

Carbon sequestration and nutrient cycling implications of the evergreen understory layer in Appalachian forests

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Abstract

Evergreen understory communities dominated by mountain laurel (*Kalmia latifolia* L.) and/or rosebay rhododendron (*Rhododendron maximum* L.) are an important but often overlooked component of Appalachian forests. In the dense thickets in which these species often occur, they have high carbon sequestration potential and play important roles in nutrient storage and cycling. We used allometric modeling of the aboveground biomass to quantify the importance of *K. latifolia* and *R. maximum*, relative to overstory tree species, in driving biogeochemical cycling in the Central Appalachian mountains. Carbon sequestration and nitrogen and phosphorus storage potentials were investigated by running 50-year simulations of the ecosystem accounting model NuCSS for two situations: forests comprising the canopy overstory layer with or without the evergreen understory layer. When simulating forests in several test watersheds based only on the composition and biomass of the overstory canopy, these forests contain between 1631 and 4825 kg/ha less in overall C content and 41–224 kg/ha less N content than if the evergreen understory layer is included. Additional N uptake by evergreen understory vegetation was estimated to amount to between 6 and 11 kg N ha⁻¹ yr⁻¹ at year 50 for the overstory-with-understory forest compared to the overstory-only forest. Vegetation pool nutrient storage was higher by 2–4% for N, and by 2–14% for P at year 50 when *R. maximum* and *K. latifolia* were included in the model. Aboveground standing biomass of *R. maximum* and *K. latifolia* accounted for only a modest portion of the C sequestered and N stored in the forest ecosystems at the watershed scale. In contrast, notably higher amounts of C and N were simulated as stored in the forest floor and soil pools when the understory was included. N storage predominated in the forest floor compared to the soil pool when a larger amount of *R. maximum* was present in a watershed, most likely due to the larger amounts of recalcitrant litter produced annually by this species compared to *K. latifolia*. In addition, storage of P in *K. latifolia* and *R. maximum* exceeded expectations compared to their watershed-scale standing biomass.

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1. Introduction

The Appalachian highlands region contains some of the most extensive contiguous area of temperate forests in eastern North America. This has resulted in part from the poor suitability of these areas for agricultural or urban land uses due to the high topographic relief (Robison, 1960), but land use pressures are increasing in this region due to development now

occurring on private lands. These forests provide a number of societal services (Daily et al., 1997), among them the maintenance of air and water quality and nutrient storage through efficient internal cycling (Perry, 1998; Aber et al., 2000). There is also growing appreciation that temperate latitudes on a global scale, particularly temperate forests, provide an important carbon sink (Schlessinger, 1977; Sedjo, 1992; Currie et al., 2003).

Forests that contain an evergreen component may be characterized by slower nutrient and C cycling compared to purely deciduous stands (McGinty, 1972; Thomas and Grigal, 1976; Day and Monk, 1977; White et al., 1988). Evidence suggests that some types of deciduous trees tend to promote more rapid nutrient cycling in forest ecosystems while some

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types of evergreen species tend to promote slower nutrient cycling by retaining nutrients in slower-decaying detritus on the forest floor (Flanagan and Van Cleve, 1983; Aerts, 1995). As a result, the amount and species composition of evergreen vegetation in eastern temperate forests are relevant to the nutrient cycling and C sequestration capacity of the forest as a whole. These capacities are expressly related to a forest's ability to protect water quality and to store atmospheric C. In Appalachian highland forests, this evergreen component includes not only overstory dominant coniferous trees. It also includes the broadleaf evergreen species present in the understory stratum, which is often dominated by mountain laurel (*Kalmia latifolia* L.) or rosebay rhododendron (*Rhododendron maximum* L.). These evergreen understories often form continuous, dense thickets beneath deciduous overstories.

In a mixed-species forest, different species may have divergent nutrient cycling capacities. These can originate from both their size and growth strategies. Overstory tree species are important in both short- and long-term nutrient cycles; nutrient-rich ground layer species are notable in the annual cycle; and evergreen species are influential in cycles of intermediate length (Day and Monk, 1977). Specifically, the evergreen understory species *K. latifolia* and *R. maximum* are significant with respect to C storage and nutrient cycling in Appalachian forests, because they produce leaf litter that decomposes slowly, thereby regulating seasonal nitrogen availability and influencing long-term patterns of organic matter accretion in early to mid-successional Appalachian forests (White et al., 1988). The lignous nature of *K. latifolia* and *R. maximum* leaves causes them to decay on the forest floor at a much slower rate compared to deciduous leaves (Thomas and Grigal, 1976). This is consistent with the broader view of higher lignin concentrations causing slower rates of plant litter decay (Moorhead et al., 1999). In fact, the ability of *K. latifolia* to inhabit dry, sterile sites has been linked to their tendency to slowly return nutrients to the soil and create tight mineral cycles through the storage of nutrients in evergreen leaves that become slowly decaying litter (Monk, 1966; Thomas and Grigal, 1976). In Newfoundland, a similar species, *Kalmia angustifolia*, was found both to thrive in and to promote nutrient-poor conditions through the production of slowly decaying humus (Bradley et al., 1997).

Evergreen understory communities dominated by *R. maximum* and/or *K. latifolia* have been estimated to cover 3 million acres of forested land in the southern Appalachian Mountains (Wahlenberg and Doolittle, 1950), while *R. maximum* is said to be the dominant subcanopy species in an estimated 74 million acres in that region (Rivers et al., 1999). Moreover, *R. maximum* and *K. latifolia* appear to have steadily increased in importance in the forests of the southern and central Appalachian mountains over the 20th century due to overstory tree disease, fire suppression, and other disturbances (Romancier, 1970; Monk et al., 1985; Phillips and Murdy, 1985; McGraw, 1989; Baker, 1994; Dobbs, 1995). The *K. latifolia*- or *R. maximum*-dominated evergreen understory layer may thus represent a significant component of the standing biomass of central Appalachian forests yet their contributions to stand biomass and C cycling have not been systematically quantified.

In the present study, the spatial extent of the *K. latifolia*- or *R. maximum*-dominated evergreen layer was evaluated using Landsat enhanced thematic mapper (ETM) imagery and topographic data in two study areas in the central Appalachian highlands; one located in the warm and dry Ridge and Valley province and another located in the cool and wet Allegheny Plateau province. Field data were used in conjunction with spatial data to estimate standing crop and growth parameters of these species, with the ultimate objective of determining their potential for C sequestration and N storage on a landscape scale. Mapping of the evergreen understory layer was undertaken because no reliable maps of evergreen understory distribution currently exist for this region. For example, the national land cover data set (NLCD), produced by the multi-resolution land characteristics (MRLC) consortium (Vogelmann et al., 2001) used Landsat thematic mapper (TM) image data to map land cover classes on a regional scale, but only identified three forested classes—deciduous, evergreen, and mixed, with no distinctions made to identify the broadleaf evergreen understory component of otherwise broadleaf deciduous forests. These forests with a substantial understory component of broadleaf evergreen shrubs were usually mapped as mixed conifer or evergreen, which are both incorrect (Chastain and Townsend, in press).

Evergreen understory communities tend to be extensive locally, but may also be absent across broad areas. We tested the importance of these species at the scale of several test watersheds having extensive evergreen understory coverage in addition to the larger study area as a whole. Watersheds represent a reasonable unit to quantify how differing assumptions about the evergreen understory may affect watershed-based budgets of nutrient cycling in forest ecosystems (Likens and Bormann, 1995). Standing biomass of evergreen understory communities is calculated using plot-level observations extrapolated to the watershed scale using measures of relative photosynthetic capacity (greenness) derived from leaf-off Landsat imagery. We estimated the C sequestration and N and P storage potential of the overall forest and the evergreen understory layer species *R. maximum* and *K. latifolia* using the nutrient cycling spreadsheet (NuCSS) model (Verburg and Johnson, 2001). This study is organized to achieve the following:

- (1) Estimate total aboveground woody and leaf biomass of *K. latifolia* and *R. maximum* in the study areas using remote sensing and forest plot survey data,
- (2) Relate the evergreen understory aboveground biomass to the overall forest biomass in seven watersheds within the Allegheny Plateau and Ridge and Valley provinces using forest inventory and analysis (FIA) data to characterize the overstory,
- (3) Use the forest overstory and evergreen understory layer biomass estimates to simulate the C sequestration and N and P accumulation potentials of forests within these watersheds,
- (4) Simulate C and N storage dynamics over time in these watersheds, and

- (5) Calculate the differences between simulating these forests as comprising only the overstory canopy versus simulating them with combined overstory and evergreen shrub understory.

