Oecologia (2002) 131:559–568
DOI 10.1007/s00442-002-0931-7

ECOSYSTEMS ECOLOGY

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Root respiration in North American forests: effects of nitrogen concentration and temperature across biomes

Received: 25 July 2001 / Accepted: 25 February 2002 / Published online: 20 April 2002
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Abstract Root respiration rates have been shown to be correlated with temperature and root N concentration in studies of individual forest types or species, but it is not known how universal these relationships are across forest species adapted to widely different climatic and edaphic conditions. In order to test for broad, cross-species relationships, we measured fine root respiration, as O_2 consumption, over a range of temperatures on excised root samples from ten forested study sites across North America in 1997. Significant differences existed among study sites in root respiration rates, with patterns among sites in respiration rate at a given temperature corresponding to differences among sites in fine root N concentrations. Root respiration rates were highly correlated with root N concentrations at all measurement temperatures (r^2>0.81, P<0.001, for 6, 18 and 24°C). Lower root respiration rates in gymnosperms than in angiosperms were largely explained by lower fine root N concentrations in gymnosperms, and root N concentrations and respiration rates (at a given temperature) tended to be lower at warm sites (New Mexico, Florida, and Georgia) than at cool sites with short growing seasons (Michigan and Alaska). Root respiration rates increased exponentially with temperature at all sites. The Q_{10} for root respiration ranged from 2.4 to 3.1, but there were no significant differences among the forest types. The average Q_{10}s for gymnosperms (Q_{10}=2.7) and angiosperms (Q_{10}=2.6) were almost identical, as were the average Q_{10}s for roots of ectomycorrhizal species (Q_{10}=2.7) and arbuscular mycorrhizal species (Q_{10}=2.6). In 1998, fine root respiration at the study sites was measured in the field as CO_2 production at ambient soil temperature. Respiration rates under field conditions were dependent on both ambient soil temperature and root N concentration. Relationships between respiration (adjusted for temperature) and root N concentration for the field measurements were similar to those observed in the 1997 laboratory experiments. For root respiration in tree species, it appears that basic relationships with temperature and nitrogen exist across species and biomes.

Keywords Root respiration · Nitrogen · Temperature · Q_{10} · Cross-biome effects

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Introduction

Root respiration can use a significant proportion of C assimilation in forests and can be a major source of soil CO_2 efflux (Ewel et al. 1987; Bowden et al. 1993; Ryan et al. 1996; Boone et al. 1998). On a global scale, the CO_2 flux from fine root respiration has been estimated to be about an order of magnitude larger than that from anthropogenic sources (Raich and Schlesinger 1992). Consequently, there is much interest in understanding the factors regulating root respiration and how it might be altered by global change.

Temperature and root N concentration have both been shown to affect root respiration rates in studies of individual forest types or species (Ryan 1991; Burton et al. 1996, 1998; Zogg et al. 1996; Pregitzer et al. 1998; Reich et al. 1998b), but it is not known how universal these effects are across forest species adapted to widely different climatic and edaphic conditions. Reich et al.

(1997, 1998a, 1999) have shown that basic fundamental relationships exist across biomes for pairs of leaf traits, including the relationship between leaf N concentration and respiration rate (Reich et al. 1998a). If similar relationships exist across species and biomes for root respiration, understanding them would greatly aid our ability to model forest C cycles at ecosystem, regional, and global scales.

In order to test for broad, cross-species relationships, we measured fine root respiration in a variety of forest ecosystems across North America. The forest types included angiosperms and gymnosperms with roots dominated by either arbuscular mycorrhizae or ectomycorrhizae. Objectives of the study were: (1) to determine the relationship across species between fine root N concentrations and root respiration rates; (2) to determine differences among species in root respiration rates, respiratory Q_{10} values, and root respiration per unit N; and (3) to determine if such differences corresponded to taxonomic group (i.e. angiosperms vs gymnosperms) or dominant type of mycorrhizal association (ectomycorrhizal vs arbuscular mycorrhizal).

Materials and methods

Study sites

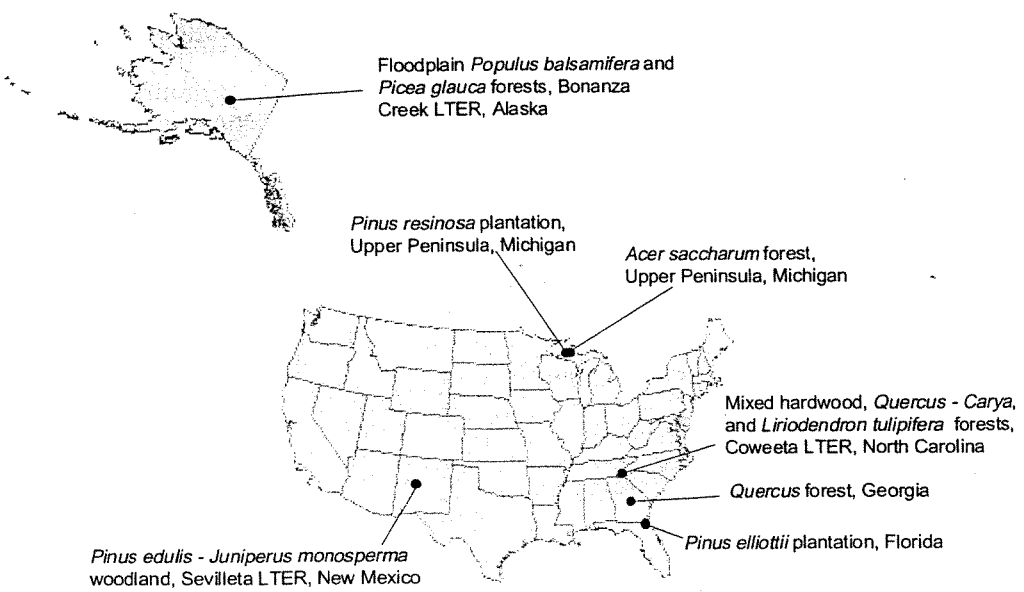
Root respiration rates were measured at ten forested study sites located across several North American biomes (Fig. 1). Boreal forests were represented by *Populus balsamifera* and *Picea glauca* stands located along the Tanana River floodplain at the Bonanza Creek LTER in interior Alaska. Cold temperate forests studied were an *Acer saccharum* dominated northern hardwood forest and a *Pinus resinosa* plantation in the Upper Peninsula of Michigan. Montane cool temperate forests, located at the Coweeta LTER in North Carolina, included mixed hardwood, *Quercus-Carya*, and *Liriodendron tulipifera* stands. Warm temperate forests in the study were a mixed *Quercus* forest in the Georgia piedmont and a *Pinus elliottii* plantation on the coastal plain in northeastern Florida. Root respiration was also measured under individual *Pinus edulis* and *Juniperus monosperma* trees in a semi-arid pinyon-juniper woodland located in the Los Pinos Mountains of the Sevilleta LTER in New Mexico. Collectively, these forests encompass a wide range of climatic conditions, with mean annual temperature ranging from −3.3 to 20.0°C and mean annual precipitation varying from 287 to 2,607 mm (Table 1). The tree species studied included gymnosperms and angiosperms, whose roots were dominated by either ectomycorrhizae or arbuscular mycorrhizae (Table 1). The sites are representative of large areas of forest land in the regions where they occur.

