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Challenges to modelling NPP in diverse eastern deciduous forests: species-level comparisons of foliar respiration responses to temperature and nitrogen

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Abstract

Modelling net primary production (NPP) in eastern deciduous forests has usually been conducted with coarse scale models that lump or simplify physiological processes. Foliar respiration (R_d) is a key physiological process in forest ecosystem C cycling; however, there are very few data on leaf respiration (R_d) for deciduous hardwood species. As a result, leaf R_d is one of the most superficially treated processes in NPP models. We hypothesize that these data are critical for understanding patterns of net primary production and for parameterizing C cycling models in diverse eastern deciduous hardwood forests. Our objectives were: (1) to determine differences in leaf R_d for seven hardwood species (*Acer rubrum*, *Liriodendron tulipifera*, *Quercus alba*, *Quercus coccinea*, *Quercus rubra*, *Quercus prinus* and *Carya glabra*) common to the canopy of southern Appalachian forests; and (2) to evaluate the effects of using 'lumped parameter' versus 'species-specific parameter' approaches to determining the leaf respiration component of NPP. We used a temperature-controlled cuvette and an infrared gas analyzer to develop temperature response curves during the night (24:00-06:00 h). Differences in leaf respiration rates (expressed on either a mass or area basis) among species were substantial, varying by greater than three-fold at high leaf temperatures (30°C). Q_{10} values ranged from 1.97 to 2.44. Some of the variation in leaf respiration rates among species was related to differences in leaf N. Comparison with a lumped parameter model of leaf respiration (PnET-II) indicated good agreement on average due primarily to combinations of species which resulted in compensating errors; however, there was the potential for considerable variation with different mixes of species.

Keywords: Leaf respiration; Model comparisons; Mixed species; Temperature response

1. Introduction

Distinct differences exist in approaches to modelling net primary production (NPP) of forests, ranging from detailed physiologically based models (e.g. BIOMASS, McMurtrie et al., 1992) to

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broader scale, more simplistic models (e.g. MBL-GEM, Rastetter et al., 1991). Reasons for the different approaches are well-known to most modelers and model users; i.e. the choice of models and approach to model development depends on the objectives (including desired spatial and temporal resolution of predictions) and the data available to parameterize the model. In most cases, as the spatial and temporal scale becomes coarser, models tend to get more simplistic in their representation of physiological processes that determine NPP. At the scale of interest of most politicians, regulators, and land managers (multiple hectares; years to decades) concerned about global climate change, most predictions of forest ecosystem response will be generated by simplistic, large area/coarse grain models. Increased computing power and Geographical Information System software have greatly facilitated the ability to generate large-area predictions, and, hence, there are numerous assessments of how climatic change will affect forests. However, in most cases we lack a thorough analysis of what the sacrifice in detail means to both prediction accuracy and understanding of the underlying mechanisms of response (e.g. are there compensating errors which preclude or lead to erroneous interpretations of response mechanisms?).

Plant respiration (R_d) is one of the most simplified represented processes in large-scale NPP models. Some models apply R_d as a simple fixed percentage of gross primary production, while others use exponential functions of temperature, with fixed coefficients, irrespective of species. Ryan (1991) has suggested a simple model, whereby nitrogen (N) is used to scale for differences among species. In forests with only a single or few dominant species, these simple approaches may be adequate. However, this might not be the case in diverse forests, such as the eastern deciduous forest type. For example, the southern Appalachian region of the eastern US exhibits both high community and species diversity. In this region, it is not uncommon for as many as 14 overstory species to co-occur within a 1-ha area, and as many as four community types to occur within a 20-ha area (Bolstad et al., 1998). Because R_d flux can be substantial, with as much as 75% of gross C gain lost via this pathway (Edwards et al., 1981), quantifying and understanding respiration rates by species is critical for developing and parameterizing NPP models. However, data required for models are not widely available, particularly those requiring individual species respiration parameters. Because of both the lack of species data and the complexity of models which account for inter-species variability, large-scale models in mixed species forests have typically used lumped parameter approaches where, for example, R_d is represented by a single response function (Aber and Federer, 1992). An inherent assumption (or hypothesis) with many of these models is that the simplification required for large-area approaches does not substantially sacrifice accuracy or interpretation of model outputs. However, if physiological response functions vary greatly among species, then variation in species composition can have a large influence on NPP.