The NuCSS model is used as an accounting tool to quantify the differences in estimated nutrient and C characteristics of a forest represented as an overstory-only entity with that of a forest represented as an overstory-with-understory entity. The objective of this study is not to assess the accuracy of the NuCSS model in estimating C sequestration and nutrient storage capacity of forests. Nor is the objective of this study to examine the effects of competition or other interactive mechanisms that occur between the forest overstory and evergreen understory layer. It is important to recognize the lack of explicit overstory–understory competition as a limitation on the interpretations that can be made from our results. At the same time, because our approach makes use of field-measured pool sizes of C and N, differences in modeled outcomes will reveal the relative importance of evergreen understory communities as structural components that contribute to the functioning of Appalachian forest ecosystems. Our results suggest that it may be important to include the understory layer in addition to the forest overstory layer when estimating overall biomass and modeling C sequestration and nutrient storage.

2. Methods

2.1. Study area

We worked in two representative study areas of the central Appalachian highlands (Fig. 1). Nineteen vegetation plots were

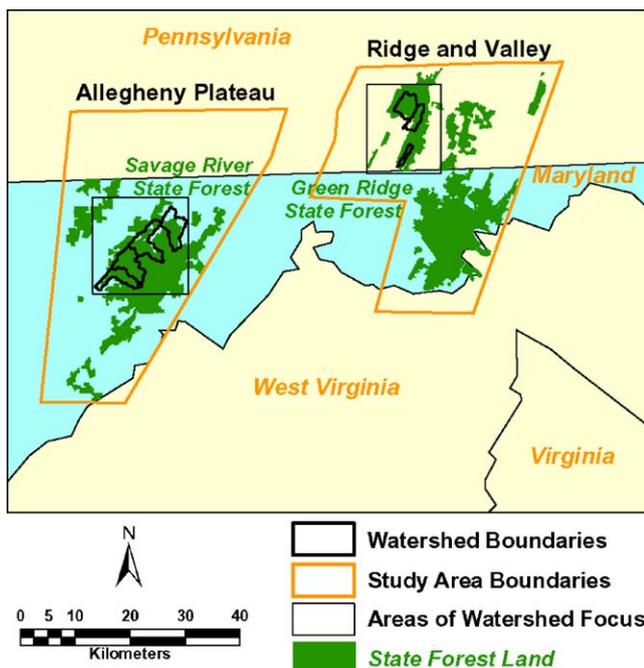


Fig. 1. Area map of present study showing the boundaries of the Allegheny Plateau and Ridge and Valley study areas, the state forest lands within these areas, and the boundaries of seven watersheds chosen for intensive study.

Table 1

Comparison of average monthly temperatures, elevation ranges, annual precipitation, and actual evapotranspiration between the Ridge and Valley and Allegheny Plateau study areas

	Ridge and Valley	Allegheny Plateau
Average monthly temperature, °C	2.3–15.8	–9.7–24.2
Elevation range, m	123–845	308–986
Average annual precipitation ^a , mm	1023	1216
Actual evapotranspiration ^b , mm/yr	537	587

^a Lynch, personal communication.

^b K. Eshelman, unpublished data.

sampled in the warm and dry Ridge and Valley physiographic province (Green Ridge State Forest, GRSF, and Buchanan State Forest, BSF). The Ridge and Valley sites are located within the historically oak–chestnut forest type (Braun, 1950). These were heavily logged and extensively burned between 1879 and 1910 (Mash, 1996), but now are largely mature 50–75-year-old forests (unpublished data, MD and PA continuous forest inventories).

We located 27 field plots on the Allegheny Plateau (Savage River State Forest, SRSF, Fig. 1) in the mixed mesophytic forest zone (Braun, 1950). Like the Ridge and Valley sites, these forests were largely cut in the early 20th century and are now dominated by oaks. The Plateau forests also have a substantial overstory component of conifers, including hemlock (*Tsuga canadensis*) and numerous pine species (*Pinus* spp.). There are substantial differences between the two study areas with respect to average monthly temperatures, yearly precipitation amounts, actual evapotranspiration, and elevation ranges (Table 1).

2.2. Watershed delineation

Three first order watersheds were selected for intensive study in the Ridge and Valley and four watersheds in the Allegheny Plateau study area. All seven watersheds exhibited a prevalence of evergreen understory communities dominated by *K. latifolia* or *R. maximum*. Overall standing biomass and leaf biomass were estimated within each watershed to characterize C content and N and P cycling. Watershed boundaries were delineated using automated tools in the Arc/Info GRID module on a 7.5 min (30 m cell) USGS digital elevation model (DEM). A 30-m map of evergreen understory communities derived from Landsat ETM data was overlaid on the watershed data to determine the coverage of *K. latifolia* and/or *R. maximum* in the individual watersheds (Table 2).

2.3. Forest aboveground biomass estimates

2.3.1. Evergreen understory layer

The aboveground biomass for *R. maximum* and *K. latifolia* was estimated using regression equations relating stem density to biomass (Monk et al., 1985). Spatial representations of stem density were obtained by regressing the stem density (stems/ha) measured on forty-six 60 m × 60 m field plots established for this research against the corresponding value of a greenness index derived from a Landsat enhanced thematic mapper

Table 2

Overall area, forested area, numbers of vegetation survey plots used to estimate biomass, and spatial extents of evergreen understory community types in each of the watersheds examined in this study

Watershed	Area (ha)	Forested area	Inventory plots	Ha <i>K. latifolia</i> cover (%)	Ha <i>R. maximum</i> cover (%)	Ha 'Mixed' cover (%)
Ridge and Valley province						
Bear Gap Run	1325.1	1308.4	7	671.9 (51.4)	9 (0.7)	–
Laurel Branch	288.36	287.1	7	123.1 (42.9)	7.3 (2.5)	–
Wildcat Run	793.6	744.7	7	333.5 (44.8)	4.4 (0.6)	–
Allegheny Plateau province						
Big Run	1979.6	1859.6	35	399.4 (21.5)	119.5 (6.4)	104 (5.6)
Bluelick Run	1898.9	1554.8	15	402.3 (25.9)	171.8 (11.0)	88.4 (5.7)
Monroe Run	1376.2	1271.3	21	256.3 (20.2)	47.6 (3.74)	48.8 (3.8)
Poplar Lick	2115.9	1885.4	22	464.6 (24.6)	206.4 (10.9)	129.5 (6.9)

Note that the parenthetically indicated percentages of cover relate only to forested portions of these watersheds. Vegetation inventory data from Continuous Forest Inventory (one plot from USFS Forest Inventory and Analysis (FIA)).

(ETM) data acquired on 31 March 2000 (Figs. 2 and 3). This index was obtained from the greenness component of a Tasseled Cap transformation of the Landsat ETM data (Huang et al., 2002). Because the March Landsat ETM image pre-dates leaf-out conditions, the image can be considered representative of evergreen (only) greenness. Observations were removed from the analysis that corresponded to field plots where understory hemlock or white pine or mixed conifer overstory were present. Areas containing evergreen understory communities dominated by *K. latifolia* or *R. maximum* in both the Ridge and Valley and Allegheny Plateau study areas had previously been mapped to better than 80% accuracy level using Landsat image data (Chastain and Townsend, in press), so these regressed stem densities were scaled up only for the areas mapped to each evergreen understory community type (*R. maximum*, *K. latifolia*, and mixed *R. maximum* and *K. latifolia*). It was assumed that the 'Mixed' evergreen understory areas in the Allegheny Plateau region contained an equal proportion of both *R. maximum* and *K. latifolia*. Although equal proportions of these species are rarely found in 'Mixed' communities, the inability to accurately discern and thus map varying proportions

of co-occurring *R. maximum* and *K. latifolia* using remote sensing necessitates this simplification. This may lead to an underestimation of the aboveground biomass for these communities. Another issue with this analysis is the presence of evergreen shrubs beneath evergreen hemlock overstories, which could not be accurately identified using remote sensing. Our field data was used to parameterize the evergreen understory component beneath areas identified as hemlock forests in the remote sensing map, such that 50% these areas were assumed to contain evergreen shrubs (25% *K. latifolia* and 25% *R. maximum*), with stem densities parameterized as the averages observed in hemlock overstory field plots.

