ECOLOGY OF FLOWERING DOGWOOD (*Cornus florida* L.) IN RESPONSE TO ANTHRACNOSE AND FIRE IN GREAT SMOKY MOUNTAINS NATIONAL PARK, USA

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2006

ACKNOWLEDGMENTS

I would like to express my thanks to my graduate committee chair, Dr. Shibu Jose, for his guidance, suggestions, and support in completing this project. Thanks also go to my committee members, Drs. Alan Long, Debbie Miller, and Wendell Cropper, for their contributions to this study. Special thanks go to committee member Dr. Mike Jenkins for his input, help, and support with all phases of this project. I am also deeply grateful to the Great Smoky Mountains National Park Inventory and Monitoring Program for providing me with data collection assistance, and an office and housing during multiple field seasons. I would also like to thank the faculty at the IFAS-Statistics Division for their help in data analyses and Ken Ford for his assistance in the potted plant experiment.

I would like to thank the National Park Service Southeast Region Natural Resources Preservation Program, Great Smoky Mountains Association, and the University of Florida College of Agriculture and Life Sciences for providing funding for this project. Without their financial support, this project would not have been possible. Finally I would like to thank my family and friends for their support and encouragement.

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ECOLOGY OF FLOWERING DOGWOOD (*Cornus florida* L.) IN RESPONSE TO ANTHRACNOSE AND FIRE IN GREAT SMOKY MOUNTAINS NATIONAL PARK, USA

By

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May 2006

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Major Department: Forest Resources and Conservation

Cornus florida L. (flowering dogwood), a common understory tree species in eastern forests, is currently threatened throughout its range by a fungus (*Discula destructiva* Redlin) that causes dogwood anthracnose. This disease rapidly kills *C. florida* trees and mortality has exceeded 90% in some forest types. The health and ecological integrity of forest ecosystems throughout the eastern United States are threatened by the decline of *C. florida* populations, but management techniques to control anthracnose have received little attention. Hence, the objectives of this project were to determine (1) the influence of past burning on *C. florida* density and health, (2) how nutrient levels influence the density and health of *C. florida*, and (3) the role of *C. florida* in calcium (Ca) cycling.

We examined *C. florida* populations in burned and unburned oak-hickory stands in Great Smoky Mountains National Park to determine if burning prior to anthracnose

infection has reduced the impacts of the disease. Burned stands contained greater *C. florida* densities and lower disease severity than unburned stands.

Nutrient availability has been hypothesized as a factor that influences dogwood anthracnose severity on *C. florida*. We studied the influence of Ca, potassium (K), and magnesium (Mg) on *C. florida* density and resistance to dogwood anthracnose. We found positive correlations between soil Ca, K, and Mg saturation and *C. florida* density in oak-hickory forests. We also found that seedlings grown in soil with lower inputs of Ca and K cations exhibited higher disease severity earlier in the growing season than seedlings grown with greater inputs of Ca and K.

Cornus florida is thought to play an important role in the Ca cycle because of the high Ca concentration found in the foliage. We quantified the relationship of *C. florida* density on Ca mineralization in the mineral soil and forest floor. Calcium mineralization occurred primarily in the forest floor and was generally greatest in the high density *C. florida* plots.

Our research showed a positive correlation between *C. florida* density and soil Ca, K, and Mg saturation. Higher levels of soil Ca and K may alleviate disease severity in *C. florida*. Further, our results indicate that prescribed fire may provide an important management tool to reduce disease incidence and severity in oak-hickory forests. We also found that the loss of *C. florida* from eastern forests has reduced the rate of soil and forest floor Ca mineralization, which may have negative effects on many associated flora and fauna.

CHAPTER 1
INTRODUCTION

Statement of the Problem

Over the last quarter century, a fungal disease has severely impacted *Cornus* (dogwood) species along the Pacific seaboard and throughout the eastern United States. Redlin (1991) identified the fungus *Discula destructiva* Redlin as the causal agent for the disease, dogwood anthracnose. Two species, *Cornus nuttallii* Aud. (Pacific dogwood) and *Cornus florida* L. (flowering dogwood), are the most susceptible to dogwood anthracnose and have experienced heavy mortality because of the disesae (Daughtery and Hibben 1994). Although not proven, it is believed that dogwood anthracnose is an exotic disease brought to North America from Asia (Britton 1994). Because *Cornus kousa* L. (Oriental dogwood) is quite resistant to anthracnose, it is suspected that the disease was brought from overseas on trees of this species that did not show symptoms (Britton 1994). In a study of *Discula* genetic diversity, Trigiano et al. (1995) found that *D. destructiva* was highly homogenous across its broad continental range compared to other *Discula* species, suggesting that *D. destructiva* is a recently introduced fungus still undergoing intense selection pressure. The sudden appearance of the disease on both coasts of the United States and its rapid spread in the eastern half of the country support this assumption.

Historically, *C. florida* was one of the most common understory trees in the eastern United States (Muller 1982, Elliott et al. 1997, Jenkins and Parker 1998). However, dogwood anthracnose has severely impacted this species and heavy mortality of *C.*

florida (attributed to dogwood anthracnose) has occurred throughout the eastern United States (Anagnostakis and Ward 1996, Sherald et al. 1996, Hiers and Evans 1997, Schwegman et al. 1998, Carr and Banas 1999, Williams and Moriarity 1999, Jenkins and White 2002). For example, Anagnostakis and Ward (1996) reported a mortality rate of 86% between 1977 and 1987 on long-term plots in Connecticut and a 77% reduction of stems was observed in Catoctin Mountain Park in Maryland between 1976 and 1992 (Sherald et al. 1996). Currently, there are no management options for controlling dogwood anthracnose in large forested areas.

Review of Literature

Cornus florida

Cornus florida is primarily an understory species found in the eastern United States, from the southern tip of Maine to the northern half of Florida and as far west as Oklahoma (McLemore 1990). Most common as a small understory tree, average height for *C. florida* ranges from 5-12 m and average stem diameter ranges from 3-8 cm. Although *C. florida* grows best on fertile well-drained soils, it can be found on Ultisols, Inceptisols, Alfisols, Spodosols, and Entisols (McLemore 1990). *Cornus florida* is a shade tolerant species and maximum photosynthesis occurs at about one-third of full sunlight (McLemore 1990). *Cornus florida* is a thin barked species that is easily damaged by logging and fire, however, it will prolifically stump sprout when damaged (Buell 1940, Kuddes-Fischer and Arthur 2002, Blankenship and Arthur 2006). Its large geographical range (Figure 1-1), ability to grow on a variety of sites, tolerance of shade, and sprouting ability enables *C. florida* to grow in association with a wide-range of tree species and in multiple stand conditions. *Cornus florida* is commonly associated with *Quercus* species and mesic hardwoods such as *Liriodendron tulipifera* L., and also occurs

under the shade of *Pinus* species (McLemore 1990). *Cornus florida* is common in many second growth forests, and is also common in old growth and undisturbed areas as well (Harrod et al. 1998, Jenkins and Parker 1998).

Biology of Dogwood Anthracnose

Dogwood anthracnose progressively attacks all aboveground parts of infected trees. Although the disease can affect trees of any size, smaller trees are more susceptible (Mielke and Langdon 1986, Hiers and Evans 1997). The edges of the leaves on the lower branches show the first symptoms of the disease, developing black spots that extend down the leaf margins under suitable conditions (Britton 1994). Anthracnose then spreads from the leaves into the twigs of the infected trees where the fungus overwinters.

In the spring, reproductive structures of *D. destructiva* form underneath leaf spots and on the surface of twig cankers. Numerous asexual spores ooze out in slimy beige droplets from buds and twigs. Local dispersal of the spores occurs by splashing rain, while longer distance dispersal may be facilitated by insects and birds (Sherald et al. 1996). The fungus eventually reaches the bole of the tree where cankers develop, girdling and killing the tree (Mielke and Langdon 1986). Trees also die from repeated defoliation, with smaller trees dying first (Britton 1994). Trees may die within 1-5 years of first infection; saplings may die in the same year they are infected.

There are many signs of dogwood anthracnose infection that can be readily identified. Leaves of infected trees typically have one or both of two types of leaf spots. Irregular light brown spots with reddish brown borders are formed when environmental conditions are less conducive to the fungus. These may be concentrated around the lower edges of the leaf, but may also appear scattered across the lamina. Under favorable disease conditions, the other type of leaf spot forms, a leaf blight with black, water-

soaked lesions typically initiating at the leaf tip and expanding upward along the mid-vein into the twig. Infected trees may display an umbrella-like canopy due to the loss of lower branches (Mielke and Langdon 1986, Daughtrey et al. 1996). In place of lower branches, epicormic shoots often develop, but are quickly infected with anthracnose. Since *C. florida* has the ability to produce stump sprouts, a dead stem surrounded by many sprouts is a common occurrence following anthracnose-caused mortality. These new shoots, however, are typically infected and will not likely mature to replace the dead tree.

Impacts of Dogwood Anthracnose

Since its first appearance in New York in 1978 (Pirone 1980), the spread of anthracnose throughout the eastern half of the United States has been rapid (Figure 1-1). The disease was widespread in nine northeastern States by 1987 (Connecticut, Delaware, Maryland, Massachusetts, New Jersey, New York, Pennsylvania, Virginia, and West Virginia) (Anderson 1991). By 1992 the disease had reached the Carolinas, Georgia, Alabama, Tennessee, and Kentucky (Knighten and Anderson 1993). Daughtrey et al. (1996) reported that the disease had also moved west to the states of Missouri, Illinois, Indiana, Ohio, and Michigan.

A recent study by Wyckoff and Clark (2002) at the Coweeta Hydrologic Laboratory in the southern Appalachian Mountains documented the rapid decline of *C. florida*, with a mortality rate of 15% within a 5 year (1993-1998) period. In Great Smoky Mountains National Park (GSMNP), analysis of long-term vegetation monitoring data revealed several alarming trends (Jenkins and White 2002). Between the two sampling intervals (1977-1979 and 1995-2000), dramatic decreases in *C. florida* stem density were observed in typic cove, acid cove, alluvial, oak-hickory, and oak-pine forest types.

Overall decline was greatest in acid cove forests, where mean *C. florida* stem density decreased by 94% (101 stems ha^{-1} to 6 stems ha^{-1}). Typic cove and alluvial forests exhibited the next greatest decreases in *C. florida* stem density (92% for both forest types). Mean density decreased from 180 stems ha^{-1} to 14 stems ha^{-1} in typic cove forests and from 364 stems ha^{-1} to 28 stems ha^{-1} in alluvial forests. The two driest forest types, oak-hickory and oak-pine, exhibited declines of 80% and 69%, respectively. Prior to anthracnose, *C. florida* stem density in oak-hickory forests was the second highest of any forest type (298 stems ha^{-1}), however, mean density decreased to 61 stems ha^{-1} in 1995-2000. Mean density decreased from 132 stems ha^{-1} to 41 stems ha^{-1} in oak-pine forests.

New *C. florida* seedlings are not replacing dead *C. florida* trees in infected stands. Trees infected with anthracnose produce fewer seeds (Rosell et al. 2001), and reduced seed production combined with the susceptibility of smaller trees to the disease has drastically decreased regeneration. Seedlings and saplings were reported to be absent in several studies (Sherald et al. 1996, Hiers and Evans 1997), indicating the severity of the problem.

Factors Affecting Dogwood Anthracnose

Many environmental variables influence the spread and virulence of dogwood anthracnose, but moisture is probably the most critical (Britton 1993). The disease is more severe on shaded and moist northeast-facing slopes than on southwest-facing slopes with open canopies (Chellemi et al. 1992, Clinton et al. 2003). In a long-term vegetation study in GSMNP, Jenkins and White (2002) reported higher levels of mortality attributed to dogwood anthracnose in more mesic forests (typic and acid coves and alluvial communities) compared to more xeric forest types (oak-hickory and oak-pine communities). Jenkins and White (2002) also reported an increased number of *C. florida*

stems on three plots after a 1976 wildfire (Figure 1-2), indicating stand conditions can be manipulated to increase *C. florida* survival from dogwood anthracnose. However, the effects of past burning on *C. florida* populations have not been fully investigated.

Although moisture may be the most important environmental variable affecting the impacts of dogwood anthracnose on *C. florida*, another key variable that has yet to be fully explored is nutrient availability. In a greenhouse study by Britton et al. (1996), simulated acid rain increased the susceptibility of *C. florida* to anthracnose. The authors hypothesized that the increase in susceptibility was largely because of soil-mediated impacts that reduced the availability of soil cations. Calcium (Ca), potassium (K), and magnesium (Mg) are nutrients that have been linked to disease resistance in other plant species and diseases (Sij et al. 1985, Anglberger and Halmschlager 2003, Sugimoto et al. 2005). Sugimoto et al. (2005) found a reduction of *Phytophthora sojae* Kaufmann and Gerdemann (stem rot) with the application of Ca on two cultivars of *Gycline max* L. Merr. cv. Chusei-Hikarikuro (black soybean) and cv. Sachiyutaka (white soybean) in Japan. Sij et al. (1985) reported that increased rates of K fertilizer significantly decreased *Colletotrichum dematium* (Pers.ex Fr.) Grove var. *truncata* (Schuv.) Arx. (anthracnose) in field grown *G. max* plants in Texas. In Austria, severity of *Sirococcus conigenus* (shoot blight) was increased on *Picea abies* (Norway spruce) trees that had needles with low levels of Mg (Anglberger and Halmschlager 2003). It is possible that bioavailability of soil Ca, K and Mg plays a role in resistance to dogwood anthracnose in *C. florida* as well.

Ecological Significance of *Cornus florida*

The loss of *C. florida* from stands throughout the eastern United States will likely have serious ecological effects. An individual tree may produce up to 10 kg of fruit each

fall (Rossell et al. 2001). There are more than 50 species of birds, including neotropical birds during fall migration, as well as a number of small game species that are known to eat the fruit (Martin et al. 1951, Stiles 1980). *Cornus florida* twigs are also an important source of browse for white-tailed deer and other herbivores (Blair 1982).

Cornus florida is also important in nutrient cycling within forest communities. In eastern mixed hardwood forests, Ca released through mineral weathering is generally insignificant (Huntington et al. 2000, Dijkstra and Smits 2002). As a result, the release of Ca through organic matter decomposition (mineralization) is considered the major source of Ca for immediate plant uptake for all tree species (Dijkstra and Smits 2002). Dijkstra (2003) reported that for most species, Ca mineralization beneath the canopy of a given species primarily occurs in the forest floor (from leaf litter) as opposed to the mineral soil. Decomposition of *C. florida* foliage is very rapid compared to other species (Blair 1988, Knoepp et al. 2005), and *C. florida* litter contains high concentrations (2.0-3.5%) of Ca (Thomas 1969, Blair 1988). Because of the high Ca concentration in its foliage, quick decomposition, and abundance in the understory, *C. florida* has long been believed to influence Ca availability in the mineral soil and forest floor by acting as a "Ca pump" in forests (Thomas 1969, Jenkins et al. 2006). High Ca concentration in *C. florida* foliage could mean potentially high rates of Ca mineralization in the forest floor and mineral soil. If high mineralization rates occur, there is a potential for high Ca availability in the soil. Apart from anecdotal evidence, the impacts of *C. florida* on Ca cycling, however, have not been quantified.

Specific Objectives

As discussed previously, the roles of past burning and bioavailability of nutrients in determining *C. florida* population dynamics following infection with dogwood

anthracnose have not been fully investigated. In addition, whether higher foliar Ca concentration in *C. florida* foliage translates into higher rates of Ca mineralization in the forest floor and mineral soil remains undetermined. Therefore, the objectives of this research project were to:

1. Determine the influence of past burning on (1) *C. florida* density and health and (2) overall stand structure and species composition in oak-hickory forests where *C. florida* is historically found.

2. Examine the effects of soil cation availability (Ca, K, and Mg) on the health and survival of *C. florida.*

3. Determine the relationship between *C. florida* density and Ca mineralization rates in two forest types (cove hardwood and oak hardwood) where *C. florida* is a common understory species.

The following three chapters describe the results of field surveys and experiments conducted in Great Smoky Mountains National Park to address these three objectives.

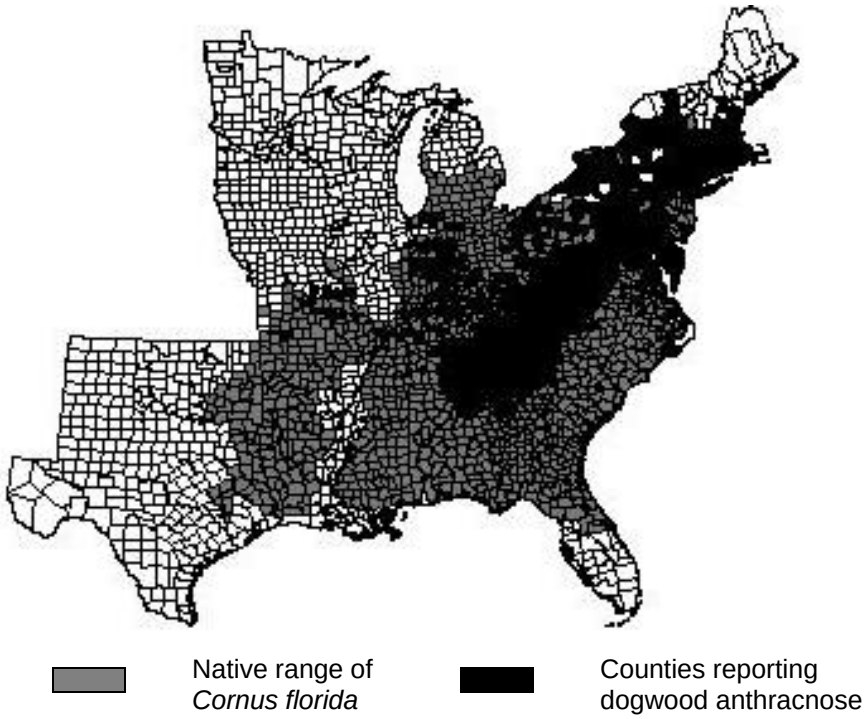

Figure 1-1. Native range of *Cornus florida* and the documented range of dogwood anthracnose in the eastern United States (Based on data from the U.S. Forest Service Southern and Northeastern Forest Research Stations).

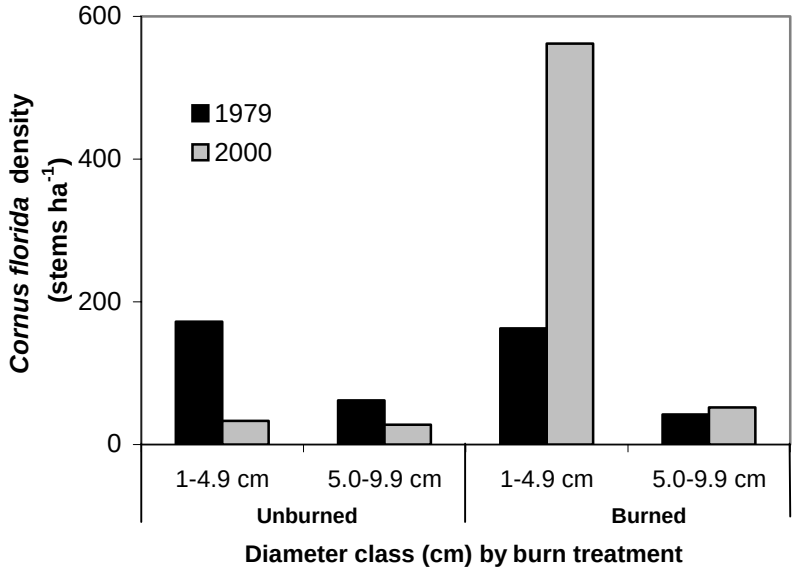

Figure 1-2. The effects of a 1976 wildfire on *Cornus florida* stem density in Great Smoky Mountains National Park. While stem density decreased drastically in unburned areas during the 21 year study period ($P < 0.001$), density increased (245%, $P = 0.159$) in the 1.0-4.9 cm class and remained stable in the 5.0-9.9 cm class in burned areas ($P = 0.334$) (Based on data from Jenkins and White 2002).