Foliar R_d represents the major fraction of plant respired C in many ecosystems (Ryan et al., 1996), and because leaves are tightly coupled to the environment, they are particularly responsive to changes in temperature and nutrient availability. Like many metabolic processes, leaf respiration is exponentially related to temperature (Kozlowski et al., 1991; Coleman et al., 1993), and is generally positively related to leaf N (Field and Mooney, 1986; Norby et al., 1986; Ryan, 1991). While leaf R_d rates and relationships between temperature and N are available for several conifer and broadleaf deciduous species throughout the world, very little leaf R_d data are available for species which occur in hardwood ecosystems in the eastern US. Furthermore, because species-level leaf R_d data are so rare, there have been no systematic evaluations of the differences in NPP predictions from 'lumped parameter' versus species specific approaches.

The objectives of this study were: (1) to determine differences in leaf R_d rates for seven hardwood species; and (2) to evaluate the effects of using 'lumped parameter' versus 'species-specific parameter' approaches to determining the leaf respiration component of NPP in eastern deciduous hardwood ecosystems.

2. Methods

2.1. Study sites

Research was conducted at the Coweeta Hydrological Laboratory located in the southern Appalachians of western North Carolina. Leaves were sampled from trees located in three control watersheds (Sites 1–3) and from a site (Site 4) near the administrative area of the laboratory. Trees at these sites were primarily composed of species that regenerated after the laboratory was logged in the early 1900s. Hence, stand age averaged ~85 years old. In Sites 1–3, we used towers to access sample leaves in the mid- and upper-crown. Towers were approximately 30 cm in cross-section and ranged from 18 to 24 m in height, allowing access to the top of the canopy (towers extended approximately 3 m above the top of the canopy). In Site 4, sample leaves were collected from branches removed with a 6-m pruning pole. Sampling from the mid- and upper-crown at all sites ensured that leaves were located in generally sunlit canopy positions. Sample sites were arrayed along an elevation gradient, spanning a range from 670 to 1430 m. Across the gradient, average annual temperature and precipitation range from 13.1°C and 1800 mm at lower elevations to 8.2°C and 2200 mm at higher elevations.

2.2. Respiration measurements

Leaf respiration was measured on seven species in late summer 1995: *Quercus alba, Quercus rubra, Quercus coccinea, Carya glabra, Quercus prinus, Liriodendron tulipifera* and *Acer rubrum.* All measurements were conducted at night (i.e. between 24:00 and 06:00 h). The sampling intensity, species sampled, and approach varied at each site due to differences in access to species and the efficacy of cutting branches. We were especially cautious in cutting branches from the tower sites because these trees are being used for long-term measurements of leaf physiology. At Site 1, in situ measurements were conducted on *Q. coccinea* (n = 2) and *L. tulipifera* (n = 2). In addition, two *L. tulipifera* branches were cut with a pruning pole and measurements (n = 2) were made on the ground within 5 min of branch cutting. At Site 2, no in situ measurements were made because the leaves were located too far from the tower to allow placement in a custom-made temperature-controlled cuvette (TCC; described in Hubbard et al., 1995). Instead, two branches of *Q. alba* were cut and measurements were made (n = 2) on the ground within 5 min of detachment. At Site 3, in situ measurements were conducted on *Q. prinus* (n = 2) and *A. rubrum* (n = 2). In addition, two *Q. rubra* branches were cut (in situ measurements were not possible), and one branch each of *A. rubrum* and *Q. prinus* were cut and measurements were made on the ground within 5 min (n = 2 for *Q. rubra* and n = 1 for *Q. prinus* and *A. rubrum*). At Site 4, branches from *L. tulipifera* (n = 1), *Carya glabra* (n = 2), and *Q. alba* (n = 2) were sampled with a pruning pole (6 m height) and measured on the ground. Cut branches from the towers and Site 4 ranged in size from approximately 2 to 4 cm diameter on the cut end. Cut branches were placed in water until leaf measurements could be made. Both in situ and ground-level measurements were conducted with the TCC and LCA-4 infrared gas analyzer (IRGA) (ADC, Hoddeson, UK). We used the TCC to develop temperature response curves for each sample, varying temperature from 10 to 30°C by 5°C increments in alternating sequences (i.e. 10-30°C on leaf sample 1, then 30–10°C on leaf sample 2). During the sample, the entire leaf (still attached to the branch on both in situ and cut branch measurements) was placed inside the cuvette. A fine-wire copper constantan thermocouple was placed against the leaf to monitor leaf temperature and this information was also used to adjust temperature to maintain the desired set-point temperature. Leaf and set-point temperature varied in most cases by $< +0.5$°C. Leaves were maintained at the set-point temperature for at least 7 and typically 10 min before IRGA respiration measurements were recorded. Time of exposure was extended as needed to ensure that steady-state values of CO_2 efflux were obtained. After the full range of temperature-response measurements was made, each leaf was removed from the cuvette, detached from the branch, and placed in