Six 30×30 m study plots were installed at all but two of the sites. Exceptions to this were the mixed hardwoods (two plots) and *Quercus-Carya* (three plots) stands in North Carolina. At these sites plots were located adjacent to existing LTER plots and fertilizer additions were not allowed, resulting in fewer plots per site. At the sites with six plots, fertilizer was applied to three of the plots beginning in late summer 1997 or early summer 1998 (100 kg N ha^{-1} $year^{-1}$) as part of a cross-site research project investigating the effects of N additions on belowground carbon allocation. The 1997 laboratory respiration measurements reported in this paper were completed before fertilization began. The 1998 field respiration measurements were made early in the growing season when only one quarter of the annual fertilizer increment had been applied.

Laboratory root respiration measurements

During the summer of 1997, root respiration, as O_2 consumption, was measured on excised fine roots from all plots at each forest site. Roots were collected from four to six random locations per plot using 10 cm deep by 5.4 cm diameter soil cores, which were transported in coolers to nearby laboratories for processing (less than 1.5 h travel time per site). At the laboratories, the cores from a plot were composited. All fine (≤1.0 mm), non-woody, live roots were then sorted by hand from the composite sample and rinsed free of soil and organic matter with deionized water. Live roots were distinguished by white, cream, red, tan or brown coloration and a smooth appearance. Dead roots had frayed, rough edges, were brittle, and often were dark brown or black in color. Excess water was blotted from the root samples, and 0.5 g (fresh weight) subsamples were used for respiration measurements. Samples for the laboratory experiments contained roots from all species present, but were comprised predominantly of the major species listed in Table 1 for each site. The understory at most sites was either very sparse (*Picea glauca, Pinus resinosa, Liriodendron tulipifera, Pinus elliottii, Pinus edulis,* and *Juniperus monosperma* sites) or

Fig. 1 Study site locations



had a species composition similar to the overstory (*Acer saccharum*, mixed hardwoods, mixed *Quercus* sites), and thus had little effect on sample composition at most sites. At the *Populus balsamifera* and *Quercus-Carya* sites, denser understory vegetation likely contributed a portion of the sampled roots, but roots of non-woody understory species and shrubs (primarily *Alnus* at the *Populus balsamifera* site) were identified and discarded when possible. Ectomycorrhizal root tips were included where they occurred.

Respiration was measured as O_2 consumption using gas-phase O_2 electrodes (model LD 2/2, Hansatech, Norfolk, England) connected to constant-temperature circulating water baths (Burton et al. 1996; Zogg et al. 1996). Root samples were allowed to equilibrate to measurement temperature for 20 min, after which time O_2 consumption was monitored for 40–60 min. Three complete O_2 electrode systems were run simultaneously, allowing respiration measurements to be performed on separate root samples at 6, 18 and 24°C within 4 h of sample collection. The time between collection and analysis differed by no more than 1 h among the sites, and there was no relationship between time since collection and respiration rate measured, indicating that the slight differences among sites in time to analysis did not influence our results. The range of temperatures was intended to encompass the actual soil temperatures existing at the site at the time of sampling, with field soil temperatures for most sites falling somewhere near the middle of the range. The actual field soil temperatures measured during 1998 field experiments suggest that this goal was achieved. Following respiration measurements, root subsamples were oven-dried (65°C, 24 h) for determination of dry weights, ground, and analyzed for N using an elemental analyzer (Carlo Erba NA 1500 N.C., CE Elantech, Lakewood, N.J.).

Root respiration rates measured in the laboratory were statistically analyzed using a two-factor (temperature and site) analysis of variance. The combined effects of root N concentration and temperature on respiration rates across sites were quantified using linear regression (within single temperatures) and non-linear regression and analysis of covariance (across all temperatures). Regressions of the natural log of respiration versus temperature were performed for each individual forest type listed in Table 1, using all the data collected from the site. The regression slope for each forest type was then used to calculate its respiratory Q_{10} ($Q_{10}=e^{10\times slope}$). All statistical analyses were performed using SYSTAT (SPSS 1998).

