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Interspecific and environmentally induced variation in foliar dark respiration among eighteen southeastern deciduous tree species

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Summary We measured variations in leaf dark respiration rate (R_d) and leaf nitrogen (N) across species, canopy light environment, and elevation for 18 co-occurring deciduous hardwood species in the southern Appalachian mountains of western North Carolina. Our overall objective was to estimate leaf respiration rates under typical conditions and to determine how they varied within and among species. Mean dark respiration rate at 20 °C ($R_{d,mass}$, μmol CO_2 (kg leaf dry mass)$^{-1}$ s^{-1}) for all 18 species was 7.31 μmol kg^{-1} s^{-1}. Mean $R_{d,mass}$ of individual species varied from 5.17 μmol kg^{-1} s^{-1} for *Quercus coccinea* Muenchh to 8.25 μmol kg^{-1} s^{-1} for *Liriodendron tulipifera* L. Dark respiration rate varied by leaf canopy position and was higher in leaves collected from high-light environments. When expressed on an area basis, dark respiration rate ($R_{d,area}$, μmol CO_2 (kg leaf dry area)$^{-1}$ s^{-1}) showed a strong linear relationship with the predictor variables leaf nitrogen (N_{area}, g N (m leaf area)$^{-2}$) and leaf structure (LMA, g leaf dry mass (m leaf area)$^{-2}$) ($r^2 = 0.62$). *This covariance* was largely a result of changes in leaf structure with canopy position; smaller thicker leaves occur at upper canopy positions in high-light environments. Mass-based expression of leaf nitrogen and dark respiration rate showed that nitrogen concentration (N_{mass}, mg N (g leaf dry mass)$^{-1}$) was only moderately predictive of variation in $R_{d,mass}$ for all leaves pooled ($r^2 = 0.11$), within species, or among species. We found distinct elevational trends, with both $R_{d,mass}$ and N_{mass} higher in trees originating from high-elevation, cooler growth environments. Consideration of interspecies differences, vertical gradients in canopy light environment, and elevation, may improve our ability to scale leaf respiration to the canopy in forest process models.

Keywords: carbon dioxide flux, forest carbon cycling, leaf gas exchange, leaf respiration, maintenance respiration.

Introduction

Plant respiration accounts for a large fraction of carbon cycling in forest ecosystems and may be of comparable importance to photosynthesis as a determinant of net primary production (Harris et al. 1975, Pearcy et al. 1987, Amthor 1989, Ryan et al. 1997). Although photosynthesis has been the focus of much measurement and modeling, less is known about plant respiration. Dark respiration rate (R_d) varies as an exponential function of temperature (Amthor 1984) and a general model that estimates maintenance respiration as a function of temperature and tissue nitrogen (N) concentration has been suggested by Ryan (1991*a*). Annual forest canopy respiratory losses can be modeled by the predicted dark respiration to N concentration relationship, annual temperature data, and estimates of total leaf biomass or surface area (Ryan 1991*b*). An important question is whether dark respiration models based on temperature and nitrogen are adequate for predicting respiration across species and environments. Our overall objective was to examine and describe variations in leaf dark respiration and nitrogen across species, canopy light environment, and elevation, for 18 co-occurring deciduous hardwood species in the southern Appalachians.

Foliar respiration rates for many tree species are currently unknown. Because of a lack of species data and thecomplexity of multi-species models, canopy or stand models of mixed-species forests have typically used mean values lumped across species (e.g., Aber and Federer 1992, Running and Hunt 1993). We sought to quantify base R_d for a large group of species and to examine the magnitude of interspecific differences in these rates within a temperate deciduous forest community.

Numerous studies have shown that leaf light environment affects leaf structure, chemistry, and the photosynthesis-light response (Norman 1980, Caldwell et al. 1986, Kull and Niinemets 1993, Walters et al. 1993, Larcher 1995, Sullivan et al. 1996, Dang et al. 1997a). Trees may deploy thicker full-sun leaves at the top of the canopy to optimize whole-canopy carbon gain, whereas a strong vertical decrease in leaf thickness and increase in leaf area may confer an advantage in competitor shading with negligible photosynthetic penalty (Gutschick and Wiegel 1988). Because photosynthesis and leaf structure both show acclimation to the integrated light environment, rates of leaf respiration may exhibit concomitant changes. For example, Ellsworth and Reich (1993) and Niinemets and Tenhunen (1997) found that leaf dark respiration in *Acer saccharum* Marsh. was influenced by the vertical canopy light gradient, but there are few other studies of R_d at multiple irradiances for deciduous tree species.

Respiration responds to growth environment temperature (e.g., Mooney 1963, Mooney and Wright 1964, Friend and Woodward 1990, Criddle et al. 1994, Larigauderie and Ko-

erner 1995, Reich et al. 1996). Leaf R_d is linked to plant temperature history as a result of acclimation (phenotypic adjustment to a change in growing temperature), or adaptation (genetic adjustment to the prevailing temperature), or both (Amthor 1984, Amthor 1989, Larcher 1995). Acclimation or adaptation may also be expressed as changes in leaf nitrogen. Many species exhibit higher N concentrations in cool-origin populations or individuals grown in cool climates (Koemer 1989, Yin 1993, Reich et al. 1996). Current models may significantly over- or underestimate respiratory carbon losses if they ignore acclimation in foliar respiration response (Larigauderie and Koemer 1995). Although we did not separate acclimation and adaptation, the mountainous region of the southern Appalachians provided an opportunity to quantify the combined acclimation/adaptation response in leaf R_d and leaf N that may arise across an elevation gradient.

We measured leaf dark respiration rates in 18 common deciduous tree species of the southeastern USA with the following objectives: (1) to determine whether respiration rates vary among species; (2) to compare rates of dark respiration at upper-, mid- and lower-canopy irradiance; (3) to ascertain if leaf respiration can be modeled as a function of leaf nitrogen for these eastern hardwood species; and (4) to examine the effects of elevation on respiration. Because interpretation of leaf respiration measurements may be affected by the base chosen to express the results (i.e., leaf surface area or dry mass), we analyzed both area-based and mass-based respiration rates.

