

ABSTRACT OF DISSERTATION

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The Graduate School
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UPLAND OAK AND RED MAPLE: COMMUNITY RESPONSE AND ECOSYSTEM
EFFECTS IN THE PRESENCE AND ABSENCE
OF FIRE DISTURBANCES

ABSTRACT OF DISSERTATION

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
College of Arts and Sciences
at the University of Kentucky

By

Heather Dawn Alexander

Director: Dr. Mary A. Arthur, Professor
Lexington, Kentucky
2008

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Shifts in forest canopy composition are increasingly common due to invasive pests and pathogens, climate change, and altered disturbance regimes. Development of restoration strategies aimed at mitigating these changes is critical, but research should also assess ecosystem-level implications given failed or limited restoration efforts. In historically oak-dominated forests of the eastern U.S., fire suppression has increased competition from fire-sensitive species, leading to decreased understory light and oak (*Quercus* spp.) regeneration problems. Prescribed fire is often used to remedy these conditions and encourage oak establishment and growth, but the efficacy of this strategy remains questionable. This dissertation describes changes in understory light and upland oak and competitor seedling survival, growth, and foliar morphology and chemistry in response to single and repeated (3x) prescribed fires over a 6-yr period (2002-2007) within eastern Kentucky. Prescribed fires led to high mortality and reduced growth of white oaks (*Leucobalanus* spp.), but a single burn with high burn temperatures and overstory mortality enhanced red oak (*Erythrobalanus* spp.) seedling growth. Among competitors, fires negatively impacted red maple (*Acer rubrum*) survival, but increased sassafras (*Sassafras albidum*) growth with virtually no effect on survival. Understory light increased temporarily post-burn and was ultimately 6% higher on repetitively-burned sites compared to those unburned or burned once. Fires altered foliar morphology and chemistry, but differences among seedling groups were either minimal or indicated an enhanced response of competitors. I also address whether a predicted shift from upland oaks to red maple, in the absence of successful restoration efforts, could influence forest hydrology and nutrient availability. Red maple funneled more precipitation and generated substantially more stemflow than oaks, leading to larger inputs of stemflow-derived nutrients. Additionally, soils underlying red maple had greater rates of net nitrogen mineralization. These findings suggest that upland oak seedlings in eastern deciduous forests are not responding to low-intensity, early growing-season prescribed fires in a manner that consistently places them in a more competitive position. In the absence of fire, increased red maple dominance could impact forest hydrology and

nutrient cycling, which has implications for disturbance regimes and future canopy and understory vegetation composition and growth.

Key words: oak regeneration, prescribed fire, stemflow, oak, red maple

Student's Signature

Date

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*To My Grandfather and Hero,
James Leonard Inabnet
(1922-2004)*

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CHAPTER 1

OVERVIEW OF TREE SPECIES EFFECTS ON ECOSYSTEM PROPERTIES AND IMPLICATIONS OF SHIFTING CANOPY COMPOSITION

Forests are biological communities dominated by trees and other woody plants (Barnes *et al.* 1998), and they are broadly classified into biomes based on climatic differences in precipitation and temperature (Whittaker 1975), physiographic features, and physiognomic similarities of dominant plants, which occur in response to environmental conditions (Barnes *et al.* 1998). While variations in environmental factors strongly influence the types and characteristics of dominant trees, plant traits also impact their surrounding environment. For example, cold temperatures and a short, cool growing season within boreal forests favor conifers, which have tough, thick, needles to minimize water loss, resist freezing, and deter herbivory. These recalcitrant conifer needles interact with climate to produce nutrient poor, acidic soils with slow decomposition and a thick organic matter layer that promotes fire disturbances. In comparison, a long, warm growing season and short, cool winter with freezing temperatures promote deciduousness in temperate forests, and annual litterfall of higher quality leaves and relatively warm climate produce faster decomposition and nutrient release into underlying soils (Barnes *et al.* 1998).

At a finer scale, individual tree species within forest types and stands can have very different impacts on ecological properties and processes. Different species produce leaves of various quantity, chemistry, and longevity, and these properties contribute to forest floor decomposition rates and recycling of essential nutrients for plant and microbial growth (Scott and Binkley 1997; Cornwell *et al.* 2008). Binkley and Giardina (1998) compiled results from experimental comparisons of species' effects on soils and found species differed by 20-50% in forest floor mass, litterfall mass and nitrogen (N) content, and net N mineralization. They further suggest a positive feedback loop between the fitness of individual trees and their own modification of understory conditions. Species differences in canopy architecture, including canopy density, branch inclination, and bark texture impact forest hydrology, understory microclimate, and nutrient inputs

via impacts on precipitation distribution (Levia and Frost 2003), light attenuation, air temperature, and humidity (Porte *et al.* 2004). Barbier *et al.* (2008) reviewed these species-specific effects on microclimate and resource availability and found they often influence understory vegetation diversity. Further, interspecific differences in tree growth rates, size, and life span affect long-term carbon (C) storage and sequestration, and consequently have implications for reforestation projects aimed at maximizing stand level C stocks and mitigating global climate change (Kirby and Potvin 2007).

While trees may have functionally overlapping characteristics, some species are so unique that dramatic declines in their abundance would have cascading impacts on the entire forest ecosystem. Ellison *et al.* (2005) defined these as ‘foundation species,’ those which define a community’s structure and function by creating locally stable conditions for other species and by modulating and stabilizing fundamental ecosystem processes. These species are by definition “irreplaceable” and play a similar role to that of keystone predators in having large impacts on community dynamics and ecosystem properties and processes, but differ because they are at lower trophic levels than predators and are usually dominant (Ellison *et al.* 2005).

Alarmingly, anthropogenic alteration of disturbance regimes has reduced numbers of foundation species at unprecedented rates (Ellison *et al.* 2005). Human impacts on disturbances include increased frequency and magnitude (*e.g.*, timber harvesting; Peres *et al.* 2006), changed mode and potency (*e.g.*, introducing pests and pathogens; Lovett *et al.* 2006)), and complete removal from the system (*e.g.*, fire suppression; Nowacki and Abrams 2008). The impacts on foundation species are far-reaching. In the eastern U.S., eastern hemlock (*Tsuga canadensis* L. (Carr)) has experienced massive die-backs because of the invasive hemlock wooly adelgid (*Adelges tsugae*; Orwig *et al.* 2002). *Acacia* spp., the dominant tree species in the Negev desert, Israel, have decreased due to water stress from aquifer pumping and poor road construction (Munzbergova and Ward 2002). Trembling aspen (*Populus tremuloides* Michx.), in the western U.S. and Canada, has declined because of reduced wildfire and overgrazing by livestock (Jones *et al.* 2005).

Oaks (*Quercus* spp.) provide another example of foundation species at threat across their range (McShea *et al.* 2007). Oaks comprise over 400 species worldwide and

dominate a variety of ecosystems, including temperate deciduous forests, chaparrals, savannahs, and broad-leaf evergreen forests (Johnson *et al.* 2002). Oaks fall into the ‘foundation species’ category in many regions because they produce a nutrient-rich hard mast consumed by numerous birds and mammals (McShea and Healy 2002), including 96 vertebrate species in North America (Martin *et al.* 1961). Additionally, they possess many adaptations to dry, fire-prone habitats that have large influences on ecosystem processes and properties. For instance, oaks have thick, corky, rough bark, which renders them fire-tolerant (Abrams 1992), but these characteristics also strongly influence precipitation distribution to forest soils via stemflow, *i.e.*, the rainwater which trees funnel down their branches and trunk to underlying soils (Andre *et al.* 2008). Oaks also have xeromorphic leaves (Abrams 1992), with a thick, waxy cuticle (Witkamp and Olson 1963) comprised of recalcitrant carbon-rich molecules (Suberkropp *et al.* 1976), which minimizes water loss but also likely slows decomposition rates and decreases nutrient availability (Shure *et al.* 1986). Oak leaf litter can also be a primary fuel source, thereby influencing susceptibility to fire disturbances (Abrams 2005).

Studies both within and outside the U.S. indicate widespread regeneration failure of many oaks. While impediments to oak regeneration may arise naturally from weather, pests, and pathogens (Johnson *et al.* 2002), studies often reveal problems in forests with considerable human influence. For instance, altered disturbance regimes in Scotland have decreased understory light and increased competition with oak seedlings (Humphrey and Swaine 1997). Habitat fragmentation and heavy urbanization have promoted large rodent populations in China, increasing acorn predation (Sun *et al.* 2004), and diseases and stress in Italy have increased overstory mortality leading to reduced acorn abundance (Vettrano *et al.* 2002).

One area where oak regeneration is particularly problematic is the deciduous forest of the eastern U.S. Here, oak forests cover over 67.3 million hectares (McWilliams *et al.* 2002), and while oak trees are often abundant, field surveys indicate a “bottleneck” between the seedling and sapling stage (Abrams and Downs 1990; Abrams and Nowacki 1992). For instance, Loftis (1988) estimated oak seedling survival of < 10% over 12 years underneath mature northern red oak (*Q. rubra* L.) in the southern Appalachian Mountains, and Lorimer (1983) measured a 90% mortality rate for overtopped red oak

saplings on a dry-mesic site in central Massachusetts. Many researchers hypothesize that this trend is due to increased cover of co-occurring competitors and low understory light resulting from more than 70 years of fire suppression (Abrams 1992; Lorimer *et al.* 1994). Oaks are only moderately shade-tolerant (Burns and Honkala 1990) and have a conservative growth strategy, which promotes root rather than shoot growth, especially in early life stages, and facilitates re-growth after topkill (Brose and Van Lear 2004). To grow to a competitive size and eventually recruit into the overstory, oaks require periodic disturbance-generated canopy gaps to increase understory light (Dey and Parker 1996). Without fire or other disturbances, oak seedlings are simply never able to grow to a sufficient size to become competitive with shade-tolerant competitors, which typically have a non-conservative growth strategy, so they overtop nearby oak seedlings, further impeding oak seedling development (Loftis 1990b; Abrams 1992; Lorimer *et al.* 1994). Other evidence supporting this ‘oak-fire hypothesis’ are pollen records, which demonstrate decreased oak pollen and increased pollen of fire-sensitive species since initiation of fire suppression ~1930 (Delcourt and Delcourt 1997), and dendrochronological analyses of fire scars, which show widespread, frequent fires during or just prior to the establishment of current oak overstories (McEwan *et al.* 2007).

Red maple is one shade-tolerant species that has exhibited a “dramatic rise” since fire suppression and “by far, the largest increase in species frequency on present-day upland oaks sites” (Abrams 2005). Red maple is a “super-generalist,” with characteristics of both early and late successional species and ability to thrive in open, recently disturbed places as well as in the shade of the forest canopy (Abrams 1998). Once limited to mesic coves, swamps, and riparian areas protected from fires (Abrams 1998), dendrochronological analyses show substantial red maple recruitment into forest overstories since fire suppression, while upland oak recruitment virtually ceased (Hutchinson *et al.* 2008). Studies evaluating red maple’s proliferation indicate increased basal area, density, importance value (Lorimer 1984; Alderman *et al.* 2005; Abrams 2005), and range expansion (Fei and Steiner 2007). Although red maple is native to the U.S., it has many invasive characteristics which have contributed to its success, including high reproductive capacity, early maturity, and flexible germination strategy (Abrams 1998; Hille Ris Lambers and Clark 2005).

Poor oak regeneration coupled with increased red maple abundance has led many researchers to predict an inevitable transition from oaks to red maple or other fire-sensitive species (Abrams 2005; McEwan *et al.* 2005; Nowacki and Abrams 2008; Fei and Steiner 2007), prompting several interrelated questions addressed in this dissertation:

Chapter 2: If this trend is driven by a lack of fire, can prescribed fire serve as a restoration tool to decrease seedling competitors, increase understory light, and promote oak seedling survival and growth? In theory, burning would preferentially select for oak seedlings and saplings because of their hypogeal germination, which places dormant buds below the soil surface and minimizes fire damage. Also, oaks have a conservative growth strategy, which promotes the development of a large belowground root system that facilitates re-growth after topkill (Brose and Van Lear 2004). In contrast, burning would target many co-occurring fire-sensitive species because of their epigeal germination and a non-conservative growth strategy, which promotes height over diameter growth (Lorimer *et al.* 1994), but often exposes dormant buds to high burn temperatures (Brose and Van Lear 2004). Decreased competition and increased light would allow oak seedlings to grow to a sufficient size to compete following a disturbance-generated canopy opening. Fire could also provide such a canopy release if post-fire mortality of overstory trees was substantial.

Chapter 3: What are the underlying, leaf-level mechanisms impacting oak and co-occurring competitor seedling response to prescribed fire? Previous work has indicated that leaf traits can provide valuable information regarding plant ecophysiological response to environmental conditions (Abrams *et al.* 1994), mechanisms affecting growth patterns and competitive interactions (Reich *et al.* 1990), and leaf susceptibility to herbivory (Rieske 2002). If fire increases light, seedlings may acclimate by increasing their total leaf area (TLA) and leaf mass per area (LMA), and if fire increases soil N availability (Wan *et al.* 2001) this should be reflected in leaf N concentration. These responses would be more pronounced in oak seedlings compared to co-occurring competitors, such as red maple and sassafras, because their conservative growth strategy promotes a large belowground root reserve, providing energy to offset costs associated with building new leaves with high C or N. Enhanced leaf characteristics may then be reflected in growth parameters, such as basal diameter.

Chapter 4: If prescribed fire does not foster oak regeneration and halt red maple proliferation, would a shift from upland oaks to red maple influence forest hydrology and nutrient cycling? Compared to oaks, red maples have a completely different set of traits, including smooth, thin bark, a dense canopy, and lignin-poor leaves. Bark and canopy traits are known to influence precipitation distribution via throughfall and stemflow (Levia and Frost 2003). Specifically, species with dense canopies often distribute less rainfall to underlying forest floors (Morris *et al.* 2003). Species with smooth bark funnel precipitation into stemflow, which concentrates precipitation in a limited area around the tree's trunk (Levia and Herwitz 2005). These general trends suggest a dominance shift from oak to red maple would alter precipitation distribution, consequently impacting the quantity and chemistry of nutrient inputs to underlying soils and soil moisture. Changes in these properties could then influence a suite of ecological parameters, including plant growth and distribution, nutrient cycling, leaching losses, litter decomposition, and fuel bed continuity (hence, propensity for fire disturbances).

These questions were addressed within second-growth (~ 80 years old) forests in the Cumberland District of the Daniel Boone National Forest of eastern Kentucky. Overstories were dominated by oaks, especially scarlet and chestnut oak (*Q. coccinea* Muench. and *Q. montana* L., respectively). However, oak saplings were rare, and red maple was a substantial understory and midstory component (Arthur *et al.* 1998; Kuddes-Fischer and Arthur 2002; Green 2005). These forests provide a unique opportunity to explore both the potential role of prescribed fire as a management tool to regenerate oaks and how a gradual shift from predominantly oaks to red maple could affect ecosystem properties and processes.

CHAPTER 2

SURVIVAL AND GROWTH OF UPLAND OAK AND CO-OCCURRING COMPETITOR SEEDLINGS FOLLOWING SINGLE AND REPEATED PRESCRIBED FIRES

ABSTRACT

Studies within and outside the U.S. indicate recurring oak (*Quercus* spp.) regeneration problems. In deciduous forests of the eastern U.S., a prevailing explanation for this trend is fire suppression leading to high competitor abundance and low understory light. In response, prescribed fire is increasingly used as a management tool to remedy these conditions and encourage future oak establishment and growth. Within eastern Kentucky, I implemented single and repeated (3x) prescribed fires over a 6-yr period (2002-2007). Pre- and post-burn, I quantified canopy cover and oak seedling survival and growth compared to other woody seedlings deemed potential competitors, primarily red maple (*Acer rubrum* L.) and sassafras (*Sassafras albidum* (Nutt.) Nees.). Burning temporarily decreased canopy cover by 3-10%, but cover rebounded the subsequent growing season. Repeated burning ultimately produced canopy cover about 6% lower than sites unburned and burned once, suggesting a cumulative effect on understory light. Red maple seedlings exhibited low survival (~ 40%) following single and repeated burns, but growth remained similar to those unburned. Burning had little impact on sassafras survival and led to total height and basal diameters 2x greater than those of unburned seedlings. A single burn had no impact on red oak (*Erythrobalanus* spp.) survival and increased height and basal diameters 25-30%, but this positive growth response was driven by seedlings on several plots which experienced high burn temperatures and consequently high overstory mortality. White oaks (*Leucobalanus* spp.), however, exhibited twice as high mortality compared to those unburned, with no change in growth parameters. Repeated burning negatively impacted survival and growth of both oak groups compared to unburned seedlings. With both burn regimes, oaks with smaller pre-burn basal diameters exhibited the lowest post-burn survival. Thus, despite the ability of prescribed burns to temporarily increase understory light and reduce red maple survival, neither single or repeated burns

placed oaks in an improved competitive position. These findings result from a combination of highly variable yet interdependent factors including the 1) life history traits of oaks compared to their co-occurring competitors, 2) pre-burn stature of pre-existing oak seedlings, and 3) variability in fire temperature and effects on understory light.

INTRODUCTION

Oaks (*Quercus* spp.) comprise a large, diverse genus of ~ 400 species worldwide distributed across various biomes, including temperate deciduous forests, chaparrals, savannahs, and broad-leaf evergreen forests (Johnson *et al.* 2002). This genus is important not only in terms of dominance, but in its production of a nutrient-rich, hard mast consumed by numerous birds and mammals (McShea and Healy 2002). Oaks have been deemed keystone species because of their cascading effects on wildlife species (Fralish 2004) and foundation species because of their direct and indirect influences on overall community dynamics and ecosystem processes (Ellison *et al.* 2005; McShea *et al.* 2007).

Studies both within and outside the U.S. indicate recurring problems with oak regeneration, a complex, lengthy process consisting of flowering and pollination, acorn production, acorn germination and seedling establishment, seedling development, and eventual overstory recruitment following canopy release. Impediments to oak regeneration may arise naturally from weather, pests, and pathogens (Johnson *et al.* 2002), but studies often reveal problems in forests with considerable human influence. For instance, altered disturbance regimes in Scotland have decreased understory light and increased competition (Humphrey and Swaine 1997). Habitat fragmentation and heavy urbanization have promoted large rodent populations in China, increasing acorn predation (Sun *et al.* 2004), and diseases and stress in Italy have increased overstory mortality leading to reduced acorn abundance (Vettraino *et al.* 2002).

In deciduous forests of the eastern U.S., a prevailing explanation for poor oak regeneration is fire suppression and consequently high competitor abundance and low understory light (Abrams 1992; Abrams and Nowacki 1992). Pollen records demonstrate decreased oak pollen and increased pollen of fire-sensitive species since initiation of fire

suppression ~1930 (Delcourt and Delcourt 1997), and dendrochronological analyses of fire scars show widespread, frequent fires during or just prior to the establishment of current oak overstories (McEwan *et al.* 2007). Paradoxically, recent modeling of climate change impacts to species in eastern U.S. forests suggest upland oak populations should increase as conditions becomes hotter and drier, while fire-sensitive species like red maple (*Acer rubrum* L.) should decrease (Iverson and Prasad 2002).

Ecologically, upland oaks have life history traits suggesting they are fire-adapted. Their conservative growth strategy promotes a large root system, which facilitates resprouting after top-kill and efficient water and nutrient use (Lorimer 1985; Abrams 1992) in dry, fire-prone habitats. Most oaks have moderate shade-tolerance (Burns and Honkala 1990) and are successful in relatively high light environments where low moisture is a key limiting factor to competitors (Abrams 1992). In contrast, many fire-sensitive species thrive in the absence of fire disturbances because of their higher shade tolerance and non-conservative growth strategy, which allow greater height growth than oaks under a dense canopy (Lorimer *et al.* 1994). Without disturbances to decrease cover of these shade-tolerant species, they can reduce understory light, further impeding oak development (Loftis 1990b; Lorimer *et al.* 1994). Small oak seedlings are often less successful following release (Loftis 1990a), primarily because they are unable to compete with faster-growing, shade-intolerant species of seed origin like yellow-poplar (*Liriodendron tulipifera* L.) and sprouts of residual stems of shade-tolerant species (Beck and Hooper 1986).

In theory, prescribed fires could enhance oak regeneration by increasing understory light and decreasing competition from co-occurring, fire-sensitive species, thereby providing a population of oak seedlings of sufficient size to compete following a disturbance-generated canopy opening. Fire could also provide a canopy release if post-fire mortality of overstory trees was substantial. To understand the ability of prescribed fire to create these conditions, I quantified pre- and post-burn canopy cover and individual oak seedling growth and survival compared to other woody seedlings deemed potential competitors, primarily red maple and sassafras (*Sassafras albidum* (Nutt.) Nees.). These species differ from oaks and each other in their life history traits, namely shade tolerance and growth strategies. This study capitalizes on sites encompassing a

diverse terrain, a large number (~ 3,000) of pre-established woody seedlings, a relatively long-term data set (6-yr), and both single and multiple (3x) burns.

METHODS

Study area

This study was conducted in the Cumberland Ranger District of the Daniel Boone National Forest (DBNF) of eastern Kentucky. Climate is humid, temperate, and continental with hot summers and mild winters. Annual air temperature averages 12.8 °C, with mean daily temperatures of 0.5 °C in January and 24 °C in July. Mean annual precipitation (122 cm) is equally distributed throughout the year (Foster and Conner 2001).

Forest stands were second-growth, about 80 yr old, and ranged in oak site index from SI 50 to 100. Pre-burn basal area of stems ≥ 10 cm diameter at breast height (DBH) was ~ 20-30 m² ha⁻¹ (Table 2.1), and oak and hickory (*Carya* spp.) dominated the overstory. Prevalent overstory red oaks (*Erythrobalanus* spp.) on mid- and upper slopes included scarlet (*Q. coccinea* Muenchh) and black (*Q. velutina* Lam.) oak, with northern red oak (*Q. rubra* L.) common on lower slopes. Prevalent white oak species (*Leucobalanus* spp.) were white (*Q. alba* L.) and chestnut (*Q. montana* L.) oak. Maples (*Acer* spp.), downy serviceberry (*Amelanchier arborea* (Michx. f.) Fern), black gum (*Nyssa sylvatica* Marshall), and sourwood (*Oxydendrum arboreum* (L.) DC.) dominated the midstory (2-10 cm DBH). Red maple comprised ~ 45% of midstory (2-10 cm DBH) stem density, while oaks comprised < 3%.

Experimental design

Within an 18-km² area, three study sites (Buck Creek, Chestnut Cliffs, and Wolf Pen) of ~ 200 to 300 ha each were subdivided into three burn treatments encompassing 58 to 116 ha. Treatments were an unburned control, less frequently burned (5+ yr interval), and frequently burned (1-2 yr interval), and were selected based on prior studies suggesting a < 5-yr burn interval to suppress growth of woody competitors, such as red maple (Sander 1988), and historical evidence that low-intensity surface fires occurred in the region every 3-4 yr (Sutherland 1997).

Within each treatment, 8 to 12 sample plots were chosen using a grid overlaid on a topographic map. Plots were 10-m wide x 40-m long and arrayed parallel to topographic contours. Plots encompassed a variety of aspects, slopes (often exceeding 60%), and elevation (260 to 360 m) and were classified as sub-xeric, intermediate, or sub-mesic (Table 2.1; McNab *et al.* 2007) to objectively account for this variability, which could affect fire behavior (Loucks *et al.* 2008).

Prescribed fires

The U.S. Forest Service conducted fires using drip torches and helicopter ignition. Frequently burned sites were burned spring 2003, 2004, and 2006, while infrequently burned sites were burned spring 2003; future references to treatments will be “Burned 1x” and “Burned 3x.” All burns were conducted between March 26 and April 16, when air temperatures were 20-27 °C, and relative humidity was 23-45% (Table 2.2). Late spring burns were used to maximize impacts on competitors during bud swell, a period when seedlings have reduced root carbohydrate reserves. The large size and highly dissected topography of the study sites and concern for personnel safety prevented assessment of flame height and spread rates (*i.e.*, fire intensity); thus, fire temperatures were recorded at four locations within each plot via pyrometers (see Loucks *et al.* 2008 for methodology). Because of the relatively steep slopes present across plots and fuel discontinuity after the previous year’s burn, several plots within Wolf Pen and Buck Creek did not burn during the 2004 fire, leading to relatively low mean burn temperatures.

Canopy cover

Canopy cover was estimated using hemispherical photography at three locations (10, 20, and 30 m) along the bottom axis of each sampling plot within the Buck Creek study site only, due to sampling logistics. Photographs were taken either before sunrise, after sunset, or when overcast to limit uneven exposure due to direct sunlight. In 2005, measurements were only taken at the 10-m location. Photographs were taken 80 cm above the forest floor using a Nikon FC-E8 183° fisheye converter attached to a digital camera, placed on a Delta-T Devices self-leveling mount, and positioned toward magnetic N. Prior to image analysis using HemiView 2.1, Adobe Photoshop® was used to remove lighted direction markers and help maximize contrast between open sky and

canopy. Images were analyzed at random and evaluated three times by a single analyst to produce an average canopy cover value for each location at each plot.

Seedling survival and growth

To determine seedling survival and growth, ~ 3,000 seedlings of oaks and their most predominant competitors were permanently tagged in June 2002 prior to burning. Any available seedling was selected from the pool of advance regeneration (98% of selected seedlings were ≤ 60 cm; mean height of 21.5 ± 14.1 cm; bud scars visible from multiple years), and no true seedlings were observed or marked. To facilitate re-measurement, seedlings were tagged with a unique identification number and mapped. Seedlings typically included 10 individuals each of the dominant white (*Leucobalanus* spp.) and red oak (*Erythrobalanus* spp.) subgenera and the most abundant competitor species, totaling ~ 30 individual seedlings per plot. On occasion, only a single oak species was present, or multiple species within subgenera were needed to obtain 10 oak seedlings. Plots encompassed a variety of species assemblages distributed across landscape positions (Table 2.3).

Annually, from 2002 to 2007, seedlings were measured during the growing season (June-August) for survival, basal diameter, total stem height, and annual height growth. Two perpendicular measurements of basal diameter were made with a digital caliper where the stem exited the soil. Total height was measured with a ruler from stem base to the leading shoot tip, and annual height growth was measured on the leading shoot from the last visible bud scar to the shoot tip. Seedlings were considered dead when no trace of shoot or root, or live tissues, was found. Seedlings recorded dead one year but that had re-sprouted the next were re-classified as alive for the prior sampling period. Seedlings not located were removed from subsequent analyses. According to pyrometer data, the 2003 and 2006 fires burned every plot, and 93 and 95%, respectively, of the seedlings in the population study which were still alive after these fires had been top-killed. The 2004 burn was patchy because of discontinuous fuels (Loucks *et al.* 2008). Ten plots did not burn, and portions of many other plots were unburned. Consequently, only 44% of seedlings still alive after burning in 2004 had been top-killed.

Statistics

For each seedling group, annual seedling survival (%) was computed across all plots within each site by treatment combination. These data were arcsine transformed to achieve a normal distribution, and analyzed as a split-plot fixed effects model with treatment blocked within study site using PROC MIXED (SAS Institute 2000). Mean basal diameter and total height were calculated for each seedling group within each plot, and analyzed similarly for temporal and treatment effects, with plot as a repeated measure. Hemispherical photographs, acquired only within Buck Creek, generated a pseudoreplicated design for canopy cover analysis. Thus, plot was used as the experimental unit. Response variables were also analyzed for differences among landscape positions; however, not all treatments within each site contained every landscape position (see Table 2.3). Thus, landscape effects were analyzed across treatments, without blocking for site. Analysis at the landscape level produced few significant results; thus, I only present data for the overall analyses without landscape position but briefly describe the effects of landscape position on survival data, which were the only response variables with a significant effect of landscape position. Site and the site*treatment interaction were considered random effects in the model when analyzed without landscape position. Fixed effects were treatment, year, seedling group, and landscape position when analyzed, and their interactions. For all analyses, Type III tests of fixed effects were used to assess significant factors and interactions ($P < 0.05$), and because the design was unbalanced, a Satterthwaite method was used to estimate degrees of freedom. For significant effects, least squares means were compared via a post-hoc Fischer's LSD test to determine differences among means at an alpha level of 0.05.

Because the same oak species did not occur across all plots, seedlings were pooled into red oak or white oak subgenera. Comparisons were made between oak subgenera, red maple, and sassafras. I chose to analyze these competitor species because of their dominance across treatments and landscape positions and because analyses of other competitors indicated that white ash (*Fraxinus americana* L.) and eastern redbud (*Cercis canadensis* L.) behaved similarly to red maple, while hickories behaved similarly to white oaks. Sugar maple (*Acer saccharum* Marshall) exhibited a distinct trend (extremely

high post-burn mortality and slow growth), but this species was primarily limited to sub-mesic plots.

Percent survival across all sites within each burn treatment based on initial basal diameter was calculated for each seedling group by grouping individual seedlings by initial diameter size classes (< 2.0, 2.1-3.0, 3.1-4.0, 4.1-5.0, and > 5.0 mm) and tallying survival in subsequent years. To determine if there were significant ($\alpha = 0.05$) linear relationships between seedling basal diameter and total height, 2007 annual height growth and previous year canopy cover, and burn temperature and seedling survival, I used the REG procedure within SAS. For each relationship, I report the p-value for the ANOVA results of the overall model and/or the coefficient of determination (R^2) to describe the strength of the relationship. For the linear regressions of basal diameter and total height, I report the equation for the regression model for each seedling group and treatment ($y = mx + b$, where the regression coefficients $m =$ slope and $b =$ y-intercept). In fall 2006, five Wolf Pen control plots were burned accidentally, and data from these plots were omitted from 2007 analyses.

RESULTS

Canopy cover

There was a significant interaction between treatment and sampling year on canopy cover ($P < 0.001$) with no effect of landscape position ($P = 0.26$; Appendix 1). On unburned sites, cover varied between 90-94% (Figure 2.1). Cover temporarily decreased ~3% ($P = 0.02$) on sites burned 1x, but values the subsequent growing season were similar to those pre-burn ($P = 0.73$). On sites burned repeatedly, the initial burn reduced cover 10% ($P < 0.01$), three times more than sites burned once ($P < 0.01$), indicating that even fires conducted at similar times can produce variable outcomes. Canopy cover rebounded the next summer and was only 2% less than pre-burn ($P = 0.08$) despite being burned a second time 3 mo prior, likely reflecting relatively mild burn temperatures (see Table 2.2). The third burn reduced canopy cover ~ 6% from the previous year ($P < 0.01$). Although cover recovered about 2% by 2007, repeatedly-burned sites still had cover 5% lower than pre-burn ($P < 0.01$) and 5 and 7% lower than sites unburned ($P < 0.01$) and burned 1x ($P = 0.03$), respectively.

