Seasonal variation in the temperature response of leaf respiration in *Quercus rubra* at the Black Rock Forest

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Abstract: Leaf respiratory temperature responses of *Quercus rubra* were measured throughout the 2003-growing season in a deciduous forest in northeastern USA, in the upper and lower portions of the canopy at two sites with different soil water availability. Consequently, stand-level canopy foliar carbon loss (R_{canopy}) was modeled for a virtual *Quercus rubra* monoculture in these two sites. The base leaf respiration rate (R_0, respiration at 10 ºC) of *Q. rubra* was significantly affected by season, site water availability, canopy height and their interactions. Upper canopy leaves generally had higher R_0 than lower canopy leaves. At the drier site, a more significant seasonal pattern in R_0 was observed, while at the more mesic site, a stronger canopy position effect was detected. By contrast, the temperature coefficient (E_0, the activation energy of respiration as a single reaction) was constant (52.5 ± 5 kJ mol^{-1}). Leaf reducing monose could partially explain the seasonality in respiration (32% - 79%), and leaf nitrogen (N_{area}) was well correlated to the canopy position effect. R_{canopy} of *Q. rubra* was first estimated by a "full distributed physiology model", which. integrates the effects of season, site, and canopy position on R_0. Sensitivity examination indicates that neglecting the season, site and canopy height effects on leaf respiration resulted in up to a 130% error on the estimation of R_{canopy}, but canopy level model parameterizations could be simplified by assuming a constant E_0 (error < 5%). From June 8th to October 28th of 2003, the modeled R_{canopy} of the virtual *Q. rubra* monoculture was 6.3 mol CO_2 m^{-2} ground, and 13.5 mol CO_2 m^{-2} ground, at the drier and the more mesic site respectively. These results suggest that the temporal and spatial heterogeneities of R_0 need to be considered in ecosystem models, but it is potentially predictable from well understood leaf properties. Meanwhile, simplifications can be made in *Q. rubra* by assuming a constant temperature coefficient (E_0, *e.g.* 52.5 kJ mol^{-1} in this study).

Data and Observations:

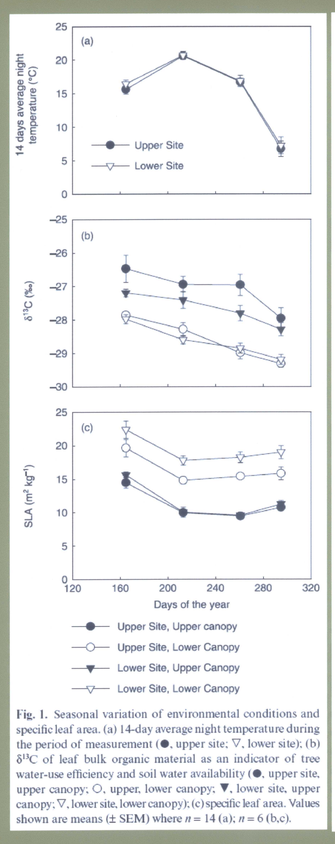


Fig. 1. Seasonal variation of environmental conditions and specific leaf area. (a) 14-day average night temperature during the period of measurement (●, upper site; ▽, lower site); (b) $\delta^{13}C$ of leaf bulk organic material as an indicator of tree water-use efficiency and soil water availability (●, upper site, upper canopy; ○, upper, lower canopy; ▼, lower site, upper canopy; ▽, lower site, lower canopy); (c) specific leaf area. Values shown are means (± SEM) where $n = 14$ (a); $n = 6$ (b,c).