CHAPTER 2
INFLUENCE OF FIRE ON THE DENSITY AND HEALTH OF *Cornus florida* L. (FLOWERING DOGWOOD) POPULATIONS IN GREAT SMOKY MOUNTAINS NATIONAL PARK

Introduction

Historically, *Cornus florida* L. (flowering dogwood) was one of the most common understory species in eastern United States hardwood forests (Muller 1982, Elliott et al. 1997, Jenkins and Parker 1998). According to McLemore (1990), *C. florida* occurs on a variety of soils (Ultisols, Inceptisols, Alfisols, Spodosols, and Entisols), is shade tolerant (maximum photosynthesis occurs at about one-third of full sunlight), and has a large geographical range (southern Maine to northern Florida and as far west as Oklahoma). These factors enable the species to grow in association with a wide-range of tree species including *Quercus* species, *Pinus* species, and *Liriodendron tulipifera* L. *Cornus florida* is most often found in post-logged secondary forests, and also occurs within tree-fall gaps of old growth forests (Muller 1982, Jenkins and Parker 1998). Because of its ability to grow in shaded conditions and thin bark, *C. florida* is not considered a fire dependent species. However, it sprouts prolifically when top-killed by fire (Kuddes-Fishcher and Arthur 2002, Blankenship and Arthur 2006).

Cornus florida is an ecologically important species in forests throughout the eastern United States. An individual *C. florida* tree may produce up to 10 kg of protein-rich fruit each fall, and more than 50 species of birds as well a number of small mammal species are known to eat the fruit (Martin et al. 1951, Rossell et al. 2001). However, *C. florida*'s most important role may be in the annual cycling of calcium in forest communities.

Cornus florida foliage decomposes very rapidly compared to other species, and *C. florida* litter contains large amounts of calcium (2.0-3.5%) (Thomas 1969, Blair 1988, Knoepp et al. 2005). As a result, *C. florida* serves an important ecological function as a calcium "pump" for associated plant species and forest floor biota.

Dogwood anthracnose, a disease caused by the fungus *Discula destructiva* Redlin (believed to be an exotic disease from Asia) has become a serious disease of *C. florida* over the past 20 years. Dogwood anthracnose was first identified in the late 1970s in New York (Pirone 1980), and has since spread rapidly throughout the eastern United States, infecting *C. florida* populations throughout much of its range (Holzmueller et al. 2006). Following infection by anthracnose, mortality rates of *C. florida* have been as high as 90% (Anagnostakis and Ward 1996, Sherald et al. 1996, Hiers and Evans 1997, Jenkins and White 2002). Although the disease can infect trees of any size, smaller trees are more susceptible than large trees and often die from repeated defoliation within 1-5 years of infection (Mielke and Langdon 1986, Hibben and Daughtery 1988). The fungus also causes twig dieback and stem cankers, which can eventually girdle the tree (Hibben and Daughtery 1988).

The rapid spread of dogwood anthracnose and high mortality of *C. florida* make it somewhat similar to the effects of *Cryphonectria parasitica* (Murill) Barr (Asian chestnut blight fungus) on *Castenea dentata* Marsh. (American chestnut). *Cryphonectria parasitica* was introduced in New York City in the early 1900s and spread rapidly down the Appalachian Mountains, infecting *C. dentata* throughout most of its range by 1926 and effectively extirpating the species by the 1950s (Anagonostakis 2001). Whereas the effects of *C. parasitica* on *C. dentata* were fairly uniform in all forest types and stand

conditions, disease severity of dogwood anthracnose is influenced by many variables, particularly shading and moisture (Britton 1993). The disease is more severe on shaded and moist northeast-facing slopes than on relatively drier southwest facing slopes with open canopies (Chellemi and Britton 1992, Chellemi et al. 1992). Britton (1993) reported that given adequate amounts of rainfall, the disease could develop throughout the growing season. In addition, Britton et al. (1996) found that acid rain increases the susceptibility of *C. florida* to anthracnose.

Since dogwood anthracnose is known to be sensitive to environmental characteristics, there is a possibility that management techniques could be used to manipulate stand structure to reduce the impacts of dogwood anthracnose. However, research examining the effects of stand manipulations on dogwood anthracnose in forest stands has been limited. Britton et al. (1994) examined the effect of past silvicultural practices on *C. florida* density and disease severity and reported *C. florida* densities were highest and disease severity lowest in stands that had been clearcut in 1939 and again in 1962. This effect was attributed to increased light levels in these plots. Prescribed burning may also offer a technique to manipulate stand conditions to favor *C. florida* survival in infected stands. Jenkins and White (2002) reported a 200% increase in *C. florida* stem density on three long-term vegetation plots that burned in 1976 in Great Smoky Mountains National Park (GSMNP), however, the effects of burning on stand structure and *C. florida* health and survival were not fully explored.

Dogwood anthracnose was first reported in GSMNP in March of 1988 when a park-wide survey revealed that 23 out of 58 plots that contained *C. florida* were infected with anthracnose (Windham and Montgomery 1990). Seven years later, in a study

conducted in the western half of GSMNP, Wilds (1997) observed signs of anthracnose on 98% of the plots on which *C. florida* occurred. By 2000, *C. florida* mortality attributed to dogwood anthracnose ranged from 69% in oak-pine stands to 94% in acid coves on long-term vegetation plots located within GSMNP (Jenkins and White 2002). Prior to anthracnose, *C. florida* was the dominant understory woody species in oak-hickory forest of GSMNP. Following anthracnose infection, *C. florida* density decreased by 80% in this forest type.

Within eastern North America, oak-hickory forests comprise over 34% of total forest cover (Smith et al. 2001). Within this forest type, fire was historically common and influenced species composition and stand structure (Brose et al. 2001). Because fire has played an important ecological role in this widely distributed forest type, we undertook a study with the following objectives: to determine the influence of past burning on (1) *C. florida* density and health and (2) overall stand structure and species composition in oak-hickory forests in GSMNP. We hypothesize that past burning has altered stand conditions (structure and species composition) in ways that reduced the impacts of dogwood anthracnose compared to unburned stands. Burning typically reduces stand density, increases light penetration through the canopy, and decreases understory moisture content, which, we hypothesize, favors *C. florida* survival. These conditions will not last indefinitely, however, and we further hypothesize that repeated burning is needed to maintain stand conditions that reduce the impacts of the disease. Because *C. florida* is a thin barked species that is frequently top-killed by fire, we further hypothesize that *C. florida* will display reduced survival once a threshold of burning frequency is reached.

Materials and Methods

Study Site

This study was conducted in GSMNP, USA, which encompasses slightly over 200 000 ha, and straddles the Tennessee and North Carolina state line. The Park is internationally renowned as a center of biological diversity within North America and was designated as an International Biosphere Reserve in 1976. Due to its biotic diversity, large size, and protected status, changes that occur within the biological communities of GSMNP often serve as baselines for comparison to other state and federal lands. Mean annual temperature in Gatlinburg, Tennessee (440 m a.s.l. and adjacent to GSMNP) is 12.9° C and mean annual precipitation is 142 cm. Our study sites ranged in elevation from 287 to 975 m. Although *C. florida* occurs in a variety of forest types, we focused our study in oak-hickory forests. These forests were typically found on moderately steep to steep slopes with southeast-south-northwest facing aspects. *Cornus florida* is a common understory species in the oak-hickory forest type, and this type has frequently burned in some areas of GSMNP over the last 30 years.

During June-August of 2001-2004, we sampled seventy-nine 0.04 ha (20 m x 20 m) plots in burned and unburned stands. Fifty-five plots were established in fourteen stands that had burned up to three times over a 20 year period (late 1960s to the late 1980s). In addition, twenty-four plots were established in six unburned stands. These areas were divided into four sampling categories: (1) single burn (seven stands, thirty plots), (2) double burn (four stands, sixteen plots), (3) triple burn (three stands, nine plots), and (4) unburned (six stands, twenty-four plots).

We used historic park maps and fire history records to select burned (single, double, and triple burns) and unburned areas. Within each burned area, we selected

stands from vegetation associations within the Montane Oak-Hickory Forest Ecological Group (White et al. 2003). Associations within this group contained *C. florida* as a major understory component prior to the onset of dogwood anthracnose (White et al. 2003). Individual polygons (stands) of each association were derived from vegetation maps of GSMNP based upon 1:12000 color-IR aerial photos (Welch et al. 2002). Unburned (reference) plots were established in nearby areas with similar slopes, aspects, topography, and vegetation associations as the burn plots. All burns selected were at least 10 hectares in size. Plots were located within the burn areas by placing a 50 m buffer inside of each area, and randomly selecting plot coordinates within appropriate vegetation associations. A minimum of three 20 x 20 m plots were placed within each burn area, with up to five plots placed in larger burns.

Field Sampling

We recorded the diameter at breast height (dbh) of all living overstory stems (> 10.0 cm dbh) by species to the nearest 0.1 cm. Living stems ≤ 10.0 cm dbh (understory) were tallied by species into four diameter classes: 0-1.0 cm, 1.1-2.5 cm, 2.6-5.0 cm, and 5.1-10.0 cm. We measured the dbh of all *C. florida* stems, regardless of overstory or understory classification, to the nearest 0.1 cm. Foliage and crown health were assessed for each living *C. florida* stem using the Mielke-Langdon Index (Mielke and Langdon 1986; Table 2-1).

Data Analysis

Data were analyzed for differences in the four sampling categories (single burn, double burn, triple burn, and unburned) for the following response variables: *C. florida* stem density, *C. florida* foliar and crown health, overstory basal area and stem density, understory basal area and stem density, understory species importance values [IV =

((relative density + relative basal area)/2)*100], *Tsuga canadensis* (L.) Carr. stem density, plot species richness, and species diversity (Shannon's diversity index). *Cornus florida* stem density differences among the four sampling categories were analyzed in three diameter classes: 0-5.0 cm, 5.1-10.0 cm, and > 10.0 cm. Total *C. florida* stem density of the four sampling categories was also analyzed. Because smaller trees are more susceptible to dogwood anthracnose (Hiers and Evans 1997, Jenkins and White 2002), *C. florida* foliage and crown health were analyzed in five diameter size classes that better represented smaller diameters: 0-1.0 cm, 1.1-2.5 cm, 2.6-5.0 cm, 5.1-10.0 cm, and > 10.0 cm. *Tsuga canadensis* stem density was analyzed in five diameter size classes (0-2.5 cm, 2.6-5.0 cm, 5.1-10.0 cm, 10.1-20.0 cm, and > 20.0 cm), plus total stem density.

Before statistical comparison, all data (except categorical) were tested for normality using the Kolmogorov-Smirnov goodness-of-fit test for normal distribution. Only the *C. florida* stem density data violated the test for normality ($P < 0.05$). These data were natural log transformed to improve normality and equalize variances. For ease of interpretation, non-transformed values are presented. All response variables were analyzed with analysis of variance (ANOVA) using the Mixed procedure in SAS (SAS 2002). The model was made up of two factors. The first factor was fixed, sampling category, and the other was random, burn area nested within sampling category. When ANOVA revealed a clear difference between the sampling categories, we used the PDIFF option for post-hoc pairwise comparisons (SAS 2002). All means presented in the paper are least square means calculated by SAS using the mixed procedure.

To test for differences in overstory and understory community composition in the four sampling categories we used MRPP (Multi-Response Permutation Procedures;

Biondini et al. 1985, Lesica et al. 1991, Peterson and McCune 2001). MRPP is a nonparametric procedure to test for multivariate differences in pre-existing groups (i.e. single burn, double burn, triple burn, and unburned stands) (Mielke 1984). It provides a test statistic (*A*) and P-value to determine whether the sampling categories occupied the same regions of species space (*A* measures within-group agreement, if $A = 1$ then items within groups are identical and 1 is the highest possible value for *A*, $A = 0$ when heterogeneity within groups equals expectation by chance, and $A < 0$ with less heterogeneity within groups than expected by chance). Interpretation of this test statistic was done using nonmetric multidimensional scaling (NMS) and indicator species analysis (IndVal) (Peterson and McCune 2001, McCune and Grace 2002). NMS is an ordination technique that is ideal for data that are nonnormal or nonlinear and contains large numbers of zero values. It uses ranked distances to linearize the relation of degrees of difference between community samples and distances on an environmental gradient, and is the most effective ordination technique available for community data (Clarke 1993, McCune and Grace 2002). IndVal is used to describe the relationship of species to categorical variables by combining species abundance in a specific category plus the faithfulness of occurrence of that species in that specific category (Dufrêne and Legendre 1997, Qian et al. 1999, Peterson and McCune 2001). The analysis produces a value of abundance for each species in each group (IndVal) and a test statistic produced from Monte Carlo tests (1000 iterations) to determine if occurrence in the maximum (indicator) group is greater than would be expected from chance.

All multivariate analyses were performed using PC-ORD (McCune and Medford 1999). To reduce the effects of rare species, we deleted those species occurring in less

than three plots prior to multivariate analyses; eight species were deleted from overstory analyses and 16 species were deleted from understory analyses (McCune and Medford 1999). MRPP and NMS were performed using the quantitative version of Sørenson's distance measure and NMS ordination was displayed on two axes. Additional axes did not significantly improve the explanatory power of the ordination.

Results

Cornus florida Stem Density

Cornus florida stem density differed significantly among sampling categories in the smallest (0-5.0 cm) size class (double burn = 691 stems ha^{-1}, triple burn = 175 stems ha^{-1}, single burn = 154 stems ha^{-1}, and unburned stands = 35 stems ha^{-1}, P = 0.0015; Figure 2-1). Double burn stands contained four times more *C. florida* stems than single burn stands (P = 0.05) and twenty times more *C. florida* stems than unburned stands (P = 0.0002). The stem density of double burn stands was not significantly different from that of triple burn stands (P = 0.39). The single burn stand and triple burn stand stem densities in this size class were not significantly different (P = 0.39), but stem densities in both of these categories were significantly greater than the unburned stand stem density (P < 0.007). There was no statistical difference between sampling categories in *C. florida* stem density in the 5.1-10 cm size class (P = 0.229; Figure 2-1). Although differences were not significant due to high inter-plot variability (P = 0.167), double and triple burn stands contained greater densities of stems >10 cm dbh (22 and 17 stems ha^{-1}, respectively) than unburned and single burned stands (5 and 6 stems ha^{-1}, respectively).

Total stem density of *C. florida* differed significantly among the four sampling categories (double burn = 770 stems ha^{-1}, triple burn = 233 stems ha^{-1}, single burn = 225 stems ha^{-1}, and unburned stands = 70 stems ha^{-1}, P = 0.0003; Figure 2-1). This difference

can be largely attributed to the greater percentage of smaller trees in burned stands. Trees in the 0-5.0 cm size class contributed 90% of the total stems ha^{-1} in double burn stands, 75% in triple burn stands, 68% in single burn stands, and just 50% in unburned stands. We observed a significantly greater total density of stems in double burn stands than in single burn stands ($P = 0.036$) and unburned stands ($P < 0.0001$), but triple burn stands did not differ significantly from double burn stands ($P = 0.53$). Single burn and triple burn stands were not significantly different from each other ($P = 0.26$), but both categories were significantly greater than the unburned stands ($P < 0.001$).

Foliage Health and Crown Dieback

Overall, mean foliage health ranged from 3.1 to 3.9 for all size classes and sampling categories, and we did not observe any differences in the foliar health among the sampling categories in each of the five size classes ($P > 0.38$; Table 2-2). Mean crown dieback ratings of all size classes ranged from 2.4 to 3.7, and there were no significant differences in crown health in three of the size classes (0-1.0 cm, $P = 0.64$; 5.1-10.0 cm, $P = 0.45$; and > 10.0 cm, $P = 0.93$; Table 2-2). However, in two of the smaller size classes (1.1-2.5 cm and 2.6-5.0 cm) there was a significant difference in mean crown dieback ratings among the four sampling categories ($P = 0.04$ and $P = 0.01$, respectively; Table 2-2). Further analyses in the 1.1-2.5 cm size class showed that the rating of unburned stands (2.4) was significantly lower (less healthy) than those of the burned stands (3.3 - 3.4, $P < 0.02$). In the 2.6-5.0 cm size class, mean crown dieback ratings for burned stands (3.6 - 3.2) were significantly higher (healthier) than that of unburned stands (2.7, $P < 0.04$). Differences among the sampling categories were not significant for the 0 – 0.1 cm class, however, plots in unburned stands did not contain any living trees in this size class.

Stand Structure

Overstory (> 10.0 cm dbh) basal area was similar among the four sampling categories (single burn = 21.7 m^2 ha^{-1}, double burn = 22.1 m^2 ha^{-1}, triple burn = 20.6 m^2 ha^{-1}, and unburned stands = 23.2 m^2 ha^{-1}, P = 0.52; Table 2-3). Overstory stem density differed significantly among the four sampling categories (single burn 436 stems ha^{-1}, double burn 323 stems ha^{-1}, triple burn 317 stems ha^{-1}, and unburned stands 564 stems ha^{-1}, P < 0.0001; Table 2-3). Comparisons of overstory stem density among the four sampling categories revealed that double and triple burn stands had similar stem densities (P = 0.92). Densities in these two categories were significantly lower than that of single burn stands (P < 0.05) and unburned stands (P < 0.001). Finally, single burn stands had significantly fewer stems than unburned stands (P = 0.016).

In the understory (≤ 10.0 cm dbh), basal area was similar between sampling categories, ranging from 6.5 - 7.4 m^2 ha^{-1} (P = 0.93; Table 2-3), while stem density was significantly different (single burn 2851 stems ha^{-1}, double burn 4594 stems ha^{-1}, triple burn 5072 stems ha^{-1}, and unburned stands 2292 stems ha^{-1}, P=0.024; Table 2-3). Comparisons of understory stem density among the four sampling categories revealed that double and triple burn stands had similar densities (P = 0.66), as did single burn stands and unburned stands (P = 0.46). Double and triple burn stands had significantly greater understory stem densities than the single burn and unburned stands (P < 0.05).

Overstory Community Composition

Shannon's diversity index did not differ significantly in the overstory in the four sampling categories (P = 0.48; Table 2-4). However, species richness of plots in the four sampling categories did differ slightly (P = 0.06), and was greatest in unburned stands compared to burned stands (6.9 versus < 5.7, respectively; Table 2-4). MRPP indicated

that species composition differed slightly between plots in the sampling categories (MRPP: $P < 0.0001$, $A = 0.09$). Three species were associated with unburned stands (*Acer rubrum* L., *Oxydendrum arboreum* (L.) DC., and *T. canadensis*) and one each for double burn stands (*Quercus alba* L.) and triple burn stands (*Quercus velutina* Lam.) (IndVal: $P < 0.08$ each; Table 2-5). These differences, however, were not strong enough to clearly separate the sampling categories in the ordination (Figure 2-2).

