

## IMPACTS OF AN EXOTIC DISEASE AND VEGETATION CHANGE ON FOLIAR CALCIUM CYCLING IN APPALACHIAN FORESTS

MICHAEL A. JENKINS,<sup>1,4</sup> SHIBU JOSE,<sup>2</sup> AND PETER S. WHITE<sup>3</sup>

<sup>1</sup>*National Park Service, Great Smoky Mountains National Park, Twin Creeks Natural Resources Center, 1314 Cherokee Orchard Road, Gatlinburg, Tennessee 37738 USA*

<sup>2</sup>*School of Forest Resources and Conservation, University of Florida, Box 110410, Gainesville, Florida 32611 USA*

<sup>3</sup>*Department of Biology—Campus Box 3280, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina 27599-3280 USA*

**Abstract.** Because of the high calcium content of its foliage, *Cornus florida* (flowering dogwood) has been described as a calcium “pump” that draws calcium from deeper mineral soil and enriches surface soil horizons. However, over the last two decades an exotic fungal disease (dogwood anthracnose, *Discula destructiva*) has decimated populations of this once-common understory species. Its loss, combined with forest stand development, could alter intra-stand calcium cycling. We used data from long-term vegetation monitoring plots to examine the ecological role of *C. florida* in calcium cycling and to identify changes in annual foliar calcium cycling over a 20-year period between two sampling intervals, 1977–1979 (pre-anthracnose) and 1995–2000 (post-anthracnose). Published equations were used to estimate foliar biomass per species for five forest types: alluvial, typic cove, acid cove, oak–hickory, and oak–pine. Calcium concentrations derived from foliage samples were used to estimate annual foliar calcium production per species for understory woody stems (<20 cm dbh) and total foliar calcium production for overstory stems (≥20 cm dbh). At a given level of soil calcium availability, *C. florida* foliage contained greater concentrations of calcium than three other dominant understory species (*Tsuga canadensis*, *Acer rubrum*, and *Rhododendron maximum*). Between 1977–1979 and 1995–2000, the annual calcium contributions of understory woody vegetation declined across all forest types, ranging from 26% in oak–pine stands to 49% in acid coves. Loss of *C. florida* was responsible for only 13% of this decline in oak–pine stands, but accounted for 96% of the decline in typic coves. In oak–hickory and oak–pine stands, we observed large increases in the foliar biomass of *T. canadensis*, a species whose calcium-poor foliage increases soil acidity. Increases in overstory foliar biomass and calcium offset understory losses in three forest types (alluvial, typic coves, and oak–pine) but not in oak–hickory and acid cove stands. Overall, calcium cycling in oak–hickory stands was more negatively affected by the loss of *C. florida* than the other forest types. Oak–hickory forests comprise over a third of the total forest cover in the eastern United States, and decreases in annual calcium cycling could have cascading effects on forest biota.

**Key words:** calcium cycling; *Cornus florida*; dogwood anthracnose; exotic disease; forest stand development; long-term monitoring; soil calcium availability; southern Appalachian Mountains; temperate forests; tree mortality; *Tsuga canadensis*; understory vegetation.

### INTRODUCTION

Calcium (Ca) serves many functions in regulating physiological and structural processes of plants (Jones 1998, McLaughlin and Wimmer 1999, Mengel et al. 2001). Despite its important role in plant metabolism and growth, Ca mobility is low and its uptake and distribution rate is a limiting factor for many key plant functions (Jones 1998, McLaughlin and Wimmer 1999). For these reasons, McLaughlin and Wimmer (1999) hypothesized that Ca supply exerts considerable control on both the structure and function of forest ecosystems.

Over the past two decades numerous studies have suggested that human activities are depleting ecosystem

Ca across a broad range of forests in eastern North America (Federer et al. 1989, Cronan and Schofield 1990, Johnson and Lindberg 1992, Huntington 2000, Huntington et al. 2000) and Europe (Matzner and Murach 1995, Jönsson et al. 2003). Most studies have identified atmospheric deposition of sulfur and nitrogen oxides as a cause of soil acidification, resulting in aluminum mobilization and cation leaching (Cronan and Schofield 1990, Likens et al. 1996, Lawrence et al. 1999, Driscoll et al. 2001). In addition, reduced atmospheric deposition of Ca (Johnson et al. 1994) and uptake of Ca into woody biomass (Johnson et al. 1988, Johnson and Todd 1990) have been implicated in losses of Ca within forest ecosystems.

Within forest stands, Ca loss occurs in forest-floor organic horizons as a result of aluminum migrating from deeper soil horizons and displacing Ca (Lawrence et al.

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<sup>4</sup> E-mail: [mike\\_jenkins@nps.gov](mailto:mike_jenkins@nps.gov)

1995). Because of their high nutrient content compared to mineral soil, organic horizons are the primary rooting layer in forests (Lawrence et al. 1995) and contain the majority of soil fauna (Pritchett and Fisher 1987). Calcium losses in this layer have had serious impacts on other organisms. For example, on low-nutrient soils in the Netherlands, loss of snail shells linked to acid deposition limited the reproductive success of the Great Tit (*Parus major*; Graveland 1996). In the central Appalachian Mountains, land snail density and species richness were positively correlated with Ca availability (Hotopp 2002), and a similar impact on other passerine birds may be occurring.

Woody-species composition strongly influences soil chemistry, including exchangeable aluminum concentration and Ca availability (Blair 1988, Finzi et al. 1998, Dijkstra and Smits 2002). Soils beneath *Acer saccharum* trees have greater Ca availability (Dijkstra and Smits 2002) and lower levels of exchangeable aluminum (Finzi et al. 1998) than soils beneath *Tsuga canadensis* trees. Thomas (1969) found significantly greater exchangeable Ca under *Cornus florida* trees than under *Pinus taeda*. Because of the high Ca content and rapid decomposition of its foliage (Thomas 1969, Blair 1988), numerous authors have suggested that *C. florida*, one of the most common understory trees in eastern North America, may have an important ecological role in the Ca economy of forest stands (Thomas 1969, McLemore 1990, Hiers and Evans 1997, Jenkins and White 2002). As with most woody plants, Ca concentrations increase in *C. florida* foliage throughout the growing season, and no net resorption of Ca prior to leaf abscission has been observed (Kost and Boerner 1985, Potter et al. 1987). While numerous studies have shown that overstory vegetation heavily dominates total stand biomass (Crow 1978, Rutkowski and Stottlemeyer 1993, Son et al. 2004), the relative contributions of overstory and understory woody vegetation to annual foliar biomass and Ca cycling have received limited attention.

*Cornus florida* is currently threatened across much of its range by *Discula destructiva* Redlin, a destructive fungus that causes dogwood anthracnose (Daughtrey and Hibben 1994, Holzmueller et al. 2006; see Plate 1). Genetic testing suggests that *D. destructiva* was introduced recently, possibly from Asia (Britton 1994). Mortality of *C. florida* has been severe over the past two decades throughout its range. In Franklin County, Tennessee (USA) Hiers and Evans (1997) observed a 98% decrease in *C. florida* density within a cove forest between 1983 and 1995. In western North Carolina (USA) Wyckoff and Clark (2002) observed a 15% annual mortality rate for *C. florida* between 1991 and 1998. In Great Smoky Mountains National Park (GSMNP) between the late 1970s and 2000, decreases in the density of *C. florida* ranged from 69% in oak-pine stands to >90% in cove forests (Jenkins and White 2002). Over this same period in GSMNP, the understory importance of *T. canadensis* has more than doubled

across forest types in response to the loss of *C. florida* and over 60 years of fire suppression (Jenkins and White 2002). Based on these changes, we hypothesized that the rapid loss of a "calcium-pumping" species (*C. florida*) combined with a drastic increase in a species with low levels of foliar Ca (*T. canadensis*), has altered Ca cycling and availability in the forest floor and surface soil horizons of these forests, possibly impacting a chain of associated flora and fauna. Further, we hypothesized that these impacts are more pronounced on sites with low levels of available Ca.