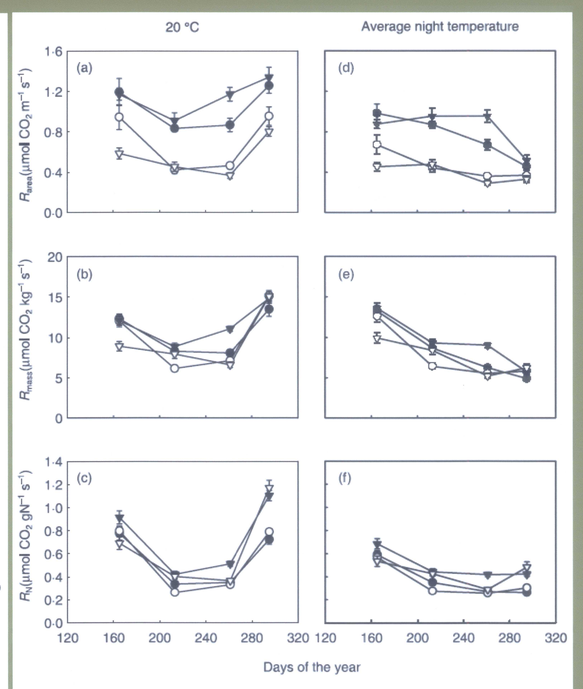


Fig. 2. Seasonal variation of dark respiration rates estimated from fitted temperature-response curves (Fig. 2) for *Quercus rubra* leaves in four site–canopy position combinations. Parameters R_{area} (upper panel); R_{mass} (middle panel); R_N (lower panel) are area-, biomass- and nitrogen-based dark respiration rates calculated from the fitted responses. Respiration rates at 20 °C (a–c) or at the 14-day average night temperature bracketing the measurement period (d–f) are plotted. Values shown are means (± SEM), $n = 6$. Symbols as in Fig. 1(b,c).

Leaf respiratory temperature responses and general leaf properties of *Quercus rubra* were measured throughout the 2003 growing season. Measurements were made in the upper and lower portions of the canopy of mature trees at two sites with different soil water availability. Correlations among respiration and various leaf properties, including SLA, N and soluble carbohydrates were examined. We hypothesized that (1) the model parameters of leaf respiratory temperature response would vary with season, site and canopy position; (2) due to the difference in light environment of the two sites, the seasonal effect would be more significant at the drier site, while the canopy effect would be more significant at the more mesic site; (3) the respiration rate would be positively related to leaf nitrogen and soluble sugars (monose and sucrose); and (4) the temporal and spatial patterns in respiration could be explained by different leaf properties (leaf nitrogen, monose and sucrose).

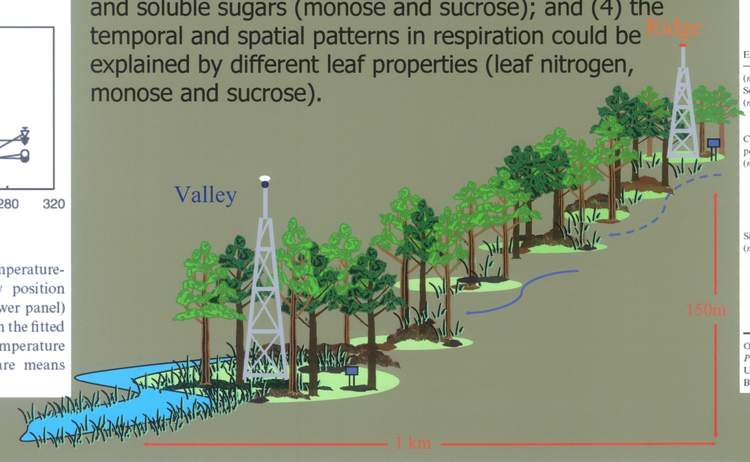


Table 1. Model parameters of respiratory temperature response in all season/site/canopy position combinations

