burning in pine and oak-pine forests

Final Report for the Joint Fire Science Program

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Summary

The last two decades have seen an increasing awareness of the importance of fire in the xeric forest communities of the southern Appalachian Mountains, an increase in its use as a management tool, and an increase in the number of studies on the role and impact of fire in these communities. In the last ten years, managers have also witnessed the invasion of *Paulownia tomentosa* (Princess tree, hereafter *Paulownia*) after some of these fires. As natural, intentional, and accidental fires are increasingly part of the landscape, it is important to determine the landscape, watershed and stand variables that favor the spread of this exotic into natural areas following fire, determine whether it is impacting native communities or species, and incorporate this knowledge into management practices and our understanding of regional fire dynamics.

The following Joint Fire Science Project has been conducted by Dane Kuppinger whose dissertation encompasses the project and has been partially funded by JFSP. Consequently, this report includes questions and analyses beyond the scope of the JFS project. Deliverables beyond the JFS project are given in the Deliverables section, his projected completion date is under the Timeline section, and additional funding sources are given in the Project description.

Utilizing plot data from five fires, this study analyzes the effects of fire severity, season of burn, environmental conditions, and the relative location of mature *Paulownia* trees on *Paulownia* seedling abundance and vigor within sampled plots to determine under what conditions *Paulownia* seedlings are likely to survive to maturity. Fire and environmental variables and the presence and abundance of *Paulownia* are analyzed to determine what effects fire and invasion have had on native species cover and diversity. Focusing on the Linville Gorge fire, watershed scale spatial data are utilized to ask what characteristics of topography, community type, and fire severity promote *Paulownia* invasion. Making use of pre and post-fire plot data available for Linville Gorge, we analyzed changes in diversity and composition and whether these are impacted by *Paulownia* presence or abundance. Three experiments are utilized to test *Paulownia* seed viability over time, the conditions under which *Paulownia* seeds survive fire, and *Paulownia*’s germination rate under different ground cover, light, and burial conditions. A seed bank study of dry forest communities in Great Smoky Mountains National Park (GRSM) documents the diversity and distribution of species encountered in the seed bank and the distribution of *Paulownia* seeds as a function of distance from mature individuals. Finally, information from the preceding analyses is synthesized to predict patterns of *Paulownia* invasion, exotic species invasions generally, and to create tools for land managers.

Deliverables

Proposed	***Accomplished/Status***
Models predicting *Paulownia* invasion in response to variation in landscape, temporal, topographic, and stand conditions	Several models have been developed predicting *Paulownia* invasion in response to landscape, topographic and stand variables from seed distribution information and field survey data. These models are presented within this report. Modeling temporal changes in invasion is underway are will be completed by September 2006.
Experiments testing: (1) Seed viability over time; (2) The impact of stand level variables on germination; (3) The conditions under which *Paulownia* seeds survive fire.	Two of the three experiments laid out in the grant have been attempted twice with inconclusive results. These experiments will be rerun during the summer of 2006 and the results will be complete by August 2006. Results from the 3rd experiment (seed viability over time) are presented in this report.
GIS landscape-scale models of susceptibility to invasion following burning across the study area.	GIS landscape-scale models of susceptibility to invasion are in development will be complete by November 2006.
Presentation laying out the study's results	Presentation of the study's results will be scheduled for the Fall of 2006

Additional Deliverables (not in proposal)

Type	***Summary/Status***
Presentations on subject	Poster presentations have been given on this study and related thesis investigations at: Association of Southeastern Biologists annual conference, Washington D.C., April 2003. Joint Fire Science Program Primary Investigator workshop, Phoenix, AZ., April 6-8th, 2004. Oral presentation have been given on this study and related thesis investigations at: Association of Southeastern Biologists annual conference,

	Memphis, TN., April 2004. Western North Carolina Alliance conference: The Role of Fire in Southern Appalachian Mountains, Asheville, NC., September 17th, 2005. Association of Southeastern Biologists annual conference, Gatlinburg, TN., March 30th, 2006. Southeast Exotic Pest Plant Council annual conference, Raleigh, NC., May 25th, 2006 A presentation on invasion patterns at Linville Gorge will be given at the Ecological Society of America's annual conference in August, 2006.
Publications	Interactions between pre- and post-fire community composition, topography, fire severity, and exotic invasion at Linville Gorge, NC. In Preparation. The effect of fire characteristics, light, surface cover, and burial depth on the germination of *Paulownia tomentosa*. In Preparation. Seed-bank components and distribution in xeric forests of the western Great Smoky Mountains National Park. In Preparation. From theory to practice: Creating *Paulownia tomentosa* management tools for land managers and conservationists. In Preparation.
Seed bank study	A seed bank study was conducted in the western portion of Great Smoky Mountains National Park in xeric forest communities to check for the presence of *Paulownia* seeds, how far they were dispersed from mature trees outside the park, and whether their distribution was affected by elevation or direction from sample to mature tree (a stand in for wind effects). All seedlings germinated from the sample were identified to species were possible giving a "complete" species list of sampled sites.
Paulownia and fire impacts on native species and communities	At Linville Gorge, resampling vegetation plots put in place before the fire enabled analyses of the impacts of fire and *Paulownia* invasion on the recovery of native species and communities. Analysis of these data will be completed by November 2006.

Timeline for completion of remaining deliverables

Temporal model of *Paulownia* invasion will be competed by September 2006.
Spatial analyses of *Paulownia* invasion rates incorporating proximity to mature trees, fire intensity, and spatial environmental variables (site dryness, community type, topographic position, slope, and aspect) will be complete by September 2006.
Impacts of fire and *Paulownia* invasion on native species and community recovery patterns will be completed by November 2006.
GIS landscape-scale model of susceptibility to invasion incorporating seed dispersal studies and predictive models derived from field survey data will be complete by November 2006.
Seminar presentation of final results will be scheduled for November 2006.
Dissertation of primary researcher Dane Kuppinger (encompassing the JFSP study) will be competed by April 2007.

Introduction

Purpose and need

Forests of the southeastern United States have endured over 60 years of fire suppression (Langdon and Johnson 1994) and although southern Appalachian xeric forest communities have not received as much attention as other fire prone communities, fire played a significant role prior to widespread suppression. Past work by Harmon (1982) and Harrod (1998) has indicated that these communities experienced regular, low intensity fires which maintained open woodlands with higher intensity fires, at approximately 100 year intervals, giving rise to the majority of pine regeneration. Managers throughout the region are currently restoring this natural process by carefully reintroducing historic fire regimes in xeric forest communities. Prescribed fire has offered land managers an important tool for restoring disturbance regimes critical to maintain many biological communities. Within the southeastern Unites States, prescribed fire has been recommended to perpetuate stands of *Pinus pungens* (table mountain pine) and *Pinus rigida* (pitch pine; Waldrop and Brose 1999, Welch et al. 2000), regenerate oak species on productive upland sites (Barnes and Van Lear 1998, Brose et al. 1999) and restore habitat for threatened and endangered species (Sparks et al. 1999, Rock 2000, Stout 2001). However, the reintroduction of historic fire regimes through prescribed burning may create conditions that allow the invasion of exotic plant species that formerly were not part of the biotic community.

Over the past several years, the use of prescribed fire has greatly increased on Forest Service and National Park Service lands. In Great Smoky Mountains National Park, the prescribed burning program has grown from a 4 ha fuel reduction burn in 1996 to approximately 1000 ha burned in 2005. The use of prescribed fire on National Forest land has been even greater. On the Cherokee National Forest in Tennessee, prescribed fire was used to treat approximately 8,500 ha in 2000. In North Carolina, prescribed fire was used to treat over 10,500 ha on the Nantahalla, Pisgah, Croatan, and Uwharrie National Forests in 2000. While these burns have been very successful in reducing fuel loads, restoring communities, and creating wildlife habitat, understanding and minimizing the detrimental effects of prescribed fire becomes critical as more hectares of forest are burned each year. Of these detrimental effects, invasion by exotic species is among the most alarming since it directly undermines the positive ecological effects produced by burning.

In Great Smoky Mountains National Park, we have observed heavy invasion of the exotic species *Paulownia* following prescribed burning in the western portion of the Park near Chilhowee Lake (Fig. 1). Following a prescribed burn in the Tabcat Creek watershed, over 1200 *Paulownia* seedlings were hand-pulled by park staff as part of an on-going control effort. *Paulownia* trees are found in great numbers growing on rock outcrops along the I-40 corridor between Knoxville, Tennessee and Asheville, North Carolina. The species is also very common along Highway 129 in southeast Tennessee and southwest North Carolina. Both of these corridors run between Park Service and Forest Service holdings (Fig. 1) and the *Paulownia* trees they contain serve as potential seed sources for invasion following prescribed burning by both agencies. If *Paulownia* established within the interior of forests following burning, these new populations could serve as “stepping stones” to further advance the species inward to new areas.

Although *Paulownia* has been a common invader along roadways and other areas significantly impacted by human activity for years (first documented in the GRSM in 1975 in association with major road cuts; Baron 1975), and occasionally a few individuals had been seen in native plant communities following hurricanes (Williams 1993), these new invasions following fire marked the first time that the species was observed in significant numbers following disturbance in plant communities dominated by native species. To date *Paulownia* is the most common exotic species observed with any regularity in these communities.

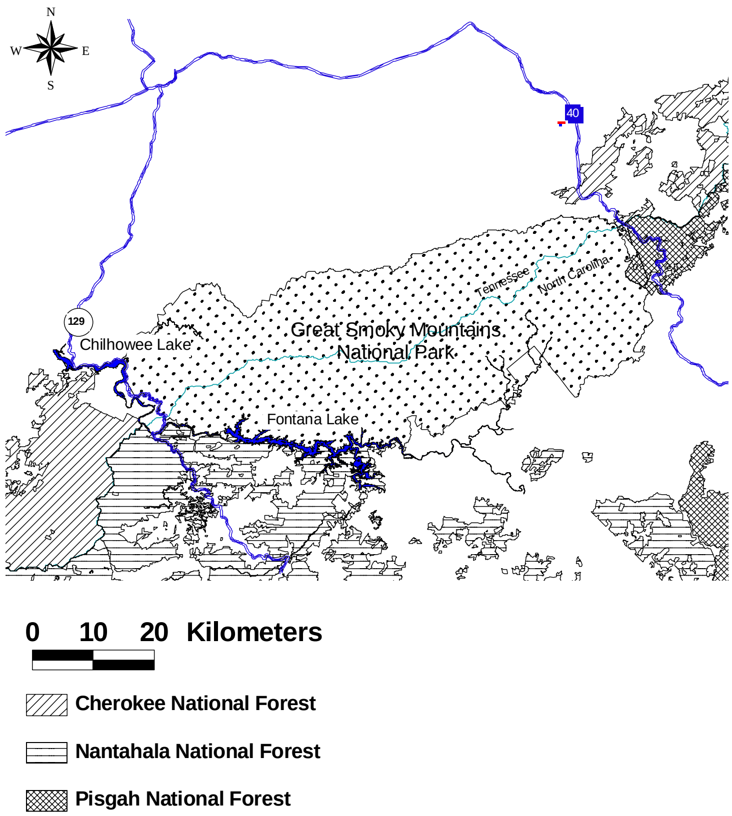


Figure 1: Cherokee National Forest, Pisgah National Forest, and Nantahala National Forest with the I-40 and 129 corridors.

Project description

Invasion of exotics is often facilitated by disturbance because they generally increase the availability of resources, including space, and/or decrease competition. However, disturbances vary considerably in severity and spatial characteristics and therefore in their effect on invasion patterns. In addition to disturbance, species availability (both native and exotic) and general habitat characteristics are important in understanding patterns of invasion (Hobbs 1992, With 2001). Species availability, habitat, and disturbance require studies at different spatial scales: species availability requires analysis at a regional to landscape scale; habitat characteristics require analysis along gradients at a watershed scale; and variation in disturbance severity requires analysis at the local to community scale. This research examines these three scales to document the role of fire in the invasion of *Paulownia tomentosa* in southern

Appalachian xeric forest communities and assesses the interactions between *Paulownia* and native plants in a community's response to fire. There is a strong applied rationale for this work: land managers seek to continue to reintroduce fire as a natural process in the southern Appalachians, but do not want to simultaneously increase the distribution and establishment of exotic species, nor affect the abundance of native fire dependent species because of this exotic invasion.

Funding from the Joint Fire Science Program was matched by inkind funding from the University of North Carolina at Chapel Hill, the Mrs. W.C. Coker Fellowship and the Alma Holland Beers Scholarship, enabling an expansion of the project to explore additional facets of this disturbance-invasion dynamic. The cumulative research project has been conducted by Dane Kuppinger at the University of North Carolina at Chapel Hill who has conducted this research as part of his dissertation (accepted dissertation proposal is attached; Appendix B). Upon its completion, a copy of his dissertation will also be submitted to the Joint Fire Science Program (see Timeline).

Objectives

In this study, we address two basic objectives concerning the invasion and persistence of *Paulownia* in burned forests. We examine each objective through a combination of field studies and experiments. Experiments will be conducted to examine the mechanisms controlling *Paulownia* invasion and establishment and field studies were used to examine how these mechanisms interact across a forested landscape.

Objective #1: What landscape, watershed, and stand conditions influence the establishment of *Paulownia* seedlings following burning?

a. *Landscape level and season-dependent variables*: We examined the relationship between *Paulownia* establishment and distance of burn areas from a known seed source. We also examined the influence of season of burn on *Paulownia* invasion. From these examinations we address the following questions:
    1. Does the overall density of *Paulownia* seedlings decrease the further a burn is located from a known seed source? Is there a discernable cut-off distance for the invasion of seeds into a burned area?
    2. Since *Paulownia* seeds are released in the fall, do early season burns allow sufficient opportunity for competing vegetation to establish and reduce the density of *Paulownia* seedlings the following spring?
    3. Does *Paulownia* seed viability change with time since dispersal in controlled experiments?

b. *Watershed level variables*: We examined the relationship between *Paulownia* establishment and the following watershed level variables: (1) aspect, (2) slope position, (3) terrain shape (McNab 1989), and (4) percent slope. From this examination we address the following questions:
    1. Does *Paulownia* seedling density increase with increasing site dryness?
    2. What is the relationship between aspect, slope position, terrain shape, slope, and site dryness and fire intensity?

3. How does intensity of burn influence *Paulownia* germination and survivorship in controlled experiments?

c. *Stand level variables*: We examined the relationship between *Paulownia* establishment and the following variables: (1) litter depth, (2) percent cover of shrub-layer species, and (3) percent canopy cover. From this examination we address the following questions:
   1. Following fire, what is the relationship between *Paulownia* seedling density and the depth of remaining litter/duff?
   2. What is the relationship between shrub-layer cover and *Paulownia* seedling density?
   3. What is the relationship between overstory cover and *Paulownia* seedling density?
   4. In experiments, how does the germination and survivorship of *Paulownia* vary with changes in litter depth and shading?

Objective #2: How does the survivorship of *Paulownia* vary with time since burning?

a. *At the stand level*: We examined the relationship between *Paulownia* survival and increased shading by addressing the following question:
   1. Does increased shading and competition levels several years after burning result in decreased survivorship of *Paulownia* individuals?
b. At the watershed level: We examined the relationship between *Paulownia* survival and topographic position by addressing the following question:
   1. Within burned areas, how does survivorship through time vary with topographic position?