paper bags for transport to the laboratory. Leaf area was determined with an area meter (CID-251 Image Analyzer), after which leaves were dried (70°C for 48 h), ground, and analyzed for total N with a Perkin–Elmer CHN analyzer. Respiration rates (μmol m^{-2} s^{-1} and nmol g^{-1} s^{-1}) were determined based on the difference in CO_2 entering and exiting the cuvette, flow rate, and leaf surface area or mass.

2.3. Statistical analyses

Within species, we combined data from both in situ and cut branch measurements and conducted analyses on species means. As observed in other studies (Walters et al., 1993), our examination of the data indicated no differences in respiration rate from in situ versus cut branch techniques. For example, for *L. tulipifera*, we measured R_d on leaves in situ, then removed the branch and re-measured the same leaves. Respiration rates and temperature response curves were essentially identical for in situ and cut branch measurements.

We used non-linear regression to develop temperature response curves and linear regression to analyze relationships between respiration rate and leaf N. For non-linear regression, we used the model:

respiration rate (μmol m^{-2} s^{-1} or nmol g^{-1} s^{-1})

$$= \beta_0^* e^{(\beta_1 T)} \quad (1)$$

where β_0 and β_1 are estimated parameters, and T is the leaf temperature. Q_{10} values were calculated for each species. Relationships between R_d and leaf N were determined with linear regression analyses. All analyses were conducted using the Statistical Analysis System (SAS Institute Inc., 1987).

2.4. Model comparisons

We used the mass-based temperature response parameters from Eq. (1) to examine the effects of species/site specific estimates of respiration versus generalized lumped parameter approaches typical of large scale models (Aber and Federer, 1992; Aber et al., 1996). For this comparison we used PnET-II, a generalized lumped-parameter model which has been applied and validated for a variety of forest types in the eastern US (Aber and Federer, 1992; Aber et al., 1996; McNulty et al., 1996). To determine leaf R_d, PnET-II scales leaf respiration (per unit weight) to N (per unit weight) driven by maximum photosynthetic rate (i.e. R = 0.10 x maximum photosynthetic rate) and uses a Q_{10} = 2, to determine a temperature response. Actual nighttime leaf respiration (R_d) is calculated using the equation:

$$R_d = (R^*(Q_{10}^{((\text{Tnight} - \text{PsnTOPT})/10)})^*\text{nightlength}) \quad (2)$$

where R_d is the leaf respiration in nmol g^{-1}, Q_{10} = 2, Tnight is the average nighttime temperature in °C, PsnTOPT is the optimal temperature for photosynthesis in °C, and nightlength is the length of nighttime in seconds. We calculated average and species specific respiration (at 10, 15, 20, 25 and 30°C) with the temperature response functions developed from our data and compared them to predictions from the general equations of Aber et al. (1996) for nighttime leaf respiration across the temperature (10-30°C) and N (1.5-3.0%) range observed in our study.