Regression equations (Table 3) were applied to estimate biomass from the stem diameters of *R. maximum* and *K. latifolia* using stem diameter data for each species collected from field plots. Wood disks (331 total) of *R. maximum* and *K. latifolia* stems were strategically collected in areas representative of various drought stress conditions and gypsy moth disturbance levels from 19 vegetation plots in the Ridge and Valley and 27 plots in the Allegheny Plateau. The average stem diameter of *K. latifolia* was 3.0 cm in both study areas. The average stem diameter for *R. maximum* was 5.3 cm in the Ridge and Valley and 4.0 cm in the Allegheny Plateau. Using these stem diameter averages and the modeled stem densities, together with species-specific regression equations (Table 3; Monk et al., 1985), we made areal estimates of the woody, foliar, and total aboveground biomass for both species on a per-hectare basis at the scales of the entire study area and selected watersheds (Tables 6 and 7).

2.3.2. Forest overstory

The aboveground biomass of the forest overstory trees was estimated from plot-level field surveys of species composition and DBH using allometric equations (Table 3) developed for tree species groups (Jenkins et al., 2003). These equations were applied to field data from 366 continuous forest inventory (CFI) plots in the Allegheny Plateau study area. Because the Ridge and Valley study area straddles two states, its forest overstory tree aboveground biomass was estimated using 463 CFI plots in Maryland and 5 forest inventory and analysis (FIA) plots

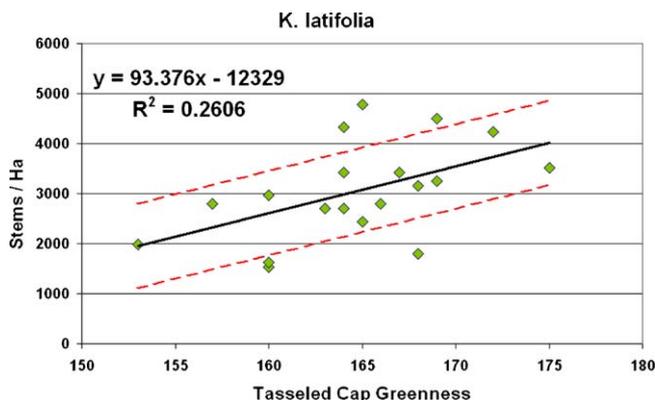


Fig. 2. Regression from which biomass estimate was based for evergreen understory communities dominated by *K. latifolia* in the Ridge and Valley study area (d.f. 1/17, $F = 5.99$, $p = 0.026$). Dotted lines represent standard error (S.E.) of predicted stem density based on tasseled cap greenness value (S.E. = 846 stems/ha).

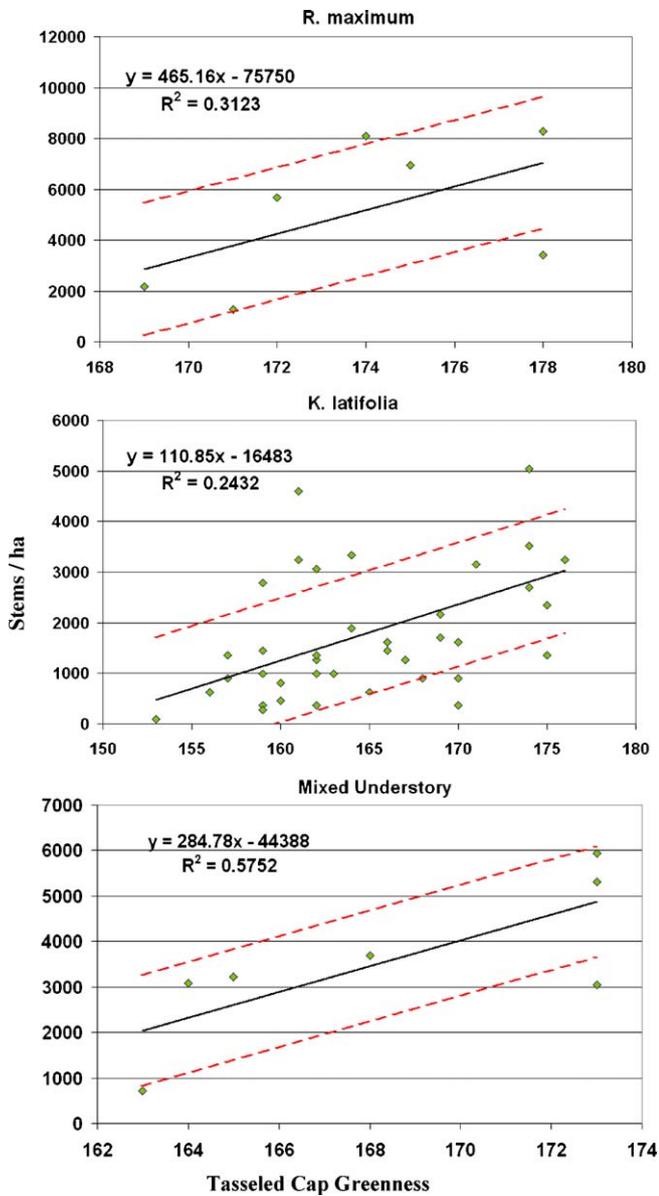


Fig. 3. Regressions from which were based the biomass estimates for *K. latifolia*, *R. maximum*, and ‘Mixed’ understory areas in the Allegheny Plateau study area (*R. maximum* d.f. 1/5, $F = 2.27$, $p = 0.192$; *K. latifolia* d.f. 1/38, $F = 12.21$, $p = 0.001$; ‘Mixed’ d.f. 1/5, $F = 6.77$, $p = 0.048$). Dotted lines represent standard error (S.E.) of predicted stem density based on tasseled cap greenness value (*R. maximum* S.E. = 2599 stems/ha, *K. latifolia* S.E. = 1225 stems/ha, ‘Mixed’ S.E. = 1218 stems/ha).

located in Pennsylvania. A subset of the CFI plots were chosen to estimate the aboveground biomass within the four watersheds in the Allegheny Plateau based on GIS overlays (Table 2). In the Ridge and Valley, only six CFI plots and one FIA plot coincided with the area encompassing the three test watersheds and were in close spatial proximity to evergreen understory communities mapped using remote sensing. In both study areas, allometric equations were used to estimate total aboveground biomass and the proportion of foliar material. The biomass estimates were applied to the CFI and FIA plots, then extrapolated to the study areas as a whole and test watersheds in particular based on the total amount of forested area as

Table 3

Allometric and linear equations used to estimate the total aboveground biomass (TAB) and leaves and bark/wood biomass from dbh (cm) for species and species groups present in the watersheds selected for this research

Species group (spp)	Equation	N
Soft maple/birch ^a	TAB = $\text{Exp}(-1.9123 + 2.3651 \ln(\text{dbh}))$	316
<i>A. rubrum</i>	Leaves = $(\text{Exp}(-4.0813 + 5.8816/\text{dbh})) \times \text{bm}$	632
<i>Betula</i> spp.		
Mixed hardwood ^a	TAB = $\text{Exp}(-2.48 + 2.4835 \ln(\text{dbh}))$	289
<i>F. Americana</i>	Leaves = $(\text{Exp}(-4.0813 + 5.8816/\text{dbh})) \times \text{bm}$	632
<i>L. tulipifera</i>		
<i>P. serotina</i>		
<i>S. albidum</i>		
<i>Tilia</i> spp.		
<i>U. Americana</i>		
Hard maple/oak/hickory/beechn ^a	TAB = $\text{Exp}(-2.0127 + 2.4342 \ln(\text{dbh}))$	485
<i>A. saccharum</i>	Leaves = $(\text{Exp}(-4.0813 + 5.8816/\text{dbh})) \times \text{bm}$	632
<i>Carya</i> spp.		
<i>Q. Alba</i>		
<i>Q. coccinea</i>		
<i>Q. prinus</i>		
<i>Q. rubra</i>		
<i>Q. velutina</i>		
Hemlock ^a	TAB = $\text{Exp}(-2.5384 + 2.4814 \ln(\text{dbh}))$	395
<i>T. canadensis</i>	Leaves = $(\text{Exp}(-2.9584 + 4.4766/\text{dbh})) \times \text{bm}$	777
Pine ^a	TAB = $\text{Exp}(-2.5356 + 2.4349 \ln(\text{dbh}))$	331
<i>P. pungens</i>	Leaves = $(\text{Exp}(-2.9584 + 4.4766/\text{dbh})) \times \text{bm}$	777
<i>P. resinosa</i>		
<i>P. rigida</i>		
<i>P. strobus</i>		
<i>P. virginiana</i>		
Spruce ^a	TAB = $\text{Exp}(-2.0773 + 2.3323 \ln(\text{dbh}))$	212
<i>Picea</i> spp.	Leaves = $(\text{Exp}(-2.9584 + 4.4766/\text{dbh})) \times \text{bm}$	777
Apen/alder/cottonwood/willow ^a	TAB = $\text{Exp}(-2.2094 + 2.3867 \ln(\text{dbh}))$	230
<i>Populus</i> spp.	Leaves = $(\text{Exp}(-4.0813 + 5.8816/\text{dbh})) \times \text{bm}$	632
<i>K. latifolia</i> leaves ^b	Leaves = $17.23 + 32.14 \times (\text{dbh})$	45
<i>K. latifolia</i> bark and wood ^b	Bark/wood = $74.92 + 842.27 \times (\text{dbh})$	45
<i>R. maximum</i> leaves ^b	Leaves = $-886.98 + 422.15 \times (\text{dbh})$	45
<i>R. maximum</i> bark and wood ^b	Bark/wood = $-9709 + 3274.44 \times (\text{dbh})$	45

^a From Jenkins et al. (2003).