Seedling survival

There was a significant three-way interaction of treatment, seedling group, and landscape position on seedling survival ($P < 0.001$; Appendix 2), but there was no relationship between burn temperature and seedling survival for any seedling group or burn ($P > 0.05$ for all). There was also a significant effect of year that was independent of other main factors ($P < 0.01$) because seedlings from earlier sampling years always had higher survival than those from later years. In the absence of fire, white oaks declined ~6% annually, compared to about 5% for red oaks and red maple (Figure 2.2a). These three seedling groups exhibited the highest mortality on sub-mesic sites (Appendix 2). Sassafras survival remained > 90% for the duration of the study. This species' mortality was greatest on intermediate sites where survival was only ~70% in 2007, but sassafras exhibited no mortality on sub-mesic sites. Red maple tended to have significantly higher survival than red oaks and sassafras on sub-xeric sites ($P = 0.05$ and 0.02 , respectively) and higher survival than sassafras, white oaks, and red oaks ($P < 0.01$, 0.02 , and 0.01 , respectively) on intermediate sites. Thus, under all moisture regimes, at least one competitor performed equivalent to or better than co-occurring oaks.

Burning 1x decreased red maple and white oak survival to 50% ($P < 0.01$) and 60% ($P = 0.06$), respectively, but survival of sassafras and red oaks remained similar to unburned controls (Figure 2.2b; $P = 0.10$ and 0.08 , respectively). Low red maple survival was due to initially high post-burn mortality on sub-xeric and intermediate sites and delayed mortality on sub-mesic sites (Appendix 2). White oak mortality was consistently high across all landscape positions.

Sites burned 3x had lower white oak and red maple survival compared to unburned sites ($P = 0.04$ and < 0.01 , respectively), but sassafras and red oaks were not significantly affected (Figure 2.2c; $P = 0.88$ and 0.30 , respectively). Importantly, survival of each seedling group was no different than that of those seedlings burned only 1x ($P = 0.54$, 0.36 , 0.27 , and 0.89 for white oaks, red oaks, sassafras, and red maple, respectively). Across landscape positions, seedling survival generally mimicked overall trends except oaks on sub-mesic sites had survival significantly lower than those on sub-xeric and intermediate sites burned 3x ($P < 0.01$ for all) and lower than unburned sub-mesic sites ($P < 0.01$ for all; Appendix 2).

Basal diameter

The effect of burn treatment on seedling basal diameter depended on its interaction with seedling group and sampling year (treatment*seedling group*year, $P < 0.001$), and was independent of landscape position ($P = 0.35$; Appendix 3). On unburned sites, mean basal diameter of all seedling groups slowly increased over the 6-yr study (Figure 2.2d). Red oaks and red maple increased from ~3.5 to 5.0 mm ($P < 0.01$ for both). White oaks grew slowest, but increased from 3.2 to 4.1 mm ($P = 0.04$). Sassafras increased from 3.5 to 5.2 mm, but this effect was not significant ($P = 0.14$).

On sites burned 1x, red oaks and sassafras exhibited large increases in mean diameter from 2002 to 2007 ($P < 0.01$ for both). By 2007, red oaks had diameters 2 mm larger than those unburned ($P = 0.02$), while sassafras diameters were 4 mm larger ($P < 0.01$; Figure 2.2e). White oak and red maple seedlings slightly increased over time but remained similar to unburned controls by 2007 ($P = 0.65$ and 0.72 , respectively) and about 2x smaller than sassafras and 1.5x smaller than red oaks.

Multiple burns reduced diameters of all seedling groups, due to top-kill and re-sprouting of new stems with smaller diameters (Figure 2.2f), although the 2004 burn had minimal impacts, likely due to relatively low burn temperatures. In 2007, no seedling group had diameters greater than those on unburned sites ($P = 0.28, 0.65, 0.06, \text{ and } 0.20$ for red oaks, white oaks, sassafras, and red maple, respectively), and diameters of red oaks and sassafras were smaller than those on sites burned 1x ($P < 0.01$ for both).

Across treatments and seedling groups, seedlings with larger initial basal diameters generally had the greatest survival over the study (Figure 2.3). On unburned sites, there were linear decreases in red and white oak survival across diameter size classes, but the slope of these lines tended to increase with decreasing size. Unburned red maple < 2 mm also exhibited a linear decrease in survival with basal diameter, but larger size classes tended to have reduced survival only in later study years. Burning also produced the lowest survival among smaller size classes, but trends were generally curvilinear, with most mortality occurring after the initial burn. Notably, single and repeated burns produced especially low survival of small red maple (< 2 mm), and small white oaks (< 3 mm) were most impacted by multiple burns. Except for a linear decrease

in small sassafras burned 1x, this seedling group exhibited few survival trends as a function of size class.

Total stem height

The effect of burn treatment on seedling total height depended on its interaction with seedling group and sampling year (treatment*seedling group*year; $P < 0.001$), and was independent of landscape position ($P = 0.86$; Appendix 4). On unburned sites, mean height of all seedling groups slowly increased from 2002 to 2007 (Figure 2.2g). Sassafras seedlings doubled in height from ~ 25 cm to 50 cm ($P < 0.01$), as did red maple, which increased from ~ 17 cm to 34 cm ($P < 0.01$). Both red oaks and white oaks grew ~ 2 cm annually, increasing significantly ($P < 0.01$ for both) in height from about 20 to 30 cm over the 6-yr period.

By 2007, sassafras and red oak seedlings burned 1x were 41 and 11 cm taller, respectively, than those unburned ($P < 0.01$ for both), but red maple and white oaks were no taller than unburned seedlings ($P = 0.72$ and 0.82 , respectively; Figure 2.2h). Sassafras quadrupled in height from 2002 to 2007 (from 23.7 to 83.2 cm; $P < 0.01$), and red oaks grew from 23.2 to 50.2 cm tall ($P < 0.01$). This large increase in red oak height (and basal diameter) was mostly on several Wolf Pen plots burned 1x, which had higher burn temperatures compared to nearby plots and consequently high reductions in overstory basal area (Figure 2.4). Red oaks on these plots were also relatively large pre-burn (basal diameter > 5 mm; total height > 30 cm).

Sassafras and red oaks burned 3x were taller in 2007 than they were in 2002 ($P < 0.01$ and 0.02 , respectively), but white oaks ($P = 0.93$) and red maple ($P = 0.08$) had heights similar to those pre-burn (Figure 2.2i). Compared to unburned seedlings, sassafras burned 3x were 28 cm taller by 2007 ($P < 0.01$), but red oaks, white oaks, and red maple remained similar to unburned controls ($P = 0.65$, 0.26 , and 0.25 , respectively). Sassafras and red oaks burned 3x were ultimately 13 and 23 cm shorter than those burned 1x ($P < 0.01$ and 0.03 , respectively), but white oaks and red maple were similar between the burn treatments ($P = 0.18$ and 0.40 , respectively).

Mean seedling basal diameter and total height measured in 2007 were strongly correlated (Figure 2.5). Except for sassafras, the regression slopes increased and y-intercepts generally decreased with burn number (Table 2.4) suggesting a greater increase

in height for every unit increase in basal diameter for seedlings burned repeatedly than seedlings unburned or burned 1x.

Lower canopy cover in 2006 was also significantly correlated with higher annual height growth (based on plot means) in 2007 (Figure 2.6; see Appendix 5 for all annual growth data) for all seedling groups except sassafras ($P = 0.24$). This correlation was strongest for red maple ($R^2 = 0.84$), but it was based on 10 plots, compared to 33 for both oaks.

DISCUSSION

Results on unburned sites exemplify the current status of oak regeneration beneath mostly closed canopies in eastern deciduous forests. Without fire, canopy cover was 90-94%, and oak seedlings exhibited high mortality and slow growth. Oak seedling total height increased only 2 cm yr⁻¹, and basal diameter increased 0.1 and 0.3 mm yr⁻¹ for white and red oak subgenera, respectively. At this rate, seedlings currently 30 cm tall would not reach 1 m high for another 35 yr. Lorimer *et al.* (1994) documented slow growth (4-6 cm yr⁻¹) of natural oak seedlings in mature stands in Wisconsin, but even these rates were 2-3x faster than those measured here. Slow growth underneath a dense canopy is not uncommon (Crow 1992; Dey and Parker 1996), and previous determinations of root age suggest oak seedlings can persist in the understory on drier sites in the absence of disturbance for 30-50 yr (Sander 1972). The consequences of slow growth and high mortality under a mature, undisturbed canopy become especially apparent when compared to red maple and sassafras, which exhibited annual height and basal diameter growth 1.5-2.5x faster than oaks. This trend is the essence of the oak regeneration problem in eastern U.S. forests, and relatively better growth and survival of fire-sensitive, shade-tolerant species have been extensively documented by other researchers (Abrams and Downs 1990; Abrams and Nowacki 1992, Arthur *et al.* 1998, Blankenship and Arthur 2006).

I hypothesized that prescribed fire would enhance oak regeneration by increasing understory light and decreasing growth and survival of competitor species, and that multiple burns conducted frequently would more effectively create these conditions. In this study, single and repeated fires temporarily increased understory light, but canopy

cover rebounded by the subsequent growing season. This transitory effect following the initial disturbance may have resulted from prolific sprouting and light occlusion. For example, Chiang *et al.* (2005), working nearby, correlated rapid light depletion with increased stem density in the shrub stratum, primarily from red maple stump sprouting, and found multiple fires did not decrease post-fire sprouting. A similar pattern of temporarily decreased canopy cover also followed the first and third burn; the second burn was mild (Table 2.2), likely from reduced fuel loads due to the prior year's burning, and consequently, changes in canopy cover were relatively small. Importantly, sites burned 3x ultimately had 5-7% lower canopy cover compared to those unburned or burned 1x, suggesting a cumulative effect of frequent, repeated burns on understory light.

Both single and repeated fires decreased survival of red maple seedlings. Because this species has epigeal germination, dormant buds along the stem's base are often above the soil surface, making them more susceptible to mortality from high burn temperatures than oaks (Brose and Van Lear 2004). This could lead to decreased sprouting ability (Brose *et al.* 2006), especially among smaller seedlings, and could partially account for the extremely high red maple mortality measured on sites burned 1x which experienced high burn temperatures. Red maple also had high mortality on sub-mesic sites several years post-burn, which may reflect a gradual depletion of belowground resources following resprouting, as species with non-conservative growth strategies often have lower root reserves (Huddle and Pallardy 1999). Importantly, repeated burning did no better at reducing red maple survival than one burn.

Fires did not reduce the growth of surviving red maple compared to those unburned. Red maple is a highly adaptable "super-generalist" (Abrams 1998), with characteristics of both early and late successional species, that thrives in open, recently disturbed places as well as in the shade of the forest canopy (Sipe and Bazzaz 1994). Following a disturbance which increases understory light, red maple quickly produces new leaves, which have low construction and maintenance costs because they are thin with few secondary compounds (Nagel *et al.* 2002). Thus, as long as red maple seedlings have sufficient belowground resources to support re-building aboveground tissues post-fire, they will be able to rapidly utilize available light.

Both single and repeated burns led to a prolific growth response in sassafras and had virtually no effect on survival. Dey and Hartman (2005) measured high sassafras survival (91%) even after four burns, and similar to findings reported here, found survival did not correlate with initial basal diameter. Early studies examining the growth habits of this species describe it as highly adaptable on a variety of soils due primarily to extensive root suckering (Duncan 1935). Root networks could provide a continual carbon source (Loehl 2000) and allow efficient re-building of fire-damaged tissues. If parent plants subsidize carbon, this could also explain sassafras survival being independent of initial basal diameter and greater height growth per unit increase in basal diameter compared to other seedlings. Additionally, sassafras roots typically grow 15-50 cm deep (Duncan 1935), which could protect them from mild, dormant season burns. Sassafras dominance may eventually decrease as individual stems self-thin. However, several studies have shown increased oak seedling survival and growth after removing competing understory and subcanopy species (Loftis 1990b; Lorimer *et al.* 1994). Thus, at this critical stage in oak development, the occurrence of a thick sassafras understory could have negative effects on growth of co-occurring oak, primarily via light occlusion.

Despite temporarily increased light and decreased red maple survival after single and repeated fires, oak survival and growth generally remained similar to or lower than on unburned controls. Upland oaks are generally considered “stress-tolerators” (*sensu* Grime 1977); thus, they are adapted to relatively stable conditions, put considerable photosynthate into storage rather than growth, and do not change their phenotype rapidly when exposed to altered conditions or resources (Dey and Parker 1996). While oaks often require high light environments for growth and survival (Johnson *et al.* 2002), their ability to effectively capture a transitory increase in light is limited by their relatively non-plastic growth strategy. In this study, lower canopy cover was positively correlated with higher annual height growth of oaks the subsequent year, and oaks burned 3x had greater height growth per unit increase in basal diameter compared to those unburned or burned 1x. However, slopes of both regressions were relatively low for oaks, suggesting light levels are still insufficient to generate significant height growth, and competing species are better adapted for rapidly utilizing this new resource than oaks.

Notably, oak's inflexible growth strategy is a major reason why researchers often report successful oak regeneration following a naturally large canopy opening (Rentch *et al.* 2003) and why some suggest prescribed fires be conducted following silvicultural canopy manipulations, which can provide long-term changes in understory light. For instance, Brose *et al.* (1999) found that medium to high-intensity growing season fires conducted 2-4 yr after a shelterwood that removed 50% of the basal area increased oak abundance and stocking. A need for long-term light increases may also explain why the greatest increases in red oak seedling development occurred on sites burned 1x, where a subset of plots experienced high temperatures and high mortality of both understory competitors and overstory trees. While these results were limited to a few plots, they are consistent with previous studies that show high-intensity fires in mature stands serve to improve oak regeneration (Swan 1970; Moser *et al.* 1996).

Generally, though, prescribed fires in this study did not place oaks in a better competitive position, and may reflect the relatively small pre-burn stature of the oak seedlings. Basal diameter often correlates with root biomass (Jacobs *et al.* 2005), which affects ability to survive fire (Brose and Van Lear 2004) and eventually allocate photosynthate to stem growth following top-kill (Lorimer 1993). However, even when a canopy opening provides sufficiently high and long-lasting light, oak seedlings must be relatively large (basal diameters > 1.9 cm; Brose *et al.* 2006) prior to burning to be competitive post-fire. Initial mean basal diameter of oak seedlings in this study was small (< 4 mm), and while fire had some positive impacts on red oak seedling development, their diameters remained < 7 mm. Thus, further growth development would be necessary for these seedlings to remain competitive following future canopy openings. Small pre-burn stature could also explain why burning was especially detrimental to white oaks. At study initiation, half as many white oaks than red oaks had diameters > 5 mm (41 compared to 85 seedlings). Additionally, many chestnut oak (*Q. montana* L.) seedlings on a nearby ridge had hollow roots and lower root mass compared to scarlet oak (*Q. coccinea* Muenchh) and red maple (Chiang 2002). If seedlings in this study had similarly low root mass, this could lead to poor sprouting ability and survival following fire and partially explain why white oaks had greater post-burn mortality even among larger diameter classes compared to red oaks.

Although not measured in this study, pre-burn seedling age could also be an important determinant of post-fire oak seedling development. Recent work by Dillaway and Stringer (2007) suggests that oak seedlings residing in the understory in a suppressed state for considerable periods may be physiologically unable to respond to increases in light (even high light provided by a release), as seedlings with older root systems (> 8 yr) had lower soluble non-structural carbohydrates, thus less potential vigor.

CONCLUSIONS

Single and repeated prescribed fires over a 6-yr period in these deciduous forests of eastern Kentucky produced variable results. The generalist red maple exhibited high post-burn mortality following a burn with high temperatures, presumably due to damage to dormant buds, but fire did not affect the growth of surviving red maple, likely due to this species' plastic morphology which allows rapid utilization of newly available resources. Sassafras, which expands clonally via root suckers, was virtually unaffected by single and multiple fires. This species produces extensive belowground root networks which are mostly protected from fire and can provide carbon sources necessary for resprouting following top-kill. While oaks are generally considered fire-adapted, pre-burn seedling stature appeared especially important. White oaks, with lower initial basal diameters and potentially lower root mass, experienced high mortality and reduced growth following prescribed fire. In contrast, high burn temperatures and consequently high overstory mortality on several plots burned 1x promoted red oak seedling growth and led to survival higher or equivalent to competitors. Notably, these seedlings, predominantly on drier sites, were also larger prior to burning. These results, as well as the relatively minor effects of the mild burns of 2004, exemplify the patchy character of fire and consequent effects on seedlings. In summary, prescribed fires produced few positive effects on oak seedling development due to transitory effects on understory light, minimal impacts on survival and growth of co-occurring competitors, the small pre-burn stature of oak seedlings, and the unpredictable nature of fire.

Table 2.1. Plot characteristics within each study site and treatment. Values are mean \pm SD. Overstory basal area refers to trees \geq 10 cm diameter at breast height (DBH). Geologic substrate classifications were acquired from the Salt Lick USGS Quadrangle and S = Siltstone, SS = Siltstone/Shale, DS = Dolomite/Shale, LS = Limestone. Landscape positions are based on McNab *et al.* (2007). SM = sub-mesic, INT = intermediate, SX = sub-xeric.

Parameter	<u>Buck Creek</u>			<u>Chestnut Cliffs</u>		
	<u>Control</u>	<u>Burned 1x</u>	<u>Burned 3x</u>	<u>Control</u>	<u>Burned 1x</u>	<u>Burned 3x</u>
Slope (%)	43.6 \pm 20.0	44.1 \pm 18.5	37.7 \pm 22.0	37.0 \pm 10.1	42.2 \pm 14.6	33.7 \pm 20.4
Elevation (m)	326 \pm 23	331 \pm 23	319 \pm 42	321 \pm 21	307 \pm 27	306 \pm 19
Overstory Basal Area (m ²)	23.1 \pm 5.6	20.1 \pm 4.5	24.4 \pm 10.0	18.9 \pm 7.4	20.3 \pm 7.8	20.6 \pm 11.8
Geologic Substrate	S/DS	S/DS	S/DS/LS	S/DS/LS	S/DS/LS	S/DS/LS
Landscape Position	3 SM, 3 INT, 4 SX	4 SM, 3 INT, 4 SX	0 SM, 8 INT, 4 SX	6 SM, 4 INT, 0 SX	3 SM, 6 INT, 1 SX	4 SM, 5 INT, 1 SX

Table 2.1, Cont.

Parameter	<u>Wolf Pen</u>		
	<u>Control</u>	<u>Burned 1x</u>	<u>Burned 3x</u>
Slope (%)	42.2 ± 12.8	51.8 ± 21.6	37.8 ± 20.8
Elevation (m)	315 ± 16	307 ± 32	314 ± 23
Overstory Basal Area (m ²)	30.9 ± 9.6	26.0 ± 8.8	23.3 ± 11.5
Geologic Substrate	S/DS	S/SS	S/SS
Landscape Position	8 SM, 2	1 SM, 7	4 SM, 3
	INT, 0 SX	INT, 4 SX	INT, 1 SX

Table 2.2. Burn parameters within the three study sites averaged throughout each fire's duration.

Burn Parameters	<u>Buck Creek</u>				<u>Chestnut Cliffs</u>			
	<u>Burned 1x</u>		<u>Burned 3x</u>		<u>Burned 1x</u>		<u>Burned 3x</u>	
Date	4/14/03	4/14/03	3/26/04	4/11/06	3/25/03	3/24/03	4/7/04	4/13/06
Time of Ignition	1130	1130	1300	1015	1130	1230	1200	1130
Ignition Method	Aerial	Aerial	Hand	Hand	Hand	Hand	Aerial	Hand
Air temperature (°C)	26.3	26.3	25.2	24.1	25.0	24.0	23.4	25.4
Relative Humidity (%)	23.2	23.2	44.6	28.0	32.5	35.0	39.7	35.0
Wind Direction	NW	NW	SW	SW	SW	W	W	S
Wind Speed (km/hr)	0-9.7	0-9.7	3.2-9.7	1.6-3.2	0-9.7	0-9	3.2-6.4	4.8-7.6
Mean Burn Temp @ 0 cm (°C)	473.2	563.7	148.5	529.0	533.1	475.0	410.5	485.1

Table 2.2. Cont.

Burn Parameters	<u>Wolf Pen</u>			
	<u>Burned 1x</u>	<u>Burned 1x</u>	<u>Burned 3x</u>	<u>Burned 3x</u>
Date	4/16/03	4/16/03	4/7/04	4/11/06
Time of Ignition	1230	1230	1200	1000
Ignition Method	Aerial	Aerial	Aerial	Hand
Air temperature (°C)	26.8	26.8	23.1	20.0
Relative Humidity (%)	38.7	38.7	39.0	30.5
Wind Direction	W	W	W	W
Wind Speed (km/hr)	0-14.48	0-14.48	8-12.9	3.2-6.4
Mean Burn Temp @ 0 cm (°C)	583.5	561.3	152.3	476.0

Table 2.3. Number of plots containing each measured seedling species across sub-mesic (sm), intermediate (int), and sub-xeric (sx) landscape positions.

Group	Species	<u>Unburned</u>			<u>Burned 1x</u>			<u>Burned 3x</u>			Tot
		sm	int	sx	sm	int	sx	sm	int	sx	
Red oaks	Black oak (<i>Quercus velutina</i>)	14	5	4	5	14	7	6	15	4	74
	Northern red oak (<i>Quercus rubra</i>)	13	-	-	4	3	3	6	2	-	31
	Scarlet oak (<i>Quercus coccinea</i>)	-	3	3	1	2	2	1	4	4	20
White oaks	White oak (<i>Quercus alba</i>)	15	5	2	4	8	3	7	6	3	53
	Chestnut oak (<i>Quercus montana</i>)	6	6	2	3	8	5	1	11	3	45
	Chinkapin oak (<i>Quercus muehlenbergii</i>)	-	-	-	-	-	-	2	-	-	2
Others	Sassafras (<i>Sassafras albidum</i>)	1	3	3	3	6	7	-	7	5	35
	Red maple (<i>Acer rubrum</i>)	4	4	1	1	8	2	-	6	1	27
	White ash (<i>Fraxinus americana</i>)	8	-	-	1	-	-	3	2	-	14
	Sugar maple (<i>Acer saccharum</i>)	3	1	-	1	1	-	5	-	-	11
	Hickory (<i>Carya spp.</i>)	1	1	-	-	1	-	-	-	-	3
	Eastern redbud (<i>Cercis canadensis</i>)	-	-	-	-	-	-	-	1	-	1

Table 2.4. Linear regression results of basal diameter vs. total height based on plot means in 2007.

Seedling group	Trt	n (# plots)	R ²	p-value	Eqn of Line
Red oaks	All	80	0.91	< 0.001	y = 8.40x - 6.48
	Unburned	23	0.87	< 0.001	y = 6.76x - 1.88
	Burned 1x	30	0.91	< 0.001	y = 8.52x - 5.70
	Burned 3x	27	0.89	< 0.001	y = 8.63x - 6.22
White oaks	All	72	0.82	< 0.001	y = 6.80x + 2.12
	Unburned	22	0.82	< 0.001	y = 5.94x + 5.71
	Burned 1x	26	0.77	< 0.001	y = 6.90x + 2.03
	Burned 3x	24	0.76	< 0.001	y = 8.89x - 4.02
Red maple	All	22	0.87	< 0.001	y = 9.59x - 3.01
	Unburned	7	0.82	0.005	y = 8.56x - 2.92
	Burned 1x	9	0.94	< 0.001	y = 10.47x - 6.88
	Burned 3x	6	0.67	0.045	y = 12.03x - 6.21
Sassafras	All	35	0.9	< 0.001	y = 11.36x - 7.54
	Unburned	7	0.98	< 0.001	y = 12.12x - 11.92
	Burned 1x	16	0.89	< 0.001	y = 11.09x - 9.09
	Burned 3x	12	0.94	< 0.001	y = 14.73x - 23.29

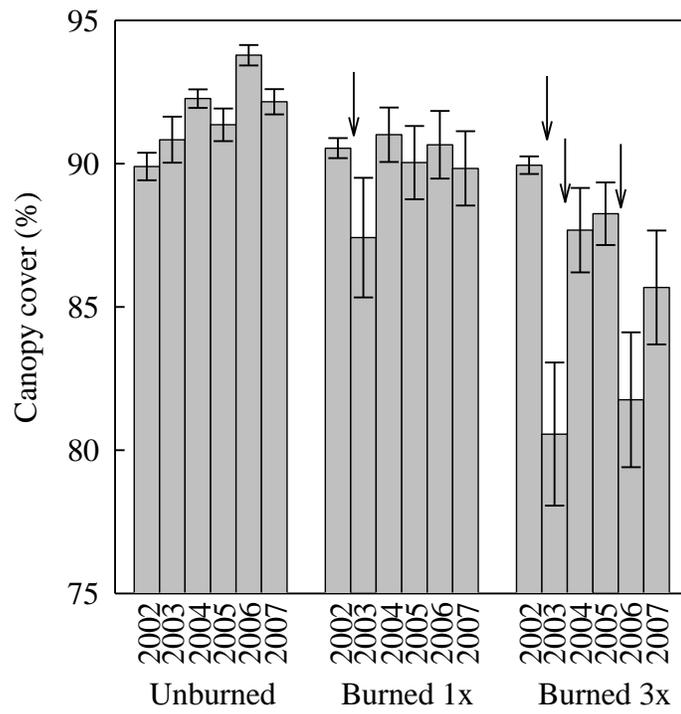


Figure 2.1. Annual canopy cover within each burn treatment at the Buck Creek study site. Mean data \pm SE. Arrows indicate burn.

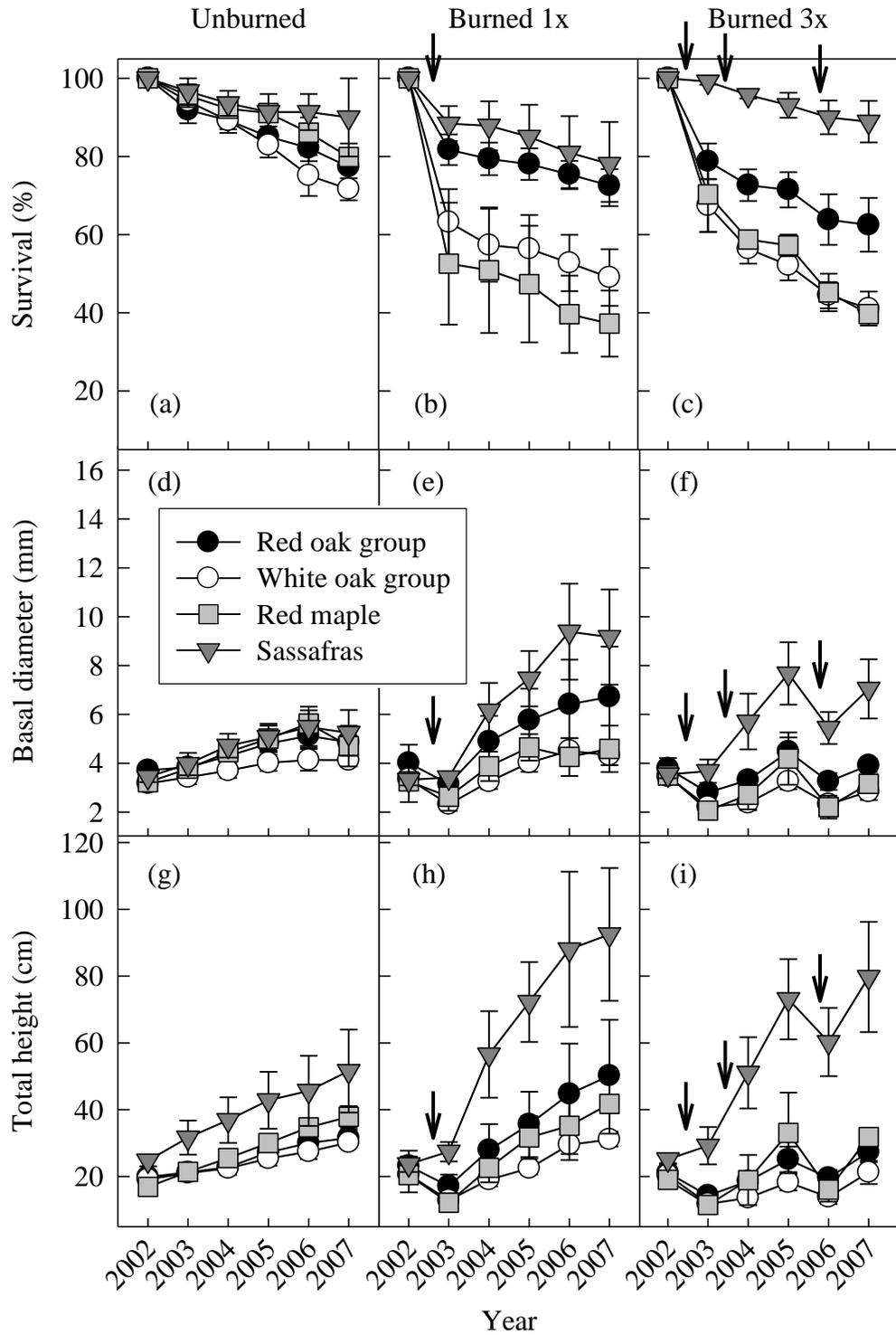


Figure 2.2. Annual survival, basal diameter, and total height (mean \pm SE) for each seedling group within each burn treatment. Arrows indicate burns.

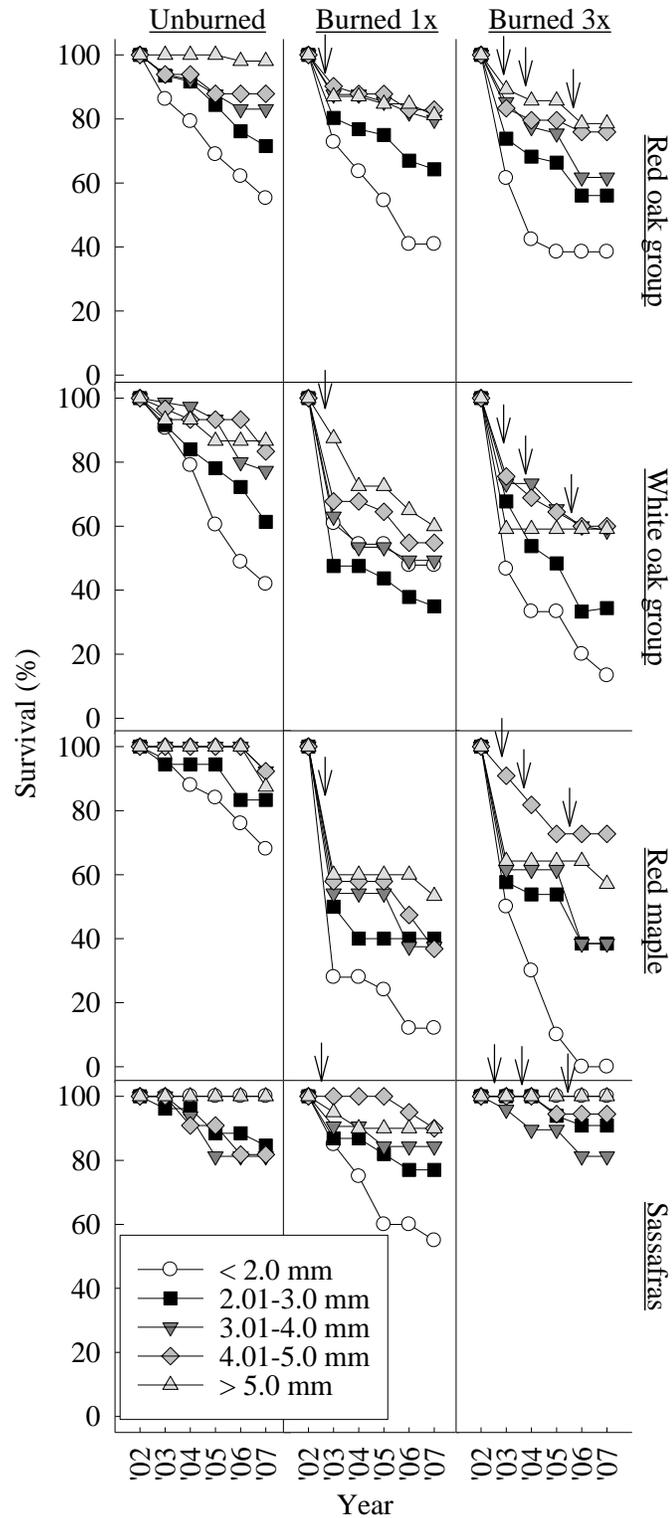


Figure 2.3. Seedling survival as a function of initial basal diameter size class tallied across sites. Arrows indicate burn. Note: Small and large sassafras symbols overlap.

