Aboveground biomass and nitrogen allocation of ten deciduous southern Appalachian tree species

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Abstract: Allometric equations were developed for mature trees of 10 deciduous species (*Acer rubrum* L., *Betula lenta* L., *Carya* spp., *Comus florida* L., *Liriodendron tulipifera* L., *Oxydendrum arboreum* (L.) DC., *Quercus alba* L., *Quercus coccinea* Muenchh., *Quercus prinus* L., and *Quercus rubra* L.) at the Coweeta Hydrologic Laboratory in western North Carolina, U.S.A. These equations included the following dependent variables: stem wood mass, stem bark mass, branch mass, total wood mass, foliage mass, total biomass, foliage area, stem surface area, sapwood volume, and total tree volume. High correlation coefficients (R^2) were observed for all variables versus stem diameter, with the highest being for total tree biomass, which ranged from 0.981 for *Oxydendrum arboreum* to 0.999 for *Quercus coccinea*. Foliage area had the lowest R^2 values, ranging from 0.555 for *Quercus alba* to 0.962 for *Betula lenta*. When all species were combined, correlation coefficients ranged from 0.822 for foliage area to 0.986 for total wood mass, total tree biomass, and total tree volume. Species with ring versus diffuse/semiring porous wood anatomy exhibited higher leaf area with a given cross-sectional sapwood area as well as lower total sapwood volume. *Liriodendron tulipifera* contained one of the highest foliar nitrogen concentrations and had consistently low branch, bark, sapwood, and heartwood nitrogen contents. For a tree diameter of 50 cm, *Carya* spp. exhibited the highest total nitrogen content whereas *Liriodendron tulipifera* exhibited the lowest.

Résumé : Des equations allométriques ont été développées pour les arbres matures de 10 espèces à feuilles caduques (*Acer rubrum* L., *Betula lenta* L., *Carya* spp., *Comus florida* L., *Liriodendron tulipifera* L., *Oxydendrum arboreum* (L.) DC., *Quercus alba* L., *Quercus coccinea* Muenchh., Quercus *prinus* L. et Quercus *rubra* L.) au laboratoire hydrologique de Coweeta, dans l'ouest de la Caroline du Nord, aux États-Unis. Ces equations incluaient les variables dependantes suivantes : la masse du bois dans le tronc, la masse de l'écorce sur le tronc, la masse des branches, la masse totale du bois, la masse du feuillage, la biomasse totale, la surface foliaire, la superficie de la surface du tronc, le volume de bois d'aubier et le volume total de l'arbre. Toutes les variables étaient étroitement corrélées (R^2) avec le diamètre du tronc. La biomasse totale de l'arbre avait le coefficient le plus élevé qui variait de 0,981 pour l'*Oxydendrum arboreum* à 0,999 pour le *Quercus coccinea*. La surface foliaire avait la plus faible valeur de R^2 qui variait de 0,555 pour le *Quercus alba* à 0,962 pour le *Betula Zenta*. Lorsque toutes les espèces étaient combinées, les coefficients de corrélation variaient de 0,822 pour la surface foliaire à 0,986 pour la masse totale de bois, la biomasse totale de l'arbre et le volume total de l'arbre. Contrairement aux espèces avec du bois à pores diffus ou à zone semi-poreuse, les espbces avec du bois à zone poreuse avaient une surface foliaire plus importante pour une surface transversale donnée d'aubier de même qu'un volume total d'aubier plus faible. Le *Liriodendmn tulipifera* avait l'une des plus-fortes concentrations d'azote foliaire et le contenu en azote de ses branches, de son écorce, de son bois d'aubier et'de son bois de cœur était toujours faible. Pour un arbre d'un diamètre de 50 cm, le *Carya* spp. avait le contenu en azote le plus élevé tandis que le *Liriodendron tulipifera* avait le plus faible.

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Introduction

The allocation of biomass, nitrogen, and sapwood within a tree all have profound impacts on the physiology, growth, and distribution of tree species. Stem cross-sectional sapwood area and total sapwood volume greatly influence foliage area, transpiration, and stem respiration. Following the pipe model theory (Shinozaki et al. 1964), leaf area is

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Table 1. Species codes and DBH (1.37 m above ground level) range of the study trees.

Species	Code	*n*	DBH (cm) Minimum	Maximum
Acer rubrum L.	Acru	11	6.3	52.4
Betula lenta L.	Bele	10	7.8	39.6
Carya spp.*	Casp	10	8.2	52.3
Comus florida L.	Cofl	4	3.8	10.2
Liriodendron tulipifera L.	Litu	10	10.2	55.8
Oxydendrum arboreum (L.) DC.	Oxar	8	4.3	34.6
Quercus alba L.	Qual	10	7.0	63.0
Quercus coccinea Muenchh.	Quco	5	15.0	43.3
Quercus prinus L.	Qupr	10	10.6	57.5
Quercus *rubra* L.	Quru	9	19.7	52.0

Note: Trees were measured from the side due to the high degree of slope at the harvest sites.
*Includes *Carya* glabra (Mill.) Sweet, *Carya ovata (Mill.) K.* Koch, and *Carya tomentosa* (Poir.) *Nutt.*

correlated with cross-sectional sapwood area (Waring et al. 1977, 1980, 1982; Rogers and Hinckley 1979; Kaufmann and Troendle 1981). In turn, sapwood area is linked to transpiration (Vertessy et al. 1995; Haydon et al. 1996) while sapwood volume is an important scalar when predicting whole-tree stem respiration (Ryan 1989).

Tissue nitrogen concentration and' allocation greatly influence the ecophysiology of successional species. Foliar nitrogen concentration is correlated with photosynthetic rates (Field and Mooney 1986; Reich et al. 1995), suggesting that species with high foliar nitrogen concentrations may possess a competitive advantage. Similarly, nitrogen concentration has been correlated with respiration in many plant species and tissues (Ryan 1991), suggesting that high levels of nitrogen in branch and stem wood tissue during the growing season, which do little to directly aid photosynthetic production, could increase stem and branch respiration. Therefore, during the growing season, species with high foliage nitrogen concentrations and low branch and stem wood nitrogen contents possess au allocational pattern that may lead to high photosynthate production and low cellular maintenance respiration in the stem and branches, thereby allowing an organism to maximize carbon gain.

Allometric equations relating tree stem diameter at breast height (DBH) to various tree biological attributes are an important tool for many types of forest scaling efforts and models. While there are regional allometric equations for Wood mass in the southern Appalachians (Clark and Schroeder 1986), there are no site-specific equations for the Coweeta Basin. Landscape-level modeling of carbon fluxes in forested ecosystems requires accurate estimations of stem surface area or preferably sapwood volume for stem respiration scaling (Ryan 1990). Likewise, photosynthetic measurements require total leaf area and (or) mass for accurate scaling (Baldocchi 1993).

The purpose of this study was fourfold: *(i)* to generate allometric relationships including foliage area, cross-sectional sapwood area, stem surface area, and sapwood volume for 10 deciduous species at the Coweeta Hydrologic Laboratory/Long Term Ecological Research (LTER) site in western North Carolina, *(ii)* to examine both the accuracy of the regional Clark and Schroeder (1986) relationships for predicting total wood mass for trees on the Coweeta Basin and the site-specific nature of allometric equations, *(iii)* to explore the relationships between leaf area and cross-sectional sapwood area at breast height for species of differing wood anatomy (i.e., ring versus diffuse/semiring porous species), and *(iv)* to compare nitrogen concentrations in the foliage, branches, and wood as a function of species and size, as well as the total nitrogen content for trees of a given diameter.