Methods

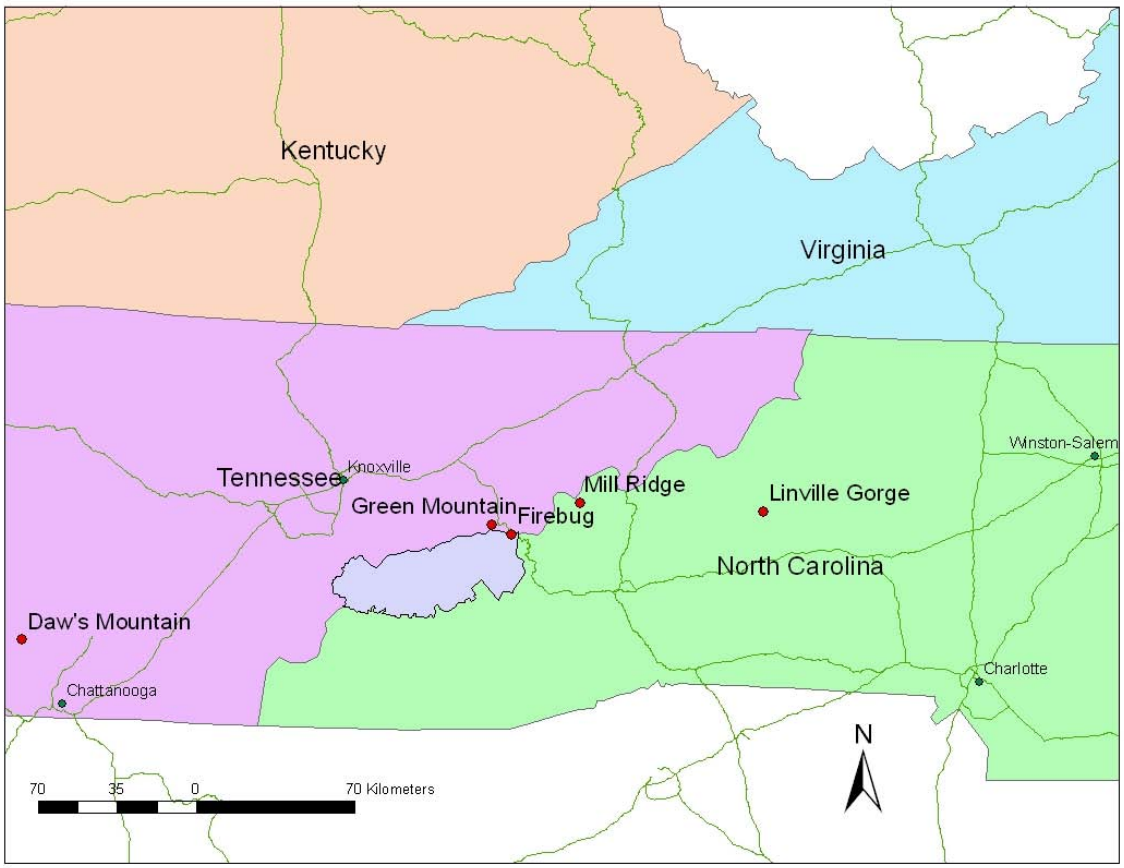
Site selection

The fires sampled in this project (Table 1, Figure 2) were chosen after a thorough survey of recent fires (burned 1-2 years prior to the beginning of the study) in the Southern Appalachian mountains on National Park (GRSM) and Forest Service (Pisgah, Cherokee, and Nantahala National Forests) properties. The majority of the work was conducted outside of GRSM because fires within the park boundary had been targeted for exotic (including *Paulownia*) control efforts. All fires 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.

Table 1: Location, number of plots, and land ownership status of each sampled fire.

Fire	# of Plots	Location/Ownership
Linville	75	Linville Gorge, Pisgah NF
Mill Ridge	13	Mill Ridge, S of Hot Springs, Pisgah NF
Green Mtn.	63	Cherokee NF, along the Foothills Parkway
Firebug	14	Cherokee NF, between I40 and GRSM, just over TN/NC line
Daw's Mtn.	18	Sequatchie Valley, Cumberland Plateau, private land north of Dunlap, TN

Figure 2: Locations of the sampled fires



Vegetation survey methodology

10x10m plots were laid down every 50 m along transects run across the slope. Transect length was determined by topography. Transect positions were chosen to maximize the range of fire intensities and landscape positions sampled within a burn. Geo-coordinates were recorded for each plot. At the Linville Gorge and Green Mountain fires, the location of mature *Paulownia* trees located in the vicinity of the fire was also recorded. All plots were surveyed according to the North Carolina Vegetation Survey (NCVS) protocol described in Peet et al. (1998) with the following variations and additions:

- Plots were subdivided into 5x5m subplots rather than the nested subplots standard to the CVS design. All ground, herb, shrub, and tree coverages and stem dbh's were recorded at the sub-plot level.
- The exact dbh of all stems >1cm was recorded. The dbh for stems that were not clearly dead prior to the fire but were now dead was recorded along with a species id and for data analysis purposes were assumed to be fire killed.
- Species cover at the shrub level was estimated for all shrubs that appeared to have died as a result of the fire.
- Estimates were made of the pre-fire cover by strata.
- A spherical densiometer was used to record canopy cover from plot center.
- Ground cover was estimated for: litter, rock (boulder and cobble), hummus, organic soil, and mineral soil. Litter depth, min. and max., was also measured along with a total hummus cover measurement including the cover of exposed hummus and that which was covered by litter. Measurements were taken at the plot and sun-plot level.
- The number and height of all *Paulownia* stems within each sub-plot was recorded.
- Fire intensity within each plot was visually estimated (1-5 scale) from percent dieback at each cover level (shrub, understory, etc), scorch height, and resprouting frequency.

Plot Data Analysis

Watershed and stand level variables were tested for significance through the use of logistic and negative binomial regressions against the presence/absence and abundance (respectively) of *Paulownia* (Tables 3, 4). These variables were also used in classification trees (Figures 3, 4) to test for congruence between model types (Table 5), to address the high levels of variance left unexplained by the regression models, and as a step towards landscape and watershed scale maps predicting areas potentially vulnerable to *Paulownia* invasion.

The significance of "Site" within the regressions when utilizing the full dataset suggested that there was a difference in invasion rates between sites. The classification tree utilizing the full data set showed that 3 sites (Linville Gorge, Daw's Mountain, and FireBug) experienced much higher invasion rates than the remaining sites. As there was some concern that this was due to varying seed availability between fires, the classification trees were rerun with only the data from these fires (Figure 4).

Experiments

<u>Experiment #1</u>

Experiment #1, a germination study, was conducted to determine germination rates over the course of a year under different storage conditions. Seeds from 4 populations were stored in 3 different ways; dry at room temperature, cold-stratified for a month prior to sowing, and buried in mesh bags under leaf litter from collection till germination. Every month for a year (January – November), 80 seeds from each population and each storage type were placed on soil trays and germinated in the greenhouse. The field stored seeds from population #3 were dug-up by an animal and not included in the study. Seeds were watered daily and germination rates for each seed batch was tracked bi-weekly for 2 months. Final germination rates for each month were compared between storage treatments (average of all populations and for individual populations) and within individual storage treatments comparing populations (Table 6, 7 Figures 5, 6, 7).

Experiments #2 and #3

Experiments #2 (Fire survival) and #3 (Effect of surface cover, light, and burial depth) have been run twice; in 2004 in the Pisgah National Forest just east of Linville Gorge (an attempt at a "natural" experiment) and again in 2005 at the Mason Farm research field at the North Carolina Botanical Garden in Chapel Hill. Both of these attempts met with very limited success (1 seedling at Linville and ~10 at Mason Farm out of ≥9,600 seeds) despite high observed germination rates (70-80%) from the same set of seeds in the germination study (Table 7). Only two other studies have tested field germination rates and they also reported very low field germination (~1% and 8% respectively) (Hyatt 2000, Longbrake 2001), but their germination rates were still orders of magnitude higher than we observed in our experiments. As mature *Paulownia* are located at the Linville Gorge study site and near the Mason Farm site, and the Mason Farm trial received very high levels of care, this was unexpected. Consequently these experiments are being rerun this summer within the greenhouse at UNC-Chapel Hill. Each "block" will consist of one quarter-flat and the "soil" used will be Promix. Although these conditions deviate significantly from "natural" conditions, the failure of previous summers' experiments has lead to a desire to conduct them in a medium where *Paulownia* seeds have demonstrated a high germination rate. Simultaneous to the experiment, *Paulownia* seed germination will be compared on soils from Linville Gorge, Mason Farm, and on Promix. Specific treatment levels for the 2006 iteration of these experiments are given below.

The Linville Gorge attempt was conducted along Forest Service road 118 which formed the eastern firebreak for the 2000 Linville Gorge fire. The area selected was patchily and lightly burned and was chosen because it was a dry forest community and there were number of immature *Paulownia* trees just outside of the experimental area indicating that *Paulownia* seeds could germinate in the soils present. It was also an area with very high levels of pine mortality from the southern pine beetle. This was important as permission was not obtained from the Forest Service to cut down any living trees and full sunlight was needed for the experiments. All downed and dead trees were cut and pulled to the side and all vegetation was clipped at ground height before the experiment was laid out. No supplemental watering was possible and below-ground vegetation was not removed. This iteration contained the following treatment levels in additional to those listed below for the 2006 attempt. Experiment #2: A no burn fire intensity level; a no seeds added burial level; and an ambient and wet soil moisture level (at the time of burn). Experiment #3: A shallow (2cm) litter level; and a no seeds added burial level.

The Mason Farm site had been covered by a light blocking landscaper's cover-cloth eliminating perennials for the previous 2 years. Subsequent to its removal, the ground was plowed with a disk plow to a depth of 16 inches and then tilled to 6 inches with a roto-tiller to further break up the soil. Once the experiment was initiated, seeds were watered every other day and the blocks were kept free of weeds. This iteration contained the following treatment levels in addition to those listed below for the 2006 attempt. Experiment #2: A no seeds added burial level; and a no burn fire intensity level. Experiment #3: A shallow (2cm) litter ground cover level; and a no seeds added burial level.

2006 design of Experiments #2 and #3

Exp #2: Fire Survival

A randomized, block design will be used to examine the effect of burial depth, fire intensity (as measured by maximum temperature), and burn season on *Paulownia* seed germination. With 5 replicates, there are a total of 30 experimental blocks (3 burial x 2 intensity x 5 replicates) each season. No unburned treatments are included because these conditions are present within experiment #3 and greenhouse space is limited. 100 *Paulownia* seeds will be added to each block.

Burning will be conducted using a "burn tool" developed by Joan Walker with the National Forest Service's Southern Research Station at Clemson University. This tool consists of an inverted propane burner attached to a tripod and lowered to the desired height above the soil surface. Temperature is recorded and displayed in real time through thermocouples at the soil surface attached to a data-logger and computer. *Paulownia* seeds will be enclosed in a wire mesh bag for the burn (done outside), retrieved, and germinated on a growing medium in the greenhouse.

Treatments:

Burial depth (3 levels): Litter surface (litter depth 5cm), soil surface, buried at 5cm

Burn season (2 levels): Spring, late summer

Fire Intensity (2 levels): Low intensity (200° C) and high intensity (500° C)

Exp#3: Effect of surface cover, light, and burial depth

Surface cover treatments and burial depths will be randomly assigned within a block design in each shade enclosure. 100 *Paulownia* seeds will be added to each block. 5 replicates results in 25 experimental blocks (3 burial x 2 cover x 5 replicates, with 1 treatment combination [bare soil ground cover and litter surface burial] removed because of impossibility) in each shade treatment. Each shade treatment will be replicated twice for a total of 100 experimental blocks.

Treatments:

Light level (2 levels): Full sun and 50% shade

Ground cover (2 levels): Litter (5cm), Bare soil

Burial depth (3 levels): Litter surface, Soil surface, 5cm into soil profile

Seed bank study

Eighty-three soil samples were collected from the western portion of the GRSM from xeric forests on southwest facing slopes in February and March of 2005. The sample area was bounded by Rich Mountain Rd., Cade's Cove loop Rd., Rabbit Creek trail, and the park boundary. Samples were taken at 3 equal distance (from park boundary) and 3 equal elevation classes (utilizing only the range of elevation within the sample area) such that 10 locations were chosen from each combination of classes where possible. At each location 10 randomly located samples within a 10m area were collected using a 5cm soil corer. Samples were then combined into a single composite sample. 9 Additional samples were taken from the base of a mature *Paulownia* located outside of the park and at 10m and 50m out in each of the cardinal directions. These samples were used to definitively determine whether *Paulownia* seeds can be germinated from soil samples and to characterize the short distance dispersal curve for *Paulownia's* seeds.

Soils were refrigerated in the days between their collection and processing. Soils were sieved at the North Carolina Botanical Garden in Chapel Hill to remove everything larger than 3cm and smaller than .25mm, the remaining mixture was spread over a growing medium in the greenhouse at UNC, and watered daily. Germination was tracked daily through November 21st (35 weeks) and all germinants were identified to species where possible. GIS was used to spatially locate soil samples, all mature (seed producing) *Paulownia* surrounding the study area, and calculate the distance from each positive sample (a sample from which *Paulownia* was germinated) to the nearest mature tree.

Modeling distance effects on *Paulownia* seedling density

A preliminary model predicting seedling density was attempted for Linville Gorge using the distance from the nearest road to each plot. These distances were plotted against the observed number of *Paulownia* seedlings. However, these data produced either a weekly positive relationship between distance and seedling density or no relationship depending on whether outliers were removed (Figure 8). The location of mature trees is being collected and the relationship will be reanalyzed once these data are in hand.

More tangible results were obtained from the seed bank study samples. The distance from each positive soil sample to the nearest mature *Paulownia* was plotted against the number of seedlings in log-log space. A least squares linear model (Figure 9, $p < .001$) was fit to the data and applied to the study area map to create predicted seed shadows and densities. (Figure 10). As this model does not incorporate additive effects (i.e. the effect of being close to multiple mature trees), it will under predict seed density, especially when mature trees occur at high densities. Further work is being done to incorporate these additive effects. Once the Linville Gorge and seed bank based models are complete they will be compared for congruence.

Results

Results presented below (following the objective they address) represent those completed to date. Work on the remaining questions presented in the Introduction and in the attached dissertation proposal are ongoing. All will be completed within the year at which time the results of all analyses (including those outside of the grant's dictates) will be submitted as an addendum to this report. For additional information on the specific statistical methods employed, see the attached dissertation proposal.

At the landscape scale, the important drivers of invasion are seed dispersal, longevity, and season. The effect of distance on *Paulownia* seedling density was modeled in two ways; from the results of a seed bank study in the western corner of the GRSM and by comparing observed invasion rates with the distance to the nearest road (Linville Gorge). Although the second approach did not give rise to conclusive results (Figure 7), the seed bank study does show a limitation to *Paulownia's* dispersal ability (Figure 11, 12).

In the seed bank study, *Paulownia* seedlings were germinated from four of the 83 samples collected within the park and eight of the nine samples collected in the immediate vicinity of a mature tree. (Figure 11, 12) The most interior positive sample was collected 1.945 kilometers from the park boundary and the farthest distance between a positive sample and the closest mature tree was 3.746 kilometers. No samples other than those collected at 20m and 50m from a mature tree contained more than one seedling suggesting that the majority of seeds, even though they are wind dispersed, do not travel far from the parent. Although some seeds did travel a long way from the nearest potential parent, there were many negative samples closer to a mature tree than these positive samples collected far from a mature tree. This suggests that *Paulownia's* seed bank is very limited, spatially heterogeneous, both, or that the sampling intensity was insufficient to capture *Paulownia* seeds. There were an insufficient number of positive samples to determine whether dispersal is directionally biased or affected by elevation. Although the seed bank model has a cut-off distance for seed dispersal (1.316 kilometers), when it is applied to Linville Gorge, it underestimates seedlings density even when based on the distance to the nearest road (rather than mature tree), a condition that grossly overestimates mature *Paulownia* density (Figure 13).