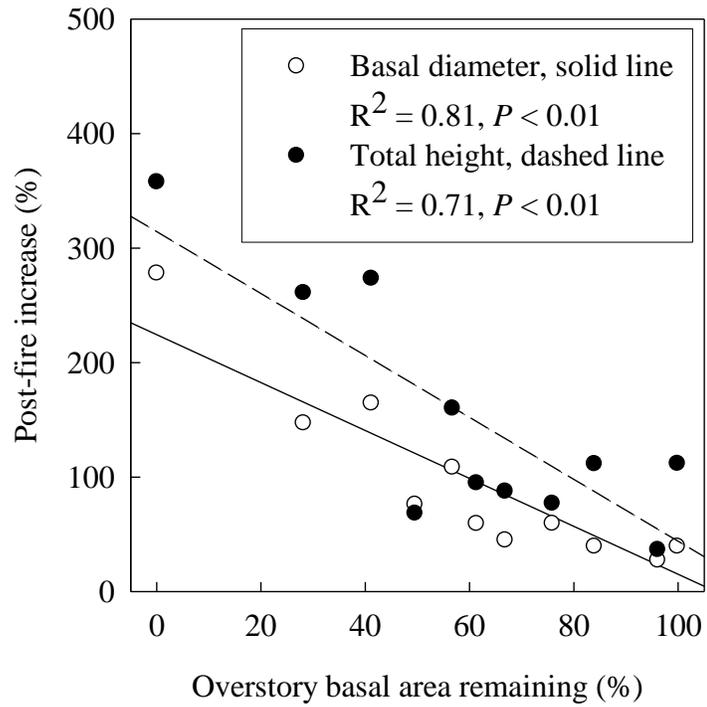


Figure 2.4. Remaining overstory (% basal area) and red oak basal diameter and total height increases from 2002 to 2007 at Wolf Pen intermediate plots burned 1x.

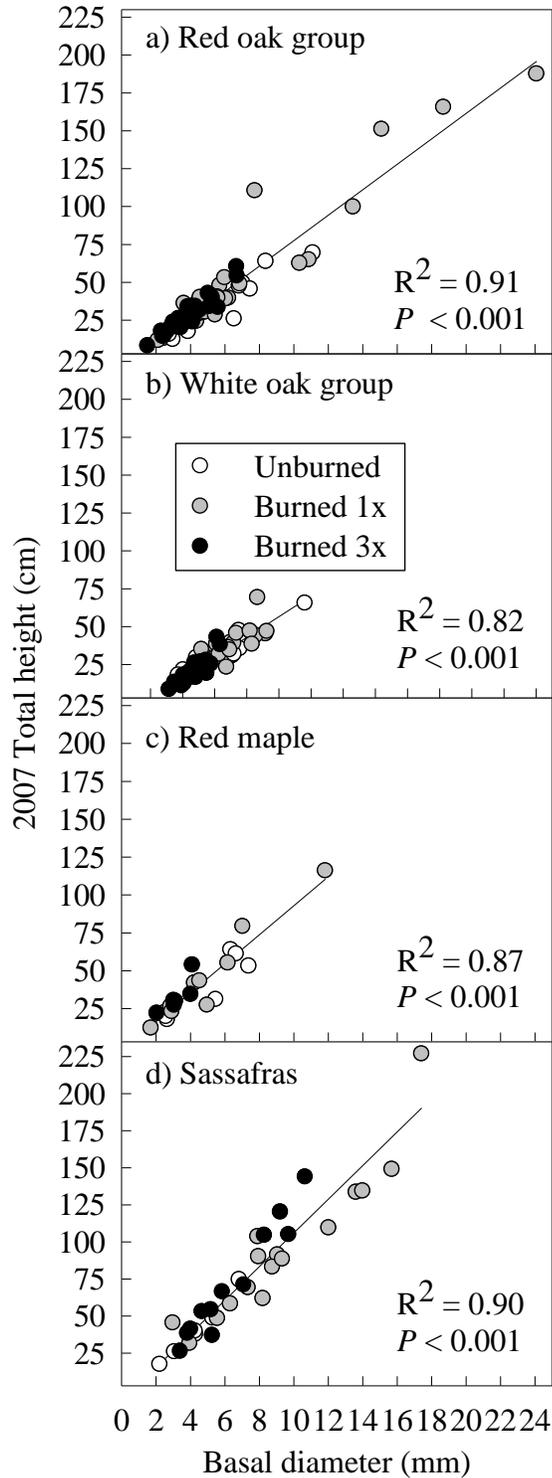


Figure 2.5. Basal diameter vs. total height of each seedling group based on plot means in 2007. Trendlines, R^2 , and p -values are for all treatments combined. For individual treatments see Table 2.4.

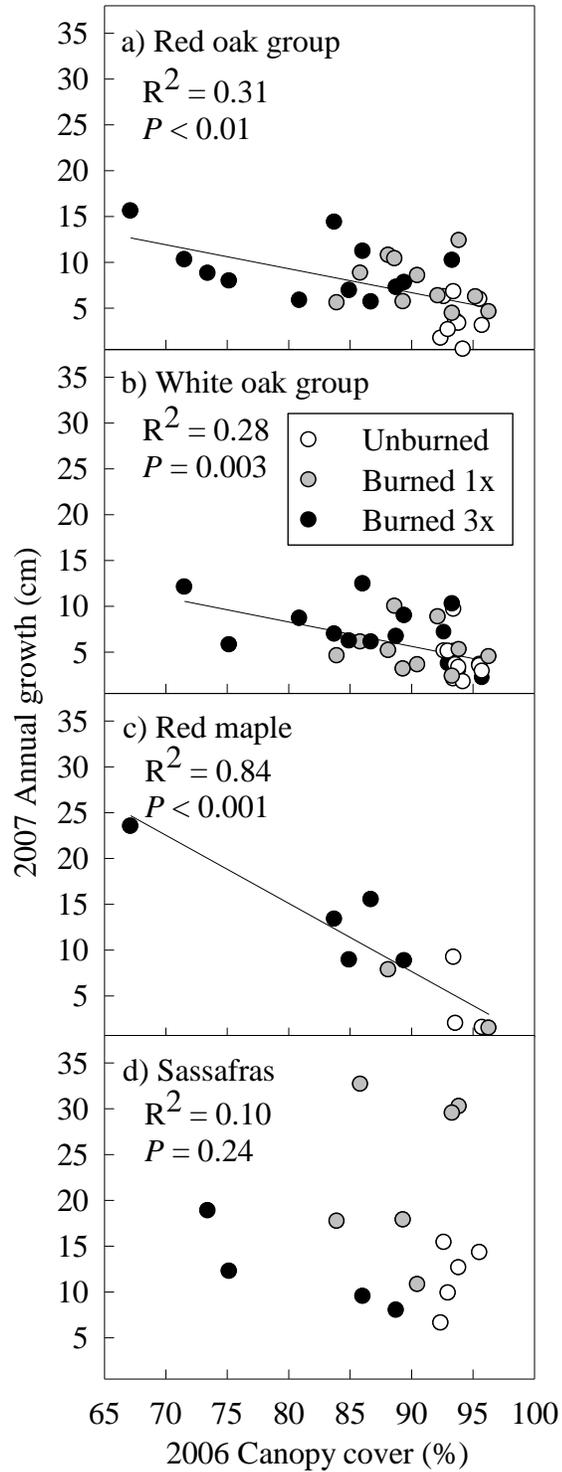


Figure 2.6. 2007 seedling growth (plot means) vs. 2006 canopy cover at Buck Creek plots only. Trendlines, R^2 , and p-values are for all treatments combined.

CHAPTER 3

FOLIAR MORPHOLOGY AND CHEMISTRY OF UPLAND OAKS, RED MAPLE, AND SASSAFRAS SEEDLINGS IN RESPONSE TO SINGLE AND REPEATED PRESCRIBED FIRES

ABSTRACT

Managers increasingly use prescribed fire to decrease competition from fire-sensitive species, increase understory light, and improve oak (*Quercus* spp.) regeneration. To better understand woody seedling response to burning, single and repeated (3x) prescribed fires were implemented over a 6-yr period (2002-2007) in eastern Kentucky and leaf traits of red (*Erythrobalanus* spp.) and white oaks (*Leucobalanus* spp.) were compared to their co-occurring competitors, red maple (*Acer rubrum* L.) and sassafras (*Sassafras albidum* Nutt.) Nees.). Burned seedlings had higher total leaf area (TLA) than those unburned, primarily due to 2-3x higher TLA of sassafras, but foliar N concentration remained unchanged. Leaf mass per area (LMA) and N content per area (N_{area}) increased post-fire but were independent of seedling identity and less pronounced following a single burn compared to multiple burns. Canopy openness during 2006, which ranged from ~ 5-30%, positively correlated with sassafras TLA, oak and sassafras N_{area} , and LMA of all seedling groups the subsequent year. In 2007, TLA, LMA, and N_{area} were positively correlated with basal diameter of all groups, but most significantly for sassafras and red maple. These findings indicate that prescribed fire can alter leaf characteristics, but suggest that this disturbance alone does not enhance oak seedling leaf traits relative to their co-occurring competitors, sassafras and red maple. This study provides additional evidence that low-intensity, early growing-season fire in the absence of additional canopy manipulation may not be an effective management tool for promoting oak regeneration in this region.

INTRODUCTION

Fire suppression in historically oak-dominated forests of the eastern U.S. has facilitated the spread of fire-sensitive tree species leading to low understory light

(Abrams 1992). Moderately shade-tolerant oaks (*Quercus* spp.; Burns and Honkala 1990) are competitively inferior under a thick mid- or understory and often experience regeneration failure (Lorimer *et al.* 1994). Without periodic disturbance, some researchers predict conversion of many forest stands from predominantly oaks to shade-tolerant, fire-sensitive species such as red and sugar maple (*Acer rubrum* L. and *A. saccharum* Marshall, respectively; Nowacki and Abrams 2008), which in many stands have already increased in density and dominance (McEwan *et al.* 2005; Blankenship and Arthur 2006). Even with disturbance, shade-intolerant species of seed origin, like yellow-poplar (*Liriodendron tulipifera* L.), and well-established shade-tolerant regeneration (Van Lear *et al.* 2000) often outcompete understory oaks, whose available resources have been suppressed by an extensive period of low light (Abrams 1992). Importantly, a canopy shift away from upland oaks has numerous ecological consequences, as many wildlife species consume acorns, and oaks have strong influences on overall community dynamics and ecosystem processes (McShea *et al.* 2007).

Current management efforts increasingly use prescribed fire with the goal of decreasing competition from fire-sensitive species, increasing understory light by removing canopy trees and sub-canopy vegetation, and promoting oak seedling growth and development. Burning is expected to preferentially enhance oak regeneration because oaks have hypogeal germination, which places dormant buds below the soil surface and minimizes fire damage, and a conservative growth strategy, which promotes a large belowground root system that facilitates re-growth after topkill (Brose and Van Lear 2004). In contrast, many co-occurring fire-sensitive species have epigeal germination and a non-conservative growth strategy, which promotes height over diameter growth (Lorimer *et al.* 1994), but often exposes dormant buds to high burn temperatures (Brose and Van Lear 2004). Thus, oaks are expected to have greater survival and growth in post-fire environments thereby enhancing their ability to compete with co-occurring woody seedlings following a subsequent canopy release (Barnes and Van Lear 1998). However, studies evaluating prescribed fire effects on oak regeneration report variable outcomes (Brose *et al.* 2006) and frequently indicate that fires without any other silvicultural manipulation (1) fail to systematically kill oak seedling competitors, including those species typically classified as “fire-intolerant” (*e.g.*, Albrecht and McCarthy 2006), (2)

produce moderate to significant mortality of oak seedlings, especially those of smaller size classes (*e.g.*, Dey and Hartman 2005), and (3) create only modest or temporary changes in light intensity (*e.g.*, Hutchinson *et al.* 2005).

In an associated seedling population study (see Chapter 2), prescribed fire effects on survival and growth of seedling sprouts (initial seedling height ≤ 60 cm) of upland oak were compared to two competitors, red maple and sassafras. White oaks (*Leucobalanus* spp.) experienced high mortality and reduced growth following prescribed fire, possibly due to relatively low initial basal diameters (< 4 mm). In contrast, high burn temperatures (surface temperatures of ~ 600 °C) and high overstory mortality ($> 50\%$ basal area reduction) on several plots burned 1x promoted growth of red oak seedlings and led to survival higher or equivalent to that of competitors. Notably, these seedlings, predominantly on drier sites, were larger prior to burning (basal diameter ≥ 6 mm). Among competitors, fires negatively impacted red maple survival, with negligible effects on growth of surviving seedlings, but fires promoted sassafras growth with virtually no impact on survival. Furthermore, understory light increased temporarily, and at study cessation, mean canopy openness on plots burned 3x was $\sim 15\%$, about 6% higher than sites unburned or burned 1x.

These and other findings suggest that fire effects on oak regeneration are inherently complicated because fire influences woody seedling dynamics at many levels. Also, species may have different growth strategies and life history traits that produce a variety of seedling responses to fire disturbances. Fire acts directly on seedling survival through heating effects, and as mentioned earlier, differences in bud exposure among species can have a large impact on relative post-fire survival (Brose and Van Lear 2004). Fire also can alter environmental conditions and resource availability, such as understory light, which often coincide with changes in other abiotic conditions (*e.g.*, water availability, soil temperature; Naidu and DeLucia 1997). While nitrogen (N) can be lost during fires due to volatilization at relatively low temperatures (200 °C; White *et al.* 1973), a meta-analysis by Wan *et al.* (2001) reported increased soil availability of NH_4^+ and NO_3^- across ecosystems and fire types for up to 1 yr following fire. These increases have been linked to pyrolysis of organic matter, post-fire changes in soil moisture and temperature that stimulate N mineralization, and leaching of N from the forest floor into

underlying soils following fire (Wan *et al.* 2001). If surviving seedlings have differing abilities to acclimate to a new set of abiotic conditions and respond rapidly to transitory increases in available resources, even small changes in light or N availability could impact seedling growth and competitive stature in post-fire environments. Further, the removal of aboveground tissues by fire may also alter leaf physiology due to changes in root:shoot dynamics (*e.g.*, Reich *et al.* 1990). Following late-spring fires in Wisconsin, Kruger and Reich (1997b) measured an increase in foliar leaf N per unit area and photosynthetic capacity of three temperate species despite finding no increase in post-fire soil N or water availability. The magnitude of these responses differed among species, suggesting variable consequences of fire-induced resprouting on seedling growth and recovery following fire (Kruger and Reich 1997a,c).

To gain further insight regarding the underlying mechanisms affecting relative differences in seedling growth previously observed in post-fire environments, this study focused on woody seedling response at the leaf level. While whole-plant responses are the best indicators of how different seedlings will respond to altered environmental conditions (Kruger and Reich 1997a,b,c; Naidu and DeLucia 1997), previous work has indicated that leaf traits also can provide additional information regarding plant ecophysiological response to abiotic factors (Abrams *et al.* 1994), mechanisms affecting growth patterns and competitive interactions (Reich *et al.* 1990), and leaf susceptibility to herbivory (Rieske 2002). Specifically, single and repeated (3x) prescribed fires were implemented over a 6-yr period (2002-2007) in mature, second-growth forests in eastern Kentucky, and pre- and post-burn changes in total leaf area (TLA), leaf mass per unit area (LMA), N content per unit leaf area (N_{area}), foliar carbon (C) and nitrogen (N) concentrations, and leaf C:N ratios were quantified annually in oak and co-occurring competitor seedlings of red maple and sassafras. To evaluate the role of understory light, these leaf characteristics were examined in 2007 in relation to the previous year's canopy openness. Leaf characteristics in 2007 also were used to assess potential links among seedling size, measured as basal diameter, and foliar morphology and chemistry. We hypothesized that seedlings would acclimate to post-fire changes in understory light by increasing their TLA and/or LMA, as these leaf traits have been previously shown to be effective strategies for increasing light interception and assimilation (DeLucia *et al.* 1998;

Aranda *et al.* 2004). We predicted that if fire increased soil N availability or altered root:shoot dynamics, this would be reflected in foliar N concentration (Reich *et al.* 1990). We further hypothesized that these responses would be more pronounced in oak seedlings compared to red maple and sassafras seedlings because oak's conservative growth strategy promotes a large belowground root reserve, providing energy to offset costs associated with building new leaves with high C or N.

METHODS

Study area

Leaf parameters were measured in forest stands within the Cumberland Ranger District of the Daniel Boone National Forest (DBNF) of eastern Kentucky. Prior to burn treatment, the overstory was second-growth (~ 80 yr old) and averaged 20-30 m² ha⁻¹ of pre-burn basal area (stems ≥ 10 cm diameter at breast height (DBH)). Oak, including scarlet (*Q. coccinea* Muenchh), black (*Q. velutina* Lam.), northern red (*Q. rubra* L.), white (*Q. alba* L.), and chestnut oak (*Q. montana* L.), and hickory, including pignut (*Carya glabra* (Mill.) Sweet var. *glabra*), bitternut (*C. cordiformis* (Wangenh.) K. Koch), and mockernut (*C. tomentosa* (Poir.) Nutt.), dominated overstory composition. Midstory (2-10 cm DBH) dominants were red and sugar maple (*A. rubrum* L. and *A. saccharum* Marshall, respectively), downy serviceberry (*Amelanchier arborea* (Michx. f.) Fern), black gum (*Nyssa sylvatica* Marshall), and sourwood (*Oxydendrum arboreum* (L.) DC.). Few oaks (< 3%) comprised midstory stem density, while red maple's density was ~ 45%.

Climate is generally humid, temperate, and continental. Mean annual air temperature is 12.8 °C, with mild winters and hot summers (mean daily temperature = 0.5 °C and 24 °C in January and July, respectively). Annual rainfall (122 cm) is equally distributed throughout the year (Foster and Conner 2001). Estimates of the Palmer Drought Severity Index (PDSI) obtained for the region from the National Climatic Data Center (<http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp#>) indicated strong interannual swings in moisture availability during the study. PDSI for 2002 (0.56) indicated an “incipient wet spell,” followed by “moderately wet” (2.71) and “extremely

wet” (4.03) years in 2003 and 2004, respectively. The PDSI during 2005 and 2006 was “normal” (0.02 and -0.20, respectively), while 2007 was a “moderate drought” (-2.47).

Experimental design

The overall study design consisted of three burn treatments (unburned, burned 1x, and burned 3x), each within three replicate study sites (Buck Creek, Chestnut Cliffs, and Wolf Pen). Study sites were within an 18-km² area and were ~ 200 to 300 ha each. Each burn treatment encompassed 58 to 116 ha (see Chapter 2 Methods for more detail) and contained 10-12 plots. Plots were chosen using a grid overlaid on a topographic map and encompassed a variety of aspects, slopes (often exceeding 60%), and elevations (260 to 360 m). Each plot was parallel to topographic contours and 10-m wide x 40-m long. Because of the logistical constraints associated with leaf-level measurements, the current study used only one site (Buck Creek; 230 ha) within the larger study. This study site contained a total of 33 plots (10 unburned, 11 burned 1x, 12 burned 3x). While each burn treatment within this site contained replication at the plot level, analysis of plot data generated a pseudoreplicated design because fire could not be applied to each plot individually. Thus, results cannot be generalized beyond Buck Creek; however, it seems reasonable that these findings are representative of the other two sites given their similar variability in aspect, slope, elevation, pre-burn basal area, soil type, and landscape position (see Chapter 2, Table 2.1). Additionally, forest stands within all treatments and study sites were mature, second-growth, originating ~ 80-100 years ago following extensive logging and showed similar dominance of overstory and midstory vegetation (see *Study area* description above).

Prescribed fires

Fires were ignited by the U.S. Forest Service using either drip torches and/or helicopter ignition. Sites burned 3x were burned in spring 2003, 2004, and 2006, while those burned 1x were burned in spring 2003. All burns were between March 26 and April 16, when air temperatures were 20-27 °C, and relative humidity was 23-45% (see Chapter 2 for further details). Flame height and spread rates (*i.e.*, fire intensity) were not measured due to the large size and highly dissected topography of the study sites and concern for personnel safety. However, variability in fire temperature was quantified using pyrometers at four locations within each plot (see Loucks *et al.* 2008, for

methodology). Fire temperatures at each site within the larger study and potential effects on whole seedling growth and survival are reported in Chapter 2.

Across Buck Creek plots, surface fire temperatures (mean \pm SD) varied with year. In 2003, temperatures were 473 ± 182 and 563 ± 77 °C at plots burned 1x and 3x, respectively. Greater variability among plots burned 1x resulted from a single plot with comparatively low temperatures. During 2004, only 50% of plots burned, likely due to greater fuel discontinuity because of burning only 1-yr prior, leading to a mean (\pm SD) surface burn temperatures of only 149 ± 172 °C. During 2006, burn temperatures were more homogeneous (529 ± 45 °C). Importantly, burn temperatures during the 2003 fire were significantly and positively ($P < 0.001$; $R^2 = 0.49$) correlated with canopy openness measured the following summer, while temperatures in subsequent fires were not, suggesting initial surface fire temperatures and associated fire behavior strongly influenced understory light.

Seedling leaf traits

Pre-burn (June 2002), seedlings of oaks and their most predominant competitors were selected from the pool of advance regeneration (98% were ≤ 60 cm height), permanently tagged with a unique identification number, and mapped as part of a long-term seedling population study to assess survival and growth in response to prescribed fire (see Chapter 2). All seedlings were well-established with mean height of 21.5 ± 14.1 cm, and were visually inspected at the root collar to ensure they were independent seedlings. No true seedlings (*i.e.*, seedlings that have not been previously top-killed and resprouted) were observed or selected. Selected seedlings included one species of the dominant white oak (*Leucobalanus* spp.), one species of the dominant red oak (*Erythrobalanus* spp.), and the most abundant competitor species, either red maple (*A. rubrum* L.), sugar maple (*A. saccharum* Marshall), sassafras (*Sassafras albidum* (Nutt.) Nees.), white ash (*Fraxinus americana* L.), hickory (*Carya* spp.), or eastern redbud (*Cercis canadensis* L.). *Leucobalanus* spp. included white oak (*Q. alba* L.; 706 seedlings ha⁻¹) and chestnut oak (*Q. montana* L.; 1302 seedlings ha⁻¹), and *Erythrobalanus* spp. included black oak (*Q. velutina* Lam.; 677 seedlings ha⁻¹), scarlet oak (*Q. coccinea* Muenchh; 421 seedlings ha⁻¹), and northern red oak (*Q. rubra* L.; 189 seedlings ha⁻¹).

Sassafras and red maple were by far the most dominant competitor species (~ 3900 and 3600 seedlings ha⁻¹, respectively).

Within a two-week period during the growing season (early-July to mid-August) from 2002 to 2007, seedlings of the 3-4 species represented in each plot as part of the seedling population study were selected within a 10-m radius outside of the periphery of the permanent demography plot for determination of leaf characteristics and basal diameter. Seedlings were marked with a metal ring to prevent re-sampling in subsequent years. Treatments, plots, and species were sampled in a different order each year to avoid any systematic bias. During 2002, only one seedling of each species at each plot was selected. This sampling approach was modified in remaining years, and two seedlings of each species at each plot were selected. Selected seedlings were of similar size as those in the long-term seedling population study, and resulted in a total of > 200 seedlings sampled annually (33 plots x ~3-4 species x 1-2 seedlings per species).

Based on estimates from the population study, the proportion of seedlings top-killed by each fire varied among burns. Of the seedlings within the larger population study which survived the initial (2003) fire at Buck Creek, ~ 95% experienced top-kill and re-sprouting. Because the 2004 fire was relatively mild, only 29% of seedlings underwent top-kill and re-sprouting. However, the 2006 fire top-killed 95% of seedlings. These levels of top-kill were relatively consistent among study sites. Importantly, burn temperature and seedling survival among all three sites were not correlated (see Results in Chapter 2).

For each selected seedling, two perpendicular measurements of basal diameter were made with a digital caliper where the stem exited the soil. Total leaf area (TLA) was obtained on each seedling by scanning every fully-expanded leaf with a portable leaf area meter (LI-3000A Area Meter, LI-COR, Inc., Lincoln, NE). To determine seedling leaf mass per unit area (LMA) and assess C and N parameters, several fully-expanded leaves with minimum insect or browse damage were excised from the upper portions of every measured seedling, placed in a dampened paper towel, and transferred in a pre-labeled plastic bag to the laboratory, where they were stored at 4 °C until further analysis. Within 2d, leaves were cleaned of any debris, scanned on a leaf area meter (LI-3100 Area Meter, LI-COR, Inc., Lincoln, NE), and placed in a 60 °C oven. Leaves were dried to a constant

weight, and within 1 wk, weighed to obtain dry mass. LMA for each seedling was calculated by dividing the dry weight of the leaves extracted from each seedling by their laboratory-determined leaf area. A 1-cm diameter disk from one randomly-selected dried leaf per seedling was removed (taking care to avoid the mid-vein), weighed to the nearest 0.0001 g, and stored at 60 °C until analysis for carbon (C) and nitrogen (N) concentrations using a Leco CN 2000 Analyzer (Leco Corporation, St. Joseph, MI). Leaf N content per unit area (N_{area}) was calculated by multiplying N concentration by LMA.

Canopy cover

Understory light was estimated annually during July by acquiring hemispherical photographs of canopy openness; however, only data from 2006 and 2007 were used in this study. To account for within-plot light variability, photographs were obtained at three locations (10, 20, and 30 m) along the bottom axis of each sampling plot, and because light conditions from a “seedling’s perspective” were desired, photographs were acquired 80 cm above the forest floor. To limit uneven exposure due to direct sunlight, photograph acquisition was restricted to either before sunrise, after sunset, or when overcast. A digital camera attached to a Nikon FC-E8 183° fisheye converter and placed on a Delta-T Devices self-leveling mount positioned toward magnetic N was used to take all photographs. Because hemispherical photographs were only used to assess canopy openness and not other light estimates which require solar tracks to be superimposed, this camera orientation was used only as a means of ensuring similar camera placement from year-to-year. Digital photographs were initially processed with Adobe Photoshop® to remove lighted direction markers and maximize contrast between open sky and canopy. Images were then analyzed in random order using HemiView 2.1 and evaluated three times by a single analyst to produce an average canopy cover value for each location at each plot.

Statistics

For statistical analyses, oak seedlings were pooled into red or white oak subgenera, and comparisons of leaf traits were made between these two oak subgenera, red maple, and sassafras. I focused on these competitor species because of their dominance across plots and because other species measured did not have sufficient replication at the treatment level to provide meaningful results. I grouped oaks into

subgenera because initial evaluations of potential species-specific differences proved minimal. Chestnut and white oak did not significantly differ with regard to any parameter. Among red oaks, black and scarlet oak were generally statistically similar, while northern red oak had greater foliar N, lower C:N ratios, lower LMA, and higher N_{area} . However, when I evaluated the impact of northern red oak on overall trends by removing these data from statistical analyses, I found no influence, likely because northern red oak represented only a small portion (~ 12%) of seedlings within the red oak subgenera. Thus, I chose to leave this species in the dataset for all analyses. All future references to the four seedling types analyzed (red oaks, white oaks, red maple, and sassafras) will be as “seedling groups.” Samples sizes differed among these four seedling groups. Both red and white oak species were sampled on every plot, and occasionally we sampled more than one red or white oak species on a single plot (see *Methods: Seedling leaf traits*), while red maple and sassafras were only sampled on plots where they were the dominant competitor. Thus, annual sample sizes per treatment ranged from 14-16, 10-12, 2-6, and 5-6 for red oaks, white oaks, red maple, and sassafras, respectively, yielding a total annual sample size across treatments of 44, 33, 11, and 16, respectively. When two seedlings per species per plot were sampled (all years except 2002), the mean of the measurements was used for statistical analyses.

Plots were treated as the experimental unit, and mean seedling data for each plot were analyzed by ANOVA as a three-way factorial (main effects = burn treatment, year, and seedling group) with repeated measures using the MIXED procedure of SAS (SAS Institute 2000). While the use of only one sampling site generates a pseudoreplicated design (Hurlbert 1984) and violates the underlying assumption of independence of experimental units, I felt the use of an ANOVA was justified given the similar pre-burn variability in aspect, slope, elevation, soil, and vegetation within each of the Buck Creek treatments (see Table 2.1). Most importantly, analysis of pre-burn leaf data indicated no treatment differences, suggesting observed post-burn differences were truly due to burning and not to some other effect. There was some variability in landscape position (classified according to McNab *et al.* 2007) among treatments, but previous analyses of landscape position indicated little to no effect on litter mass or woody fuels (Loucks *et al.* 2008), no effect on canopy openness and seedling growth, and only limited effects on

seedling survival (see Chapter 2). Since there were no detectable landscape position effects on seedling total height, annual height growth, or basal diameter, it is unlikely that this variable accounted for the observed post-burn differences in leaf characteristics.

TLA data did not meet the underlying assumptions of homogeneity of variance and normality and were log-transformed prior to analyses. For all analyses, Type III tests of fixed effects were used to assess significant factors and interactions ($P < 0.05$), and because the design was unbalanced, the Satterthwaite method was used to estimate degrees of freedom. For all significant effects, least squares means were compared via a post-hoc Fischer's LSD test to determine differences among means at $\alpha = 0.05$.

Because the temperate species evaluated typically have determinate growth and a second flush on seedlings was rarely observed, light conditions from any particular year were expected to be most influential on leaf parameters the subsequent year. However, light conditions within a particular year likely influence leaf parameters as well. Thus, I explored relationships between burn-induced changes in canopy openness in 2006 and leaf parameters in 2007 as well as canopy openness and leaf parameters in 2007 using linear regression and correlation procedures (PROC REG of SAS). Comparison of the two analyses indicated more significant correlations and stronger trends (i.e., higher R^2) using 2006 canopy openness; thus, I only present those findings here. Notably, the calculation of canopy openness at the plot level probably fails to incorporate the complete light environment experienced by a seedling because it does not consider sunflecks (Rich *et al.* 1999) and was not assessed immediately above each individual seedling.

Seedling basal diameter is an important indicator of seedling belowground resources (Jacobs *et al.* 2005), and in a companion study (see Chapter 2), exhibited a strong positive correlation with seedling total height among seedling groups and treatments. To determine if leaf parameters were correlated with this measurement of seedling size, I evaluated 2007 seedling basal diameter and leaf parameters. Differences between slopes and y-intercepts of trendlines for each seedling group were evaluated by ANCOVA.