Table 1 Study site descriptions and dominant overstory species sampled. Sites are ordered by increasing mean annual temperature

Forest site	Location	Basal (m^2 ha^{-1})	Dominant overstory species (% of basal area)	Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Taxonomic group	Dominant mycorrhizal type
Populus balsamifera, Bonanza Creek LTER, Alaska, USA	64°40′N, 148°15′W	37	94% *Populus balsamifera*	126	–3.3	287	Angiosperm	Ectomycorrhizal
Picea glauca, Bonanza Creek LTER, Alaska, USA	64°41′N, 148°14′W	34	98% *Picea glauca*	122	–3.3	287	Gymnosperm	Ectomycorrhizal
Acer saccharum, Upper Peninsula, Michigan, USA	46°39′ N, 88°28′W	34	92% *Acer saccharum*	427	3.8	841	Angiosperm	Arbuscular
Pinus resinosa, Upper Peninsula, Michigan, USA	47°6′ N, 88°39′W	34	100% *Pinus resinosa*	321	3.8	883	Gymnosperm	Ectomycorrhizal
Mixed hardwoods, Coweeta LTER, North Carolina, USA	35°3′N, 83°25′W	34	26% *Betula alleghaniensis* and 20% *Quercus rubra*	1347	9.4	2607	Angiosperm	Ectomycorrhizal
Quercus-Carya, Coweeta LTER, North Carolina, USA	35°3′N, 83°25′W	35	30% *Quercus prinus*	1101	11.1	2502	Angiosperm	Ectomycorrhizal
Liriodendron tulipifera, Coweeta LTER, North Carolina, USA	35°4′N, 83°26′W	34	85% *Liriodendron tulipifera*	772	12.7	1816	Angiosperm	Arbuscular
Pinus edulis, Sevilleta LTER, New Mexico, USA	34°24′N, 106°31′W	NA[a]	Individual *Pinus edulis* trees	1993	12.7	388	Gymnosperm	Ectomycorrhizal
Juniperus monosperma, Sevilleta LTER, New Mexico, USA	34°24′N, 106°31′W	NA[a]	Individual *Juniperus monosperma* trees	1993	12.7	388	Gymnosperm	Arbuscular
Mixed *Quercus*, Georgia, USA	33°25′N, 83°25′W	26	68% *Quercus* spp.	166	16.5	1263	Angiosperm	Ectomycorrhizal
Pinus elliottii, Florida, USA	30°37′N, 81°43′W	24	100% *Pinus elliottii*	10	20.0	1303	Gymnosperm	Ectomycorrhizal

[a] Basal area is not applicable to the pinyon-juniper woodland. Total ground coverage by the canopies of woody vegetation was 0.30 m^2 m^{-2} in the pinyon-juniper woodland, with 0.13 m^2 m^{-2} *Pinus edulis* and 0.15 m^2 m^{-2} *Juniperus monosperma*. Sampling was performed under individual *Pinus* and *Juniperus* trees

Field root respiration measurements

In the summer of 1998, root respiration, as CO_2 production, was measured in the field at ambient soil temperature at each forest site. Samples for field root respiration measurement consisted of fine roots (≤1 mm diameter) collected from the top 5 cm of organic matter and mineral soil at three to four locations within each plot at a site and composited. Root samples from the mixed-hardwood forest in North Carolina were collected adjacent to *Quercus rubra* trees, samples from the *Quercus-Carya* forest in North Carolina were collected adjacent to *Quercus prinus* trees, and samples from the mixed *Quercus* forest in Georgia were collected adjacent to *Quercus alba* trees. Field comparisons of the morphological characteristics of the sample roots to those attached to seedlings and small saplings indicated the field respiration samples were comprised predominantly of the targeted species for these three sites and of the dominant overstory species listed in Table 1 for the other study sites.

The roots were brushed free of loose soil and organic matter, but were not washed or rinsed. Total collection time was about 15 min, and samples (ca. 2 g fresh weight) were then immediately placed in a respiration cuvette attached to an infra-red gas analyzer (IRGA, CIRAS-I portable gas analyzer, PP Systems, Haverhill, Mass.). Root samples typically consisted of five to seven excised root mats, each of which was comprised of an intact network of root segments containing primarily first, second and third order roots. During excision, roots were only damaged at the locations where the intact root networks were detached (i.e. five to seven locations per sample). Detailed examinations of similar root mats suggest that first order roots contributed about 50% of the root length sampled and second order roots contributed about 25% (Pregitzer et al. 2002). One or two samples were analyzed from each plot at a site.

The IRGA and cuvette were configured in an open system, with respiration rate determined by the difference in the amounts of CO_2 entering and leaving the cuvette. Steady respiration rates were achieved within 15 to 20 min after placing a sample in the cuvette. The input $[CO_2]$ for the cuvette was maintained at 1,000 µmol/mol, in order to approximate soil $[CO_2]$. The base of the aluminum respiration cuvette was 5 cm diameter, with an internal chamber for roots of 76 cm^3. Beneath the respiration chamber was a solid aluminum plug 12 cm in length. The entire 17 cm long aluminum base was inserted into the soil and acted as a heat sink, allowing the roots inside to be maintained at ambient soil temperature during the measurement period (verified by comparing temperatures measured by a thermistor inside the cuvette, in contact with the root sample, to soil temperatures adjacent to the cuvette). Following respiration measurements, root samples were placed in coolers, or frozen, until they could be returned to the laboratory for cleaning of any adhering soil and organic debris (≤5% of sample mass), determination of dry weights, and N analysis. Microbial respiration in the adhering soil and organic debris would have been measured as root respiration, but rates of microbial respiration per gram of forest soil material (Zak et al. 1999) are often orders of magnitude less than those we measured per gram of root tissue. Thus the contribution of these materials to measured root respiration rates should be much less than 5% of the reported values.

The 1998 field respiration measurements were conducted shortly after N fertilization treatments had begun, so the possible effects of N additions on root N concentration and root respiration rate were tested for using a two-factor (study site×fertilizer) analysis of variance for root N concentration and a two-factor analysis of covariance (study site×fertilizer, with temperature as a covariate) for the natural log of root respiration. Non-linear regression was used to examine the combined effects of root N concentration and temperature on field-measured rates of root respiration across the study sites.

Root respiration rates of tree species may, in some cases, be affected by the $[CO_2]$ at which measurements are made (Qi et al. 1994; Burton et al. 1997), with higher $[CO_2]$ resulting in lower respiration rates. However, recent reports suggest that this CO_2 effect does not exist for roots of many species (Bouma et al. 1997a, b; Bryla et al. 2001; Burton and Pregitzer 2002). To avoid potentially confounding our results, we measured root respiration in the field using the same measurement $[CO_2]$ for all sites. The value chosen (1,000 µl l^{-1}) is just slightly lower than the $[CO_2]$ typically found near the soil surface where our root samples were taken (1,200 µl l^{-1} in Burton et al. 1997; 1,350 µl l^{-1} in Yavitt et al. 1995; 1,023 – 2,152 µl l^{-1} in Fernandez et al. 1993). We did test a subsample of our field root respiration samples for a possible $[CO_2]$ effect by determining respiration rates at both 350 and 1,000 µl l^{-1}, and found no effect of $[CO_2]$ on field root respiration measurements over that concentration range (Burton and Pregitzer 2002).