Understory Community Composition

Shannon's diversity index and species richness did not differ in the understory among the four sampling categories ($P = 0.81$ and $P = 0.48$, respectively; Table 2-4). Species composition did differ slightly between the sampling categories (MRPP: $P < 0.0001$, $A = 0.06$). Numerous species were indicative of sampling categories, primarily in the triple burn stands (unburned: *T. canadensis*; double burn: *C. florida* and *Tilia americana* L.; triple burn: *Carya alba* L., *Carya glabra* Mill., *Pinus virginiana* Mill., *Q. alba*, *Quercus prinus* L., *Quercus rubra* L., *Q. velutina*, and *Robinia pseudoacacia* L.; Table 2-5). These differences, however, were not strong enough to clearly separate the sampling categories in the ordination (Figure 2-2).

Importance Values for Understory Species

In addition to greater stem densities, mean importance value (IV) of *C. florida* was four times greater in double burn stands than in unburned stands (IV = 21.6 versus 5.1, $P = 0.001$; Table 2-6). *Cornus florida* importance values were also significantly greater in single burn (IV = 12.1) and triple burn (IV = 14.8) stands compared to unburned stands (IV = 5.1, $P = 0.05$). *Cornus florida* had the greatest importance value of any species in double burn stands and second highest in the triple and single burn stands. Six other species had higher importance values than *C. florida* in unburned stnads, including *T.*

canadensis, which was ten times greater in importance in unburned stands compared to burned stands ($P < 0.05$; Table 2-6).

In triple burn stands, the importance values for *A. rubrum* (IV = 7.8) was significantly lower ($P = 0.03$) than that of single burn stands (IV = 24.2). Also within triple burn stands, *C. glabra* and *C. alba* L. importance values were three times greater than in any other category ($P < 0.004$ and $P < 0.01$, respectively). In addition, the *R. pseudoacacia* importance value was three times greater in triple burn stands compared to the other sampling categories ($P < 0.04$) and the importance value of *P. virginiana* was greatest in the triple burn stands.

***Tsuga canadensis* Stem Density**

Overall, total *T. canadensis* stem density was significantly greater in unburned stands (216 stems ha^{-1}) compared to single burn (42 stems ha^{-1}), double burn (23 stems ha^{-1}), and triple burn stands (11 stems ha^{-1}, $P < 0.001$; Figure 2-3). Most of the *T. canadensis* stems were in the smallest (0-2.5 cm) size class, *T. canadensis* stem density was over four times greater in unburned stands (83 stems ha^{-1}) compared to single (18 stems ha^{-1}), double (14 stems ha^{-1}), and triple burn stands (11 stems ha^{-1}, $P < 0.001$; Figure 2-3). Unburned stands had significantly more *T. canadensis* stems ha^{-1} in the 2.5-5.0 cm, 5.1-10.0 cm, and 10.1-20.0 cm size classes as well ($P < 0.005$). In the largest diameter classes (> 20 cm), single burn stands and unburned stands were similar (4 and 6 stems ha^{-1}, respectively, $P = 0.49$). This size class was absent on plots in double and triple burn stands.

Discussion

The results of our study demonstrate the potential role of fire in regulating population dynamics of *C. florida* in post-anthracnose stands. Overall, burned stands in

our study had greater *C. florida* stem densities, *C. florida* trees with healthier crowns, and higher *C. florida* importance values than unburned stands. The greater *C. florida* stem densities and healthier *C. florida* trees in burned stands are likely the result of reduced shading following the burns that created a relatively drier microclimate that was less favorable to *D. destructiva*. Studies have shown that shaded conditions increase the severity of dogwood anthracnose (Gould and Peterson 1994, Erbaugh et al. 1995). For example, Chellemi and Britton (1992) reported an inverse relationship between evaporative potential and disease severity on *C. florida* in the southern Appalachians. *Discula destructiva* growth has been found to be greater under moist conditions. In a study involving artificial inoculation of *C. florida* with dogwood anthracnose, Ament et al. (1998) reported that *D. destructiva* lesions on *C. florida* leaves were five times larger when placed inside moistened bags for seven days compared to lesions that developed on leaves that spent four, two, and zero days inside moistened bags.

In our study, the greatest densities of *C. florida* stems were found in double burn stands. Although single burn stands had greater *C. florida* stem densities than unburned stands, it appears that a single burn within a 20 year period is not sufficient to maintain *C. florida*. Increases in overstory stem densities following a single burn appear to provide sufficient shading for anthracnose to increase in virulence. Studies have shown repeated burns better maintain lower overstory stem densities in oak forests (Huddle and Pallardy 1996, Peterson and Reich 2001, Hutchinson et al. 2005), which favors *C. florida* survival from dogwood anthracnose. Our results indicate, however, that benefits of multiple burns are reduced when burning is increased to three burns in a 20 year period. It appears that although larger (> 5 cm) *C. florida* trees survived the third burn, smaller trees displayed

less resprouting after the third burn. This reduction in resprouting may be attributed to fire induced mortality of smaller stems, as opposed to lack of root carbohydrates, resulting in fewer stems per hectare capable of producing sprouts (Arthur et al. 1998), and suggests that this was too short an interval between burns. Increased importance values of *R. pseudoacacia* and *P. virginiana* on triple burn stands, (indicator species of triple burn stands as well), suggest that the third burn shifted stands towards an earlier successional composition (Harrod et al. 1998). This shift to an earlier successional composition may perhaps be another reason for decreased *C. florida* stem densities in triple burn stands.

Although there were some differences in overstory community composition among the sampling categories, these differences were not strong enough to classify the sampling categories as unique communities. However, the identification of *A. rubrum*, *O. arboreum*, and *T. canadensis* as indicator species in unburned stands suggest that this sampling category is shifting to a later successional stage. This is not surprising, however, considering the lack of disturbance in these stands for the past 80-100 years.

In the understory, we found that differences in overall community composition were present, but limited to a few species, such as *C. florida* and *T. canadensis*. We observed higher understory stem densities in multiple burn stands, which is a result of reprouting by deciduous trees and is consistent with other studies (McGee et al. 1995, Elliott et al. 1999, Kuddes-Fischer and Arthur 2002). However, while burned stands had greater total understory stem densities, fire decreased the density and importance of *T. canadensis* in the understory of burned stands. In fire suppressed stands, this species often dominates the understory and produces a dense sub-canopy that results in moist,

heavily shaded conditions (Godman and Lancaster 1990, Woods 2000, Jenkins and White 2002, Galbraith and Martin 2005) that favor dogwood anthracnose development (Chellemi and Britton 1992). Therefore, the reduction in *T. canadensis* density following fire has likely contributed to the greater densities of *C. florida* in burned areas.

In our study, the positive effects on *C. florida* density observed in burned stands were likely a result of the indirect effects of fire, produced by changes in stand structure and composition. The direct effects of fire (smoke and heat) on *D. destructiva* are unknown. However, studies suggest that fire may reduce the amount of inoculum of fungal diseases (Parmeter and Uhrenholdt 1975, Schwartz et al. 1991). In laboratory experiments, Parmeter and Uhrenholdt (1975) found that exposure to smoke from burning pine needles reduced the amount of rust and gall fungi on cellophane sheets. Schwartz et al. (1991) suggested that smoke from upland fires may have settled into unburned mesic ravines and helped reduce mortality of the endangered *Torreya taxifolia* Arnott (Florida torreya) by reducing fungal disease. In addition, burning typically produces a flush of nutrients in the soil after a burn (Kutiel and Shaviv 1992, Boerner et al. 2004, Tuininga and Dighton 2004). This flush in nutrients, especially cations such as calcium, magnesium, and potassium, may benefit *C. florida* survival. Studies have documented the importance of nutrients in plant survival from diseases (Sij et al. 1985, Yamazaki et al. 1999, Sugimoto et al. 2005). Holzmueller et al. (2006b) reported that cation availability played a role in *C. florida* survival and resistance to dogwood anthracnose.

We observed prolific sprouting by *C. florida* in stands that burned prior to anthracnose infection in our study. However, the use of fire as a management tool for

anthracnose is dependent upon the ability of diseased and weakened trees to resprout after fire in anthranconse-infected stands. Encouragingly, Blankenship and Arthur (2006) reported high levels of *C. florida* sprouts in recently burned areas that had been previously infected with dogwood anthracnose. However, the long-term survival rate of these sprouts in anthracnose-infected stands is unknown. In addition, in the burned stands we sampled, most living *C. florida* stems were relatively small in diameter. The amount of fruit produced by these populations of smaller individuals relative to pre-anthracnose production is unknown. The amount of fruit and seeds produced is critical to the successful reproduction of *C. florida* and its role as a source of soft mast for wildlife.

Prescribed fire may offer the best means of control of dogwood anthracnose in oak-hickory forest stands. Although Britton et al. (1994) documented the highest stem densities of *C. florida* in clearcut areas in a study of timber harvest practices on *C. florida* populations, it is unlikely that clearcutting large areas for the benefit of a single understory species would fit into many ecosystem management plans. Furthermore, in clearcut stands, the overstory will likely redevelop during the stem exclusion stage within 20 years after a harvest (Oliver and Larson 1990), and shading will again increase. The return interval for clearcutting (60-100 years) will likely be too long to serve as an effective long-term control. Prescribed burning in oak forests may offer a more applicable management technique across large forested areas and multiple ownerships, particularly those where mechanical harvests are not an option. Although eastern oak forests have been subjected to fire suppression for about 100 years, resource managers have increased efforts to manage oak forests with prescribed fire (Brose et al. 2001), and these efforts offer a framework for managing *C. florida* populations as well. Burning on a

10-15 year return interval would probably be best for *C. florida* survival, and would fit in with the historic fire regime of eastern oak-hickory forests (Harmon 1982). In single, double, and triple burned stands in our study, we observed less crown dieback compared to unburned stands, however, the lack of difference in foliar infection may indicate that the interval since the last burn (nearly 20 years) has allowed anthracnose to return to a level of infection similar to unburned stands. This suggests that these stands will require additional burns to slow the loss of *C. florida*.

Management Implications

Our results suggest that prescribed fire may offer an effective and practical management technique to alleviate the symptoms of anthracnose in oak-hickory and, perhaps, oak-pine forests. Other forest types, such as cove and alluvial forests, where *C. florida* was once a frequent component (Jenkins and White 2002) burned infrequently, if at all, in the past. Therefore these forest types are unlikely to sustain fire frequencies of 10-15 years; the frequency that appears to best reduce the effects of anthracnose. Although this study was conducted in GSMNP, we believe that its methods and results are applicable across the eastern United States in forest types that contain *C. florida* and have regimes of relatively frequent fire.

It is unlikely, however, that burning could be returned to all oak-hickory and oak-pine forests due to many external factors such as time and budget constraints and management objectives. Consequently, certain areas may be deemed higher in priority for burning. These areas include currently uninfected stands that are in close proximity to infected areas, stands only recently showing signs of infection, or infected stands with large *C. florida* populations. Land managers would be more successful using prescribed

burning in maintaining *C. florida* populations than attempting to reintroduce *C. florida* to areas where it once occurred.

Conclusion

The results of our study suggest that burning has reduced the impacts of anthracnose on *C. florida* populations. Burned stands, especially double burn stands, had significantly greater *C. florida* stem densities than unburned stands. In addition, the density of *T. canadensis*, a species that creates stand conditions favorable for dogwood anthracnose, was greatly reduced in burned stands. Past burning did not drastically affect overall overstory or understory species composition, but the importance values of selected overstory and understory species were highly indicative of specific burn frequencies. The results indicate that prescribed burning may offer an effective and practical technique to control the impacts of dogwood anthracnose and prevent the loss of *C. florida* from oak-hickory forests.

Table 2-1. Scales for foliage health (% of foliage with signs of anthracnose) and crown dieback (% of crown dieback) used to assess the level of disease severity of dogwood anthracnose on *Cornus florida* trees (based on the Mielke-Langdon Index, Mielke and Langdon 1986).

Rating	Foliage health	Crown dieback
1	>76	>76
2	51-75	51-75
3	26-50	26-50
4	1-25	1-25
5	none	none

Table 2-2. Mean foliage and crown health (± 1 SE) for *Cornus florida* for five diameter classes in the four different sampling categories using the Mielke-Langdon Index (Mielke and Langdon 1986).

Diameter class (cm)	Single burn	Double burn	Triple burn	Unburned	P-value[1]
Foliage Health					
0 - 1.0	3.6 (0.2)	3.5 (0.2)	3.1 (0.3)	A[3]	0.38
1.1 - 2.5	3.6 (0.2)	3.6 (0.2)	3.6 (0.2)	3.7 (0.3)	0.94
2.6 - 5.0	3.6 (0.2)	3.8 (0.2)	3.6 (0.3)	3.7 (0.3)	0.88
5.1 - 10.0	3.8 (0.1)	3.7 (0.1)	3.9 (0.2)	3.8 (0.3)	0.90
>10.1	3.6 (0.3)	3.6 (0.2)	3.7 (0.2)	3.6 (0.3)	0.99
Crown Dieback					
0 - 1.0	3.2 (0.3)	3.5 (0.3)	3.0 (0.5)	A	0.63
1.1 - 2.5	3.3 (0.2) [a2]	3.4 (0.2) [a]	3.3 (0.3) [a]	2.4 (0.3) [b]	0.04
2.6 - 5.0	3.3 (0.1) [a]	3.6 (0.2) [a]	3.2 (0.2) [a]	2.7 (0.3) [b]	0.01
5.1 - 10.0	3.3 (0.1)	3.4 (0.2)	3.7 (0.2)	3.3 (0.3)	0.45
>10.1	3.5 (0.4)	3.7 (0.4)	3.4 (0.5)	3.2 (0.3)	0.93

[1] P-value from ANOVA

[2] Means followed by the same letter in the same row are not statistically different ($P < 0.05$) using post-hoc pairwise comparisons among sampling categories when ANOVA P-value < 0.05

[3] A = Absent, no trees from this sampling category were found in this size class

Table 2-3. Mean understory and overstory basal area and stem density (± 1 SE) in the four sampling categories.

Understory	Basal Area (m^2 ha^{-1})	Stem density (stems ha^{-1})
Single burn	7.1 (0.5)	2851 (360) [b2]
Double burn	6.9 (0.7)	4594 (726) [a]
Triple burn	6.5 (1.0)	5072 (1090) [a]
Unburned	7.4 (0.4)	2292 (274) [b]
P-value	0.93[1]	0.024
Overstory		
Single burn	21.7 (0.8)	436 (31) [b]
Double burn	22.1 (1.1)	323 (46) [c]
Triple burn	20.6 (1.8)	317 (43) [c]
Unburned	23.2 (0.8)	564 (25) [a]
P-value	0.52	<0.0001

[1] P-value from ANOVA

[2] Means followed by the same letter in the same column for understory and overstory are not statistically different ($P < 0.05$) using post-hoc pairwise comparisons among sampling categories when ANOVA P-value < 0.05

Table 2-4. Mean species richness and Shannon's diversity index (± 1 SE) for the understory and overstory in the four sampling categories.

Understory	Species richness	Shannon's diversity index
Single burn	11.4 (0.9)	1.9 (0.08)
Double burn	11.0 (1.3)	1.9 (0.11)
Triple burn	13.5 (1.5)	2.0 (0.12)
Unburned	10.7 (1.0)	1.9 (0.09)
P-value	0.48[1]	0.81
Overstory		
Single burn	5.7 (0.4)	1.3 (0.09)
Double burn	5.4 (0.5)	1.2 (0.12)
Triple burn	5.2 (0.7)	1.2 (0.14)
Unburned	6.9 (0.4)	1.4 (0.09)
P-value	0.06	0.48

[1] P-value from ANOVA

Table 2-5. Overstory and understory indicator values (IndVal) (percent of perfect indication) and associated sampling category. P-value represents the proportion of randomized trials that the indicator value was equal to or exceeded the observed indicator value.

Species	IndVal	P-value	Indicator group
Overstory			
Acer rubrum	32.2	0.080	Unburned
Oxydendrum arboreum	29.8	0.073	Unburned
Quercus alba	47.4	0.001	Double burn
Quercus velutina	29.7	0.026	Triple burn
Tsuga canadensis	36.0	0.006	Unburned
Understory			
Carya alba	46.0	0.001	Triple burn
Carya glabra	42.6	0.012	Triple burn
Cornus florida	40.2	0.015	Double burn
Pinus virginiana	31.5	0.018	Triple burn
Quercus alba	18.9	0.065	Triple burn
Quercus prinus	37.8	0.033	Triple burn
Quercus rubra	42.5	0.002	Triple burn
Quercus velutina	22.3	0.076	Triple burn
Robinia pseudoacacia	42.9	0.005	Triple burn
Tilia americana	18.7	0.023	Double burn
Tsuga canadensis	46.9	0.007	Unburned

Table 2-6. Mean importance values (± 1 SE) of selected understory species in the four sampling categories.

Species	Single burn	Double burn	Triple burn	Unburned
Acer pensylvanicum	9.6 (5.5)	3.5 (7.3)	A	9.8 (6.0)
Acer rubrum	24.2 (3.3) [a]	17.8 (4.4) [ab]	7.8 (1.8) [b]	19.2 (3.6) [ab]
Carya alba	0.9 (0.9) [a]	2.0 (1.8) [a]	7.0 (1.5) [b]	2.1 (1.0) [a]
Carya glabra	1.6 (1.0) [a]	1.8 (2.5) [a]	10.3 (2.0) [b]	2.5 (1.2) [a]
Cornus florida	12.1 (2.3) [a]	21.6 (3.2) [b]	14.8 (4.2) [ab]	5.1 (2.6) [c]
Halesia tetraptera	3.2 (1.7)	3.4 (2.4)	A	1.8 (1.9)
Kalmia latifolia	5.3 (3.6)	2.8 (4.8)	5.4 (6.0)	6.6 (4.0)
Liriodendron tulipifera	4.9 (1.6) [a]	2.4 (2.2) [ab]	0.3 (2.6) [ab]	0.4 (1.8) [b]
Nyssa sylvatica	6.4 (1.8) [ab]	9.6 (2.3)	0.9 (3.1) [a]	6.1 (1.9) [ab]
Oxydendrum arboreum	6.3 (1.7)	7.3 (2.3)	6.4 (2.9)	5.2 (1.9)
Pinus strobus	3.1 (2.0)	1.6 (2.6)	A	4.9 (2.2)
Pinus virginiana	0.2 (0.7) [a]	0.8 (0.9) [ab]	2.5 (1.1) [b]	1.1 (0.8) [ab]
Quercus prinus	3.8 (1.0)	1.3 (1.4)	3.0 (2.2)	2.4 (1.2)
Quercus rubra	0.7 (0.3) [a]	0.8 (0.4) [ab]	2.0 (0.6) [b]	0.1 (0.4) [a]
Quercus velutina	0.5 (0.7) [a]	0.6 (0.9) [a]	3.1 (1.0) [b]	0.4 (0.8) [a]
Rhododendron maximum	4.3 (2.3)	0.3 (3.1)	2.0 (3.8)	4.1 (2.5)
Robinia pseudoacacia	1.3 (0.9) [a]	2.0 (1.2) [a]	6.4 (1.6) [b]	0.2 (1.0) [a]
Sassafras albidum	1.5 (0.7)	1.1 (0.9)	2.9 (1.2)	1.3 (0.8)
Tsuga canadensis	0.9 (2.6) [a]	0.5 (3.5) [a]	0.3 (4.2) [a]	9.9 (2.8) [b]

[1] Means followed by the same letter in the same row are not statistically different ($P < 0.1$) using post-hoc pairwise comparisons among sampling categories when ANOVA P-value < 0.05

[2] A = Absent, no trees from this sampling category were found in this size class

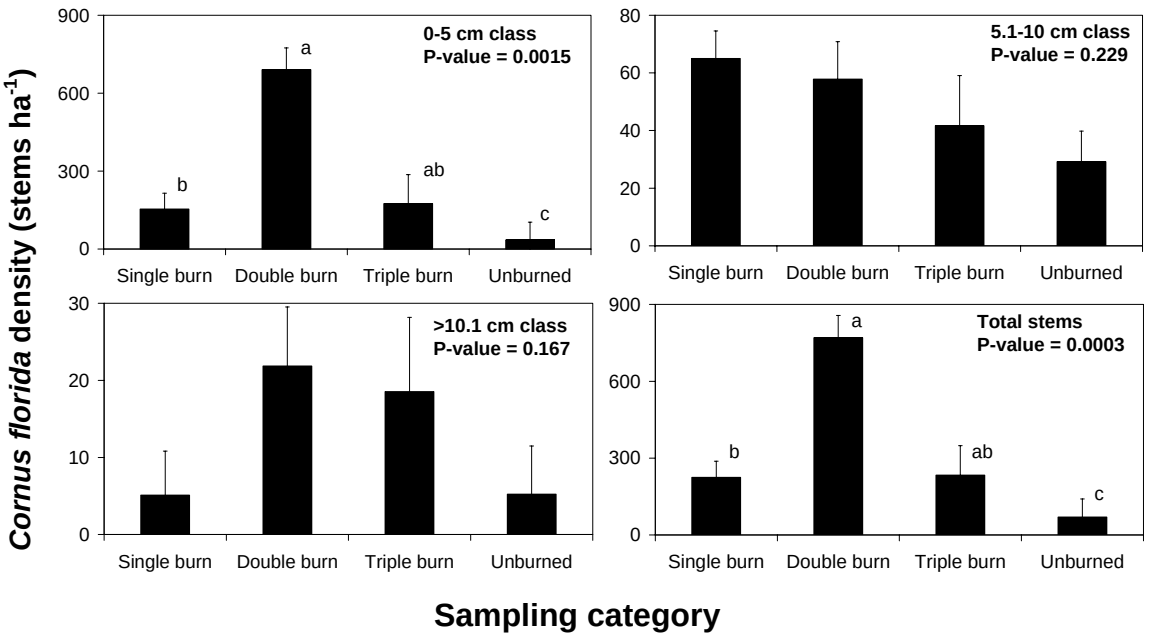

Figure 2-1. Mean *Cornus florida* stem density (± 1 SE) in the four sampling categories for three diameter classes and total stems ha^{-1} for all diameter classes. Within each graph, P-value is from ANOVA, and bars with same letters are not significantly different from each other ($P < 0.05$) using post-hoc pairwise comparisons among sampling categories when ANOVA P-value < 0.05; note the scale of the y-axis for each graph.