In this paper, we use data from a network of permanent vegetation plots in GSMNP to examine how the loss of *C. florida* trees and other changes in forest composition and structure have affected the annual cycling of Ca to the forest floor. More specifically, we address the following questions: (1) How does the Ca concentration of different understory woody species vary? (2) Does *C. florida* concentrate more Ca into its foliage than other dominant understory species on sites with low Ca availability? (3) Based upon calculated foliar biomass and Ca content, how did the amount of Ca returned to the forest floor annually by *C. florida* and other understory woody species change over a 20-year period (between 1977–1979 and 1995–2000) following anthracnose infection? (4) Based upon calculated foliar biomass and Ca content, how did the relative contributions of overstory and understory woody vegetation to foliage biomass and annual Ca cycling change over a 20-year period following anthracnose infection?

## METHODS

### *Study site*

Because of its biotic diversity, large size (>200 000 ha), and protected status, Great Smoky Mountains National Park (GSMNP), USA, is internationally renowned as a center of biological diversity. Complex ecological gradients combine to create a diverse mosaic of biological communities. Elevations in the Park range from 267 m to 2025 m and the rugged topography includes rocky summits, incised drainages, talus slopes, and level valleys. Annual rainfall varies from 140 cm at low elevations to >200 cm on some high peaks. Seventy-nine unique vegetation associations comprised of nearly 1600 species of vascular plants have been identified within GSMNP (White et al. 2003, NPSpecies 2006). Because over 20% of the Park was never cleared of timber, GSMNP also contains one of the largest tracts of primary forest in eastern North America (Pyle 1988).

Between 1977 and 1979, 287 permanent 0.1-ha (50 × 20 m) vegetation plots were established in the western end of GSMNP (White and Busing 1993). Watersheds were divided into sample sites based upon elevation, slope position, and aspect, and plots were randomly located within each sample site. These plots cover a broad range of site conditions and disturbance histories and include areas of mature forest, abandoned agricul-

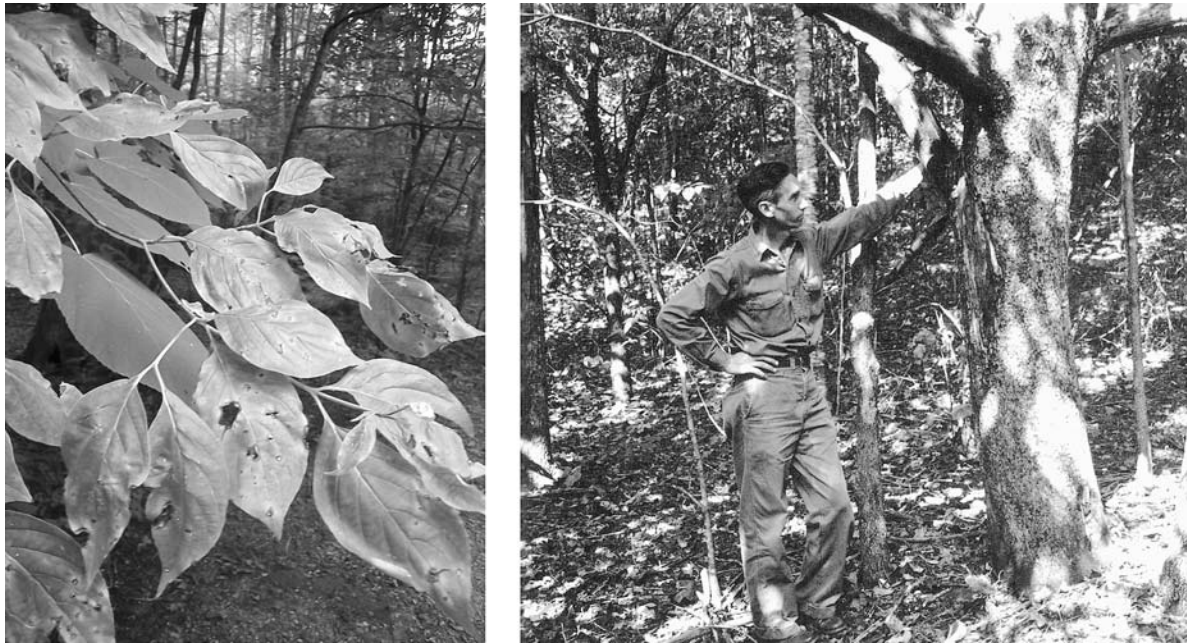


PLATE 1. (Left) Flowering dogwood (*Cornus florida*) foliage during the early stage of infection with dogwood anthracnose (*Discula destructiva*). The edges of the leaves show the first symptoms of the disease, developing spots that extend down the leaf margins as the disease progresses. The fungus eventually reaches the bole of the tree where cankers develop, girdling and killing the tree. Infected trees growing in shaded conditions may die within 1–3 years of first infection; saplings may die in the same year they are infected. Photo credit: National Park Service. (Right) Photographed in 1959, this *C. florida* tree was thought to be the largest ever documented in GSMNP. Prior to anthracnose, *C. florida* often dominated the understory of stands that regenerated after logging and agricultural use. Photo credit: National Park Service.

tural land, limestone substrates, and past burning. For this study, we used data from 84 plots that contained *Cornus florida* and were resampled as part of GSMNP's long-term monitoring program and other research projects. Plot data were used to classify plots into five broad forest types: acid cove, typic cove, alluvial, oak–hickory, and oak–pine (Jenkins and White 2002). Recent evaluation of data from plots that did not contain dogwood in 1977–1979 revealed that there has been little or no invasion of *C. florida* into new areas.

Acid cove forests were on gentle to moderately steep slopes and flats between 430 and 860 m elevation. They were often located near streams within concave and v-shaped drainages. Typic cove forests were in more-protected topographic positions on gentle to moderate slopes with northerly aspects and elevations of 410–890 m. Alluvial forests were found on flats along medium-sized perennial streams between 330 and 640 m elevation. Soils underlying this forest type were relatively deep and loamy with large rocks. Most alluvial forest stands were formerly cleared for farming and settlement (Pyle 1988). Oak–hickory forests were generally on moderately steep northwest to south facing slopes ranging from 310 to 1020 m elevation and oak–pine forests were typically found on narrow ridges and knobs, middle and upper slopes, and other exposed sites. Aspects were generally southeast–northwest and slopes were gentle to moderately steep.

#### Field sampling and laboratory analysis

Data were collected from 84 permanent plots during two sampling intervals: 1977–1979 and 1995–2000. Plots were distributed across five forest types, alluvial forests ( $n = 11$ ), typic cove forests ( $n = 16$ ), acid cove forests ( $n = 13$ ), oak–hickory forests ( $n = 34$ ) and oak–pine forests ( $n = 10$ ). Within each  $20 \times 50$  m plot, the dbh (diameter at breast height = 1.37 m) of all living stems  $\geq 1$  cm dbh was measured to the nearest 0.1 cm and recorded by species during the 1977–1979 survey, and for 76 of 84 plots remeasured during the 1995–2000 survey. For eight plots remeasured between 1995 and 2000, the density of all trees  $< 10$  cm dbh were tallied by species into two dbh classes: 1–4.9 cm and 5.0–9.9 cm. On these eight plots, the dbh of all trees  $\geq 10$  cm was measured and recorded by species.