In our laboratory experiments, the $[CO_2]$ within the cuvettes during the measurement period ranged from approximately 3,000 to 24,000 µl l^{-1}. These estimates are based on the assumption that increases in $[CO_2]$ are approximately equal to measured decreases in $[O_2]$. The range in $[CO_2]$ is a result of differences among sites and temperatures in respiration rates. In all cases, these $[CO_2]$s are in a range where $[CO_2]$ appears to have only a small affect on root respiration rates (Burton et al. 1997; Qi et al. 1994), so we feel that the patterns we measured in our laboratory studies are real. If high measurement $[CO_2]$ did slightly reduce respiration rates, then the actual differences among sites and temperatures would be slightly greater than we report, since it is the sites and temperatures with the highest respiration rates that generated the greatest $[CO_2]$ within the cuvette and would be most inhibited.

Results

Laboratory root respiration measurements

Significant differences existed among the study sites in respiration rates (Tables 2, 3), with patterns among sites in root respiration rate at a given temperature corresponding to differences among sites in fine root N concentration (Fig. 2). At the site level, mean root respiration rates were highly correlated with mean root N concentration at each temperature. The strongest relationship occurred at 18°C (Fig. 3), but the relationships at 6 and 24°C were also highly significant:

$$\begin{aligned} &6°C: R_{O2} = -0.449 + 0.147\,N \quad (r^2 = 0.81,\ P < 0.001) \\ &18°C: R_{O2} = -0.878 + 0.424\,N \quad (r^2 = 0.91,\ P < 0.001) \\ &24°C: R_{O2} = -2.418 + 0.829\,N \quad (r^2 = 0.82,\ P < 0.001) \end{aligned} \tag{1}$$

where R_{O2} is fine root respiration as O_2 consumption in nmol O_2 g^{-1} s^{-1} and N is fine root nitrogen concentration in g kg^{-1}.

When all temperatures were combined, a predictive relationship with respiration rate linearly related to N and exponentially related to temperature explained nearly 90% of the variation in the overall data set:

$$R_{O2} = (-0.185 + 0.083\,N)\, e^{0.092\,T} \quad (R^2 = 0.88,\ P < 0.001) \tag{2}$$

where T is temperature in °C. Temperature alone explained slightly more than half of the variability in the data set (r^2=0.58), with root N concentration explaining much of the remaining variation in root respiration rates.

Although N concentration explained a large proportion of the differences among sites in mean respiration rate (Figs. 2, 3), it did not fully account for the site-to-site variation observed. Analysis of covariance indicated some re-

Table 2 Regression coefficients and Q_{10} values for root respiration, as O_2 consumption (nmol O_2 g^{-1} s^{-1}), over the temperature range of 6–24°C. Slopes and intercepts are for individual site regressions between the natural logarithm of respiration and temperature

Study site	Slope	Intercept	Q_{10}	r^2	Significance[a] without root N as covariate (model 1)	Significance[a] with root N as covariate (model 2)
Populus balsamifera – Bonanza Creek LTER, Alaska	0.088	0.132	2.4	0.93	b	a
Picea glauca – Bonanza Creek LTER, Alaska	0.107	–0.439	2.9	0.95	cd	a
Acer saccharum – Upper Peninsula, Michigan	0.100	–0.152	2.7	0.95	bc	ab
Pinus resinosa plantation – Upper Peninsula, Michigan	0.111	–0.651	3.0	0.90	de	ab
Mixed hardwoods – Coweeta LTER, North Carolina	0.088	–0.056	2.4	0.86	bcd	a
Quercus-Carya – Coweeta LTER, North Carolina	0.113	–0.581	3.1	0.94	bcdef	abc
Liriodendron tulipifera – Coweeta LTER, North Carolina	0.096	0.252	2.6	0.95	a	ab
Pinus edulis – Sevilleta LTER, New Mexico	0.097	–0.792	2.6	0.92	g	c
Juniperus monosperma – Sevilleta LTER, New Mexico	0.089	–1.071	2.4	0.94	h	d
Mixed *Quercus* – Georgia	0.088	–0.419	2.4	0.89	efg	bc
Pinus elliottii plantation – northeastern Florida	0.092	–0.471	2.5	0.96	ef	ab
All gymnosperms			2.7 (0.3)[b]			
All angiosperms			2.6 (0.3)			
All ectomycorrhizal species			2.7 (0.3)			
All arbuscular mycorrhizal species			2.6 (0.1)			

[a] Sites with different letters in the significance columns have regression lines which differ in elevation at $P<0.05$
[b] Values are the arithmetic mean of the Q_{10} values listed above for all species within the group, with standard deviation in parentheses

maining differences among sites after adjusting for the effects of N. Lower respiration rates per unit N occurred at the *Juniperus monosperma* and *Pinus edulis* sites in New Mexico and the mixed *Quercus* site in Georgia (Table 2).

There also was variation within sites in laboratory measured root respiration rates. In contrast to the between-site variation, much of the within-site variation could not be accounted for by root N concentration. At a given temperature, root respiration rates for individual samples within sites were only occasionally correlated with root N concentration (Table 4).

A specific contrast between gymnosperms and angiosperms in respiration rate indicated that the gymnosperms in this study had lower fine root respiration rates ($P<0.001$). These differences were largely explained by lower fine root N concentrations in the gymnosperms; when N concentration was used as a covariate, root respiration rates were not significantly different among gymnosperms and angiosperms ($P=0.214$).

Root respiration rates increased exponentially with temperature at all sites (Fig. 2, Table 2). The Q_{10} for root respiration ranged from 2.4 to 3.1, but there were no significant differences among sites in Q_{10}, as indicated the lack of a site×temperature interaction in the overall regression model (Table 3). The average Q_{10}s for gymnosperms and angiosperms were almost identical, as were the average Q_{10}s for ectomycorrhizal species and arbuscular mycorrhizal species (Table 2).