^b From Monk et al. (1985).

identified from a remote sensing classification (Chastain and Townsend, in press).

2.4. Simulation of carbon and nitrogen storage and cycling

2.4.1. Nutrient cycling spreadsheet model (NuCSS)

The nutrient cycling spreadsheet model (NuCSS, Verburg and Johnson, 2001) was applied to estimate C sequestration and to evaluate N and P storage over time for the forests occurring within the seven test watersheds. NuCSS is a spreadsheet-based compartment model that tracks C and nutrient storage, fluxes, and cycling through standing biomass, the forest floor, and soil storage pools. Designed to serve as a tool for nutrient management, it is intermediate in complexity between simple budget calculations and complex, process-based ecosystem models. For example, there is no feedback between the soil nutrient availability and tree growth. Exchangeable soil cation and N pools become negative if nutrient requirements of tree growth exceed what is available in these pools (Verburg and Johnson, 2001).

The growth model within the NuCSS model allows the user to simulate the growth of a forest community over 50 1-year time steps using a logistic-like growth function for foliage, branch, bole, and coarse and fine root compartments. Initial and maximal biomass by species are required model inputs to initialize simulations. The equation used in the NuCSS model to ‘grow’ these vegetation compartments is:

$$W(t) = W_{\max} / (1 + \alpha e^{-\mu t})$$

where $W(t)$ is biomass at time t , W_{\max} is the maximal biomass, α is the parameter that describes the steepness of the exponential growth slope, μ is the relative growth rate, and t is time in years (Verburg and Johnson, 2001).

The N cycle is simulated in NuCSS by allowing N to enter the litter pool from live foliage, branches and fine roots (Verburg and Johnson, 2001). The N in the litter pool is either mineralized or immobilized by microorganisms, depending on the C/N ratio of the substrate, the fraction of C in the litter, microbial C/N, and microbial C use efficiency. The N present in the OM that exceeds what is necessary for microbial biomass production is mineralized (Verburg and Johnson, 2001). The NuCSS model allows the forest floor C/N and SOM to vary over time based on changes in N mineralization and immobilization rates. Decomposition and mineralization of leaf, woody, fine root litter, and soil organic matter is simulated in NuCSS using an exponential decay function defined by decomposition rate constants (k -value) specified separately for leaf litter, wood, and fine roots.

The uptake of N by vegetation is computed as the vegetation N increment minus the amount of N lost in foliage, woody, and fine root litter. Because exchangeable N in soil rarely exceeds 40 kg ha⁻¹, if the total amount of exchangeable N surpasses this amount, the excess will leach (Verburg and Johnson, 2001). The cycling of P in NuCSS differs from N cycling in that weathering of parent material is an additional source of P. Also, P mineralization and P in litterfall are not simulated explicitly. Rather, P mineralization is assumed to equal P litterfall.

We estimated the input parameters required by the model from the literature and from our own field surveys. Parameters also included an array of ecosystem, biogeochemical, and soil properties (Table 4). The values used for the present analyses were derived to reflect the forest structure and composition, climatic characteristics, foliar and litter chemistry, and soil properties encountered in the different study watersheds (Tables 4 and 5). The fraction of live leaf material entering the forest floor pool as litter and litter decomposition rates (k -value) were based on the structure and floristic composition of the forest overstory (and evergreen understory layer) in each study watershed. Because it was anticipated that differences between model results would be caused primarily by the amount and physical properties of the recalcitrant litter of *K. latifolia* and *R. maximum*, separate litter decomposition rate parameters were obtained from the literature for all of the component species of the forests present in the different watersheds examined. Model defaults were used when no specific value for the watersheds studied were available. This was considered reasonable, as this version of NuCSS was developed for the eastern deciduous biome (P. Verburg, personal communication).

Our first run of the NuCSS model for each watershed employed a growth model run for overstory trees that used maximal biomass parameters for overstory tree foliar and total aboveground biomass compartments (overstory-only model run). A second run of the model was conducted with a separate growth model for overstory trees and an evergreen understory component using parameters for maximal aboveground and leaf biomass for evergreen understory communities (overstory-with-understory model run). Belowground biomass compartments were estimated as the model default 26% (24% coarse and 2% fine root) of the total aboveground biomass for both the overstory and evergreen understory layer vegetation. These values are conservative, but reasonable estimates for belowground biomass in Appalachian deciduous forests (McGinty, 1976).

Because the NuCSS model does not limit vegetation growth based on nutrient constraints, the overstory and understory layer vegetation do not compete for available nutrients, nor can one limit the growth of the other. This and the omission of other ecological interactions represents a limitation in the use of NuCSS. It is, for example, known that competition for resources may inhibit the regeneration of forest overstory trees (Nilsen et al., 2001). A limitation of NuCSS is that it cannot be used to assess feedbacks arising from ecological interactions. If *K. latifolia* and *R. maximum* were hypothetically able to impede overstory regeneration, their presence could increase over time in a manner not accounted for by NuCSS.

2.5. Leaf decomposition data

The use of scalars to adjust reported decomposition rates is justified by evidence that macroclimate acts as a dominant predictor of leaf litter decay rates, both as a controller of microbial activity and through its influence on litter chemistry (Meentemeyer, 1978; Aerts, 1997). The adjustment scalar is

Table 4

Values and sources for input parameters used in NuCSS model simulations run for the seven selected watersheds examined in this study

Parameter	Unit	Value	Source
Initial biomass (foliage, branch, bole, coarse and fine roots)	kg/ha	100 for trees; 50 for shrubs	Model default
Maximum biomass (foliage, branch, bole, coarse and fine roots)	kg/ha	<i>Trees</i>	
		8000 foliage	Model default
		16000 branch	Model default
		80000 bole	Model default
		25000 coarse roots	Model default
		2000 fine roots	Model default
		<i>Shrubs</i>	
		Based on actual Biomass estimates	Field observations extrapolated Using tasseled cap greenness
N, P, K, Ca, and Mg content (foliage, branch, bole, coarse and fine roots)	%	<i>Trees</i>	
		2.25 foliage N	Unpublished data from study areas
		Other nutrients	Defaults (from Duke Forest, NC)
		<i>K. latifolia</i>	
		1.26 foliage N	Monk et al. (1985)
		0.26 wood N	Monk et al. (1985)
		0.17 foliage P	Monk et al. (1985)
		0.11 wood P	Monk et al. (1985)
		<i>R. maximum</i>	
		1.35 foliage N	Monk et al. (1985)
		0.35 wood N	Monk et al. (1985)
		0.13 foliage P	Monk et al. (1985)
		0.10 wood P	Monk et al. (1985)
		N, S, P, K, Ca, Mg, Na, and Cl deposition	
K, Ca, Mg, Na, Cl	National Atmospheric Deposition Program (http://nadp.sws.uiuc.edu/)		
Fraction N translocated from foliage before senescence	–	0.70	Model default
Soil chemical and physical properties	Dekalb soil series		Values for soil layer depths, bulk density, mineral content, CEC, etc. from the NRCS National Lab database (online)
Initial forest floor leaf, woody, and fine root litter weight	kg/ha	0.1	Model default
Fraction C in organic matter	–	0.52	W. Currie (unpublished data)
Decomposition rate constant for leaf, woody, and fine root litter and SOM	Fraction/yr	<i>Leaf</i> : see Table 6	Based on actual forest composition
		<i>Wood</i> : 0.1	Model default
		<i>Fine root</i> : 0.5	Model default
		<i>SOM</i> : 0.001	Model default
Fraction humified	–	<i>Leaf</i> : 0.2	W. Currie (unpublished data)
		<i>Wood</i> : 0.1	W. Currie (unpublished data)
		<i>Fine root</i> : 0.1	W. Currie (unpublished data)
Fraction live foliage, branches, and fine roots entering litter pool annually	Fraction/yr	<i>Leaf</i> : varies by watershed	Based on actual forest composition
		<i>Branch</i> : 0.05	Model default
		<i>Fine roots</i> : 0.5	Model default
Microbial C/N ratio	–	<i>Leaf</i> : 0.15	Model default
		<i>Wood, fine roots, SOM</i> : 0.15	Model default
Microbial carbon use efficiency	–	<i>Leaf, wood, fine roots, SOM</i> : 0.15	Model default

applied using actual evapotranspiration (AET) to account for climatic differences between our sites and those where litter decay rates were measured (Table 5). A composite decomposition rate was then calculated for the individual watersheds using a weighted average of the specific decomposition rates of all species present. Allometric biomass estimates of leaf weight

of individual overstory tree species identified in field surveys (CFI and FIA) were used to estimate the contribution of deciduous overstory tree species, and that amount was divided by two as a conservative estimate of the litter contributions of evergreen conifer tree species (Reich et al., 1995). The leaf litter contributions of the evergreen understory was estimated