Soil was sampled at 8 to 10 points throughout each plot and pooled into one sample per plot. At each sampling point within a plot, a hand spade was used to collect a sample of mineral soil from the A-horizon. Sampling depth was  $\sim 10$  cm on most plots. Samples were dried at  $43^\circ\text{C}$  for 8 h, ground, and sifted through a 2-mm (number 10 mesh) sieve. Calcium and other cations were extracted from the soil by mixing 25 mL of 1 mol/L neutral, ammonium acetate with 5 g of soil and shaking for 30 min (Suarez 1996). The filtered extract was analyzed with an inductively coupled plasma atomic emission spectrometer to determine the molar equiva-

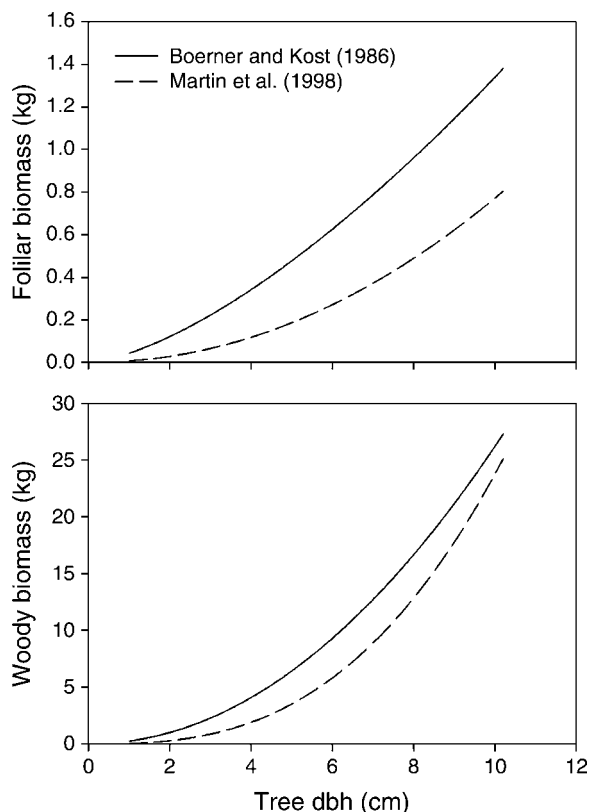


FIG. 1. Woody and foliar biomass curves for *Cornus florida* based upon equations developed by Boerner and Kost (1986) and Martin et al. (1998). Boerner and Kost (1986) equations were developed prior to the onset of dogwood anthracnose; Martin et al. (1998) equations were developed after impacts of anthracnose. The two sets of equations yield similar results for woody biomass, but Martin et al. (1998) yields much less foliar biomass for a given tree diameter.

lents of cations, including calcium (ICP-AES [inductively coupled plasma atomic emission spectrometer]; Soltanpour et al. 1996). This procedure saturates all soil exchange sites with ammonium ions (Sumner and Miller 1996). The ammonium ions are then dislodged with an acidic extractant and the cation exchange capacity (CEC) is calculated from the amount of ammonium thus displaced. The molar equivalents of individual cations (including calcium) are compared to the CEC and the base saturation percentage of each cation is determined. All soil analyses were performed by A&L Analytical Laboratories, Memphis, Tennessee, USA.

Between late August and late October of both 2001 and 2003 we collected foliage from *C. florida* trees across the 84 plots we resampled. We also sampled the two or three most common understory woody species other than *C. florida* present in each plot. Typically, three individual trees of each species were sampled. However, no living *C. florida* trees remained on 16 plots, and on many plots there were fewer than three living *C. florida* trees. We used telescopic pole cutters to collect foliage at

various positions in the crown to account for leaf development in response to varying light levels within the canopy. Specifically, the crown was divided into four quarters and leaves were collected from throughout each quarter when possible. A cord with a weight attached was thrown over higher branches and used to bend them down for sampling with the pole cutters. Generally, we were unable to collect foliage samples from overstory trees ( $\geq 20$  cm dbh). We combined all leaves from each tree into a single composite sample.

All samples were dried at  $65^{\circ}\text{C}$  for 72 h and fine-ground using a coffee grinder. All subsequent analyses were performed at the Analytical Research Laboratory of the University of Florida in Gainesville, Florida, USA. Samples were digested in a muffle furnace at  $500^{\circ}\text{C}$  for five hours before being dissolved in 6 mol/L HCl. Concentrations of Ca were determined on an inductively coupled plasma emission spectrometer (Perkin-Elmer Plasma 400ICP/AES; Perkin-Elmer, Norwalk, Connecticut, USA). All Ca concentrations are presented as milligrams per liter, mg/L.

#### Foliar biomass

Foliar biomass was calculated from dbh data using allometric equations (Appendix A). We did not calculate foliar biomass of *Rhododendron maximum* or *Kalmia latifolia*. All published biomass equations for these two species were based upon diameter at ground level, which is not measured as part of the GSMNP Vegetation Monitoring Protocols.

*Cornus florida* foliar biomass from the 1977–1979 sampling interval was estimated using a species-specific equation developed by Boerner and Kost (1986) prior to infection by dogwood anthracnose. For the 1995–2000 remeasurement, *C. florida* biomass was calculated with both the Boerner and Kost (1986) equation and a species-specific equation developed by Martin et al. (1998) in the southern Appalachians after dogwood anthracnose infection. While the equations of Boerner and Kost (1986) and Martin et al. (1998) show similar relationships between dbh and woody biomass, the output of the Martin et al. (1998) equation suggests that post-anthracnose stands are producing considerably less foliar biomass (Fig. 1). All foliar biomass values were converted to kilograms per hectare, kg/ha. Mean foliar biomass was calculated per species for each of the five forest types. Biomass was calculated separately for understory ( $< 20$  cm dbh) and overstory ( $\geq 20$  cm dbh) vegetation. We used 20 cm dbh as the break between understory and overstory vegetation since it represented the maximum diameter for *C. florida* trees in both temporal sample intervals.

#### Foliar calcium

On each plot, foliar Ca concentrations (in milligrams per liter, mg/L) of all trees were averaged by species. To determine foliar Ca content of each species on a plot, we converted this average Ca concentration to a percentage

TABLE 1. Tree sampling data for the 84 Great Smoky Mountains National Park (USA) resampled plots together with calcium concentration data for the various species, arranged in descending order of Ca concentration.