Field root respiration measurements

Fertilizer treatments had been initiated at the study sites prior to the 1998 field root respiration measurements, but only a portion (25 kg N ha^{-1}) of the annual increment had been applied and this initial amount of fertilizer N did not alter either root N concentration or field root respiration rates at the sites (Table 5).

Table 3 Analysis of variance and analysis of covariance of the effects of temperature, study site and fine root N concentration on fine root respiration rates measured in the laboratory as O_2 consumption

Source	*df*	MS	*F* ratio	*P*
Analysis of variance (model 1)				
Study site	10	2.66	57.28	<0.001
Temperature	2	40.68	876.50	<0.001
Study site×Temperature	20	0.06	1.19	0.274
Error	142	0.05		
Analysis of covariance with N as covariate (model 2)				
Study site	10	0.68	16.92	<0.001
Temperature	2	40.16	1,003.81	<0.001
Study site×Temperature	20	0.05	1.30	0.187
Nitrogen concentration	1	0.95	23.71	<0.001
Error	141	0.04		

Soil temperatures at which root respiration were measured in the field ranged from 8°C in the Alaska *Populus balsamifera* stand to 27°C in the Florida *Pinus edulis* plantation (Fig. 4). Root respiration rates measured in the field (as CO_2 production) represented the combined effects of these widely varying soil temperatures and the N concentrations of the fine root samples (Fig. 4). At the New Mexico, Florida and Georgia sites, lower inherent rates of root respiration associated with low root N concentrations were at least partially offset by higher growing season soil temperatures. Together, temperature and root N concentration explained 60% of the variation in the field root respiration data set:

$$R_{O2}=(-0.185+0.083\,N)\,e^{0.092\,T}\ (R^2=0.88,\ P<0.001) \quad (3)$$

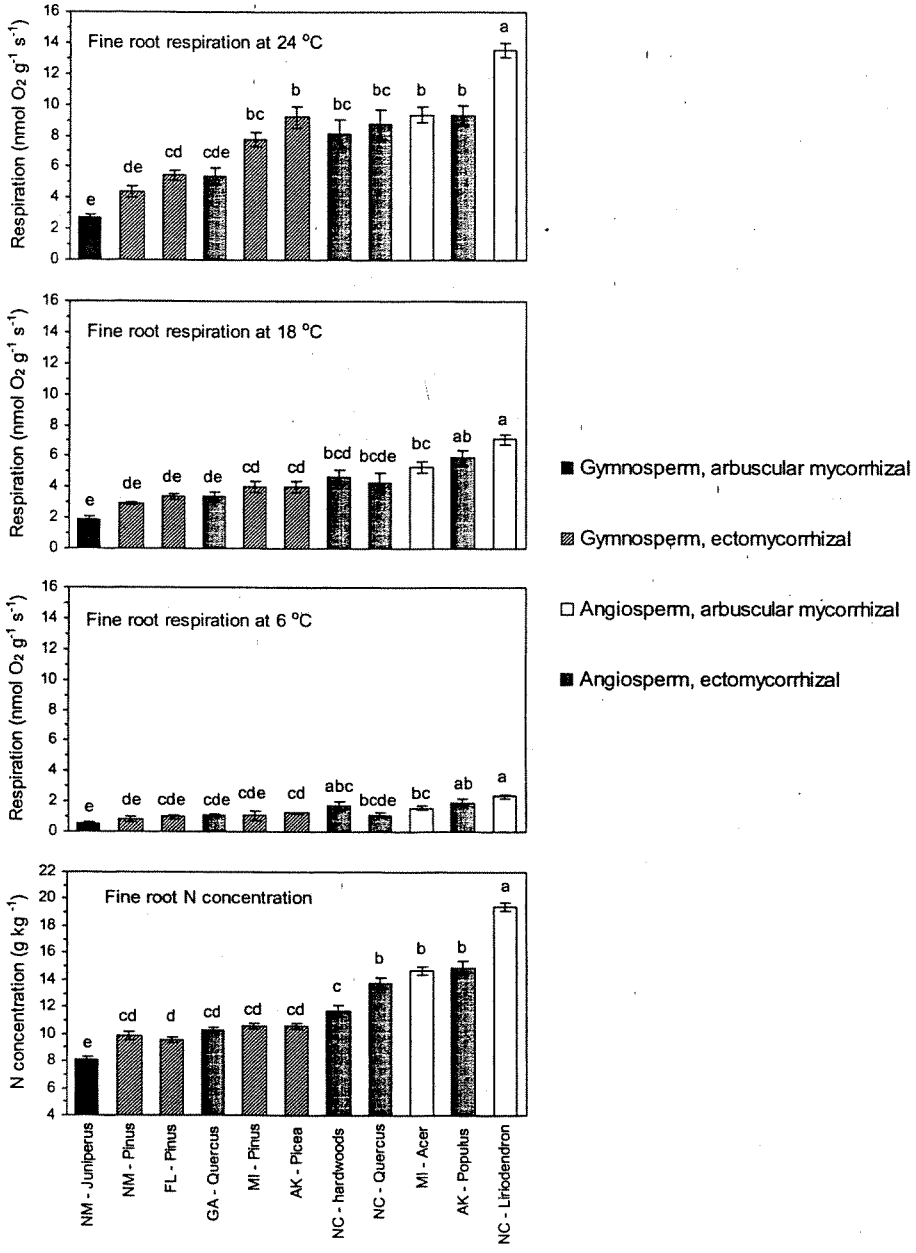


Fig. 2 Fine root respiration rates at 6, 18 and 24°C measured in the laboratory as O_2 consumption and fine root N concentrations. *Error bars* indicate one standard error of the mean. Site location abbreviations are: *NM* New Mexico, *FL* Florida, *GA* Georgia, *AK* Alaska, *MI* Michigan, and *NC* North Carolina. Bars without common letters indicate sites that differ significantly at $P<0.05$ (Tukey's HSD test)

Root N concentration was the more important of the two factors, explaining 43% of the variation.