Material and methods

Study area

Trees were sampled in the southern Appalachian Mountains in western North Carolina at the Coweeta Hydrologic Laboratory (35°N, 83°W) as well as in au area 4 km to the south, both areas are on the Nantahala National Forest. All trees were selected from mature stands (i.e., >80 years old) containing mixed oak (white oak (*Quercus alba* L.), scarlet oak (*Quercus coccinea* Muenchh.), chestnut oak (*Quercus prinus* L.), red oak (*Quercus rubra* L.), and black oak (Quercus *velutina Lam.)),* hickory (pignut hickory *(Carya glabra* (Mill.) Sweet), shagbark hickory *(Carya ovata (Mill.) K.* Koch), and mockemut hickory *(Carya tomentosa* (Poir.) *Nutt.)),* red maple (*Acer rubrum* L.), sourwood (*Oxydendrum arboreum* (L.) DC.), sweet birch (*Betula lenta* L.), flowering dogwood (*Cornus florida* L.), and tulip-tree (*Liriodendron tulipifera* L.). The mean annual precipitation, generated by an average of 133 storm events per year, is 2035 mm (Swift et al. 1988). Steep topography at the Coweeta Hydrologic Laboratory and in the surrounding area ranges in elevation from 675 to 1592 m. The soils are Inceptisols and Ultisols with A and B horizon depths ranging from trace covering to 70 cm (Velbel 1988). The younger Jnceptisols occur at higher elevations and on rocky substrates and are typically Umbric Dystrochrepts and Typic Dystrochrepts (Thomas 1996). Inceptisols are also located in coves and are represented by Typic Haplumbrepts. The older Ultisols, found on mountain slopes, are depicted by Typic Hapludults and Humic Hapludults (Thomas 1996).

Field measurements

Trees used in this study were selected by species, size, and location and were harvested between June and August to reduce the effects of decreasing specific leaf area (SLA) (Kloeppel et al. 1993) and nitrogen retranslocation on nitrogen tissue concentrations (Day and Monk 1977). The range of species and sizes was selected to represent the distribution observed in over 400 permanent plots across the Coweeta Basin (Douglas and Hoover 1988). Trees were selected using a stratified random design (Avery and Burkhart 1994) so that sample trees would represent a wide diameter range (Table 1). After locating trees of a desired species, the individuals were examined for gross anomalies such as severe pathogen

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damage or atypical crown architecture due to broken tops, or due to proximity to gaps or roads; atypical trees were excluded from sampling. The study trees were chosen from numerous locations within the study area to encompass a wide range of sites for each species; no trees were taken from treatment watersheds. Once suitable trees were identified and DBH (1.37 m) measured, they were felled using a chainsaw and the following variables were measured.

Using a 25-m steel tape, we measured the height from the base of the tree to the base of the live crown (BLC), crown length, and total height to the nearest centimetre. The stem was divided into 1- or 2-m sections, depending on the size of the sample tree, and marked with spray paint; the crown (BLC to the top of the tree) was subsequently divided into thirds and marked. All limbs were removed and separated into crown position (e.g., lower, middle, and upper) based on the origin of the branch. A subsample branch was selected from each crown position to quantify the variation in the ratio of foliage mass to branch mass that occurs from the lower to the upper portion of the crown. This subsample was then weighed with a 125 ± 0.05 kg digital scale (Intercomp, ST2000, Minneapolis, Minn.). We then weighed the remaining branches by crown position.

The bare stem was cut into 1- or 2-m sections and the individual log sections were weighed. We then cut a disk approximately 4 cm thick from the base of each log section to be used for determining water content and bark to wood ratios. Additional disks were cut from the base of the tree, DBH, and BLC and were used to determine cross-sectional sapwood area and sapwood volume. If a tree was too large to weigh (i.e., the l-m stem sections would exceed the capacity of the 125-kg scale), log volume from the base of the tree up to the point of feasible weighing was calculated using Newton's log rule (Avery and Burkhart 1994). Disks were cut from the bottom, middle, and top of the log and their circumferences as well as the total length of the log were recorded.

Laboratory analysis

We separated the crown subsamples into foliar and branch components, which were then dried to a constant mass at 65°C and weighed to determine moisture content. Prior to drying the foliage, we selected 10 representative leaves from each of the canopy section subsamples and separated the petioles from the leaf blades; The total area of the leaf blades was measured using a leaf area meter (LI-COR 3100, LI-COR, Inc., Lincoln, Nebr.); the blades and petioles were dried (65°C) and weighed to determine SLA and the ratio of leaf blade mass to total leaf mass.

The fresh mass and circumference (outside bark) were recorded for the disks sampled from the base of each log section; bark and wood were then separated. We dried the disks (65°C) and weighed the wood and bark separately to determine wood mass to total mass and bark mass to total mass ratios as well as the moisture content of the total disk. The disks taken from the base of the tree, DBH, and BLC were stained with a potassium iodide solution to determine heartwood-sapwood boundaries (Kutscha and Sachs 1962). We traced the total disk area and the heartwood-sapwood delineation on.acetate sheets and painted them to make them opaque. We then measured heartwood and sapwood area from these tracings on a leaf area meter. The disks from the large stem sections, where volumetric estimations were needed, had a 10" wedge cut from the center to the outside edge of the disk (including bark). Wedge volume was found by volumetric displacement (Heimichs and Lassen 1970), and mass was measured after drying to a constant mass *(65°C)* to calculate specific gravity. The total log section mass was then calculated by multiplying the average specific gravity of the wedges for each species by the volume of the log section.

Integrating

The total dry mass of the foliage or branches for a given section was calculated by multiplying the ratio of dried foliage or dried branches to the total dried mass of the crown section subsample by the total crown section dry mass. The foliage mass of the crown section is then multiplied by the SLA and by the leaf blade mass to total leaf mass ratio to determine total leaf area for a given crown section. The correction of the leaf blade mass to total leaf mass ratio is necessary because the petiole, which is not used in the leaf area calculations, accounted for 5–13% of the total leaf mass in this study for *Quercus alba* and *Carya* spp., respectively. The total foliage mass, branch mass, and foliage area for the tree is then summed across all three canopy positions. Similarly, we determined the log section dry mass by multiplying (1 – moisture content) by the field wet mass and then calculated total wood mass and bark mass for the section from the ratios of bark or wood to the total disk dry mass. Stem surface area was calculated by multiplying the log section length (e.g., 1 or 2 m) by the average of the circumferences from the disks at the base and top of the log and summing over all sections. Similarly, we calculated stem volume by multiplying the surface area of the disks by the log section lengths and summing over all sections. The top log section was considered to be conical. The surface area of the volumetrically estimated logs was calculated using a modified version of Newton's log formula where disk circumference was substituted for disk surface area (Avery and Burkhart 1994).

Total sapwood volume for a tree is given by the sum of the sapwood volume of the branches and the sapwood volume of the stem, which is the difference between the total wood volume (inside bark) and the heartwood volume. For this study, the branch volume was assumed to be entirely sapwood; although larger branches can certainly have a large proportion of heartwood, we feel that the contribution to total heartwood is minimal. It follows that the branch volume is then equal to the total branch dry mass divided by the branch specific gravity (see Clark and Schroeder 1986). The geometric solids of total wood volume and heartwood volume were computed by summing the volumes for the 'base to DBH" section (frustrum of a neiloid), the "DBH to BLC" section (frustrum of a paraboloid), and the "BLC to the top" section (paraboloid) (Husch et al.1972).