3. Results

3.1. Differences in leaf R_d among species

We found substantial differences in leaf R_d expressed on an area (umol m^{-2} s^{-1}) and mass (nmol g^{-1} s^{-1}) basis and the shape of the temperature response curves among species (Fig. 1 (a, b)). For example, at 25°C there was up to a three-fold difference among species (i.e. 0.32 umol m^{-2} s^{-1} for *C. glabra* versus 0.90 umol m^{-2} s^{-1} for *Q. rubra*). For all species except *Q. coccinea*, the non-linear model of R_d versus temperature response was significant (i.e. β_0 and β_1 95% confidence intervals did not encompass zero; Table 1). For *Q. coccinea*, the β_0, parameter 95% confidence interval encompassed zero. Q_{10} values ranged from 1.97 to 2.44 (Table 1).

3.2. Role of nitrogen

When expressed on an area basis (μmol m^{-2} s^{-1} at 15°C), variation in R_d among species was linearly related ($r^2 = 0.52$; $P < 0.05$) to variation in leaf N (Fig. 2a). Similar patterns were observed when leaf respiration and leaf N were expressed on a mass basis (i.e. nmol g^{-1} s^{-1} at 15°C vs. leaf N in percent dry weight; Fig. 2b); however, the data were too variable to establish statistically significant mass-based relationships. Collectively, leaf N and temperature explained 73% of the variation in leaf R_d among species (leaf respiration [μmol m^{-2} s^{-1}] = - 1.046 + 0.034(leaf temperature in °C) + 0.384(leaf N in percent); $P = 0.0001$; mean square error = 0.02695) with both parameters highly significant ($P < 0.0001$; $n = 20$). Although respiration and temperature were exponentially related (Fig. 1 (a, b)), logarithmic transformations of either the dependent or independent variables did not improve the regression.

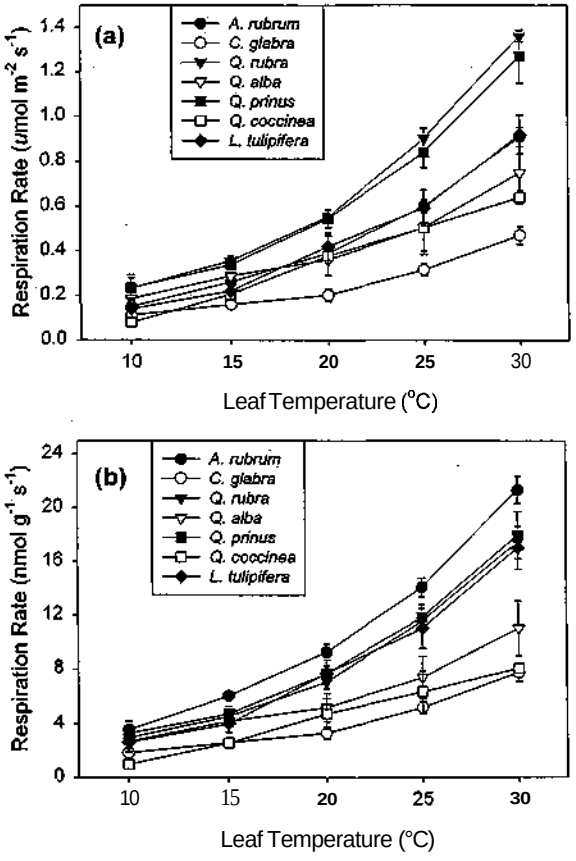

Fig. 1. Leaf respiration temperature-response curves for all species based on: (a) area (μmol m^{-2} s^{-1}); and (b) mass (nmol g^{-1} s^{-1}). Data are the means of observations from independent leaf samples. Bars on data points represent standard error of the means.

3.3. Lumped versus species specific approaches to modelling leaf R_d

We compared our mass based individual species and lumped models to the mass- and N-based predictions of PnET-II (Aber et al., 1996) and found a high correlation between the average mass-based temperature-response function (Table 1) and the mass-based PnET-II functions ($r^2 = 0.99$; $P < 0.0001$; $n = 5$); however, the PnET-II estimates were consistently 1.4 nmol g^{-1} s^{-1} greater than the Coweeta-specific temperature-response curve estimates (intercept = 1.38, slope = 1.01; Fig. 3). At warmer temperatures (i.e. higher respiration rates), a 1.4 nmol g^{-1} s^{-1} bias results in less than a 10% difference between observed and predicted R_d. At cooler temperatures (i.e. lower respiration rates), this bias becomes more pronounced. With the exception of *A. rubrum*, individual species respiration estimates were generally greater with the mass-based PnET-II functions (Fig. 3).