Materials and methods

Study sites and canopy access

Research was conducted on mixed deciduous hardwood forests in the southern Appalachian mountains. Sampling was concentrated in two areas, the first centered at the United States Forest Service (USFS) Coweeta Hydrological Laboratory (35°3′ N, 83°25′ W) located in western North Carolina. Elevations in the Coweeta basin range from 675 to 1592 m and climate is characterized by mild temperatures and high precipitation. Mean annual temperature and precipitation range from 13 °C and 1800 mm at lower elevations, to 8.2 °C and 2200 mm at higher elevations (Swift et al. 1988). A second, lower-elevation sampling site was located near Toccoa, Georgia, 45 km south of Coweeta. The Toccoa site has an elevation of approximately 300 m with a mean annual temperature of 16 °C and a mean annual precipitation of 2400 mm. Characteristic forest cover of the study areas includes mesic cove species (*Liriodendron tulipifera* L., *Tsuga canadensis* (L.) Carrière), xeric oak and pine species on ridges and drier low-elevation sites (*Pinus rigida* Mill., *Quercus coccinea* Muenchh., *Q. prinus* L.), northern hardwood species on higher elevation sites (*Acer saccharum, Betula alleghaniensis* Britt., *Q. rubra* L.), and mixed deciduous communities over a range of intermediate elevations and environmental conditions (including *A. rubrum* L., *Carya* spp., and Q. *alba* L.).

Leaf respiration was measured both *in situ* and on detached material from several locations. Four permanent towers, 18 to 28 m in height, permitted access to all or portions of the canopy of 11 species, including the uppermost leaves of dominant species. Towers were located in the Coweeta basin study area and arrayed across an elevation gradient ranging from 740 to 1430 m (described in Sullivan et al. 1996). Of the 438 leaves sampled, 132 leaves were collected from these towers. A pole pruner and ladders were used to access additional trees from locations widely distributed across the Coweeta site and for all sampling done in the Toccoa area. Temporary scaffolds ware also erected to obtain the all-night gas exchange measurements.

Plant materials

Eighteen species were sampled. Of these, eight were intensively sampled, with a minimum of 25 leaves each: *Acer rubrum* (red maple), *Betula* spp., (*B. lenta* L. and *B. alleghaniensis*, sweet birch and yellow birch), *Carya* spp., (*C. glabra* Mill. and C. *tomentosa* Nutt., pignut hickory and mockemut hickory), *Liriodendron tulipifera* (tulip poplar), *Quercus alba* (white *oak), Quercus coccinea* (scarlet oak), *Quercus prinus* (chestnut *oak),* and *Quercus rubra* (northern red oak). Ten species had a minimum sample size of 12 leaves: *Acer pensylvanicum* L. (striped maple), *Cornus florida* L. (flowering dogwood), *Fraxinus* spp., (*E americana* L. and *F. pennsylvanica* Marsh., white ash and green ash), *Magnolia fraseri* Walt. (umbrella tree), *Nyssa sylvatica* Marsh. (black gum), *Oxydendrum arboreum* L. DC. (sourwood), *Rhododendron maximum* L. (rhododendron), *Robinia pseudoacacia* L. (black locust), *Platanus occidentalis* L. (sycamore) and *Tilia americana* L. (basswood) (Table 1).

Data were collected during three sampling periods in summer 1996: early summer (June 20 to June 31), mid-summer (July 20 to August 11), and late summer (September 1 to September 14). Only fully expanded leaves from mature individuals in mixed-species stands were sampled. Species were sampled across a wide span of elevations (Table 1). *Acer rubrum, Carya* spp., *Quercus alba, Q. prinus* and *Q. rubra* occur up to 1500 m, the highest elevation in Coweeta. *Acer rubrum, Carya* spp. and *Q. alba* also occur at the Toccoa study area, permitting sampling of these three species across a gradient of over 1200 m. Two species were included specifically for their foliar N characteristics, *Robinia pseudoacacia, an* N-fixing tree with high foliar *N,* and *Rhododendron maximum,* a semievergreen species with low leaf N.

Canopy light environment, sampling methods and gas exchange measurements

Dark respiration rates were measured on leaves sampled from three light environments defined by canopy position and exposure to direct sunlight. h-radiances were categorized as high light, medium light or low light based on independent photosynthetic photon flux density (PPFD) measurements made in upper-, mid-, and lower-canopy positions at the four tower sites (described in Sullivan et al. 1996). Leaves in the high-light environment (PPFD > 1000 $\mu mol\ m^{-2}\ s^{-1}$) were from the upper-canopy crown or from exposed side-branches and received full direct sun for more than 10 h each day during the

Table 1. Summary statistics of leaf traits and dark respiration (at 20 °C) by species and canopy position irradiances. High light (H): upper crown or exposed side-branch leaves that received full sun for more than 10 h each day. Medium light (M): main portion of the canopy; leaves received direct sun during part of the day, less than 6 h total, and diffuse light the remainder of the day. Low light (L): lower portion of dominant tree canopy, or sub-canopy trees; leaves were shaded all day. Values are means ± SE.