Model parameter	Sampling period	Upper site		Lower site	
		Upper canopy	Lower canopy	Upper canopy	Lower canopy
E_0 (kJ mol^{-1})	06/11–06/16	51·0 (3·0)^{abc}	54·8 (1·9)^{ab}	57·6 (1·1)^{a}	51·2 (1·3)^{bc}
	07/30–08/01	52·5 (1·9)^{bc}	52·1 (1·3)^{bc}	49·5 (2·4)^{bc}	56·7 (3·1)^{ab}
	09/17–09/18	55·4 (1·5)^{ab}	55·1 (2·7)^{abc}	47·0 (2·4)^{c}	55·6 (1·9)^{ab}
	10/20–10/23	52·0 (1·2)^{bc}	49·7 (2·7)^{bc}	51·5 (2·8)^{abc}	48·2 (3·2)^{bc}
R_0 (area, 10 °C) (μmol m^{-2} s^{-1})	06/11–06/16	0·64 (0·06)^{a}	0·43 (0·06)^{bcd}	0·51 (0·03)^{ab}	0·28 (0·03)^{e}
	07/30–08/01	0·39 (0·01)^{d}	0·20 (0·02)^{f}	0·45 (0·05)^{bcd}	0·21 (0·03)^{ef}
	09/17–09/18	0·39 (0·04)^{d}	0·21 (0·02)^{ef}	0·60 (0·05)^{a}	0·17 (0·01)^{f}
	10/20–10/23	0·59 (0·04)^{ab}	0·47 (0·06)^{abcd}	0·64 (0·06)^{a}	0·40 (0·03)^{cd}
R_0 (mass, 10 °C) (μmol kg^{-1} s^{-1})	06/11–06/16	8·5 (0·42)^{a}	8·0 (0·57)^{ab}	7·9 (0·42)^{ab}	6·1 (0·44)^{cd}
	07/30–08/01	3·9 (0·19)^{ef}	2·9 (0·18)^{h}	4·4 (0·29)^{e}	3·6 (0·43)^{efgh}
	09/17–09/18	3·6 (0·25)^{efg}	3·2 (0·29)^{fgh}	5·6 (0·32)^{d}	3·0 (0·20)^{gh}
	10/20–10/23	6·3 (0·39)^{cd}	7·4 (0·54)^{abc}	7·1 (0·47)^{bc}	7·6 (0·53)^{abc}

E_0 is a parameter equivalent to the energy of activation for respiration as an overall reaction, and is similar, but not identical, to the energy of activation for a single enzyme reaction.
R_0 (on an area basis and a mass basis) is the base respiration rate at 10 °C.
Values shown are means (± SEM) where $n = 6$. Means were compared in pairs among all 16 season/site/canopy position combinations by *t*-test. If two values are followed by the same letter, they are not significantly different at $P = 0{\cdot}05$.

$$R = R_0 e^{\frac{E_0}{R_g}\left(\frac{1}{T_0}-\frac{1}{T_a}\right)}$$

Table 2. Summary of multivariant correlation analysis between R at 20 °C (R_{20}) and leaf properties (leaf nitrogen, reducing monose and sucrose) in *Quercus rubra*