RESULTS

Total leaf area (TLA)

Unburned seedlings had significantly lower mean TLA (0.024 m^2) than those burned 1x (0.033 m^2) and 3x (0.034 m^2 ; $P = 0.003$ and < 0.001 , respectively), but burning 3x did not significantly alter TLA compared to burning only 1x ($P = 0.76$; Figure 3.1). There was also a steady and significant ($P < 0.001$) increase in TLA from 2002 (0.023 m^2) to 2007 (0.063 m^2), which was independent of treatment ($P = 0.07$), but varied by seedling group ($P < 0.001$). By 2007, red oaks had greater TLA (0.069 m^2) than red maple (0.042 m^2 ; $P = 0.03$) and white oaks (0.040 m^2 ; $P = 0.001$), but sassafras had 2-4x greater TLA (0.139 m^2) than all other seedling groups ($P < 0.001$ for all). There was no treatment*seedling group effect on TLA ($P = 0.30$), suggesting species-specific effects were not sufficiently large to generate significant variation by treatment. However, burned sassafras seedlings clearly had higher TLA than other seedling groups from 2005-2007.

Leaf mass area (LMA)

Seedlings burned 3x had significantly greater LMA (52.1 g m^{-2}) than those burned 1x (46.2 g m^{-2} ; $P < 0.001$), which were significantly greater than those unburned (41.9 g m^{-2} ; $P = 0.002$), but these treatment effects were independent of seedling group ($P = 0.35$; Figure 3.2). Pre-burn, LMA was statistically similar across treatments ($P > 0.05$ for all), but after the first burn in 2003 and continuing throughout the study, unburned seedlings had significantly lower LMA than seedlings burned 3x ($P < 0.01$ for all years). In contrast, seedlings burned 1x had significantly higher LMA from those unburned only during the first year post-burn ($P < 0.001$).

There were interannual fluctuations in LMA that varied with seedling group ($P < 0.001$). Across treatments, LMA of red maple and sassafras seedlings peaked in 2004, the wettest year. Red maple LMA was also relatively high in 2007, a very dry year. LMA of both oaks peaked in 2003 on burn sites, which led to significantly higher LMA of oak seedlings in 2003 than in 2002 ($P < 0.01$). This effect was temporary, and oaks in 2004 no longer significantly differed from those in 2002 ($P = 0.95$).

Foliar nitrogen (N)

There was no overall treatment effect on seedling foliar N concentration ($P = 0.86$; Figure 3.3), although this parameter varied among seedling groups ($P < 0.001$). Red maple had the lowest overall foliar N concentration (1.54%). Red and white oaks were

intermediate (1.80% and 1.97%, respectively), and sassafras was highest (2.07%). There was significant interannual variability ($P < 0.001$), apparently driven by changes in precipitation. Across seedling groups, N concentrations were high in 2004 and low in 2002 and 2007. There also were significant treatment*year ($P = 0.008$) and treatment*year*seedling group ($P = 0.02$) effects, which appeared to be driven by decreased foliar N concentrations of red maple seedlings in 2007 on burned sites.

When expressed as foliar N content per unit area (N_{area} ; Figure 3.4), there were significant burn effects ($P < 0.001$). Seedlings burned 3x had significantly greater N_{area} (9.5 g m^{-2}) than those burned 1x (8.5 g m^{-2} ; $P = 0.001$), which were significantly greater than those unburned (7.7 g m^{-2} ; $P < 0.001$). Burn effects depended on year ($P < 0.001$), but did not vary with seedling group ($P = 0.30$). Immediately after the first fire, seedlings burned 1x and 3x had significantly higher N_{area} (8.7 and 9.6 g m^{-2} , respectively) than those unburned (7.0 g m^{-2} ; $P = 0.002$ and < 0.001 , respectively). Burned seedlings also had statistically higher N_{area} than pre-burn ($P < 0.001$ for both burn treatments), while unburned seedlings did not ($P = 0.19$), suggesting that despite some pre-burn variability, changes in N_{area} of burned seedlings from 2002 to 2003 were due to burning and not to some other factor common across treatments. Burn effects were not consistent throughout the years, as N_{area} of unburned seedlings was statistically similar to those burned 1x ($P = 0.33$) and 3x ($P = 0.09$) in 2004, during or following relatively wet years, but differed again in 2005 and 2007. In 2006, immediately following the third burn on plots burned 3x, N_{area} of seedlings burned 3x was higher than those unburned and burned 1x ($P < 0.001$ for both), which were not significantly different from each other ($P = 0.96$). All seedling groups except red and white oaks differed from one another ($P < 0.01$), but these effects depended on sampling year ($P < 0.001$). Notably, in 2004, N_{area} of all seedling groups was similar, but in all other years, oaks had higher N_{area} than both red maple and sassafras.

In 2007, mean N_{area} within each seedling group from each plot was positively correlated with mean LMA, except for red maple ($R^2 = 0.15$; $P = 0.24$; Appendix 6). This trend was stronger for red and white oaks ($R^2 = 0.70$ and 0.72 , respectively; $P < 0.001$ for both) than sassafras ($R^2 = 0.33$; $P = 0.02$). Oaks also exhibited a greater increase in N_{area} per unit change in LMA than sassafras, as indicated by higher slopes (slope = 2.1 and 1.8

for red and white oaks, respectively, compared to sassafras slope = 1.4; $P < 0.001$ for all comparisons) of the regression trendlines.

Foliar carbon (C)

There were significant treatment effects on foliar C concentration ($P = 0.009$; Figure 3.5), but these were independent of year ($P = 0.25$) and seedling group ($P = 0.99$). Seedlings burned 3x had slightly higher mean C concentration (49.1%) compared to those burned 1x (48.8%; $P = 0.02$) and unburned (48.2%; $P = 0.005$). Seedling group also affected foliar C concentration ($P < 0.01$). Red maple and sassafras did not significantly differ ($P = 0.22$) but had higher C (49.5 and 49.3%, respectively) than red (48.5%) and white (48.3%) oaks, which were not significantly different ($P = 0.09$). Carbon also varied by year ($P < 0.001$) and was lowest during or following dry years, 2002 and 2007.

Mean foliar C concentration in 2007 exhibited a positive linear correlation with mean LMA for red oaks ($R^2 = 0.31$; $P < 0.001$), red maple ($R^2 = 0.42$; $P = 0.03$), and sassafras ($R^2 = 0.56$; $P < 0.001$), but not white oaks ($R^2 = 0.00$; $P = 0.65$; Appendix 7). Trendline slopes were not significantly different among species ($P = 0.92$), but y-intercepts differed ($P < 0.001$) because at any given C concentrations, red oak LMA was higher than red maple, which was higher than sassafras.

C:N

There was no treatment effect on seedling foliar C:N ($P = 0.64$), but all seedling groups significantly differed from each other ($P < 0.01$ for all comparisons; Appendix 8). C:N was highest for red maple (33.2), intermediate for oaks (red = 27.7, white = 25.2), and lowest for sassafras (24.8). There was also significant interannual variation ($P < 0.01$). Foliar C:N decreased from 30.6 in 2002, a relatively dry year, to 24.5 in 2004, a very wet year, and increased again to 28.9 in 2007, a very dry year. Red maples had the greatest variability in C:N ratios, with C:N occasionally being higher on burned plots, but mean values were never statistically different among treatments ($P > 0.05$)

Canopy cover and leaf parameters

Several trends emerged for mean leaf parameters measured at each plot in 2007 and regressed against previous year mean canopy openness (expressed as open sky; Figure 3.6). Mean TLA of sassafras increased significantly ($R^2 = 0.41$; $P = 0.0007$) with increasing open sky, whereas mean LMA increased significantly ($P < 0.001$ for all) with

increasing understory light for all seedling groups (R^2 ranged from 0.40 for white oaks to 0.79 for sassafras). The regression slopes indicated a similar increase in LMA per unit increase in open sky for both oaks and sassafras (slope = 0.09-1.0; $P = 0.09$), but y-intercepts significantly differed ($P < 0.001$) such that LMA at any given light level was highest for red oaks, intermediate for white oaks, and lowest for sassafras. The slope of red maple's trendline (0.70) was ~ 30% lower than other seedling groups ($P < 0.05$ for all comparisons), although the y-intercept was similar to red oaks. Foliar N concentration and C:N ratios did not vary with understory light for any seedling group, but N_{area} significantly increased with increasing light for red oaks ($R^2 = 0.31$; $P < 0.001$), white oaks ($R^2 = 0.17$; $P = 0.02$), and marginally for sassafras ($R^2 = 0.23$; $P = 0.05$), but not red maple ($R^2 = 0.06$; $P = 0.47$). Foliar C concentration of red oaks ($R^2 = 0.25$; $P = 0.003$) and sassafras ($R^2 = 0.30$; $P = 0.03$) increased significantly with increasing light.

Leaf parameters and seedling size

Seedling size, measured as basal diameter, exhibited positive linear correlations with several leaf traits. TLA was strongly and positively correlated (R^2 ranged from 0.57 for white oaks to 0.93 for red maple; $P < 0.001$ for all) with seedling basal diameter across seedling groups (Figure 3.7). The response was strongest for red maple, which had a slope 3x steeper (0.0063) than oak or sassafras, whose slopes were statistically similar ($P = 0.09$). LMA and N_{area} were both positively correlated with basal diameter, but these trends were strongest for red maple and sassafras ($R^2 = 0.55$ and 0.47, respectively), which had slopes 2-4x greater than either oak. C and N concentrations and foliar C:N exhibited no correlations with basal diameters.

DISCUSSION

The primary impetus for using prescribed fire to enhance oak regeneration is the assumption that fire can decrease competition from fire-sensitive species and increase understory light. Combined, these altered understory conditions are expected to promote oak seedling growth and development, thereby enhancing their ability to compete with co-occurring woody seedlings which also survived burning or established following fire disturbance. Surviving oaks are hypothesized to gain a competitive edge following disturbance because their conservative growth strategy promotes development of

belowground resources which facilitate re-growth after top-kill (Larsen and Johnson 1998). Leaf alterations that promote interception and assimilation of newly available understory light or minimize water loss could also prove beneficial. Also, seedlings able to utilize a temporary increase in N availability could have an important growth advantage, and this should be reflected in foliar N concentrations. Overall, changes in oak seedling leaf characteristics in response to fire and the reflection of these leaf changes in growth parameters and competitive stature depend on a combination of interacting factors: 1) extent and duration of change in the abiotic parameter, 2) inherent phenotypic plasticity and ability to capture a transitory versus a long-lived change in resource availability, and 3) relative response of competing seedlings.

One way a seedling could take advantage of increased understory light post-fire is to increase TLA. In this study, burned seedlings had higher TLA, primarily due to a 2-3 fold increase in sassafras leaf area, but this response was not magnified by repeated burning. This change appeared related to understory light, as indicated by the positive correlation of TLA in 2007 with previous year canopy openness. Increasing TLA in response to increased light could be an effective strategy for early successional, shade-intolerant species like sassafras, which are not adapted to residing in the understory for long periods. In contrast, later successional species may not use this strategy because leaves are costly, both in terms of construction and maintenance (Barthod and Epron 2005), and low leaf area may confer a lower risk of herbivory and exposure to pathogens (DeLucia *et al.* 1998) and lower susceptibility to temporary decreases in water availability. For some species, increasing TLA may only be advantageous under conditions of permanently high light availability. For example, Sipe and Bazzaz (1994) found that red maple produced many small leaves generating higher total leaf area ($\sim 350 \text{ cm}^2$) in large gaps (300 m^2), but in small gaps (75 m^2), leaf area was 4 times smaller ($\sim 80 \text{ cm}^2$). While fire led to a wide range of canopy openness among plots, large canopy gaps were relatively rare and often only temporary due to prolific resprouting of mid- and understory species, which occluded a substantial portion of understory light the subsequent year (unpubl. data).

Seedlings could also increase their photosynthetic capacity in response to post-fire conditions by increasing their LMA and foliar N_{area} . Increased LMA with increased

irradiance is common (*e.g.*, Ellsworth and Reich 1993) and represents a change in a seedling's leaf dry-mass investment per unit of area available for light interception, resulting from either increased leaf thickness or density (Wright *et al.* 2004). These changes can increase the concentration of nitrogen-rich photosynthetic enzymes like RUBISCO and lead to a concomitant increase in N_{area} , which often leads to greater photosynthetic capacity per unit leaf area (Ellsworth and Reich 1993) and return of assimilated carbon (Aranda *et al.* 2004). N_{area} can also increase in response to increased foliar N concentrations due to increased soil N availability.

In this study, LMA and N_{area} were higher in burned seedlings, but there were no differences among seedling groups. These changes likely reflect increased understory light, as these parameters were positively correlated with canopy cover. The lack of fire-induced changes in foliar N concentration in this study, and strong correlations of LMA and N_{area} , suggest changes in LMA were responsible for changes in N_{area} in all seedling groups but red maple. Enhanced LMA post-fire contrasts with both Gilbert *et al.* (2003), working on a nearby ridge in Kentucky, and Reich *et al.* (1990), in central Wisconsin, who found no or few significant differences between LMA of seedlings on burned and unburned sites. These studies both evaluated a single burn, and neither reported variations between pre- and post-burn understory light, suggesting limited changes in LMA could be due to minimal changes in light.

Increased LMA post-fire also could result from changes in foliar C concentration. If fire leads to high evaporative losses through reduced forest floor mass and/or increased light, seedlings may respond through increased epidermal or cuticle thickness (Ashton and Berlyn 1994), which could increase foliar C concentrations. In this study, LMA was positively correlated with foliar C concentration of red oaks, red maple, and sassafras when considered across treatments. This trend emerged because foliar C tended to increase with burn number. Niinemets *et al.* (1999) measured increased foliar lignin, a C-rich compound, with increasing light, and suggested that this could be a side effect of light-induced water stress. Adams and Rieseke (2003) measured elevated foliar tannins in white oaks on burned sites, presumably from increased light (Dudt and Shure 1994).

We expected foliar N concentration to increase if fire increased soil N availability (Wan *et al.* 2001) or altered root:shoot dynamics (Kruger and Reich 1997b). However,

there was a lack of foliar N response to burning. Loucks *et al.* (2008) measured few burn effects on forest floor organic matter after the 2003 and 2004 fires; thus, these low-intensity fires may not have increased soil N availability. Alternatively, fire-induced increases in available soil N may have been transitory and dissipated in the 4-mo period between burning and sampling. Blankenship and Arthur (1999) measured only a 1-d increase in soil N following a single fire in eastern Kentucky. Gilbert *et al.* (2003), working in the same study site, found only a 4-mo post-fire increase in foliar N, which they speculated may have been due to the dilution of foliar N as seedling growth increased in response to fire (Reich *et al.* 1990).

All seedling groups exhibited positive correlations between basal diameter and TLA, LMA and N_{area} , but the trendline slopes were often highest for red maple and sassafras. Differences among seedling groups may result from different costs associated with constructing and maintaining leaves (Nagel *et al.* 2002; Barthod and Epron 2005). Increased LMA can lead to increased cell lignification (Baruch and Goldstein 1999) and increased epidermal and cuticle thickness (Ashton and Berlyn 1994), which entail investment in costly C molecules. Constructing and maintaining leaves with greater N per unit leaf area is also costly (Poorter and Villar 1997). If leaves already contain high levels of these expensive compounds, as do oak leaves, increased costs could lead to lower gains in photosynthate and consequent ability to invest in growth.

CONCLUSIONS

The results presented here represent the second part of a long-term study to assess prescribed fire effects on upland oak and co-occurring woody seedling growth and survival and provide another level of detail to help us understand how and why different woody seedlings respond to post-fire conditions in a specific manner. These findings suggest that low-intensity, early growing-season fires can alter foliar morphology and chemistry, especially TLA, LMA, and N_{area} , of upland oak and co-occurring competitor seedlings. These changes were often related to altered canopy cover conditions and were positively correlated with increased seedling basal diameter. However, differences in leaf parameters among seedling groups were either minimal or indicated an enhanced response of the competitors, red maple and sassafras. Thus, even when oak seedling foliar

characteristics responded positively to fire, their competitors performed equivalently or better.

Many of the survival, growth, and leaf-level differences observed in this and the companion study reflected differences in growth strategies and allocation patterns among seedling groups, which are important determinants of phenotypic plasticity and ability to capture a transitory versus a long-lived change in resource availability. Sassafras, an early successional, shade-intolerant species with clonal ramets, consistently exhibited greater survival, total height, and basal diameter growth following fire, and results of this study suggest one way that this species may be able to achieve superior stature following fire disturbance is by producing greater TLA and more effectively being able to increase basal diameter with every incremental increase in LMA and N_{area} . Red maple, a “super-generalist” with adaptations to various environments (Abrams 1998), exhibited reduced survival post-fire but no alterations in growth. Post-fire variations in leaf traits were also comparatively small in this species. Red and white oaks, with their moderate shade tolerance and “stress-tolerator” growth strategy, responded differently to burning. Fires were detrimental to white oak growth and survival, while red oaks had moderate post-fire survival and stimulated growth on plots with heavy overstory mortality. Both subgenera exhibited increased LMA and N_{area} post-fire, but these increases were always similar to co-occurring species, likely due to the relatively high costs of constructing and maintaining C and N-rich leaves.

The combined findings of the two companion studies provide further evidence that upland oak seedlings in the deciduous forests of eastern Kentucky are not responding to low-intensity, early growing season prescribed fires, conducted singly or repetitively, in a manner that consistently places them in a better competitive position. This lends credence to the idea that prescribed fires without silvicultural manipulation are not an especially effective management tool for enhancing oak regeneration in this region.

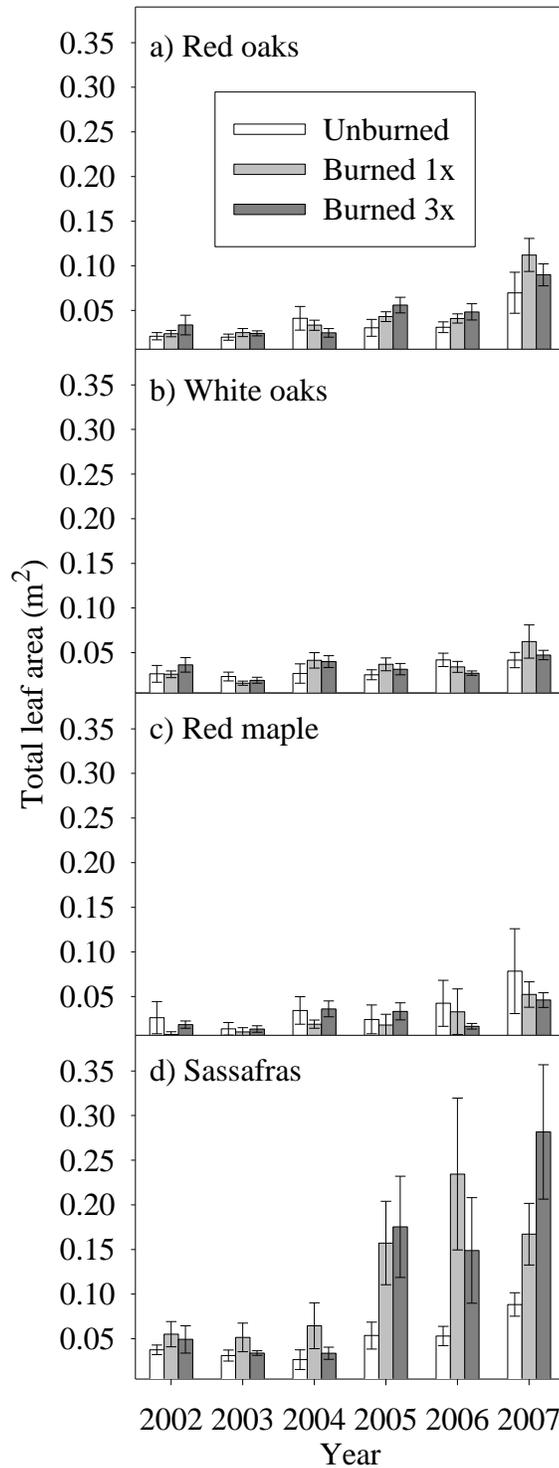


Figure 3.1. Mean annual total leaf area \pm SE for each seedling group across each treatment. Seedlings burned 1x were burned in spring 2003, and those burned 3x were burned in spring 2003, 2004, and 2006.

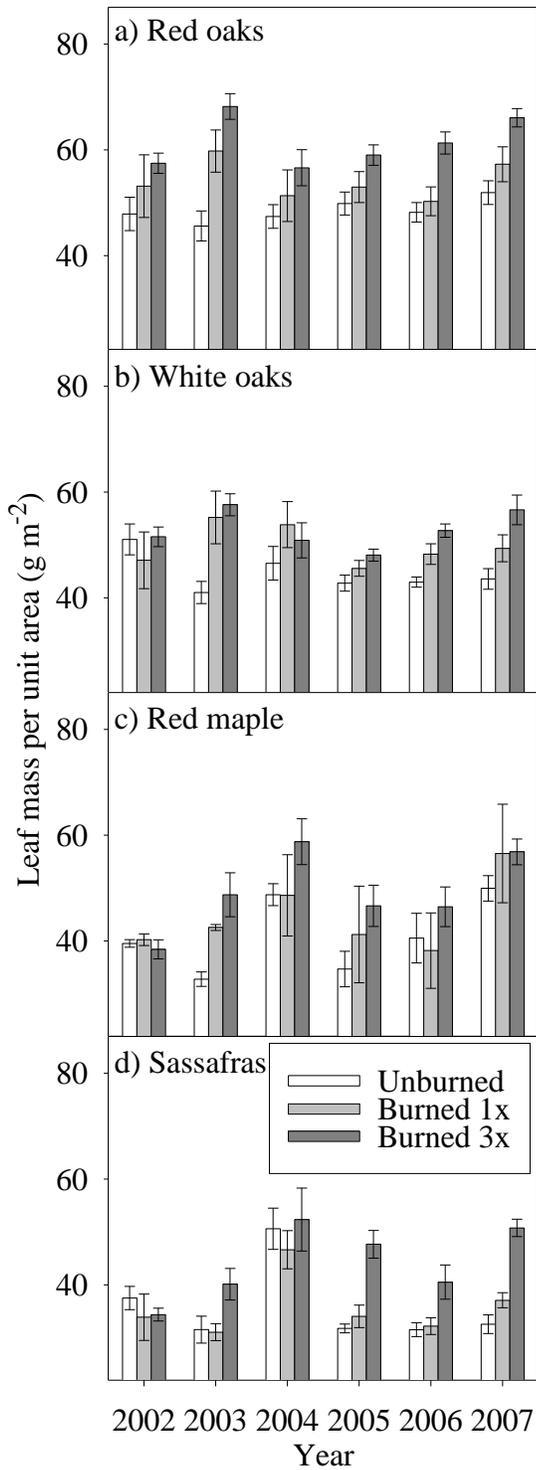


Figure 3.2. Mean leaf mass per unit area \pm SE for each seedling group across each treatment. Seedlings burned 1x were burned in spring 2003, and those burned 3x were burned in spring 2003, 2004, and 2006.

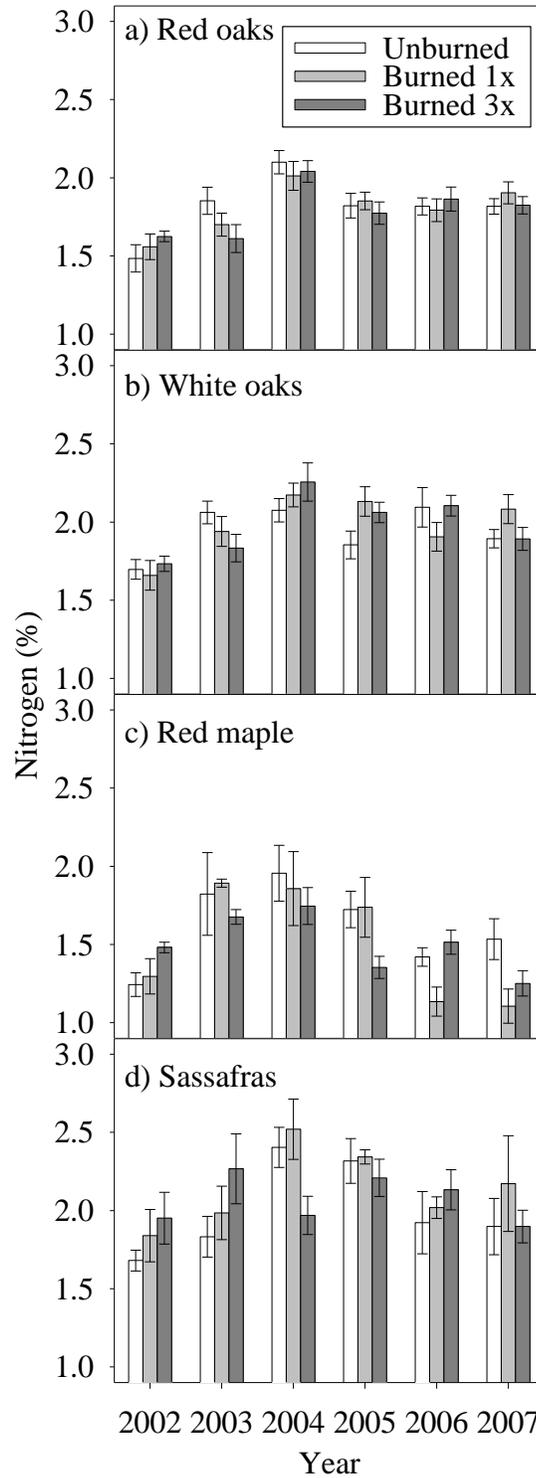


Figure 3.3. Mean foliar nitrogen \pm SE for each seedling group across each treatment. Seedlings burned 1x were burned in spring 2003, and those burned 3x were burned in spring 2003, 2004, and 2006.

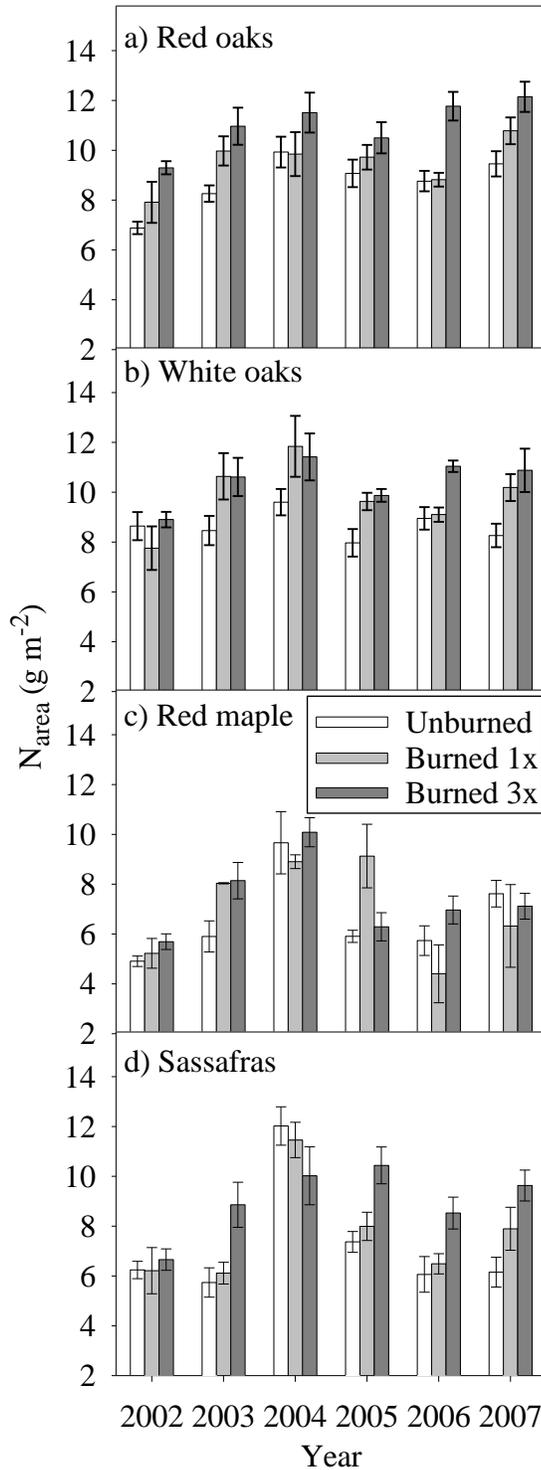


Figure 3.4. Mean foliar nitrogen content per unit area ($N_{\text{area}} \pm \text{SE}$) for each seedling group across each treatment. Seedlings burned 1x were burned in spring 2003, and those burned 3x were burned in spring 2003, 2004, and 2006.

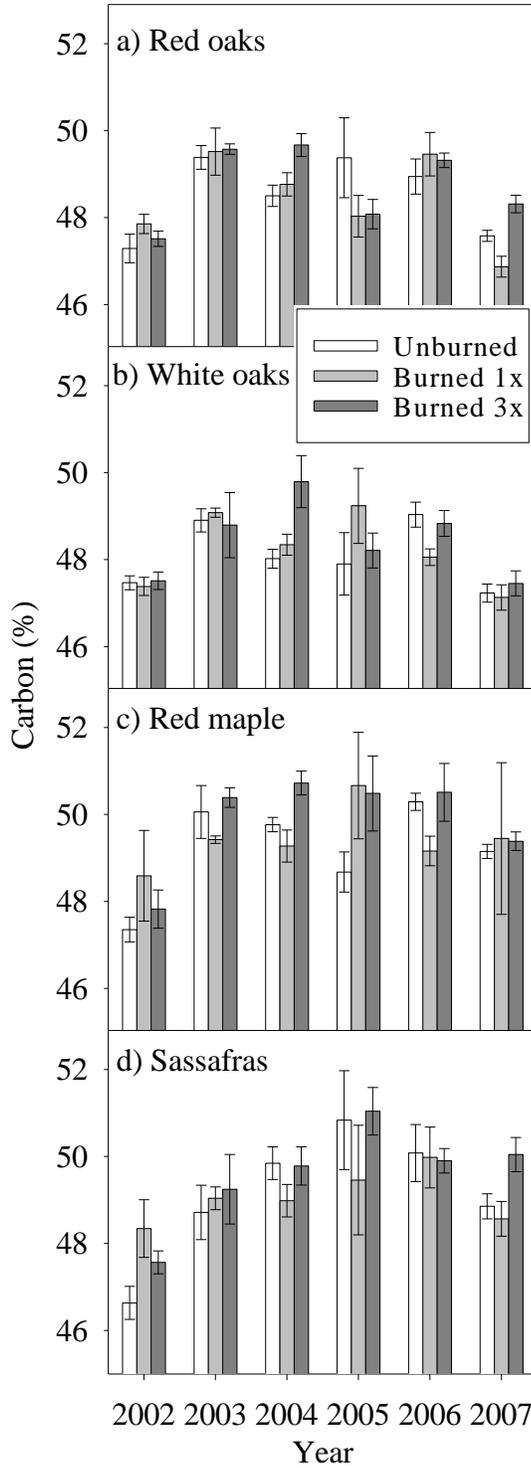


Figure 3.5. Mean foliar carbon \pm SE for each seedling group across each treatment. Seedlings burned 1x were burned in spring 2003, and those burned 3x were burned in spring 2003, 2004, and 2006.