Species	Common name	No. sampled	Freq.†	Ca concentration (mg/L)‡	
				Mean ± SE	Range§
<i>Tilia americana</i>	American basswood	2	13	22 300 ± 5610	16 690–27 910
<i>Liriodendron tulipifera</i>	tulip poplar	7	34	17 400 ± 2692	8120–27 170
<i>Cornus florida</i>	flowering dogwood	120	68	17 302 ± 621	3289–34 460
<i>Fraxinus americana</i>	white ash	2	18	14 870 ± 4470	10 400–19 340
<i>Acer saccharum</i>	sugar maple	15	25	13 109 ± 758	8520–20 560
<i>Halesia tetraptera</i>	mountain silverbell	41	47	13 002 ± 431	8500–19 280
<i>Carpinus caroliniana</i>	American hornbeam	6	14	12 745 ± 1477	9490–19 400
<i>Rhododendron maximum</i>	rosebay rhododendron	42	25	11 705 ± 362	4551–16 890
<i>Acer pensylvanicum</i>	striped maple	5	47	11 014 ± 2234	7240–19 610
<i>Carya</i> spp.	hickory species	3	49	9823 ± 382	9070–10 300
<i>Betula lenta</i>	black birch	2	45	9575 ± 2175	7400–11 750
<i>Magnolia</i> spp.	magnolia species	3	35	9560 ± 1494	7220–12 340
<i>Kalmia latifolia</i>	mountain laurel	6	15	9205 ± 357	8240–10 740
<i>Oxydendrum arboreum</i>	sourwood	9	54	9120 ± 880	6420–14 960
<i>Lindera benzoin</i>	spicebush	3	6	8483 ± 1651	6430–11 750
<i>Acer rubrum</i>	red maple	117	81	8268 ± 238	3677–17 230
<i>Nyssa sylvatica</i>	blackgum	18	49	7862 ± 362	5440–10 670
<i>Quercus</i> spp.	oak species	8	50	7341 ± 677	5730–11 130
<i>Tsuga canadensis</i>	eastern hemlock	184	76	4632 ± 114	1826–10 370
<i>Pinus</i> spp.	pine species	3	18	3601 ± 780	2041–4400
<i>Pinus strobus</i>	white pine	24	54	2920 ± 158	1951–4859

† Frequency = number of plots (out of the total 84 plots) on which the species was found.

‡ Calcium concentration of foliage.

§ Calcium concentration range by species across all plots sampled in 1995–2000.

and multiplied this value by the foliar biomass of each species. On plots with 100% *C. florida* mortality, Ca concentration values of the nearest plot of the same forest type were used to calculate foliar Ca content in 1977–1979. Since some of the species on our plots are conifers that do not drop all their leaves in a given year, we used leaf life-span values determined by Reich et al. (1999) to estimate the proportion of leaves dropped yearly for each species. These values were: 60 months for *T. canadensis*, 21 months for *P. strobus* and 33 months for yellow pine species (*Pinus echinata*, *P. rigida*, and *P. virginiana*). While we did not collect foliage samples from several less common species, on average our Ca concentration data allowed us to determine the Ca content of >96% of the foliar biomass calculated for each plot. All Ca-content values were converted to kilograms per hectare, kg/ha. Mean values were calculated by species for understory vegetation (<20 cm dbh) in each of the five forest types.

#### Data analysis

We used nonlinear regression to examine how the four dominant understory species (*C. florida*, *Tsuga canadensis*, *Acer rubrum*, and *R. maximum*) differ in their ability to concentrate foliar Ca on sites with low Ca availability. A nonlinear response curve was used to describe the relationships between foliar Ca content of each species (response variable) and percentage soil Ca saturation (predictor variable). We used percentage Ca cation saturation to represent available soil Ca since this measurement best represents the ease with which Ca may be displaced and taken up by plants (Brady 1990).

A nonlinear function was also used to examine the relationship between the foliar-to-soil Ca ratio and percentage soil Ca saturation. We estimated four parameters using the Marquardt-Levenberg nonlinear least squares algorithm. Plots of Studentized residuals vs. fitted values were used to assess the regression assumption of constant variance (Neter et al. 1996). Residual plots and standard techniques were used to screen for and evaluate the influence of potential outliers (Neter et al. 1996).

We used two-way repeated-measures ANOVA with sampling interval as the repeated factor and forest type as the nonrepeated factor to compare changes in individual understory species (including *C. florida*) biomass and Ca between sampling intervals and among forest types. Two-way repeated-measures ANOVA was also used to compare changes in total understory foliar biomass, total overstory foliar biomass, and total foliar biomass (understory and understory). Changes in total overstory Ca content were also compared using two-way repeated-measures ANOVA. Log<sub>10</sub>- and square-root transformations were used to homogenize variances and improve normality when necessary. Nontransformed summary data are presented for ease of interpretation.

## RESULTS

### Understory foliar calcium concentrations and uptake

The foliar Ca concentration of understory woody vegetation varied greatly (Table 1). Concentrations ranged from 2920 mg/L for *Pinus strobus* to 22 300 mg/L for *Tilia americana*. *Cornus florida* and *Liriodendron tulipifera* foliage contained the next highest Ca

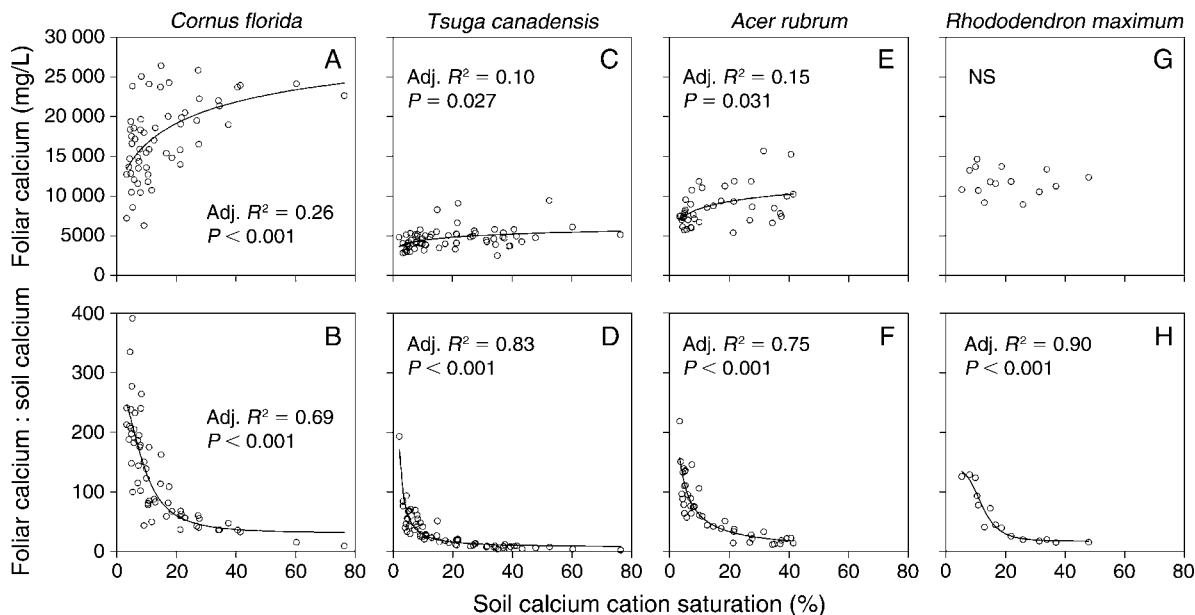


FIG. 2. Regression curves of foliar calcium and the ratio of foliar Ca to soil Ca vs. percentage soil Ca cation saturation for (A and B) *Cornus florida*, (C and D) *Tsuga canadensis*, (E and F) *Acer rubrum*, and (G and H) *Rhododendron maximum*. Curves were fit with the equation  $f = (a - d) / [1 + (x/c)^b] + d$ .

concentrations (17 302 and 17 400 mg/L, respectively). Among the dominant understory species (*C. florida*, *Acer rubrum*, *Tsuga canadensis*, and *Rhododendron maximum*), *C. florida* foliage contained the greatest concentration of Ca. The Ca concentration of *A. rubrum* (8268 mg/L) was less than half that of *C. florida*, and that of *T. canadensis* was less than a third (4632 mg/L). Compared to *A. rubrum* and *T. canadensis*, *R. maximum* foliage was relatively rich in Ca (11 705 mg/L). *Cornus florida* foliage exhibited the greatest range of Ca concentrations and highest single-plot value of any species (34 460 mg/L).