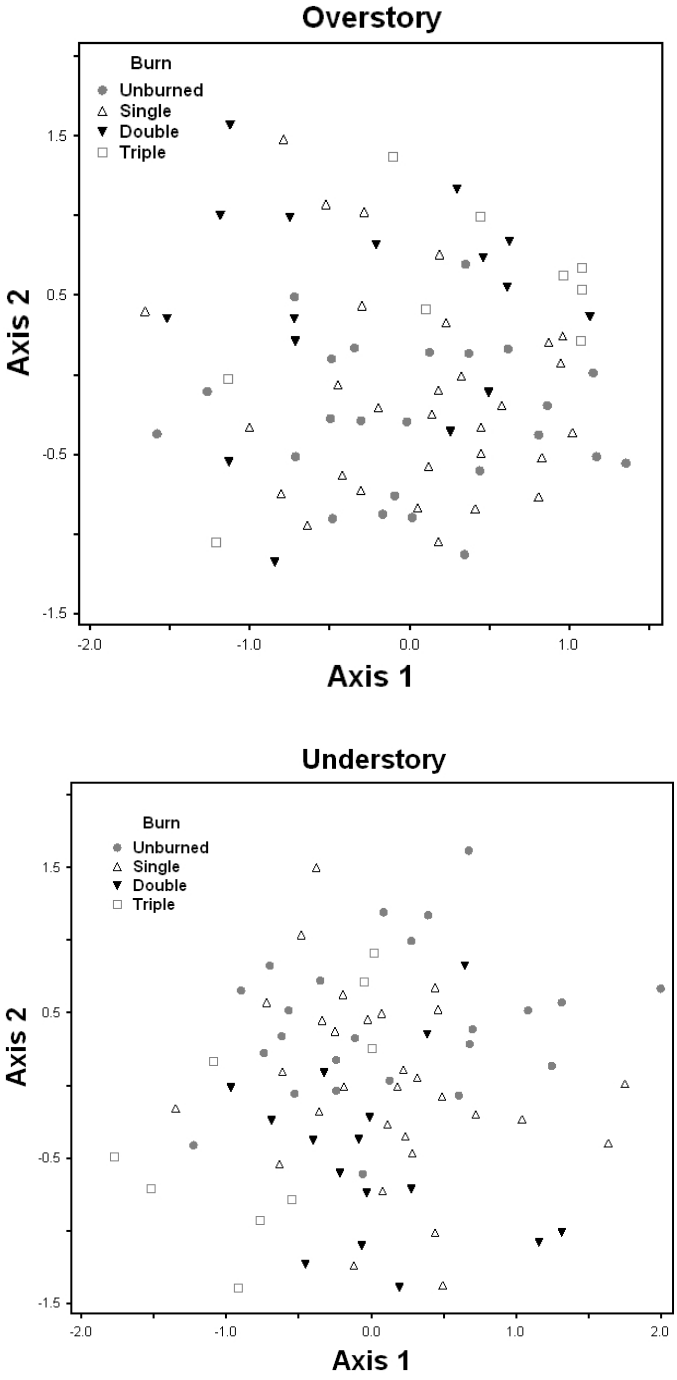

Figure 2-2. Nonmetric multidimensional scaling sample ordination of overstory and understory communities, showing the relative differences in community composition separated by sampling categories. Graphs indicate a lack of distinct compositional changes in overstory or understory with respect to burn frequency.

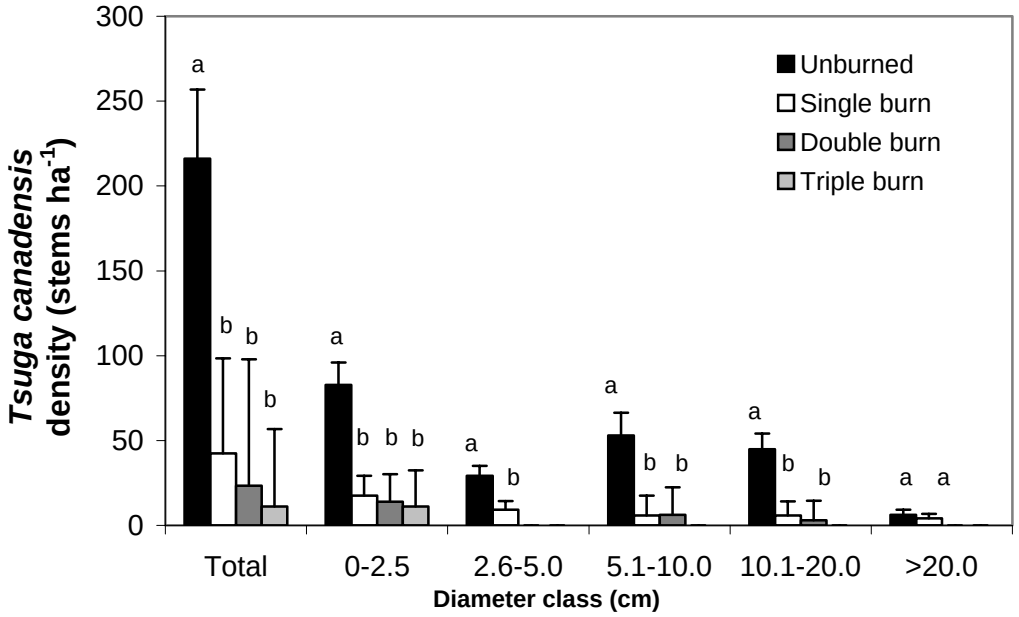

Figure 2-3. Mean *Tsuga canadensis* stem density (± 1 SE) in five diameter size classes and total (all diameter classes combined) in the four sampling categories. Same letters in each diameter class represent no significant differences in mean stems ha^{-1} ($P < 0.05$) using post-hoc pairwise comparisons among sampling categories when ANOVA P-value < 0.05.

CHAPTER 3
INFLUENCE OF CALCIUM, POTASSIUM, AND MAGNESIUM ON *Cornus florida* L. DENSITY AND RESISTANCE TO DOGWOOD ANTHRACNOSE

Introduction

Dogwood anthracnose, caused by the fungus *Discula destructiva* Redlin, is a major disease of *Cornus florida* L. in forests of the eastern United States. Where dogwood anthracnose is present, mortality rates of *C. florida* have been up to 90% (Sherald et al. 1996, Hiers and Evans 1997). The fungus causes leaf necrotic blotches, leaf blight, twig dieback, and stem cankers, which eventually lead to tree death (Hibben and Daughtery 1988). Disease severity and rate of infection, however, vary with several environmental factors. The disease is most severe in cool, wet areas of high elevation with shaded slopes (Chellemi et al. 1992). Within individual stands, disease severity increases with decreased light availability, increased moisture, and decreased evaporative potential of the leaf surface (Chellemi and Britton 1992).

While the link between mineral nutrition and resistance to dogwood anthracnose has not been examined in detail, soil availability of cations may reduce the impacts of the disease and increase the survival of *C. florida* trees. Britton et al. (1996) found that disease severity did not increase with application of pH 2.5 simulated rain to the foliage, but did increase with application of pH 2.5 simulated rain to the growing medium. Consequently, the increase in the severity of infection was attributed to nutrient bioavailability, not foliar damage. However, since soil nutritional changes were not quantified, this hypothesis still remains unproven. In a review of calcium (Ca) physiology

and terrestrial ecosystem processes, McLaughlin and Wimmer (1999) hypothesized that low Ca saturation decreases the natural resistance of *C. florida* to dogwood anthracnose. Anderson et al. (1991) reported that liming reduced disease severity of anthracnose on ornamental *C. florida* trees.

While the link between soil cation availability and anthracnose has not been examined, calcium applications have been shown to reduce the impacts of fungal disease on soybeans (*Glycine max* (L.) Merr.) and bacterial wilt on tomato (*Lycopersicon esculentum* L.) seedlings (Muchovej et al. 1980, Sugimoto et al. 2005, Yamazaki et al. 1999). Other cations, particularly potassium (K) and magnesium (Mg), have also been linked to disease resistance in plants. Sij et al. (1985) reported that increased rates of K fertilizer significantly decreased the impacts of a fungal disease on field grown soybean plants. Jeffers et al. (1982) reported lower numbers of seeds infected with seed mold on tomato plants fertilized with K. Likewise, the severity of fungal shoot blight was greater on *Picea abies* (Norway spruce) trees whose needles contained low levels of Mg (Anglberger and Halmschlager 2003).

Calcium, K, and Mg play essential roles in plant growth and development (Epstein 1972, Mengel et al. 2001). Calcium strengthens plant cell walls, which may help in disease resistance (Muchovej et al. 1980, Conway et al. 1992, Sugimoto 2005). Potassium and Mg are essential for many plant metabolic functions (Epstein 1972, Mengel et al. 2001). Disease resistance with optimal K and Mg nutrition may be attributed to increased energy used to offset the impact of plant diseases (Mengel et al. 2001). In addition, K may also increase disease resistance by increasing the thickness of outer walls in epidermal cells (Mengel et al. 2001)

The objective of this chapter was to determine whether the availability of soil cations (Ca, K, and Mg), influence the health and survival of *C. florida.* Because high levels of Ca, K, and Mg have been associated with fungal disease resistance in other plant species, we hypothesize (hypothesis 1) that forested stands with high densities of *C. florida* trees would have higher concentrations of these cations in the soil. We further hypothesize (hypothesis 2) that additional input of soil cations decreases disease severity of dogwood anthracnose on *C. florida*.

Materials and Methods

Study Site

This study was conducted in Great Smoky Mountains National Park (GSMNP), USA. Great Smoky Mountains National Park straddles the Tennessee and North Carolina state line, encompassing slightly over 200 000 ha in the southern Appalachian Mountains. The varied geology and topographic structure of GSMNP results in a wide-range of soil conditions and associated vegetation communities. Mean annual temperature in Gatlinburg, Tennessee (440 m a.s.l. and adjacent to GSMNP) is 12.9° C and mean annual precipitation is 142 cm. Our study sites ranged in elevation from 287 to 975 m. Although *C. florida* occurs in a variety of forest types, from mesic coves to xeric oak-pine woodlands, we focused our study on oak-hickory forests on moderately steep to steep slopes with southeast-south-northwest facing aspects. Oak-hickory is a major forest type in GSMNP, covering 43,337 ha, (21% of the Park's total forest cover; Madden et al. 2004) and prior to anthracnose *C. florida* was the dominant woody species in the understory (Jenkins and White 2002).

Forest Soil Sampling

During June-August of 2001-2004 soil samples were collected from seventy-nine long-term vegetation plots (20 m x 20 m; 0.04 ha) established in twenty oak-hickory stands in GSMNP. *Cornus florida* stem density in the stands ranged from 0 to 1150 stems ha^{-1} and basal area ranged from 0 to 0.7 m^2 ha^{-1}. Mineral soil was collected from four random locations within each plot and then pooled together to create one composite sample per plot. Samples were collected by scraping away the forest floor and collecting the top 10 cm of mineral soil (A and upper B horizons).

Lab Analysis

Samples were analyzed for soil Ca, K, and Mg by A&L Analytical Laboratories, Inc., Memphis, Tennessee and respective soil cation saturation (%) was calculated. Samples were dried at 36° C for 6 hours, and then sieved through a 2 mm sieve. A 3 g sample of dried soil was shaken with 30 mL of Mehlich III extracting solution (Mehlich 1984) for 5 minutes and then centrifuged. The solution was analyzed for Ca, K, Mg, and Na by using an inductively coupled plasma emission spectrometer. Exchangeable hydrogen (H) was calculated by leaching 5 g of dried soil with, 20 mL of 0.2 M triethanolamine and 0.25 M barium chloride buffer solution (pH 8.1), then by 20 mL of 0.25 M barium chloride solution. The amount of standard acid needed to back titrate the leachate to the methyl red and bromcresol green endpoint was used to calculate the concentration of exchangeable acidity. Cation exchange capacity (CEC) was determined by the summation of exchangeable base cations (Ca, K, Mg, and Na) and exchangeable H. Soil cation saturation was calculated as the percentage of the respective cation that contributed to total CEC.

Potted Plant Experiment

We tested the influence of three cations (Ca, K, and Mg) on *C. florida* seedling survival and resistance to dogwood anthracnose by using a potted plant experiment. Six hundred 1-0 bareroot *C. florida* seedlings were purchased from a commercial nursery in Bartow, Florida, located approximately 65 km east of Tampa, Florida. Dogwood anthracnose has not been reported in Florida; therefore these seedlings were presumed to be disease free and showed no evidence of anthracnose infection before the experiment began. The 1-0 seedlings were transplanted into three-gallon pots in a 40% Florida peat, 40% pine bark, and 20% sand mixture and grown in a nursery for one year. The seedlings were watered every other day during the growing season. During the transplant into the three-gallon pots, the seedlings were randomly selected to receive one of twelve fertilization treatments. The treatments included three cations (Ca, K, and Mg) at four levels (0, 50, 100, and 200%) of a standard nursery fertilization rate. Fertilization mixes for the twelve treatments were mixed separately at the nursery using a base mix (Table 3-1) with the addition of the appropriate amount of Ca, K, and Mg to create the required treatments (Table 3-2). The seedlings were fertilized three times; the first fertilization treatment was at the time of transplant (May 2003), the second was in October 2003, and the final fertilization treatment was in March 2004, before leaf onset occurred. Depending on the treatment, 59 to 68 g (base rate + the treatment addition) of fertilizer was placed within each pot during each fertilization period.

In April 2004, the seedlings were transported to Twin Creeks Natural Resources Center in GSMNP (35° 42’ 51”N, 83° 30’ 37”W). Dogwood anthracnose has been widely reported in GSMNP, and heavy *C. florida* dieback has been reported in every forest type

where *C. florida* is found (Jenkins and White 2002). Seedlings were placed under infected *C. florida* trees in a 70 year-old *Liriodendron tulipifera* L. and *Acer rubrum* L. stand. This allowed *C. florida* trees infected with dogwood anthracnose to serve as a source of natural inoculum (Britton et al. 1996). All seedlings were placed directly underneath the *C. florida* canopy in a randomized complete block design with four blocks.

Foliage samples were collected from the *C. florida* seedlings one day prior to inoculation to test for foliar nutrient concentration. After collection, samples were dried in an oven at 65º C for 72 hours and then ground using a tissue grinder. Analysis of foliage samples was performed using an inductively coupled plasma emission spectrometer (ICPES) at the University of Florida Analytical Research Lab (Gainesville, Florida). A 750 mg sample of dried plant material was weighed into a 20 mL high form silica crucible and dry ashed at 485° C for 12 hours. The ash was equilibrated with 5 mL of 20% HCl at room temperature for 30 minutes. Then 5 mL of deionized water was added, gently swirled and the sample was allowed to settle for 3 hours. The solution was decanted into a 15 ml plastic vial for direct determination by ICPES. Results of tissue concentrations are presented in mg g^{-1}.

Seedlings were measured for height and root collar diameter in April 2004 before inoculation and no significant differences were found among treatments ($P > 0.36$). After inoculation, seedling foliage was assessed every 2 weeks for presence of anthracnose. Any nonanthracnose lesions were disregarded. We used a scale based on the Mielke-Langdon index (Mielke and Langdon 1986) to assess disease severity on the seedlings (Table 3-3).

Statistical Analysis

Forest Soil

In order to reduce plot variability found in the forest soil data, plot values were averaged together for each stand. We then used linear regression models to describe the relationship between soil cation saturation (Ca, K, and Mg) and *C. florida* stem density and basal area. All statistical analyses were done using SAS (SAS 2002).

Potted Plant Experiment

In the potted plant experiment, ANOVA was conducted to test for differences in infection ratings among the treatments. When ANOVA revealed significant main effects, we separated the means with post-hoc pairwise comparisons. A logistical model was used to test for differences in seedling mortality at the end of the experiment. We used curvilinear regression to describe the relationship between *C. florida* tissue concentration of Ca, K, and Mg to fertilization input. All statistical analyses were done using SAS (SAS 2002).

Results

Forest Soil Cation Saturation

We found significant positive correlations between the three cations (Ca, K, and Mg) and *C. florida* stem density and basal area. Soil Ca saturation ranged from 5.7 - 26.3% and exhibited the strongest relationship of the three cations with *C. florida* stem density ($R^2 = 0.70$, $P < 0.0001$; Figure 3-1). Soil Mg saturation ranged from 2.3 - 8.2% and soil K saturation ranged from 2.0 - 5.0%. We also found significant relationships of soil K saturation ($R^2 = 0.54$, $P < 0.001$; Figure 3-2) and soil Mg saturation ($R^2 = 0.62$, $P < 0.0001$; Figure 3-3) with *C. florida* stem density.