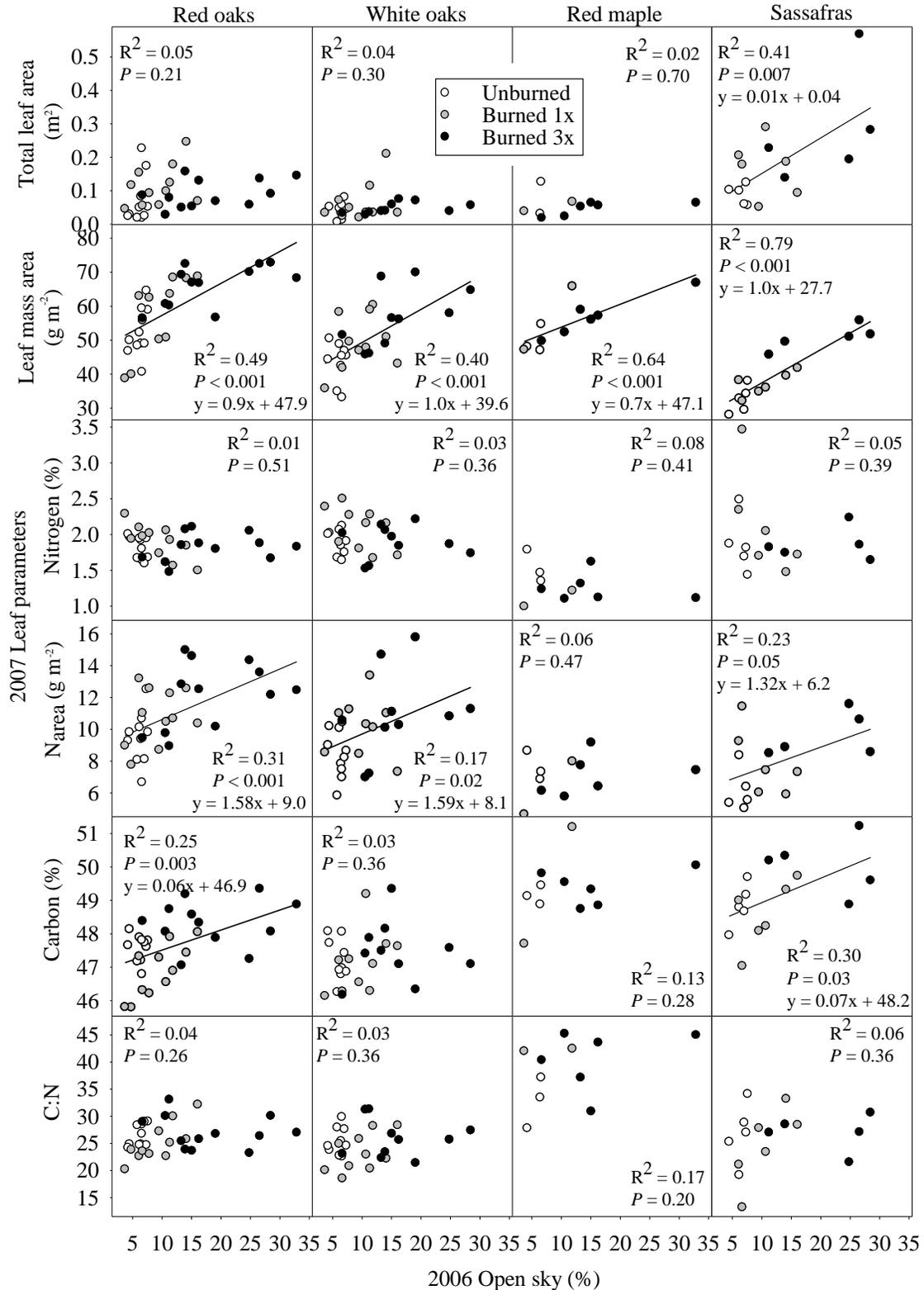


Figure 3.6. Mean leaf parameters for each plot in 2007 regressed against 2006 open sky (%) for each seedling group across each treatment. Seedlings burned 1x were burned in spring 2003, and those burned 3x were burned in spring 2003, 2004, and 2006.

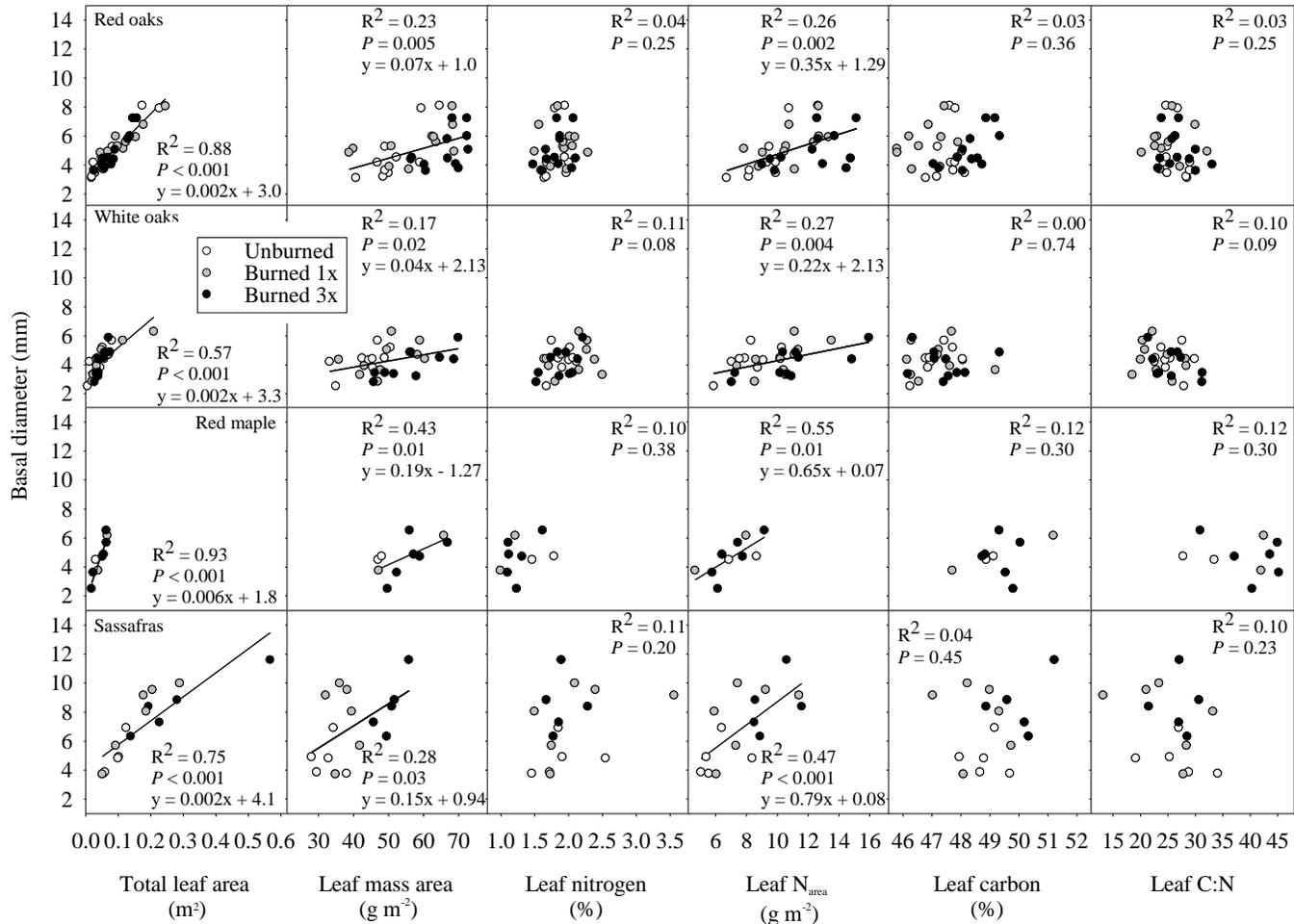


Figure 3.7. Mean leaf parameters for each plot regressed against mean basal diameter in 2007 for each seedling group across each treatment. Seedlings burned 1x were burned in spring 2003, and those burned 3x were burned in spring 2003, 2004, and 2006.

CHAPTER 4

IMPLICATIONS OF A SHIFT FROM UPLAND OAKS TO RED MAPLE ON FOREST HYDROLOGY AND NUTRIENT AVAILABILITY

ABSTRACT

Discerning impacts of different tree species on forest ecosystem dynamics is increasingly important as shifts in canopy composition increase due to invasive pests and pathogens, climate change, and altered disturbance regimes. In historically oak-dominated forests of the eastern U.S., fire suppression has facilitated the spread of red maple (*Acer rubrum* L.), a fire-sensitive, yet highly adaptable species. In this study, I address whether a predicted shift from upland oaks to red maple could influence ecosystem hydrology and nutrient availability due to species-specific effects on precipitation distribution and inorganic nitrogen (N) cycling. In eastern Kentucky, I measured seasonal variations in chestnut oak (*Q. montana* L.), scarlet oak (*Q. coccinea* Muench.), and red maple throughfall and stemflow following discrete precipitation events and assessed net N mineralization in underlying soils over a 2-yr period (2006-2008). Throughfall quantity and chemistry varied little among species, but red maple funneled more precipitation and generated 2-7x more stemflow than either oak, leading to larger inputs of stemflow-derived nutrients. Soils underlying red maple also had 5x greater rates of winter net nitrification compared to both oaks and 20-30% greater rates of net ammonification compared to chestnut oak. Combined, these traits could impact future canopy and understory composition and growth through effects on plant available nutrients, leaching losses, fuel discontinuity, fire disturbances, and forest management practices utilizing prescribed fire. Thus, shifting canopy dominance from oaks to red maple as a consequence of changing management practices and altered fire regimes has important implications for ecosystem properties and processes via species-specific effects.

INTRODUCTION

Individual tree species comprising forest communities can have important influences on ecosystem properties and processes. Species-specific differences in leaf litter quantity and quality influence decomposition rates and nutrient availability (Scott and Binkley 1997; Cornwell *et al.* 2008). Interspecific variation in canopy architecture, leaf area, and bark texture influence precipitation distribution, which affects evaporation, water status, understory microclimate, nutrient inputs, and leaching (Levia and Frost 2003). Species impact carbon storage through variable growth rates, allocation, and longevity (Kirby and Potvin 2007), and can shape regional climate through differential albedo and evapotranspiration (Amiro *et al.* 2006). Differences in susceptibility to wind (Papaik and Canham 2006), flood (Kozlowski 1997), ice (Tremblay *et al.* 2005), or fire (Hengst and Dawson 1994) can lead to species-specific impacts of disturbance and controls on disturbance intensity and magnitude. Discerning these individual tree species' impacts on forest community and ecosystem dynamics is increasingly important as shifts in canopy composition become common under the influence of invasive pests and pathogens (Lovett *et al.* 2006), climate change (Iverson *et al.* 2008), and altered disturbance regimes (Nowacki and Abrams 2008).

Fire suppression over the last 7+ decades has facilitated the spread of the “super-generalist” red maple (*Acer rubrum* L.; Abrams 1998) into historically oak-dominated forests of the eastern U.S. (Lorimer 1984; Fei and Steiner 2007). Red maple was once a minor forest constituent, limited to mesic coves, swamps, and riparian areas protected from fires (Abrams 1998). Dendrochronological analyses indicate substantial red maple recruitment into forest overstories following fire suppression, while upland oak recruitment virtually ceased (Hutchinson *et al.* 2008). Today, red maple can be found across sites of varying edaphic conditions (Abrams 1998), and studies indicate increased basal area, density, importance value (Lorimer 1984; Alderman *et al.* 2005; Abrams 2005), and range expansion (Fei and Steiner 2007). While a native tree, red maple has many invasive characteristics which have contributed to its success, including high reproductive capacity, early maturity, flexible germination strategy (Hille Ris Lambers and Clark 2005), and ability to act as both an early and late successional tree species

(Abrams 1998). Notably, Uva *et al.* (1997) classify red maple as weedy and/or invasive species in the northeast U.S.

On many sites, red maple's increase has coincided with a substantial decline in oak regeneration, presumably from decreased understory light and increased competition as red maple and other shade-tolerant species proliferate without fire disturbances to suppress their growth and expansion (Lorimer *et al.* 1994; Abrams 2005). This trend has led many researchers to predict an inevitable transition from oaks to red maple or other fire-sensitive species (Abrams 2005; McEwan *et al.* 2005; Fei and Steiner 2007; Nowacki and Abrams 2008). While prescribed fires have been increasingly implemented in an attempt to curb red maple proliferation and promote oak regeneration, results thus far suggest fire alone cannot achieve these results (Hutchinson *et al.* 2005; see Chapter 2). Beyond the detriments to wildlife of losing an essential mast species such as oak, the ecological consequences of this shift have been largely untested. Anecdotally, red maple exhibits many traits that differ from co-occurring oak species such as thinner leaves, denser canopies, and smoother bark, and the few studies evaluating red maple and oak characteristics suggest different leaf litter chemistry, which may differentially impact nutrient cycling within underlying soils (Finzi *et al.* 1998; Washburn and Arthur 2003).

Species-specific differences between red maple and upland oaks could have important implications for forest hydrology, nutrient cycles, disturbance regimes, and future canopy and understory composition. In this study, I address whether a shift from upland oaks to red maple predicted in the continued absence of fire or other management practices could influence forest hydrology and nutrient cycling due to species-specific effects on precipitation distribution and inorganic nitrogen (N) cycling. I measured seasonal variations in chestnut oak (*Q. montana* L.), scarlet oak (*Q. coccinea* Muench.), and red maple throughfall and stemflow quantity and quality following discrete precipitation events and assessed net ammonification, nitrification, and N mineralization in underlying soils. I hypothesized that red maple would have a denser canopy and generate less throughfall compared to oaks. Nutrient concentrations of red maple throughfall would be relatively higher because greater canopy surface area would allow more nutrient leaching and collection from foliar and bark surfaces; however, throughfall nutrient inputs would be lower because of less total volume. I further hypothesized that

because of smoother bark red maple would have higher stemflow volume and funneling effects. Greater stemflow volume would lead to higher nutrient loading, but not nutrient concentrations, because the rough bark of oaks would create greater surface area to concentrate airborne or leached nutrients. Greater stemflow volume and higher nutrient inputs from red maple could then lead to higher net rates of N mineralization due to greater soil moisture and carbon (C) and inorganic N inputs.

METHODS

Study area

Studies were conducted on Klaber and Whittleton Ridges in the Cumberland Ranger District of the Daniel Boone National Forest (DBNF) of eastern Kentucky, USA. These ridges were non-contiguous and separated by ~ 8.5 km. Soils were a silt loam, moderately deep, well-drained and generally acidic (Hayes 1993). Climate was temperate, humid, and continental, with a mean annual temperature of 12 °C and annual precipitation (113 cm yr⁻¹) fairly well-distributed throughout the year (Foster and Conner 2001). Study areas along each ridge encompassed ~ 15 ha with similar slope (< 20% grade) and elevation (~ 400 m). These areas had minimum human influence and no recent fires (> 25 yr; Blankenship and Arthur 2006).

Forest stands were second-growth (~ 60-80 yr; Washburn and Arthur 2003) and comprised a diverse assemblage of tree species. Total overstory (≥ 10 cm diameter at breast height (DBH)) basal area and stem density were approximately 26.5 m² ha⁻¹ and 532 trees ha⁻¹, respectively (calculated from Blankenship and Arthur 2006). Oaks dominated overstory basal area (19.5 m² ha⁻¹) and stem density (242 trees ha⁻¹), and included scarlet oak (*Quercus coccinea* Muench.), chestnut oak (*Q. montana* Willd.), white oak (*Q. alba* L.), and black oak (*Q. velutina* Lam.). Red maple (*Acer rubrum* L.) comprised a relatively small portion of overstory basal area (4.0 m² ha⁻¹), but stem density (215 trees ha⁻¹) was only 11% less than all oaks combined. Total midstory basal area and density were about 1.9 m² ha⁻¹ and 808 trees ha⁻¹. Red maple comprised substantially greater midstory basal area (1.1 m² ha⁻¹) and density (403 trees ha⁻¹) than oaks (0.01 m² ha⁻¹ and 2.5 trees ha⁻¹, respectively). Chestnut and scarlet oak seedlings were relatively abundant on the forest floor (1800 and 900 stems ha⁻¹, respectively), but

red maple seedling density was greater (10675 stems ha⁻¹; Green 2005) than these two oaks species combined.

Study design

From summer 2006 to spring 2008, I assessed throughfall and stemflow quantity and quality of red maple and two upland oak species (chestnut and scarlet oak) seasonally (February, May, August, and November) during discrete precipitation events. Seasonal sampling was employed to capture changing canopy cover and weather patterns. I chose these two oak species because initial surveys of stand composition indicated that they were the most dominant representatives of the red (*Erythrobalanus* spp.) and white (*Leucobalanus* spp.) oak subgenera. I sampled a single canopy dominant or co-dominant tree (20-30 cm DBH) of each species within five blocks (~ 0.1 ha each) along each ridge (n = 10 trees per species), resulting in a randomized complete block design with block nested within ridge. Small midstory trees whose canopy overlapped with the target tree were manually removed prior to sampling to minimize influences due to non-target species. Incident precipitation quality and quantity were simultaneously collected in adjacent open areas (~ 0.5 ha) near each ridge.

To determine if these two upland oak species cycle inorganic N differently than red maple, I initiated seasonal sampling of *in situ* N mineralization within underlying mineral soils in May 2006. I used a similar study design as that detailed above using a different subset of trees. In August 2006, a “no tree” area, which was devoid of tree boles > 2 cm DBH within a 2-m radius, was added to each block to allow assessment of N mineralization in the absence of a tree’s presence.

Tree characteristics

Each sampled tree was assessed for several characteristics prior to initial sampling. Crown height and width were measured with a Vertex hypsometer. Crown width was estimated in the four cardinal directions by walking out the estimated width of the crown and measuring distance back to the edge of the tree bole. Crown area was calculated by averaging the four crown widths, then using this width from bole as the radius of a circle to estimate area. Crown volume was estimated only on throughfall/stemflow trees by assuming the canopy occupied a cylindrical volume and multiplying the crown depth by the crown area. Bark roughness was estimated as the

mean depth of bark fissures measured ~ 1.5 m aboveground in the four cardinal directions. Percent cover of bark epiphytes was visually estimated in the four cardinal directions within a 10 cm² area at ~ 1.5 m aboveground using the following categories: 0 = < 20%, 1 = 21-40%, 2 = 41-60%, 3 = 61-80%, and 4 = 81-100%.

Water collection

Throughfall was collected on opposite sides of each tree, ~ 0.5 m from the base of the bole and ~ 0.75 m aboveground, using a 20-cm diameter (314 cm²) polyethylene funnel attached to a 2-L amber, polyethylene bottle. Two similar collectors for incident precipitation were installed in an open area adjacent to each ridge. The neck of each funnel contained glass wool to prevent entry of debris. Collectors were cleaned between precipitation events using deionized water, and new glass wool filters were installed.

Stemflow was collected using polyurethane foam collars adhered to the bole of each tree ~ 120 cm aboveground and angled slightly downward to facilitate collection (see Appendix 9 for detailed methodology). Each collar was attached to an 80-L collection vessel using 1.25-cm diameter silicone tubing. Prior to each event, collection bins were tightly covered, lined with chemically inert polypropylene bags, and tested for leaks using deionized water. Points along the collar with leakage were re-sealed with silicone sealant.

Incident precipitation, throughfall, and stemflow were collected within 48 hrs of each precipitation event, which was the time required to access both ridges. Total volume, pH, and electrical conductivity (EC) were measured in the field, the pH and EC using a portable meter (Hanna Instruments, Model HI 98129, Woonsocket, RI, USA) calibrated prior to each sampling. One 500-mL stemflow and one throughfall sample (pooled from the two collectors per tree) were obtained from each tree. When volumes were sufficient, random, duplicate throughfall and/or stemflow samples were collected from individual trees and analyzed to test for variation within the experimental unit (*i.e.*, tree). The proportion of precipitation collected as throughfall was calculated as: Throughfall Volume/Precipitation Volume. The funneling ratio (Herwitz 1986), which provides an estimate of the branch-funneling effect and the aboveground woody surface area contacted by stemflow drainage (*i.e.*, contribution from the branches in generating stemflow), was computed for each tree and event as $F = S/PB$, where F is the funneling

ratio, S is the stemflow volume for the given tree (ml), P is the rainfall depth (cm), and B is the basal area of the tree (cm^2). A funneling ratio of 1.0 indicates that measured stemflow volume would be equal to the measured volume from a hypothetical rain gauge with a collecting area the size of the basal area of the tree. A ratio greater than 1.0 indicates a contribution from branches in funneling water to the stem and increasing the total volume of water captured from the tree.

On occasion, the stemflow collecting apparatus malfunctioned for various reasons (*e.g.*, extreme weather pulling the collection tube from the vessel or debris falling on the device) resulting in some variation in the number of experimental units on several sampling dates. Precipitation collectors for Whittleton Ridge were tampered with during the February 2007 sampling, rendering these data unavailable. In addition, sampling equipment at Whittleton Ridge was destroyed by a black bear during fall 2007, limiting sampling to Klaber Ridge. Devices were re-installed in February 2008.

Water samples were returned to the laboratory on ice where a sub-sample was immediately filtered through a $0.45 \mu\text{M}$ membrane filter for future analysis of cations, anions, and dissolved organic carbon (DOC). All samples were kept in the dark at 4°C until analysis. Within 24 hr, inorganic N ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^- + \text{NO}_2^-\text{-N}$) was analyzed colorimetrically with an automated continuous-flow analyzer (Bran+Luebbe Autoanalyzer III, Bran-Luebbe, Chicago, IL), and within 1 wk, water samples were digested with potassium persulfate and analyzed colorimetrically to obtain total N concentration. Within 72 hr, base cations (Ca^{2+} , Mg^{2+} , Na^+ , and K^+) were measured using an atomic absorption spectrometer (Avanta AAS, GBC Scientific Equipment, Hampshire, IL), and anions (SO_4^- , PO_4^{3-} , and Cl^-) were assessed via ion chromatography (ICS-2000, Dionex Corporation, Sunnyvale, CA). Inorganic phosphate concentrations were below detection limits (0.03 mg L^{-1}) on most sampling dates, so are not reported here. Total carbon (TC), total organic carbon (TOC), and dissolved organic carbon (DOC) were analyzed within 72 hr with a total organic carbon analyzer (TOC 5000-A, Shimadzu Scientific Instruments, Columbia, MD). Total carbon was obtained on unfiltered samples; TOC was analyzed on unfiltered, acidified samples; and, DOC was analyzed on filtered and acidified samples. During October 2006, I noticed a few samples with TOC concentrations less than DOC concentrations and determined this discrepancy to be due

to a faulty filtering system. These DOC data were eliminated from further analyses. Ten percent of all samples were analyzed as replicates. Mean concentrations are volume-weighted (concentration/mean volume). Inputs were calculated as content (concentration*volume) divided by the collecting area, which was either the area of the funnel(s) or basal area of the tree.

Soil moisture

To determine if differences in stemflow and throughfall inputs impacted underlying mineral soil moisture, I determined gravimetric soil moisture beneath trees of each species after each rainfall event. Trees sampled were of similar size and adjacent to trees equipped with stemflow collars. Soils were sampled to a mineral soil (A-horizon) depth of 5 cm at a distance 0.5 m from the edge of each tree bole and in the center of each “no tree” area using a 2.5-cm diameter metal t-collector. The O horizon was removed prior to collection. Soils were stored in the laboratory at 4 °C until processed within 1 d of collection. Each sample was weighed, dried to constant weight at 105 °C, and reweighed. Values are reported on a soil dry weight basis: soil moisture (%) = (wet weight – dry weight)/dry weight.

Leaf litter

Because net N mineralization rates are often correlated with leaf litter quality (Scott and Binkley 1997), I estimated leaf litter contribution beneath each target tree and “no tree” area. Before leaf fall in 2006, I installed a 1-m² mesh screen ~ 0.5 m from the bole of each tree and in the center of each “no tree” area. I collected litter weekly throughout leaf fall; litter was then air-dried, sorted by species, dried at 60 °C, and weighed to determine mass and species composition. This estimation method assumes that litter displaced from the collecting screen between sampling dates due to wind or other mechanisms was similarly replaced.

Net N mineralization

To assess species-specific variation in net rates of seasonal (February, May, August, and November) inorganic N cycling, I collected two replicate soil samples 0.5 m from the bole of each tree and near the center of each “no tree” area using a 4-cm diameter PVC corer. Organic horizons were removed in the field and upper mineral soils (0 – 5 cm) placed in separate polyethylene bags and returned to the laboratory on ice for

analysis of initial inorganic N concentrations ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$; $\mu\text{g N g}^{-1}$ soil). *In situ* net N mineralization was determined using two PVC soil incubation tubes driven ~ 10 cm into the soil, which were loosely covered with duct tape and left in place for 28-d, when the upper mineral soils (0 – 5 cm) were removed and analyzed in the same manner as initial samples. Upon return to the laboratory, soil samples were stored at 4 °C and processed within 1 d of collection. Mineral soils were sieved through a 2-mm mesh sieve to homogenize the sample and remove large rocks, debris, and root material. A 10 g subsample was placed in extraction cups with 50 ml of 1 mol/L KCl and shaken for 1 hr. The solution was filtered on No. 40 Whatman paper, and the supernatant analyzed colorimetrically for available inorganic N ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$) with a Bran Luebbe Autoanalyzer III. Net N mineralization was calculated as the total inorganic N ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$; $\mu\text{g N g}^{-1}$ soil d^{-1}) accumulated over the 28-d incubation period. Net nitrification was the total $\text{NO}_3^-\text{-N}$ ($\mu\text{g N g}^{-1}$ soil d^{-1}) and net ammonification the total $\text{NH}_4^+\text{-N}$ accumulated over the 28-d incubation period.

Statistics

Differences among water and soil variables were analyzed in a factorial treatment arrangement (season and species as fixed effects) within a randomized complete block design with ridge and block nested within ridge as random factors using PROC MIXED (SAS Institute 2000). Tree and leaf litter characteristics were assessed similarly but without the seasonal component. Because the initial models consistently revealed statistically significant differences between stemflow and throughfall, these variables were analyzed and presented separately. Differences between precipitation and throughfall and precipitation and stemflow were analyzed by subtracting throughfall and/or stemflow from precipitation and testing whether these values differed from 0. Statistics for pH were analyzed using H^+ concentration, but I present mean pH for simplicity. All variables were tested for normality and homogeneity of variance prior to analyses and were transformed when they did not meet these underlying assumptions. For all significant factors and interactions ($P < 0.05$), least squares means were compared via a post-hoc Fischer's LSD test to determine differences among means at $\alpha = 0.05$.

RESULTS

Tree characteristics

Red maple differed from both oaks with regard to most tree parameters (Table 4.1). Red maple trees were smaller, with significantly lower mean DBH, basal area, and height than chestnut and scarlet oak ($P < 0.01$ for all comparisons). Red maple average crown width from the bole was ~ 0.5 m greater than chestnut ($P = 0.05$) and scarlet oak ($P < 0.01$), and encompassed 11 ($P = 0.04$) and 14 ($P = 0.01$) m² more area, respectively. Red maple mean crown depth was 0.8 and 2.3 m less than scarlet and chestnut oak, respectively, and while these differences were not significant ($P = 0.12$), red maple's smaller crown depth resulted in similar crown volume among species ($P = 0.58$). Red maple's bark was 2 and 5x smoother than both oaks ($P < 0.001$ for both), and scarlet oak was twice as smooth as chestnut oak ($P < 0.001$). Epiphyte cover was similar between red maple and chestnut oak ($P = 0.24$), which had cover twice as high as scarlet oak ($P = 0.04$ and < 0.01 , respectively).

Water quantity

Throughfall volume was always less than precipitation volume ($P < 0.01$ for all comparisons), and seasonal variations ($P < 0.01$) were driven by those in precipitation. Throughfall volume was similar among species ($P = 0.15$; Figure 4.1A), but red maple received a lower percentage of precipitation as throughfall (69%) than scarlet (72%; $P = 0.05$) or chestnut oak (78%; $P < 0.001$; Figure 4.1B).

Red maple generated 2-7x more stemflow and funneled 2-7x more precipitation than either oak ($P < 0.001$ for both comparisons), while scarlet oak produced more stemflow and often had a funneling ratio 20-55% higher than chestnut oak ($P < 0.001$ for both; Figure 4.1C). Seasonal variations ($P < 0.001$) in stemflow volume reflected those in precipitation, but stemflow volume was substantially larger than precipitation volume ($P < 0.001$). Notably, red maple's funneling capacity varied little across seasons and events of different magnitude (Figure 4.1D).

Water quality

Precipitation and throughfall NH₄⁺ concentrations did not differ from each other ($P > 0.05$ for all species; Figure 4.2A), but NH₄⁺ inputs via throughfall were always less than precipitation because of low volume ($P < 0.01$ for all species; Figure 4.2B),

especially in spring and summer, when trees were in full canopy. Throughfall NH_4^+ concentrations and inputs were similar among tree species ($P = 0.96$ and 0.28 , respectively), but varied seasonally ($P < 0.001$), with high concentrations in winter ($P < 0.01$ for all comparisons) and low inputs in spring. NH_4^+ stemflow concentrations were higher than precipitation ($P < 0.001$ for all species), but there were no difference among tree species ($P = 0.78$). NH_4^+ stemflow concentrations varied seasonally ($P < 0.001$), with summer values (0.38 mg L^{-1}) ~ 2-3x more than spring (0.22 mg L^{-1}) and winter (0.12 mg L^{-1} ; Figure 4.2C). However, red maple generated 2-3x more NH_4^+ input (87 mg m^{-2}) than chestnut (29 mg m^{-2} ; $P < 0.001$) or scarlet oak (38 mg m^{-2} ; $P < 0.001$), while the two oaks did not differ ($P = 0.13$; Figure 4.2D).

Precipitation and throughfall NO_3^+ concentrations and input (Figures 4.2E and 4.2F) did not vary from each other ($P > 0.05$ for all comparisons), and there were no significant differences among tree species for these two parameters ($P = 0.31$ and 0.68 , respectively). NO_3^+ concentration and input varied seasonally ($P < 0.001$), with high values in winter. Stemflow NO_3^+ concentrations and input (Figures 4.2G and 4.2H) exhibited a similar seasonal trend ($P < 0.001$), and were higher than precipitation in winter and spring ($P < 0.05$ for all comparison). Red maple had higher concentrations (0.35 mg L^{-1}) than chestnut oak (0.15 mg L^{-1} ; $P < 0.001$), but not scarlet oak (0.31 mg L^{-1} ; $P = 0.57$). Red maple input (133 mg m^{-2}) was 8x greater than chestnut oak (16 mg m^{-2} ; $P < 0.001$) and 2x greater than scarlet oak (66 mg m^{-2} ; $P < 0.001$).

Total nitrogen (TN) concentration was significantly lower in precipitation than in throughfall and stemflow ($P < 0.05$ for all comparisons), but tree species did not differ with regard to throughfall TN concentration ($P = 0.22$; Figure 4.3A), throughfall TN input ($P = 0.97$; Figure 4.3B), or stemflow TN concentration ($P = 0.85$; Figure 4.3C). However, TN input via stemflow exhibited a species effect ($P < 0.001$), as red maple generated 2-3x more TN than either chestnut or scarlet oak ($P < 0.001$ for both comparisons; Figure 4.3D). All parameters varied seasonally ($P < 0.05$ for all), with high throughfall and stemflow TN concentrations in winter and spring, respectively, and relatively high TN inputs in fall.