When the Q_{10} values for the individual sites (Table 2) were used to adjust the field respiration rates to a common temperature (18°C), the resulting pattern among sites in root respiration (Fig. 4) generally corresponded to the pattern among sites in fine root N concentration (Fig. 2). At the site level, root N concentration explained 73% of the variation among sites in mean respiration rate adjusted to a common temperature (18°C). Unlike the laboratory experiments, much of the within-site variation in field respiration rates could be related to root N concentration (Table 4).

Field respiration rates as CO_2 production agreed well with laboratory respiration rates as O_2 consumption. The individual site equations in Table 2 (derived from the laboratory measurements) were used to estimate the rate of root respiration, as O_2 consumption, that would occur at the 1998 field soil temperatures. Across sites, the ratio of O_2 consumption to CO_2 production was slightly, but not significantly, less than 1:1 (Fig. 5). Field measurements had the advantage of immediate determination of respiration at ambient soil temperature, while laboratory measurements allowed respiration to be determined across a range of temperatures at one time, eliminating the need to make numerous visits per year to each field location. The longer time between sample collection and analysis for the laboratory samples may have contributed to the tendency for laboratory O_2 consumption rates at a given temperature to be lower than field CO_2 production rates, despite the fact that respiration rates expressed as O_2 consumption often are slightly higher than rates ex-

Table 4 Within-site correlations between root respiration rate and root N concentration and the coefficient of variation (CV) for root N concentration for the laboratory and field experiments. Data for the laboratory experiments are grouped by measurement temperature. Site location abbreviations are as given for Fig. 2. Significant correlations ($P \leq 0.10$) are indicated in boldface type

Study Site	Laboratory data[a] 6°C			Laboratory data[a] 18°C			Laboratory data[a] 24°C			Field data			
	r	*P*	CV	*r*	*P*	CV	*r*	*P*	CV	*r*	*P*	CV	*n*
Populus balsamifera, AK	0.39	0.45	0.13	**0.93**	**0.01**	0.15	**0.73**	**0.10**	0.11	**0.69**	**0.01**	0.10	12
Picea glauca, AK	–0.05	0.93	0.06	**0.90**	**0.02**	0.05	0.40	0.43	0.11	**0.75**	**<0.01**	0.19	12
Acer saccharum, MI	–0.24	0.64	0.10	0.48	0.33	0.09	0.22	0.67	0.03	–0.29	0.58	0.07	6
Pinus resinosa, MI	0.58	0.23	0.11	0.26	0.62	0.04	0.22	0.67	0.09	**0.88**	**<0.01**	0.11	7
Mixed hardwoods, NC	–0.08	0.95	0.09	0.87	0.33	0.19	0.77	0.44	0.27	**0.73**	**0.10**	0.22	6
Quercus-Carya, NC	ND[b]	ND	ND	ND	ND	ND	ND	ND	ND	–0.41	0.73	0.07	3
Liriodendron tulipifera, NC	0.52	0.29	0.09	**0.75**	**0.08**	0.13	0.45	0.37	0.07	**0.79**	**0.02**	0.10	12
Pinus edulis, NM	0.63	0.25	0.12	–0.18	0.74	0.07	0.65	0.16	0.20	**0.58**	**0.05**	0.18	12
Juniperus monosperma, NM	0.65	0.23	0.09	–0.30	0.57	0.03	0.39	0.45	0.11	**0.79**	**<0.01**	0.15	12
Mixed *Quercus*, GA	0.17	0.75	0.09	–0.45	0.38	0.07	0.57	0.24	0.06	**0.65**	**0.02**	0.16	12
Pinus elliottii, FL	0.18	0.74	0.16	–0.21	0.69	0.09	–0.35	0.50	0.05	**0.56**	**0.10**	0.26	12

[a] Sample size for laboratory data was six per temperature, except for the mixed hardwoods (n=3) and *Quercus-Carya* (n=2) sites
[b] Not determined due to sample size of two

Table 5 Analysis of variance for the effects of fertilizer addition on root N concentration and analysis of covariance for the effects of fertilizer addition on root respiration rates measured in the field at ambient soil temperature. The natural log of root respiration was the dependent variable in the analysis of covariance, with temperature as a covariate

Source	*df*	MS	*F* ratio	*P*
Analysis of variance for effects of fertilizer on root N concentration				
Study site	8	150.87	36.74	<0.001
Fertilizer	1	8.91	2.17	0.145
Study site×Fertilizer	8	2.81	0.68	0.704
Error	73	4.11		
Analysis of covariance for effects of fertilizer on root respiration, temperature as covariate				
Study site	8	2.303	25.89	<0.001
Fertilizer	1	0.003	0.03	0.861
Study site×Fertilizer	8	0.158	1.78	0.096
Temperature	1	0.452	5.09	0.027
Error	72	0.089		

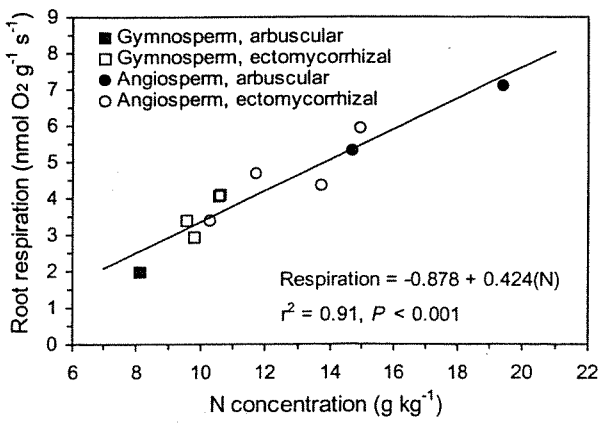


Fig. 3 Relationship between fine root N concentration and fine root respiration at 18°C measured in the laboratory as O_2 consumption for roots from North American forest types. Values are site means for respiration rate and N concentration for the forest sites listed in Table 1.