Nitrogen analysis

Foliar tissue nitrogen concentration was determined from approximately 50 leaves from each dried, crown position subsample. Branch tissue nitrogen concentration was determined on a representative branch from each crown position subsample. The tree as a whole was the experimental unit, so the mean of the three crown positions was used-in all nitrogen analyses. For stem tissue nitrogen analysis, bark, sapwood from the last 2 years of growth, and a 10" wedge from the remaining wood were sampled from disks equally spaced within the stem (sensu Son and Gower 1991). We sampled three to five disks per tree depending on tree size. On the smaller trees (<15 cm DBH), up to one half of the bark and sapwood from each disk was used. All samples were ground with a Wiley mill to pass through a 0.5-mm^2 screen (size 40) and analyzed with a combustion elemental analyzer (2400CHN, Perkin Elmer, Norwalk, Conn.). Nitrogen content per component per tree was found by multiplying the nitrogen concentration for each tissue sample by the total dry mass of that component. Stem wood nitrogen content (excluding bark) was calculated following Son and Gower (1991).

Statistical analysis

Simple linear regressions (PROC REG, SAS Institute Inc. 1985) were computed using $\log_{10}$-transformed data (to linearize) and took the form

$$[1] \quad \log_{10} Y = a + b \cdot \log_{10} x$$

where X is the stem DBH (centimetres), Y is the dependent variable

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Table 2. Specific leaf area (SLA) for 10 southern Appalachian tree species in western North Carolina, U.S.A.

Species code	n	SLA ($cm^2 \cdot g^{-1}$) Minimum	Maximum	Mean (SE)
ACN	11	114.2	162.3	144.2*bcd* (4.7)
Bele	10	161.8	538.2	333.0*a* (45.3)
Casp	10	90.9	259.1	142.7*bcd* (15.5)
Cofl	4	255.7	439.0	345.5*a* (38.8)
Litu	10	150.8	224.2	186.0*bc* (7.4)
oxar	8	131.6	273.6	196.4*b* (20.1)
Qual	10	101.6	225.4	136.8*bcd* (12.7)
Quco	5	95.1	127.4	112.6*d* (5.2)
Qupr	10	98.0	212.1	123.0*d* (11.4)
Quru	9	107.0	152.3	129.5*cd* (6.0)

Note: Means followed by tbe same letter are not significantly different (LSD mean separation test at a = 0.05). See Table 1 for species codes.

Table 3. Wood specific gravity (including bark) for converting volumetric estimates of large logs to mass estimates.

Species code	Observed specific gravity (SE)	Reference specific gravity (SE)*
Acru	0.558*cd* (0.014)	0.522 (0.009)
Bele	0.609*bc* (0.006)	0.616 (0.007)
Casp	0.658*ab* (0.011)	0.631 (0.006)
Litu	0.440*e* (0.020)	0.403 (0.005)
Qual	0.5571 (0.016)	0.587 (0.005)
Quco	0.522*d* (0.021)	0.568 (0.005)
Qupr	0.664*a* (0.020)	0.599 (0.004)
Quru	0.571*cd* (0.015)	0.576 (0.003)

Note: Means followed by the same letter are not significantly different (LSD mean separation test at a = 0.05). See Table 1 for species codes.
*Reference specific gravities are from Clark and Schroeder (1986).

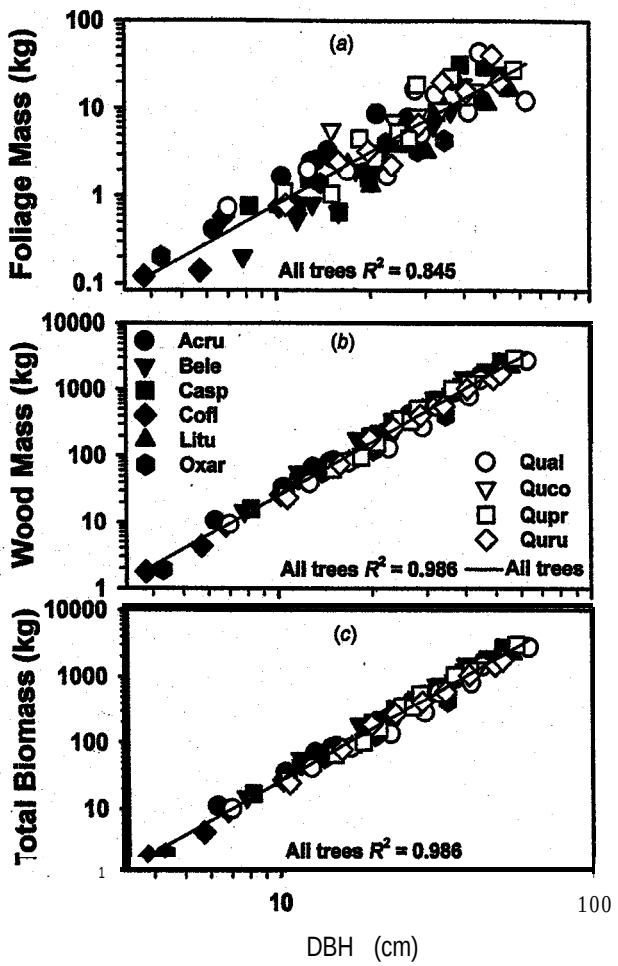
(e.g., stem wood, stem bark, sapwood volume, etc.), and *a* and *b* are the intercept and slope, respectively. Means were compared using the LSD mean separation test at the a = 0.05 level for SLA and specific gravity (PROC MEANS, SAS Institute Inc. 1985). Pairwise comparisons of regression coefficients (PROC REG, SAS Institute, Inc. 1985) were performed for the ring porous and diffuse/semiring porous models relating sapwood volume to DBH and foliage area to cross-sectional sapwood area (Chatteijee and Price 1977). Regression analysis was also performed on tissue nitrogen content versus DBH to calculate values for predicted trees of diameters 10, 30, and 50 cm (PROC REG, SAS Institute, Inc. 1985).

Results

Specific leaf area

Mean SLA by species ranged from 112.6 $cm^2 \cdot g^{-1}$ for ***Quercus coccinea*** to 345.5 $cm^2 \cdot g^{-1}$ for ***Comus florida*** (Table 2). ***Betula Zenta*** and ***Comus florida*** had similar and significantly greater SLA (LSD mean separation test at a = 0.05) thau all other species. Foliage crown position was determined by the location of branch origin and is not an indication of foliage height or light interceptance. Therefore, an analysis of the relationship of SLA to crown position is not appropriate; however, SLA was evaluated as a function of stem DBH. ***Betula lenta***, ***Carya*** spp., ***Quercus alba***, and ***Quercus rubra*** exhibited the only significant decline for SLA versus DBH with *p* values of 0.009, 0.033, 0.011, and 0.017, respectively. Stem diameter explained between 38 and 55% of the variation in SLA for ***Carya*** spp. and ***Betula lenta***, respectively.

Fig. 1. Allometric relationships for (a) foliage mass, (*b*) wood mass (stem wood, bark, and branches), and (c) total biomass (wood and foliage) versus tree stem DBH at the Coweeta Hydrologic Laboratory in western North Carolina, U.S.A. Note the different scale in Fig. 1a.