When *C. florida* basal area was used as the independent variable, R^2 and P-values decreased for every cation. The strongest relationship was observed between soil Ca saturation and *C. florida* basal area ($R^2 = 0.59$, $P = 0.001$; Figure 3-1). A weak relationship was observed between soil K saturation and *C. florida* basal area ($R^2 = 0.23$, $P = 0.08$; Figure 3-2), but a significant relationship was observed between soil Mg saturation and *C. florida* basal area ($R^2 = 0.45$, $P = 0.008$; Figure 3-3)

Potted Plant Experiment

Calcium Treatments

Among the four levels in the Ca treatments, the seedlings did not show a significant difference among treatments until 6 weeks after inoculation. After 6 weeks, the 0% treatment had the lowest (less healthy) infection rating (Table 3-4). Eight weeks after inoculation, all treatments except for the 100% treatment, which had a higher (healthier) infection rating, were statistically the same ($P > 0.19$; Table 3-4). This trend continued until the end of the experiment. At the end of the experiment, mortality for the Ca treatments ranged from 62 - 100% and was significantly different among the four treatments ($P = 0.0013$; Figure 3-4). The 0% and 200% Ca treatments had 100 and 87% mortality, respectively, which was significantly greater than the 72% mortality observed in the 50% Ca treatment and 62% mortality observed in the 100% Ca treatment ($P < 0.05$).

Potassium Treatments

Seedlings in the K treatments began to show significant differences in infection ratings 4 weeks after inoculation ($P = 0.025$; Table 3-4). Throughout the experiment, the 0% treatment had the lowest (less healthy) infection rating and the highest mortality (Table 3-4 and Figure 3-4). The 100% treatment had a high (healthier) infection rating in

the beginning of the experiment and after 10 weeks was significantly higher (healthier) than all other treatments ($P < 0.02$; Table 3-4). After 14 weeks, there were no significant differences in infection ratings among the four K treatments ($P = 0.44$) and by the end of the experiment (24 weeks) all treatments had suffered heavy mortality (> 85%, $P = 0.26$; Figure 3-4).

Magnesium Treatments

There appeared to be very little difference in the anthracnose infection ratings among the Mg treatments. Infection ratings were similar throughout the experiment; however, the 200% treatment did have slightly lower (less healthy) infection ratings in weeks 4 and 6 (Table 3-4). After 10 weeks there were no significant differences among treatments ($P = 0.17$; Table 3-4), and at the end of the experiment there were no significant differences in mortality among the four Mg treatments (> 88%, $P = 0.26$; Figure 3-4).

Foliar Cation Concentrations

Mean Ca concentration in the foliage of the Ca treatments ranged from 3.59 mg g^{-1} (0% treatment) to 3.66 mg g^{-1} (100% treatment). There was not a significant relationship between foliar Ca concentration and Ca input, perhaps due to the high sample variability ($R^2 = 0.17$, $P = 0.43$; Figure 3-5). In the K treatments, mean K concentration was highest in the 100% treatment (2.05 mg g^{-1}) and lowest in the 0% and 200% treatments (1.76 and 1.77 mg g^{-1}, respectively). The relationship between K concentration and K input was significant ($R^2 = 0.61$, $P = 0.02$; Figure 3-5). In the Mg treatments, Mg concentration was greatest in the 50% treatment (0.83 mg g^{-1}) and lowest in the 200% treatment (0.72 mg g^{-1}). In general, after peaking in the 50% treatment, Mg concentration decreased as input

increased in the Mg treatments although the relationship was weak ($R^2 = 0.40$, $P = 0.098$; Figure 3-5).

Discussion

We found significant positive correlations between *C. florida* (stem density and basal area) and soil Ca, K, and Mg saturation. Although correlation does not imply causation, there are several possible explanations for these strong correlations. One explanation is that higher soil cation concentrations help maintain healthy *C. florida* populations even in the presence of dogwood anthracnose. Because these nutrients are readily available in the forest soil, there is a decrease in inter and intraspecific competition for nutrient resources. This enables *C. florida* to obtain more nutrients to be used for plant defense and allocate more resources to developing stronger cells walls to resist infection of *D. destructiva*. The higher nutritional status could also help in replacing lost foliage and or repairing stem cankers arising from anthracnose infections.

It is also reasonable to argue that nutrient levels are greater on high *C. florida* stem density sites because of the presence of *C. florida*. Multiple studies have shown the influence of individual species on forest floor and mineral soil nutrient levels (Dijkstra and Smits 2002, Washburn and Arthur 2003, Fujinuma et al. 2005), which occurs through several different mechanisms. Certain species are able to uptake higher levels of nutrients than others and secure nutrients in biomass before they are lost through soil leaching (Dijkstra and Smits 2002). Another mechanism is the influence of plant species on chemical weathering of the soil by modifying soil acidity (Augusto et al. 2000). It has been hypothesized that because of the high Ca concentration and rapid decomposition of *C. florida* foliage (Blair 1988, Knoepp et al. 2005) compared to other associated species, *C. florida* acts as a "Ca pump" in forest soils (Thomas 1969). In addition to high

concentration of Ca in *C. florida* foliage, studies performed in western North Carolina found that *C. florida* foliage contained high concentrations of K and Mg compared to other species in oak hardwood forests (Day and Monk 1977, Elliot et al. 2002; Table 3-5). High levels of these nutrients, particularly Mg, compared to other species were also found in the wood, twigs, and bark of *C. florida* (Day and Monk 1977). High soil K and Mg saturation in stands with high densities of *C. florida* indicates that this species may also be acting as K and Mg "pumps" as well. It is possible that these two hypotheses are not independent of each other.

The results of our potted plant experiment showed greater inputs of Ca and K cations slowed the rate of anthracnose infection. We observed differences in the rates of infection over the 6 month period with respect to the treatments. Calcium nutrition has been linked to the resistance of many plant species to fungal and bacterial diseases (Muchovej et al. 1980, Yamazaki et al. 1999, Sugimoto et al. 2005). Calcium plays a key role in development of plant cell walls (Epstein 1972, Mengel et al. 2001) and studies suggest that disease severity is reduced due to increased Ca concentrations in cell walls (Muchovey et al. 1980, Conway et al. 1992, Sugimoto 2005). In our experiment, seedlings in the 100% Ca treatment exhibited fewer signs of anthracnose and lower mortality compared to 0% and 200% Ca treatments throughout the experiment. At the end of the experiment, mortality for the Ca treatments were significantly greater in the 0% and 200% treatment compared to the 50% and 100% treatments. This indicates that Ca availability is an important factor in *C. florida* resistance to dogwood anthracnose. However, we did not see a relationship between foliar Ca concentration and Ca inputs.

Perhaps the high variability in foliar Ca concentration within each treatment precluded a significant relationship (Figure 3-3).

Potassium is a macronutrient essential to the performance of multiple plant enzyme functions (Epstein 1972, Mengel et al. 2001). Studies have indicated higher disease resistance with increased levels of K (Jeffers et al. 1982, Sij et al. 1985), which, although the mechanisms are not completely understood, may be attributed to increased energy and epidermal wall thickness (Mengel et al. 2001). In our experiment, the 100% K treatment had a healthier infection rating in the early weeks of the experiment. After 10 weeks, the infection rating was still significantly healthier than all other treatments. The 100% K treatment also had the highest foliar concentration of K compared to other K treatments (Figure 3-3). Therefore, increased disease resistance may be attributed to increased K foliar concentration. Despite the additional K inputs in the 200% K treatment, this treatment had lower K foliar concentration levels and unhealthier infection ratings compared to the 100% K treatment. Decreased foliar concentration in the 200% K treatment compared to the 100% K treatment can be attributed to nutrient imbalances created by excess soil K; similar results have been reported by Wilmot et al. (1996).

Although we found a significant relationship between *C. florida* density and soil Mg saturation, it did not appear that Mg input had any effect on disease severity or mortality. Other studies of plant disease have found similar results (Nwoboshi 1980, Wisniewski et al. 1995). Nwoboshi (1980) found that Mg fertilization rates had no effect on the resistance of *Manihot esculenta* L. (cassava) to anthracnose. Wisniewski et al. (1995) reported that Mg did not inhibit the germination or growth of two fungal diseases, *Botrytis cinerea* Pers. or *Penicillium expansum* Link, whereas increased Ca

concentrations decreased spore germination and growth of both pathogens. Although Anglberger and Halmschlager (2003) reported that severity of *Sirococcus* shoot blight decreased on *P. abies* trees that had needles with high levels of Mg, in our experiment we found that the treatment that produced the highest concentration of foliar Mg (50% treatment) fared just as poorly as the other treatments.

Overall, all treatments suffered heavy mortality by the end of the growing season after they were exposed to *D. destructiva* (62-100%; Figure 3-2). This is not particularly surprising considering the fact that multiple studies have shown smaller trees to be very susceptible to the disease and often die within the first year of to exposure the disease (Mielke and Langdon 1986, Hibben and Daughtery 1988, Hiers and Evans 1997). In addition, it should be noted that the 2004 growing season (year of the potted plant experiment) had above average precipitation in GSMNP (National Climatic Data Center 1999-2004; Figure 3-6) and dogwood anthracnose throughout the Park was virulent (personal observation). The overwhelming presence of the disease might have decreased some of the differences among the treatments. Dogwood anthracnose is a disease that is most severe in cool, moist, and heavily shaded conditions (Chellemi and Britton 1992, Chellemi et al. 1992, Britton 1993), and higher levels of mortality have been reported in mesic forests compared to xeric forests (Jenkins and White 2002).

Britton (1993) reported that given adequate amounts of rainfall, dogwood anthracnose could develop throughout the growing season. Factors affecting relative humidity and evaporative potential of leaf surfaces in a stand, such as stand density, slope, and elevation, probably influence impacts of dogwood anthracnose on *C. florida* more than nutrient conditions. We still conclude, however, that low availability of Ca and

K in forested stands containing *C. florida* increases the susceptibility of *C. florida* to dogwood anthracnose. Decreased nutrient availability in eastern forests from acid deposition (Likens et al. 1996, McLaughlin and Wimmer 1999) has likely had a negative impact on remaining *C. florida* populations, which may further inhibit the annual calcium cycling of cations by *C. florida* (Holzmueller et al. 2006c).

Conclusion

The results of this project indicate that there is a correlation between soil cation saturation (Ca, K, and Mg) and *C. florida* stem density and basal area in oak-hickory forests. High concentrations of these cations in *C. florida* foliage suggest that this species may play an important role in nutrient cycling by acting as a "pump" that draws cations from deeper in a soil profile and cycles them through the forest floor and surface soil. The results of this project also suggest that increased levels of Ca and K in the soil may lead to increased resistance to dogwood anthracnose. We conclude that soil fertility in forest stands should not be overlooked when applying management techniques to reduce the impacts of dogwood anthracnose.

Table 3-1. Content of the base fertilizer mix.

Element	Rate (%)
NH_4	6.8
NO_3	5.2
P_2O_5	6.0
AgSul 90	6.2
$FeSO_4$	0.8
$MnSO_4$	0.3
$ZnSO_4$	0.1
$CuSO_4$	0.05

Table 3-2. Inputs (%) added to the base fertilizer mix (separately) for each treatment.

Treatment	Calcium ($CaSO_4$) rate (%)	Potassium (K_20) rate (%)	Magnesium ($MgSO_4$) rate (%)
Ca 0%	**0.0**	8.0	1.8
Ca 50%	**0.75**	8.0	1.8
Ca 100%	**1.5**	8.0	1.8
Ca 200%	**3.0**	8.0	1.8
K 0%	1.5	**0.0**	1.8
K 50%	1.5	**4.0**	1.8
K 100%	1.5	**8.0**	1.8
K 200%	1.5	**16.0**	1.8
Mg 0%	1.5	8.0	**0.0**
Mg 50%	1.5	8.0	**0.9**
Mg 100%	1.5	8.0	**1.8**
Mg 200%	1.5	8.0	**3.6**

Table 3-3. Scale used to assess the severity of dogwood anthracnose infection on the foliage of *Cornus florida* seedlings. Scale was based on the Mielke-Langdon Index (Mielke and Langdon 1986).

Rating	% of foliage with signs of anthracnose
0	Dead
1	76-100
2	51-75
3	26-50
4	1-25
5	0

Table 3-4. Biweekly infection ratings for *Cornus florida* seedlings for length of the experiment.

Treatment	Week 2	Week 4	Week 6	Week 8	Week 10	Week 12	Week 14	Week 16	Week 18	Week 20	Week 22	Week 24
Ca												
0%	3.9 [a1]	3.5 [a]	2.8 [a]	2.5 [a]	1.5 [a]	1.1 [a]	0.8 [a]	0.6 [a]	0.4 [a]	0.1 [a]	0.1 [a]	0.0 [a]
50%	3.8 [a]	3.8 [a]	3.4 [b]	2.9 [ab]	1.9 [a]	1.6 [a]	1.4 [ab]	1.1 [ab]	1.1 [ab]	0.7 [ab]	0.6 [ab]	0.4 [ab]
100%	3.8 [a]	3.8 [a]	3.4 [b]	3.2 [b]	2.8 [b]	2.3 [b]	1.7 [b]	1.3 [b]	1.2 [b]	0.8 [b]	0.7 [b]	0.4 [b]
200%	3.8 [a]	3.6 [a]	3.0 [a]	2.7 [a]	1.8 [a]	1.3 [a]	0.9 [a]	0.8 [a]	0.7 [a]	0.3 [a]	0.3 [a]	0.2 [a]
SE	0.1	0.1	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.1	0.1	0.1
K												
0%	4.0 [a]	3.3 [a]	2.5 [a]	1.3 [a]	0.8 [a]	0.6 [a]	0.5 [a]	0.3 [a]	0.1 [a]	0.1 [a]	0.1 [a]	0.1 [a]
50%	3.8 [a]	3.6 [b]	2.9 [ab]	1.8 [b]	1.1 [a]	0.9 [ab]	0.6 [a]	0.4 [a]	0.4 [a]	0.3 [a]	0.3 [a]	0.2 [a]
100%	3.8 [a]	3.7 [b]	3.2 [b]	2.0 [b]	1.7 [b]	1.2 [b]	0.7 [a]	0.6 [a]	0.5 [a]	0.3 [a]	0.2 [a]	0.2 [a]
200%	4.0 [a]	3.7 [b]	3.2 [b]	1.7 [a]	1.2 [a]	0.8 [ab]	0.6 [a]	0.4 [a]	0.4 [a]	0.2 [a]	0.2 [a]	0.2 [a]
SE	0.1	0.1	0.2	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1
Mg												
0%	3.9 [a]	3.9 [a]	3.4 [a]	2.1 [a]	1.6 [a]	0.9 [a]	0.6 [a]	0.5 [a]	0.5 [a]	0.3 [a]	0.2 [a]	0.2 [a]
50%	3.8 [a]	3.6 [ab]	3.0 [ab]	1.9 [ab]	1.2 [a]	0.9 [a]	0.6 [a]	0.4 [a]	0.3 [a]	0.1 [a]	0.1 [a]	0.1 [a]
100%	3.7 [a]	3.8 [a]	3.4 [a]	2.4 [a]	1.6 [a]	1.2 [a]	1.0 [a]	0.8 [a]	0.8 [a]	0.3 [a]	0.3 [a]	0.2 [a]
200%	3.9 [a]	3.4 [b]	2.6 [b]	1.5 [b]	1.2 [a]	0.7 [a]	0.7 [a]	0.7 [a]	0.6 [a]	0.4 [a]	0.3 [a]	0.3 [a]
SE	0.1	0.1	0.2	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1

[1] Means with different letters in same column for each cation for each week are statistically different ($P < 0.05$) using post-hoc pairwise comparisons among sampling categories when ANOVA P-value < 0.05

Table 3-5. Foliar calcium (Ca), potassium (K), and magnesium (Mg) concentrations (%) for selected species in a southern Appalachian forest. Data presented is from Day and Monk (1977).

Species	Foliar concentration (%)		
	Ca	K	Mg
Cornus florida	1.60	1.18	0.90
Quercus alba	0.50	0.75	0.14
Quercus coccinea	0.45	0.62	0.14
Quercus prinus	0.59	1.09	0.19
Quercus rubra	0.75	0.89	0.33
Quercus velutina	0.71	0.95	0.17
Acer rubrum	0.62	0.53	0.20
Carya glabra	0.95	0.58	0.82
Liriodendron tulipifera	1.39	1.04	0.61
Oxydendrum arboreum	0.96	0.78	0.27
Nyssa sylvatica	0.96	1.04	0.51
Magnolia fraseri	1.07	1.25	0.38
Betula lutea	1.11	1.10	0.37
Sassafras albidum	0.52	1.08	0.27

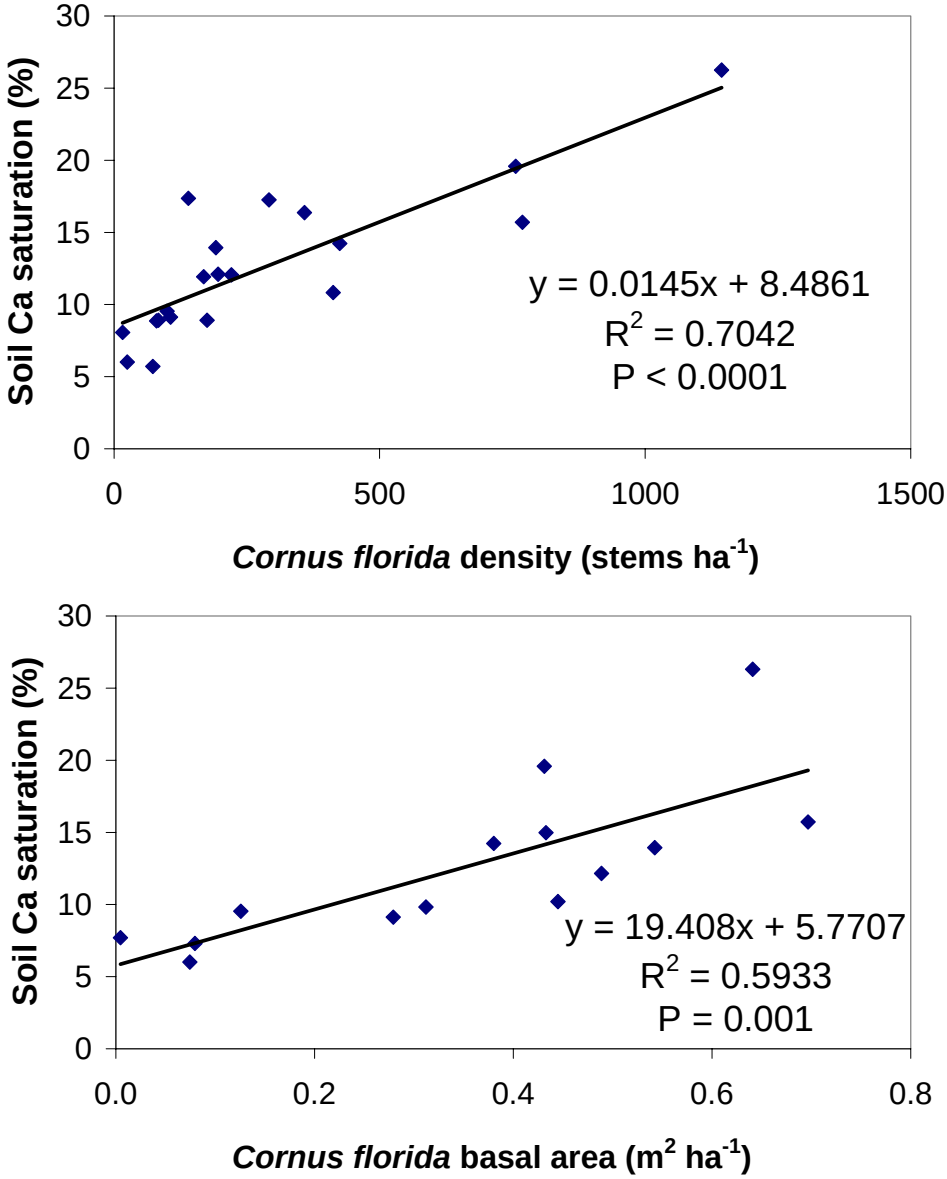

Figure 3-1. Linear regression between soil calcium (Ca) saturation and *Cornus florida* stem density and basal area.