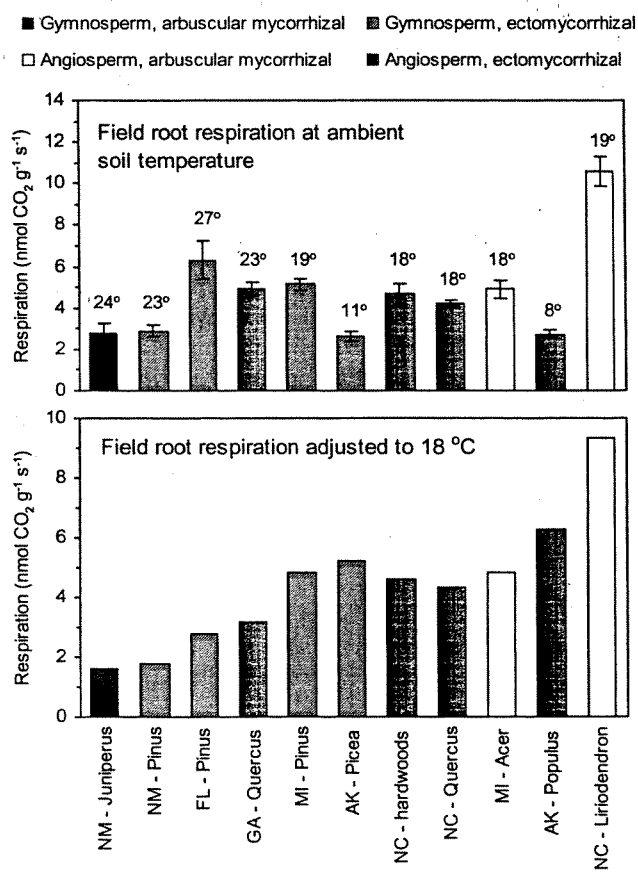


Fig. 4 Root respiration rates measured in the field as CO_2 production at ambient soil temperatures (*upper plate*) and respiration rates adjusted to a common temperature of 18°C (*lower plate*) using the Q_{10} values in Table 2. Error bars indicate one standard error of the mean. Soil temperatures at the time of respiration measurement are indicated above the bars in the upper plate of the figure. Site location abbreviations are as given for Fig. 2

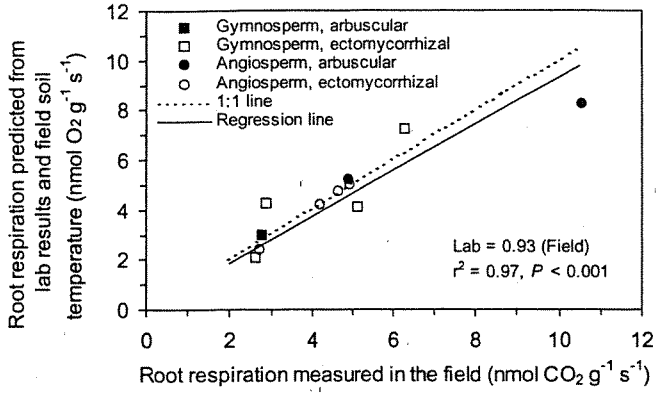


Fig. 5 Relationship between root respiration measured in the field as CO_2 production at ambient soil temperature and root respiration as O_2 consumption predicted for the same temperature using the laboratory-derived individual site relationships in Table 2

pressed as CO_2 production (Edwards and Harris 1977; Carpenter and Mitchell 1980; Burton et al. 1996).

Discussion

The relationship we observed between root respiration and root N concentration was not unexpected, as it is has been shown that a linear relationship often exists between N concentration and respiration for plant tissues (Ryan 1991, 1995; Reich et al. 1996; Maier et al. 1998), including the roots of trees (Burton et al. 1996, 1998; Zogg et al. 1996; Pregitzer et al. 1998; Reich et al. 1998b). What was surprising is how much of the variation among the forest sites in fine root respiration was explained by site-to-site differences in fine root N concentration (Fig. 3), despite the large differences among sites in vegetation, climate, and edaphic conditions. In data from our laboratory experiments, the use of root N as a covariate in analysis of variance removed almost all the between-site differences in respiration rate at a given temperature (Table 2) and eliminated significant differences between the gymnosperm and angiosperm groups in root respiration rate. Only a few sites had root respiration rates lower than would be predicted from their root N concentrations: *Pinus edulis* and *Juniperus monosperma* in New Mexico, and, to a lesser degree, mixed *Quercus* in Georgia (Table 2). These sites regularly experience warm, dry soil conditions during the growing season. Lower rates of respiration per unit N at these sites may have been a consequence of dry soil conditions during the time of sampling, as it is known that drought can cause reductions in root respiration (Gansert 1994; Bryla et al. 1997, 2001; Burton et al. 1998).

In the field measurements, we often found a strong within-site relationship between root respiration and N concentration, while in the laboratory experiments, we typically did not. The collection method for the laboratory experiments produced samples within a site that did not vary as much in N concentration as those used in the field experiments (see coefficients of variation for N in Table 4). Roots used in the laboratory experiments were composited to a greater degree than those used for field measurements, which could have contributed to lower within-site variation in root N concentrations for the laboratory experiments. Also, roots used in the laboratory experiments were rinsed while roots used in the field experiments were not. The laboratory roots tended to have slightly lower N concentrations (circa. 10%) than the field roots, thus leaching of N during rinsing may also have been a factor. The greater range of within-site sample N concentrations and higher number of samples per site in the field experiment enabled us to detect statistically significant within-site relationships between root respiration and N concentration that were not apparent in the laboratory experiments. Pregitzer et al. (1998) previously noted that relationships between N concentration and root respiration became apparent only when a sufficiently large range of N concentrations was examined. Root age, nutrients other than N, and soil moisture availability may account for some of the remaining differences in root respiration, both within and among sites, that were not explained by N concentration.