Trends in DOC, TOC, and TC were similar; thus, I only present findings for TC. Precipitation TC concentration and inputs were lower than throughfall ($P < 0.05$ for all

comparisons) except during winter, but there were no species differences in throughfall TC concentrations or inputs ($P = 0.76$ and 0.52 , respectively; Figures 4.4A and 4.3B). Stemflow TC concentrations were always higher in stemflow than precipitation ($P < 0.05$ for all comparisons). Red maple stemflow TC concentrations (Figure 4.4C) were significantly lower (17 mg L^{-1}) than chestnut (42 mg L^{-1}) and scarlet oak (36 mg L^{-1} ; $P < 0.001$), which were similar ($P = 0.38$), but inputs did not vary by species ($P = 0.34$; Figure 4.4D). Markedly high values in spring drove seasonal effects in throughfall and stemflow TC parameters ($P < 0.01$ for all).

Throughfall pH and EC did not vary by species ($P = 0.74$ and 0.97 , respectively), but exhibited significant seasonal effects ($P < 0.01$ and 0.02 , respectively) due to higher pH and lower EC in fall and winter compared to spring and summer (Appendix 10). Stemflow pH and EC varied seasonally ($P < 0.001$ for both) in a manner similar to throughfall, but chestnut oak had lower pH and higher EC than both red maple and scarlet oak ($P < 0.01$ for all), while red maple had lower pH and EC ($P < 0.001$ and 0.008 , respectively) than scarlet oak (Appendix 10).

Cation and anion concentrations were generally enriched in throughfall compared to precipitation, but they never varied among tree species ($P > 0.05$ for all; Appendix 10). However, Mg^{2+} and K^+ input via chestnut oak throughfall were $\sim 20\%$ higher than scarlet oak or red maple ($P < 0.05$ for all; Appendix 2). Stemflow concentrations were generally highest from chestnut oak and lowest from red maple, but red maple inputs were consistently greater ($P > 0.05$ for all comparisons; Appendix 10 and 11).

Soil moisture

The effect of species on mineral soil moisture depended on season (species*season $P < 0.001$; Figure 4.5). In winter, red maple had higher soil moisture than chestnut oak ($P = 0.05$) only, while in spring, scarlet oak had higher soil moisture than chestnut oak ($P = 0.01$). In summer, “no tree” areas had lower soil moisture than all tree species ($P < 0.05$ for all), and in fall, there were no differences among treatments.

Leaf litter

Total litter mass (without woody debris) beneath sampled trees was $400\text{-}464 \text{ g m}^{-2}$, and did not vary among species ($P = 0.09$; Figure 4.6). Contributions from chestnut oak, scarlet oak, red maple, and “other” species were similar underneath different tree

species ($P = 0.53, 0.17, 0.37,$ and $0.88,$ respectively). Chestnut and scarlet oak litter comprised 30-40% each of total leaf litter mass, while red maple and “other” species contributed about 20% and 8%, respectively.

Net ammonification, nitrification, and N mineralization

Net ammonification varied by season ($P < 0.001$) and species ($P = 0.01$; Figure 4.7A). Rates were highest in spring/summer and lowest in fall/winter. Red maple had significantly greater rates than chestnut oak ($P = 0.01$), but not scarlet oak ($P = 0.18$) or “no tree” areas ($P = 0.63$). There was a significant season*species effect on net nitrification ($P < 0.001$; Figure 4.7B). Species differences were negligible except in winter when nitrification underneath red maple was $\sim 5x$ greater ($0.04 \mu\text{g-N g}^{-1} \text{ dry soil d}^{-1}$) than underneath chestnut ($-0.01 \mu\text{g-N g}^{-1} \text{ dry soil d}^{-1}$; $P < 0.001$) and scarlet oak ($0.003 \mu\text{g-N g}^{-1} \text{ dry soil d}^{-1}$; $P = 0.003$). Net nitrification in “no tree” areas were similar to red maple ($P = 0.96$). Net N mineralization mimicked trends in ammonification (Figure 4.7C), as most mineralization occurred via this process.

DISCUSSION

I hypothesized that, compared to oaks, red maple canopies would be denser, leading to less throughfall volume and greater throughfall nutrient concentrations, but lower throughfall nutrient inputs. While not significant, total throughfall volume beneath red maple was slightly lower than both oaks', and the percentage of incident precipitation received as throughfall was always significantly lower beneath red maple. Species differences were least apparent in winter, suggesting leaf area could be an important parameter affecting this trend. However, these trends did not coincide with greater nutrient concentrations or lower nutrient inputs. The only species-specific differences in throughfall chemistry were greater Mg^{2+} and K^+ inputs from chestnut oak during spring and summer. Chestnut oak foliage is known to have greater Mg^{2+} concentrations than scarlet oak or red maple (Rieske *et al.* 2002), and previous work has indicated throughfall enrichment of Mg^{2+} and K^+ due to foliar leaching (Hermann *et al.* 2006). A noticeable lack of other species-specific effects on throughfall may suggest canopy properties known to affect throughfall quantity or quality (*e.g.*, leaf area, branch angle; Levia and Frost 2003) were not sufficiently different to elicit variability, or differences may have

existed, but were not detected because of the difficulty of ascertaining individual tree canopy effects in a mixed species stand. For instance, while I made attempts to select trees with independent canopies, there was still an unavoidable degree of canopy overlap, such that throughfall likely passed through leaves and branches of several trees before reaching the collectors.

As hypothesized, red maple had the smoothest bark and generated 2-7x more stemflow volume than oaks. Smooth bark has low water storage capacity (Herwitz 1985), low resistance to flow (Voigt 1960), and few obstacles to generate canopy drip (Carlyle-Moses and Price 2006). In north-central Florida, Lui (1998) found smooth-barked black gum (*Nyssa sylvatica* var. *biflora* Marshall) had 5 times lower water storage capacity than rough-barked cypress (*Taxodium aschdens* Brongn.). In a mixed oak-beech stand in Belgium, André *et al.* (2008) evaluated stemflow production across rain events of different magnitude and found that European beech (*Fagus sylvatica* L.), with thin, smooth bark, consistently generated between 1.5 and 22 times more stemflow volume than sessile oak (*Quercus petraea* Liebl.), with thick, rough bark.

The capacity to funnel precipitation and produce large stemflow yields suggests that as red maple dominance increases, there will be less precipitation distributed across the forest floor and more precipitation concentrated within limited areas surrounding tree boles. While stemflow is generally restricted to an area ~ 0.5 – 1 m from the tree bole (Voigt 1960; Chang and Matzner 2000), a zone of high water inputs and relatively high moisture could create fuel discontinuity, decreasing flammability of whole forest stands. Nowacki and Abrams (2008) argue that red maple and other shade-tolerant species create cool, damp conditions in their understory through their thick, dark canopies and easily decomposable leaf litter. This “mesophication” process creates a positive feedback loop that promotes fire-intolerant species and renders forests less conducive to fire disturbances, suggesting current restoration practices using prescribed fire to regenerate oaks will become less effective over time (Abrams 2005).

While high stemflow volume from red maple did not always produce greater moisture in upper mineral soils, this does not mean that greater water inputs are trivial. Measurements within the upper mineral soil (0-5 cm) probably do not capture the actual impacts of red maple’s stemflow loading throughout the soil profile. Stemflow also tends

to move along “preferential flow paths” (Johnson and Lehmann 2006), which are paths of least resistance often created by root growth through the soil. Thus, measuring soil moisture of the bulk soil may underestimate the magnitude of water flowing through soils. The large magnitude of differences in stemflow inputs between red maple and oaks can be demonstrated by projecting stemflow volume over the total growing season (April 1st-August 31st) using average precipitation values during 2006-2008. Based on stemflow generation observed during the lowest and highest magnitude growing-season events (1.2 cm and 2.78 cm in May and August 2007, respectively) and calculated per unit trunk basal area, red maple stemflow depth equivalents would be ~857-1000 cm compared to only 175-389 cm for chestnut oak and 425-467 cm for scarlet oak. These differences are considerable, and when accumulated over time and space, suggest that high stemflow generation may provide an additional avenue by which increased red maple dominance would contribute to the “mesophication” of forest stands.

Red maple’s greater ability to channel precipitation as stemflow could also decrease susceptibility to water shortages, allowing red maple to improve its own understory conditions. Stemflow can be an important mechanism of groundwater recharge to deep soils (Durocher 1990; Taniguchi *et al.* 1996), and trees and shrubs in semiarid and arid regions have been shown to uncouple from short-term drought conditions by storing stemflow-derived water at their bases (Martinez-Meza and Whitford 1996). An ability to funnel even small precipitation volumes could be an effective strategy in temperate regions if trees grow on xeric, sandy soils, such as those sampled here because summer droughts are common across the eastern U.S., and fluctuations in climatic extremes are predicted to increase with global warming (Watson *et al.* 1998). Notably, Abrams and Mostoller (1995) found red maple saplings had the largest percentage decrease in photosynthesis during drought of six tree species in central Pennsylvania, and Abrams and Kubiske (1990) found red maple seedlings had limited ability to adjust osmotically during drought. Both findings suggest a high sensitivity of physiological processes to low water availability in seedling and sapling stages that could be partially overcome as an adult through stemflow channelization to deeper rooting regions. This may also be advantageous to young red maple growing in this zone of relatively greater water inputs.

As hypothesized, nutrient concentrations were often greater in oak stemflow, while red maple produced higher stemflow-derived nutrient inputs. These findings are likely attributable to differences in bark characteristics. Because rough-barked species have higher water holding capacity and generate less stemflow (Herwitz 1987), rainfall tends to stay on the surface longer, chemically enriching the stemflow (André 2007); however, low volume produces low nutrient inputs. Similar to findings here, Levia and Herwitz (2005) documented substantially enriched stemflow nutrient concentrations but low inputs from pignut hickory (*Carya glabra* Mill.), a rough-barked species, compared to smooth-barked sweet birch (*Betula lenta* L.). In this study, oaks never had significantly higher N concentrations than red maple, and especially in winter, chestnut oak stemflow NO_3^- concentrations were well below red maple and scarlet oak. Epiphytes, which had higher cover on chestnut oak bark, are known to take up inorganic N from stemflow (Liu *et al.* 2002), and Levia (2002) document significant sequestering of nitrate by corticolous macrolichens during winter rainfall events. Unexpectedly, large differences in stemflow C concentrations between oaks and red maple occurred during spring, which also coincided with abnormally high throughfall C concentrations across all species. Values were driven by spring 2008 values, which were acquired during the emergence of 17-year cicadas (*Magicicada* spp.). As no other nutrients increased, high C concentrations may have been due to their newly shed exoskeletons.

High inputs of stemflow-derived nutrients could create a zone of nutrient-rich soils at the base of red maple trees. Stemflow can be 30-40 times more enriched than throughfall (Durocher 1990) due to the greater leachability of bark compared to leaves (Foster and Nicolson 1988) and the longer residence time of stemflow along the tree's surface (Soulsby and Reynolds 1994). Nutrient variability within stemflow can produce similar variability within underlying forest soils, and this trend has been shown to be most pronounced in fine-textured soils beneath smooth-barked species which produced the greatest stemflow volume (Gersper and Holowaychuk 1971). Conversely, red maple's high stemflow volume coupled with large nutrient inputs could lead to leaching losses. Chang and Matzner (2000) measured 4 times higher seepage fluxes of mineral elements in areas proximal to the stems of European beech compared to those distal. Gersper and Holowaychuk (1971) described large leaching losses from smooth compared to rough-

bark species as well as lower extractable Ca^{2+} and Mg^{2+} in soils adjacent to high flow sides of trees. Leaching losses could be accentuated in winter, due to higher NO_3^- inputs, as NO_3^- is a highly mobile anion. Leaching potential may also reflect soil characteristics, with more freely draining soils experiencing greater losses. In a previous study on ridges sampled here, Washburn and Arthur (2003) measured higher concentrations of extractable Ca^{2+} , Mg^{2+} , K^+ , and total N in mineral soils underneath red maple compared to chestnut oak, lending credence to the idea that higher stemflow nutrient inputs leads to increased nutrient concentrations in underlying soils, at least in this region. Interestingly, red maple may be redistributing nutrients within a readily accessible zone, which could act as a fertilization process, providing another potential means by which red maple improves its own understory conditions.

Soils near red maple boles exhibited higher rates of net ammonification and net N mineralization compared to chestnut oak and higher rates of net winter nitrification compared to both oaks. I hypothesized that greater inputs of stemflow-derived nutrients and higher water inputs would contribute to these findings. Boerner and Koslowsky (1989) measured a zone of high N mineralization near the trunks of sugar maple (*Acer saccharum* Marshall), American beech (*Fagus grandifolia* Ehrh.), and white ash (*Fraxinus americana* L.), and suggested stemflow nutrients as causal factors. Chang and Matzner (2000) measured increased nitrification rates in areas proximal to European beech stems, and linked this to higher soil moisture due to high stemflow volume. While these studies do not specifically address species differences, they do point to stemflow as an important factor affecting N mineralization. Notably, most studies of tree species' effects on N cycling focus on leaf litter chemistry, as species having lower litter lignin:N and C:N have been shown to have to greater net rates of N mineralization within underlying soils (Scott and Binkley 1997). Finzi *et al.* (1998) measured summer net N mineralization rates twice as high underneath red maple compared to northern red oak (*Q. rubra* L.) and attributed these findings to interspecific variability in leaf litter quality. Analysis of leaf litter composition beneath each tree species indicated no differences in litter mass or relative litter contribution among species, suggesting that if there were litter quality differences among species, these differences were not the primary factor affecting N mineralization differences within underlying soils of different trees. High winter net

nitrification beneath red maple corresponded with relatively higher stemflow inputs of TON, NH_4^+ (the precursor to nitrate), and NO_3^- as well as slightly higher soil moisture. Greater net ammonification could also reflect relatively higher TON or NH_4^+ inputs.

CONCLUSIONS

The results presented here represent the first part of a two-part study to highlight how a shift in forest canopy composition from oak to red maple dominance could impact ecosystem dynamics. In this study, red maple altered hydrology by funneling more precipitation and generating 2-7x greater stemflow volume. Greater water movement through soils underlying red maple could decrease fuel continuity and disrupt the success of future oak restoration practices using prescribed fire (Abrams 2005). Fewer fires could create a positive feedback by promoting red maple dominance in eastern forests (Nowacki and Abrams 2008). High stemflow and consequently greater yields of water and nutrients could also promote conditions which favor red maple by providing resources in a limited zone near red maple's bole during stressful conditions, such as short-term water shortages and or low nutrient availability. Binkley and Giardina (1998) suggested that the influence of underlying soils by individual trees may directly or indirectly improve their status or decrease that of their competitors. These results hint at how red maple's unique characteristics and potential impacts on surrounding soils could do just that, and may help explain red maple's ability to establish and grow on a variety of sites in the absence of fire. These findings further suggest that an increase in red maple dominance could have various effects on several ecosystem properties and processes, including forest hydrology, nutrient cycling, and disturbance regimes.

Table 4.1. Characteristics of red maple, chestnut oak, and scarlet oak trees prior to sampling initiation along two ridges in the Daniel Boone National Forest of eastern Kentucky. Values are mean \pm SE. Different lower case letters indicate significant differences ($P < 0.05$).

Tree Characteristic	Red maple	Chestnut oak	Scarlet oak
DBH (cm)	22.2 \pm 0.6a	26.1 \pm 0.6b	27.7 \pm 0.5b
Basal Area (cm ² tree ⁻¹)	387.1 \pm 30.2a	535.0 \pm 25.5b	604.8 \pm 22.1b
Height (m)	16.2 \pm 0.4a	18.2 \pm 0.5b	18.5 \pm 0.4b
Crown Width (m)	4.1 \pm 0.1a	3.7 \pm 0.1b	3.5 \pm 0.2b
Crown Area (m ²)	54.5 \pm 3.8a	43.1 \pm 2.9b	40.7 \pm 5.0b
Crown Depth (m)	11.8 \pm 0.9a	14.1 \pm 1.0a	12.6 \pm 0.7a
Crown Volume (m ³)	634.6 \pm 65.7a	668.3 \pm 98.5a	549.7 \pm 103.1a
Bark Roughness (mm)	2.6 \pm 0.4a	12.1 \pm 0.5b	5.3 \pm 0.4c
Bark Epiphyte Index	1.7 \pm 0.3a	2.1 \pm 0.2a	1.0 \pm 0.2b

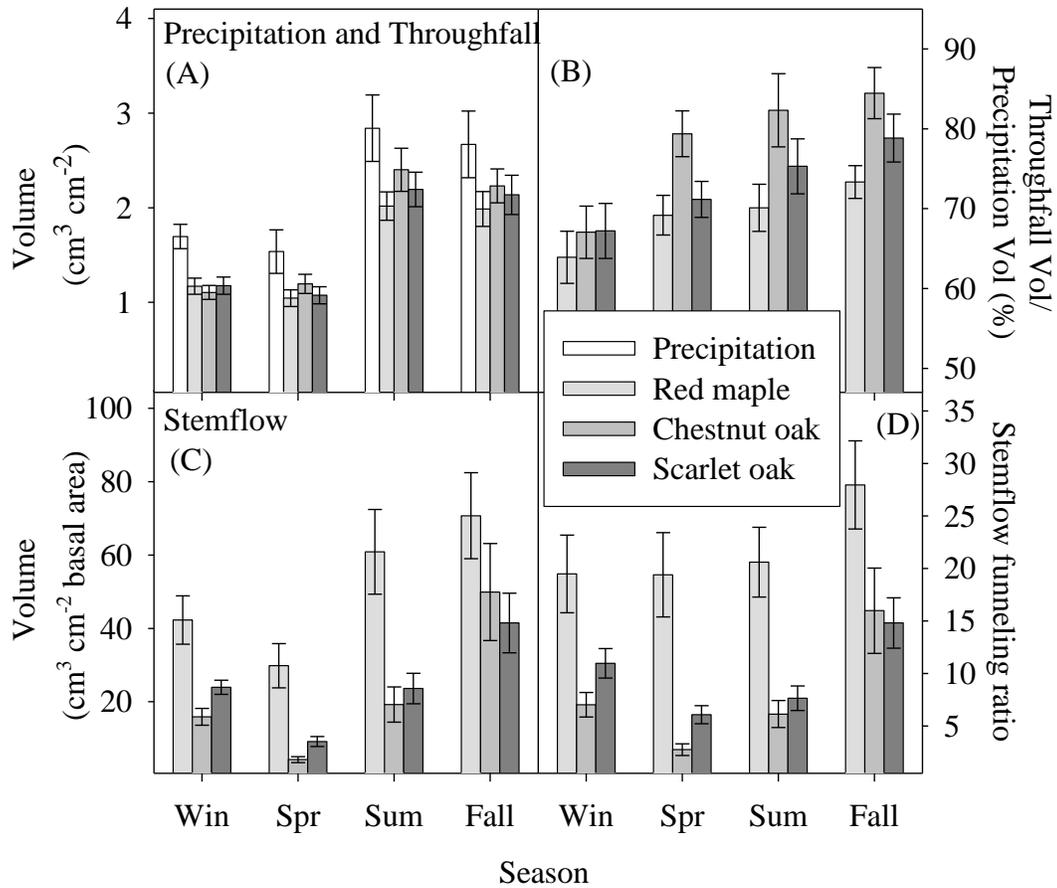


Figure 4.1. Incident precipitation and throughfall volume (A), percent of precipitation passing through the canopy as throughfall (B), stemflow volume (C), and funneling ratio (D) on a seasonal basis from 2006-2008 for red maple, chestnut oak, and scarlet oak. Means are \pm SE. Throughfall and stemflow volume are expressed as depth equivalents with incident precipitation based on the area of the collecting funnels and basal area of the tree. Note different scales for throughfall and stemflow volume.

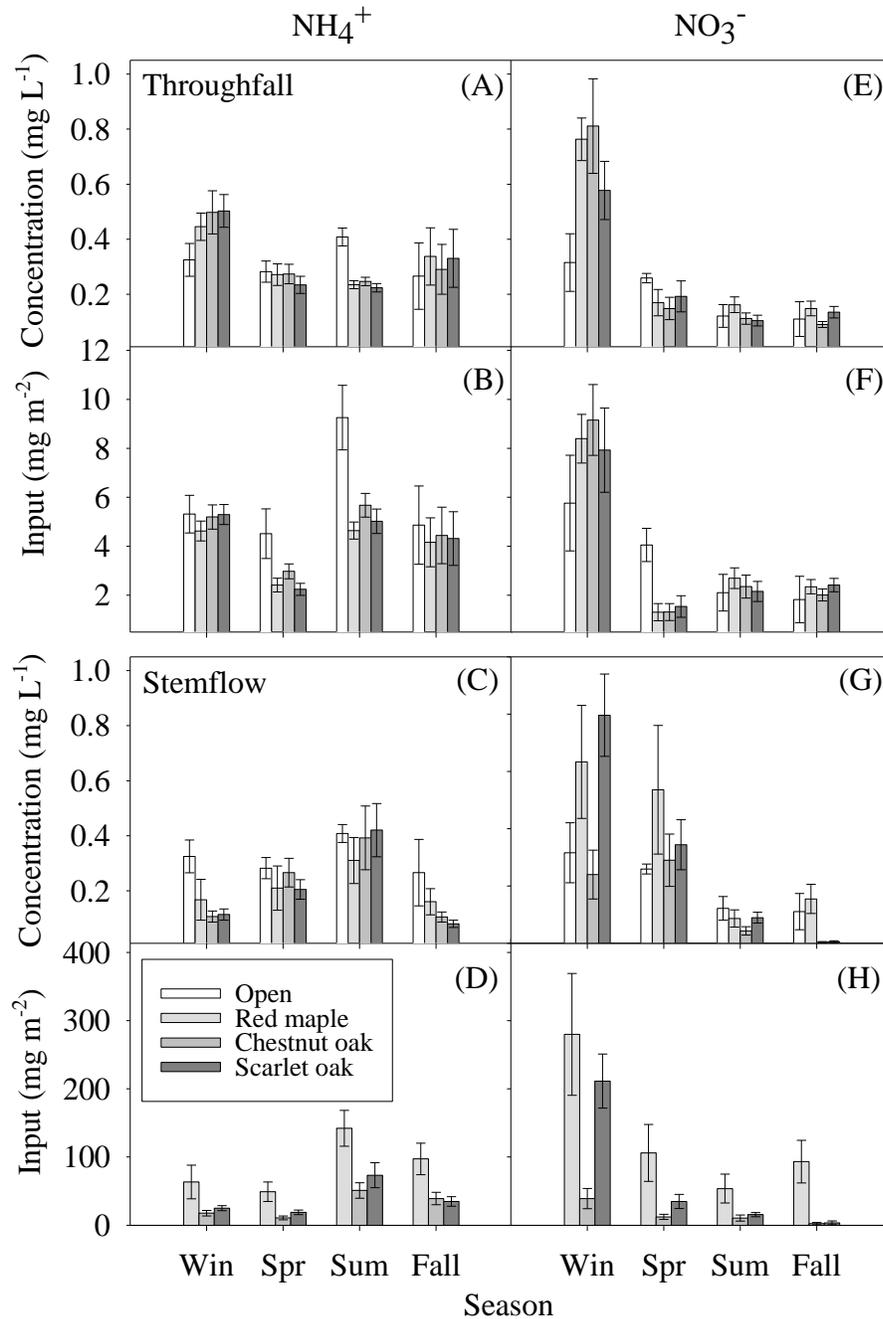


Figure 4.2. Open area precipitation, throughfall, and stemflow NH_4^+ and NO_3^- mean concentration (volume-weighted) and input for red maple, chestnut oak, and scarlet oak on a seasonal basis from 2006-2008. Open area precipitation inputs are not shown with stemflow inputs because there are substantially lower. Note different axes scales for throughfall and stemflow NH_4^+ and NO_3^- input. Means are \pm SE.

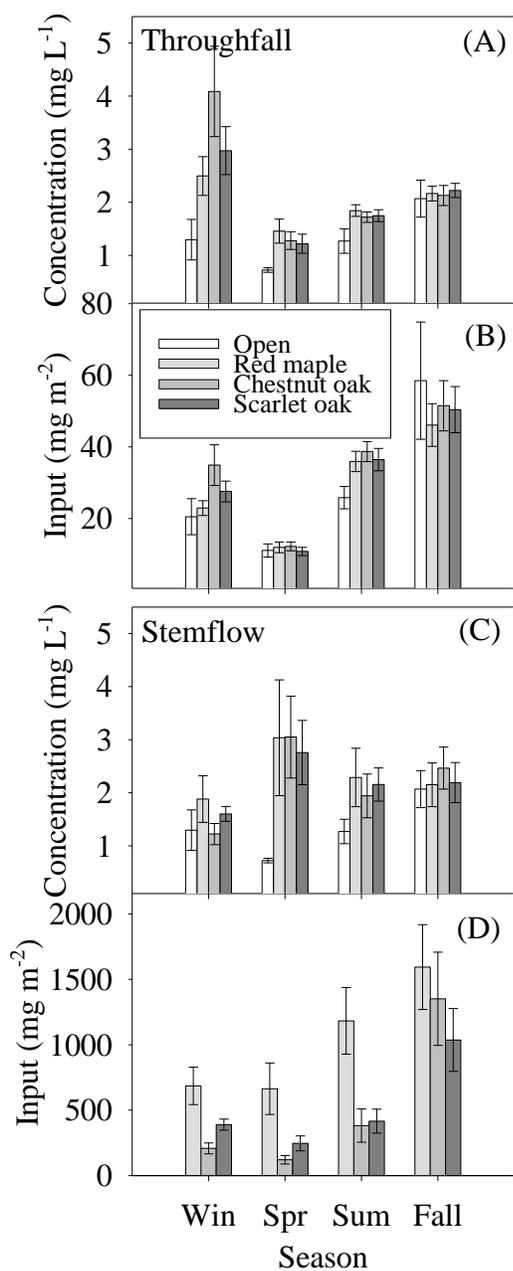


Figure 4.3. Open area precipitation, throughfall, and stemflow total nitrogen (TN) mean concentration (volume-weighted) and input for red maple, chestnut oak, and scarlet oak on a seasonal basis from 2006-2008. Open area precipitation inputs are not shown with stemflow inputs because there are substantially lower. Note different axes scales for throughfall and stemflow TN input. Means are \pm SE.

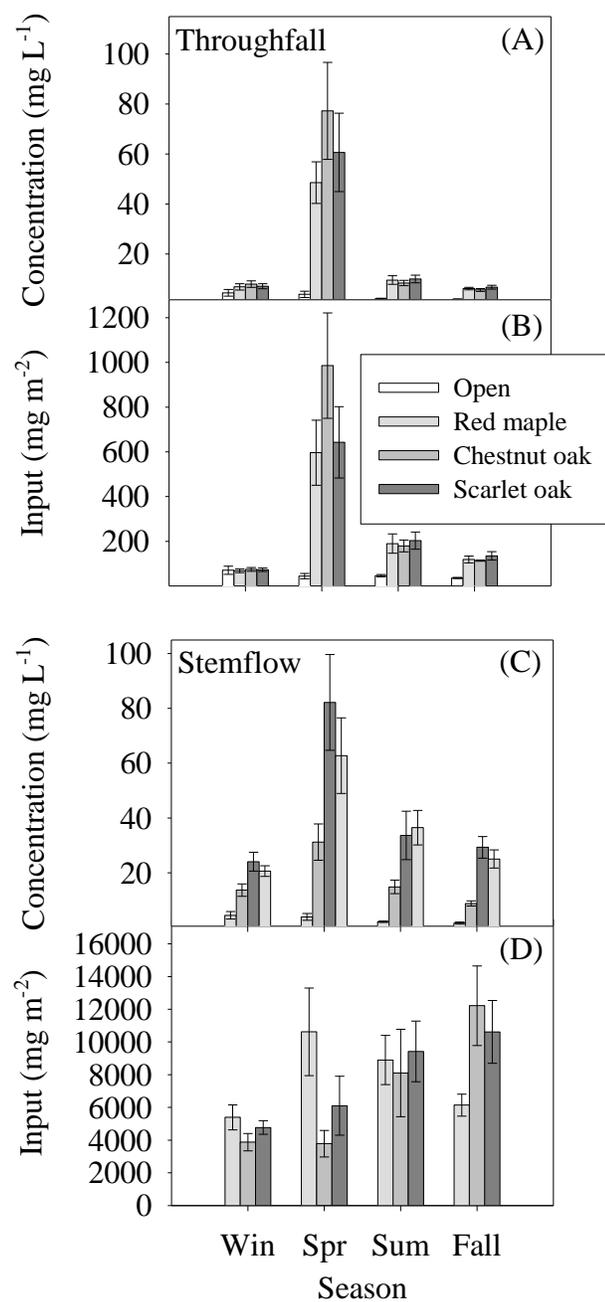


Figure 4.4. Open area precipitation, throughfall, and stemflow total carbon (TC) concentration (volume-weighted) and input for red maple, chestnut oak, and scarlet oak seasonally from 2006-2008. Open area precipitation inputs are not shown with stemflow inputs because there are substantially lower. Note different axes scales for throughfall and stemflow TC input. Means are \pm SE.

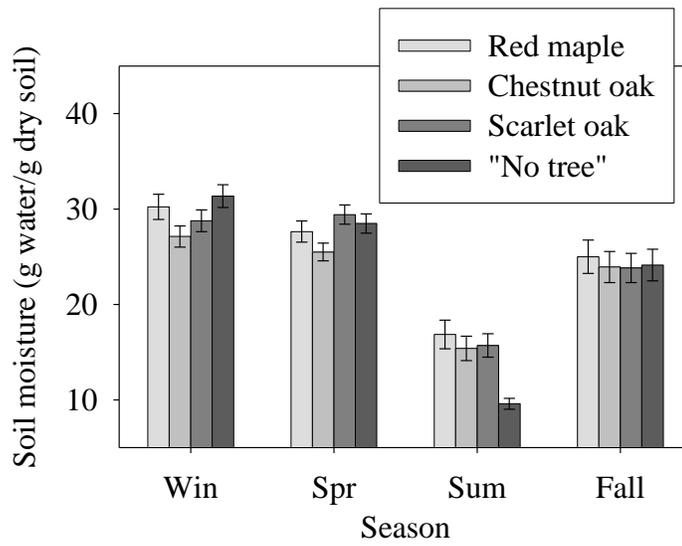


Figure 4.5. Seasonal gravimetric soil moisture of soils underneath red maple, chestnut oak, scarlet oak, and “no tree” areas from 2006-2008. Means are \pm SE.