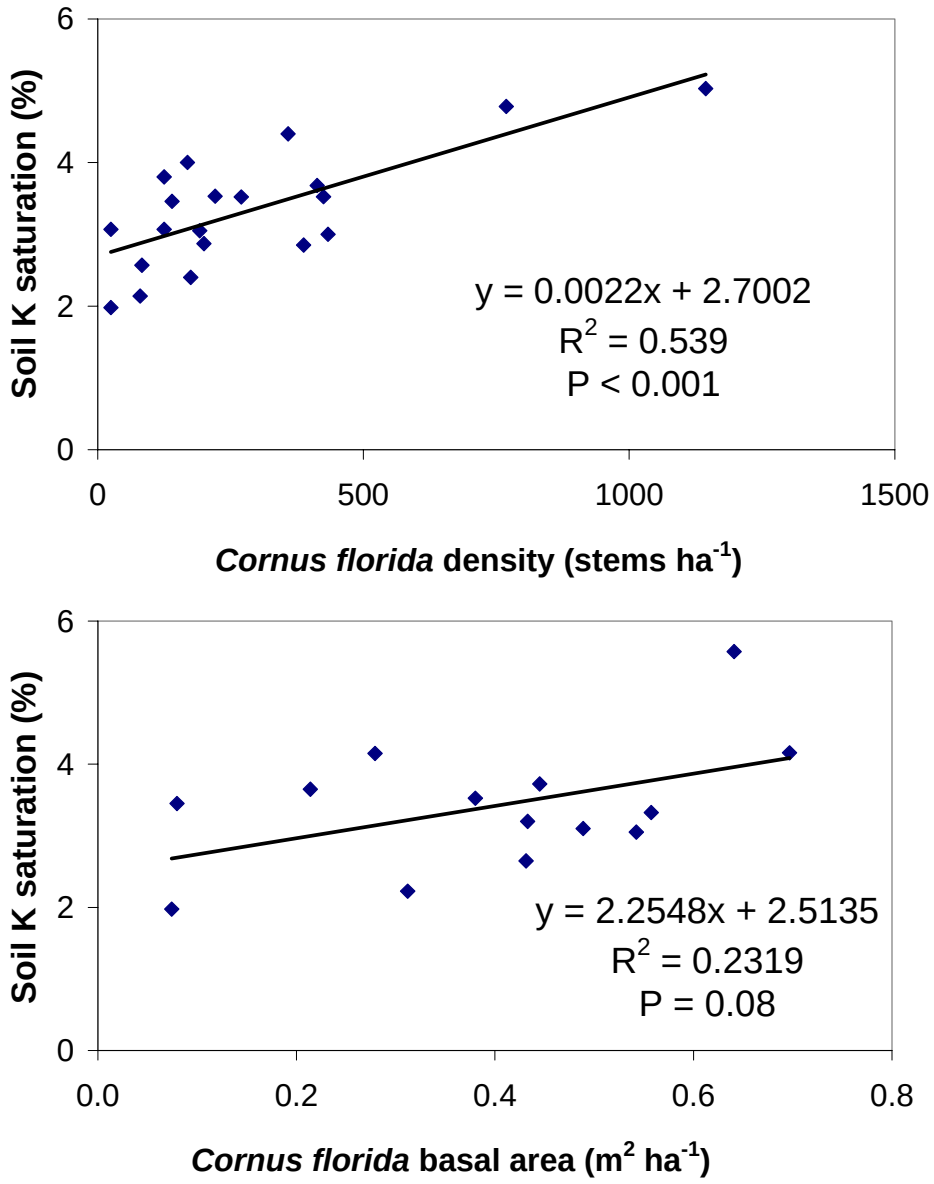

Figure 3-2. Linear regression between soil potassium (K) saturation and *Cornus florida* stem density and basal area.

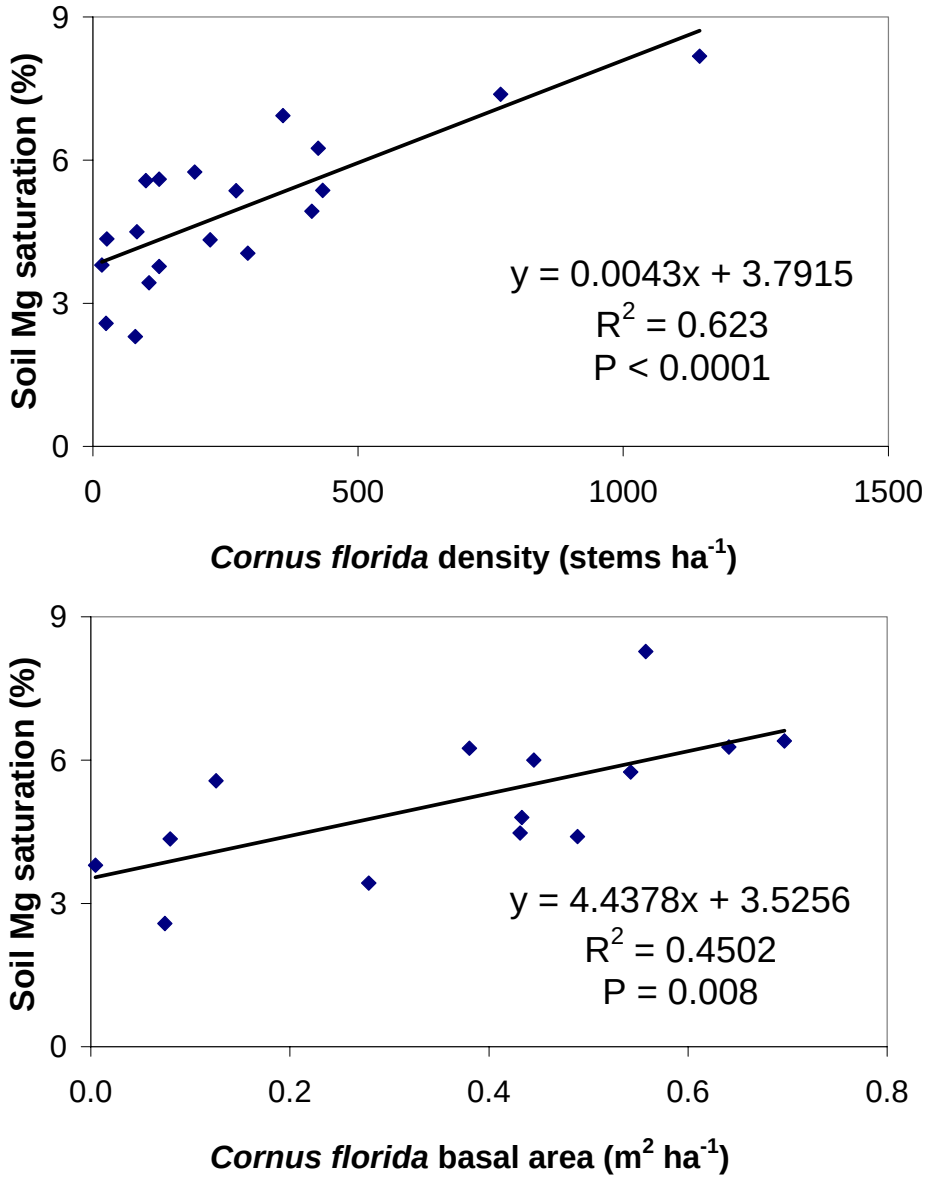

Figure 3-3. Linear regression between soil magnesium (Mg) saturation and *Cornus florida* stem density and basal area.

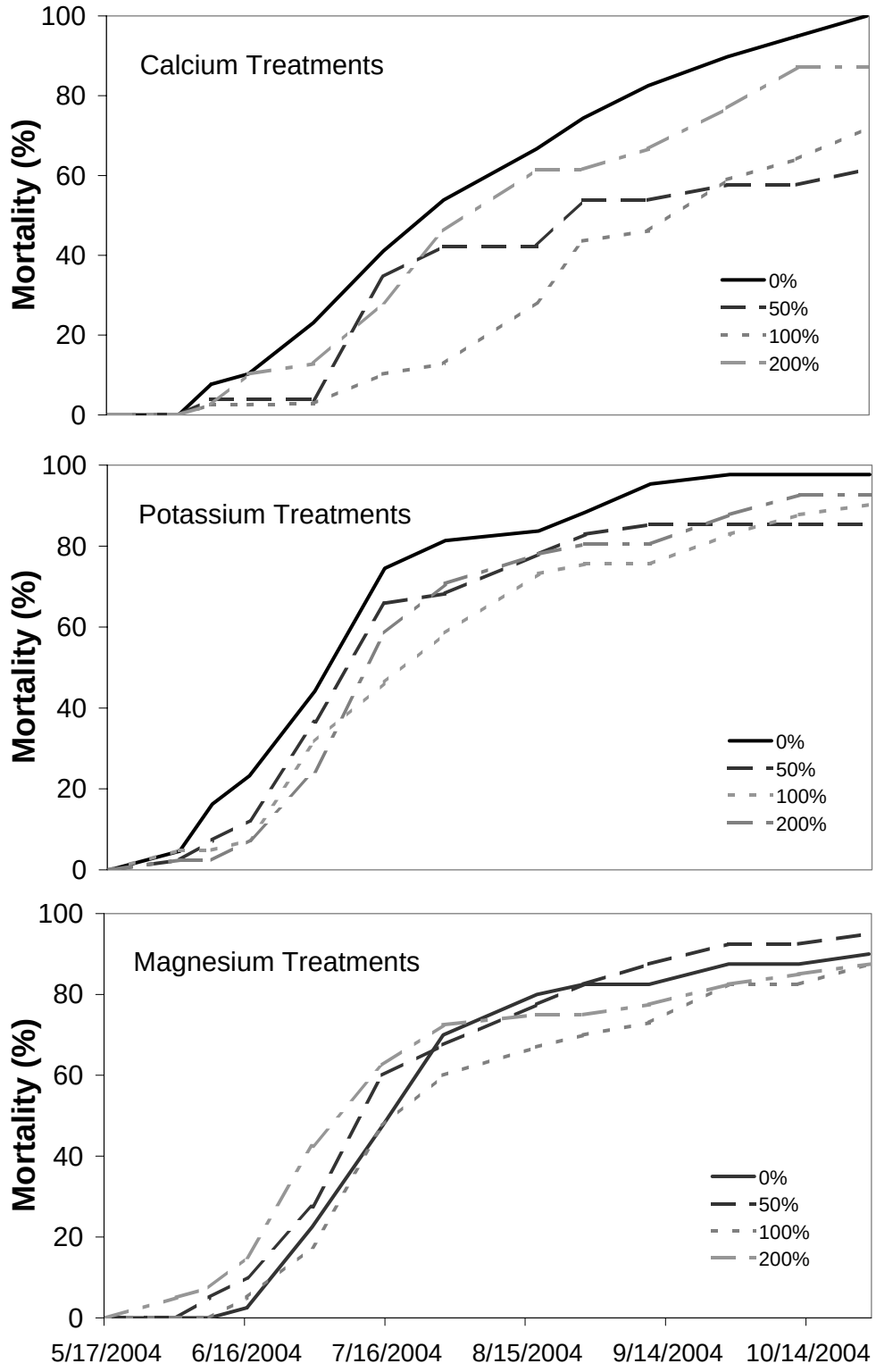

Figure 3-4. Biweekly mortality (%) of *Cornus florida* seedlings for the four treatment levels of each cation.

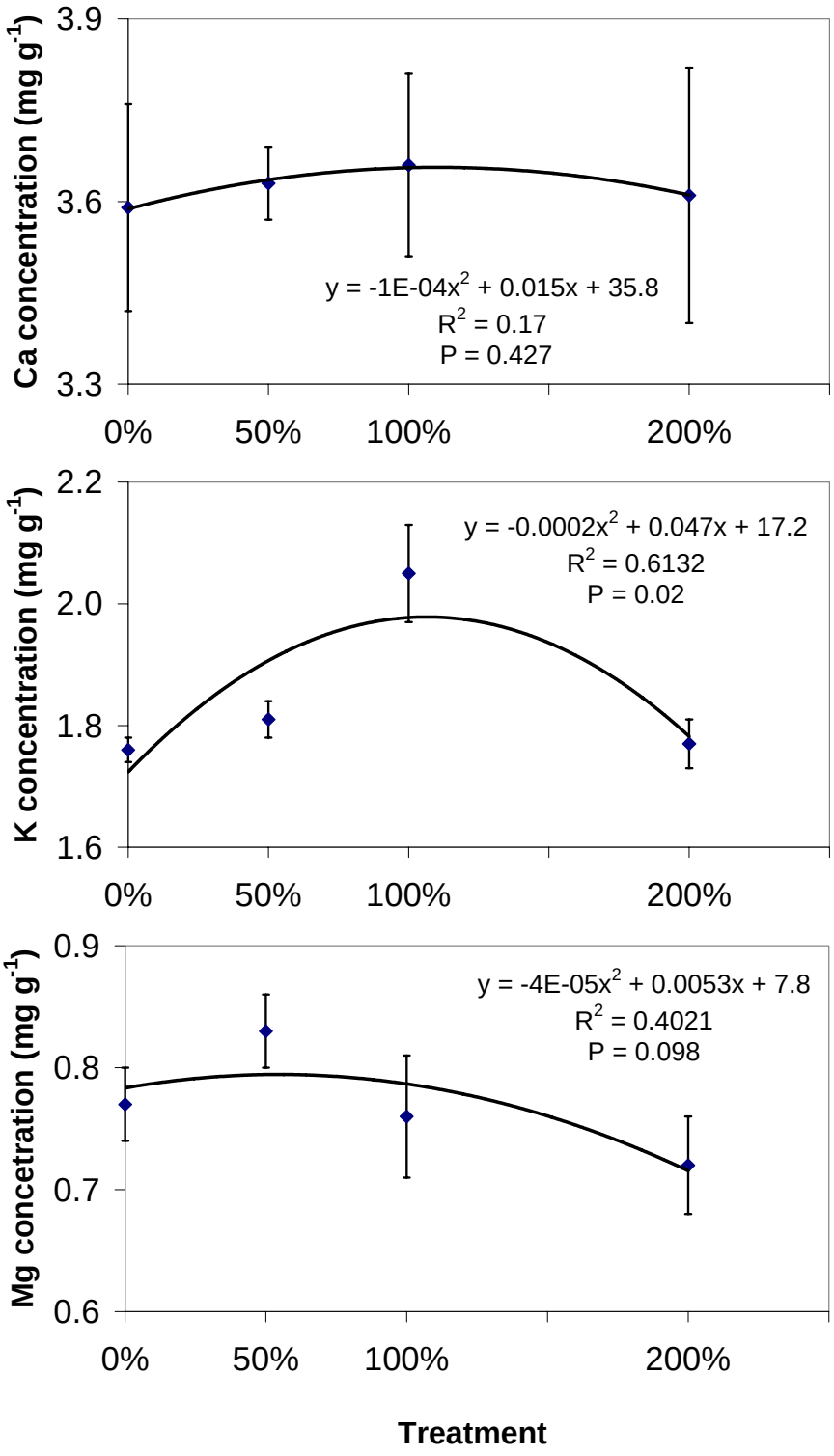

Figure 3-5. Foliar calcium (Ca), potassium (K), and magnesium (Mg) concentrations of *Cornus florida* seedling foliage for the four treatment levels of each cation.

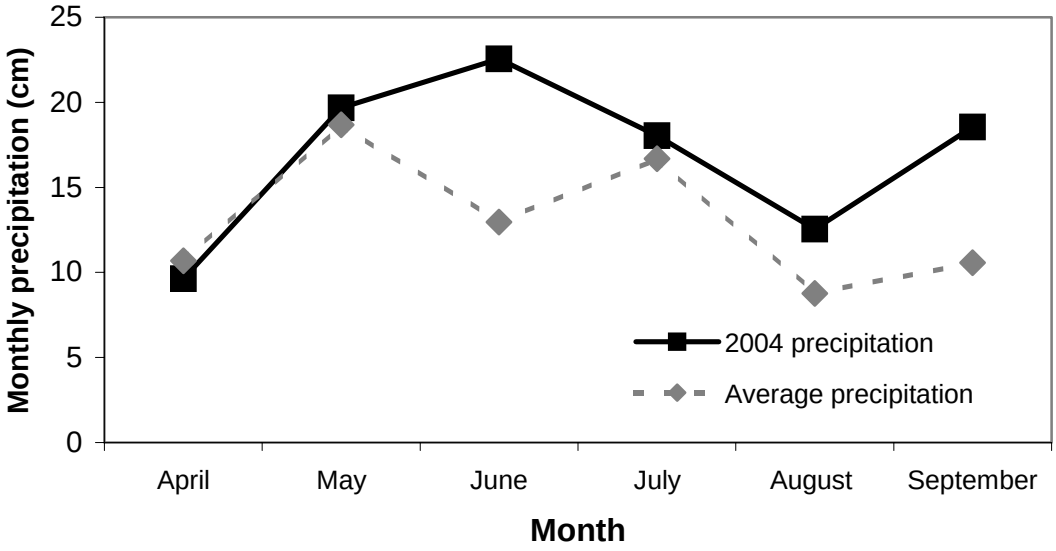

Figure 3-6. Precipitation data for 2004 and previous 5 year average (1999-2003) during April-September at the Twin Creeks Natural Resources Center, Great Smoky Mountains National Park (Data from National Climatic Data Center 1999-2004).

CHAPTER 4
INFLUENCE OF *Cornus florida* L. ON CALCIUM MINERALIZATION IN TWO SOUTHERN APPALACHIAN FOREST TYPES

Introduction

Over the past two decades, numerous studies have raised concerns about calcium (Ca) depletion in forest soils of the eastern United States (Likens et al. 1998, Huntington et al. 2000, Johnson et al. 2000, Yanai et al. 2005). In many forests, this depletion has been well documented. For example, between 1965-1992, Likens et al. (1998) estimated a loss of 9.9-11.5 kmol ha^{-1} of total Ca from the complete soil profile at Hubbard Brook Experimental Forest in New Hampshire. In a 60-80 year old southern Piedmont forest in Georgia, Huntington et al. (2000) estimated that the soil Ca depletion rate was 12.7 kg ha^{-1} y^{-1}. Calcium depletion has been attributed to leaching caused by acid deposition (Lawrence et al. 1995, Likens et al. 1996) and uptake and sequestering of nutrients in woody biomass (Johnson and Todd 1990, Huntington et al. 2000). The ecological consequences of soil Ca depletion could be devastating since long-term forest ecosystem health and sustainability have been closely linked to pools of available Ca in the soil (Graveland et al. 1994, NAPAP 1998, Driscoll et al. 2001, Hamburg et al. 2003).

In mixed hardwood forests of eastern North America, Ca released through mineral weathering is generally an insignificant contributor to total calcium cycling (Huntington et al. 2000, Dijkstra and Smits 2002). As a result, the release of Ca through organic matter decomposition (mineralization) is considered the major source of Ca for immediate uptake by forest plants (Likens et al. 1998, Dijkstra and Smits 2002). In a

study in northwestern Connecticut, Dijkstra (2003) reported that Ca mineralization occurred primarily in the forest floor (from leaf litter) as opposed to the mineral soil. Foliar Ca concentrations vary greatly among tree species (Metz 1952, Day and Monk 1977, Elliot et al. 2002), which influences the amount of Ca mineralized in the forest floor beneath the canopy of a given tree species (Dijkstra 2003).