Species	Elevation range (m)	*n*	Irradiance	N_{mass} (mg N g^{-1})	N_{area} (g N m^{-2})	SLA (cm^2 g-t)	$R_{d,mass}$ (μmol kg^{-1} s^{-1})	$R_{d,area}$ (μmol m^{-2} s^{-1})
Acer pensylvanicum (AP)	1128-1430	6	M	19.8 ± 0.11	0.78 ± 0.06	257 ± 6.8	7.35 ± 0.42	0.29 ± 0.01
		8	L	18.4 ± 0.07	0.63 ± 0.02	296 ± 16.4	5.33 ± 0.35	0.18 ± 0.01
Acer rubrum (AR)	274–1524	8	H	18.0 ± 0.09	1.45 ± 0.12	129 ± 11.7	6.39 ± 0.39	0.52 ± 0.05
		30	M	18.9 ± 0.05	1.35f0.07	151 ± 8.4	6.18 ± 0.28	0.44 ± 0.02
		14	L	17.8 ± 0.05	0.82 ± 0.07	230 ± 12.5	5.28 ± 0.19	0.24 ± 0.02
Betula spp. (BE)	671-1430	11	H	19.5 ± 0.08	1.18 ± 0.07	170 ± 17.5	8.09 ± 0.40	0.5 1 ± 0.04
		8	M	21.5 ± 0.10	0.95 ± 0.09	244 ± 34.0	8.05 ± 0.47	0.36 ± 0.04
		10	L	21.7 ± 0.05	0.78 ± 0.04	285 ± 16.3	6.19 ± 0.41	0.23 ± 0.02
Carya spp. (CA)	274-1509	10	H	24.5 ± 0.12	2.11 ± 0.15	119 ± 7.9	6.36 ± 0.48	0.54 ± 0.03
		14	M	22.9f0.11	1.66 ± 0.06	140 ± 8.9	5.96 ± 0.41	0.43 ± 0.02
		14	L	22.4 ± 0.07	1.15 ± 0.06	201 ± 10.9	5.62 ± 0.47	0.29 ± 0.03
Cornus florida (CF)	671-930	4	H	17.4 ± 0.07	1.19f0.09	148 ± 5.6	7.06 ± 0.41	0.48 ± 0.02
		6	M	15.1 ± 0.08	0.76 ± 0.07	207 ± 23.6	7.48 ± 0.24	0.39 ± 0.05
		5	L	18.7 ± 0.06	0.71 ± 0.04	264 ± 6.6	7.56 ± 0.72	0.29 ± 0.04
Fraxinus spp. (FR)	671-869	4	H	19.2 ± 0.14	1.59f0.12	125 ± 18.3	7.83 ± 0.47	0.69 ± 0.14
		6	M	20.7 ± 0.09	1.16 ± 0.12	191 ± 23.5	6.52 ± 0.40	0.37 ± 0.05
		8	L	19.2 ± 0.14	1.16 ± 0.10	170 ± 10.9	6.93 ± 0.53	0.43 ± 0.05
Liriodendron tulipifera (LT)	686-1052	8	H	21.3 ± 0.17	1.59f0.10	134 ± 8.3	8.25 ± 0.51	0.63 ± 0.06
		14	M	22.3 ± 0.12	1.07 ± 0.12	223 ± 13.0	8.47 ± 0.43	0.39 ± 0.02
		10	L	23.7 ± 0.12	1.12 ± 0.06	214 ± 11.2	6.87 ± 0.22	0.33 ± 0.02
Magnolia fraseri (MF)	808-1070	4	H	22.9 ± 0.05	1.09f0.18	227 ± 36.9	6.94 ± 0.88	0.35 ± 0.09
		5	M	22.5 ± 0.07	0 97 ± 0.13	252 ± 40.2	7.41 ± 0.57	0.32 ± 0.04
		4	L	23.6 ± 0.16	0.85 ± 0.17	293 ± 32.3	5.58 ± 1.05	0.20 ± 0.04
Nyssa sylvatica (NS)	716-1052	7	M	18.4 ± 0.19	1.01 ± 0.06	183 ± 16.3	7.02 ± 0.30	0.40 ± 0.04
		5	L	17.2 ± 0.08	0.78 ± 0.06	225 ± 23.1	7.10 ± 0.57	0.33 ± 0.04
Oxydendron arboreuwt (OA)	671-716	2	H	18.6 ± 0.12	0.71 ± 0.05	262 ± 0.9	7.70 ± 0.12	0.29 ± 0.00
		6	M	20.0 ± 0.17	0.94f0.12	221 ± 11.6	5.47 ± 0.31	0.25 ± 0.02
		6	L	15.8 ± 0.05	0.60 ± 0.06	270 ± 18.8	5.62 ± 0.67	0.22 ± 0.03
Platanus occidentalis (PO)	671-716	2	H	20.7 ± 0.03	1.42 ± 0.01	145 ± 1.1	5.08 ± 0.05	0.35 ± 0.00
		6	M	17.2 ± 0.03	1.04 ± 0.07	167 ± 8.4	5.84 ± 0.36	0.35 ± 0.03
		6	L	17.3 ± 0.07	0.85 ± 0.06	209 ± 8.4	5.75 ± 0.35	0.28 ± 0.03
Quercus alba (QA)	274-1524	15	H	23.2 ± 0.14	2.25 ± 0.09	103 ± 5.0	8.08 ± 0.64	0.78 ± 0.04
		26	M	24.0 ± 0.08	1.57 ± 0.10	166 ± 10.0	7.59 ± 0.35	0.49 ± 0.03
		16	L	23.7 ± 0.12	1.58 ± 0.13	159 ± 9.7	7.72 ± 0.38	0.5 1 ± 0.04
Quercus coccinea (QC)	274-854	8	H	19.1 ± 0.04	2.03 ± 0.08	95 ± 4.8	5.17f0.30	0.56 ± 0.05
		10	M	20.2f0.12	2.01 ± 0.10	101 ± 6.0	3.91 ± 0.29	0.40 ± 0.03
		10	L	20.6 ± 0.07	1.61 ± 0.10	132 ± 8.6	4.50 ± 0.34	0.36 ± 0.04
Quercus prinus (QP)	412-1430	12	H	23.9 ± 0.08	2.74 ± 0.18	89 ± 3.6	8.34 ± 0.58	0.93 ± 0.07
		10	M	27.1 ± 0.12	2.04 ± 0.14	140 ± 12.9	8.29 ± 0.5 1	0.65 ± 0.08
		12	L	24.1 f0.12	1.27 ± 0.08	197 ± 14.5	8.49 ± 0.50	0.44 ± 0.03
Quercus rubra (QR)	671-1524	6	H	28.7 ± 0.23	2.75 ± 0.14	104 ± 6.2	7.41 ± 0.45	0.72 ± 0.04
		12	M	23.8 ± 0.13	1.85 ± 0.23	157 ± 24.8	5.83 ± 0.24	0.45 ± 0.06
		18	L	26.4 ± 0.16	1.50f0.13	181 ± 13.3	5.02 ± 0.38	0.29 ± 0.03
Rhododendron maxim um (RM)	671-1430	11	M	10.2 ± 0.04	1.27 ± 0.10	85 ± 7.1	2.03 ± 0.18	0.25 ± 0.03
		3	L	10.4 ± 0.03	1.18 ± 0.10	90 ± 9.7	1.58 ± 0.01	0.18 ± 0.02
Robinia pseudoacacia t (RP)	671-1070	3	H	31.7f0.51	2.37 ± 0.14	132 ± 13.6	7.32 ± 0.57	0.56 ± 0.06
		7	M	38.6f0.18	2.19f0.10	177 ± 9.4	8.21 ± 1.02	0.46 ± 0.04
		4	L	38.5 ± 0.33	2.14 ± 0.46	195 ± 25.3	9.73 ± 0.41	0.52 ± 0.05

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Species	Elevation range (m)	*n*	Irradiance	N_{mass} (mg N g^{-1})	N_{area} (g N m^{-2})	SLA (cm^2 g^{-1})	$R_{d,mass}$ (μmol kg-' s^{-1})	$R_{d,area}$ (μmol m^{-2} s^{-1})
Tilia americana (TA)	671-1070	5	H	28.8 ± 0.16	1.99f0.15	150f20.1	6.94 ± 0.61	0.48 ± 0.04
		4	M	28.1f0.19	1.66zt0.23	175 ± 16.8	6.43f0.59	0.38 ± 0.05
		5	L	28.1f0.18	1.04 ± 0.17	308f58.0	6.57f0.47	0.25 ± 0.05
All species pooled		102	H	22.4 ± 0.05	1.91 ± 0.06	129f4.7	7.31 f0.18	0.62 ± 0.02
		188	M	21.5 ± 0.04	1.41 ± 0.04	169f4.7	6.56f0.15	0.41 ± 0.01
		148	L	21.6 ± 0.04	1.12 ± 0.04	213 ± 5.6	6.29 ± 0.16	0.32 ± 0.01

growing season. Leaves in the medium-light environment (PPFD 500-1000 μmol m^{-2} s^{-1}) were from the main portion of the canopy and received direct sun for less than 6 h during the day, and indirect light the remainder of the day. Low-light environment leaves (PPFD < 500 μmol m^{-2} s^{-1}) were from the lower portion of the dominant tree canopy or from sub-canopy trees and were shaded all day. Measurement of integrated daily or maximum daily PPFD for each tree and leaf sampled was not practical with our large sample size. However, resulting data gradients in leaf traits indicated categorization of leaves by light environment was consistent for the high-light upper-canopy and low-light lower-canopy classes, and more variable for the medium-light mid-canopy designation. Branches with mature fully expanded leaves were harvested predawn (0400-0600 h EST). Harvested branches were quickly transported to the laboratory and the stems recut under water. Branches were kept hydrated and stored in darkness until leaf gas exchange measurements were made within 12-h of harvesting.