Specific gravity

Wood specific gravity, which was used for the volume to mass conversion of the large log sections, varied considerably among species (Table 3). As expected, ***Liriodendron tulipifera*** exhibited the lowest specific gravity (0.440) whereas ***Quercus prinus*** exhibited the highest (0.664) using the LSD mean separation technique at the a = 0.05 level. Our observed values were not significantly different (95% confidence intervals) from those reported by Clark and Schroeder (1986) except that for ***Quercus prinus***, which was significantly higher in this study (Table 3).

Allometric relationships

The coefficients for the mass and geometric variables (e.g., area and volume) for the log_{10}-transformed linear regressions are given in Table 4. Stem diameter explained between ***68% (Quercus alba)*** and ***95% (Oxydendrum arboreum)*** of the variation in foliage mass (Fig. 1a) and between 56% ***(Quercus alba)*** and 96% ***(Betula Zenta)*** of the

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Table 4. Regression equations for estimating component dry mass, leaf area, stem surface area, sapwood volume, and total tree volume for 10 tree species at the Coweeta Hydrologic Laboratory in western North Carolina, U.S.A.

Species code		*a* (SE)	*b* (SE)	MSE	R^2	CF
Stem wood mass (kg)						
Acru	11	-1.215 (0.055)	2.575 (0.042)	0.001	0.997	1.003
Bele	10	-1.221 (0.160)	2.594 (0.121)	0.007	0.981	1.019
Casp	10	-1.441 (0.104)	2.728 (0.075)	0.003	0.993	1.008
Cofl	4	-1.421 (0.139)	2.585 (0.171)	0.003	0.987	1.008
Litu	10	-1.522 (0.149)	2.737 (0.102)	0.005	0.988	1.013
oxar	8	-1.439 (0.209)	2.646 (0.167)	0.016	0.973	1.043
Qual	10	-1.581 (0.126)	2.732 (0.088)	0.006	0.991	1.016
Quco	5	-1.756 (0.204)	2.876 (0.142)	0.002	0.980	1.005
Qupr	10	-1.778 (0.152)	2.918 (0.107)	0.005	0.988	1.013
Quru	9	-1.416 (0.187)	2.639 (0.129)	0.007	0.981	1.019
All trees	87	-1.436 (0.051)	2.685 (0.037)	0.009	0.984	1.024
Stem bark mass (kg)						
Acru	11	-1.913 (0.140)	2.462 (0.107)	0.009	0.981	1.024
Bele	10	-1.858 (0.206)	2.436 (0.156)	0.012	0.964	1.032
Casp	10	-1.682 (0.145)	2.358 (0.104)	0.006	0.983	1.016
Cofl	4	-3.040 (0.209)	3.040 (0.259)	0.006	0.979	1.016
Litu	10	-1.588 (0.096)	2.302 (0.066)	0.002	0.993	1.005
oxar	8	-2.274 (0.155)	2.583 (0.124)	0.009	0.984	1.024
Qual	10	-2.212 (0.152)	2.548 (0.107)	0.008	0.984	1.021
Quco	5	-2.504 (0.379)	2.938 (0.263)	0.008	0.969	1.021
Qupr	10	-1.964 (0.180)	2.564 (0.127)	0.007	0.978	1.019
Quru	9	-1.846 (0.178)	2.441 (0.123).	0.006	0.980	1.016
All trees	87	-2.344 (0.097)	2.764 (0.071)	0.032	0.946	1.089
Branch mass (kg)						
Acru	11	-2.056 (0.168)	2.733 (0.128)	0.013	0.979	1.035
Bele	10	-3.086 (0.197)	3.505 (0.149)	0.011	0.984	1.030
Casp	10	-2.970 (0.532)	3.323 (0.382)	0.087	0.892	1.260
Cofl	4	-2.214 (0.201)	3.133 (0.248)	0.006	0.981	1.016
Litu	10	-2.160 (0.368)	2.591 (0.252)	0.028	0.921	1.077
Oxar	8	-2.017 (0.266)	2.579 (0.213)	0.025	0.954	1.069
Qual	10	-1.806 (0.475)	2.409 (0.333)	0.079	0.851	1.233
Quco	5	-1.657 (0.832)	2.425 (0.576)	0.040	0.807	1.112
Qupr	10	-2.871 (0.550)	3.238 (0.389)	0.063	0.884	1.182
Quru	9	-2.660 (0.5 11)	3.026 (0.352)	0.053	0.901	1.151
All trees'	87	-2.114 (0.128)	2.691 (0.094)	0.056	0.906	1.160
Total wood mass (kg) (stem wood, stem bark,' and branches)						
Acru	11	-1.096 (0.054)	2.591 (0.042)	0.001	0.997	1.003
Bele	10	-1.254 (0.148)	2.728 (0.112)	0.006	0.985	1.016
Casp	10	-1.349 (0.075)	2.773 (0.054)	0.002	0.997	1.005
Cofl	4	-1.384 (0.152)	2.760 (0.188)	0.003	0.986	1.008
Litu	10	-1.258 (0.118)	2.646 (0.080)	0.003	0.992	1.008
Oxar	8	-1.279 (0.179)	2.623 (0.143)	0.011	0.980	1.030
Qual	10	-1.317 (0.149)	2.640 (0.104)	0.008	0.986	1.021
Quco	5	-1.389 (0.026)	2.750 (0.018)	0.001	0.999	1.003
Qupr	10	-1.619 (0.151)	2.926 (0.106)	0.005	0.988	1.013
Quru	9	-1.279 (0.137)	2.651 (0.094)	0.004	0.990	1.011
All trees	87	-1.281 (0.048)	2.681 (0.035)	0.008	0.986	1.021
Foliage mass (kg)						
Acru	11	-1.620 (0.200)	1.778 (0.153)	0.019	0.931	1.052
Bele	10	-3.086 (0.231)	2.628. (0.175)	0.015	0.961	1.041
Casp	10	-2.595 (0.491)	2.356 (0.353)	0.074	0.829	1.217

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Table 4 (continued).