		$R_{20(area)}$ (μmol CO_2 m^{-2} s^{-1})				$R_{20(mass)}$ (μmol CO_2 kg^{-1} s^{-1})				$R_{20(N)}$ (μmol CO_2 g^{-1} N s^{-1})		
			Partial correlation coefficient				Partial correlation coefficient				Partial correlation coefficient	
Effects isolated	Data group	R^2	N_{area} (mmol N m^{-2})	M_{area} (g m^{-2})	S_{area} (g m^{-2})	R^2	N_{mass} (mmol N g^{-1})	M_{mass} (g g^{-1})	S_{mass} (g g^{-1})	R^2	M_N (g g^{-1} N)	S_N (g g^{-1} N)
($n = 96$)	All	**0·36*****	**0·39*****	**0·46*****	−0·007 ns	**0·22*****	−0·03 ns	**0·32****	−0·12 ns	**0·42*****	**0·61*****	−0·04 ns
Season ($n = 24$)	UU	**0·40***	−0·19 ns	**0·54****	−0·07 ns	**0·66*****	−0·35 ns	**0·51***	−0·56**	**0·48****	**0·57****	−0·25 ns
	UL	0·29 ns	−0·18 ns	**0·46***	0·04 ns	**0·44****	−0·28 ns	0·39 ns	−0·20 ns	**0·41*****	**0·57****	0·04 ns
	LU	0·23 ns	0·26 ns	0·39 ns	−0·27 ns	**0·34***	0·10 ns	0·31 ns	−0·36 ns	**0·57*****	**0·72*****	−0·24 ns
	LL	**0·64*****	−0·19 ns	**0·73*****	0·14 ns	**0·66*****	0·26 ns	**0·72*****	0·11 ns	**0·80*****	**0·89*****	0·11 ns
Canopy position ($n = 12$)	13 Jun US	**0·73***	0·62 ns	0·30 ns	**0·66***	0·19 ns	−0·04 ns	0·06 ns	0·41 ns	0·41 ns	0·30 ns	0·53 ns
	13 Jun LS	**0·91*****	**0·93*****	−0·08 ns	−0·72*	0·54 ns	0·25 ns	−0·67*	−0·61 ns	0·41 ns	−0·57 ns	−0·63*
	31 Jul US	**0·91*****	**0·86****	−0·57 ns	0·02 ns	0·73*	0·49 ns	−0·79**	0·11 ns	**0·50***	−0·70*	0·03 ns
	31 Jul LS	**0·92*****	**0·85****	−0·12 ns	0·23 ns	0·32 ns	0·48 ns	−0·13 ns	0·15 ns	0·12 ns	0·05 ns	0·30 ns
	21 Sep US	**0·91*****	**0·68***	0·29 ns	0·44 ns	0·43 ns	0·53 ns	0·20 ns	0·39 ns	0·13 ns	0·04 ns	0·27 ns
	21 Sep LS	**0·99*****	**0·97*****	−0·63 ns	0·06 ns	**0·87****	**0·81****	−0·70*	−0·04 ns	0·56*	−0·61*	0·42 ns
	17 Oct US	0·92*	**0·93*****	0·36 ns	−0·04 ns	0·73*	0·60 ns	0·43 ns	−0·56 ns	0·54 ns	0·39 ns	−0·50 ns
	17 Oct LS	**0·92*****	**0·90*****	0·59 ns	−0·26 ns	0·21 ns	0·34 ns	0·13 ns	−0·12 ns	0·47 ns	**0·64***	−0·31 ns
Site ($n = 12$)	13 Jun UC	0·47 ns	−0·26 ns	**0·64***	0·23	0·32 ns	−0·48 ns	0·22 ns	−0·18 ns	0·44 ns	0·61 ns	0·27 ns
	13 Jun LC	**0·85*****	**0·85****	0·05 ns	−0·29*	0·35 ns	0·59 ns	−0·02 ns	−0·10 ns	0·02 ns	−0·04 ns	−0·12 ns
	31 Jul UC	0·37 ns	0·48 ns	0·04 ns	−0·17 ns	0·22 ns	−0·30 ns	0·16 ns	−0·44 ns	0·13 ns	−0·17 ns	0·35 ns
	31 Jul LC	0·21 ns	0·39 ns	0·10 ns	−0·07 ns	0·06 ns	−0·03 ns	0·02 ns	−0·19 ns	0·33 ns	0·49 ns	−0·11 ns
	21 Sep UC	0·23 ns	0·23 ns	0·27 ns	0·20 ns	0·22 ns	−0·29 ns	0·41 ns	0·29 ns	0·17 ns	0·26 ns	0·37 ns
	21 Sep LC	**0·77****	**0·67***	0·50 ns	0·42 ns	0·47 ns	0·44 ns	0·48 ns	0·41 ns	0·32 ns	0·57 ns	0·42 ns
	17 Oct UC	**0·67***	**0·79****	**0·69***	−0·25 ns	**0·61***	0·59 ns	**0·67***	−0·38 ns	**0·82*****	**0·90*****	−0·08 ns
	17 Oct LC	0·72*	**0·79***	**0·70***	−0·08 ns	0·21 ns	0·28 ns	0·43 ns	0·13 ns	**0·77****	**0·85****	−0·13 ns