Seed longevity was tested by comparing germination rates from different populations and under different storage treatments. Looking at germination rates over time within storage treatments and between populations, although there are significant differences between populations in some months, there is no significant trend for one population to have consistently higher germination rates (Figure 7). Additionally, there is no trend towards decreased seed viability over the course of the study (Figure 5, 6, 7). Comparing storage treatments, there are significant differences treatments (Figure 5). The field and dry storage treatments exhibited moderate to high germination rates throughout the year while the stratified treatment exhibited low germination rates until mid summer.

At the watershed scale, factors which influence fire intensity are the dominant drivers of invasion rate. Initial analyses show *Paulownia* to be most frequently present and in greatest abundance on high benches followed by crests and high slopes (Table 2). Slope was also significantly related to *Paulownia* presence and abundance in all model types (Table 3, 4, Figure 3, 4) and aspect was an important variable in the classification tree generated from the data subset. Terrain shape has not yet been thoroughly analyzed. All of these variables are associated with site dryness and fire intensity, the variable most closely correlated with *Paulownia* invasion rate, and by their nature have significant spatial components. Ongoing spatial analyses of these data and experimental tests of the influence of burn intensity on seed survival will hopefully clarify these relationships.

Table 2: Number of plots located at each topographic position, the number of these plots which are invaded and the abundance of *Paulownia* within invaded plots.

Topographic Position	Number of plots	Number of stems	Average abundance	Number of invaded plots	Proportion invaded
Crest	21	19	0.90	10	0.48
High level	10	202	20.20	10	1.00
High slope	62	316	5.10	27	0.44
Mid slope	60	206	3.43	13	0.22

At the scale of the individual stand (plot), the significant variables were those that influenced the ability of *Paulownia*'s seeds to germinate and grow, namely those that affected light levels and ground cover. The most important of these was the amount of cover above one meter (as recorded by a spherical densiometer). This proved to be a better predictor of invasion success that the cover of any one strata layer (only canopy cover was significant as an individual strata layer). This is consistent with *Paulownia*'s adaptation for high light environment. It is also the variable most highly correlated with fire intensity measurements. No significant relationships were found between shrub-layer cover and *Paulownia* seedling density or presence/absence in any of the models tested (Tables 3, 4, Figures 3, 4)

Of the ground cover variables, only the summed cover of exposed soil plus exposed humus (organic + mineral soil cover + humus cover) and litter cover and depth were found to be significant. Mineral and organic soil cover, and humus cover were individually all positively, but not significantly, correlated with *Paulownia* invasion. Combined (hereafter soil exposure) they represent the total proportion of ground with conditions favorable for *Paulownia* seed germination. Soil exposure was found to be highly significant ($p<.001$) in regressions predicting both the presence and abundance of *Paulownia*, and in the classification tree based on the entire data set (labeled "Bare.soil" in the regression tables and "sum.soil.hum" in the classification tree). No regressions showed a significant relationship between litter depth and the abundance or presence/absence of *Paulownia* (Tables 3, 4) though litter depth was used in both classification trees (Figures 3, 4) and litter cover was used in the tree built from the complete dataset (Figure 3) suggesting that litter depth and litter cover are significant factors but not driving factors. The other variables found to be significant in the regression and tree models were watershed (aspect, slope, topographic position) or landscape (site) level factors (Table 5).

A number of analyses remain to be completed in the coming year. The effect of burn season is being examined by comparing invasion rates between fires from different seasons utilizing data from all sampled plots and fires. The spatial components of fire and landscape as captured by site dryness (TCI, topographic convergence index), insolation (Hillshade), fire severity (changes in NDVI before and after the fire), vegetation community, and the spatial location of each plot (in case of a spatial effect not captured by these other indices) are being analyzed for their ability to significantly predict *Paulownia* invasion. Although fire intensity data are only available for the Green Mountain and Linville Gorge fires, the other variables will be analyzed across all sampled fires. This summer, experimental tests of the ability of *Paulownia* seeds to survive fire and germinate under different light and ground cover conditions will be conducted once again, and plots at Linville gorge will be resampled to measure

Paulownia survival over time under varying levels of shading and at different topographic positions within the landscape. Finally, vegetation data from all sampled plots will be analyzed for impacts of *Paulownia* invasion on native species diversity, composition, or cover.

Discussion

Invasive species pose interesting and often novel problems for land managers interested in restoring disturbance regimes. On one hand disturbance is an essential part of ecosystems and may be necessary for the continued reproduction or survival of many important native species. On the other hand, disturbances are often implicated in the invasion of exotics because they create openings in resources space which may be usurped by the invader. They question to managers then is: how to allow or introduce disturbance without facilitating exotic invasion.

With *Paulownia* and fire, this question becomes: What drives invasion at the landscape, watershed, and stand scales. What factors must be present at each scale for *Paulownia* to make use of the post-disturbance environment? With this information hand, managers can then look to see how or where they can reintroduce fire without fear or invasion and where they need to be vigilant and enact post-disturbance monitoring and control measures.

At the landscape scale, seed availability is a controlling factor. The seed bank study found *Paulownia* seeds dispersed 3.746 kilometers from the nearest potential parent, but this dispersal model demonstrably under predicted invasion rates at Linville Gorge even under grossly unrealistic assumptions about the abundance of mature trees in the landscape. Further work on dispersal models continues, but this initial estimate of 3.746 kilometers as the maximum dispersal distance at least gives a distance over which managers should be aware that the potential for invasion exists when other conditions are met. Although this study has no further light to shed on the effects on season of burn on invasion (in progress) or seed longevity (no trends), other work on longevity (Longbrake 2001) has shown that seeds remain highly viable in the soil for two years and suggested that seeds may remain viable in the soil for 15 years. If this is indeed the case, and if seeds are able to survive fire, the potential exists for a sizable seed bank to be built up over time.

At the watershed scale, seed availability may still be an important factor at the most remote locations, but the pattern of *Paulownia*'s invasion is most closely tied to the pattern of fire intensity as evidenced by the significance of remaining vegetation cover as a predictor of invasion success. Although this is not a perfect measure of fire intensity (variation in cover exists before fire and afterwards independent of it), fire intensity measures are not available for all studied fires, so vegetation cover (as measured by the densiometer) is a stand-in variable. Although fire intensity and effects at a specific point may be greatly affected by 'local' variables (ex. fuel availability), at the watershed scale it is driven by the patterns of aspect, slope, xeric microsites, and vegetation communities. Although aspect and slope have been shown to be significant in some of the models presented here, teasing apart the reasons why is more complicate. Are they significant because certain aspects and slopes are correlated with increased fire intensities which result in increased invasion frequency or because *Paulownia* germinate better within a particular range of aspects and slopes? Determining the influence of slope, aspect and other watershed-scale spatial variables will require spatial analyses which are not yet complete.

At the stand or plot scale, invasion success is influenced by variables dominant at both larger spatial scales as well as a suite of variables which vary over the scale of meters. Canopy cover (a stand level variable) is the most significant predictor of *Paulownia* invasion overall, but this is influenced by watershed-level patterns of fire intensity. The fact that this is the most important variable in determining the degree of invasion by *Paulownia* (as measured by abundance) and whether *Paulownia* is present at all also suggests causal reasons as to why this species is not found more frequently following other types of disturbance- namely that fire often has a much greater impact on overstory cover across both spatial and temporal scales. Spatially, fires can be quite large and more severely burned areas (highest levels of overstory death) within burns can likewise be large. The temporal differences between fire and other disturbances may be even more significant as fires can significantly impact below ground resources (seeds, root collars that support resprouting) that are often not as extensively impacted by other disturbance types. Consequently, *Paulownia* may present a particular invasive potential following fire because regrowth rates are slower, resulting in decreased competition during *Paulownia*'s early development. This invasive potential may be tempered if *Paulownia*'s seeds exhibit high levels of mortality during fire making the species more dependent on post-fire seed dispersal.

The only other stand level variable that was a significant predictor of invasion in regressions was the amount of exposed soil. The significance of this variable is not surprising as *Paulownia* is known to germinate best on bare soil since it has few carbohydrate reserves available to put down a long primary root through thick litter. The inverse (though not tight or one-to-one) relationship between soil exposure and litter cover and depth (the result of fire removing litter and thereby exposing soil) explains the significance of both variables. One (soil exposure) leads to an increased chance of invasion success and the other (litter cover/depth) creating conditions which prevent or limit invasion. The use of litter depth in the lower branches of the classification tree helps to explain why it was not found to be a significant variable in the regression models; namely that although it is important, it is less important that other variables although a high level of litter cover may prevent invasion, this is less important than the amount of sunlight available. Further, since vegetation cover and litter cover are negatively correlated as a result of fire effects, much of the variation in litter depth is accounted for in the first split of the tree. That it is present at all illustrates the greater ability of classification trees to illuminate complex variable interactions than regressions.

The ability of all model types to capture the significance of litter cover and depth and soil exposure is also limited by the time delay between invasion and sampling and the spatial variability of these factors. Measurements made at the 5x5m scale 1-2 years after invasion has occurred are not measurements of conditions at the time and place of germination. Even if these variables have not changed between invasion and sampling, the sampling scale may decrease the recorded correlation between invasion and these variables, thereby limiting the ability to detect a relationship even where it exists.

Experiments being rerun this summer will (hopefully) shed further light on the significance of these variables.

Finally, although the variables used in the tree models have been discussed individually, it is worth discussing generally the similarities and differences between them. Both models do a good job of predicting *Paulownia's* absence (95.3% full, 91.3% subset), but the tree built from the subset of the data is better at predicting the presence of *Paulownia* (75.2% vs. 87.3%). This supports the theory that there is something about the excluded fires that has limited *Paulownia*'s invasion, that there are sites where one would expect to find *Paulownia* from which it is absent. Consequently, when these fires are included in the model, the presence prediction accuracy is decreased because *Paulownia* is absent from areas where it is expected to be present. Unfortunately, it is as yet unclear whether this is the result of an unrecorded environmental variable or the result of limited seed availability. It is also reassuring that there is as much congruence between the models as there is. The densiometer reading is the most important factor in both models and the "level" of the split is relatively constant (38.5% vs. 46% for the full and subset models respectively). Additionally, 2 of the 3 other variables used in the full model (not including site as that would be expected to drop out) are also used in subset model.

Conclusion

Although there this project is not yet complete, the work done to date demonstrates that the pattern of *Paulownia* invasion can be predicted. Predicting patterns of invasion is essential for effective control over the long term and demonstrates that with focused treatment further invasion of this species can be prevented in natural areas of the Southern Appalachians.

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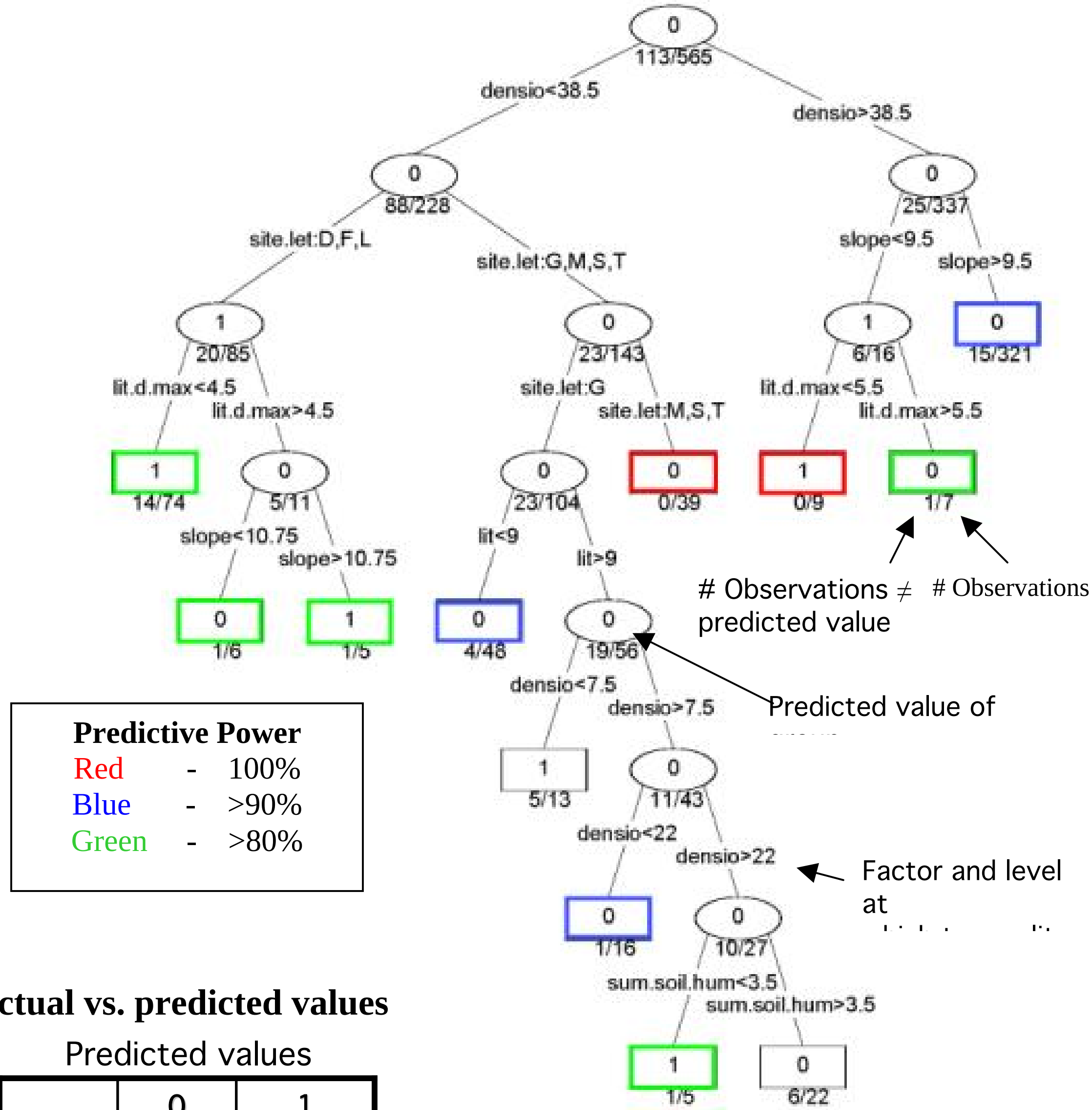
Appendix A – Figures and Tables

Coefficient	DF	Deviance	Residual DF	Residual Dev.	Pr(ChiSq)
NULL	1		559	741.3389	**0.000000**
Densiometer	1	202.638	558	538.7009	**0.000000**
Bare Soil	1	63.7623	557	474.9385	**0.000000**
Site	1	58.9973	556	415.9412	**0.000000**
Topographic Position	4	81.2429	552	334.6983	**0.000000**
Slope	1	7.7386	551	326.9597	**0.005405**
Litter	1	2.5645	550	324.3952	0.109284
Max. litter depth	1	2.2814	549	322.1138	0.130933
Densio:Slope	1	0.2249	548	321.8889	0.635359
Densio:Site	1	2.3274	547	319.5615	0.127113

Table 3. ANOVA tables for negative binomial regression. Model: # *Paulownia* stems ~ densio + bare.soil + site + topo.position + slope + litter + Max litter depth + densio*slope + densio*site. Additional variables and interaction terms were tested and found to be non-significant.