4. Discussion

Leaf R_d and Q_{10} values observed in our study are within the range of values observed for both hardwoods and conifers in other studies (Walters et al., 1993; Ryan et al., 1996). The wide variation in leaf R_d rates among species indicates potentially large differences in net canopy carbon gain in forests with spatial or temporal variation in species composition (i.e. altered diversity via succession or management). However, variation in leaf R_d does not directly translate into variation in canopy C gain. Variation in net photosynthesis (A), leaf area index (LAI), and vertical LAI distribution also need to be considered because they can offset or further emphasize the importance of

Table 1
Species-specific leaf nitrogen (N in %), specific leaf weight (SLW in g cm^{-2}), and parameters for temperature response function based on area (μmol m^{-2} s^{-1}) and mass (nmol g^{-1} s^{-1})[a]

Species	Leaf characteristics		Temperature-response parameters					
	N	SLW	Area			Mass		
			β_0	β_1	Q_{10}	β_0	β_1	Q_{10}
Acer rubrum	2.09	0.42	0.070(0.003)	0.086(0.002)	2.36	1.666(0.016)	0.085(0.002)	2.34
Carya spp.	1.90	0.61	0.048(0.005)	0.076(0.004)	2.14	0.786(0.086)	0.076(0.004)	2.13
Liriodendron tulipifera	1.99	0.54	0.064(0.009)	0.089(0.005)	2.44	1.188(0.158)	0.089(0.005)	2.44
Quercus alba	2.10	0.68	0.095(0.010)	0.068(0.004)	1.97	1.349(0.138)	0.069(0.004)	1.99
Quercus coccinea	2.10	0.80	0.072(0.025)	0.074(0.013)	2.10	0.909(0.312)	0.086(0.001)	2.35
Quercus prinus	2.75	0.71	0.097(0.003)	0.086(0.001)	2.36	1.385(0.142)	0.086(0.001)	2.36
Quercus rubra	2.21	0.78	0.094(0.005)	0.089(0.002)	2.44	1.226(0.063)	0.089(0.002)	2.44
All species	2.10	0.65	0.077(0.005)	0.082(0.002)	2.27	1.201(0.051)	0.083(0.001)	2.10

[a] Numbers in parentheses are standard errors of the temperature response function parameter estimates.

leaf R_d differences among species. To illustrate this point, we used previously published data on in situ A (Sullivan et al., 1996) and vertical LAI distribution (Vose et al., 1995) collected from the same towers used in this study. Ratios of leaf level A to R_d (area based) at light saturation (i.e. 1200 μmol m^{-2} s^{-1}) indicate that the greatest potential per leaf for C gain occurs for *Q. coccinea* and *C. glabra* and the lowest potential per leaf for *A. rubrum* and *Q. rubra* (Fig. 4). The low A/R_d values for *A. rubrum* and *Q. rubra* occur for different reasons; i.e. relatively low A_{max} for *A. rubrum* and high R_d for *Q. rubra.* Under low light levels (i.e. 300 μmol m^{-2} s^{-1}), these patterns shift slightly, with *Q. alba* and *C. glabra* having the highest ratios and by *A. rubrum* and *C. glabra* which comprise 33 and 19% of the total stand LAI (average stand LAI = 4.7), respectively, with most of that LAI displayed in the mid- and lower canopy. The high LAI of *A. rubrum* may offset the low A/R_d values observed at high and low light levels. LAI for oak species ranges from 5 *(Q. rubra)* to 15% *(Q. coccinea)* of the total LAI with most distributed in the upper third of the canopy. Based on patterns of A/R_d and LAI amount and vertical distribution, we would predict the greatest net canopy C fixation for *C. glabra* and *Q. coccinea.*