*Cornus florida* displayed greater uptake of Ca into its foliage than did the other dominant understory species. *Cornus florida* foliage contained more Ca at a given level of soil Ca saturation than *T. canadensis*, *A. rubrum*, or *R. maximum* (Fig. 2). In addition, *C. florida* Ca concentration continued to increase with increasing soil Ca saturation after the curves of the other species leveled off. *Cornus florida* exhibited a much greater relative concentration of Ca in its foliage on low-Ca sites than did the other three dominant species, and *C. florida* also exhibited a much higher ratio of foliar Ca to soil Ca than other species on sites with low soil Ca saturation. The foliar Ca concentrations and foliar Ca to soil Ca ratios of the other three species showed much less change with increasing soil Ca saturation compared to *C. florida*.

#### Changes in understory foliar biomass and calcium content

Both understory foliar biomass and foliar Ca contributions have declined within the five forest types (Appendix B). Typic coves exhibited the greatest decline

in foliar biomass (from 683 kg/ha in 1977–1979 to 365 kg/ha in 1995–2000; 47% decline) and alluvial and oak–pine stands exhibited the least decline (from 1339 kg/ha to 1039 kg/ha and from 1492 kg/ha to 1157 kg/ha, respectively; a 22% decline for both types). Oak–hickory and acid cove stands exhibited moderate decreases in foliar biomass. Foliar biomass declined 34% in oak–hickory forests (from 1238 kg/ha to 818 kg/ha) and 38% in acid coves (from 925 kg/ha to 569 kg/ha). However, acid cove and oak–hickory stands exhibited the greatest decrease in total foliar Ca content. In acid cove understories, foliar Ca inputs declined from 8.16 kg/ha to 4.16 kg/ha; a 49% decline. In oak–hickory stands, Ca inputs declined from 11.57 kg/ha to 6.73 kg/ha; a 42% decline. Calcium input declines in the understories of the other three forest types ranged from 23% in typic coves (from 7.76 kg/ha to 5.95 kg/ha) to 27% in alluvial stands (11.14 kg/ha to 8.08 kg/ha).

We observed a significant interaction ( $P < 0.001$ ) between forest type and sampling interval for total understory foliar biomass, indicating differences in the decline among forest types. In 1977–1979 there were no significant differences in biomass among forest types. However, in 1995–2000 typic coves contained less foliar biomass than the other three forest types ( $P < 0.001$  for all types). In addition, oak–pine stands also contained greater foliar biomass than acid cove stands in 1995–2000 ( $P < 0.001$ ). While two-way repeated-measures ANOVA revealed a significant interaction between forest type and sampling interval for total biomass (combined overstory and understory) post hoc tests showed no significant differences ( $P > 0.1$  for all types).

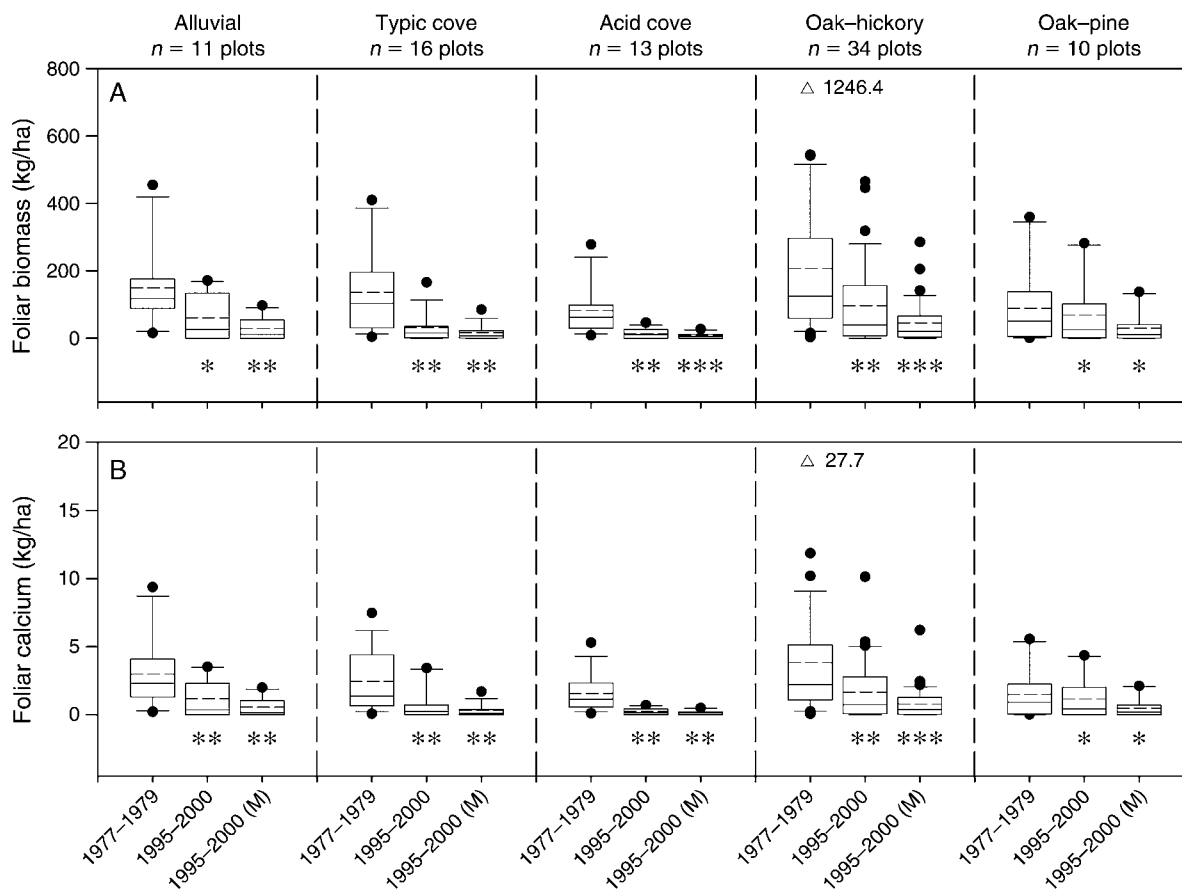


FIG. 3. Annual foliar (A) biomass and (B) calcium inputs from *Cornus florida* on five forest types. Values for the 1977–1979 and 1995–2000 sampling intervals were calculated using the foliar biomass equation developed by Boerner and Kost (1986). The equation developed by Martin et al. (1998) was also used to calculate values for the 1995–2000 sampling interval [“1995–2000 (M)”]. Plots show means (dashed horizontal lines), medians (solid horizontal lines), 25th and 75th percentiles (box ends), and 10th and 90th percentiles (whiskers). All outliers are also depicted (●). Values are provided for two outliers (Δ) in oak–hickory forests that were outside the range of the y-axis. Two-way repeated-measures ANOVA with Tukey’s multiple-comparison tests were used to compare 1977–1979 means to 1995–2000 and 1995–2000 (M) means across all forest types: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

#### Changes in the contribution of *C. florida* to foliar biomass and calcium cycling

The loss of *C. florida* between 1977–1979 and 1995–2000 has resulted in a loss of *C. florida* foliar biomass and foliar Ca content within the five forest types (Fig. 3). Prior to the onset of dogwood anthracnose infection, mean *C. florida* foliar biomass ranged from 81 kg/ha on acid cove plots to 207 kg/ha on oak–hickory plots. The decrease in biomass and Ca content was greatest in acid coves, where *C. florida* foliar biomass and Ca content declined by 84 and 85%, respectively. However, *C. florida* foliar biomass and Ca content were greatest in oak–hickory stands, where mean foliar Ca contributions declined from 3.84 kg/ha in 1977–1979 to 1.66 kg/ha in 1995–2000. Interestingly, foliar Ca contributions in 1977–1979 showed a large range on individual plots across forest types, varying from a low of 0.24 kg/ha in acid cove stands to a maximum of 27.72 kg/ha in oak–hickory stands. Following the impacts of anthracnose, oak–hickory stands still contained the greatest *C. florida*

foliar biomass and Ca content, although inputs declined by 53 and 57%, respectively. Following anthracnose infection, the range of Ca inputs from *C. florida* on individual plots ranged from a low of 0 kg/ha and to a maximum of 10.13 kg/ha in oak–hickory stands. Foliar Ca inputs after anthracnose infection, based upon the foliar biomass equation developed by Martin et al. (1998), were much lower than pre-anthracnose levels, with no forest type exceeding a mean input of 1 kg/ha. In addition, the maximum input on an individual plot was only 6.23 kg/ha in an oak–hickory stand.