Coefficient	DF	Deviance	Residual DF	Residual Dev	Pr(ChiSq)
NULL	1		559	629.8154	
Densiometer	1	107.7607	558	522.0547	**0.000000**
Bare soil	1	26.331	557	495.7237	**0.000000**
Site	1	47.8155	556	447.7237	**0.000000**
Topographic position	4	24.9365	552	422.9717	**0.000052**
Slope	1	0.0629	551	422.3427	0.427724

Table 4. ANOVA table for Logistic regression. Model: *Paulownia* presence/absence ~ densio + bare.soil + site + topo.position + slope. Additional variables and interaction terms were tested and found to be non-significant.



Actual vs. predicted values

Predicted values (columns); Actual values (rows)

	0	1
0	431	21
1	28	85

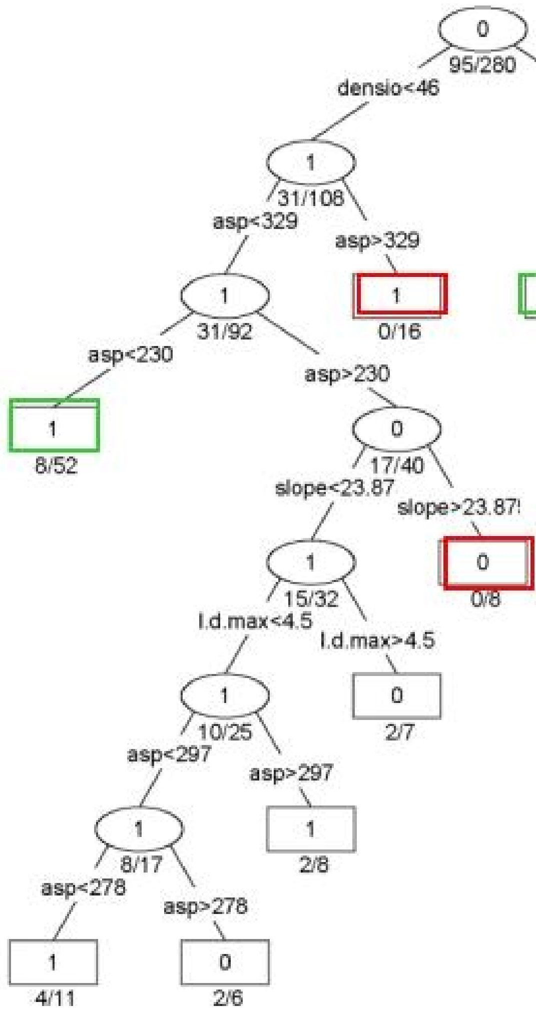
Tree classification rates

Overall misclass rate	8.67
Overall Class accuracy	91.33
Pres. predict accuracy	75.22
Abs. predict accuracy	95.35

Legend

densio	=	Densiometer recorded cover
site.let	=	Studied fire D – Daw's Mountain F – Firebug L – Linville Gorge G – Green Mountain M – Mill Ridge
lit.d.max	=	Maximum litter depth
slope	=	Slope
lit	=	Litter cover
sum.soil.hum	=	Summed organic, mineral, and hummus cover

Figure 3. Classification tree built from the entire dataset that predicts the presence/absence of *Paulownia*.



Predictive Power

Red - 100%
Blue - >90%
Green - >80%

Actual vs. predicted values

Actual values \ Predicted values	0	1
0	169	16
1	12	83

Legend

densio	=	Densiometer recorded cover
asp	=	Aspect
slope	=	Slope
lit.d.max	=	Maximum litter depth

Tree classification rates

Overall misclass. rate	10
Overall class. accuracy	90
Pres. predict accuracy	87.36
Abs. predict accuracy	91.35

Figure 4. Classification tree built from the plots at Linville Gorge, Firebug, and Daw's Mountain that predicts the presence/absence of *Paulownia.*

Factor	Model			
	Neg. bin.	Logistic	Full tree	Subset tree
Remaining cover	X	X	X	X
Site	X	X	X	
Topo. position	X	X		
Bare soil	X	X		
Slope	X		X	X
Aspect				X
Litter cover			X	
Max lit. depth			X	X

Table 5. Comparison of regression and tree results. Amount of variance explained decreases from red to green to blue. In the trees, the green factors determined the second splits. Factors with a black X were either significant (regressions) or used in the model (later splits of the trees).

Germ. start date	Pop #1			Pop #2			Pop #3			Pop #4		
	Dry	Strat.	Field	Dry	Strat	Field	Dry	Strat	Field	Dry	Strat	Field
January	0.30	N/A	0.34	0.56	N/A	0.63	0.40	N/A	N/A	0.41	N/A	0.38
February	0.24	0.00	0.18	0.35	0.04	0.55	0.20	0.04	N/A	0.60	0.03	0.45
March	0.01	0.01	0.45	0.05	0.08	0.08	0.08	0.04	N/A	0.16	0.01	0.15
April	0.51	0.04	0.09	0.24	0.01	0.15	0.09	0.05	N/A	0.28	0.00	0.13
May	0.66	0.00	0.76	0.65	0.00	0.50	0.36	0.01	N/A	0.71	0.00	0.83
June	0.48	0.00	0.78	0.65	0.00	0.40	0.30	0.00	N/A	0.48	0.00	0.71
July	0.61	0.06	0.66	0.83	0.39	0.60	0.68	0.35	N/A	0.88	0.11	0.64
August	0.19	0.43	0.48	0.23	0.58	0.53	0.35	0.43	N/A	0.10	0.08	N/A
September	0.69	0.34	0.46	0.73	0.63	0.35	0.64	0.23	N/A	0.71	0.40	0.68
October	0.73	0.39	0.91	0.70	0.11	0.10	0.65	0.48	N/A	0.75	0.25	0.09
November	0.48	0.64	N/A	0.79	0.49	N/A	0.56	0.33	N/A	0.65	0.60	N/A

Table 6. Final germination rates for *Paulownia* seeds.

Germination start date	Storage treatment		
	Dry	Stratified	Field
January	0.42	N/A	0.45
February	0.35	0.03	0.39
March	0.08	0.03	0.23
April	0.28	0.03	0.12
May	0.60	0.00	0.70
June	0.48	0.00	0.63
July	0.75	0.23	0.63
August	0.22	0.38	0.50
September	0.69	0.40	0.50
October	0.71	0.31	0.37
November	0.62	0.51	N/A

Table 7. Average germination rates for each storage treatment.

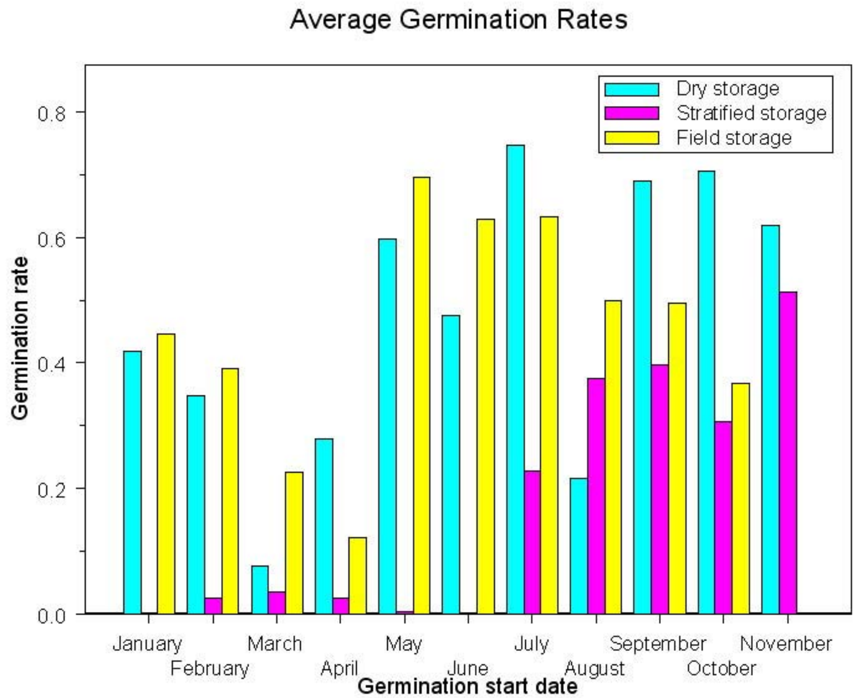


Figure 5. Germination rate by storage treatment averaged for all populations.

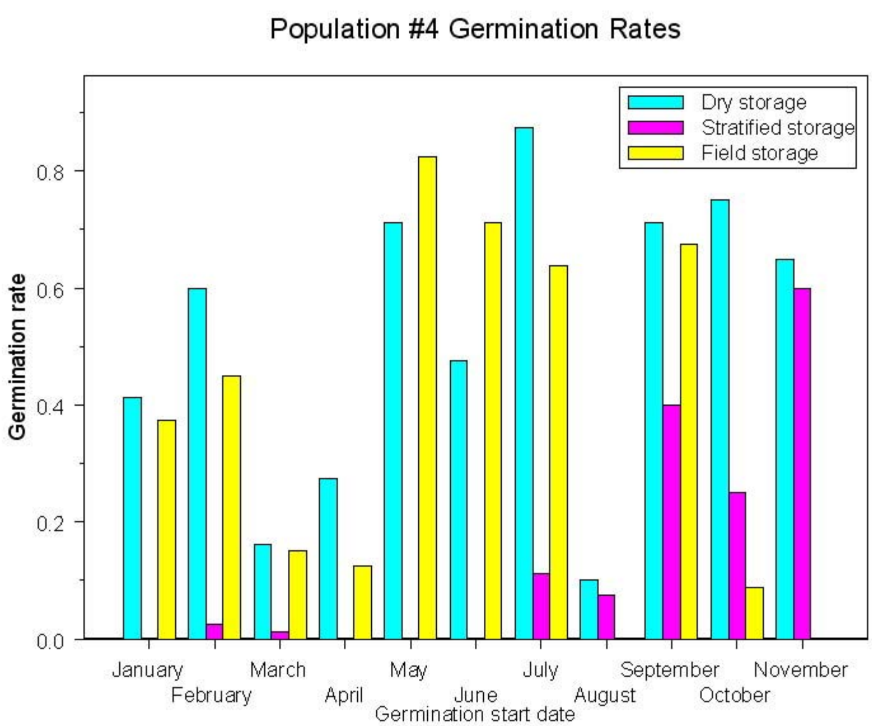


Figure 6.. Germination rate by storage treatment for Population #4.

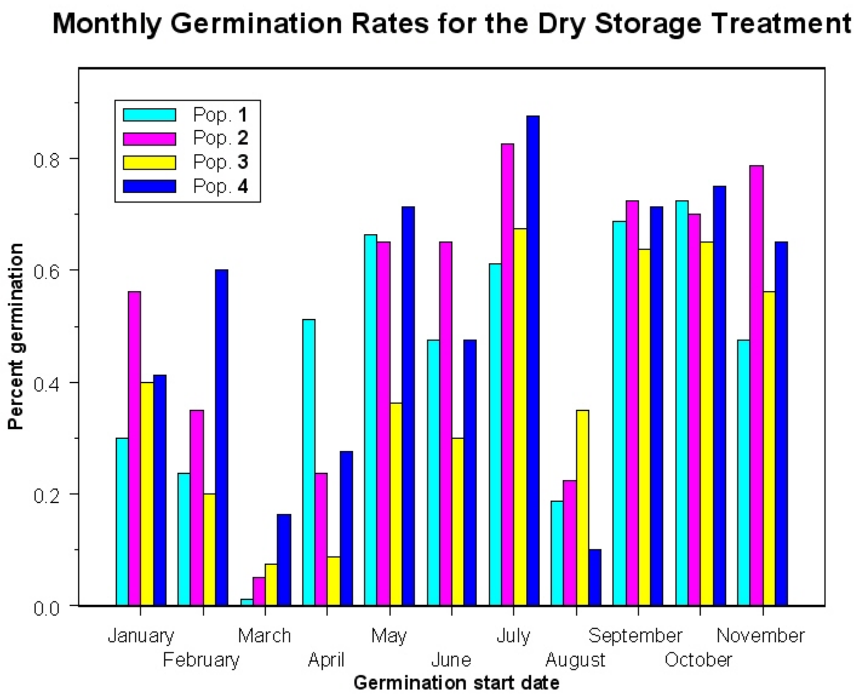


Figure 7. Germination rate for each population – Dry storage treatment

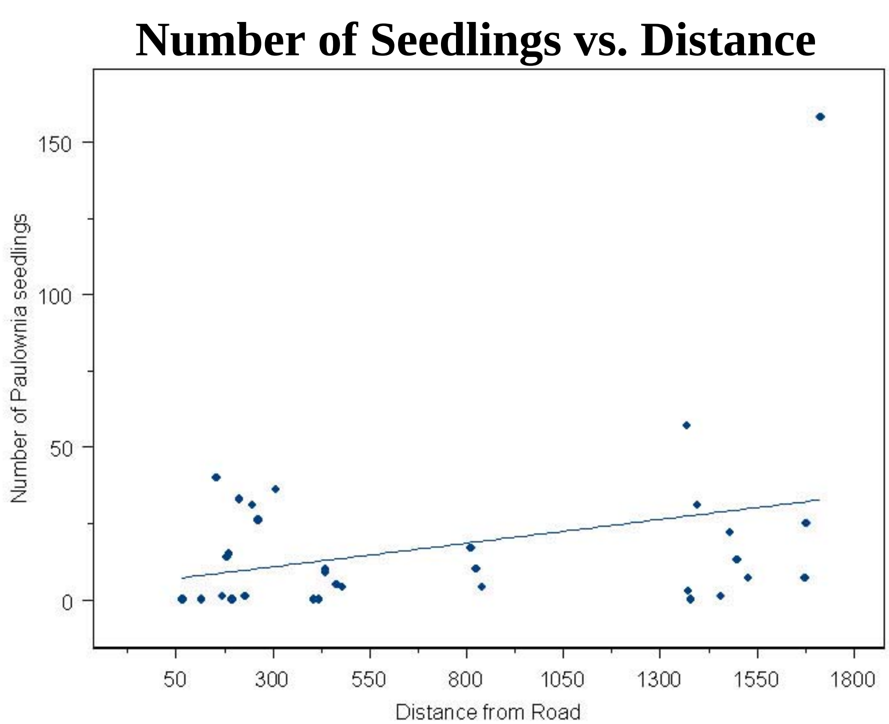


Figure 8. Relationship between distance and seedling density at Linville Gorge

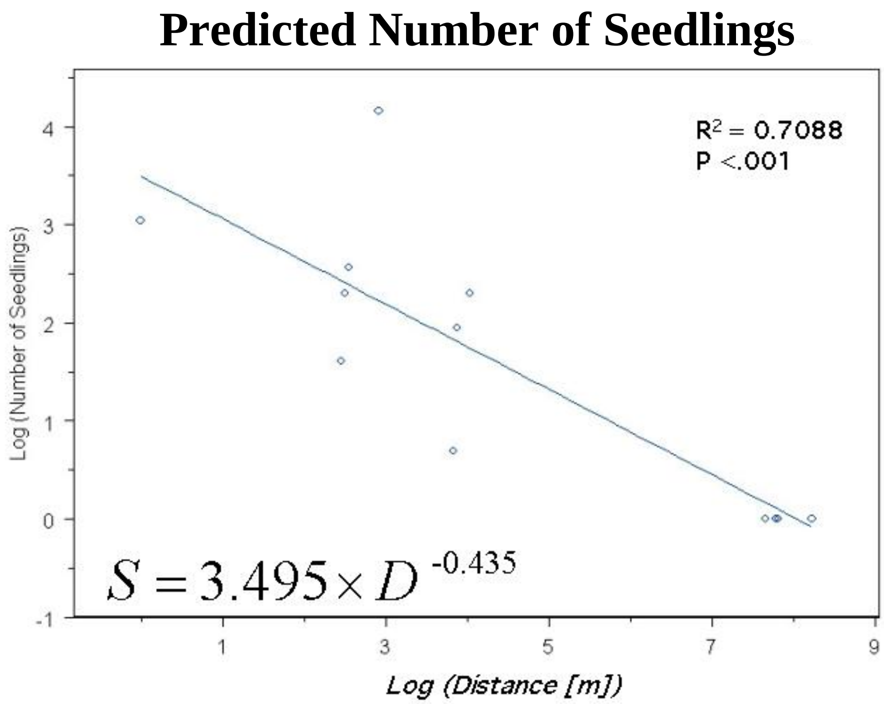


Figure 9. Least Squares linear model of relationship between distance and seedling density.