The relationship between leaf respiration and nitrogen provides further evidence for the linkage of tissue N levels to respiration (Ryan, 1995; Ryan et al., 1996). Variation within and among species in tissue N levels will influence leaf respiration, and the tissue N-respiration relationship has been suggested as an approach to account for species differences (Ryan, 1991). However, it should be noted that in our study, leaf N and leaf R_d were correlated only when R_d was expressed on an area basis and N on a mass basis. Hence, some of the correlation may be due to differences in leaf structural characteristics. When expressed using similar units (i.e. both on a mass basis or an area basis), the relationship is considerably weaker, which suggests that at least in hardwoods, the leaf N-respiration relationship may not be robust enough to use as a scaling tool.

Results from comparing leaf R_d using lumped versus species-specific approaches indicated that for the seven species we studied at Coweeta, the general equations from the mass-based PNET functions adequately predict N and temperature-dependent respiration rate for the average of all species, although predictions were generally higher than those derived from site-specific temperature-response curves. In stands with varying proportions of species (e.g. predominately *Q. rubra),* the differences in mass-based respiration rate between the general equation and species-specific equations could become more significant and influence productivity estimates. For example, in

the southern Appalachians, most stands are dominated by two to three species. Does a mixture of species minimize the inaccuracies of individual species predictions? To examine this question, we used data from 297 permanent plots located in the Coweeta Hydrologic Laboratory (Elliott et al., 1999). Averaged across all plots, the dominant species occurring in the 2185 ha basin are *Q. prinus* (5.88 m^2 ha^{-1}), *A. rubrum* (3.89 m^2 ha^{-1}), *Q. coccinea* (2.44 m^2 ha^{-1}), *Q. rubra* (2.03 m^2 ha^{-1}), *L. tulipifera* (1.95 m^2 ha^{-1}), and *Carya* spp. (1.65 m^2 ha^{-1}) (Table 2). Several community types are also present (based on discriminant analyses; Elliott et al. (1999)) within the basin, with very different species composition patterns than those observed at the basin level (Table 2). We weighted leaf respiration estimates derived from species-specific equations by their relative basin-level basal area, and for four community types (Dry Oak, Mixed Deciduous, Mesic Oak, and Xeric Oak) comprised of species for which we derived specific equations (Table 1). At the basin-level and for most community types, there was generally good agreement between the PnET-II leaf respiration estimates and the weighted species-

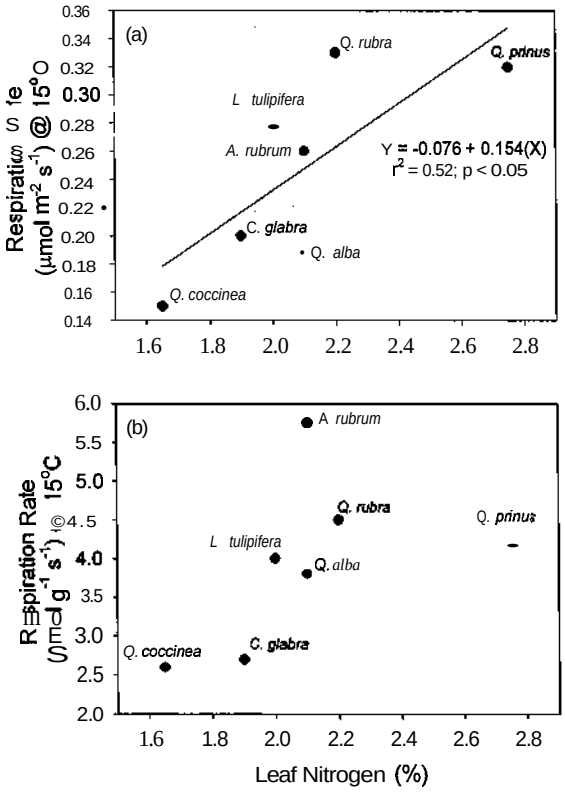

Fig. 2. Relationship between leaf N (% dry weight) and leaf respiration (μmol m^{-2} s^{-1} and nmol g^{-1} s^{-1} at 15°C).