Table 5
First-year decay constants (k) for leaves of species found in the two study areas

Species	k (1/y)	Source	Source AET	Adjusted k (1/y) using AET	
				Ridge and Valley	Allegheny Plateau
<i>A. rubrum</i>	0.5597	Mudrick et al. (1994) (WV)	587 (Savage River data)	0.5115	0.5597
<i>A. saccharum</i>	0.667	Boerner and Rebbeck (1995) (WV)	587 (Savage River data)	0.6096	0.667
<i>Betula</i> spp.	0.4483	Magill and Aber (1998) (Harvard Forest, MA)	578 (Harmon, 1992)	0.4161	0.4553
<i>Carya</i> spp.	0.5	Default parameter	–	0.5	0.5
<i>F. americana</i>	0.47	Mellilo et al. (1982) (Hubbard Brook, NH)	552 (Harmon et al., 1999)	0.4568	0.4998
<i>K. latifolia</i>	0.2148	J. Webster, personal communication (Coweeta, NC)	779 (Sun et al., 1999)	0.1479	0.1619
<i>L. tulipifera</i>	0.8965	Mudrick et al. (1994) (WV)	587 (Savage River data)	0.8193	0.8965
<i>N. sylvatica</i>	0.5979	Kelly (1973) (TN)	652 (observed 1969–2001)	0.4921	0.5384
<i>P. rigida</i>	0.1849	Hubbard Brook, NH (LIDET data)	552 (Harmon et al., 1999)	0.1797	0.1966
<i>P. pungens</i>	0.1849	Hubbard Brook, NH (LIDET data)	552 (Harmon et al., 1999)	0.1797	0.1966
<i>P. strobes</i>	0.2173	Andrews experimental forest (OR)	552 (Harmon et al., 1999)	0.2112	0.2311
<i>P. virginiana</i>	0.1849	Hubbard Brook, NH (LIDET data)	552 (Harmon et al., 1999)	0.1797	0.1966
<i>P. serotina</i>	0.1849	Hubbard Brook, NH (LIDET data)	552 (Harmon et al., 1999)	0.1797	0.1966
<i>Q. alba</i>	0.5924	McClougherty et al. (1985) (WI)	535 (McClougherty et al., 1985)	0.594	0.65
<i>Q. coccinea</i>	0.395	Harvard Forest (MA)	578 (Harmon et al., 1999)	0.3666	0.4012
<i>Q. prinus</i>	0.3334	Mudrick et al. (1994) (WV)	587 (Savage River data)	0.3047	0.3334
<i>Q. rubra</i>	0.395	Magill and Aber (1998) (Harvard Forest, MA)	578 (Harmon et al., 1999)	0.3666	0.4012
<i>Q. velutina</i>	0.3323	Magill and Aber (1998) (Harvard Forest, MA)	578 (Harmon et al., 1999)	0.3084	0.3375
<i>R. maximum</i>	0.1812	J. Webster, personal communication (Coweeta, NC)	779 (Sun et al., 1999)	0.1248	0.1365
<i>T. canadensis</i>	0.3566	McClougherty et al. (1985) (WI)	535 (McClougherty et al., 1985)	0.3576	0.3913

using the previously established leaf biomass estimates, with *K. latifolia* estimates divided by two and *R. maximum* estimates divided by four to reflect their average leaf longevity (Monk et al., 1985).

The fraction of live leaf material entering the forest floor annually and the litter decomposition rate (k -value) were the two primary parameters altered for the NuCSS simulations of overstory-only and overstory-with-understory forest types. As such, a sensitivity analysis was performed for the Bluelick Run watershed in the Allegheny Plateau province to compare the k -value and annual fraction of litter from live leaves parameter values used in the overstory-only and overstory-with-understory forests with parameter values that would be used for wholly coniferous and deciduous idealized forest types. For this analysis, the NuCSS model's default litter decomposition rate (k -value) and annual fraction of litter from live leaves parameter values were both set at 0.25 for an entirely coniferous forest, and 0.5 and 1.0, respectively, for a purely deciduous forest (Verburg and Johnson, 2001). The values used for the k -value and annual fraction of litter from live leaves parameters for the overstory-only model simulation were 0.485 and 0.849, respectively, for the Bluelick Run watershed based

on actual vegetation assemblages. The parameter values used in this watershed for the k -value and annual fraction of litter from live leaves for the overstory-with-understory model simulation were 0.471 and 0.786, respectively. This analysis was useful as an illustration of where NuCSS model results for overstory-only and overstory-with-understory forest types lie in the broader range of NuCSS model results defined by extremes in the input values for these two parameters.

3. Results

3.1. Aboveground biomass estimates

The estimated proportion of the evergreen understory component of the overall forest standing biomass was very small for the two study areas taken in their entirety, but greater when examined at the level of the selected watersheds (Tables 6 and 7). Aboveground biomass of the evergreen understory layer was estimated to be less than half of 1% of the overall forest standing biomass in the Ridge and Valley and 1% of the Allegheny Plateau study area.

Table 6
Estimated total aboveground and leaf biomass amounts of *Kalmia latifolia* and *Rhododendron maximum* in kilograms and percentages of total forest aboveground and leaf biomass of the forested area within the Ridge and Valley province as well as the Bear Gap Run, Laurel Branch, and Wildcat Run watersheds

	<i>R. maximum</i> biomass (%)		<i>K. latifolia</i> biomass (%)		Total evergreen understory biomass (%)	
	Aboveground	Leaf	Aboveground	Leaf	Aboveground	Leaf
Ridge and Valley forests	8×10^6 (0.06)	1.2×10^6 (0.36)	4.51×10^7 (0.33)	1.89×10^6 (0.57)	5.31×10^7 (0.38)	3.09×10^6 (0.93)
Bear gap run	2.83×10^5 (0.21)	4.25×10^4 (1.26)	5.55×10^6 (3.99)	2.32×10^5 (6.86)	5.83×10^6 (4.2)	2.75×10^5 (8.12)
Laurel branch	2.55×10^5 (0.86)	3.83×10^4 (5.05)	8.82×10^5 (2.92)	3.69×10^4 (4.87)	1.14×10^6 (3.78)	7.52×10^4 (9.93)
Wildcat run	1.74×10^5 (0.23)	2.61×10^4 (1.36)	2.83×10^6 (3.59)	1.19×10^5 (6.19)	3.01×10^6 (3.82)	1.45×10^5 (7.56)

Table 7

Estimated total aboveground and leaf biomass amounts of *Kalmia latifolia* and *Rhododendron maximum* in kilograms and percentages of total forest aboveground and leaf biomass of the forested area within the Allegheny Plateau province as well as the Big Run, Bluelick Run, Poplar Lick, and Monroe Run watersheds

	<i>R. maximum</i> biomass (%)		<i>K. latifolia</i> biomass (%)		Total evergreen understory biomass (%)	
	Aboveground	Leaf	Aboveground	Leaf	Aboveground	Leaf
Allegheny Plateau forests	1.19×10^8 (0.58)	2.28×10^7 (4.88)	9.38×10^7 (0.46)	3.93×10^6 (0.84)	2.13×10^8 (1.04)	2.67×10^7 (5.72)
Big run	2.47×10^6 (0.65)	4.72×10^5 (5.19)	2.34×10^6 (0.62)	9.8×10^4 (1.08)	4.81×10^6 (1.26)	5.7×10^5 (6.26)
Bluelick run	3.59×10^6 (1.41)	6.88×10^5 (9.62)	2.47×10^6 (0.97)	1.03×10^5 (1.45)	6.07×10^6 (2.37)	7.91×10^5 (11.07)
Poplar lick	4.3×10^6 (0.67)	8.22×10^5 (7.41)	2.84×10^6 (1.01)	1.19×10^5 (1.07)	7.14×10^6 (1.68)	9.41×10^5 (8.48)
Monroe run	9.27×10^5 (0.35)	1.77×10^5 (2.85)	1.42×10^6 (0.53)	5.93×10^4 (0.95)	2.34×10^6 (0.87)	2.37×10^5 (3.8)