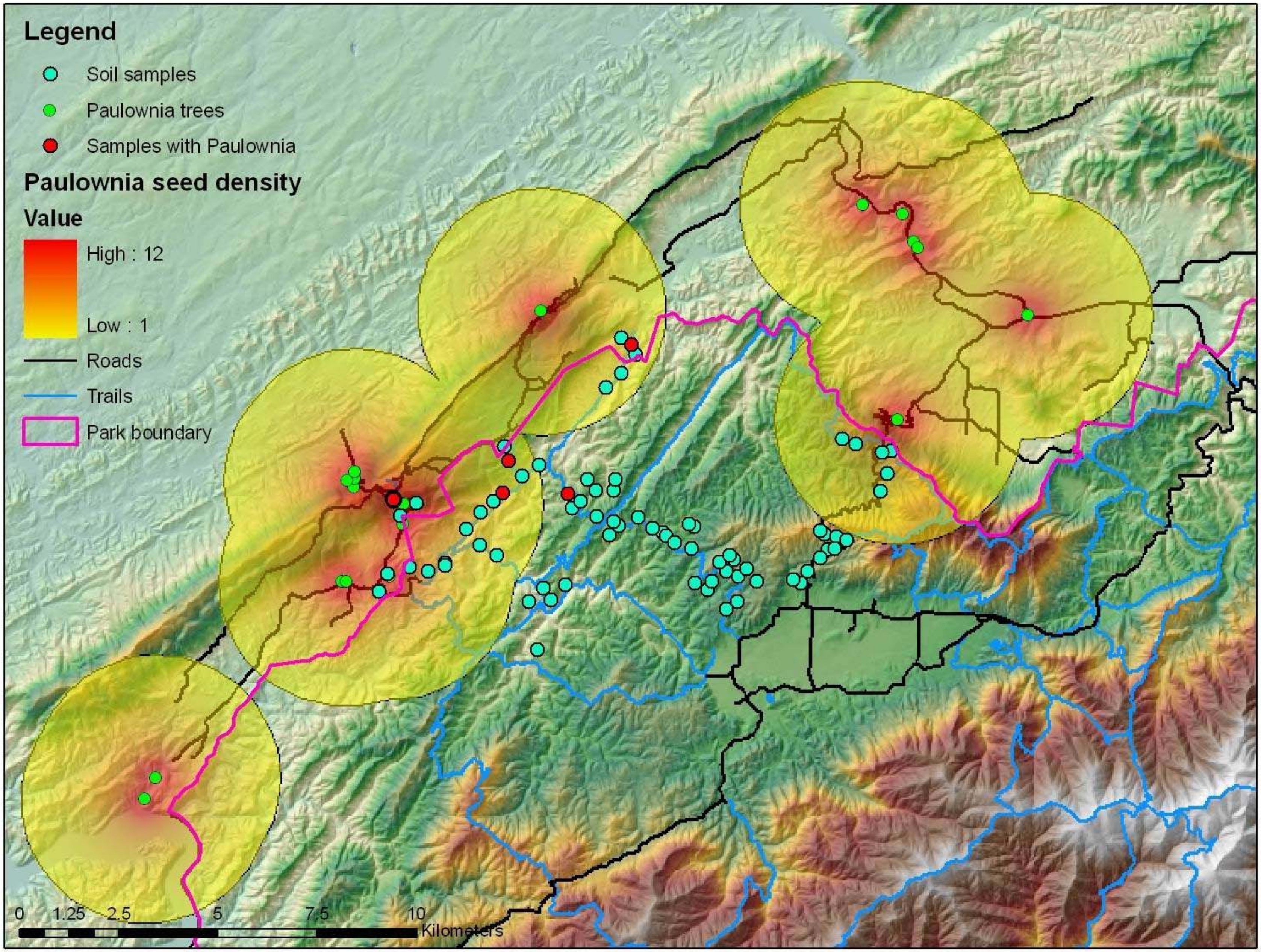


Figure 10. Least-squares model (Figure 9) applied to the Great Smoky Mountains National Park study area to predict seed shadow and densities.

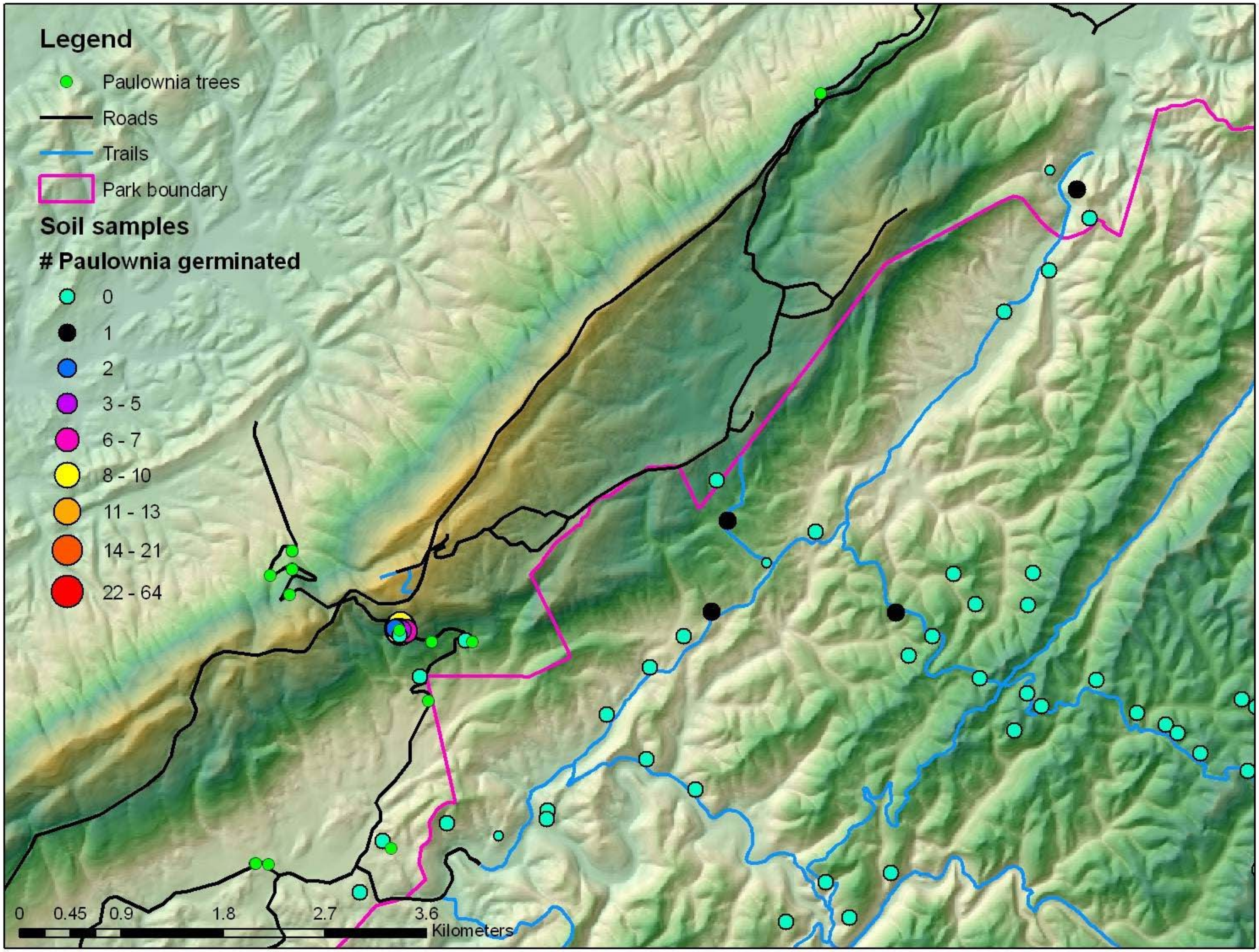


Figure 11. Abundance of *Paulownia* seeds in soil samples collected in and around western Great Smoky Mountains National Park.

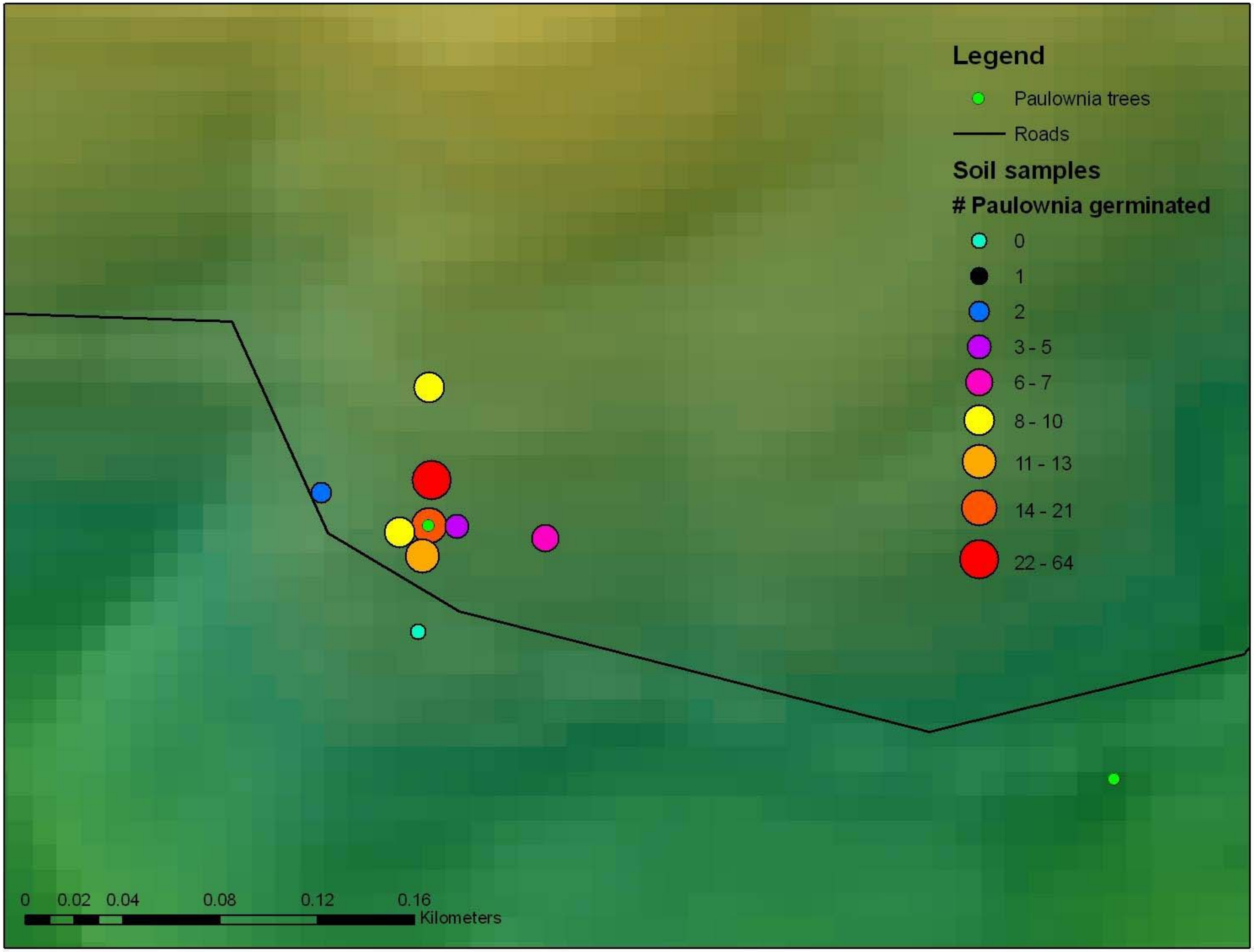


Figure 12. Abundance of *Paulownia* seeds in soil samples collected near a mature tree.

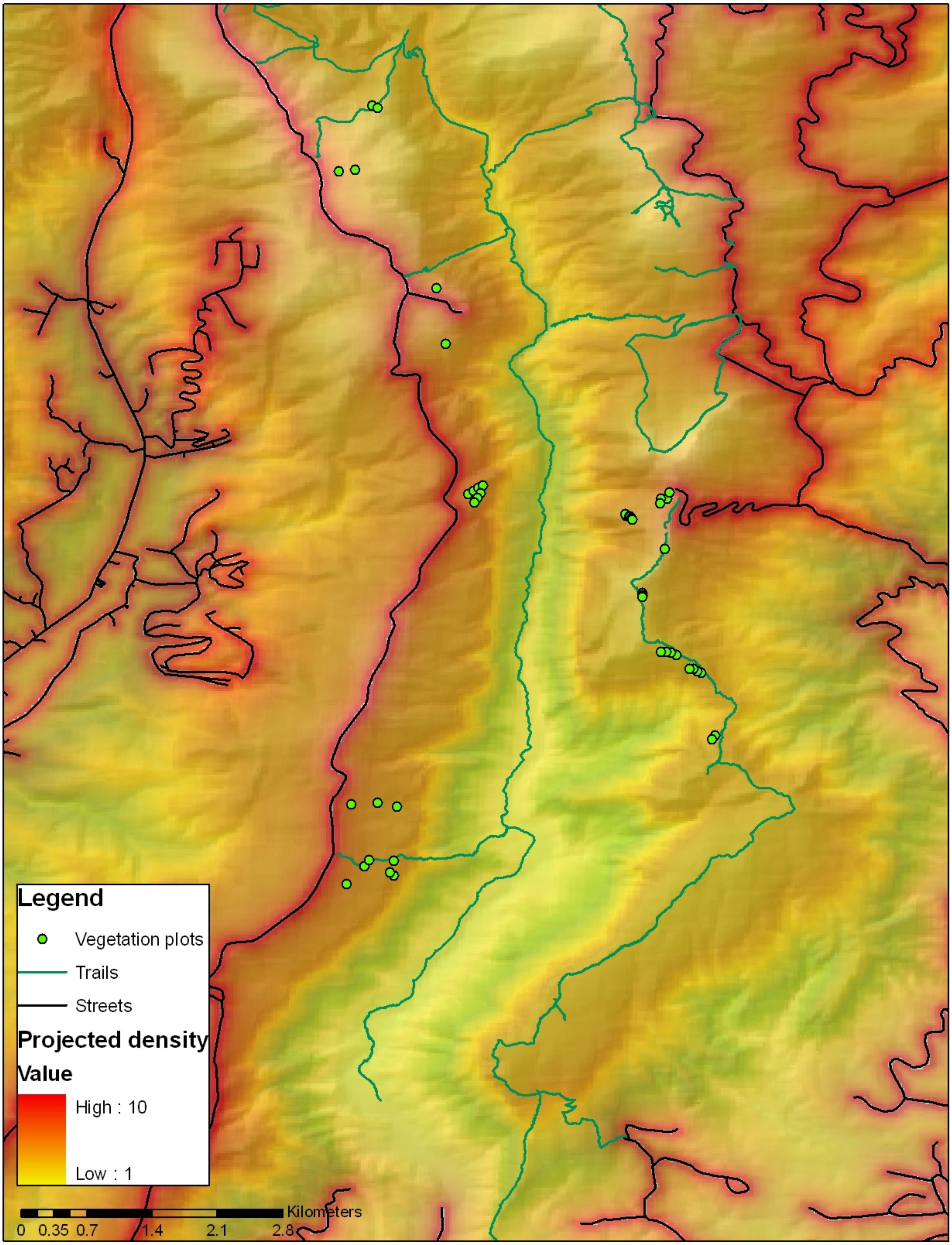


Figure 13. *Paulownia* seedling density at Linville Gorge based on seed bank derived dispersal curve.