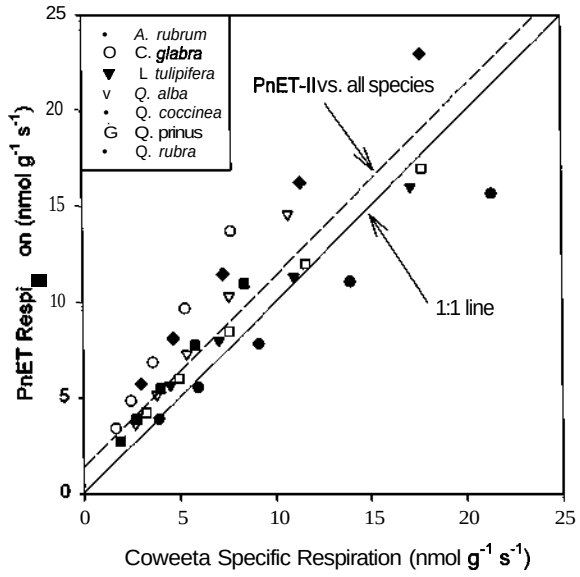

Fig. 3. Comparison of nighttime leaf respiration (nmol g^{-1} s^{-1}) estimated with the lumped parameter approach from Aber et al. (1996) (with species specific N values from Coweeta) and the mass-based species temperature-response curves from Coweeta.

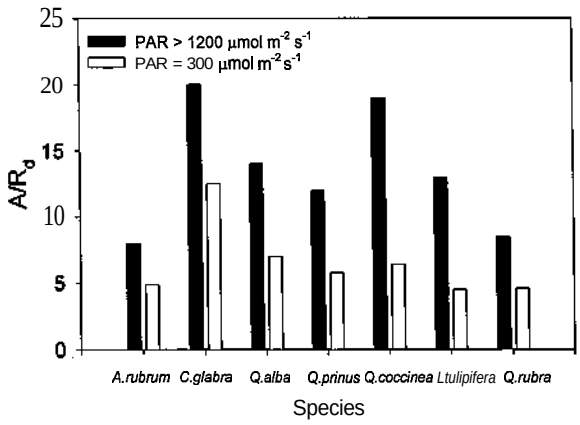

Fig. 4. Ratios of maximum net photosynthesis (*A* at > 1200 μmol m^{-2} s^{-1}; Sullivan et al., 1996) to leaf respiration (μmol m^{-2} s^{-1} at 20°C).

Table 2
Species composition (basal area in m^{-2} ha^{-1}) of overstory vegetation at the Coweeta Hydrologic Laboratory[a]

Species	Community type							
	Basin	Northern	Dry	Mixed	Cove	Mesic	Xeric	Pine
	Wide	Hardwood	Oak	Deciduous	Hardwood	Oak	Oak	Hardwood
Acer rubrum	3.9(0.2)		2.3(0.1)	3.3(0.4)			1.5(0.1)	
Betula lenta	20.7(0.6)			2.6(0.2)				
Carya spp.	1.7(0.1)				2.5(0.2)	3.6(0.2)		
Liriodendron tulipifera	2.0(0.1)				8.9(0.6)			
Pinus rigida								6.3(0.4)
Quercus coccinea	2.4(0.1)		2.5(0.1)	2.2(0.3)			11.3(0.7)	5.6(0.4)
Quercus prinus	5.9(0.3)		12.7(0.7)	2.6(0.3)		4.2(0.3)	4.2(0.3)	3.8(0.2)
Quercus rubra	2.0(0.1)	4.3(0.1)				8.4(0.5)		
Tila Americana		12.3(0.3)						

[a] Basin wide species composition is based on the top sk species, and community types are based on the top three species. Numbers in parentheses are the percent basal area of each species relative to the total for each community type.

cies-specific estimates (Fig. 5). This was especially true at leaf temperatures greater than 25°C. At lower leaf temperatures, PnET-II estimates were 15-20% greater. Only the Xeric-Oak community type diverged substantially from the PnET-II estimates, and differences were greatest at the higher leaf temperature. These results indicate that at the level of the community and greater, mixtures of species (with the exception of the Xeric-Oak type) tend to result in convergence, primarily because of compensating errors. In our analyses, the occurrence of *A. rubrum* was most important to this convergence, as R_d for *A. rubrum* was underestimated by PnET-II, while all other species were overestimated.