Foliar dark respiration was measured with an open system infrared gas analyzer operated in differential mode (LCA-3, Analytical Development Company, Hoddesdon, Herts., England) and equipped with a custom temperature-controlled leaf cuvette. The cuvette (Hubbard et al. 1995) was heated and cooled with a Peltier unit, controlled by a data logger (Campbell 21X, Campbell Scientific, Logan, UT). Entire leaves were placed in the cuvette (volume -200 cm'). Ambient reference air was drawn through a mixing ballast at a flow rate of 200 μmol s^{-1}. Leaf temperature was monitored with a thermocouple and sampling temperatures remained within 0.05 °C of set-point temperature. Respiration was measured at 10, 15, 20, 25 and 30 °C. Flux was recorded after the difference in CO_2 concentration between reference and chamber had been stable for a minimum of 3 min. Leaves were typically held at each set-point temperature for 5 to 10 min. Leaf area was measured with a CID-251 Image Analyzer, then leaves were dried at 70 °C for 48 h, weighed to 0.001 g and analyzed for N concentration with a Perkin-Elmer CHN analyzer. Metrics of leaf structure, LMA, leaf mass per unit of leaf area and SLA, leaf area per unit of mass, were obtained from fresh leaf area and dried leaf mass.

In situ versus detached branch measurements

Dang et al. (1997b) have shown that leaf gas exchange from detached branch samples is relatively stable up to 14 h after harvesting. To test whether measured respiration rates were being affected by the sampling methodology, we compared *in situ* and detached branch leaf CO_2 flux for four species: *Acer rubrum, Liriodendron tulipifera, Quercus alba* and *Q. rubra. In situ* measurements were made on mid- to upper-canopy leaves by housing the IRGA and temperature controlled cuvette equipment on a portable scaffolding. Gas exchange measurements at 20 °C were taken every hour from nightfall onward on a set of three or four leaves. Before sunrise (between 0400 and 0630 h), two additional leaves were measured at all five temperature settings. After *in situ* measurements, the branch that held the sampled leaves was cut and treated as per field collection methods. Carbon dioxide flux was then measured on two or more leaves per detached branch at mid-morning (4 h after harvest) and late afternoon (8-12 h after harvest). The 28 *in situ* leaf measurements were added to the final data set.

Data analysis

All analyses were based on dark respiration rates at 20 °C except for the comparison of R_d in cut and detached leaves. A companion study (Bolstad et al. 1999, this issue) reports the nonlinear temperature-respiration response curves obtained from the 10, 15, 20, 25 and 30 °C measurements. Statistical analysis was done with the Statistical Analysis System software package (SAS version 6.11, SAS Institute, Cary, NC). A combination of outlier tests, including box-whisker plots, Cook's D, and analysis of residuals, led to omission of 14 leaves from the data set; a total of 438 leaves remained. Data were tested for normality and equality of variance. Analysis of variance was used to test, models and, if the ANOVA was significant, then Duncan's new multiple-range test (NMRT) was applied to test differences in leaf structure, N, and respiration rate caused by it-radiance, elevation and taxon. Differences were accepted as statistically significant if $P < 0.05$. All data ($n = 438$ leaves) were used in the analysis of both canopy position light environment effects and the relationship of respiration to nitrogen. A subset of data was extracted to test elevation effects. It consisted of 143 high-light upper canopy leaves from the five taxa common across the full elevation gradient (*Acer rubrum, Carya* spp., *Quercus alba, Q. prinus* and *Q. rubra).* Another subset of data was extracted for interspecies comparisons. This subset contained leaves from mid- and upper-canopy positions and included 290 leaves from all 18 taxa.

Results

detached branches and seasonal variation

There were no significant differences in dark respiration rates on a mass basis ($R_{d,mass}$, μmol CO_2 (kg leaf dry mass)$^{-1}$ s^{-1}) between *in situ* leaves and leaves from detached branches for any of the four species tested ($P < 0.001$). For example, in *Liriodendron tulipifera,* mean $R_{d,mass}$ values at 15, 20 and 25 °C were 6.5, 10.0 and 14.7 μmol kg^{-1} s^{-1} for cut-branch leaves versus 6.4, 9.9 and 14.2 μmol kg^{-1} s^{-1} for *in situ* measurements. Nonlinear regression of $R_{d,mass}$ as an exponential function of temperature (T) (i.e., $R_{d,mass} = \beta_0 \exp(\beta_1 T)$) showed no difference between the β_0 and β_1 parameters of attached leaves versus detached-branch leaves for *L. tuliptfera,* nor for any of the other three species, nor for the pooled data set (Figure 1).

Dark respiration and N concentration exhibited no significant seasonal changes across the sampling period. Foliar N concentration is known to be high in early spring then to decrease sharply to a plateau for most of the growing season before declining at the onset of leaf senescence (Day and Monk 1977). In the Coweeta basin, bud burst and leaf expansion begin in early April at low elevations and in early May at high elevations, whereas leaf senescence begins in late September. Our sample dates, from June 20 to September 14, thus encompassed the stable period of leaf N concentration and we observed no correlation between $R_{d,mass}$ and Julian day ($P > 0.174$). Varying concentrations of nonstructural carbohydrates (NSC) throughout the growing season could alter mass-based respiration rate analysis; however we did not measure NSC. The relationship between $R_{d,mass}$ and leaf N concentration was stable across the July through September sampling dates. However, there was a slightly stronger linear $R_{d,mass}$ versus N_{mass} relationship for the June sampling period ($r^2 = 0.20$, $n = 75$) than for the remainder of the season ($r^2 = 0.10$, $n = 363$). Differences in the June data were not considered large enough to warrant segregation by season.