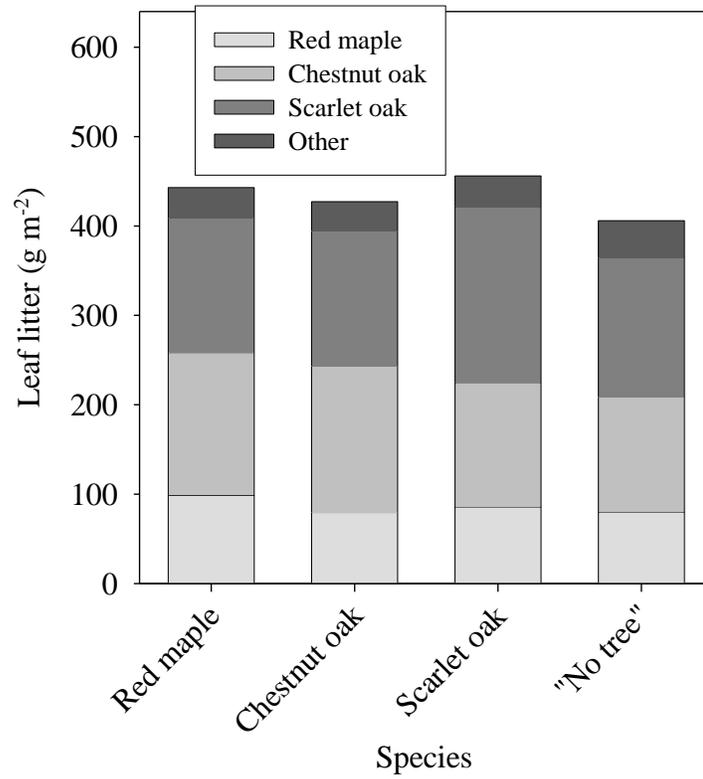


Figure 4.6. Leaf litter mass of scarlet oak, chestnut oak, red maple, and all “other” species measured in fall 2006 underneath each target species and “no tree” areas.

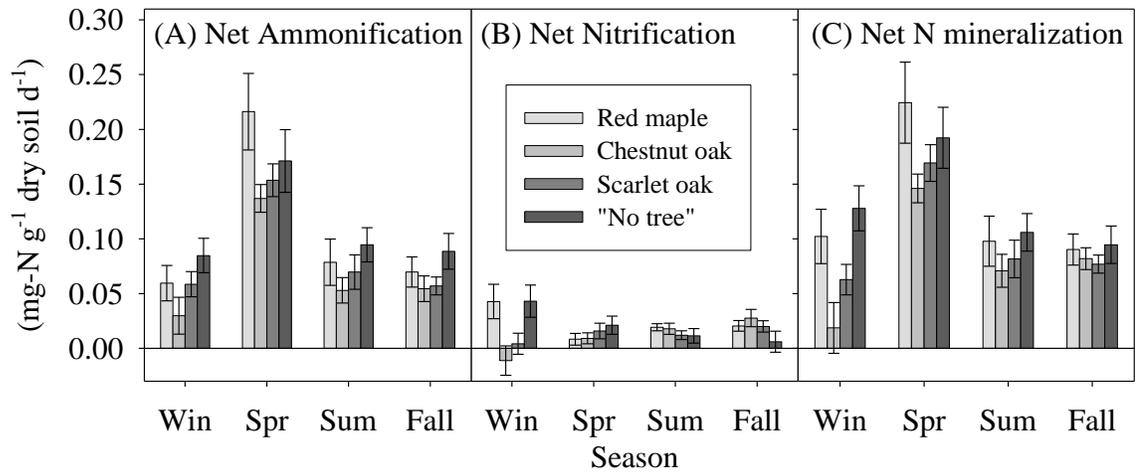
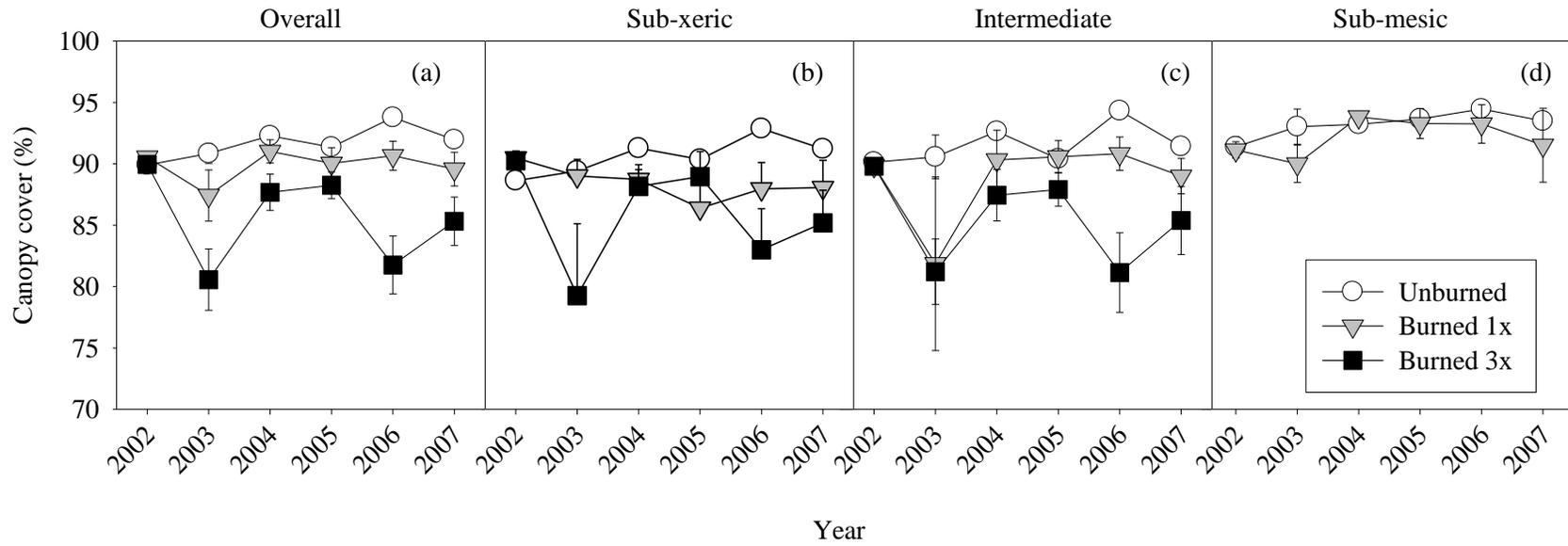
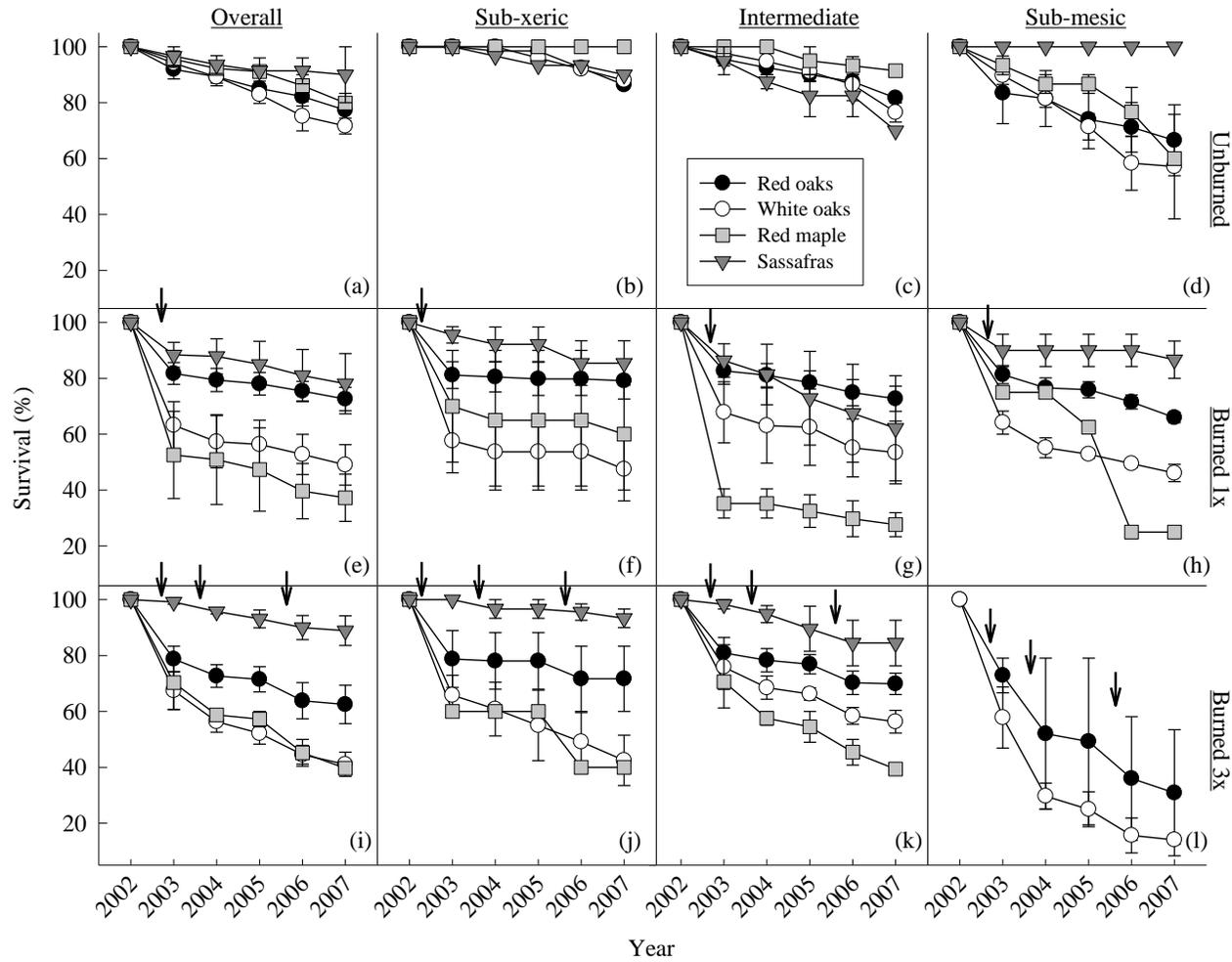


Figure 4.7. Seasonal *in situ* net rates of ammonification, nitrification, and N mineralization in underlying soils of red maple, chestnut oak, scarlet oak, and “no tree” areas from 2006-2008. Means are \pm SE.

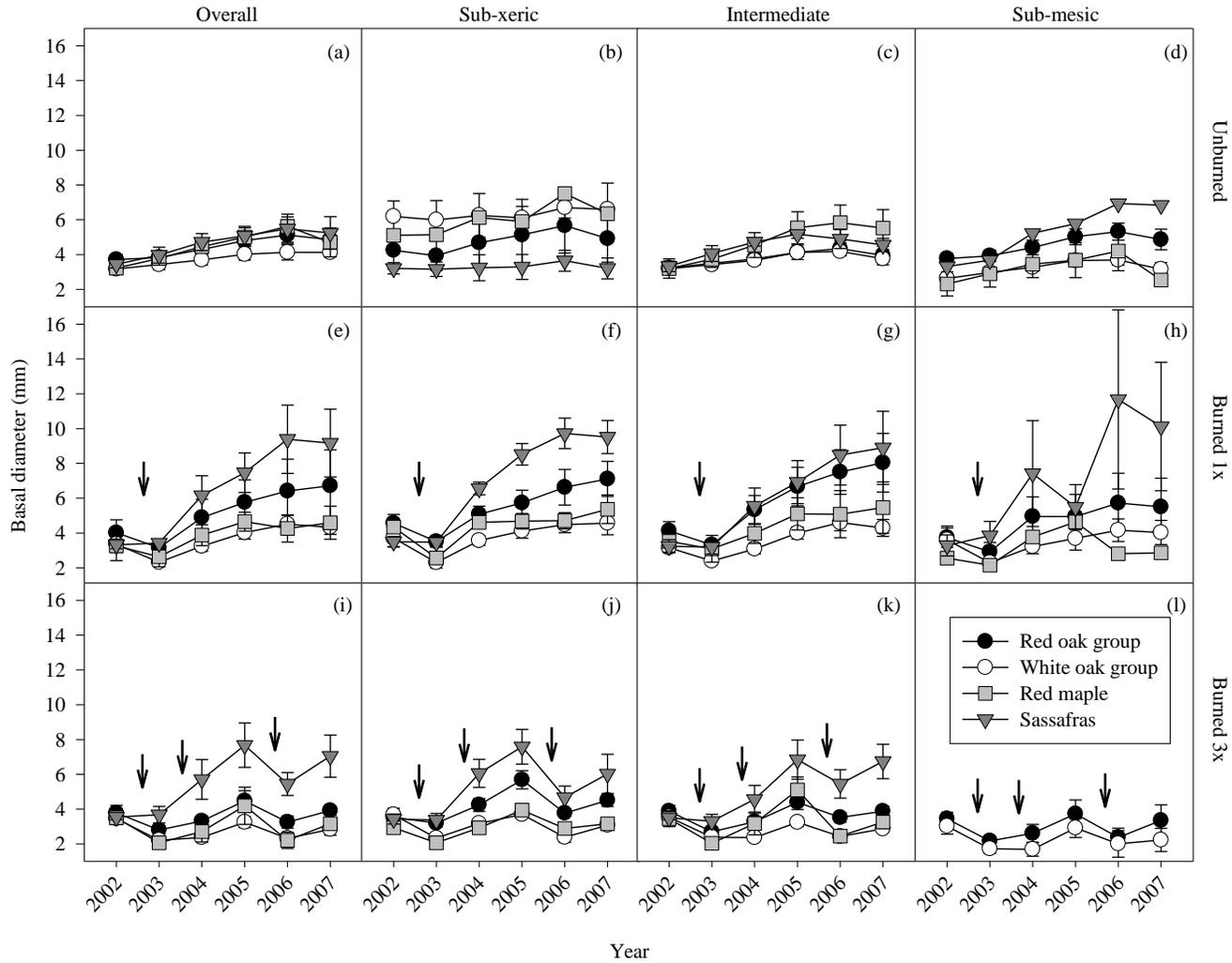
APPENDICES



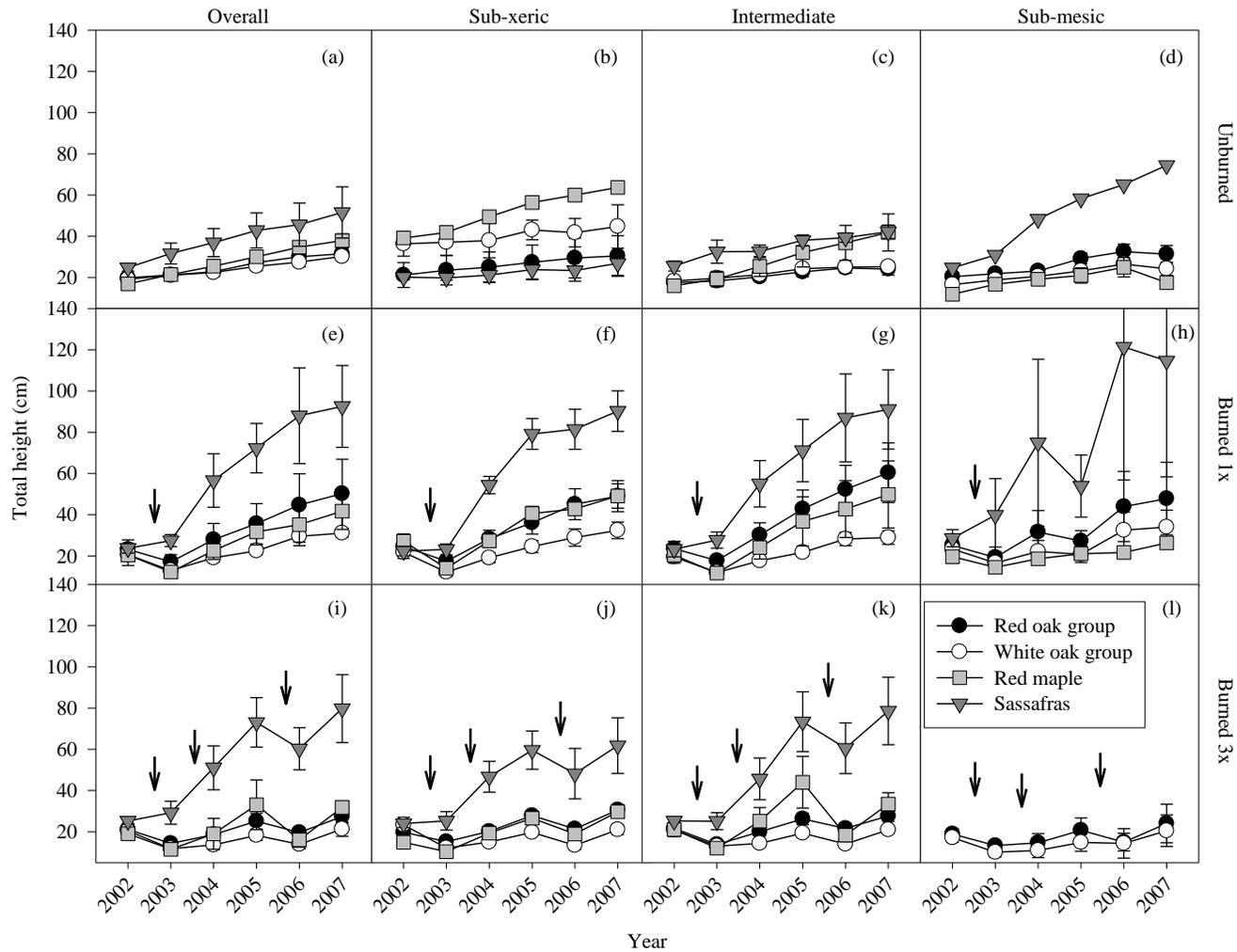
Appendix 1. Annual canopy cover at Buck Creek. Mean data \pm SE for each treatment include averages across landscape positions (a; overall) and within sub-xeric (b), intermediate (c), and sub-mesic (d) landscape positions.



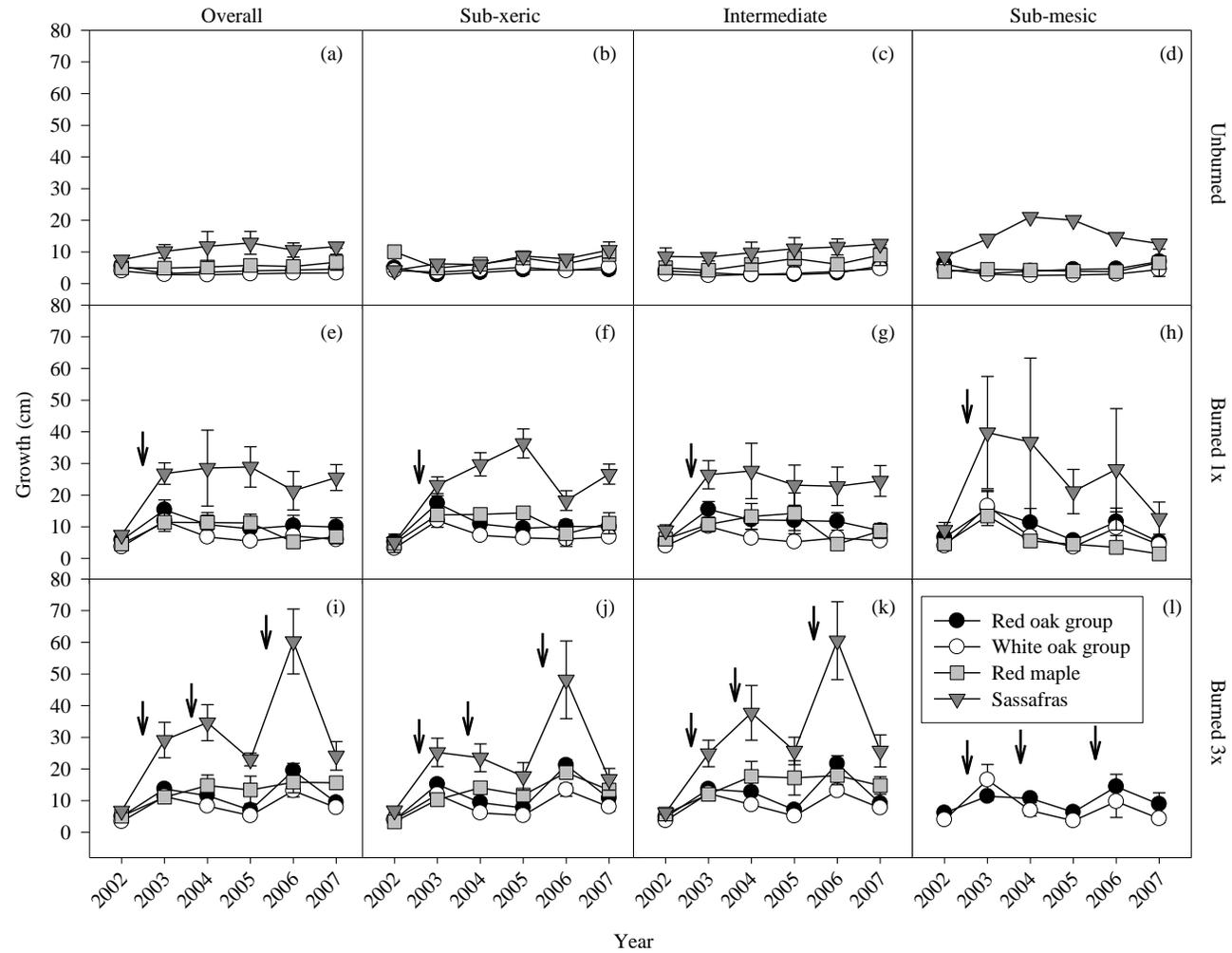
Appendix 2. Mean \pm SE annual survival of each seedling group across each treatment (overall) and within sub-xeric, intermediate, and sub-mesic landscape positions. Arrows indicate burns.



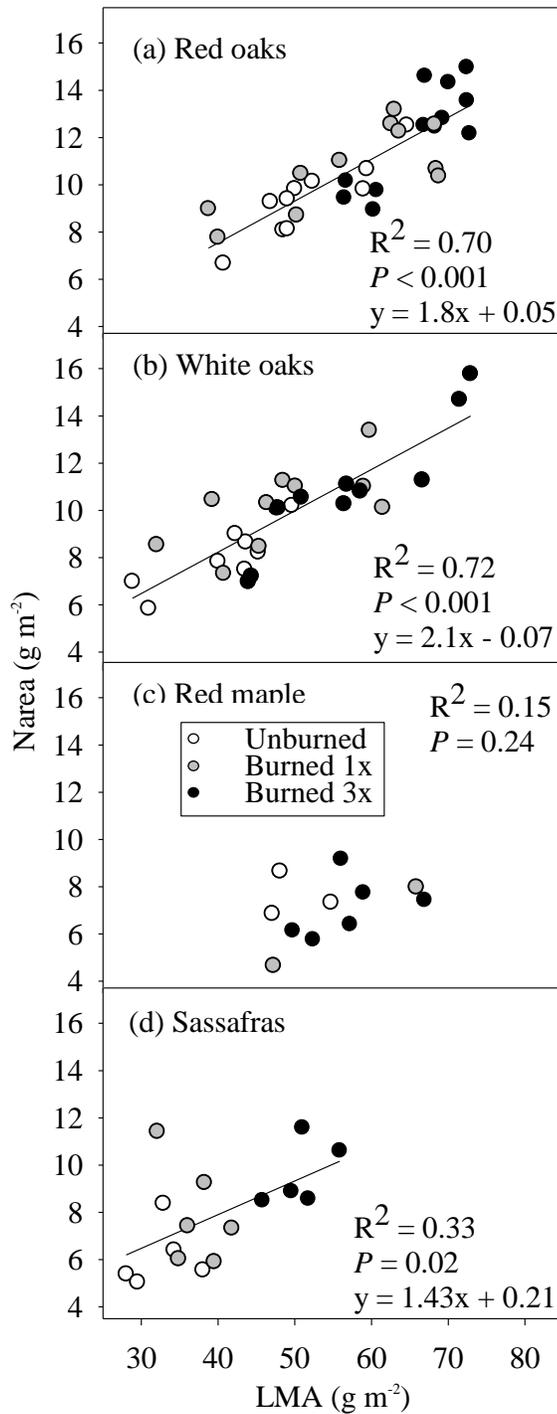
Appendix 3. Mean \pm SE annual basal diameter of each seedling group across each treatment (overall) and within sub-xeric, intermediate, and sub-mesic landscape positions. Arrows indicate burns.



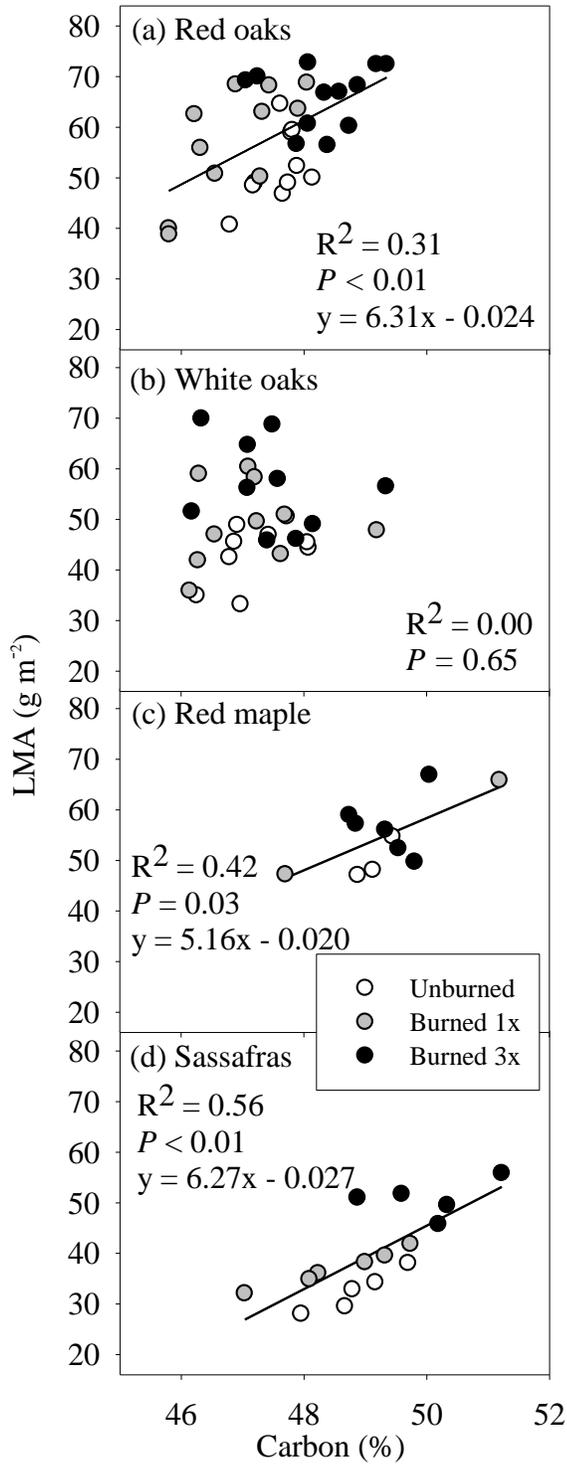
Appendix 4. Mean \pm SE annual total height of each seedling group across each treatment (overall) and within sub-xeric, intermediate, and sub-mesic landscape positions. Arrows indicate burns.



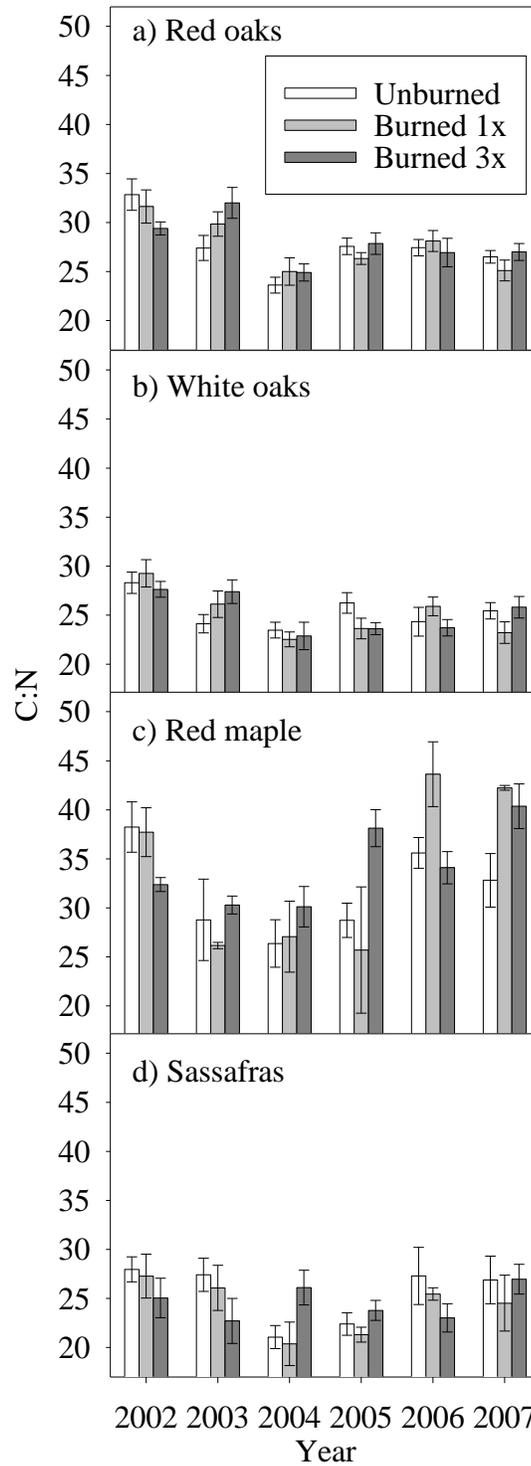
Appendix 5. Mean \pm SE annual height growth of each seedling group across each treatment (overall) and within sub-xeric, intermediate, and sub-mesic landscape positions. Arrows indicate burns.



Appendix 6. Mean leaf mass per area (LMA) for each plot in 2007 regressed against foliar nitrogen content per unit area (N_{area}) for each seedling group across each treatment. Seedlings burned 1x were burned in spring 2003, and those burned 3x were burned in spring 2003, 2004, and 2006.



Appendix 7. Mean leaf mass per unit area (LMA) for each plot in 2007 regressed against foliar carbon concentration for each seedling group across each treatment. Seedlings burned 1x were burned in spring 2003, and those burned 3x were burned in spring 2003, 2004, and 2006.



Appendix 8. Mean foliar C:N \pm SE for each seedling group across each treatment. Seedlings burned 1x were burned in spring 2003, and those burned 3x were burned in spring 2003, 2004, and 2006.

Appendix 9. Methodology used for construction of stemflow collars.



Step 1: Construct aluminum foil mold around bole of tree ~ 1 m aboveground so that one side is at a slight downward angle (this will facilitate water flow into collection vessel.)



Step 2: Fill mold with spray polyurethane foam, making sure to fill all bark fissures.



Step 3: Let foam expand and harden (at least 1 hr), and carefully cut trough around collar using hawk-billed, tiler's knife. The trough should slant inward so that outside edge is higher than inner part. Make sure not to puncture the foam during cutting.



Step 4: Gently create a hole (slightly larger than tubing diameter) with a rubber stopper borer in each collar at the point of lowest inclination. Adhere tubing to collar with silicone. Also, check collar for leaks with distilled water and fill areas with leakage with silicone.



Step 5: Connect tube to collection bin, and stabilize connection with duct tape.

Appendix 10. Seasonal cation and anion concentrations (volume-weighted; mg L⁻¹), pH, and electrical conductivity (EC; μS) of incident precipitation, throughfall, and stemflow for red maple, chestnut oak, and scarlet oak from 2006-2008. Values are mean ± SE.