Species code	*n*	*a* (SE)	*b* (SE)	MSE	R^2	CF
Cofl	4	-2.160 (0.616)	2.048 (0.761)	0.055	0.676	1.157
Litu	10	-2.192 (0.378)	1.981 (0.258)	0.029	0.865	1.080
oxar	8	-1.675 (0.161)	1.546 (0.129)	0.009	0.953	1.024
Qual	10	-1.599 (0.536)	1.673 (0.375)	0.101	0.677	1.307
Quco	5	-0.380 (0.268)	0.928 (0.185)	0.004	0.858	1.011
Qupr	10	-2.323 (0.486)	2.214 (0.344)	0.050	0.818	1.142
Quru	9	-2.514 (0.417)	2.326 (0.287)	0.035	0.890	1.097
All trees	87	-2.122 (0.127)	2.022 (0.093)	0.055	0.845	1.158
Total biomass (kg) (stem wood, stem bark, branches, and foliage)						
ACN	11	-1.060 (0.050)	2.574 (0.038)	0.001	0.998	1.003
Bele	10	-1.248 (0.148)	2.726 (0.112)	0.006	0.985	1.016
Casp	10	-1.326 (0.075)	2.762 (0.054)	0.002	0.997	1.005
Cofl	4	-1.339 (0.170)	2.730 (0.211)	0.004	0.982	1.011
Litu	10	-1.236 (0.114)	2.635 (0.078)	0.003	0.992	1.008
oxar	8	-1.218 (0.171)	2.582 (0.137)	0.010	0.981	1.027
Qual	10	-1.266 (0.157)	2.613 (0.110)	0.009	0.984	1.024
Quco	5	-1.283 (0.012)	2.685 (0.009)	0.001	0.999	1.003
Qupr	10	-1.587 (0.151)	2.910 (0.107)	0.005	0.988	1.013
Quru	9	-1.259 (0.130)	2.644 (0.090)	0.003	0.991	1.008
All trees	87	-1.247 (0.047)	2.663 (0.035)	0.008	0.986	1.020
Foliage area (m^2)						
ACN	11	-0.494 (0.190)	1.762 (0.145)	0.017	0.936	1.046
Bele	10	-0.829 (0.175)	2.008 (0.133)	0.009	0.962	1.024
Casp	10	-1.027 (0.592)	1.996 (0.426)	0.108	0.700	1.332
Cofl	4	-0.510 (0.347)	1.827 (0.430)	0.018	0.851	1.049
Litu	10	-0.816 (0.397)	1.877 (0.272)	0.032	0.839	1.089
oxar	8	-0.132 (0.144)	1.293 (0.115)	0.007	0.947	1.019
Qual	10	0.030 (0.524)	1.284 (0.367)	0.097	0.555	1.293
Quco	5	0.400 (0.261)	1.091 (0.181)	0.004	0.899	1.011
Qupr	10	-1.033 (0.448)	2.041 (0.317)	0.042	0.818	1.118
Quru	9	-1.182 (0.414)	2.141 (0.285)	0.035	0.874	1.097
All trees	87	-0.491 (0.114)	1.674 (0.084)	0.045	0.822	1.126
Stem surface area (m^2)						
ACN	11	-1.360 (0.074)	1.665 (0.056)	0.003	0.989	1.008
Bele	10	-1.223 (0.115)	1.583 (0.087)	0.004	0.973	1.011
Casp	10	-1.488 (0.145)	1.731 (0.104)	0.006	0.968	1.016
Cofl	4	-1.783 (0.265)	1.862 (0.327)	0.010	0.916	1.027
Litu	10	-1.444 (0.143)	1.775 (0.098)	0.004	0.973	1.011
oxar	8	-1.595 (0.155)	1.815 (0.124)	0.009	0.968	1.024
Qual	10	-1.821 (0.101)	1.889 (0.071)	0.004	0.987	1.011
Quco	5	-1.772 (0.278)	1.907 (0.192)	0.004	0.961	1.011
Qupr	10	-1.499 (0.107)	1.706 (0.075)	0.002	0.983	1.005
Quru	9	-1.388 (0.210)	1.641 (0.145)	0.009	0.941	1.024
All trees	87	-1.574 (0.054)	1.791 (0.040)	0.010	0.960	1.027
Sapwood volume (m^3) (stem sapwood and branches)						
Acru	11	-3.642 (0.086)	2.441 (0.066)	0.004	0.993	1.011
Bele	10	-3.817 (0.163)	2.554 (0.124)	0.008	0.979	1.021
Casp	10	-4.081 (0.189)	2.637 (0.136)	0.011	0.977	1.030
Cofl	4	-3.994 (0.452)	2.634 (0.559)	0.030	0.876	1.083
Litu	10	-3.581 (0.131)	2.318 (0.089)	0.004	0.987	1.011
oxar	8	-3.876 (0.214)	2.507 (0.172)	0.016	0.968	1.043
Qual	10	-3.577 (0.295)	2.072 (0.206)	0.031	0.917	1.086
Quco	5	-3.619 (0.471)	2.184 (0.326)	0.013	0.916	1.035
Qupr	10	-4.033 (0.290)	2.486 (0.205)	0.018	0.942	1.049

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Table 4 (concluded).

Species code	*n*	*a* (SE)	*b* (SE)	MSE	R^2	CF
Quru	9	-4.179 (0.125)	2.465 (0.086)	0.003	0.990	1.008
All trees	87	-3.695 (0.108)	2.315 (0.079)	0.040	0.909	1.111
Total tree volume (m^3) (stem and branches)						
Acru	11	-3.885 (0.079)	2.616 (0.061)	0.003	**0.995**	1.008
Bele	10	**-4.005** (0.134)	2.724 (0.102)	0.005	**0.988**	1.013
Casp	10	4.296 (0.081)	2.856 (0.058)	0.002	**0.996**	1.005
Cofl	4	4.239 (0.267)	2.878 (0.332)	0.010	0.961	1.027
Litu	10	-4.035 (0.145)	2.742 (0.099)	0.004	0.988	1.011
Oxar	8	4.049 (0.093)	2.693 (0.074)	0.003	0.995	1.008
Qual	10	**-4.021** (0.142)	2.607 (0.100)	0.007	0.987	1.019
Quco	5	-4.118 (0.066)	2.738 (0.045)	0.001	0.999	1.003
Qupr	10	**-4.230** (0.158)	2.797 (0.112)	0.005	0.986	1.013
Quru	9	**-4.088** (0.220)	2.700 (0.151)	0.010	0.975	1.027
All trees	87	-4.061 (0.048)	2.705 (0.035)	0.008	0.986	1.021

Note: Equations for all variables are of the form $\log_e Y = a + b\log_e X$ where Y is the dependent variable (e.g., stem wood mass (kg)) and X is stem DBH (1.37 m) (cm). CF is the correction factor where CF = exp ((SEE x 2.303)²/2) (Sprugel 1983); SEE. = $\sqrt{MSE}$. See Table 1 for species codes.

Table 5. Differences in predicted total wood mass between this study and Clark and Schroeder (1986) using trees with diameters of 10, 30, and 50 cm.

Species	Total wood mass (kg)						% difference*		
	This study			Clark and Schroeder (1986)					
code	10 cm	30 cm	50 cm	10 cm	30 cm	50 cm	10 cm	30 cm	50 cm
Acru	31	540	2029	30	488	—	3	11	—
Bele	30	606	—	45	551	—	-32	10	—
Casp	27	561	2314	26	656	2309	4	-14	<1
Litu	25	451	1742	19	402	1477	31	12	18
Qual	21	391	1504	31	574	2254	-30	-32	-33
Quco	23	489	—	29	547	1897	-21	-11	—
Qupr	21	511	2279	23	553	1867	-9	-8	22
Quru	24	438	1697	40	585	2012	-40	-25	-16
All trees	26	487	1914	30	516	1873	-14	-6	2

Note: Missing values are due to predicted tree diameter hemg beyond the range of the equations. See Table 1 for species codes.

*Difference in total wood mass prediction for this study compared with Clark and Schroeder (1986).

variation in foliage area (Fig. 2*a*). Foliage mass and foliage area inherently had the highest variability and therefore the lowest R^2 values of all allometric variables (Table 4). The R^2 of the total tree biomass relationship with DBH ranged from 0.981 in *Oxydendrum arboreum* to 0.999 in *Quercus coccinea* and was equally high for all tree species combined, R^2 = 0.986 (Table 4; Fig. lc).