COMMUNITY RECOVERY AND INVASION BY *PAULOWNIA TOMENTOSA* FOLLOWING FIRE IN XERIC FORESTS OF THE SOUTHERN APPALACHIANS

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Abstract

The last two decades have seen an increase in the awareness of fire's importance in xeric southern Appalachian forest communities, an increase in its use as a management tool, and an increase in the number of studies in the role and impact of fire on these communities. In the last ten years, managers have also witnessed the invasion of *Paulownia tomentosa* after some of these fires. As natural, intentional, and accidental fires are increasingly part of the landscape, it is important to determine the landscape, watershed and stand variables that favor the spread of this exotic species into natural areas following fire, determine if it is impacting native communities or species, and incorporate this knowledge into management practices and our growing understand of regional fire dynamics. This thesis addresses both the invasion of *Paulownia* and the role of fire in the southern Appalachians in five chapters (not including chapter I, the introduction).

Utilizing plot data from five fires, the second chapter analyzes the effects of fire severity, season of burn, environmental conditions, and the relative location of mature *Paulownia* trees on *Paulownia* seedling abundance and vigor within sampled plots and asks whether *Paulownia* seedlings are likely to survive to maturity. Fire and environmental variables and Paulownia presence and abundance of *Paulownia* are analyzed to determine what effects fire and invasion have had on native species cover and diversity.

The third chapter focuses on one fire, Linville Gorge. It utilizes watershed scale spatial data to ask what characteristics of topography, community type, and fire severity promote *Paulownia* invasion. Making use of pre and post-fire plot data, it analyses changes in diversity and composition and whether these are impacted by *Paulownia* presence or abundance. And finally, it asks whether the observed patterns of community recovery agree with those predicted by Ryan's fire severity matrix.

In the fourth chapter, two experiments are utilized to test the conditions under which *Paulownia* seeds survive fire, and to test *Paulownia*'s germination rate under different ground cover, light, and burial conditions.

A seed bank study of dry forest communities of the Great Smoky Mountains National Park documents the diversity and distribution of species encountered in the seed bank and the distribution of *Paulownia* seeds as a function of distance from mature individuals.

The final chapter synthesizes information from the preceding chapters to predict patterns of *Paulownia* invasion, exotic species invasions generally, and to create tools for land managers.

Chapter I: Introduction

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 of invasion patterns. In addition to disturbance, species availability (both native and exotic) and general habitat characteristics are important in understanding patterns of invasion (Hobbs 1992, With 2001). Species availability, habitat, and disturbance require studies at different spatial scales: species availability requires analysis at a regional to landscape scale; habitat characteristics require analysis along gradients at a watershed scale; and variation in disturbance severity requires analysis at the local to community scale. This thesis examines these three scales in documenting the role of fire in the invasion of *Paulownia tomentosa* in the southern Appalachians and assesses the interactions between *Paulownia* and native plants in a community's response to fire. There is a strong applied rationale for this work: land managers are seeking to reintroduce fire as a natural process in the southern Appalachians, but do not want to simultaneously increase the distribution and establishment of exotic species, nor affect the abundance of native fire dependent species because of this exotic invasion.

In order to understand the relationship between fire and invasion, it is important that we first understand the factors that affect the range of effects that fire and invasion can have upon native species' recovery. 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 (Figure 1, 2). 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 3). The matrix's two axes (above and below ground fire effects) enclose a domain in which Ryan placed the recovery strategies (resprouting, dispersal, etc) described as "first vital processes" by Nobel and Slayter (1980).

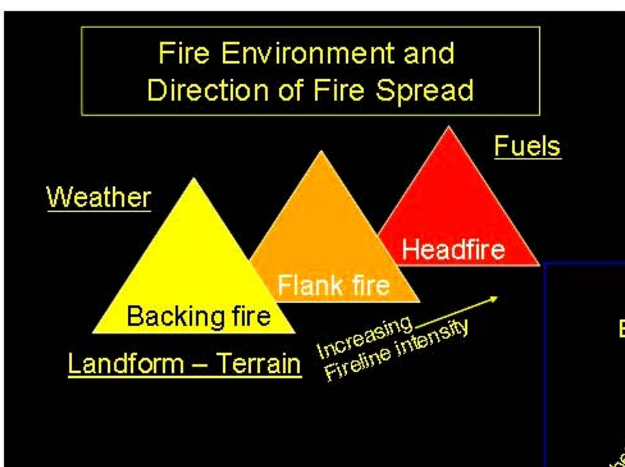
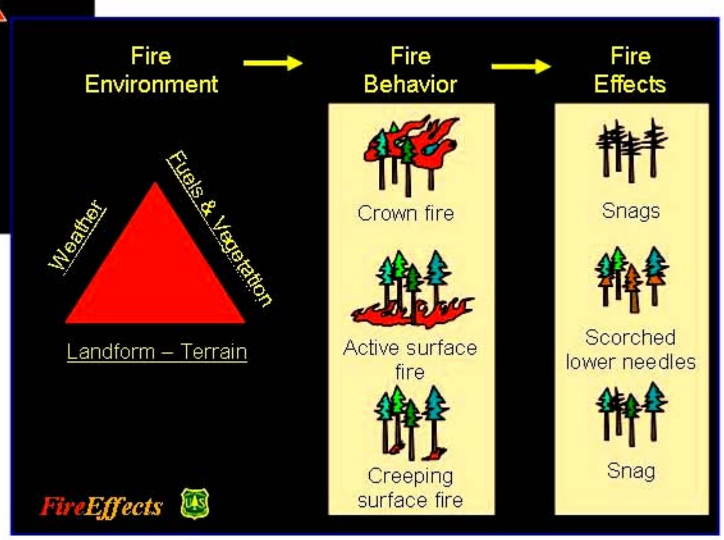


Figure 1: From Ryan 2002
Fire environment as affected by weather, terrain, fuels, and position within the fire.

Figure2: from Ryan 2002
Interactions between fire environment, behavior, and effects



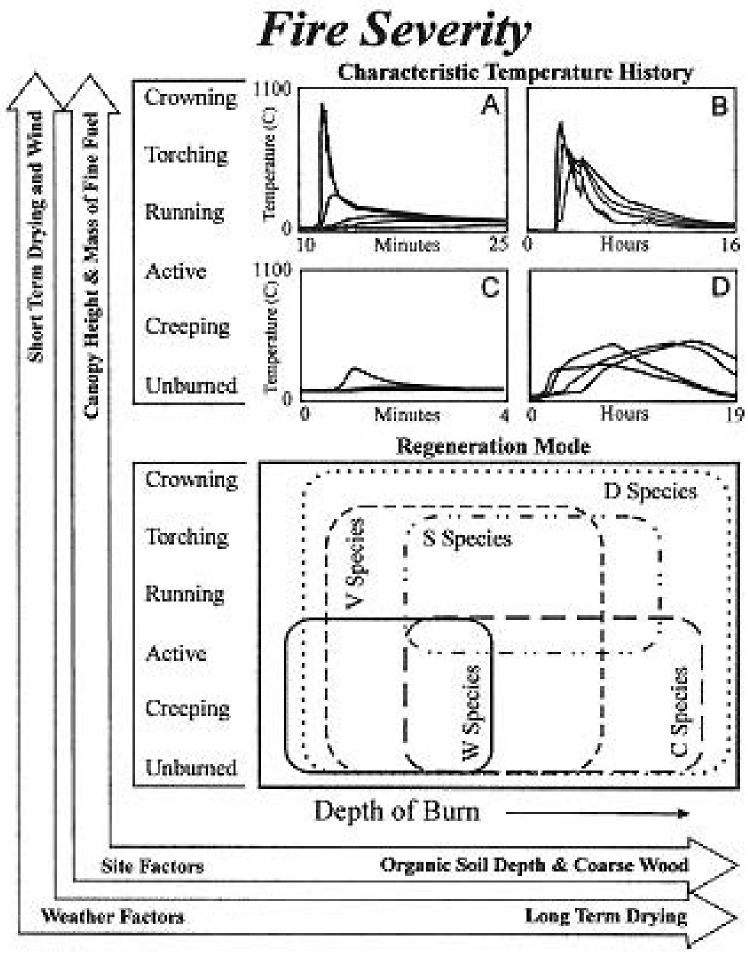


Figure 3: Fire Severity Matrix from Ryan 2002

Top: 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

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 net to affect fire intensity.

Bottom: Regeneration schemes favored under different circumstances. Definitions in Table #1

Table 1: From Ryan 2002, Modes of regeneration and reproduction – first vital processes of Noble and Slatyer (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 it (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

This matrix (fig. 3) suggests that surface fire intensity, and depth/degree 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 singe regeneration mode is in effect. From Ryan's work we can further predict that low levels of soil heating and low surface 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 dispersal across the landscape. In contrast, species' responses to higher levels of soil heating and fire intensity will be less predictable as spatially and temporally variable post-fire seed-rain 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 spatial patterns of fire intensity and refugia (surviving seed producing individuals) found to be significant by these studies.

The pattern of post-fire invasion and recovery can affect the pattern of community development for many years. Some species that resprout or invade following fire may persist in the community for many years and be able to regenerate in the absence of further disturbance, while other species will not be able to regenerate without future disturbances. Even though some invading species may only have a transient presence in the post-disturbance community due to an intolerance of competition, they may affect the presence or abundance of later successional species through changes they cause in the local environment. This cascading effect can result in a "ghost of impacts past" that is observable in the community's makeup well after the transient species has disappeared from the community.

Fire, the communities that experience them, and the effects of fire on said communities are often highly spatially variable and an understanding of the role of fire in these communities must incorporate this spatial component. As previous studies have documented, landscape patterns of topography, community type, and community structure affect the process of fire and vice versa (Turner 1989). As such, in studying fire effects it is necessary to look beyond the scale of the individual and plot to the scale of the watershed and landscape and backwards in time to the pre-fire conditions to understand fire's effects on patterns of community and species recovery.

Case study:

In this thesis, the pattern of succession after fire is studied in the dry pine and oak-pine forest communities of the Southern Appalachians. I also study the factors influencing patterns of invasion by focusing on the invasion of an exotic tree, *Paulownia tomentosa*, into these communities and compare the establishment and early survival of *Paulownia* to the native species that also respond to disturbance.

Although southern Appalachian dry pine and oak-pine communities have not received as much attention as other fire prone communities, fire played a significant role prior to widespread suppression (Harmon 1982, Harrod 1998). Past work by Harmon (1982) and Harrod (1998) has indicated that these communities experienced regular, low intensity fires which maintained open woodlands with higher intensity fires, at approximately 100 year intervals, giving rise to the majority of pine regeneration. As interest in these communities has increased, there has been a corresponding increase in the use of prescribed fires to mimic their historic fire regime.

In the 1990's researchers and land managers began to see *Paulownia* establishment after burning in native 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 documented in the GRSM in 1975 in association with major road cuts (Baron 1975)), and occasionally a few individuals had been seen in native plant communities following hurricanes (Williams 1993), these new invasions following fire 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 communities. As managers increasingly turn to prescribed fires to restore natural processes and encourage and perpetuate certain native plant communities and species, there is a concern that these practices may also result in an increase in the frequency of *Paulownia* in wild areas. As such, there is an increasing interest in the relationship between *Paulownia* and wildfire.

In addressing issues of significance to land managers with regards to this species, we can also test ideas and ask questions relevant to factors influencing patterns of disturbance and invasion generally. By looking at patterns of *Paulownia* invasion and native species establishment and recovery we can ask how fire severity causes differences in species response, how severity affects the importance of the seedbank, and whether these results are supportive of Ryan's placement of modes of regeneration within his Fire Severity Matrix. By comparing fires that burned in different seasons and by experimentally manipulating the season of burn, we can ask how much the season of burn matters to post-fire recovery for both *Paulownia* and native species. Analyzing the spatial distribution of *Paulownia* seeds in the soil will increase knowledge about patterns of seed dispersal and provide a framework for studying seed dispersal in other species. By comparing *Paulownia* invasion within and across fires, we can assess the degree to which *Paulownia* represents a risk to native communities, whether it influences the post-fire dynamics, species composition, or the density of native species. Methods used to predict patterns of *Paulownia* invasion can be generalized to provide guidelines for determining the invasive potential, impact, and necessary control efforts for other exotic species.

The goal of my research is to address the issues and questions outlined above in order to increase the general knowledge about the relationships between fire and the patterns of species recovery and invasion. The focus on *Paulownia* in particular will increase the depth of knowledge about this species and provide managers better tools for the control of exotic species in general and *Paulownia* in particular.

Chapter summaries

The summaries below present the general outline and foci of each chapter. The specific questions addressed in each chapter are listed within the body of that chapter. Further information on data collection methodology and the data used in each chapter and with each question can be found in Appendix I.

Chapter II: Relationships across fires

Utilizing data collected from five fires, this chapter analyzes how fire severity, season of burn, environmental conditions, and the presence and abundance of *Paulownia* affect patterns of native species cover and diversity. The first three of these factors plus the relative location of mature *Paulownia* trees are analyzed to determine their effects on the *Paulownia* seedling abundance and vigor within sampled plots and to ask whether *Paulownia* seedlings are likely to survive to maturity.

Chapter III: Linville Gorge

This chapter focuses on one fire (Linville Gorge) for which pre and post-fire data and spatial vegetation community data is available. It utilizes the watershed scale spatial data to ask what characteristics of topography, community type, and fire severity promote *Paulownia* invasion. Making use of pre and post-fire plot data, it analyses changes in diversity and composition and whether these are impacted by *Paulownia* presence or abundance. And finally, it asks whether the observed patterns of community recovery agree with those predicted by Ryan's fire severity matrix.

Chapter IV: Experiments

The first experiment tests the conditions under which *Paulownia* seeds survive fire while the second tests *Paulownia*'s germination rate under different conditions. The results of the second experiment are then compared with field survey data.

Chapter V: Seed bank

This chapter analyzes the results of a seed bank study undertaken on southwesterly facing dry forest communities of the GRSM. All germinating individuals were identified and the resulting composition compared with the above ground community's. The location of *Paulownia* germinants was analyzed to measure its abundance within the seed bank as a function of elevation and the relative location of mature individuals.

Chapter VI: Synthesis

This chapter gathers together the information obtained from the preceding chapters' analyses to make predictions about patterns of *Paulownia* invasion and exotic species invasions generally. The aim of this chapter is as much to create tools that will be useful to managers concerned with controlling *Paulownia,* as it is to synthesize and summarize the work of preceding chapters.