Season	Ion	Precip	<u>Throughfall</u>			<u>Stemflow</u>		
			Red maple	Chestnut oak	Scarlet oak	Red maple	Chestnut oak	Scarlet oak
Winter	Ca ²⁺	0.31 ± 0.04	0.74 ± 0.16	0.64 ± 0.09	0.58 ± 0.08	3.14 ± 0.85	3.92 ± 0.70	3.54 ± 0.40
	Mg ²⁺	0.12 ± 0.01	0.22 ± 0.02	0.22 ± 0.02	0.22 ± 0.02	0.60 ± 0.27	1.29 ± 0.26	0.64 ± 0.07
	Na ⁺	0.91 ± 0.30	1.26 ± 0.21	1.27 ± 0.23	1.17 ± 0.20	1.05 ± 0.27	1.04 ± 0.23	1.06 ± 0.16
	K ⁺	0.19 ± 0.11	0.69 ± 0.14	0.57 ± 0.07	0.72 ± 0.15	4.31 ± 0.59	10.96 ± 1.64	10.95 ± 0.91
	SO ₄ ⁻	2.10 ± 0.18	4.05 ± 0.81	3.23 ± 0.27	3.42 ± 0.32	9.73 ± 1.27	18.10 ± 2.04	15.08 ± 1.69
	Cl ⁻	1.30 ± 0.20	1.32 ± 0.15	1.47 ± 0.16	1.34 ± 0.13	2.61 ± 0.52	5.03 ± 1.19	3.50 ± 0.44
	pH	5.4 ± 0.2	4.9 ± 0.1	5.2 ± 0.1	5.3 ± 0.1	4.2 ± 0.1	4.3 ± 0.1	4.6 ± 0.1
	EC	15.0 ± 1.2	22.6 ± 2.3	22.3 ± 2.6	24.5 ± 2.3	81.2 ± 8.9	127.8 ± 11.5	89.7 ± 6.7
Spring	Ca ²⁺	0.35 ± 0.05	1.28 ± 0.18	1.25 ± 0.12	1.59 ± 0.27	1.87 ± 0.41	5.48 ± 0.95	3.99 ± 0.57
	Mg ²⁺	0.07 ± 0.02	0.51 ± 0.05	0.54 ± 0.05	0.49 ± 0.05	0.23 ± 0.04	1.60 ± 0.29	0.46 ± 0.05
	Na ⁺	0.98 ± 0.08	1.32 ± 0.11	1.13 ± 0.08	1.27 ± 0.10	0.51 ± 0.11	1.19 ± 0.19	0.76 ± 0.14
	K ⁺	0.43 ± 0.09	4.60 ± 0.22	5.36 ± 0.31	4.93 ± 0.50	6.64 ± 1.23	11.21 ± 1.82	9.13 ± 1.07
	SO ₄ ⁻	1.86 ± 0.26	5.70 ± 0.76	5.67 ± 0.77	6.52 ± 0.94	8.48 ± 1.16	21.34 ± 3.32	10.81 ± 1.19
	Cl ⁻	0.70 ± 0.17	1.48 ± 0.09	1.59 ± 0.18	1.51 ± 0.16	1.83 ± 0.40	4.15 ± 0.50	2.59 ± 0.33
	pH	5.7 ± 0.1	4.8 ± 0.1	4.8 ± 0.1	4.8 ± 0.1	4.0 ± 0.1	3.9 ± 0.1	4.3 ± 0.1
	EC	9.9 ± 0.9	40.8 ± 2.7	38.9 ± 2.4	38.0 ± 2.7	73.1 ± 8.1	114.7 ± 7.2	81.0 ± 8.1

Appendix 10, cont.

Season	Ion	Precip	<u>Throughfall</u>			<u>Stemflow</u>		
			Red maple	Chestnut oak	Scarlet oak	Red maple	Chestnut oak	Scarlet oak
Summer	Ca ²⁺	0.34 ± 0.10	0.87 ± 0.09	0.87 ± 0.11	0.84 ± 0.09	0.95 ± 0.18	2.96 ± 0.61	2.82 ± 0.38
	Mg ²⁺	0.10 ± 0.03	0.28 ± 0.04	0.31 ± 0.04	0.27 ± 0.04	0.24 ± 0.05	0.97 ± 0.22	0.45 ± 0.06
	Na ⁺	0.69 ± 0.19	0.93 ± 0.17	0.80 ± 0.12	0.87 ± 0.16	0.37 ± 0.09	0.45 ± 0.12	0.47 ± 0.09
	K ⁺	0.12 ± 0.05	2.53 ± 0.32	2.80 ± 0.34	2.54 ± 0.26	8.54 ± 2.02	11.19 ± 2.66	13.16 ± 1.71
	SO ₄ ⁻	1.85 ± 0.33	3.73 ± 0.35	3.74 ± 0.38	3.41 ± 0.38	9.41 ± 2.75	14.11 ± 4.22	12.13 ± 2.49
	Cl ⁻	1.13 ± 0.25	1.00 ± 0.18	1.05 ± 0.19	1.16 ± 0.20	1.87 ± 0.55	2.95 ± 1.14	2.26 ± 0.54
	pH	5.7 ± 0.4	5.2 ± 0.1	5.1 ± 0.1	5.2 ± 0.1	4.4 ± 0.2	3.9 ± 0.2	4.6 ± 0.1
	EC	14.2 ± 3.3	25.3 ± 2.8	26.8 ± 2.8	24.3 ± 2.8	56.6 ± 8.0	74.1 ± 6.3	76.7 ± 10.0
Fall	Ca ²⁺	0.01 ± 0.01	0.40 ± 0.06	0.45 ± 0.10	0.38 ± 0.08	0.72 ± 0.23	1.19 ± 0.31	0.48 ± 0.10
	Mg ²⁺	0.05 ± 0.02	0.17 ± 0.01	0.18 ± 0.02	0.18 ± 0.01	0.35 ± 0.07	0.27 ± 0.10	0.15 ± 0.06
	Na ⁺	0.42 ± 0.08	0.73 ± 0.12	0.75 ± 0.13	0.62 ± 0.10	0.50 ± 0.11	0.69 ± 0.15	0.55 ± 0.11
	K ⁺	0.24 ± 0.05	1.18 ± 0.14	1.33 ± 0.20	1.27 ± 0.14	4.63 ± 0.55	7.20 ± 1.09	7.38 ± 0.90
	SO ₄ ⁻	1.19 ± 0.58	1.85 ± 0.41	1.85 ± 0.48	2.26 ± 0.55	5.54 ± 1.40	6.83 ± 1.36	5.94 ± 1.74
	Cl ⁻	0.89 ± 0.53	0.80 ± 0.26	0.78 ± 0.26	0.78 ± 0.25	1.26 ± 0.27	1.02 ± 0.23	0.93 ± 0.27
	pH	5.9 ± 0.3	5.7 ± 0.1	5.6 ± 0.2	5.5 ± 0.2	5.1 ± 0.1	4.6 ± 0.1	5.2 ± 0.1
	EC	3.8 ± 1.8	12 ± 1.9	12.6 ± 2.8	13.5 ± 2.9	32.5 ± 6.4	49.2 ± 7.6	38.2 ± 6.3

Appendix 11. Seasonal cation and anion inputs (mg m^{-2}) of incident precipitation, throughfall, and stemflow for red maple, chestnut oak, and scarlet oak from 2006-2008. Values are mean \pm SE.

Season	Ion	Precip	<u>Throughfall</u>			<u>Stemflow</u>		
			Red maple	Chestnut oak	Scarlet oak	Red maple	Chestnut oak	Scarlet oak
Winter	Ca ²⁺	5.14 \pm 0.61	6.96 \pm 1.00	6.52 \pm 0.64	6.44 \pm 0.83	1129.67 \pm 266.07	640.92 \pm 125.25	790.47 \pm 77.27
	Mg ²⁺	2.12 \pm 0.28	2.26 \pm 0.14	2.42 \pm 0.16	2.48 \pm 0.23	220.55 \pm 84.62	204.15 \pm 34.46	155.92 \pm 18.61
	Na ⁺	14.36 \pm 3.96	11.70 \pm 1.46	11.77 \pm 1.72	11.02 \pm 1.39	390.27 \pm 88.46	157.26 \pm 30.80	232.27 \pm 30.36
	K ⁺	2.81 \pm 1.53	6.47 \pm 0.97	5.82 \pm 0.62	7.37 \pm 1.62	1647.87 \pm 177.82	1737.32 \pm 247.78	2525.99 \pm 208.16
	SO ₄ ⁻	35.22 \pm 3.11	41.53 \pm 8.00	35.50 \pm 2.38	39.16 \pm 4.76	3810.11 \pm 433.64	3562.75 \pm 562.82	3430.63 \pm 299.73
	Cl ⁻	21.37 \pm 2.31	13.13 \pm 1.07	15.76 \pm 1.09	14.52 \pm 1.22	985.31 \pm 170.77	763.88 \pm 133.61	817.08 \pm 114.18
Spring	Ca ²⁺	4.81 \pm 0.39	13.21 \pm 1.05	12.94 \pm 0.64	14.45 \pm 2.07	460.68 \pm 74.84	235.49 \pm 39.26	373.94 \pm 70.23
	Mg ²⁺	0.95 \pm 0.22	4.76 \pm 0.32	5.69 \pm 0.28	4.55 \pm 0.27	66.43 \pm 9.77	67.50 \pm 11.53	42.90 \pm 7.15
	Na ⁺	13.88 \pm 0.88	12.65 \pm 0.81	12.43 \pm 0.53	12.35 \pm 0.58	154.74 \pm 33.24	48.95 \pm 11.13	66.64 \pm 10.32
	K ⁺	6.91 \pm 2.03	49.09 \pm 5.28	64.18 \pm 6.27	52.07 \pm 5.42	1957.95 \pm 362.77	476.89 \pm 88.39	850.46 \pm 132.68
	SO ₄ ⁻	26.62 \pm 3.07	60.74 \pm 8.84	72.85 \pm 11.49	70.73 \pm 10.17	2477.54 \pm 358.66	924.65 \pm 163.15	990.94 \pm 170.10
	Cl ⁻	8.58 \pm 1.78	16.25 \pm 2.14	19.75 \pm 2.76	15.37 \pm 1.51	524.66 \pm 103.59	171.62 \pm 29.81	239.66 \pm 41.53

Appendix 11. Cont.,

Season	Ion	Precip	<u>Throughfall</u>			<u>Stemflow</u>		
			Red maple	Chestnut oak	Scarlet oak	Red maple	Chestnut oak	Scarlet oak
Summer	Ca ²⁺	6.26 ± 1.53	15.56 ± 0.93	17.34 ± 1.10	16.15 ± 1.34	518.53 ± 70.75	496.55 ± 85.58	501.63 ± 68.82
	Mg ²⁺	1.91 ± 0.65	4.82 ± 0.43	6.04 ± 0.47	4.88 ± 0.45	128.88 ± 19.30	155.51 ± 31.14	79.14 ± 10.69
	Na ⁺	14.73 ± 3.73	14.54 ± 1.64	15.20 ± 1.29	14.70 ± 1.57	208.24 ± 56.84	96.00 ± 29.93	111.52 ± 26.62
	K ⁺	2.03 ± 1.03	46.31 ± 5.45	57.50 ± 3.98	50.55 ± 5.38	4377.85 ± 607.50	1781.38 ± 364.40	2444.66 ± 368.21
	SO ₄ ⁻	39.92 ± 6.09	68.31 ± 3.55	80.09 ± 6.40	66.65 ± 5.49	5302.87 ± 1633.90	1806.49 ± 318.51	1866.50 ± 243.42
	Cl ⁻	29.97 ± 8.95	17.81 ± 3.12	23.49 ± 4.41	26.18 ± 5.56	980.34 ± 228.56	305.64 ± 49.72	341.16 ± 56.88
Fall	Ca ²⁺	0.26 ± 0.16	8.28 ± 1.63	10.71 ± 2.81	8.37 ± 2.04	522.13 ± 166.50	586.24 ± 209.97	195.50 ± 54.24
	Mg ²⁺	1.85 ± 0.69	3.29 ± 0.38	3.66 ± 0.20	3.60 ± 0.32	238.15 ± 51.54	26.46 ± 16.13	53.95 ± 28.11
	Na ⁺	9.60 ± 0.88	11.72 ± 0.94	15.25 ± 3.06	11.10 ± 0.93	380.64 ± 88.87	404.90 ± 115.21	273.26 ± 65.47
	K ⁺	5.92 ± 1.17	22.64 ± 3.71	25.96 ± 2.11	25.50 ± 3.10	3162.05 ± 347.60	2822.19 ± 628.51	2968.39 ± 482.85
	SO ₄ ⁻	21.07 ± 8.08	26.64 ± 3.23	30.77 ± 5.66	34.37 ± 5.25	3375.86 ± 721.64	2025.20 ± 390.04	1807.63 ± 292.62
	Cl ⁻	14.16 ± 8.09	9.48 ± 2.59	11.83 ± 3.58	10.06 ± 2.70	829.68 ± 162.88	462.31 ± 112.44	338.36 ± 61.64

Appendix 12. Brief summary of companion study to Chapter 4 evaluating ecosystem effects of increasing red maple dominance on litter decomposition and net N mineralization.

In a companion study, I addressed the implications of increased contributions of red maple leaf litter on decomposition rates (see Appendix 13 for methodology), net N mineralization, and soil moisture (see Appendix 14 for methodology) over a 1-yr period, and found that red maple leaf litter had initially low nitrogen concentrations, high C:N ratios, but lower lignin:N (Appendix 15). Rates of mass loss were greatest for red maple leaf litter and decreased with increasing oak litter contribution. However, despite high decomposition rates, red maple leaf litter displayed increased N concentrations and decreased C:N over time (Appendix 16) and lower rates of net ammonification and net N mineralization. Repressed N cycling was limited to the upper organic layers (Appendix 17), and was not evident in upper mineral soils (0 – 5 cm; Appendix 18).

Appendix 13. Decomposition and leaf litter chemistry methodology.

To determine if an increase in red maple leaf litter would alter decomposition rates, I implemented a traditional decomposition bag study in March 2007. Treatments included leaf litter assemblages of the following: (1) red maple (RM) only, (2) scarlet oak (SO) only, (3) chestnut oak (CO) only, (4) RM (25%) + SO (37.5%) + CO (37.5%), (5) RM (50%) + SO (25%) + CO (25%), (6) RM (75%) + SO (12.5%) + CO (12.5%). I began collecting leaf litter in September 2006, which continued weekly throughout leaf fall (November 2006). A total of 10-g (dry weight) of litter from each treatment was placed into a 20 x 20-cm plastic bag with a 1 x 2-mm mesh size (large enough to allow entry of small soil fauna and permit aerobic microbial activity; Melillo *et al.* 1982), tightly sealed, and labeled with a unique identification number. Bags were installed in five blocks along both Klaber and Whittleton Ridges, resulting in a randomized complete block design nested within ridge. Blocks consisted of areas predetermined to have similar red maple and oak litterfall and overstory influence to minimize potential confounding differences in N mineralization due to initial substrate. A preliminary study conducted along these ridges in summer 2005 provided the requisite data to locate these areas. Each area had a 7.5-m radius, incorporating a total area of 177 m².

Prior to installation, the Oi layer was carefully removed, and bags were arrayed in a random grid on top of the Oe layer. Bag locations were at least 0.5-m distant from a tree bole, and ~ 20 cm apart. Bags were secured to the forest floor with metal pins, and their locations mapped to facilitate re-location. One bag per block per was removed at 3-mo intervals beginning at time 0 (spring 2007) until time 4 (spring 2007). Bags were then collected at a 6-mo interval in spring and fall 2008. An additional 6-mo pick-up is scheduled for spring 2009 and another pick-up is for scheduled for summer 2012 for long-term assessment of decomposition. In total, the sampling design consisted of 480 bags (2 ridges, 5 blocks, 6 treatments, 8 pick-ups).

Upon removal from the field, contents of each bag were returned to the laboratory, cleaned of external debris and invertebrates, dried at 60 °C for 48 hr, and weighed. Mass remaining was calculated as the initial dry mass (M_0)/dry mass at time t

(M_t). Leaf decomposition rate over the study period will eventually be calculated using an exponential decay model (Olson 1963):

$$\ln (M_0 / M_t) = k * t$$

where M_0 = mass of litter at time 0, M_t = mass of litter at time t, t = time of incubation (usually in years), k = decomposition rate constant.

After determination of mass loss, each sample was dried at 60 °C to a constant weight and ground to a fine powder. Carbon (C) and nitrogen (N) concentration were determined by the University of Kentucky Regulatory Services using a Leco CN 2000 Analyzer (Leco Corporation, St. Joseph, MI). Lignin concentration of fresh leaf litter of each species was determined using the Ankom Technology Method for Determining Acid Detergent Lignin.

Appendix 14. Leaf litter effects on moisture, net ammonification, net nitrification, and net N mineralization methodology.

To determine if increases in red maple leaf litter will alter moisture and net inorganic N cycling in organic and upper mineral soil horizons due to species-specific litter differences, I installed a field experiment where I manually manipulated the type of leaf litter on the ground. Plots were installed in five blocks along both Klaber and Whittleton Ridges, resulting in a randomized complete block design nested within ridge. Blocks consisted of areas predetermined to have similar red maple and oak litterfall and overstory influence to minimize potential confounding differences in N mineralization due to initial substrate. A preliminary study conducted along these ridges in summer 2005 provided the requisite data to locate these areas. Each area had a 7.5-m radius, incorporating a total area of 177 m² and coincided with areas identified for litter decomposition experiment (Appendix 13).

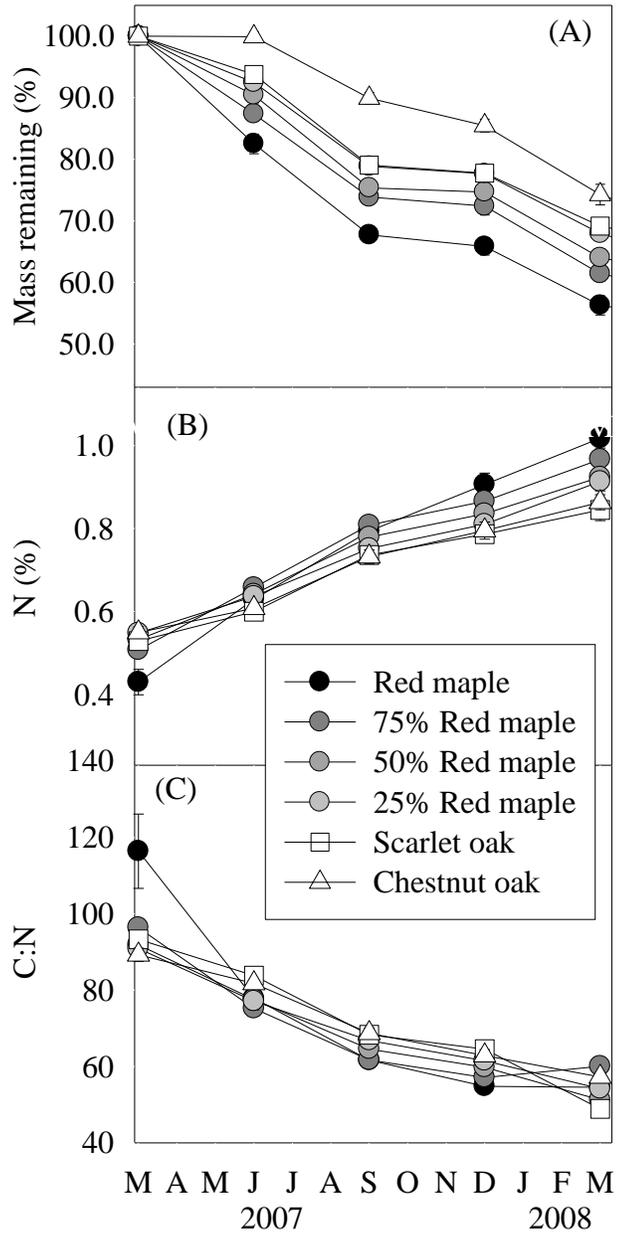
Seven 1-m² plots were delineated within each area and randomly assigned to one of seven leaf litter assemblage treatments: (1) 100% red maple (RM), (2) 100% scarlet oak (SO), (3) 100% chestnut oak (CO), (4) 25% RM + 37.5% SO + 37.5% CO, (5) 50% RM + 25% SO + 25% CO (6) RM (75%) + SO (12.5%) + CO (12.5%), (7) unmanipulated control. Litter was collected weekly from end of September 2006 through leaf fall using 1-cm² mesh nets suspended between trees about 1-1.5 m aboveground. Approximately 132 m² of netting was used on each ridge. Fresh litter was immediately returned to the laboratory, air dried in cardboard boxes, and sorted by species.

Plots were separated by at least 0.5 m and were > 1 m from a tree bole. Vegetation within each plot was manually clipped to ground level and maintained at this state throughout the study to minimize any confounding effects due to nutrient uptake or input via plants. The Oi layer was removed by hand, and each plot was covered with 400 g (air-dry weight) of its randomly assigned litter treatment. This amount was based on an average pre-determined amount of litter received during litterfall in adjacent “no tree” areas. Plots were then covered with plastic mesh to prevent additional leaf litter entry but allow rainfall passage and adhered to the ground with landscape pins. During fall, plots were regularly cleared of outside litter. To simulate natural leaf fall, leaf litter was

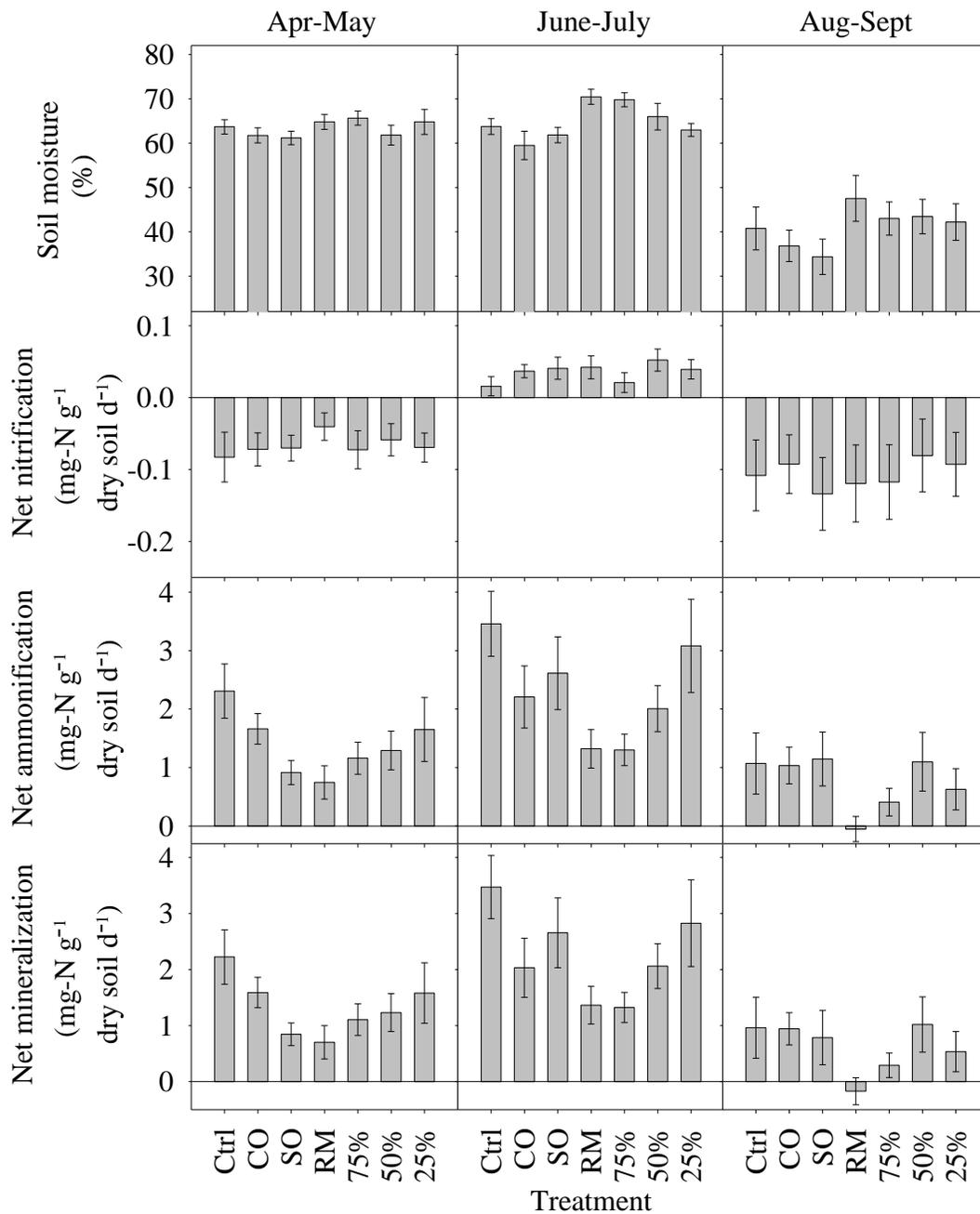
similarly allocated to each plot in 2007 immediately after leaf fall, although fresh litter was collected from the ground by hand rather than using nets. Because a lag time occurs between litter allocation and the time it takes litter to start decomposing, plots remained untouched for 1.5 yr (April 2008). In April, June, and August 2008, 28-d *in situ* incubations were used to assess net inorganic N cycling within the organic layer and upper mineral soils. Methods were similar to those described in Chapter 4, but used the buried bag method rather than the core method. This method was used to prevent damage by wildlife which had previously occurred when using the core method.

Appendix 15. Initial leaf litter lignin concentration, nitrogen (N) concentration, lignin:N, and carbon (C): N ratio of red maple, chestnut oak, and scarlet oak. Values are mean (\pm SE). Different letters represent significant differences ($P < 0.05$) for the observed parameter.

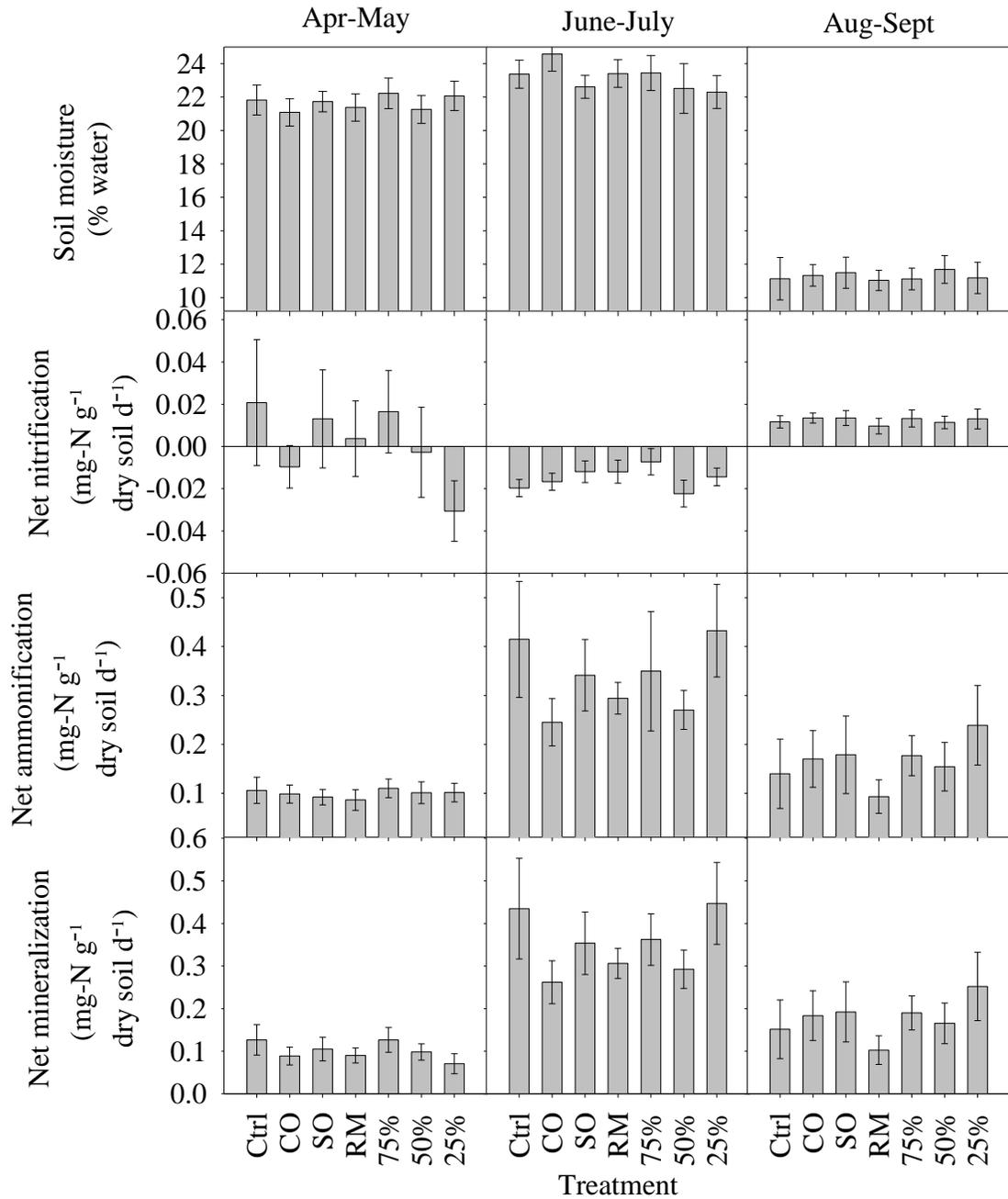
Species	Lignin (%)		Nitrogen (%)		Lignin:N		C:N	
Red maple	10.57	(0.35)a	0.43	(0.03)a	25.97	(2.37)a	116.37	(9.72)a
Chestnut oak	19.81	(1.14)b	0.55	(0.01)b	36.29	(2.30)b	89.24	(1.76)b
Scarlet oak	14.75	(0.68)c	0.53	(0.01)b	28.18	(1.80)a	93.27	(1.48)b



Appendix 16. Mass remaining (A), nitrogen (N) concentration (B), and C:N ratios (C) for different litter treatments used in the decomposition litter bag study over a 1-yr period.



Appendix 17. Initial soil moisture, net nitrification, net ammonification, and net N mineralization for organic material (O_i) underneath various litter treatments during three separate *in situ* (28-d) buried bag incubations throughout spring and summer 2008.



Appendix 18. Initial soil moisture, net nitrification, net ammonification, and net N mineralization for upper mineral soils (0-5 cm) underneath various litter treatments during three separate *in situ* (28-d) buried bag incubations throughout spring and summer 2008.

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- University of Kentucky Barnhart Fund for Excellence (representing the Forestry Department Graduate Student Association, 2007)
- Third Place for Poster and Display Presentation, University of Kentucky Graduate Student Interdisciplinary Conference (2007)
- Best Poster, Joint Fire Science Principal Investigator Meeting (2005)
- People's Choice Best Overall Poster, Estuarine Research Federation Conference (2003)

Professional Publications

Peer-reviewed publications

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- upland oaks, red maple, and sassafras seedlings in response to single and repeated prescribed fires. *Canadian Journal of Forest Research*.
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