Cornus florida L. foliage, on average, has a higher Ca concentration (2.0-3.5%) and more rapid decomposition than that other woody species (Thomas 1969, Blair 1988, Knoepp et al. 2005). *Cornus florida* was, historically, one of the most common understory species in eastern United States hardwood forests (Muller 1982, Elliott et al. 1997, Jenkins and Parker 1998). Because of the high Ca concentration of its foliage, rapid decomposition of its litter and its abundance in the understory, *C. florida* has long been believed to influence Ca availability in the soil and forest floor by acting as a "Ca pump" that draws calcium from deep in the soil profile and deposits it on the biotically-rich forest floor and surface soil (Thomas 1969, Jenkins et al. 2006). However, during the past 20 years, *C. florida* has suffered heavy mortality (over 90% in some forest types) throughout most of its range due to the rapid spread of the fungus *Discula destructiva* Redlin, which causes the disease dogwood anthracnose (Anagnostakis and Ward 1996, Sherald et al. 1996, Hiers and Evans, 1997, Jenkins and White 2002, Holzmueller et al. 2006). The loss of *C. florida* foliar biomass from the understories of eastern hardwood forests has the potential to further reduce Ca availability in these forests.

Although many have suggested that *C. florida* plays an important role in Ca cycling and availability in eastern forests (Thomas 1969, Hiers and Evans 1997, Jenkins and White 2002), no studies have been conducted to quantify the impact of *C. florida* on Ca

mineralization in forests where the species occurs. Understanding the influence of *C. florida* on the mineralization rate of forest stands is critical to understanding the impacts of dogwood anthracnose on calcium cycling. The objective of this study was to quantify Ca mineralization in the forest floor and mineral soil along natural gradients of increasing *C. florida* stem density. Because *C. florida* litter decomposes very rapidly compared to other species (Thomas 1969, Blair 1988, Knoepp et al. 2005), and its foliage contains high concentration of Ca (Thomas 1969, Blair 1988), we hypothesized that stands with high densities of *C. florida* have higher rates of Ca mineralization than stands with lower *C. florida* densities.

Materials and Methods

Study Area

We conducted this study in the north-central portion of Great Smoky Mountains National Park (GSMNP), near Gatlinburg, Tennessee. Mean annual temperature in Gatlinburg, Tennessee (440 m a.s.l.) is 12.9° C and mean annual precipitation is 142 cm. Study site elevation ranged from 487 to 762 m. All sampling was performed in two forest types; oak hardwood and cove hardwood. The most common species in the oak hardwood forest type were *Quercus alba* L., *Quercus prinus* L., *Quercus coccinea* Muenchh., *Carya alba* (L.) Nutt., *Pinus strobus* L., *Oxydendrum arboreum* (L.) DC., and *Nyssa sylvatica* Marsh. In the cove hardwood forest type, the most common species were *Liriodendron tulipifera* L., *Acer rubrum* L., *Tsuga canadensis* (L.) Carr., *Fagus grandifolia* Ehrh., *Betula lenta* L., and *Magnolia fraseri* Walt. All study sites were located in secondary forests that were logged prior to park establishment in 1934 (Pyle 1988). Soils in this area were predominantly Junaluska-Tsali complex, Soco-Stecoah complex, and Spivey-Santeetlah-Nowhere complex. These complexes, found in both forest types, are typically

well drained, form on moderate slopes (15-45%), are sometimes stony, and are derived from soft metasandstone (Anthony Khiel, soil scientist, NRCS, personal communication).

Field Sampling

We determined Ca mineralization in the forest floor and mineral soil using the buried bag *in situ* incubation method described by Eno (1960). This technique has recently been utilized to quantify Ca mineralization in forested ecosystems (Dijkstra 2003) and is commonly used to estimate N mineralization as well (Prescott et al. 2003, Allen et al. 2005). We collected data for 2 years; bags were buried in early June 2003/2004 (summer incubation) and again in early December 2003/2004 under freshly fallen leaf litter (winter incubation). Overall, sixty-eight 10 m x 10 m plots were sampled every year, thirty in the cove hardwood forest type and thirty-eight in the oak hardwood forest type. For each forest type, plots were divided into three sampling categories based on *C. florida* stem density: (0 stems ha^{-1}, 200-300 stems ha^{-1}, and > 600 stems ha^{-1}), hereafter referred to as zero, low, and high density, respectively. Each plot was surrounded by a 20 m buffer from the outside edge of the plot that was void of other *C. florida* stems. There was a minimum of 100 m separating plots from each other.

In each plot, two forest floor samples (20 cm x 20 cm) were taken underneath the canopy of the *C. florida* trees, but were at least 1 m away from the nearest tree base. Forest floor mass and depth were determined from these samples. On plots where no *C. florida* trees were present, two forest floor samples were randomly collected within the 10 m x 10 m plot, and were at least 1 m away from the nearest tree base. Where the forest floor was removed, a soil core (4 cm x 15 cm) was extracted. Each forest floor and underlying soil sample was divided into two equal parts, transferred to polyethylene bags, and closed with a knot. Two litter and two soil bags (initial sample) from each plot were

returned to the lab to determine dry mass, pH, and exchangeable Ca. The remaining sample bags (final sample) on each plot were then returned to the spot from which they were collected, and the soil bags were buried in the core holes and the forest floor bags were placed in the litter layer. The bags containing the forest floor were covered with fresh forest litter. Six months after incubation, the bags were retrieved and brought back to the laboratory for further analysis.

Laboratory Analysis

Once in the lab, the contents of the bags were dried in an oven at 70° C for 72 hours. After drying, the mineral soil was sieved through a 2 mm sieve and the forest floor was ground using a tissue grinder. Subsamples of the forest floor and mineral soil were dried at 105° C for 48 hours to measure gravimetric moisture content. Samples of the forest floor and mineral soil were then measured for pH in de-ionized water slurry (10:1 ratio for the forest floor and 2:1 ratio for the soil). Samples were stirred initially and again after 15 minutes. After settling for 30 minutes following the final stirring, pH was measured. We extracted both the mineral soil and forest floor (separately) samples using 10 g of mineral soil and 5 g of forest floor mixed with 100 ml of 0.1M $BaCl_2$ in a 120 ml vial. Samples were shaken for 2 hours on a soil shaker and filtered after settling for 24 hours using a coffee filter. Exchangeable Ca was measured using an inductively coupled plasma emission spectrometer at the University of Florida Analytical Research Laboratory (Gainesville, Florida). Calcium mineralization was determined as the difference between final and initial exchangeable Ca in the bags.

Statistical Analysis

Summer and winter initial Ca concentrations and pH for the 2 years were compared using paired t-tests. Because there was no statistical difference ($P > 0.05$) between the 2

years for any variable the data were combined for further analysis. Differences between initial and final pH, exchangeable Ca from initial summer and initial winter periods, and Ca mineralization from summer and winter incubations were tested using paired t-tests for each forest type. ANOVA was used to test for differences of forest floor mass and depth, initial exchangeable Ca concentrations, and Ca mineralization for the three *C. florida* densities for each forest type. We also tested the relationship between Ca mineralization and stem density, basal area, and foliar biomass (Martin et al. 1998) using step-wise multiple regression. Step-wise multiple regression did not yield any significant relationships among any variables and as a result data are not shown. All statistical analyses were done using SAS (SAS 2002).

Results

Forest Floor Mass and Depth

There were no significant differences in forest floor mass (2.5 - 2.9 kg m^{-2}) in cove hardwood plots for both summer and winter periods ($P > 0.61$). There also were no significant differences in forest floor mass (2.7 - 3.1 kg m^{-2}) in oak hardwood plots during summer and winter periods ($P > 0.37$). There were no significant differences in forest floor depth (3.4 - 4.0 cm) in cove hardwood plots during summer and winter periods ($P > 0.39$). There were also no significant differences in forest floor depth (3.5 - 3.8 cm) in the oak hardwood plots during summer and winter periods ($P > 0.47$).

Soil pH

In cove hardwood plots, mean forest floor pH ranged from 4.63 to 5.77 in the forest floor and from 4.01 to 4.95 in the mineral soil (Table 4-1). In oak hardwood plots, mean forest floor pH ranged from 4.01 to 5.40 and mean mineral soil pH ranged from 3.65 to 4.49 (Table 4-1). In cove hardwood plots, the mean pH of the forest floor increased

slightly during summer incubation on zero and low density plots ($P < 0.01$), but did not significantly change on high density plots ($P = 0.50$). Mean mineral soil pH did not change significantly for any density class during either incubation period ($P > 0.43$). In oak hardwood plots, mean pH increased slightly in the forest floor and mineral soil of zero density plots ($P = 0.1$ and $P = 0.01$) and in the forest floor of low density plots ($P = 0.005$). During the winter incubation, there was a significant increase in pH between the initial and final samples in both forest types for all *C. florida* densities ($P < 0.001$; Table 4-1).

Initial Exchangeable Ca

Initial mean values for exchangeable Ca varied with *C. florida* density in both the forest floor and mineral soil for both forest types. Mean forest floor values in the cove hardwood plots ranged from 5.5 to 8.4 g kg^{-1}, which was about ten times greater than mean values found in the cove hardwood forest mineral soil 0.45 to 0.85 g kg^{-1} ($P < 0.001$; Figure 4-1). In oak hardwood plots, forest floor mean values ranged from 3.6 to 7.4 g kg^{-1}, and mineral soil mean values ranged from 0.19 to 0.68 g kg^{-1} (Figure 4-1). Initial exchangeable Ca mean values generally increased with *C. florida* density for both forest types for summer and winter incubation periods and were significantly greater in the high *C. florida* density plots compared to the zero density plots in both the forest floor and mineral soil in both forest types ($P < 0.01$). Comparisons of initial exchangeable Ca mean values made between the winter and summer incubations showed no significant differences between the two periods (Figure 4-1).

Ca mineralization

Ca mineralization was greater in the forest floor than in the mineral soil for both forest types ($P < 0.0001$). Mean values ranged from 2.09 to 9.16 mg kg^{-1} day^{-1} for the

cove hardwood forest floor and from -1.10 to 0.20 mg kg^{-1} day^{-1} in the cove hardwood mineral soil (Figure 4-2). For the oak hardwood forests, mean values ranged from 1.31 to 7.16 mg kg^{-1} day^{-1} in the forest floor and from -0.40 to 0.23 mg kg^{-1} day^{-1} in the mineral soil (Figure 4-2). Mean values for the winter incubation period were significantly lower than summer incubation period for most of the mineral soil comparisons, but were not significantly different from the summer incubation periods for the forest floor comparisons for both forest types ($P > 0.21$). *Cornus florida* density had an effect on the forest floor in both forest types ($P < 0.1$), with increasing *C. florida* density leading to increased Ca mineralization (Figure 4-2).

Yearly Ca mineralization was greater in the high *C. florida* density plots compared to the zero density plots for both forest types; cove hardwood, high density (3.3 g kg^{-1} yr^{-1}) versus zero density (0.6 g kg^{-1} yr^{-1}, $P = 0.04$) and oak hardwood, high density (2.4 g kg^{-1} yr^{-1}) versus zero density (1.1 g kg^{-1} yr^{-1}, $P = 0.09$; Table 4-2). In most cases, yearly Ca mineralization in the mineral soil was negative, indicating Ca immobilization.

Discussion

Most of the yearly Ca mineralization in our study can be attributed to the forest floor, which is similar to Dijkstra's (2003) findings in northwestern Connecticut that, under most tree species, forest floor Ca mineralization far exceeded mineral soil Ca mineralization. The two species that did have mineral soil exchangeable Ca inputs that were comparable to the forest floor in Dijkstra's (2003) study were *Acer saccharum* Marsh. and *Fraxinus americana* L., and this increase in mineral soil inputs was attributed to high earthworm activity. Neither of these two species was in high abundance in either forest type in our study. In addition, in glaciated areas, such as Connecticut, exotic earthworm species tend to dominate over native species. The exotic species tend to break

down litter and duff at a much more rapid rate than natives. In non-glaciated areas, such as the southern Appalachians, native earthworms dominate and the break down of coarse organic matter is much slower (Hendrix and Bohlen 2002).

Ca mineralization differed significantly in the forest floor among the three *C. florida* densities in both forest types and incubation periods. Within the forest floor, Ca mineralization was significantly higher in the high density *C. florida* plots, except for the winter incubation period in the oak hardwood forest type which did not show a significant difference due to high plot variability. Increased mineralization in high density *C. florida* plots could be attributed to the high Ca concentration (Thomas 1969, Blair 1988) and rapid decomposition of *C. florida* foliage (Thomas 1969, Blair 1988, Knoepp et al. 2005). Mineralization in the forest floor did not differ between winter and summer incubation periods for any density level or forest type. Dijkstra (2003) reported Ca mineralized was greater in the summer incubation period compared to the winter incubation period and attributed this to warmer temperatures during the summer incubation period. The warmer winters of Tennessee compared to Connecticut may have offset this difference and resulted in comparable winter and summer values. It should be noted though, that mineral soil Ca mineralization values were significantly lower during the winter incubation period of our study.

Initial exchangeable Ca values in the zero density *C. florida* plots were slightly higher in the cove hardwood forest type than in the oak hardwood forest type in both the mineral soil and forest floor ($P < 0.001$). This result could be attributed to the different Ca concentrations found in the foliage of the dominant species in each forest type. Numerous studies have shown how soil properties can be influenced by tree species (Boettcher and

Kalisz 1990, Finzi et al.1998, Dijkstra and Smits 2002, Fujinuma et al.2005). The cove hardwood forest type was primarily dominated by *L. tulipifera*, which has an average of 1.74% Ca concentration in its foliage, compared to the dominant species in the oak hardwood forest type, *Q. alba*, which has much lower average Ca foliar concentration (0.73%) (Jenkins et al. 2006) (See Table 4-3 for a listing of species and corresponding Ca concentration).

Despite the differences in initial values of exchangeable Ca between the two forest types, values for initial exchangeable Ca were significantly greater in high density *C. florida* plots compared to zero density plots in both the forest floor and mineral soil for both forest types for both incubation periods. While previous research has focused on the relationship between overstory trees and soil chemistry, our study shows that a single understory woody species can have considerable influence on soil chemical properties. One would assume that given the larger size of overstory trees, most of the forest floor biomass comes from overstory trees and not from understory trees, therefore overwhelming any effect understory trees might have on soil chemical properties. However, in a study by Jenkins et al. (2006) in GSMNP, the authors reported that understory foliar biomass contributed up to 49% of total stand foliar biomass, depending on forest type and stand developmental stage.

Because of dogwood anthracnose, *C. florida* density has greatly declined across the eastern United States (Anagnostakis and Ward 1996, Sherald et al. 1996, Hiers and Evans 1997, Jenkins and White 2002), dramatically reducing *C. florida* foliar biomass added to the forest floor. In GSMNP, there has been a significant reduction in the amount of Ca cycled to the forest floor in forest types containing *C. florida*. Typic cove forests

experienced a 86% decline in *C. florida* leaf litter over a 20 year period since 1977, resulting in a corresponding decline (85%) in annual Ca inputs and oak-hickory forests experienced a 78% reduction in *C. florida* leaf litter during the same period, resulting in a 78% reduction in annual Ca inputs (Jenkins et al. 2006). Throughout much of the Park, and likely across the southern Appalachians as well, *C. florida* trees have largely been replaced by *T. canadensis*, a species with more acidic litter that contains little Ca (Jenkins and White 2002). Increased *T. canadensis* densities in the forest understory could further disrupt Ca cycling in eastern forests. In a study that compared base cation levels beneath three tree species (*Acer saccharum* Marsh., *Tilia Americana* L., and *Tsuga canadensis*) in Ottawa National Forest in western Upper Michigan, the authors reported high levels of base cation leaching underneath *T. canadensis* canopies which was attributed to the low uptake of these cations by *T. canadensis* (Fujinuma et al. 2005). The hemlock woolly adelgid (*Adelges tsugae* Annand), however, is spreading rapidly within GSMNP, and forests across the southern Appalachians may experience heavy *T. canadensis* mortality, similar to that observed in the northeastern United States (Johnson et al. 1999). If this occurs, the importance of shade tolerant hardwood species, such as *A. rubrum*, may increase in the forest types we sampled. While this and other hardwood species typically contribute more calcium to annual cycling than *T. canadensis*, their contributions are still much lower than that of *C. florida*.

In a study of regional forest plant species diversity in central Europe, Cornwell and Grubb (2003) reported the highest levels of plant species richness were found on nutrient rich soils. Although it is not clear how loss of Ca inputs from *C. florida* has affected the vigor and growth of other species and the overall stand dynamics in eastern hardwood

forests, several other common species co-occurring with *C. florida* (*Q. coccinea*, *Q. rubra* L., and *Robinia pseudoacacia* L.) have been reported to show increased levels of mortality in the southern Appalachian Mountains while dogwood anthracnose has been dramatically reducing *C. florida* in eastern forests (Wyckoff and Clark 2002). *Cornus florida* litter is a major source of Ca and a decline in foliar biomass could negatively affect Ca mineralization in the soil, the primary source of uptake in eastern forests (Dijkstra and Smits 2002), disrupting the Ca cycle (Figure 4-3). This negative impact, combined with acid deposition, may eventually result in further Ca depletion (Hamburg et al. 2003), which has been associated with canopy dieback in some eastern hardwood forests (Wilmot et al. 1996).

Lack of Ca can affect other components of forest ecosystems, including soil fauna. Decreased land snail abundance has been correlated with decreased exchangeable Ca levels in Sweden (Wäreborn 1992) and the central Appalachian Mountains (Hotopp 2002). In the Netherlands, poor reproductive success in *Parus major* L. (great tit, a passerine bird) because of a lack of Ca in eggshells was attributed to reduced snail abundance on soils depleted of calcium by acid deposition (Graveland et al. 1994, Graveland 1996).

Because of the important role *C. florida* plays in the Ca cycle, preventing its loss may be of critical importance in eastern forests. This is a difficult task due to the presence of dogwood anthracnose. However, there has been some indication that prescribed burning with proper frequency can help retain *C. florida* as a component of stands infected with this disease (Holzmueller et al. 2006a).

Conclusion

These results suggest that *C. florida* density significantly affects Ca mineralization in both cove hardwood and oak hardwood forest types, primarily in the forest floor. The influence of *C. florida* on Ca mineralization may be attributed to the high Ca concentration and rapid decomposition of its foliage. Because mineralized Ca in the forest floor is the primary source of available Ca in eastern hardwood forests, loss of *C. florida* may further alter Ca cycling in these forests with subsequent negative impacts on associated flora and fauna.

Table 4-1. Mineral soil and forest floor mean pH (± 1 SE) for summer and winter incubations in the cove hardwood and oak hardwood forest types.