Chapter II: Effects of fire severity and site conditions on post-fire native and exotic species recovery and invasion patterns in the southern Appalachians

Rationale

Many native species are dependent on recurrent disturbance, including fire. Studying patterns of native establishment as a function of fire intensity will increase understanding of the fire-related processes that lead to community differentiation and local variation in species composition. Insight into the effect of fire severity upon *Paulownia* establishment will increase knowledge about the factors controlling its pattern of invasion. A comparison of these patterns will allow for a better understanding of the potential effects of *Paulownia* upon native species and enable managers to make more informed decisions regarding the use and effects of fire. This chapter attempts this through an extensive analysis conducted across fires and geography.

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 invasion. As land managers are increasingly interested in the use of prescribed fires and allowing wildfires to burn to encourage regeneration of native, fire-adapted pine and oak-pine communities, this represents a potentially significant problem.

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 more generally, have been explained by two basic constraints: spatial-temporal constraints and environmental constraints. Either a species is not there (has not yet invaded the habitat) because it has not yet gotten there due to dispersal limitations (spatial-temporal constraints) or the local site characteristics are not suitable to allow the species to germinate, grow, compete, and reproduce (environmental constraints). As *Paulownia* invades following disturbance (fire), environmental constraints that may affect the pattern of invasion include environmental conditions that are the result of fire effects in addition to inherent site environmental variables such as topographic position, slope, and aspect. Potential spatial constraints include distance from seed source, position within the landscape, or the direction from a site to seed sources. Direction and distance from each locality to seed source would be relevant as surrogates for the effect of wind patterns on seed availability. Wind-dispersed seeds, like those of *Paulownia*, are significantly affected by weather patterns and wind direction at the time of seed dispersal. Directly measuring these variables is intractable given the complexity of wind patterns and high levels of local variation. Direction and distance from the locality to neighboring seed trees is a substitute variable that, with today's GIS software, is relatively easy to calculate.

Another question of relevance to land managers is how long *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. Alternatively, if *Paulownia* presence and cover are not shown to have an impact on native species occurrence or recovery patterns (Chapter III), then control efforts may not be necessary in some situations. However, if *Paulownia* is able to establish a self-perpetuating population, and its presence does impact native species, then managing agencies must adopt a long-term approach to control.

Questions addressed and Methods utilized

Details about collection methodology, fire locations, and the data utilized in each question are included in Appendix I.

1. ***Question:*** How do fire severity, season of burn, environmental conditions, and the spatial location of mature *Paulownia* trees interact to control patterns of native species cover and diversity and *Paulownia* abundance and vigor within and across fires?

   a. What are the relationships between fire severity (as measured by light and soil disturbance), fire season, site-specific environmental variables (as measured by topographic position, slope, aspect, slope shape, elevation, and soil type and chemistry), and native species cover and diversity?

   Analyses: Regressions and regression trees will be used to look at ability of fire effect and environmental variables to predict the cover and diversity of native species. Ordination will be used to group plots into community types and fire intensity will be examined to see if it correlates with differences in community type or composition.

   b. Do the effects of fire severity as measured by light and soil disturbance, fire season, or site-specific environmental variables (as measured by topographic position, slope, aspect, slope shape, elevation, and soil type and chemistry) correlate with increased *Paulownia* invasion as measured by the number of seedlings and their height?

   Analyses: Classification and regression trees will be used to look at the ability of environmental and fire effects variables to predict the presence/absence and height respectively of *Paulownia*. Negative binomial regressions will look at the significance of these same variables as they predict the number of *Paulownia* stems and their height and a logistic regression will do the same to assess their relationship to the presence or absence of *Paulownia*. The community plot groupings in Q1a will be compared to see if Paulownia presence or abundance is associated with particular community types.

c. What is the relationship between *Paulownia* invasion and the relative spatial location of mature (seed producing) *Paulownia* trees?

i. Does *Paulownia* invasion increase as the distance to mature *Paulownia* trees decreases?

ii. Is *Paulownia* invasion impacted by the direction to mature trees?

Analyses: Distance and direction from each plot to the nearest mature Paulownia tree will be calculated with ArcMap using GIS coordinates of the plots and mature trees. These values will be added into the above data analyses to test whether they are significant predictors)

2. <u>*Question:*</u> How long does *Paulownia* persist following invasion under various physical conditions?

Analyses: Although sufficient time has not passed since the fires to observe whether or not the *Paulownia* seedlings survive to maturity and give rise to a subsequent generation, recounts of the # and height of *Paulownia* stems were conducted 1 or 2 years following the initial vegetation surveys. Regressions and classification trees will be used to see if the same variables, and the same level of these variables in the case of the classification trees, predict the presence and # of seedlings. Ordination will also be used to see if the plots that retain the highest number and healthiest (as measured by height) seedlings form a subset of the originally invaded plots that is identifiable by a particular variable(s). The condition of variables will then be assessed to see if they are likely to remain constant for the time period necessary for *Paulownia* to reach maturity.

Target for publication: *Biological Invasions* or *Biological Conservation*

Chapter III: Interactions between pre- and post-fire community composition, topography, fire severity, and exotic invasion at Linville Gorge, NC.

Rationale

Although it is generally accepted that pre-fire conditions influence fire intensity, the nature of the immediate post-fire community, and its subsequent recovery, researchers rarely possess data sets that enable them to test the interaction among these factors. Fortuitously, such an opportunity is present in Linville Gorge due to the establishment of plots by Claire Newell in 1992 prior to the November 2000 wildfire within the gorge, the resampling of these plots by Matt Reilly in 2003, and placement of further plots by myself in 2002 and 2003. The invasion of the burn by *Paulownia* combined with the pre- and post-fire plot data allows one to address the relationships between pre- and post-fire conditions, fire intensity, and native and exotic species recovery and invasion at the plot scale. At the watershed scale, knowledge of fire-intensity, the vegetation communities of the gorge, and the distribution of *Paulownia* seedlings across the burn allow a watershed-scale analysis of the interactions among these factors. This chapter differs from the preceding one in that it is an intensive study of a landscape rather than an extensive study across several. Further, the greater availability of data (temporal and spatial) for this landscape allows for a different suite of questions to be asked.

Research into these dynamics will allow researchers to derive better models of community response to fire in general, and fire response within southern Appalachian oak-pine and pine forests in particular. These data will also enable examination of the effect of pre-fire conditions on *Paulownia* invasion and the effect of *Paulownia* on recovery patterns, the first of which is not possible with other data sets used in this thesis.

Questions addressed Methods utilized

Details about collection methodology, fire locations, and the data utilized in each question are included in Appendix I.

A. *At the Watershed scale*

1. *Question:* Does Paulownia invasion increase with increasing site exposure, from mesic to xeric sites, and from less to more severely burned patches?

Analyses: ArcGIS will be used to create a combined map of fire intensity, community type, topography, the location of mature *Paulownia*, and the location of each plot and the number and height of Paulownia stems in each plot to look for correlations between these variables. Regression trees and correlations between the number and height of *Paulownia* stems, environmental and fire effects variables, and community type, will analyze the significance of each variable on the presence and abundance of *Paulownia*.

B. *At the stand (plot) scale*

1. *Question:* Does the diversity or composition of a particular strata increase as fire severity increases.

Analyses: Pre and post-fire species richness grouped by growth form will be analyzed using paired randomization tests of the difference in richness over time. Changes in composition will be analyzed using multi-response permutation procedure (MRPP) and non-metric multidimensional scaling (NMS) to look at the consistency of changes in composition. Gathered environmental variables, including the measurements of fire severity, will be overlaid on the NMS ordination to asses whether species composition varies with environmental variables, including fire severity.

2. *Question:* Does *Paulownia* cover, density, or height negatively correlate with the cover and diversity of other species at the range of sampled scales (5x5m and 10x10m)?

Analyses: Measures of *Paulownia* invasion success (# and height) will the regressed against native species cover (overall, dominant, by strata, and rare species) and diversity to test for significance.

3. *Question*: Do the observed patterns of community regeneration agree with those predicted by Ryan's fire severity matrix and are these affected by *Paulownia*?

Is community regeneration more heavily influenced by outside colonization

Target for publication: *Biological Invasion*s or *Biological Conservation*

Chapter IV: The effect of fire characteristics, light, surface cover, and burial depth on *Paulownia* germination

Rationale

There are two sets of factors relative to fire that control how well a species does in vegetation communities where fire plays a role: fire survival, and post- fire recovery and growth. If a species is not able to survive a fire in adult form, then it must be able to recolonize from seed. *Paulownia,* like other species whose life history strategy can be characterized along the Ruderal-Competitor side of Grime's Triangle (1977), is not found in "mature" pre-disturbance communities. These species are therefore faced with the challenge of invading the site after the disturbance. In order to do so species depend upon either survival in the seed bank, a yearly input of seeds (known as seed rain), or a combination of the two. Dependence on yearly seed rain requires the species to produce a great number of widely dispersed seeds every year. Additionally, for invasion to occur, a mature individual must be sufficiently close for its seeds to have a chance of arrival. Seed banking is also widely used by species, especially when the habitat conditions to which they are adapted are sufficiently uncommon in space or time such that that there is a low probability of seeds arriving at a suitable site in any given year. The seed bank is comprised of seeds that can remain dormant in the soil, sometimes for many years, till appropriate conditions are present. These two strategies are not mutually exclusive and many species rely on a combination of the two to ensure their continued existence. Although previous work has established that *Paulownia* seeds can be germinated under laboratory conditions after burial in the soil profile for two years (Longbrake 2001), the importance of seed banks to its invasion success and the effect of fire upon seed banks is unknown. Given the highly dispersed nature of *Paulownia's* seeds and the number of seeds that are produced by each tree every year, the yearly seed rain is also bound to be very important.

The first experiment addressed in this chapter will look at the importance of seedbanks for *Paulownia* following fire (through the surrogate measure of fire's impact on buried seeds). If fire characteristics affect the seedbank (though seed mortality), then this information can help land managers use prescribed fires that minimize the influence of seed banks (by killing the seeds within them) thereby increasing the dependence of invasion upon seed rain. If there is a spatial constraint to seed rain (Chapter V), then land managers can concentrate their post-fire control efforts on areas likely to receive the highest levels of seed rain. If there isn't a spatial constraint to seed rain, prescribed fires can still be designed to allow native species at least a season's worth of growth before faced with competition from *Paulownia* if *Paulownia* seeds are killed in the fire. If, on the other hand, fire characteristics have no effect upon the seed bank (seeds survive all natural fire types), then knowing the post-fire conditions which increase invasion success will help managers focus their control efforts (Chapter II, III).

The second experiment addressed in this chapter will measure the importance of different environmental characteristics (surface cover type and light level) upon the germination and growth of *Paulownia.* Although field surveys and observations can measure correlations between *Paulownia* and environmental variables such as surface cover type and light levels, they cannot directly test these relationships. Additionally, field surveys can only measure these environmental conditions at the time of the survey, conditions which may have changed since germination. Again, this is something that can only be determined through direct experimentation. Agreement between field surveys and experimental observations would give added weight to the significance of the findings, and experiments also allow the researcher to separate the influence of factors that may be confounding in the field (such as light and soil exposure).

For conservationists, knowing the germination and growth rates of *Paulownia* under different conditions will shed light on questions about *Paulownia's* potential to impact native species composition, frequency, and post- fire recovery; all significant issues for the conservation of native species and communities.

Questions addressed

1. *<u>Question:</u>* What is the effect of fire upon *Paulownia's* seedbank and early regeneration?
   a. Do *Paulownia* seeds survive fire and if so under what conditions do they survive? (Exp #1)
      i. What effect does seed position within the soil profile have upon germination?
      ii. What effect does fire intensity (maximum temperature) have upon germination?
      iii. What effect does the season of burn have upon germination?
   b. How does the germination of *Paulownia* affected by different conditions? (Exp #2)
      i. What effect does the amount of sunlight have upon germination?
      ii. How well do seeds germinate under different surface conditions
      iii. What effect does different burial depth have upon germination when combined with the surface conditions listed above?

Methods:

Although a direct test of the impact of fire on a potential *Paulownia* seedbank is logistically difficult if not impossible (due to the unknown quantity of seeds in the bank and their small nature making finding and counting them difficult to impossible), burying a known quantity of seeds and burning them allows for an approximation of this interaction that is experimentally tractable. Though the planned experiment will use only seeds from the previous fall (while a seed bank might contain seeds from many years), given the current complete lack of knowledge about the relationship between fire and seed survival from this species, the planned experimental design is a logical place to start.

These experiments have been run twice now, in 2004 in the Pisgah National Forest to the east of Linville Gorge (an attempt at a "natural" experiment) and again in 2005 at Mason Farm research field at the North Carolina Botanical Garden in Chapel Hill. Both of these attempts met with very limited success (1 seedling at Linville and ~10 at Mason Farm) despite high observed germination rates (70-80%) from the same set of seeds in the germination study. Only two other studies have tested field germination rates and they also reported very low field germination (~1% and 8% respectively) (Hyatt 1988, Longbrake 2001), but their germination rates were still orders of magnitude higher than the ones found in either summer. As mature Paulownia individuals are located at the Linville study site and the Mason farm trial received very high levels of care, this is unexpected. It may be that the seeds dried out after germination was initiated or seedlings were eaten by deer in the Linville Gorge trail, but supplemental watering and a deer fence should have prevented this problem at Mason farm. Based on conversations with Carol Baskin (of Baskin and Baskin's *Seeds*, 1996) it is suspected that soil texture may be a factor (seed viability having been ruled out by monthly germination trials). If so, this would indicate a previously unknown constraint on invasion success. Consequently, the experimental design has been retooled to test this possibility and minimize its effects when evaluating the effect of other variables. As a result, these experiments are being rerun in the spring/summer of 2006 within the greenhouse at UNC-Chapel Hill. Each "block" will consist of one quarter-flat and the “soil” used will be Promix. Although these conditions deviate significantly from “natural” conditions, the failure of previous summers’ experiments has lead to a desire to conduct them in a medium where *Paulownia* seeds have demonstrated a high germination rate. Simultaneous to the experiment, *Paulownia* seeds germination will be compared on soils from Linville Gorge, Mason Farm, and on Promix. Details on the Linville Gorge and Mason Farm trials are included in Appendix II.

Exp #1: Fire Survival

A randomized, block design will be used to examine the effect of burial depth, fire intensity (as measured by maximum temperature), and burn season on *Paulownia* seed germination. With 5 replicates, there are a total of 30 experimental blocks (3 burial x 2 intensity x 5 replicates). No unburned treatments are included because these conditions are present within experiment #2 and greenhouse space is limited. 100 *Paulownia* seeds will be added to each.

Burning will be conducted using a “burn tool” developed by Joan Walker with the National Forest Service’s Southern Research Station at Clemson University. This tool consists of an inverted propane burner attached to a tripod and lowered to the desired height above the soil surface. Temperature is recorded and displayed in real time through thermocouples at the soil surface attached to a data-logger and computer. *Paulownia* seeds will be enclosed in a wire mesh bag for the burn (done outside), retrieved, and germinated on a growing medium in the greenhouse.