In our laboratory experiments, species from cool sites (Alaska and Michigan) had root N concentrations and respiration rates at a given temperature that were as high or higher than those for species from warm sites (New Mexico, Florida, and Georgia) (Fig. 2). Higher root N concentration at our cooler sites would be consistent with an adaptive strategy in which the work of the root system is accomplished by greater amounts of proteins and amino acids (i.e. higher N concentration) performing their functions more slowly due to cooler ambient temperatures. Reich et al. (1996) similarly suggested that high needle N concentrations in *Pinus sylvestris* populations from cold environments might be an adaptive feature that allowed for greater total metabolic activity and growth rate under the low temperatures of their native environment. The root respiration rates we measured in the field (Fig. 4), which represent the combined effects of ambient soil temperature and root N, indicate that high growing season soil temperatures at the warmest sites (New Mexico, Florida, Georgia) did not result in much larger rates of root respiration than at the cooler sites, due to the lower root N at the warm sites. Across all of our sites, however, root N and mean annual temperature were not significantly correlated, due largely to very high root N concentrations at the intermediate temperature *Liriodendron tulipifera* site in North Carolina. Thus growing season soil temperature is, at best, only one of several factors which interact to determine root N concentration and respiration rate at a given temperature.

The response of root respiration to increasing temperature was quite similar at all sites, despite the wide variety of tree species, mycorrhizal associations, climates, and edaphic conditions studied. The range among sites in Q_{10} in this study (2.4–3.1) is narrower than the range in Q_{10} values reported in the literature for roots of other common North American tree species (2.7, Cox 1975;

1.9–2.1, Cropper and Gholz 1991; 1.5–3.0, Lawrence and Oechel 1983; 2.0, Sowell and Spomer 1986; 2.1, Zogg et al. 1996; 2.7, Burton et al. 1996; 2.0, Ryan et al. 1996). A possible factor contributing to the smaller range in Q_{10}s in our study may be the use of a variety of different experimental designs and temperature ranges by the various other investigators. It is known that Q_{10} can depend on the temperature range over which it is determined (Schleser 1982; Lawrence and Oechel 1983; Ryan 1991), with higher values for Q_{10} occurring when cold temperature ranges are examined. Our use of the same range of temperatures for all species studied was intended to avoid this potential problem and facilitate between-species comparisons. Our Q_{10} values for *Liriodendron tulipifera* and *Populus balsamifera* (2.6 and 2.4, respectively) are nearly identical to those measured over a similar temperature range (5–25°C) by Cox (1975) (2.7 for *Liriodendron tulipifera*) and Lawrence and Oechel (1983) (2.35 for *Populus balsamifera*).

Overall, our laboratory results suggest that the rate of increase in fine root respiration with temperature is generally similar for many tree species. However, the applicability of these laboratory results for predicting root respiration in the field must be assessed. If root respiration in the field acclimates to changing soil temperatures during the year, then the Q_{10} determined from a temperature series in the laboratory will not accurately predict root respiration rates in the field over the entire range of soil temperatures encountered during a growing season or year. Our field respiration rates corresponded quite well to respiration rates predicted for the same temperatures using our laboratory-derived respiration/temperature relationships (Fig. 5), but the 1997 laboratory experiments and 1998 field experiments were both performed during the summer months, and soil temperatures at each site were fairly similar between years. Thus agreement between the 1997 and 1998 results does not preclude the possibility that root respiration acclimates to temperature in the field. It only indicates that our laboratory results are valid for soil temperatures typical during the warmer, middle portion of the growing season.

To validate our laboratory estimates for colder temperatures, we would need additional field measurements during times when soil temperatures were colder. Time and travel limitations precluded the possibility of performing such field experiments for all of the species studied, but in research conducted in Michigan, we have measured root respiration rates in the field over the course of two entire growing seasons (April to November) for *Pinus resinosa* and *Acer saccharum*. In those experiments, we found that Q_{10} values for the two species were the same to slightly lower than those measured in the laboratory in this study (3.0 v 3.0 for *Pinus resinosa* and 2.4 vs 2.7 for *Acer saccharum*) (A.J. Burton, unpublished data). This would suggest that little, if any, detectable temperature acclimation occurs within a growing season for root respiration of these two species in the field and that the use of laboratory temperature series for determining the response of root respiration to temperature is reasonably accurate. For *Picea glauca*, another of the species we studied, Weger and Guy (1991) found no evidence that root respiration acclimated to temperature. Similarly, no evidence of temperature acclimation has been found for root respiration in *Picea engelmannii* or *Abies lasiocarpa* (Sowell and Spomer 1986). However, in seedlings grown at a elevated constant temperatures (Bryla et al. 1997; Tjoelker et al. 1999) and young citrus trees grown at elevated field temperatures (Bryla et al. 2001), root respiration has acclimated to temperature. This suggests that species may differ in their ability to acclimate to temperature. It is also possible that acclimation only occurs above a certain temperature threshold (Bryla et al. 2001) or that near-constant temperatures are needed to cause measurable acclimation in tree species, and that the natural diurnal and day-to-day soil temperature fluctuations that occur in temperate and boreal forests might prevent acclimation from occurring to any large degree in the field. Additional research is needed to determine whether significant acclimation does occur under field conditions for roots of some trees species. Such research is especially relevant today, since acclimation could significantly alter the way in which root respiration might respond to global warming.

Root N concentration and temperature explained most of the variability observed in root respiration in both the laboratory and the field. Remaining unexplained variation in respiration occurred primarily within study sites and might be related to a variety of factors, such as root age, the concentrations of nutrients other than N, or drought. The effects of temperature and N concentration on root respiration were generally similar across species, despite large differences in climatic and edaphic conditions and regardless of whether roots were from angiosperms or gymnosperms, or dominated by ectomycorrhizae or arbuscular mycorrhizae. For root respiration in tree species, it appears that basic, broad-scale relationships with temperature and nitrogen concentration exist across species and biomes.

Acknowledgements The authors thank Rodney Will, Jack McFarland, Lee Ogden, Trish Burton, Neeti Bathala, Jennifer Lansing, Cara Cario, Kendra Calhoun, Christina Doljanin, and Shannon Brown for their assistance in the field and lab, and Bob Parmenter, Jim Vose and Tom Fox for their logistical support. We also acknowledge the Coweeta, Bonanza Creek, and Sevilleta LTERs, Mead Corporation, Rayonier Corporation, Container Corporation of America, Champion International, the U.S.D.A. Forest Service, and the U.S. Fish and Wildlife Service for providing study site locations and field laboratories. This research was funded by the U.S. National Science Foundation Ecosystem Studies Program (collaborative awards DEB 9615509, 9616537, 9616538, and 9996211; and grant DBI 9413407).

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