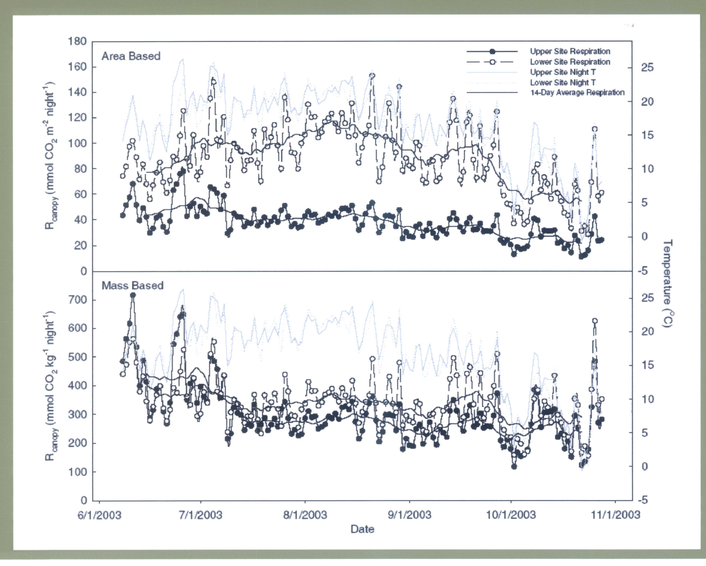
Original data were log-transformed. Multiple correlation coefficients (R^2), partial correlation coefficients (r) of each leaf property and statistical significance levels are shown (*, $P < 0{\cdot}05$; **, $P < 0{\cdot}01$; ***, $P < 0{\cdot}001$).
UU, Upper site, upper canopy; UL, upper site, lower canopy; LU, lower site, upper canopy; LL, lower site, lower canopy; US, upper site; LS, lower site; UC, upper canopy; LC, lower canopy.
Bold type highlights significant R^2, which can be attributed to some positive partial correlations, and all significant positive partial correlation coefficients.

Model Calculations:

$$R_{canopy} = \sum_i R_{0i} e^{\frac{E_{0i}}{R_g}\left(\frac{1}{T_0}-\frac{1}{T_a}\right)} \times LAI_i$$

We scaled up the foliar respiration measurements to estimate the canopy foliar carbon loss (R_{canopy}) according to stand leaf area index (LAI), and night temperature of the two research sites. The leaf level results were used to parameterize an Arrhenius function model that integrated season, site, and canopy position effects on leaf respiratory temperature responses to estimate R_{canopy} for a virtual monoculture forest of *Q. rubra* in the growing season of 2003. We further (1) estimated the error caused by a series of simplified parameterization scenarios, which respectively neglect the effect of specific environmental or biological factors and (2) established a reasonable simplifying procedure for the model. Firstly, we modeled R_{canopy} during four 14-day periods bracketing the days when leaf respiratory temperature responses were measured. Secondly, the sensitivity of the model was tested to five simplified parameterization scenarios, in which respiratory parameters and specific leaf area were assumed to be constant throughout (1) the growing season, (2) canopy depth, (3) the whole virtual *Q. rubra* stand (neglecting site heterogeneity) respectively; moreover (4) E0 was assumed to be constant across all season/site/canopy position combinations; and (5) the temperature fluctuations during each night were ignored.