Loss of *C. florida* accounted for much of the loss in understory Ca cycling across the five forest types (Appendix B). In typic cove stands, the loss of *C. florida* was responsible for 96% of the observed decrease in calcium inputs between 1977–1979 and 1995–2000. The loss of *C. florida* accounted for 59% of the observed loss in alluvial stands, 45% in oak–hickory stands, and 33% in typic cove stands. The loss of *C. florida* made

relatively minor contribution (13%) to the total loss of Ca in oak–pine stands.

We observed a significant interaction between forest type and sampling interval for *C. florida* foliar biomass, indicating differences in the decline among forest types. Results from Tukey pairwise multiple-comparison tests show no significant differences in foliar biomass for the first sampling interval (1977–1979;  $P$  values ranged from 0.061 to 0.983). However, in 1995–2000 oak–hickory plots contained greater foliar biomass than did acid cove plots ( $P = 0.006$ ). The interaction between forest type and sampling interval was insignificant for foliar Ca content ( $P = 0.212$ ).

#### *Changes in the contributions of other understory species to foliar biomass and calcium content*

In addition to changes in understory foliar biomass and Ca content resulting from the loss of *C. florida*, we observed changes in the foliar biomass and Ca of other species across the five forest types (Appendix B). In alluvial understories, foliar biomass from *Pinus* spp. declined from 175 kg/ha to 24 kg/ha and foliar Ca content declined from 0.63 kg/ha to 0.09 kg/ha ( $P < 0.05$  and  $P < 0.001$ , respectively). In addition, Ca inputs from *L. tulipifera* decreased from 1.80 kg/ha to 1.17 kg/ha ( $P < 0.1$ ), but inputs from *T. canadensis* increased slightly from 0.69 kg/ha to 0.83 kg/ha ( $P < 0.05$ ). In typic coves, understory foliar biomass and Ca contributions from *Halesia tetraptera* declined ( $P < 0.05$  and  $P < 0.001$ , respectively). Calcium contributions from understory *L. tulipifera* trees also declined in typic coves (from 0.94 kg/ha to 0.38 kg/ha;  $P < 0.01$ ). In acid coves, the foliar biomass and Ca contributions of *Oxydendrum arboreum* and *Carya* spp. declined. Oak–hickory stands exhibited declines in the foliar biomass and calcium contributions of *A. rubrum*, *Carya* spp., *O. arboreum*, and *Quercus* spp. The inputs of foliar Ca from *T. canadensis* increased in oak–hickory stands from 0.61 kg/ha to 0.94 kg/ha. This increase only offset a small portion of the total Ca loss in this forest type (4.84 kg/ha between 1977–1979 and 1995–2000). In 1977–1979, *Quercus* spp. contributed more foliar biomass and Ca than any other species in oak–pine stands (531 kg/ha and 3.9 kg/ha, respectively). However, in 1995–2000 both foliar biomass (163 kg/ha) and Ca (1.24 kg/ha) contributions from *Quercus* spp. declined greatly (69% and 68%, respectively).

Two-way repeated-measures ANOVA revealed a significant interaction between sampling interval and forest type for foliar biomass of *Quercus* spp. However, post hoc tests revealed no changes in relative foliar biomass of *Quercus* spp. among forest types between sampling intervals. During both sampling intervals, oak–pine and oak–hickory stands contained greater *Quercus* spp. foliar biomass than the other forest types ( $P < 0.05$  for all types). Analyses also revealed a significant interaction for *A. pensylvanicum*. In 1977–1979, the foliar biomass of *A. pensylvanicum* did not

differ among forest types ( $P > 0.05$  for all types). In 1999–2000, oak–hickory stands contained greater foliar biomass of this species than either alluvial or oak–pine stands ( $P = 0.006$  and  $P = 0.040$ , respectively).

Several individual species or species groups (*O. arboreum*, *Carya* spp., *Pinus* spp., and *Quercus* spp.) exhibited significant interactions between forest type and sampling interval for foliar Ca content. In 1977–1979, understory *O. arboreum* trees in typic cove stands contributed less Ca than in any other forest type ( $P < 0.05$  for all types). In 1995–2000, contributions of Ca from this species were significantly greater in alluvial stands than in typic coves ( $P = 0.006$ ), but no other differences existed among forest types. In 1977–1979, Ca contributions from *Carya* spp. were greater in oak–hickory stands than in any other forest type ( $P < 0.01$  for all types). In 1995–2000, the difference in Ca contributions was no longer significant between oak–hickory stands and alluvial stands ( $P = 0.134$ ). In 1977–1979, alluvial and oak–pine stands received significantly greater Ca contributions from *Pinus* spp. than did the other forest types ( $P < 0.001$  for all types). However, in 1995–2000, alluvial stands no longer received greater contributions from this species group ( $P > 0.7$  for all types). In 1977–1979, oak–pine stands received significantly greater Ca contributions from *Quercus* spp. than typic cove, acid cove, alluvial, and oak–hickory stands ( $P < 0.001$  for all types). In addition, oak–hickory stands received greater contributions than typic cove, acid cove, and alluvial stands ( $P < 0.001$  for all types). In 1995–2000, oak–pine stand contributions were still significantly greater than the other four forest types ( $P < 0.05$  for all types), but differences between oak–hickory stands and the other forest types were no longer significant ( $P > 0.1$  for all types).

#### *Changes in relative contributions of understory and overstory vegetation*

Foliar biomass of the understory layer varied by forest type and generally decreased between the 1977–1979 and 1995–2000 sampling intervals (Fig. 4). In 1977–1979, the woody understories of oak–pine and alluvial forest stands contributed 44% and 49% of total foliar biomass, respectively. However, by 1995–2000, this contribution declined to 32% for both forest types. Understory vegetation contributed 33% of foliar biomass in oak–hickory stands in 1977–1979, but only 24% in 1995–2000. Typic and acid cove stands exhibited similar decreases in the percent of foliar biomass contributed by understory vegetation, a decrease from approximately 25% in both types to 15% and 18%, respectively. Losses of understory foliar biomass were offset in alluvial and oak–pine stands by increases in overstory foliar biomass (Fig. 4). Overstory foliar biomass increased from  $1721 \pm 318$  kg/ha to  $2201 \pm 293$  kg/ha (28%;  $P = 0.007$ ) in alluvial stands and from  $1542 \pm 298$  kg/ha to  $2460 \pm 397$  kg/ha (60%;  $P = 0.007$ ) in oak–pine stands (all data: means  $\pm$  SE).