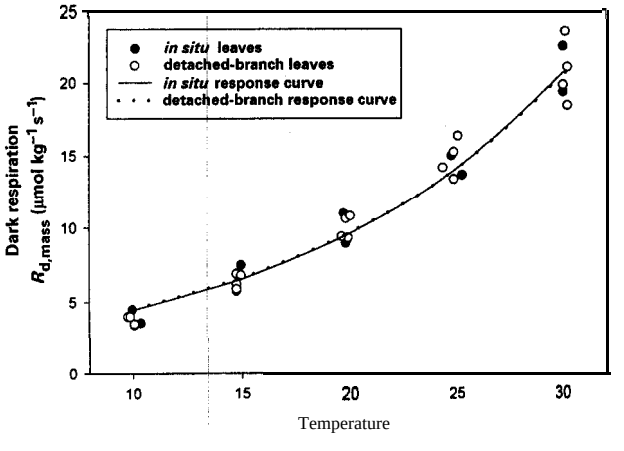

Figure 1. Comparison showing no difference in dark respiration temperature response curves for detached-branch leaves and in *situ* leaves fom *Liriodendron tulipifera.* Leaves from detached branches were measured 4-12 h after harvest. Equation is $R_{d,mass} = \beta_0 \exp(\beta_1 T)$. *Liriodendron tulipifera* detached-branch leaves had $\beta_0 = 2.11$, $\beta_1 = 0.076$ and $n = 4$, whereas *in situ* leaves had $\beta_0 = 2.06$, $\beta_1 = 0.077$ and $n = 2$.

Canopy position effects on leaf structure, nitrogen, and respiration rates

Canopy position and hence leaf light environment significantly affected leaf structure. Smaller, thicker leaves occurred in high-light upper-canopy positions and proportionally larger, thinner leaves occurred in low-light lower-canopy positions. Specific leaf area, a metric for leaf thickness (SLA, cm^2 leaf area (g leaf dry mass)$^{-1}$), was strongly related to canopy position irradiance ($P < 0.01$) for most species (exceptions for which $P > 0.05$ were *Magnolia fraseri, Nyssa sylvatica* and *Rhododendron maximum).* Pooled data for all species showed SLA increased 65% from upper to lower canopy leaves (129 versus 213 cm^2 g^{-1}) (Table 1). Nitrogen per unit leaf area (N_{area}, g N m^{-2}) was also related to canopy position ($P < 0.01$) and decreased by 41% from upper to lower canopy leaves (1.9 1 versus 1.12 g N m^{-2}). However, there was no significant difference in leaf N among leaves from different canopy position light environments when compared on a mass basis ($P > 0.43$ 1). For all species pooled, N_{mass} (mg N (g leaf dry mass)$^{-1}$) was 22.4 and 21.6 mg N g^{-1} for upper- and lower-canopy leaves, respectively.

Leaf dark respiration at 20 °C differed significantly among leaves from different canopy position light environments when expressed on an area basis ($R_{d,area}$, μmol CO_2 (m leaf area)$^{-*}$ s^{-1}). Across all species, $R_{d,area}$ was 48% less for lower-canopy leaves (0.32 μmol m^{-2} s^{-1}) than for upper-canopy leaves (0.62 μmol m^{-2} s^{-1}). Leaves from the mid-canopy medium-light environment generally had intermediate $R_{d,area}$ values. *Robinia pseudoacacia* was the only exception to this overall trend, and this discrepancy could be associated with the small sample size.

Mass-based dark respiration ($R_{d,mass}$, μmol kg^{-1} s^{-1}) was also influenced by canopy position, but did not show as consistent or as strong an association as area-based estimates. Mass-based dark respiration was related to canopy position irradiance ($P < 0.01$) for all species pooled, and mean $R_{d,mass}$ for lower-canopy leaves (6.29 μmol kg^{-1} s^{-1}) was 14% less than for upper-canopy leaves (7.31 μmol kg^{-1} s^{-1}). On an individual species basis, seven of the eighteen species had statistically significant decreases in $R_{d,mass}$ for lower-canopy positions compared with upper-canopy positions. However, within the eight species of the study with sample sizes greater than 25 leaves, five showed a significant decrease in $R_{d,mass}$ at lower-canopy positions ($P < 0.05$): *Acer rubrum, Betula spp., Liriodendron tulipifera, Quercus coccinea,* and *Q. rubra.*

Respiration-nitrogen relationships

Area-based measures of dark respiration, nitrogen, and leaf thickness co-varied. Leaf mass per unit area was used as a measure of leaf thickness (LMA, leaf dry mass per leaf area, g m^{-2}) to allow comparisons on an area basis. Linear regression showed that $R_{d,area}$ was strongly related to LMA ($r^2 = 0.57$, $P < 0.01$) and N_{area} ($r^2 = 0.58$, $P < 0.01$) for the data set of 424

leaves (17 deciduous species, excluding mum) (Figures 2a and 2b). A linear $R_{d,area}$–N_{area} model was statistically signifidant when fit to the pooled data and when fit for each species. Values of r^2 for individual species were between 0.50 and ***0.93,*** except for ***Robiniapseudoacacia*** (r^2 = 0.07) and ***Acerpensylvanicum*** (r^2 = 0.38). Nitrogen concentration, N_{mass}, was fairly constant vertically through the canopy. However, changes in leaf thickness in sunlit- versus shaded-canopy positions translated into changes in N_{area}, because N_{area} is the product of LMA and N_{mass} (Figure 2c) (Ellsworth and Reich 1993). Therefore, the positive linear relationship between $R_{d,area}$ and N_{area} is primarily related to changes in leaf structure (i.e., leaf thickening in upper-canopy high-light environments) that alter the amount of respiring tissue per unit area. The $R_{d,}$–N relationship may be better illustrated by multiple linear regression analyses of $R_{d,area}$ as a function of both N_{mass} and LMA, rather than using their product variable N_{area}. Multiple linear regression gave the equation for $R_{d,area}$ at 20 °C as: $R_{d,area}$ = 0.1324 + 0.0749 N_{mass} + 0.0062 LMA (r^2 = ***0.62,*** $P < 0.01$, ***n = 424).***

Mass-based measurements of dark respiration, nitrogen, and leaf thickness did not co-vary as did the area-based variables. Neither $R_{d,mass}$ nor N_{mass} was correlated with changes in leaf thickness, SLA (Figures 2e and 2f), although they were significantly related to one another (linear regression, $P < 0.01$) (Figure 2d). Because $R_{d,mass}$ differed less between sunlit upper-canopy leaves and shaded lower-canopy leaves, and N_{mass} is constant across canopy positions, the relationship between $R_{d,mass}$ and N_{mass} was little affected by changes in leaf structure associated with growth light environment. Regression of $R_{d,mass}$ and N_{mass} showed the variables were linearly related with r^2 = 0.18 for the entire data set of all leaves (n = 438) and r^2 = 0.11 for the data set of broad-leaved deciduous species (n = 424) (Figure 2d). The $R_{d,mass}$–N_{mass} relationships for individual species were inconsistent and linear correlations between the two variables showed positive slopes, negative