Sites and Days		Upper Site					Lower Site				
		159-172	206-219	254-267	288-301	All 4 periods	159-172	206-219	254-267	288-301	All 4 periods
14-Day Average R_{can-a} (mmol C m^{-2} night^{-1})		47.0	44.7	39.4	23.8	38.7	81.9	100.8	107.6	51.3	85.4
Seasonally Constant Physiology Model	13-June	--	+68.4%	+62.2%	+5.4%	+36.4%	--	+28.8%	+1.0%	-22.4%	+5.4%
	31-July	-41.0%	--	-4.2%	-38.4%	-14.9%	-19.3%	--	-19.1%	-32.7%	-15.5%
	17-Sept	-38.6%	+6.0%	--	-38.2%	-20.5%	+0.03%	+22.0%	--	-13.9%	+5.8%
	21-Oct	-5.0%	+60.0%	+54.0%	--	+37.6%	+20.8%	+50.3%	+21.2%	--	+27.2%
Canopy Constant Physiology Model	Upper Canopy	+6.7%	+11.5%	+10.8%	+4.3%	+7.2%	+11.3%	+11.4%	+17.1%	+8.3%	+10.7%
	Lower Canopy	-25.4%	-43.3%	-40.5%	-16.3%	-32.3%	-38.4%	-42.8%	-64.1%	-31.3%	-44.2%
Site Constant Physiology Model	Upper Site	--	--	--	--	--	+22.6%	-9.1%	-23.9%	-4.3%	-5.7%
	Lower Site	-18.8%	+10.1%	+32.1%	+4.5%	+6.5%	--	--	--	--	--
Constant E_0 Model		-3.9%	+0.1%	-3.0%	4.1%	-2.1%	-4.2%	+3.5%	+5.5%	-0.2%	+3.5%
14-Day Average R_{can-m} (mmol C kg^{-1} night^{-1})		444.0	290.6	266.1	253.4	313.5	426.5	335.7	336.4	297.5	349.0
Seasonally Constant Physiology Model	13-June	--	+136%	+136%	+36.7%	+40.4%	--	+94.1%	+74.7%	+5.2%	+29.4%
	31-July	-57.9%	--	-0.6%	-43.0%	-43.6%	-46.5%	--	-7.2%	-39.4%	-33.6%
	17-Sept	-57.8%	+2.2%	--	-44.9%	-42.9%	-42.2%	+6.3%	--	-32.5%	-23.4%
	21-Oct	-26.8%	+73.0%	+72.7%	--	+20.0%	-10.9%	+67.1%	+54.6%	--	+22.1%
Canopy Constant Physiology Model	Upper Canopy	+0.4%	+4.2%	+1.8%	-2.7%	+1.0%	+4.2%	+1.2%	+4.0%	-1.0%	+2.5%
	Lower Canopy	-2.0%	-23.0%	-10.8%	+14.8%	-6.3%	-22.6%	-8.2%	-32.3%	+6.1%	-19.6%
Site Constant Physiology Model	Upper Site	--	--	--	--	--	10.0%	-12.4%	-18.8%	-10.2%	-7.4%
	Lower Site	-9.5%	+14.2%	+23.8%	+11.5%	+7.1%	--	--	--	--	--
Constant E_0		-1.6%	+0.1%	-3.0%	+4.1%	-0.4%	-4.2%	+3.5%	+5.5%	-0.2%	+0.9%



Site and Unit Basis	Upper Site		Lower Site	
	Ground Area Based (mmol C m^{-2} night^{-1})	Biomass Based (mmol C kg^{-1} night^{-1})	Ground Area Based (mmol C m^{-2} night^{-1})	Biomass Based (mmol C kg^{-1} night^{-1})
Average R_{canopy}	37.5	301.8	88.0	337.6
Maximum R_{canopy}	77.6	716.5	152.7	624.9
Minimum R_{canopy}	11.1	116.2	28.2	155.4
CV (%)	32.8%	35.2%	29.7%	26.0%

Conclusions:

- At 20°C area-based leaf respiration rates were higher in both the early and late growing season than in the mid-growing season.
- Upper-canopy leaves generally had higher respiration rates than lower-canopy leaves.
- At the drier site a more significant seasonal pattern in respiration was observed, while at the more mesic site a stronger canopy-position effect was detected.
- E_0 , a model variable related to the overall energy of activation of respiration, varied only slightly and was not influenced by season, site or canopy position.
- Leaf properties (specific leaf area, nitrogen, soluble sugars) also varied with season, site and canopy position.
  - Leaf N and reducing monose were positively correlated with leaf respiration rates.
  - Reducing monose could partially explain the seasonality in respiration (32-79%)
  - leaf N (N_{area}) was well correlated with the canopy-position effect.
- Our results suggest that the temporal and spatial heterogeneities of respiration need to be considered in ecosystem models, but significant simplifications may be made in *Q. rubra* by assuming a constant temperature coefficient or predicting the base respiration rate (R_0) from well understood leaf properties.
  - Neglecting the season, site or canopy position effects on respiration results in considerable error in the estimation of R_{canopy}.
  - Assuming a constant E_0 or constant night temperature (average nighttime temperature) results in only a small error.
- From June 8th to October 28th of 2003, the modeled R_{canopy} of the virtual *Q. rubra* monoculture was 5.4 mol m^{-2}, and 12.6 mol m^{-2}, at the drier and mesic sites

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