Treatments:

Burial depth (3 levels): Litter surface (litter depth 5cm), soil surface, buried at 5cm
Burn season (2 levels): Spring, late summer
Fire Intensity (2 levels): Low intensity (200° C) and high intensity (500° C)

Exp#2: Effect of surface cover, light, and burial depth

Surface cover treatments and burial depths will be randomly assigned within a block design in each shade enclosure. 100 Paulownia seeds will be added to each block. 5 replicates results in 25 experimental blocks (3 burial x 2 cover x 5 replicates, with 1 treatment combination [bare soil ground cover and litter surface burial] removed because of impossibility) in each shade treatment. Each shade treatment will be replicated twice for a total of 100 experimental blocks.

Treatments:

Light level (2 levels): Full sun and 50% shade
Ground cover (2 levels): Litter (5cm), Bare soil
Burial depth (3 levels): Litter surface, Soil surface, 5cm into soil profile

Data, Analyses, and Results

The experiments did not yield sufficient germinants in 2004 or 2005 for any analyses. They will be conducted once more in the spring/summer of 2006

Target for publication: *AVS*

Chapters V: Modeling seed-banking across the landscape

Rationale

As pointed out previously, there are two fundamental constraints that limit the distribution of all species: environmental constraints and spatial-temporal constraints. Where previous chapters have addressed questions surrounding the spatial and environmental constraints that determine the distribution of *Paulownia* and other species' seedlings, this chapter addresses spatial constraints at the level of seed dispersal.

The invasion of species like *Paulownia* that are not present in the pre-disturbance community depends upon either a seed bank or post-disturbance seed rain. Species present in the pre-disturbance community may also rely upon seeds for recruitment or re-invasion if they do not survive the fire. Unfortunately, for most species the importance and spatial pattern of the seeb bank and seed rain is not known. Having such knowledge would greatly increase the ability to predict patterns and probabilities of recolonization and invasion for native and exotic species following disturbances and would be useful for conservationists working to protect or restore native plant populations and prevent exotic invasions.

Describing the seed dispersal (seed distribution) curve is, however, often difficult as it requires a great deal of data including: the identification of mature (seed producing) individuals, the collection of dispersed seeds, and the identification of distance and frequency determinants for the rare long-distance dispersal event. For common native species, the identification of seed sources and determining the source of collected seeds is particularly problematic. However for an exotic species like *Paulownia* where mature individuals are scattered, locatable, and absent from a nearby portion of the landscape, determining the dispersal curve may be possible. If seeds can be collected from soil samples taken across the uninvaded landscape, then the number of seeds at each sampled point can be used to build a dispersal curve. Such a method doesn't guarantee that the tail of the distribution will be captured but it does enable a characterization of the body of the curve. The spatial structure of the seed distribution and the circumstances under which *Paulownia* seeds survive fire will determine the best approach to limiting this species' spread and increase manager's ability to predict potential patterns of invasion. More generally, this knowledge will further efforts to create general models of seed dispersal for other wind-dispersed seeds.

For species with high rates of induced dormancy following a first growing season with conditions inappropriate for germination and growth, separation of the seed bank from the seed rain may be possible. Those that germinate readily can be assumed to be from the seed rain and those that require additional time or some manner of pre-treatment can be assumed to be from the seed bank. Unfortunately, *Paulownia* seeds stored in the field have been shown to have high levels of germination in the greenhouse and low rates of induced dormancy over the first two years following dispersal (Longbrake 2001). Consequently, there is no way to distinguish between the two. Soil sampling can however still build a composite curve of the number of viable, non-dormant seeds present in the soil at that time as a result of past seed dispersals.

Questions addressed

1. *Question:* What species are found in the seed bank of dry forest communities and how are they distributed spatially?
2. *Question:* How different is the composition of the seedbank from the plant communities of these sites as recorded in vegetation sample plots in dry forest communities?
3. *Question:* Does *Paulownia* occur in the dormant seed pool and is its presence a function of distance or direction from the Park boundary, or of elevation?

Methods

ArcGIS was used to select sites within the western portion of the GRSM on southwest facing slopes with xeric or sub-xeric vegetation types. These vegetation types were chosen because they are potentially burnable and hence invadable communities. Soil sampling sights were randomly selected from these areas within three elevation classes and three distance (from the park boundary) classes such that 10 sampling sites were chosen from every combination of elevation and distance classes where sufficient numbers of sites could be located. Sampling in this manner enabled a measurement of the effect of distance and elevation on seed abundance. The location of all *Paulownia* trees located in the vicinity of the park boundary were GPS'ed and the derived distance measurements used in subsequent analyses. Samples were collected in February and March of 2005 (seed dispersal occurs from the end of October through early December). Additional soil samples were taken from the base of a mature *Paulownia* tree located outside of the park and at 10m and 50m in each of the cardinal directions (N, S, E, W) from that tree. Said tree was chosen, as it was the closest to the park boundary. These 5 samples were used to definitively determine whether *Paulownia* seeds can be germinated from soil samples and to look at the short distance dispersal curve for *Paulownia's* seeds. As previous studies have shown that *Paulownia* seed survive well in the soil, have low rates of induced dormancy, and germinate readily in the greenhouse after two years of "storage" in the soil (Longbrake 2001), no follow up collections will be made as there is no way to determine a difference between the seed bank and the previous years seed rain in a soil sample. Soils were sieved to remove particles larger than 3cm and smaller than .25 mm and the remaining soil and seed mix was spread over a growing medium (Promix) with water and light provided. Germination is being tracked and will continue through November. All individuals that germinate will be identified to species where possible and if not to genus or family. Identifying all individuals that germinate rather than just *Paulownia* will increase knowledge about the seed bank in theses communities and will also suggest which species, like *Paulownia*, may be dependent upon fire or other disturbances for germination and which species *Paulownia* may compete with in the case of said event.

Data

Data on mature *Paulownia* tree locations from Michelle Crawley, the park service, and myself. Number of *Paulownia* and other species germinants found in each soil sample, The GPS'ed location of all soil samples, and the derived distance and direction from these soil samples to mature *Paulownia*.

Target for publication: *Natural Areas Journa*l

Chapter VI: From theory to practice: Creating *Paulownia* management tools for land managers and conservationists

Rationale

While knowledge gained form the work in the preceding chapters will prove useful to ecologists interested generally in patterns and mechanisms of invasion, and more specifically in patterns of *Paulownia* invasion, it will be most valuable to land managers and others concerned with controlling the spread of *Paulownia*. However, as long as this research remains solely academic in nature, describing mechanisms that control *Paulownia* invasion generally, it is likely to be of limited utility for land managers who have little time to translate the work into specific predictions for the properties they manage. Consequently, the knowledge gathered above will see the widest application and use if translated into a case study map illustrating the invasion threat to specific areas of the southern Appalachians (in this case Linville Gorge and the Western portion of the GRSM) and accompanied by decision trees for managers to use to determine appropriate steps to prevent of control *Paulownia* invasion.

Creating these predictive tools for *Paulownia* will also enable the creation of general methods and guidelines by which managers can create predictive tools and maps for other exotic species. Although different factors will undoubtedly be important with other species, the questions asked and methods used will be more generally applicable as steps to determine potential impact and pattern of invasion for other exotic species.

Questions addressed

1. *Question*: What predictions can be made about patterns of *Paulownia* invasion within communities, within a particular fire, and across the landscape?
2. *Question:* What questions, results, or methods from this work are applicable to land managers in other regions concerned with controlling *Paulownia* or other exotic species?
   a. Using the data gathered in the preceding chapters, what factors can be used in a decision tree that would be generally applicable to land managers in other areas where *Paulownia* is a species of concern?
   b. What generalities and predictive tools can be taken from this work with *Paulownia* and applied to predicting exotic species invasions generally?

Data

Data used will be the data gathered together in the preceding chapters

Results/Analyses:

No results or analyses have yet been generated. A predictive map will be created for two case study areas: Linville Gorge and the western portion of the GRSM (that portion covered in the seed bank study of Chapter V). A table of the factors used in the creation of the above maps and how the data relevant to them was collected will also be created to facilitate the collection of predictively useful data by land managers elsewhere. Finally, I will attempt to identify generalities that can be taken from this work and applied to the collection of data on other exotics for the purpose of predicting patterns of invasion.

Target for Publication: *Natural Areas Journal*

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Appendix I: Plot data collection methodology, plot locations, and chapter use

Data Collection Methodology

10x10m plots were laid down every 50 m along transects run across the slope. Transect length was determined by topography. Transect positions were chosen to maximize the range of fire intensities and landscape positions sampled within a burn. Geo-coordinates were recorded for each plot. At the Linville Gorge and Green Mountain fires, the location of mature *Paulownia* trees located in the vicinity of the fire was also recorded. All plots were surveyed according to the basic North Carolina Vegetation Survey (NCVS) protocol described in Peet et al. (1998) with the following variations and additions:

- Plots were subdivided into 5x5m subplots rather than the nested subplots standard to the CVS design. All ground, herb, shrub, and tree coverages and stem dbh's were recorded at the sub-plot level.
- The exact dbh of all stems >1cm was recorded. The dbh for stems that were not clearly dead prior to the fire but were now dead was recorded along with a species id and for data analysis purposes were assumed to be fire killed.
- Species cover at the shrub level was estimated for all shrubs that appeared to have died as a result of the fire.
- Estimates were made of the pre-fire cover by strata.
- A spherical densiometer was used to record canopy cover from plot center.
- Ground cover was estimated for: litter, rock (boulder and cobble), hummus, organic soil, and mineral soil. Litter depth, min. and max., was also measured along with a total hummus cover measurement including the cover of exposed hummus and that which was covered by litter. Measurements were taken at the plot and sun-plot level.
- The number and height of all *Paulownia* stems within each sub-plot was recorded.
- Fire intensity within each plot was visually estimated (1-5 scale) from percent dieback at each cover level (shrub, understory, etc), scorch height, and resprouting frequency.

Plots used in each Chapter

Of the plots listed above the following were used in Chapters II and III. All plots at a given fire were used unless noted otherwise. All plots will be used in every question except in chapter II, Question 2 where only the Linville Gorge and Green Mountain plots will be used.

Chapter II: All Fires

Linville: My plots + 1 randomly selected 10x10m from each Reilly and Kuppinger plot
Mill Ridge
Green Mountain
Firebug
Daw's Mountain

Chapter III: Linville

All of my Linville plots
Intensive modules from Newell's plots that were resampled by Reilly and myself
All of Matt Reilly's plots

Plot locations

Plots were located at the following fires. Within each fire, plots were laid out to maximize the variation in topographic position and fire intensities covered by the plots. Due to the inherent nature of fires, some locations have a limited representation of certain topographic positions and/or fire intensities.

Fire	Collected by	# of Plots	Location
Linville	Dane Kuppinger	55	Linville Gorge, Pisgah NF
Linville	Claire Newell Matt Reilly	188	Linville Gorge, Pisgah NF
Linville	Dane Kuppinger	20 burned, 5 unburned	Linville Gorge, Pisgah NF, resampling of Claire Newell's plots
Mill Ridge	Dane Kuppinger	13	Mill Ridge, S of Hot Springs, Pisgah NF
Green Mountain	Dane Kuppinger	63	Cherokee NF, along Foothills Parkway
Firebug	Dane Kuppinger	14	Cherokee NF, between I40 and GRSM, just over TN/NC line
Daw's Mountain	Dane Kuppinger	18	Sequatchie Valley, Cumberland Plateau, private land North of Dunlap
Tabcat	GRSM staff	3 burn, 3 unburn, pre and post burn	GRSM, Tabcat ridge

Appendix II: Methods of the 2004 and 2005 experiments on *Paulownia* germination

<u>*2004 Linville Gorge trail*</u>

The Linville Gorge attempt was conducted along Forest Service road 118 which formed the eastern firebreak for the 2000 Linville Gorge fire. The area selected was patchily and lightly burned and was chosen because it was a dry forest community and there were number of immature *Paulownia* trees just outside of the experimental area indicating that *Paulownia* seeds could germinate under in the soils present. It was also an area with very high levels of pine mortality from the pine beetle. This was important as I was not given permission from the Forest Service to cut down any living trees and I needed full sunlight for the experiments. All downed trees were cut and pulled to the side and all ground vegetation was clipped at ground height before the experiment was laid out. No supplemental watering was possible and below ground vegetation was not removed.

At both the Linville Gorge and Mason Farm trials Table Mountain Pine (*Pinus pungens*) seeds were added to the treatment blocks in experiment #2 so that the relative germination rates of these species could be compared. *P. pungens* was chosen as a species of interest to conservationists as a southern Appalachian endemic, one of the prime foci of fire management in these xeric communities, and as an often used measure (via regeneration rates) of the success of fire reintroduction programs. Although experimental measures of the germination success of *Paulownia* and *P. pungens* under different conditions is not a complete test of *Paulownia's* potential ability to impact native species and communities, it would shed some light on this question. It could also be argued that there are species with seeds that are more similar to *Paulownia's* (ex. a small seeded ericad), but such seeds are much more difficult to obtain and for many species, including the ericad's in these habitats, vegetative regrowth plays a bigger role in species' post-fire recovery than establishment of new individuals from seed. *P. pungens* will not be included in the 2006 trial due to difficult of collection, greenhouse space limitations, and a desire (given the previous failures) to simplify the experiment as much as possible.

2005 Mason Farm trial

The Mason Farm site had been covered by a light blocking landscaper's cover eliminating perennials for the previous 2 years. Subsequent to its removal, the ground was plowed with a disk plow to a depth of 16 inches and then tilled to 6 inches with a roto-tiller to further break up the soil. Once the experiment was initiated, seeds were watered every other day and the blocks were kept free of weeds. The Mason Farm layout was the same as at Linville Gorge except for the removal of the Soil moisture treatment in experiment #1.

Exp #1: Fire survival

A randomized, block design was used to examine the effect of burial depth, fire intensity (as measured by maximum temperature), and burn season on *Paulownia* seed germination. With 5 replicates, there were a total of 100 20x20cm experimental blocks (80 burn blocks [4 burial x 2 intensity x 2 moisture x 5 replicates] and 20 unburned blocks [4 burial x 5 replicates]) for the spring burn and the same in the fall. 100 Paulownia seeds were added to each 20x20cm block. The late summer burn was not done because of the extremely low germination rates.

Burning was conducted using a "burn tool" developed by Joan Walker with the National Forest Service's Southern Research Station at Clemson University. This tool consists of an inverted propane burner attached to a tripod and lowered to the desired height above the soil surface. Temperature is recorded and displayed in real time through thermocouples at the soil surface attached to a data-logger and computer. Soil moisture was measured with a sol probe immediately prior to burning.

Treatments

Burial depth (4 levels): No seeds added, litter surface (depth 4cm), soil surface, buried at 5cm
Burn season (2 levels): Spring, late summer
Fire Intensity (2 levels): Unburned, low intensity (200° C), and high intensity (500° C)
Soil Moisture (2levels): Ambient, Wetted

Exp#2: Effect of surface cover, light, and burial depth

Surface cover treatments and burial depths were randomly assigned within a block design in each shade enclosure. 100 Paulownia seeds were added to each 20x20cm block and 5 *P. pungens* seeds were added to replicates 1, 3, and 5 within each light treatment (with the exception of the No seeds added treatment level in the burial treatment). 5 replicates resulted in 55 20x20cm experimental blocks (4 burial x 3 cover x 5 replicates, with 1 treatment combination [bare soil ground cover and litter surface burial] removed because of impossibility) in each shade treatment. Each shade treatment was replicated twice for a total of 220 experimental blocks.

Treatments

Light level (2 levels): Full sun and 50% shade
Ground cover (3 levels): Deep litter (5cm), Shallow litter (2cm), Bare soil
Burial depth (4 levels): None (no seeds added), Litter surface, Soil surface, 5cm into soil profile