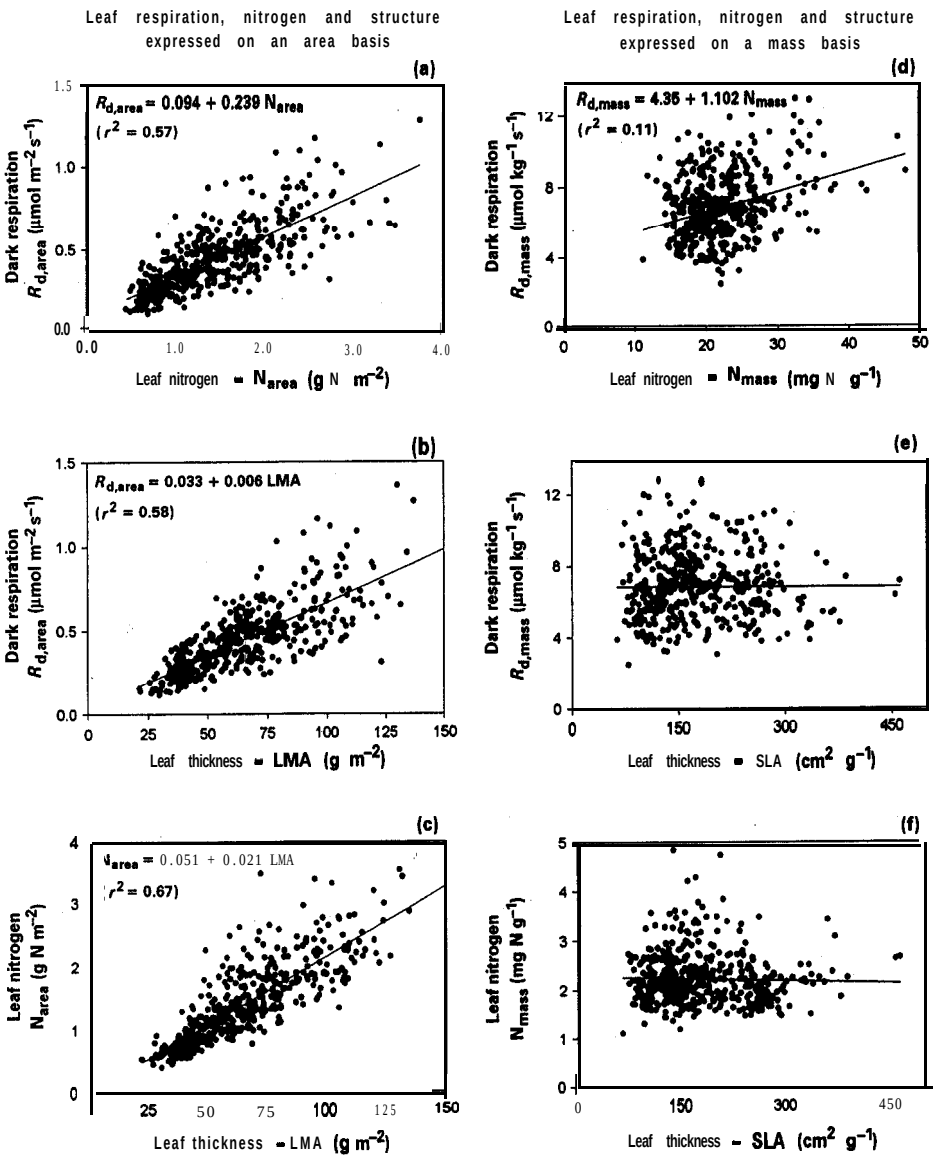

Figure 2. Relationships between dark respiration, leaf nitrogen and leaf thickness. Linear relationships of area-based (a-c) and mass-based (d-f) measures. Dark respiration was measured at 20 °C, n = 424 leaves of 17 deciduous species.

slopes, and no slope. There were low or negative correlations between $R_{d,mass}$ and N$_{mass}$ for *Acer rubrum, Betula* spp., *Cornus florida, Liriodendron tulipifera, Magnolia fraseri, Platanus occidentalis, Quercus coccinea, Q. prinus* and *Rhododendron maximum,* whereas positive slopes were seen for *A. pensylvanicum, Carya* spp., *Nyssa sylvatica, Oxydendron arboreum, Q. alba* and *Q. rubra.*

Elevational gradient, in nitrogen and dark respiration

High-elevation trees had higher foliar dark respiration rates and higher foliar N concentrations than low-elevation trees. Five species were sampled across an elevation gradient from 198 to 1524 m: *Acer rubrum, Carya* spp., *Quercus alba, Q. prinus* and Q. *rubra.* Only leaves from the upper canopy were included in the analysis (n = 143). Linear regression for the five species pooled showed both N$_{mass}$ and $R_{d,mass}$ were significantly correlated with elevation ($P < 0.01$, $r^2 = 0.09$ for N$_{mass}$, r^2 = 0.15 for $R_{d,mass}$). Multiple regression analysis of N$_{mass}$ and elevation together explained 31% of the variation in $R_{d,mass}$ (Figure 3). Trees growing at higher elevations in the Coweeta basin (1350 to 1525 m) had a mean $R_{d,mass}$ of 7.77 µmol kg^{-1} s^{-1}, 36% more than the 5.70 µmol kg^{-1} s^{-1} mean for trees growing at low elevation sites in Toccoa (200-420 m) (Table 2). Mean N$_{mass}$ for these five species was 24.0 mg N g^{-1} for high-elevation leaves, 14% higher than the mean of 21.1 mg N g^{-1} for low-elevation leaves. Foliar N$_{mass}$ and $R_{d,mass}$ were positively related to each other (linear regression, $P < 0.01$, $r^2 = 0.24$) and this correlation was partly a result of the simultaneous effects of elevation on both variables.

At any given elevation there was considerable variability in respiration rates among the individual species (Table 2). *Quercus alba* and *Q. prinus* had consistently higher mean $R_{d,mass}$ than *Acer rubrum, Carya* spp. and *Q. rubra.* However, each of the five species showed increased $R_{d,mass}$ at higher elevations, and regression of $R_{d,mass}$ as a function of elevation showed significant linear relationships for each species ($P < 0.05$), with r^2 values ranging from 0.19 to 0.40. *Acer rubrum* did not show an elevational gradient in N$_{mass}$, but did show increasing $R_{d,mass}$ with elevation ($P < 0.05$, r^2 = 0.19). *Quercus prinus* showed no relationship between foliar N and elevation (n = 2). The magnitude of change in $R_{d,mass}$ with elevation differed substantially among species. For example, mean $R_{d,mass}$ increased 22% in *A. rubrum* (5.62 to 6.86 µmol kg^{-1} s^{-1}) and 59% in *Q. alba* (6.18 to 9.83 µmol kg^{-1} s^{-1}) across the same elevational span.