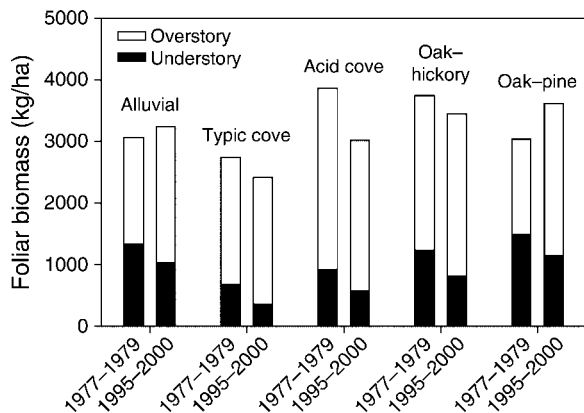


FIG. 4. Changes in the relative contribution of understory and overstory woody vegetation to foliar biomass of five forest types between 1977–1979 and 1995–2000.

While all forest types exhibited decreases in Ca contributed by understory vegetation, inputs from the overstory increased on four forest types (Fig. 5). Foliar Ca content in oak–pine stands increased from  $8.8 \pm 1.5$  kg/ha to  $14.4 \pm 1.5$  kg/ha ( $P = 0.004$ ), a 64% increase. In alluvial stands, inputs of Ca from overstory foliage increased from  $9.6 \pm 2.3$  to  $13.2 \pm 2.4$  kg/ha ( $P = 0.001$ ), a 36% increase. Calcium inputs from overstory foliage increased less in typic cove and oak–hickory stands (17% and 6%, respectively). In typic coves, Ca inputs from overstory foliage increased from  $24.8 \pm 4.1$  to  $29.1 \pm 2.5$  kg/ha ( $P = 0.041$ ). In oak–hickory stands, inputs increased from  $18.5 \pm 2.3$  to  $19.6 \pm 1.2$  kg/ha ( $P = 0.033$ ). Foliar Ca inputs from overstory vegetation did not change significantly in acid cove stands ( $24.0 \pm 5.7$  kg/ha to  $20.0 \pm 2.3$  kg/ha;  $P = 0.469$ ). Our analyses revealed no significant interactions between forest type and sampling interval for understory or overstory foliar Ca content.

DISCUSSION

Calcium uptake by *C. florida* and other understory species

In our study, *Cornus florida* concentrated more Ca in its foliage on low Ca sites than other common understory species (*Tsuga canadensis*, *Acer rubrum*, or *Rhodendron maximum*). The ratio of foliar to gross soil Ca was remarkably higher on sites with low levels of available Ca. Kost and Boerner (1985) observed that *C. florida* trees accumulated Ca most efficiently on the least fertile sites, producing 30–35% more leaf mass per unit Ca in mixed oak vs. mixed mesophytic forests. In a comparative study of *A. saccharum* and *T. canadensis*, Dijkstra and Smits (2002) found that most Ca cycling occurs in surface soils, and a relatively small amount of Ca uptake from deep soil is able to sustain high amounts of available Ca in the surface soil.

Future stand development could further decrease available Ca in the forest floor and surface soils. Exchangeable Ca in the forest floor and surface soil

horizons decreases through time, primarily due to high rates of Ca incorporation into the woody tissue of overstory trees (Johnson et al. 1988). Without *C. florida* serving as a “calcium pump” for the forest floor, the effects of Ca locked up for decades into woody tissue are augmented. In additions to its high rate of Ca uptake, *C. florida* litter decomposes more quickly than competing species. Blair (1988) found that *C. florida* litter decomposed more rapidly than both *A. rubrum* and *Quercus prinus*. Because of its higher initial Ca concentration, efficient production of foliar biomass, and rapid decomposition, *C. florida* provided sustained and regular inputs of Ca into the forest floor prior to anthracnose infection.

Changes in the contribution of *C. florida* to annual calcium cycling

Our results show that the loss of *C. florida* trees that resulted from dogwood anthracnose has reduced the amount of calcium annually cycled through the leaf litter of understory vegetation. Much of this loss in alluvial, typic cove, and oak–pine stands may have been counterbalanced by increased contributions from overstory foliage (Fig. 5). However, acid cove and oak–hickory stands, the two forest types that experienced the greatest loss in annual Ca contributed by understory foliage, exhibited slight (oak–hickory) or no (acid cove) increase in overstory foliar Ca inputs to compensate for understory losses.

The biological significance of net losses in annual Ca distributed to the forest floor is difficult to assess. Because we were unable to collect litter samples from overstory trees, direct comparisons between overstory and understory foliar Ca must be made with caution. Foliar Ca concentrations have been shown to vary within species as a result of age, height, crown class, and microenvironment (Van Den Driessche 1974). The concentrations of Ca in our study are similar to those determined by Day and Monk (1977) in a study conducted at Coweeta Hydrologic Laboratory (Otto,

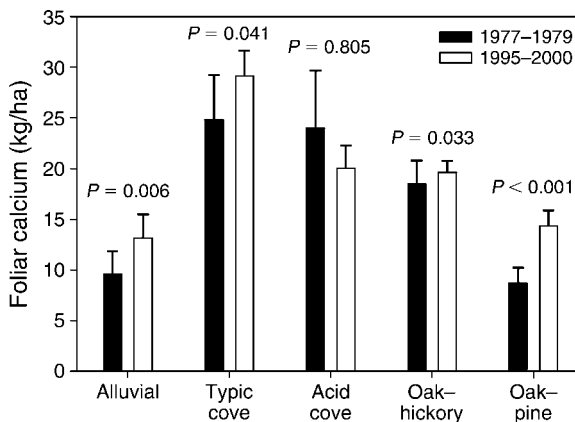


FIG. 5. Changes in foliar calcium of overstory vegetation from five forest types between 1977–1979 and 1995–2000.

North Carolina, USA) that included both understory and overstory trees. In addition, the relative concentrations of foliar Ca across species is nearly identical between Day and Monk (1977) and our study. However, given the potential limitation of our Ca concentration data, we have only made temporal comparisons (1977–1979 vs. 1995–2000) of relative changes in overstory foliar Ca and do not present our results as a definitive quantification of overstory Ca contents of individual species.

The summed overstory and understory contribution prior to anthracnose from our study (30 kg/ha) is similar to those reported for another oak–hickory forest in east Tennessee, USA (34 kg/ha; Johnson and Todd 1990), and a mixed-hardwood forest adjacent to Great Smoky Mountains National Park (GSMNP) (27 kg/ha; Gist and Crossley 1975) for the same period. If we assume that our total foliar Ca value is an acceptable approximation, then the oak–hickory stands we sampled have sustained a 12% decline in annual foliar Ca contributions. More striking, prior to anthracnose across the five forest types, we observed a wide range in the amount of foliar Ca contributed by *C. florida* in individual stands: from 0.2 kg/ha to 27.7 kg/ha. This suggests that *C. florida* trees may have created “hot spots” of Ca within forest stands.

In a study conducted in the southern Appalachians (USA), Knoepp et al. (2005) found that the initial concentration of Ca in *C. florida* after leaf fall declined 18% between 1969–1970 and 1992–1993 sampling intervals. In addition to Ca, Knoepp et al. (2005) also observed overall declines in concentrations of phosphorus, magnesium, and potassium for *C. florida*, *Q. prinus*, *Q. alba*, *A. rubrum*, and *Pinus strobus* for the same time intervals. This suggests that the cation concentration of leaf litter in the southern Appalachians may have declined, regardless of species. Consequently, our estimates of foliar Ca contributions in 1977–1979 may underestimate actual values since we derived our Ca concentration data from samples gathered in 2001 and 2003.