The leaf biomass estimates of the evergreen understory layer made up a more substantial portion of overall leaf biomass, with total percentage nearly doubling in the Ridge and Valley (0.9%) and increasing to 5.7% in the Plateau. In the seven watersheds examined in this study, leaf biomass of *R. maximum* (and to a lesser extent *K. latifolia*) ranked higher than other component overstory species with much higher overall standing biomass. For example, *R. maximum* was ranked 14th (of 25 total species) in total aboveground biomass in the Bluelick Run watershed in the Allegheny Plateau study area, but fourth in total leaf biomass due to its thick, sclerophyllous leaves. Likewise, in the Poplar Lick watershed in the Allegheny Plateau study area, *R. maximum* ranked 18th (of 25 total species) in total aboveground biomass among the woody species present, but its leaf biomass was the ranked fifth in total leaf biomass among the species identified in the CFI plots within that watershed. *R. maximum* is more important in terms of leaf biomass amount in the Poplar Lick watershed than *Q. prinus*, one of the dominant tree species in this watershed.

3.2. Simulation modeling of carbon and nitrogen pools

The NuCSS model was not designed to test hypotheses regarding specific mechanistic processes associated with nutrient cycling; rather this model was intended to integrate numerous observations, account for pools of C, N, and other nutrients, and perform scenario analysis (Verburg and Johnson, 2001). The modifications made on the NuCSS model for this study represents an ideal application of this moderately complex compartment model, in that it facilitates comparisons of amounts and locations of nutrient and C storage pools by examining scenarios in which a forest is represented as a overstory-only entity compared to a overstory-with-understory entity.

For the sensitivity analysis performed for the Bluelick Run watershed, the modeled accumulations of C and N in the forest floor and soil pools in the overstory-only and overstory-with-understory forest types over 50 years were bracketed by the C and N accumulations modeled for the idealized pure deciduous

Table 8

Size of C pools after 50 years of simulation using the NuCSS model for overstory-only forests (Can) and forests with the overstory and evergreen understory communities dominated by *K. latifolia* and/or *R. maximum* (Can + Und)

Watershed	Area (ha)	Total C (kg/ha)	Total C in vegetation (kg/ha)	Total C in soil (kg/ha)	Total C in forest floor (kg/ha)
Bear Gap Run (Can)	1308.4	1.81×10^5	6.65×10^4	1.0×10^5	1.42×10^4
Bear Gap Run (Can + Und)		1.85×10^5	6.94×10^4	1.01×10^5	1.5×10^4
Difference		4429	2915	694	820
Laurel Branch (Can)	287.1	1.81×10^5	6.65×10^4	1.0×10^5	1.42×10^4
Laurel Branch (Can + Und)		1.84×10^5	6.9×10^4	1.0×10^5	1.47×10^4
Difference		3366	2591	270	505
Wildcat Run (Can)	744.7	1.81×10^5	6.65×10^4	1.01×10^5	1.45×10^4
Wildcat Run (Can + Und)		1.85×10^5	6.91×10^4	1.0×10^5	1.55×10^4
Difference		4825	2641	1148	1037
Big Run (Can)	1859.6	1.78×10^5	6.64×10^4	9.99×10^4	1.18×10^4
Big Run (Can + Und)		1.8×10^5	6.81×10^4	1.0×10^5	1.2×10^4
Difference		2086	1691	163	232
Bluelick Run (Can)	1554.8	1.76×10^5	6.65×10^4	9.9×10^4	1.09×10^4
Bluelick Run (Can + Und)		1.79×10^5	6.9×10^4	9.91×10^4	1.12×10^4
Difference		2864	2549	34	281
Monroe Run (Can)	1271.3	1.78×10^5	6.64×10^4	9.99×10^4	1.21×10^4
Monroe Run (Can + Und)		1.8×10^5	6.77×10^4	1.0×10^5	1.23×10^4
Difference		1631	1210	214	208
Poplar Lick (Can)	1885.4	1.77×10^5	6.65×10^4	9.91×10^4	1.15×10^4
Poplar Lick (Can + Und)		1.8×10^5	6.9×10^4	9.94×10^4	1.18×10^4
Difference		3104	2493	258	353

Table 9
Size of N pools after 50 years of simulation using the NuCSS model for overstory-only forests (Can) and forests with the overstory and evergreen understory communities dominated by *K. latifolia* and/or *R. maximum* (Can + Und)

Watershed	Area (ha)	Total N (kg/ha)	Total N in vegetation (kg/ha)	Organic soil N (kg/ha)	Exchangable soil N (kg/ha)	Total forest floor N (kg/ha)
Bear Gap Run (Can)	1308.4	16158	351	15336	−103	573
Bear Gap Run (Can + Und)		16317	366	15442	−121	630
Difference		159	15	106	−19	57
Laurel Branch (Can)	287.1	16158	351	15336	−103	573
Laurel Branch (Can + Und)		16242	365	15378	−115	615
Difference		84	14	41	−12	42
Wildcat Run (Can)	744.7	16153	351	15331	−118	588
Wildcat Run (Can + Und)		16377	365	15506	−151	656
Difference		224	14	175	−33	68
Big Run (Can)	1859.6	16134	351	15305	14	463
Big Run (Can + Und)		16179	360	15330	1	488
Difference		46	9	25	−13	25
Bluelick Run (Can)	1554.8	15987	351	15172	40	423
Bluelick Run (Can + Und)		16030	365	15177	40	448
Difference		43	13	5	0	25
Monroe Run (Can)	1271.3	16142	351	15313	0	477
Monroe Run (Can + Und)		16183	358	15346	−23	502
Difference		41	6	33	−23	25
Poplar Lick (Can)	1885.4	16023	351	15197	25	351
Poplar Lick (Can + Und)		16101	364	15237	21	364
Difference		78	13	39	−4	13

and pure coniferous forest types the Bluelick Run watershed. Moreover, the C and N pool sizes in the overstory-only and overstory-with-understory forest types were more similar to the deciduous compared to the coniferous forest type, which was expected considering that the actual forest modeled in the Bluelick Run watershed is dominated by deciduous trees.

The inclusion in NuCSS of evergreen understory communities in simulated forests yielded dramatic increases in the estimated amounts ecosystem C sequestration and N storage. When simulating forests in the test watersheds based only on the composition and biomass of the overstory layer, these forests have between 1631 and 4825 kg/ha less in overall C content (Table 8) compared to when the evergreen understory layer is included. This discrepancy amounts to between 0.9 and 2.6% of overall C in these watersheds. A total of 41–224 kg/ha less in overall N content (Table 9), or between 0.3 and 1.4%, is present in the test watersheds in overstory-only model runs compared to when the evergreen understory layer is included.

Differences in the size and location of C and N storage pools were also evident between NuCSS simulations run for forests modeled as overstory-only and overstory-with-understory. The addition of standing and belowground biomass in the form of *K. latifolia* and *R. maximum* in the watershed-scale NuCSS simulations accounted for the largest increases in C storage (Table 8), followed by gradually increasing pools of forest floor and soil C (Figs. 4 and 5). Some of the variability in the soil C and N pools was related to differences in the composition in the evergreen understory layer in the watersheds examined. Specifically, the smallest increases for each study area in C and N storage in the overstory-with-understory simulations

were observed in the soil pools of watersheds where the biomass of *R. maximum* was highest relative to overall forest aboveground biomass (e.g. Bluelick Run and Laurel Branch). In the other watersheds, where evergreen understory aboveground biomass was dominated by *K. latifolia*, the amount of C stored in the soil pool was comparable to that found in the forest floor pool (Table 8), whereas the soil pool N amounts were greater than or equal to that found in the forest floor pool (Table 9).

4. Discussion

The NuCSS model was implemented in this study to facilitate the comparison of the sizes of C, N, and P pools when the forest was simulated as overstory-only or as overstory-with-understory. The NuCSS simulations showed that increases in the overall C, N, and P pools in the modeled watersheds were larger than those accounted for by the biomass additions of evergreen understory species *K. latifolia* and *R. maximum* alone, with noteworthy increases in the forest floor and soil pools. These results were obtained by changing only parameter inputs related to vegetation biomass, annual proportional litter contributions, and decomposition rates.