Table 2. Foliar N$_{mass}$ and $R_{d,mass}$ (at 20 °C) by elevation class for the five species spanning the full elevation range of the study. Only upper- and mid-canopy leaves were measured, n = 143. Means ± SE followed by a different letter are significantly different ($P < 0.05$, Duncan's NMRT).

Species	Elevation range (m)	n	N$_{mass}$ (mg N g^{-1})	$R_{d,mass}$ (µmol kg^{-1} s^{-1})
Five species pooled				
	200-420	26	21.1 ± 0.08	**5.70 ± 0.218 a**
	600-1100	66	22.6 ± 0.05	6.88 ± 0.216 b
	1350-1525	51	24.0 ± 0.07	7.77 ± 0.274 c
Total/Mean		143	22.8 ± 0.04	6.98 ± 0.157
Individual species				
A. rubrum	200-420	8	1.97 ± 0.068	5.62 ± 0.203 a
	600-1100	10	1.65 ± 0.079	5.44 ± 0.458 b
	1350–1525	20	1.93 ± 0.050	6.86 ± 0.320 b
C. glabra	200-420	6	1.89 ± 0.090	4.59 ± 0.200 a
	600-1100	15	2.55 ± 0.087	6.67 ± 0.382 b
	1350-1525	3	2.33 ± 0.043	6.49 ± 0.490 b
Q. alba	200-420	10	2.19rt0.162	6.18f0.395 a
	600-1100	21	2.20 ± 0.054	7.55 ± 0.336 b
	1350-1525	10	2.92f0.131	**9.83 ± 0.657 c**
Q. prinus	200-420	2	2.89 ± 0.065	7.03 ± 0.314 a
	600-1100	13	2.54f0.103	**7.86 ± 0.518 a**
	1350-1525	7	2.42 ± 0.132	9.36 ± 0.534 b
Q. rubra	600-1100	7	2.15 f0.133	5.52f0.365 a
	1350-1525	11	2.79f0.144	**6.89 ± 0.307 b**

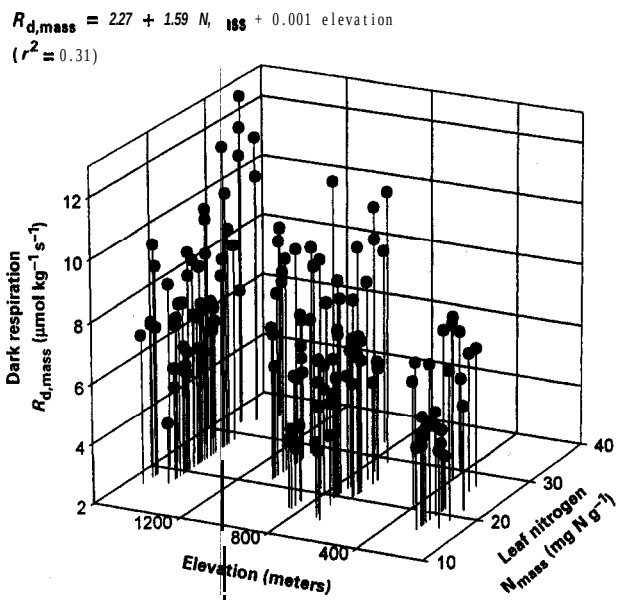

Figure 3. Leaf $R_{d,mass}$ I ...otted against leaf N$_{mass}$ and elevation for 143 leaves from five species! *A. rubrum, C. glabra, Q. alba, Q. prinus,* and Q. *rubra).* Dark respira ...on was measured at 20 °C in leaves collected from mid-canopy and ... ...per-canopy positions.

Interspecific variation in foliar respiration

There was substantial variation in leaf dark respiration rates among species (Table 1). For interspecies comparison we used data for leaves from the mid and upper canopy; 290 leaves from 18 species were analyzed (Figure 4). There were significant differences among species in mean $R_{d,mass}$ at 20 °C ($P <$ 0.01) and Duncan's NMRT showed four groupings of statistically different means (Figure 4a). *Liriodendron tulipifera, Quercus prinus* and the *Betula* spp. had the highest observed rates, whereas *Platanus occidentalis* and *Q. coccinea* had among the lowest rates. The more shade-tolerant species, such as *Acer rubrum, Cornus florida, Nyssa sylvatica and Oxydendron arboreum,* generally had mid to low $R_{d,mass}$ values. Dark

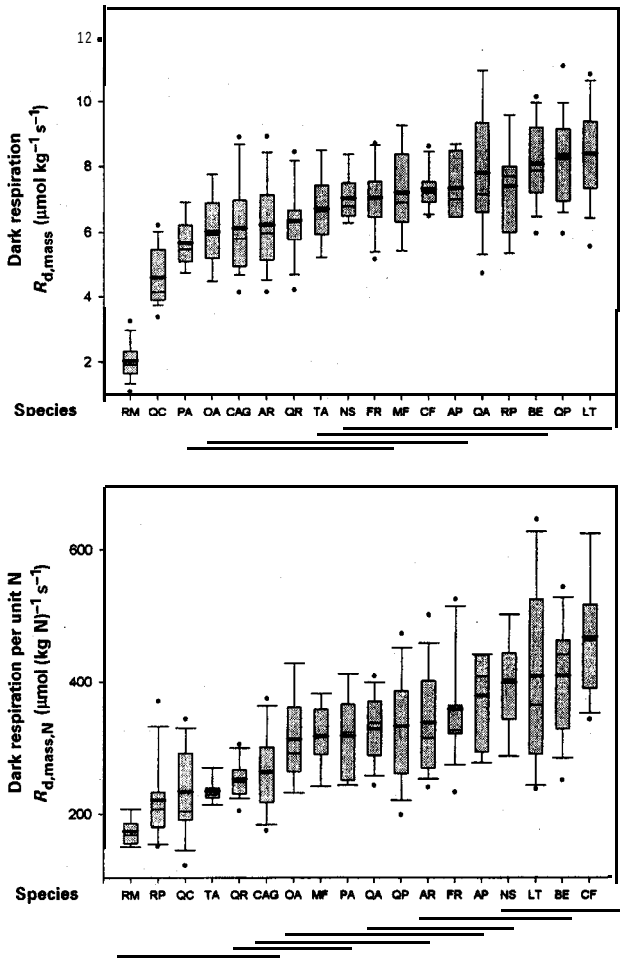

Figure 4. Interspecies comparison of leaf dark respiration at 20 "C: (a) mean $R_{d,mass}$ and (b) mean $R_{d,mass,N}$. Species codes on the y axis are genus or genus-species abbreviations (see Table 1). Leaves were from the mid and upper canopy (n per species as per Table 1). Box plots show median value in light line, and mean value in thick line. Outliers are 5th/95th percentile. Duncan's NMRT was used to test for significant differences in means; lines below show Duncan's groupings.