#### *Contributions of other understory species to foliar biomass and annual calcium cycling*

Within our study area, the relative importance of *T. canadensis* in the understory increased over time in all forest types (Jenkins and White 2002). While the gross contribution of *T. canadensis* to annual foliar biomass and Ca increased in oak–hickory and oak–pine forests, its relative contributions increased for all forest types. Most striking was the increase in *T. canadensis* foliar biomass in oak–hickory stands, where the contribution from this species increased from 10% to 26% of total foliar biomass. In addition, the contribution of hardwood trees in oak–hickory stands to foliar biomass declined from 64% to 48% between sampling intervals. The forest floor and surface soil under canopies of *T. canadensis* have been shown to have lower pH, reduced

exchangeable Ca and Mg, and greater exchangeable Al and Fe than that which occurs under hardwood canopies (Finzi et al. 1998). Because *T. canadensis* saplings grow more rapidly in low-calcium soils (Kobe 1996), the loss of *C. florida* from the forest understory may have contributed to the rapid increase in *T. canadensis* dominance. *Tsuga canadensis* is highly shade tolerant and the loss of *C. florida* and subsequent replacement by *T. canadensis* has accelerated succession in these stands. Further, increased soil acidity and reduced cation availability have been shown to increase the virulence of dogwood anthracnose (Britton et al. 1996; Holzmüller et al., *in press*). Consequently, increased soil acidification and cation leaching resulting from *T. canadensis* litter and atmospheric deposition may have accelerated foliage loss and mortality of *C. florida* trees due to anthracnose.

If understory *T. canadensis* trees are able to persist and reach the canopy, the amount of exchangeable Ca in the surface soil in these stands may be drastically reduced. A model derived by Dijkstra and Smits (2002) showed that on sites with high total mineral Ca concentrations, dominance by *T. canadensis* reduced exchangeable Ca in the surface soil by ~75% in 150 years. However, with the recent onset of the exotic hemlock woolly adelgid (*Adelges tsugae*) in GSMNP, *T. canadensis* will likely experience heavy mortality (Taylor 2002), further altering species composition and nutrient cycling within these stands.

Because of the lack of suitable biomass equations, we did not include foliar biomass or Ca contributions from *R. maximum* or *Kalmia latifolia* in this study. *Kalmia latifolia* was not a major understory species in the stands we sampled, but *R. maximum* was the second most dominant understory species in acid coves, second only to *T. canadensis* (Jenkins and White 2002). However, the importance of this species was unchanged between 1977–1979 and 1995–2000 (Jenkins and White 2002). Consequently, the contributions of *R. maximum* to foliar biomass and Ca cycling can likely be viewed as a constant input between sampling intervals. In addition, our results show that *R. maximum* foliage contains a relatively moderate concentration of Ca ( $11705 \pm 362$  mg/L) compared to other species we sampled, and according to Reich et al. (1999) the life span of *R. maximum* leaves is 48 months, suggesting that it is less of a contributor to yearly foliar biomass cycling than most deciduous species.

#### *Relative contributions of understory and overstory vegetation*

The results of our study show that understory vegetation is a major contributor to total foliar biomass in some forest stands. In the 1970s, understory vegetation in GSMNP contributed up to 49% of total stand foliar biomass. In three 31–34 yr-old mixed-oak stands in Korea, Son et al. (2004) found that understory vegetation contributed only 3–13% of the stands total

foliar biomass. However, these stands were still in the stem-exclusion stage of stand development (Oliver and Larson 1996) and other studies have shown that total foliage biomass increases with stand age (Long and Turner 1975, Santa Regina et al. 2001). Across all forest types in this study, foliar biomass contributed by understory vegetation decreased between sampling intervals. The plots we sampled in this study were in areas that were subjected to logging, broadcast burning, and livestock grazing prior to the creation of GSMNP (Pyle 1988). Due to ongoing stand development, canopies on these plots likely have become more closed since the 1970s, resulting in reduced understory density and biomass. The contribution of the overstory to foliar biomass and calcium content has increased as a result of crown expansion and canopy closure.

As stands reach the understory reinitiation stage of development, the woody understory will become more developed (Oliver and Larson 1996) and may make a larger contribution to total foliar biomass and Ca content. As canopy trees begin to decline and die, the contribution of the overstory to foliar biomass and calcium content may decrease. Because the woody-species compositions of the overstory and understory layers are often very different, the contribution of Ca per unit mass from the two layers may differ. For example, throughout much of the Midwestern United States the understories of oak stands are dominated by *Acer saccharum* (Pallardy et al. 1988, Jenkins and Parker 1998), a species whose litter is typically much richer in calcium than oaks (Table 1).

#### *Ecological impacts and management implications*

Our results suggest that oak–hickory forests are the most likely of the five forest types to have been affected by decreased cycling of Ca resulting from the loss of *C. florida* and the drastic increase in the understory importance of *T. canadensis*. This forest type experienced a 42% decline in the amount of Ca cycled by understory woody vegetation; a loss that was not completely offset by increased overstory contributions. In the eastern United States, oak–hickory forest comprises 34% of the total forest area ( $53 \times 10^6$  ha; Smith et al. 2001). In GSMNP, oak–hickory forest covers ~64 600 ha (31% of the Park's total forest cover; Madden et al. 2004). The geographic range of *C. florida* encompasses most of the area covered by oak–hickory forest in eastern North America. Whether other forests in the East have experienced changes in Ca cycling due to dogwood anthracnose is unknown. Differences in understory species composition and variations in parent material fertility could influence Ca cycling. For example, sites where hardwood species such as *A. saccharum* have replaced *C. florida* in the understory will exhibit less change in intra-stand Ca cycling than southern Appalachian sites where *C. florida* was replaced by *T. canadensis*.

The loss of Ca from the forest floor and surface soil of eastern forests may have cascading effects on a range of biota. Studies have shown that the density of snails and millipedes is strongly correlated with the local availability of Ca (Gist and Crossley 1975, Hotopp 2002). Reductions in forest-floor Ca caused by acid deposition results in lower densities of snails, which in turn causes decreased reproduction by passerine birds that depend upon Ca in snail shells for eggshell production (Graveland et al. 1994). Within the southern Appalachians, GSMNP serves as a substantial population source for Wood Thrush and other songbirds (Wilcove 1988, Simons et al. 2000). The loss of Ca from the forest floors of hardwood stands, combined with impacts of acid deposition at higher elevations (Hames et al. 2002), could have long-term negative impacts on songbird populations throughout the region.

Because of the ecological importance of *C. florida*, active management should be used to prevent the loss of this species from eastern forests. While techniques exist for controlling anthracnose in horticultural settings, techniques for controlling the disease across large areas of continuous forests have proved elusive. Britton et al. (1994) found clearcut harvesting reduced the severity of dogwood anthracnose in post-harvest stands. However, creating large clearcuts to benefit a single understory species would be inappropriate and impractical for most ecosystem management plans and is not a management option on parkland such as GSMNP. Recent work in GSMNP has shown that past burning has reduced the impacts of dogwood anthracnose by creating more open stand conditions that reduce the virulence of the fungus (Holzmueller 2006), suggesting that prescribed fire may offer the best option to prevent the loss of *C. florida* from oak–hickory and oak–pine forests. Based upon our research, preventing the loss of *C. florida* may be important to maintaining the long-term health of eastern forests.

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#### APPENDIX A

Allometric equations used to determine foliar biomass of 35 woody species across five forest types. (*Ecological Archives* A017-032-A1)

#### APPENDIX B

Tables reporting changes in foliar biomass and calcium content of selected understory species and summed totals of all understory species across five forest types. (*Ecological Archives* A017-032-A2)