	Summer		Winter	
	Initial	Final	Initial	Final
Cove hardwood				
Forest Floor				
None	4.63 (0.20)	5.31 (0.25)***	4.71 (0.15)	5.38 (0.21)*** [1]
Low	5.30 (0.19)	5.77 (0.15)**	5.30 (0.17)	5.72 (0.19)***
High	5.14 (0.17)	5.20 (0.25) ns	5.31 (0.12)	5.71 (0.14)***
Mineral Soil				
None	4.26 (0.16)	4.19 (0.16) ns	4.01 (0.11)	4.95 (0.09)***
Low	4.29 (0.12)	4.27 (0.15) ns	4.15 (0.09)	4.60 (0.09)***
High	4.26 (0.11)	4.11 (0.07) ns	4.04 (0.07)	4.63 (0.07)***
Oak hardwood				
Forest Floor				
None	4.13 (0.11)	4.35 (0.16)*	4.01 (0.08)	4.41 (0.07)***
Low	4.47 (0.19)	4.78 (0.20)**	4.41(0.12)	4.77 (0.15)**
High	5.23 (0.19)	5.40 (0.22) ns	5.11 (0.10)	5.48 (0.16)**
Mineral Soil				
None	3.65 (0.05)	3.49 (0.08) **	3.65 (0.27)	4.14 (0.04)***
Low	3.74 (0.14)	3.76 (0.19) ns	3.86 (0.09)	4.45 (0.16)***
High	4.02 (0.12)	3.95 (0.18) ns	4.01 (0.09)	4.49 (0.11)***

[1] Statistical comparisons were made between the initial and final samples for each density in each forest type using paired t-tests, ns = $P > 0.1$, * = $P < 0.1$, ** = $P < 0.01$, *** = $P < 0.001$

Table 4-2. Mean yearly Ca mineralization (± 1 SE) in forest floor, mineral soil, and combined total (forest floor plus mineral soil) for the three *Cornus florida* sampling densities in the cove hardwood and oak hardwood forest types.

	Forest Floor ($g\ kg^{-1}\ yr^{-1}$)	Mineral Soil ($g\ kg^{-1}\ yr^{-1}$)	Total ($g\ kg^{-1}\ yr^{-1}$)
Cove hardwood			
Zero	0.7 (0.8) [a1]	-0.1 (0.05) [b]	0.6 (0.8) [a]
Low	1.1 (0.9) [a]	-0.2 (0.07) [a]	0.9 (0.9) [a]
High	3.3 (0.8) [b]	0.0 (0.04) [c]	3.3 (0.8) [b]
Oak hardwood			
Zero	1.1 (0.8) [a]	-0.04 (0.01) [a]	1.1 (0.8) [a]
Low	2.6 (0.8) [b]	-0.04 (0.04) [a]	2.5 (0.8) [b]
High	2.4 (0.9) [b]	-0.03 (0.07) [a]	2.4 (0.9) [b]

[1] Means with different letters in same column for each forest type are statistically different ($P < 0.1$) using post-hoc pairwise comparisons among categories when ANOVA P-value < 0.1

Table 4-3. Foliar calcium concentrations (%) from dominant species in the two forest types (oak hardwood and cove hardwood) sampled in this study. Data from trees sampled within Great Smoky Mountains National Park on long-term vegetation plots (NPS unpublished data).

Cove hardwood species	Calcium concentration (%)	Oak hardwood species	Calcium concentration (%)
Liriodendron tulipifera	1.74	*Quercus* spp.	0.73
Acer rubrum	0.82	*Carya* spp.	0.98
Tsuga canadensis	0.46	Pinus strobus	0.29
Betula lenta	0.95	*Oxydendrum arboreum*	0.91
Magnolia fraseri [1]	1.07	*Nyssa sylvatica*	0.78
Cornus florida	1.73	*Cornus florida*	1.73

[1] Data from study by Day and Monk (1977) in Coweeta Hydrologic Laboratory located in southwestern North Carolina

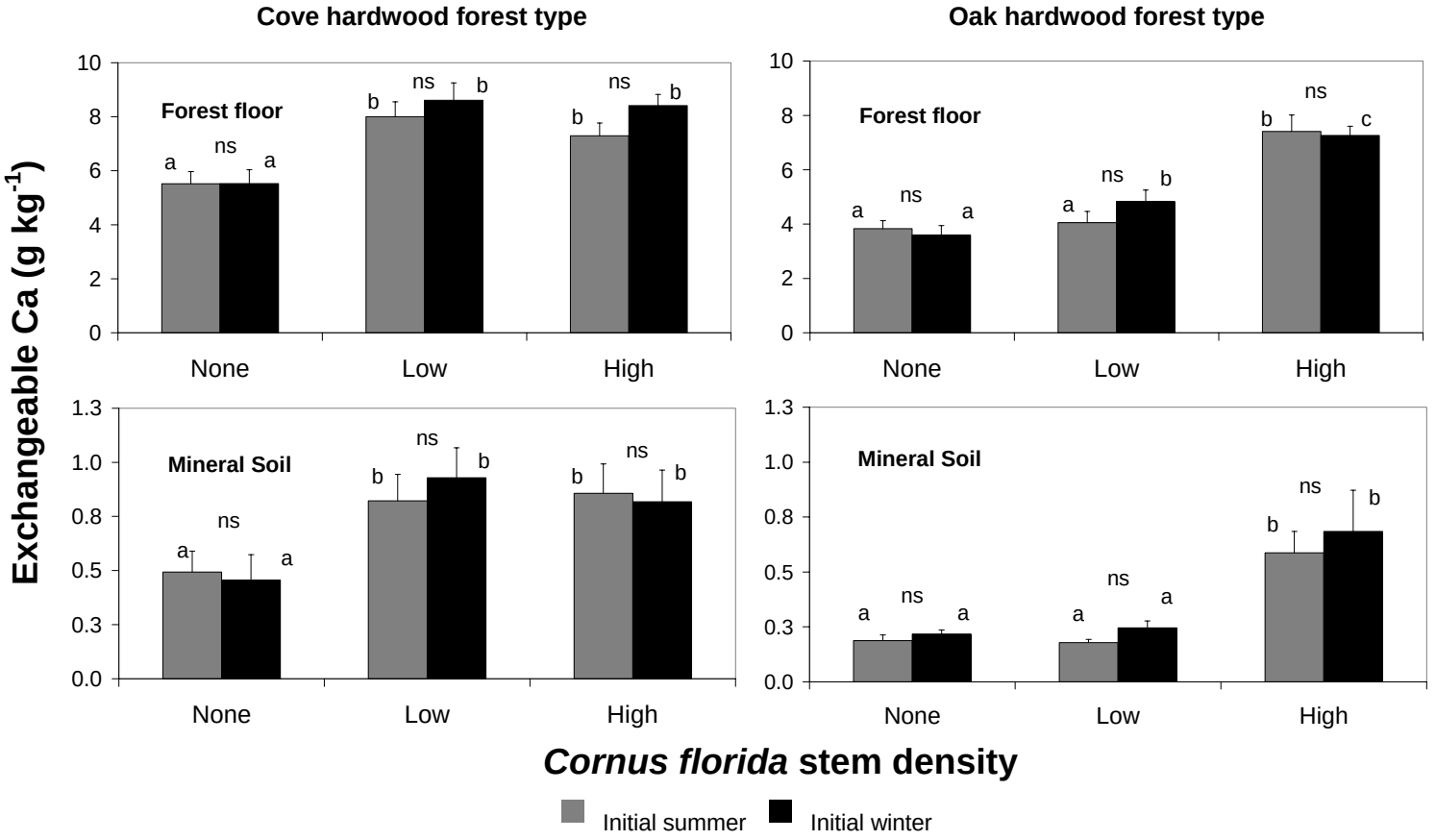

Figure 4-1. Mean initial exchangeable Ca levels (± 1 SE) in the forest floor and mineral soil in the cove hardwood and oak hardwood forest types during summer and winter collection times. Comparisons between summer and winter values in each panel were made for each density; all were nonsignificant (ns; $P > 0.05$). Bars for the same collection period in each panel with different letters are significantly different ($P < 0.05$) using post-hoc pairwise comparisons among categories when ANOVA P-value < 0.05.

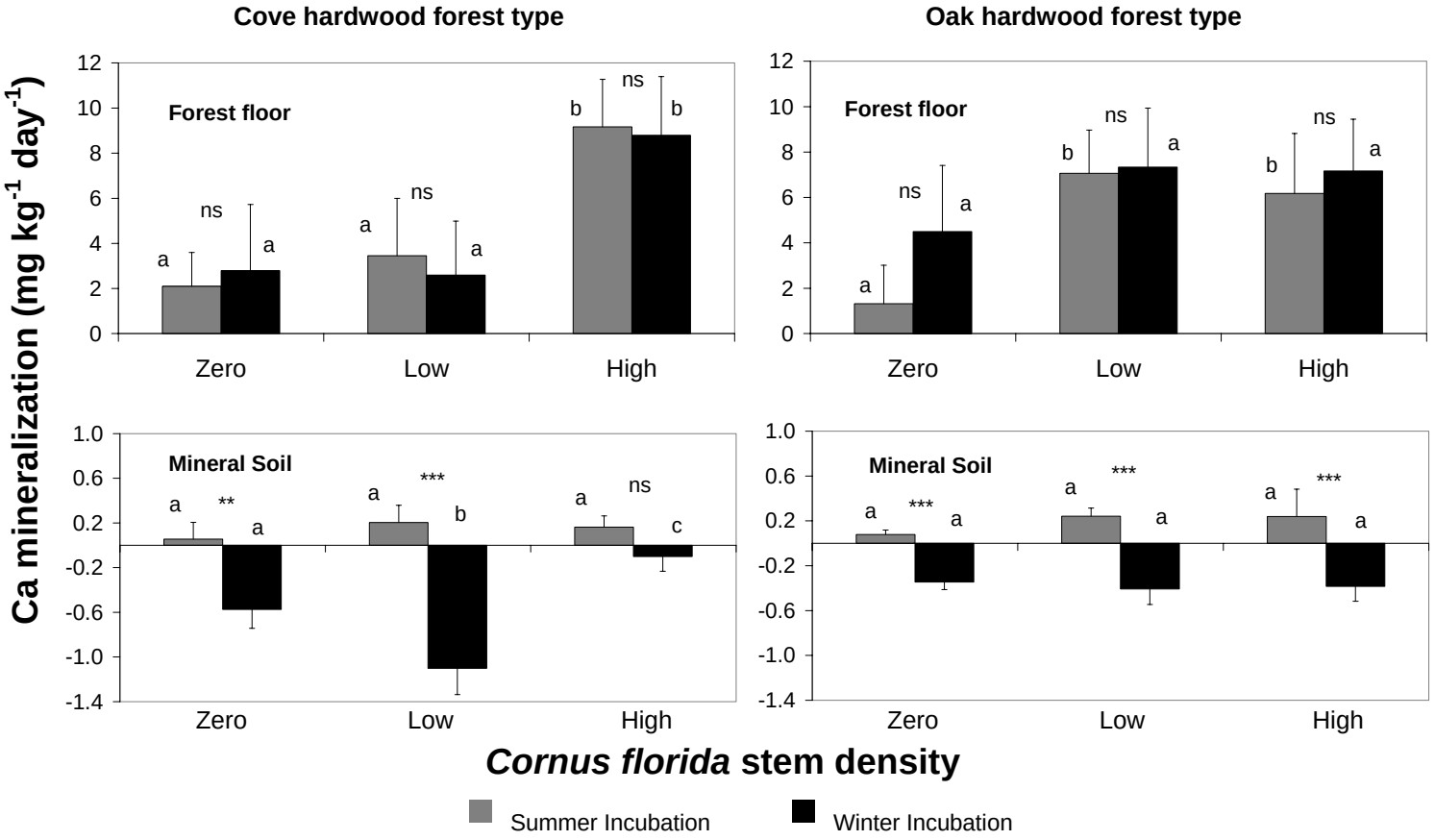

Figure 4-2. Mean Ca mineralization (± 1 SE) for the forest floor and mineral soil in the cove hardwood and oak hardwood forest types during summer and winter incubation periods. Comparisons between summer and winter values in each panel were made for each density (ns = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.001$, *** = $P < 0.0001$). Bars from the same incubation period in each panel with different letters are significantly different ($P < 0.1$), using post-hoc pairwise comparisons among categories when ANOVA P-value < 0.1.

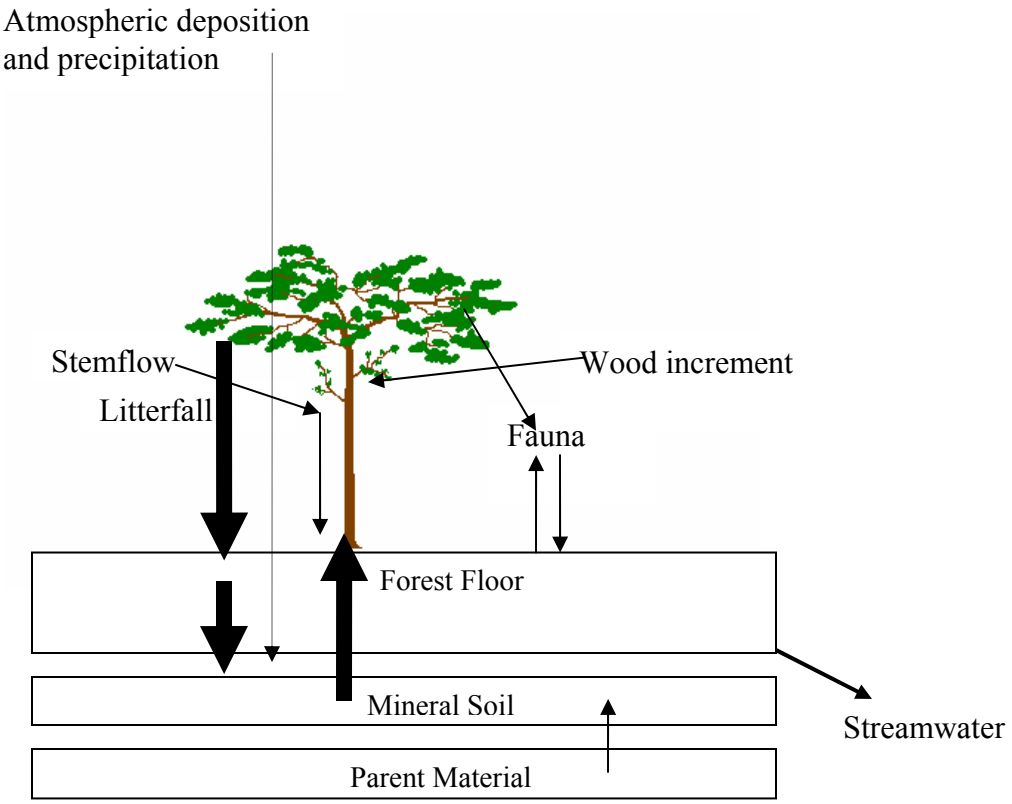

Figure 4-3. Conceptual model of calcium (Ca) cycling in an eastern United States hardwood forest. Arrow thickness indicates amount of Ca movement and box size indicates size of available Ca pool based on data from Johnson et al. (1985) and Yanai et al. (2005). Loss of *Cornus florida* may decrease the size of the forest floor Ca pool and therefore overall Ca availability may be less in oak hardwood and cove hardwood forest types.

CHAPTER 5
SUMMARY AND CONCLUSION

This research project examined the influence of dogwood anthracnose and the ecological role of *Cornus florida* L. in Great Smoky Mountains National Park (GSMNP). Specifically, the effects of past burning on *C. florida* survival and health (Chapter 2), the effects of calcium (Ca), potassium (K), and magnesium (Mg) on dogwood density and health (Chapter 3), and role of *C. florida* in Ca mineralization (Chapter 4) were examined over a three year period. Findings from these three interrelated studies are briefly summarized below.

In Chapter 2, we examined *C. florida* populations in burned and unburned oak-hickory stands to determine if burning prior to anthracnose infection has reduced the impacts of anthracnose. We hypothesized that fire has altered stand structure and created open conditions less conducive to dogwood anthracnose, which is most virulent in moist heavily shaded stands. We compared *C. florida* density, *C. florida* foliar infection and crown dieback, stand structure, species composition, *Tsuga canadensis* (L.) Carr. density, plot species richness, and plot diversity among four sampling categories: unburned stands, and stands that had burned once, twice, and three times (single, double, and triple burn stands, respectively) over a 20 year period (late 1960s to late 1980s). We also analyzed community composition using multivariate analyses. Double burn stands contained the greatest density of *C. florida* stems (770 stems ha^{-1}) followed by triple burn stands (233 stems ha^{-1}), single burn stands (225 stems ha^{-1}) and unburned stands (70 stems ha^{-1}). While foliar infection ratings did not differ between categories, we observed

less crown dieback in small trees (< 5 cm dbh) in burned stands than in unburned stands ($P < 0.05$). Total overstory density was greater in unburned stands (564 stems ha^{-1}) than in double and triple burned stand (317-436 stems ha^{-1}, $P < 0.0001$), but understory stem density was greater in burned stands (2851-5072 stems ha^{-1}) than unburned stands (2292 stems ha^{-1}, $P = 0.024$). However, the understory density and importance value of *T. canadensis*, a coniferous species that creates heavy shading in forest understories, were considerably greater in unburned stands than in burned stands. The results of our study suggest that prescribed fire may offer a management tool to reduce the impacts of dogwood anthracnose in eastern hardwood forests.

In Chapter 3 we found positive correlations between soil Ca, Mg, and K saturation and *C. florida* stem density and basal area. We tested the effect of these cations at four levels (0, 50, 100, and 200%) of a standard nursery fertilization rate on *C. florida* seedling survival and resistance to dogwood anthracnose. Although most of the seedlings died after one season of exposure to dogwood anthracnose, we found that seedlings that had lower inputs of Ca and K cations showed higher levels of disease severity sooner than seedlings in other treatments, suggesting these nutrients play a role in *C. florida* survival from anthracnose. Magnesium treatment levels did not appear to have an effect on *C. florida* disease severity or mortality.

In Chapter 4 we sampled sixty-eight 10 m x 10 m plots in two forest types, cove hardwood and oak hardwood, to quantify the influence of *C. florida* density on initial exchangeable Ca and Ca mineralization in the mineral soil and forest floor. *Cornus florida* density was classified into three levels in both forest types (zero = 0 stems ha^{-1}, low = 200-300 stems ha^{-1} and high = > 600 stems ha^{-1}). We found significantly greater

levels of initial exchangeable Ca on high density plots, compared to low density plots in both forest types in the forest floor and mineral soil ($P < 0.01$). Calcium mineralization occurred primarily in the forest floor and not in the mineral soil in both forest types. Yearly Ca mineralization was greatest in the high density *C. florida* plots (cove hardwood, high density 3.3 g kg^{-1} yr^{-1} versus zero density 0.6 g kg^{-1} yr^{-1}, $P = 0.04$ and oak hardwood, high density 2.4 g kg^{-1} yr^{-1} versus zero density 1.1 g kg^{-1} yr^{-1}, $P = 0.09$). These results indicate that the loss of *C. florida* from eastern United States forests will further alter the Ca cycle and may negatively affect the health of eastern hardwood forests.

Overall, this project indicates that nutrient availability plays a role in *C. florida* survival from dogwood anthracnose. Our results also indicate that prescribed burning offers a management technique to maintain *C. florida* as a component in eastern hardwood forests. Additionally, our project showed the importance of *C. florida* in the Ca cycle in eastern hardwood forests. Although this project took place in Great Smoky Mountains National Park, because of the large study area and wide distribution of the forest types we sampled, we believe that our findings are applicable in forests across the eastern United States where *C. florida* occurs.

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BIOGRAPHICAL SKETCH

Eric Holzmueller was born in Des Moines, Iowa, in 1978. He received a Bachelor of Science and master's degree in forestry in 1999 and 2002, respectively, from Iowa State University, Ames, Iowa. In May of 2002 he began field work for his doctoral degree in Great Smoky Mountains National Park and began taking classes in September 2002 at the University of Florida, Gainesville, FL. After graduation, Eric will continue to work at the University of Florida School of Forest Resources and Conservation as a Postdoctoral Research Associate with his advisor, Dr. Shibu Jose.