The C and nutrient storage capacity of evergreen understory species *K. latifolia* and *R. maximum* is greater than their aboveground biomass and areal coverage suggests. Their sclerophyllous evergreen leaves are higher in biomass than typical of deciduous leaves in Appalachian forests (Day and McGinty, 1975). The evergreen habit in which *R. maximum* retains its leaves for an average of 4 years and *K. latifolia* for 2

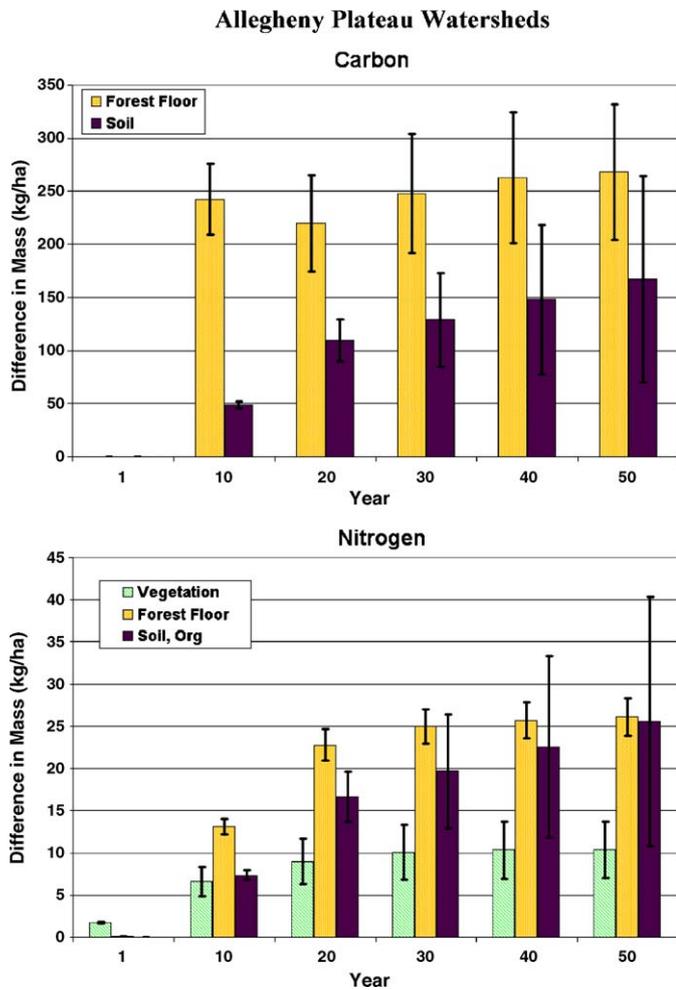


Fig. 4. Differences between NuCSS model simulation results for C and N storage pools resulting from overstory-only and overstory-with-understory forest input parameters averaged over the four test watersheds examined in the Allegheny Plateau study area.

years further expands their capacity to sequester C and retain nutrients in their leaf tissue on the watershed scale (Lipscomb and Nilsen, 1990). For example, N uptake by evergreen understory vegetation was estimated by NuCSS to increase by between 6 (Bluelick Run) and 11 (Wildcat Run) $\text{kg N ha}^{-1} \text{yr}^{-1}$ at year 50 for the overstory-with-understory forest compared to the overstory-only forest (Fig. 6). In addition, vegetation pool nutrient storage increased between 2 and 4% for N, and between 2 and 14% for P at year 50 when *R. maximum* and *K. latifolia* were included in the model (Table 10). Increases in overall forest C and N pools in *R. maximum* and *K. latifolia* simulations are especially noteworthy in the Allegheny Plateau watersheds where *R. maximum* is more prevalent (Bluelick Run and Poplar Lick compared to Monroe Run), because the relatively larger leaf and overall mass of *R. maximum* compared to *K. latifolia*. Finally, the comparatively large additional storage of P in forests with *R. maximum* and *K. latifolia* indicated by NuCSS concurs with Thomas and Grigal (1976), in which P was found to be conserved as a function of the high leaf lifespans and recalcitrant litter produced by these species.

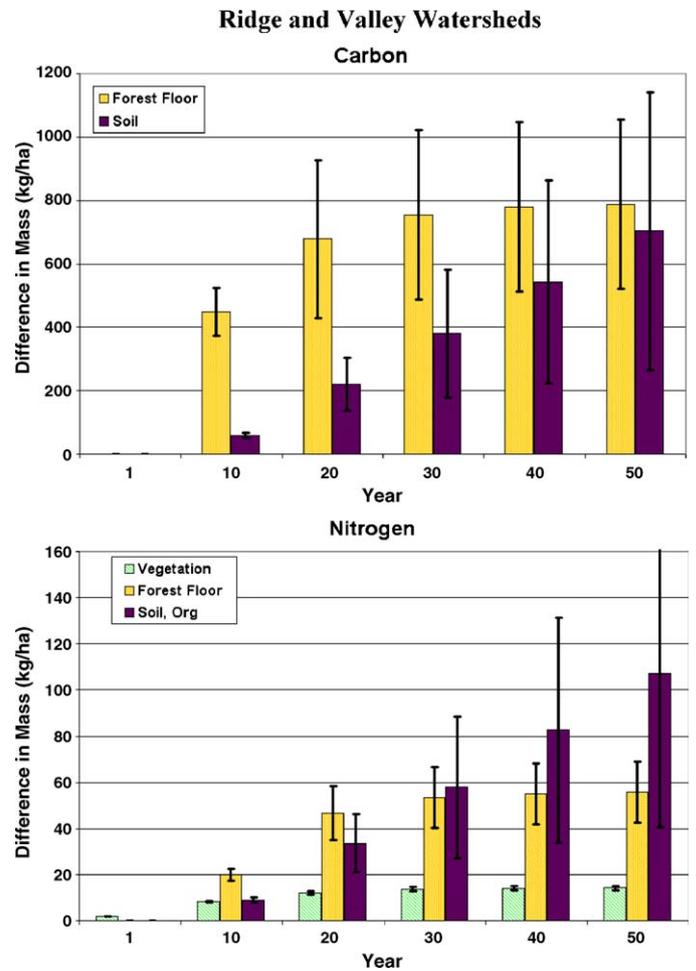


Fig. 5. Differences between NuCSS model simulation results for C and N storage pools resulting from overstory-only and overstory-with-understory forest input parameters averaged over the three test watersheds examined in the Ridge and Valley study area.

Although NuCSS is a less complex ecosystem model than others (e.g., BIOME-BGC, PnET, LINKAGES, CENTURY, etc), predictions of overall C and N sequestration in the forests simulated using this model are comparable to sequestration amounts obtained elsewhere. For example, the sequestration rates of forests growing on abandoned farmland in Rhode Island were found to be similar in estimated overall C ($1.75 \times 10^5 \text{ kg ha}^{-1}$), with comparable proportions of C in the vegetation, soil, and forest floor pools for the central Appalachian forest and the Rhode Island forest (Hooker and Compton, 2003). However, the N sequestered after 50 years (5400 kg ha^{-1}) by the Rhode Island forests was only about one-third what was predicted by the NuCSS model. This difference was due to much lower soil N in the Rhode Island forest compared to the Central Appalachian forest (approximately 1600 compared to 4500 kg ha^{-1} , respectively), which may result from differing soil types and substrates (glacial till versus highly weathered crystalline bedrock). Nonetheless, the size of the N pools in the vegetation (400) and forest floor (500) were comparable for these two forests (Hooker and Compton, 2003).