Stem surface area and sapwood volume also exhibited significant relationships with DBH (Fig. 2*b* and 2*c*). For stem surface area, R^2 ranged from 0.916 for *Cornus florida* to 0.989 for *Acer rubrum* and was 0.960 for all species combined (Table 4). Sapwood volume regressions also had high R^2 values, ranging from 0.916 to *0.993* for *Quercus coccinea* and *Acer rubrum*, respectively; however, differences among species with varying wood anatomy were apparent (Fig. 2*c*). Diffuse/semiring porous species (*Acer rubrum*, *Betula lenta*, *Carya* spp., *Cornus florida*, *Liriodendron tulipifera*, and *Oxydendrum arboreum*) exhibited a greater total sapwood volume for a given stem diameter than the ring porous species (*Quercus alba*, *Quercus coccinea*, *Quercus prinus*, and *Quercus rubra*). Regression analysis of the two groups yields R^2 values of 0.976 for diffuse/semiring porous species and 0.925 for ring porous species. The slopes of these two lines were significantly different (p = 0.042), but the intercepts were similar (p = 0.934).

Nitrogen concentration

Figure 3 shows the tissue nitrogen concentrations for the 10 species, which are arranged by decreasing foliar nitrogen concentration. Regression analysis of the tissue concentrations with DBH yielded no significant relationships for any of the species or tissue components. 'Mean foliage nitrogen concentration was equally high for *Betula Zenta*, *Quercus rubra*, *Quercus prinus*, *Liriodendron tulipifera*, and Quercus

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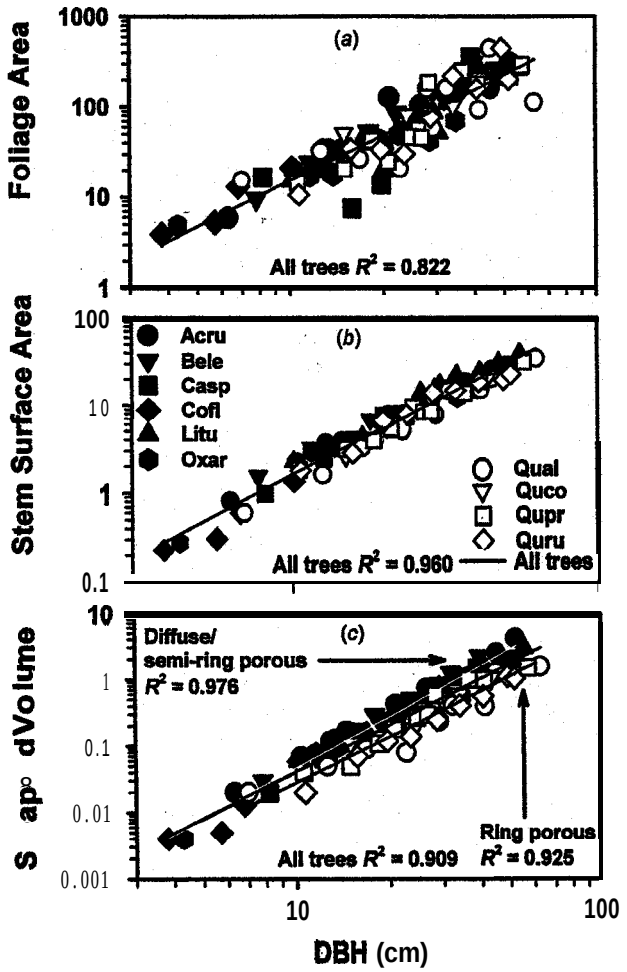
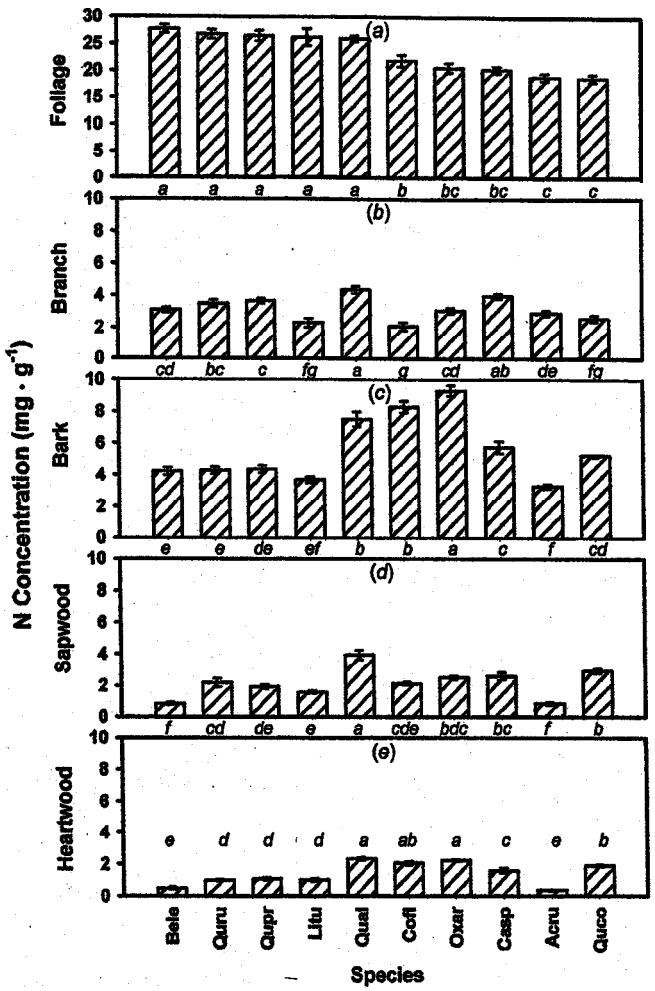
Fig. 2. Allometric relationships, for (a) foliage area, (*b*) stem surface area, and (c) total sapwood volume (stem sapwood and branches) versus tree stem DBH at the Coweeta Hydrologic Laboratory in western North Carolina, U.S.A. See Table 1 for species codes.



Fii. 3. Tissue nitrogen concentrations for (*a*) foliage, (b) branches, (*c*) bark, (*d*) the last 2 years of sapwood, and (e) heartwood for 10 deciduous species arranged by decreasing foliar nitrogen concentration. Species with the same letter below were not significantly different using the LSD mean separation test at the a = 0.05 level. See Table 1 for species codes.



alba (LSD mean separation test at a = 0.05), and these species' nitrogen concentrations were significantly greater than those of *Cornus florida*, *Oxydendrum arboreum*, *Carya* spp., *Acer rubrum*, and *Quercus coccinea* (Fig. *3a*). *Quercus alba* and the *Carya* spp. exhibited the highest mean branch nitrogen concentration, while *Cornus florida* had the lowest (Fig. *3b*); the remaining species were statistically similar despite low standard errors. Bark nitrogen concentration was highest in *Oxydendrum arboreum* and was significantly greater than in *Quercus alba* and *Comus florida*, which had significantly greater nitrogen concentrations than the remaining species (Fig. 3*c*). Sapwood nitrogen concentrations were highest in *Quercus alba* and lowest in *Acer rubrum* and *Betuka lenta* (Fig. 3*d*); no trends in sapwood nitrogen concentration versus xylem morphology (e.g., diffuse/semiring or ring porous) were apparent. Similarly, no trends were observed in heartwood nitrogen concentrations (Fig. 3e) where, again, *Quercus alba* had the highest and *Acer rubrum* and *Betula lenta* had the lowest; *Oxydendrum arboreum* and *Quercus alba* nitrogen concentrations were not significantly different (LSD mean separation test at CC = 0.05).