respiration rates can also be expressed on a nitrogen basis as CO_2 flux per unit Of leaf nitrogen ($R_{d,mass,N}$, μmol CO_2 (kg leaf N)$^{-1}$ s^{-1}). Ranking of differences among species based on $R_{d,mass,N}$ differs from that based on $R_{d,mass}$ (Figure 4b). Three shade-tolerant understory tree species, C. *jlorida, N. sylvatica* and *A. pensylvanicum,* had among the highest observed $R_{d,mass}$. *Robinia pseudoacacia* had very low $R_{d,mass}$ per unit N despite having high rates of $R_{d,mass}$ compared with Other species.

Discussion

Dark respiration rate varied vertically through the canopy, and was lower in leaves from low-light, lower-canopy environments. The differentiation between upper- and lower-canopy positions, and hence high-light versus low-light growth environments, was apparent on both area-based and mass-based calculations of respiration. However, $R_{d,mass}$ varied less between the upper and lower canopies than $R_{d,area}$. Changes in leaf thickness, reflected in leaf mass per area, appear to underlie the strong covariance between within-canopy light gradient and area-based expressions of leaf N and leaf R_d (Brooks et al. 1991, Brooks et al. 1996, Niinemets and Tenhunen 1997). When considered on a mass basis, leaf N was consistent across canopy positions, and mass-based R_d did not change with changes in leaf structure. These results are consistent with other research showing foliar N per unit leaf mass does not decline with canopy depth, and the decrease in foliar N per unit area is a result of changes in leaf structure rather than changes in N concentration (Caldwell et al. 1986, Hollinger 1989, Ellsworth and Reich 1993). Our large data set supports the idea that sun and shade leaves are differentiated both by changes in their area to mass relation and in their dark respiration rate, and suggests that models scaling leaf respiration to the canopy may need to incorporate vertical differences in leaf acclimation to light.

General models relating maintenance respiration to tissue nitrogen concentration are based on the premise that N is a surrogate measurement for protein concentration and that a general relationship exists between proteins and respiration rates (Ryan 1991*a*, 1991*b*). We found that a linear model of mass-based foliar dark respiration as a function of N concentration was only moderately predictive (explaining 11% of the variation). The linear relationship between R_d and leaf N on an area basis, however, was much more predictive (explaining 62% of the variation). Our data illustrate two factors that can influence or confound efforts to estimate general R_d–N models. First, area-based and mass-based measures of R_d to N may lead to different interpretations of the same data, because area-based measures combine leaf structure with tissue chemistry, whereas mass-based measures may be more directly linked to chemistry and metabolism (Reich and Walters 1994). The variation we observed in $R_{d,area}$ and N_{area} within the canopy was mostly a result of the scaling of N_{area} across the light gradient by changes in leaf thickness and size. Second, in forest communities where most species have relatively similar leaf traits, such as the broad-leaved southeastern deciduous tree species in this study, minimal or weak relationships between $R_{d,mass}$ and leaf N_{mass} may occur (Reich 1993). Across broader gradients of species types, life forms and environments, a mass-based R_d–N relationship may be observed and may be part of a fundamental set of co-occurring leaf structural, chemical and metabolic traits (Lambers and Poorter 1992, Reich et al 1992, 1995, 1998). Ryan (1995) found a strong linear relationship between leaf nitrogen and respiration rates among sub-alpine and boreal trees and shrubs. However it should be noted that Ryan's study included diverse life forms: coniferous life forms with low leaf N concentrations (*Abies, Picea* and *Pinus*), broad-leaved deciduous species with intermediate N concentrations (*Populus* and *Betula*), and small-leaved species of open habitats (*Alnus* and *Salix*, with *Alnus* an N-fixing species). Our data set also exhibited a higher r^2 value for the $R_{d,mass}$–N_{mass} relation when *Rhododendron maximum,* a semievergreen shrub with low leaf N, was included (r^2 = 0.18, but 0.11 without *R. m&mum).* We would

anticipate a still stronger regression relationship if we had included coniferous species in our study (cf. Ryan 1995, Reich et al. 1998).

We found distinct elevational trends in both leaf dark respiration rates and N concentration as has been shown in other studies (Mooney 1963, Pearcy 1977, Chapin and Oechell983, Friend and Woodward 1990, Larigauderie and Koemer 1995, Reich et al. 1996). Within tree species, individuals originating from cooler growing temperatures will display increased leaf N and greater R_d at a given temperature; however, the acclimation/adaptation response varies considerably by species (Tjoelker et al. 1999*a*, 1999*b*). Climate is an important driving variable in most forest ecosystem models. Because temperature, leaf N, and respiration rates co-vary with elevation, modeling in complex mountainous landscapes such as the southern Appalachians may need to account for the spatial variation in these parameters.

Although interspecies differences in leaf dark respiration are not typically accounted for in forest carbon cycling models, there was a nearly 2-fold variation in mean $R_{d,mass}$ at 20 °C among 18 co-occurring species at our study site. Species differences in dark respiration suggest that models assuming constant respiration parameters across species may benefit from stand-specific parameters based on species composition. This conclusion was also drawn from The Boreal Ecosystem-Atmosphere Study (BOREAS) that found large differences in respiratory parameters across sites and among three boreal tree species (Lavigne and Ryan 1997, Ryan et al. 1997). Although differences in mean $R_{d,mass}$ existed among our study species, they were only partly explained by interspecific variation in leaf N_{mass}. The ability to reduce the diverse R_d responses of multiple deciduous tree species to simpler functional groups would simplify carbon flux modeling in complex mixed-species forests (Smith et al. 1997). Our data did not clearly delineate such functional groups. However, the high rates of respiration per unit nitrogen observed in most sub-canopy species may indicate the need for further research on model classification of deciduous tree species by shade tolerance.

We conclude that consideration of interspecies differences, vertical gradients in canopy light environment, and elevation, may improve our ability to scale leaf respiration to the canopy in forest process models. These conclusions need to be assessed with landscape-level simulations that compare a null model assuming a mean respiration rate per unit nitrogen with a model that includes variability in species, canopy position and elevation.

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