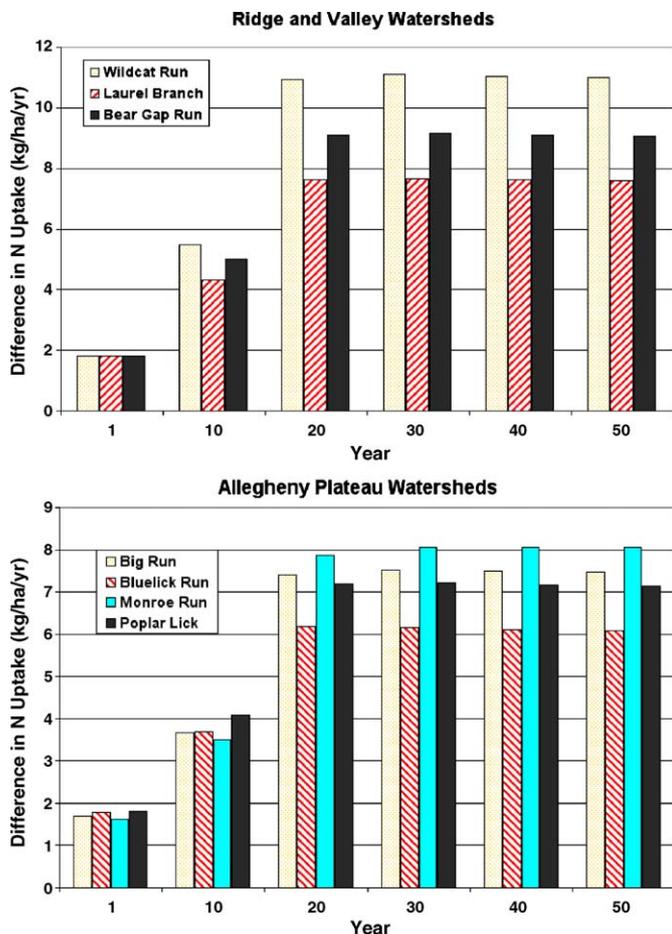


Fig. 6. Differences between NuCSS model simulation results for vegetation uptake of N for overstory-only and overstory-with-understory forest input parameters in the test watersheds examined in the Ridge and Valley and Allegheny Plateau study areas.

The NuCSS simulations showed significant increases in carbon sequestration and nutrient storage attributable to the presence of an evergreen understory at the scale of the watershed, and may act to mitigate the effects of certain disturbances,

Table 10

Amount of additional C, N, and P (kg/ha) added to the total vegetation pools (standing and belowground biomass) at year 50 by including *K. latifolia* and *R. maximum* to the forests simulated for NuCSS model runs in the seven watersheds

Watershed	Aboveground biomass	Carbon	Nitrogen	Phosphorus
Ridge and Valley				
Bear Gap Run	4458.3 (4.2)	2914.9 (4.2)	15.2 (4.1)	2.3 (5.5)
Laurel Branch	3961.5 (3.8)	2590.6 (3.8)	13.5 (3.7)	2.1 (4.9)
Wildcat Run	4039.5 (3.8)	2640.8 (3.8)	13.8 (3.8)	2.1 (5.0)
Allegheny Plateau				
Big Run	2585.9 (1.3)	1691.3 (2.5)	8.8 (2.4)	1.4 (3.2)
Bluelick Run	3901.4 (2.4)	2549.1 (3.7)	13.3 (3.6)	6.04 (14.2)
Monroe Run	1844.4 (0.9)	1210.2 (1.8)	6.3 (1.8)	1 (2.3)
Poplar Lick	3785.5 (1.7)	2492.6 (3.6)	13.1 (3.6)	2 (4.7)

Values in parentheses indicate the addition, within each column, to simulated forest vegetation pools that resulted in simulations that included the understory evergreen shrubs *K. latifolia* and *R. maximum*.

such as gypsy moth defoliation. For example, when the effects of this disturbance was examined in the Big Run watershed, stream discharge of N increased to indicate an export of about $3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Eshleman and Morgan, 1998; Eshleman, 2000), which is roughly half of the annual N deposition of $6.02 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in the Allegheny Plateau region. Similarly, Lovett et al. (2002) found that stream export of N in gypsy moth defoliated watershed in Virginia and West Virginia was roughly half of the $8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ annual N deposition. In this research, NuCSS results for the Big Run watershed indicated that accounting for the evergreen understory layer increased N mineralization by $7.8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and vegetation uptake by $7.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. The soil and forest floor pools stored an additional $0.3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. Likewise, in the Poplar Lick watershed N mineralization increased by $7.9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, vegetation uptake increased by $7.1 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, and the soil and forest floor pools increased by $0.8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ due to the inclusion of the evergreen understory. This additional N throughput and storage may have enough of an influence on the watershed scale to attenuate N leakage caused by insect defoliation, especially if most of the N released during this disturbance is in fact redistributed from the overstory to other ecosystem pools such as the forest floor (Lovett et al., 2002). Following defoliation of either the overstory or of the entire vegetation community, if tree and shrub mortality is not complete, the presence of a shrub understory with its N uptake demand could provide an increased N sink over that of an overstory alone, providing a more effective means for the vegetation community to retain mobilized N.

The capacity of North American forests to act as C sinks is considered important in strategies for reducing effects of increased atmospheric greenhouse gas emissions (Sedjo, 1992; Myneni et al., 2001), and a number of estimates of forest C and nutrient storage capacity on the regional and continental scales have been enabled by the use of remote sensing (Potter, 1999; Myneni et al., 2001). In a number of these investigations, estimates of C and nutrient storage capacity were found to be sensitive to regional differences in dominant life form (coniferous or broad leaved) and species composition (Fan et al., 1998; Myneni et al., 2001). Similarly, in this study we demonstrate the regional relevance of the evergreen understory layer in C and nutrient storage in Appalachian forests. While regional C pool accounted for by the presence of evergreen understory communities dominated by *R. maximum* and/or *K. latifolia* in these central Appalachian forests does not account for the “missing” C in global budgets, our results suggest that evergreen understory communities are an integral part of the functioning of Appalachian forests. This may be especially true for southern Appalachian forests, where increased rainfall and moisture availability may contribute to more ideal growing conditions for *R. maximum*, hence increasing the importance of evergreen understory vegetation as a component of forests in that region (White et al., 2001). For example, evergreen shrubs were found to comprise 8.8% of the overall aboveground biomass of a 50-year-old forest growing in one Coweeta watershed ($12,344 \text{ kg ha}^{-1}$ out of $139,900 \text{ kg ha}^{-1}$) (Day and Monk, 1974). As such, a detailed accounting of

the species present in the understory as well as the overstory of Appalachian forests is necessary.

The primary objective of this research was to examine the magnitude of the underestimation of biomass as well as carbon and nutrient storage caused by ignoring the presence of the evergreen understory communities when modeling Appalachian forest stands. It is important to recognize the benefits and limitations of this approach where overstory–understory competition is concerned. As a limitation, the model we used did not explicitly include overstory–understory competition for light or nutrients. However, a strength of our empirical approach was that our results implicitly include any effects of such competition, because our measures of C and N pools in biomass are based on field measurements.

The C and nutrient storage potential of the evergreen understory layer is small but in places considerable. Forest managers and others involved in landscape management should therefore consider the capacity of such forests to retain additional C and nutrients when evaluating management plans. Evergreen understory communities dominated by *K. latifolia* and *R. maximum* play a role in C and N sequestration that is out of proportion to their living biomass in the system, because the litter decomposes more slowly than that from the overstory trees. Indeed, the importance of *R. maximum* (and to a lesser extent *K. latifolia*) leaf biomass as a component of overall forest leaf biomass that were seen in NuCSS modeling results for this study area have also been observed in the southern Appalachian mountains, and are thought to have a noteworthy impact on watershed-level nutrient dynamics in this region (Day and Monk, 1977). Specifically, our results indicate that in evergreen understory communities dominated by *R. maximum* the percentage of total forest C and N sequestration is 1.5–2 times that of the total aboveground biomass accounted for by the evergreen understory, with noteworthy sequestration occurring in the forest floor and soil pools. Moreover, while simulated rates of C and N sequestration in the forest floor pool leveled off after about 30 years of growth, sequestration in the soil pool continued to increase over a time scale of 50 years. In addition, rates of N uptake by evergreen understory vegetation leveled off at between 6 and 11 kg N ha⁻¹ yr⁻¹ after about 20 years of growth in the test watersheds. The N uptake and C and N storage capacity of *R. maximum* and *K. latifolia* therefore seem to peak at approximately 20 or 30 years after the initiation of their growth, indicating that they will effectively retain additional N and act as an additional C sink within this time frame after becoming established in a forested area.

The presence of thickets of *R. maximum* and *K. latifolia* in forest understories has been found to inhibit overstory tree regeneration and therefore lead to declines in timber output (Minkler, 1941; Neary et al., 1984; Phillips and Murdy, 1985; Clinton et al., 1994; Waterman et al., 1995; Clinton and Vose, 1996; Walker et al., 1999; Nilsen et al., 2001). However, the fact that these species account for a larger amount of the C and nutrient component of forests in proportion to their biomass suggests that they may provide an important ecological service with respect to water quality. These species may be able to partially attenuate stream nitrate export response to gypsy moth

defoliation (Eshleman and Morgan, 1998; Eshleman, 2000), and other disturbances, such as wind or ice storm damage. In addition, their C and nutrient storage capacities may meaningfully contribute to the air quality maintenance and climate change mitigation services provided by Appalachian forests. The trade-off involved in removing evergreen understory species to maximize timber output should be balanced against their role in the overall functioning of the forest with respect to other important societal services.

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