Discussion

Mass predictions

Using equations from this study and the regional equations from Clark and Schroeder (1986), we predicted biomass estimates. for trees with DBH = 10, 30, and 50 cm (Table 5). When our total predicted wood masses (stem wood, stem bark, and branch mass) were compared with those predicted by Clark and Schroeder (1986), considerable differences were apparent, suggesting that site-specific or at least localized allometric equations for the Coweeta Hydrologic Laboratory are warranted. For the *Carya* spp. and all trees combined, the two equations differed only slightly (Table 5). However, *Liriodendron tulipifera* at Coweeta had a consistently higher wood mass (31, 12, and 18% for trees with diameters of 10, 30, and 50 cm, respectively), while *Quercus alba* and *Quercus rubra* wood masses were consistently lower at Coweeta (from 16 to 40%) (Table 5). For *Quercus coccinea* and *Quercus prinus trees* with diameters of 10 and 30 cm, wood mass was also lower in the Coweeta

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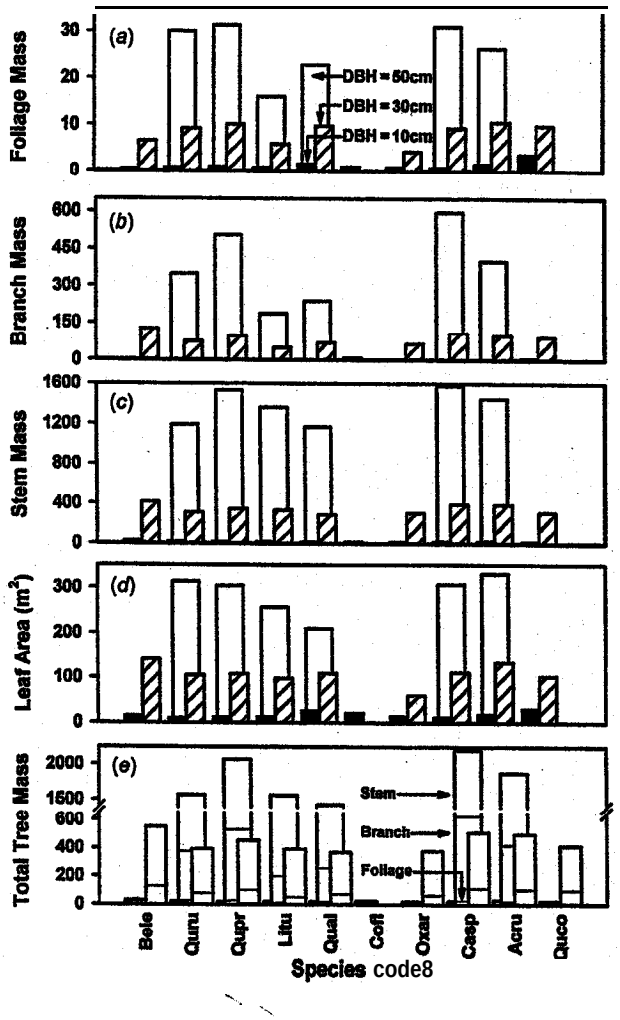
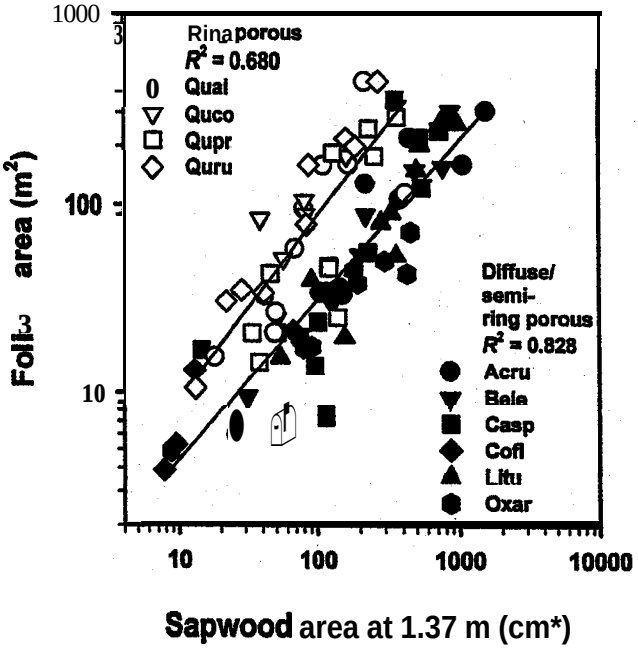
Fig. 4. Biomass allocation for trees calculated with stem DBH (1.37 m) = 10, 30, and 50 cm for (a) foliage mass, (*b*) branch mass, (*c*) stem mass (sapwood, heartwood, and bark), (*d*) leaf area, and (*e*) all aboveground components combined for 10 deciduous species arranged by decreasing foliar'uitrogen concentration. Mass values are kilograms. See Table 1 for species codes.



Basin; however,' for. ***Quercus prims*** with a diameter of 50 cm, wood mass was 22% higher than that predicted by Clark and Schroeder (1986). These discrepancies suggest that, for trees of equal DBH, the Coweeta Basin is more conducive for greater standing biomass ***in Liriodendron tulipifera*** and Quercus ***prims*** and less so for biomass in ***Quercus alba***, ***Quercus coccinea,*** and ***Quercus rubra*** when compared with the greater southern Appalachian region as sampled by Clark and Schroeder (1986).

The variation between predicted wood mass for the local and regional sampling areas could be a result of differing wood specific gravities and (or) heights. ***Quercus prinus*** had a significantly higher specific gravity in the Coweeta Basin (Table 3), which suggests that wood specific gravity may be a cause of the higher observed wood ***mass in Quercus prinus*** for a given diameter. ***Liriodendron tulipifera,*** which has a similar wood specific gravity at Coweeta when compared with the areas sampled by Clark and Schroeder (1986), has a higher predicted wood mass at Coweeta (Table 5), possibly indicating more favorable conditions for increased height (a higher site index) versus the areas sampled by Clark and Schroeder (1986).

Fig. 5. Allometric relationships of ring porous aud diffuselsemiriug porous species for foliage area versus cross-sectional sapwood area at breast height (1.37 m). For ring porous species, $\log_{10}$ Y = -0.006 + 0.969·$\log_{10}$ X ($p < 0.001$); for diffuse/semiring porous species, $\log_{10}$ Y = -0.197 + 0.843·$\log_{10}$ X ($p < 0.001$). See Table 1 for species codes.



Variation in biomass allocation

Tree species vary greatly in their biomass allocation and morphology. 'Using the allometric equations in Table 4, we compared the 10 species by predicting allocation of biomass for trees of DBH = 10, 30, and 50 cm. ***Liriodendron tulipifera*** and ***Quercus alba*** have relatively low predicted branch masses for trees of DBH = 30 and 50 cm (Fig. 4), ***while Liriodendron tulipifera*** has a noticeably lower foliage mass and leaf area (Figs. 4*a* and 4*d*). ***Although Liriodendron tzdipifera*** allocates less biomass to canopy structure, it still maintains a relatively high stem mass (Fig. 4*c*).

Relative to the ***other*** species, ***Quercus alba*** and ***Quercus rubra*** of DBH = 50 cm have lower predicted stem masses (Fig. 4*c*). Conversely, ***Carya*** species and ***Quercus prinus*** have relative high stem masses at DBH = 50 cm (Fig. 4*c*); this may be a result of their high wood' specific gravities (Table 3). Because of the combination of high stem and branch mass (Fig. 4*b*), ***these two*** species also rank the highest for total tree mass when DBH = 50 cm (Fig. 4e).