5. Conclusions

Our data indicate that there is wide variation in leaf R_d among species. Because leaf N and respiration were only weakly correlated, leaf N does not appear to be a robust indicator for scaling variation in R_d in eastern deciduous hardwood forests. While we recognize that these interpretations are based on limited data, the strength of the relationships and the correlations between our temperature-response functions and those derived from more extensive data sets (Aber and Federer, 1992; Aber et al., 1996) indicates our results are generally applicable. In addition, our temperature-response functions are well within the range of those derived from more extensive sampling in the southern Appalachian region (Bolstad et al., 1999; Mitchell et al., 1999). Clearly, additional data are needed to support the robustness of these relationships in different regions and during different times of the growing season. The variation

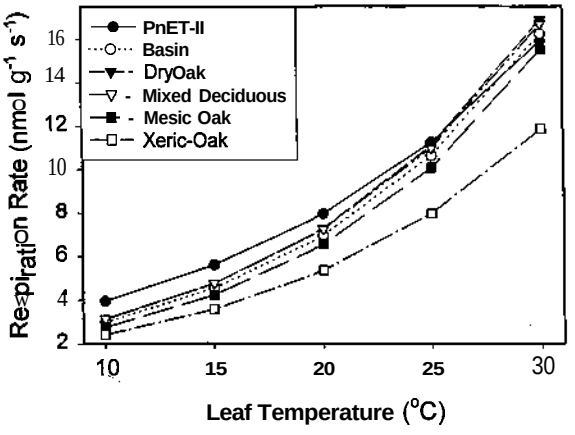

Fig. 5. Community-type and basin scale estimates of average leaf respiration (weighted by basal area distribution) vs. leaf temperature using the lumped-parameter approach from Aber et al. (1996) and the mass-based species temperature response curves from Coweeta.

in leaf respiration we observed among species cannot by itself explain variation in NPP in diverse landscapes. These data will need to be integrated in a modelling context with variation in leaf area, photosynthesis, respiration of other components, and carbon allocation.

Will detailed physiological data from all species (or at least the canopy dominants) be required to model NPP in eastern deciduous forests? Based on the species- and community-level variation we observed, it is clear that the success or failure of accurately predicting the leaf R_d component of NPP will depend on species composition. In the present analysis, there were often large differences in R_d estimates at the individual species level, but predictions using PnET-II (Aber and Federer, 1992; Aber et al., 1996) at the stand or community level, indicated that for leaf R_d, the lumped parameter approach worked well at both large (i.e. multiple community types) and small (within community types) spatial scales, largely because the mixture of species resulted in compensating errors. This was especially true for stands that contained *A. rubrum*, whose low PnET-II estimates of leaf R_d offset overestimates for other species. The greatest potential for error occurs where one or two species dominate the stand. As the ~85-year-old stands at Coweeta develop further, we would expect a shift in species composition (in the absence of disturbance) towards fewer and more shade-tolerant species.

Based on the results of these analyses and several other studies examining differences in fundamental physiological processes regulating NPP among species (Sullivan et al., 1996; Bolstad et al., 1999; Mitchell et al., 1999), we contend that future directions in modelling stand-level NPP in eastern deciduous forest should be species-based. Because of the complexity of parameterizing a multi-species model, most physiologically-based NPP models have been developed in single-species stands (e.g. BIOMASS) or have lumped parameter values across species (e.g. PnET-II). These approaches will provide inaccurate estimates of NPP in stands without the right 'mix' of species to offset over- and under-estimates or in stands where species composition is changing due to succession or changes in climatic conditions. Even in stands where overall predictions of stand- or community-level NPP predictions are correct, underlying inaccuracies in the parameters and/or algorithms severely limit the ability to interpret mechanisms regulating predicted NPP responses to altered climate, fertilization, or other changes in abiotic or biotic driving variables.

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