Sapwood and foliage area relationships

When foliage area is plotted against cross-sectional sapwood area at breast height, a clear distinction in xylem morphology is apparent (Fig. 5). Although slopes and intercepts were not significantly different (p = 0.436 and 0.298, respectively) for the ring porous and diffuse/semiring porous regressions, ring porous trees, namely the ***Quercus*** spp., had a noticeably greater foliage area per unit of sapwood area. Using linear regression techniques, foliage area was

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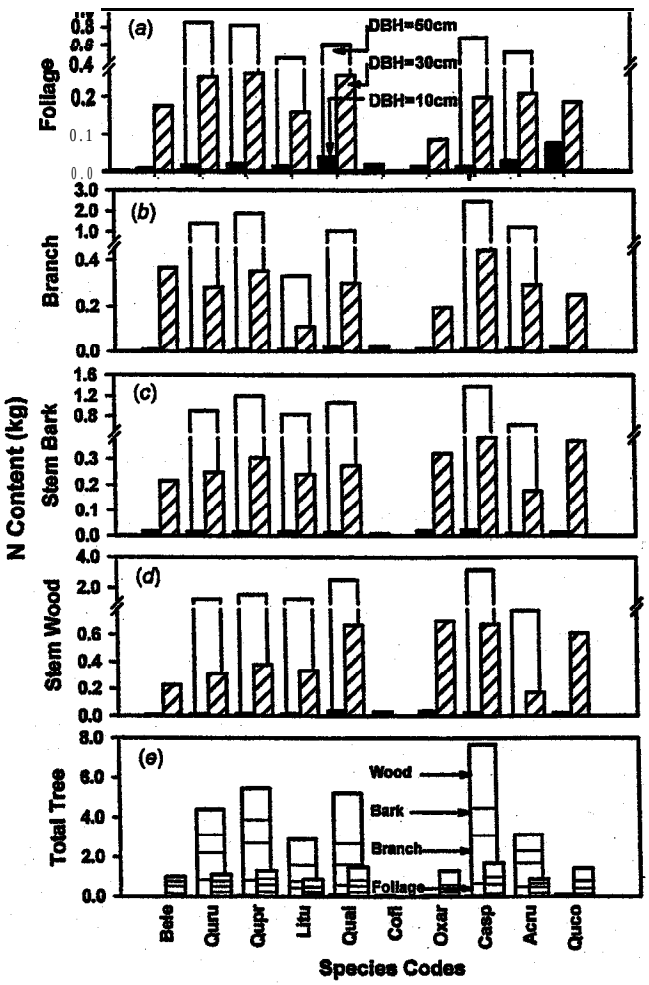
Fig. 6. Tissue nitrogen content for trees calculated with stem DBH (1.37 m) = 10, 30, and 50 cm for (*a*) foliage, (*b*) branches, (*c*) bark, (*d*) stem wood (sapwood and hearhvood), and (e) all aboveground components combined for 10 deciduous species arranged by decreasing foliar nitrogen concentration. Predictions for trees of DBH = 30 or 50 cm are only included for species sampled in that range. See Table 1 for species codes.



predicted for sapwood areas of 20 and 300 cm^2. Ring porous species supported foliage areas 117-206% greater than diffuse/semiring porous species for sapwood areas of 20 and 300 cm^2, respectively (i.e., 9.4 versus 20.4 m^2 and 92.0 versus 281.3 m^2). The support of a given foliage area with less sapwood is possible because the larger vessels of the ring porous anatomy reduce hydraulic resistance compared with diffuse/semiring porous species (Zimmermann and Brown 1971; Ni and Pallardy 1990), which results in faster sap movement (Zimmermann and Brown 1971; Hinckley et al. 1978; Kramer and Kozlowski 1979). Although the larger vessels tend to increase risk of cavitation (Tyree and Dixon 1986), Abrams (1990) noted that when cavitation occurs in ring porous species, water movement can still proceed through the smaller late-wood vessels, thereby allowing slower but sustained sap flow during drought.

Sapwood also requires respirational costs involved in cell maintenance and growth (Sprugel 1990). Since total tree sapwood volume is less in ring versus diffuse/semiring porous species, for a given stem diameter (Fig. 2*c*), total sapwood respiration may be less for ring porous species if respiration per unit volume of sapwood is similar. Respiration costs become important as tree size increases (Waring and Schlesinger 1985; Kaufmann and Ryan 1986; Ryan 1989; but see Gower et al. 1996), which suggests that sapwood respiration costs would be less for large ring porous *Quercus* spp. than for similar sized, diffuse/semiring porous species.

Nitrogen concentration

Nitrogen allocational patterns provide insight into the ecology of individual species, since nitrogen is correlated with photosynthesis (Field and Mooney 1985; Reich et al. 1995) and with respiration (Ryan 1991). ***Liriodendron tulipifera*** is characterized by a relatively high growth rate (Doolittle 1958; Buckner and McCracken 1978) and has high foliage nitrogen concentration (Day and Monk 1977) and low bark, sapwood, and heartwood nitrogen contents when compared with other species in this study (Figs. *3a* and *6c–6e*). Additionally, ***Liriodendron tulipifera*** has one of the lowest branch nitrogen contents (Fig. *6b*), indicating that it possesses a nitrogen allocational pattern for maximizing carbon assimilation by allocating less nitrogen to the non-photosynthetic tissues and more to the foliage. Although ***Liriodendron tulipifera*** is a diffuse porous species and has a large sapwood volume (Fig. 2*c*), -its low wood nitrogen concentrations suggest that it may have reduced stem respirational costs.

Nitrogen content

The predicted nitrogen content of all tissue components (Pigs. *6a–6d*) and of the total tree (Fig. 6e) for three calculated individuals, DBH = 10, 30, and 50 cm, indicates allocational differences as a function of ecophysiology and wood properties. ***Quercus rubra*** and Quercus ***prinus*** exhibited the highest foliar nitrogen content (Fig. *6a*) due to the high foliage nitrogen concentration (Fig. *3a*) and the high foliar mass. Similarly, ***Carya*** spp. had a high branch nitrogen concentration (Pig. *3b*) and a high branch biomass; therefore; it has the highest branch nitrogen content (Fig. *6b*). These allocational patterns are compounded by the high wood specific gravity of the ***Carya*** spp. (Table 3), which gives ***Carya*** spp. the highest overall stem wood nitrogen content (Fig. *6d*). The result of the high nitrogen concentration and high biomass of the stem and branch components allows ***Carya*** spp. to exhibit the highest overall nitrogen content on a per tree basis. Total tree and even stem removal of ***Carya*** spp. in harvesting operations has the potential to reduce total site nitrogen more than' any other tree species in this study (Fig. 6e). In addition, this may also be true for the economically important species such as ***Quercus rubra, Quercus alba,*** and Quercus ***prinus,*** which also have relatively high total nitrogen content per tree (Fig. 6e).

Large differences in allometric relationships warrant the need for site-specific models, while analysis of wood anatomy indicates differences in cross-sectional area of respiring sapwood for a given stem diameter. Nitrogen allocational patterns suggest a possible explanation for maximizing photosynthesis and growth, and combining biomass models with nitrogen concentration data allows a comparison to examine the effects of removing different species and their tissue

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components from the forest nitrogen pool. Further analysis of these topics is warranted.

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