1999

Below-Ground respiratory Responses of Sugar Maple and Red Maple Saplings to Atmospheric CO_2 Enrichment and Elevated Air Temperature

Nelson Edwards
Oak Ridge National Laboratory, Oak Ridge, TN

Richard Norby
Oak Ridge National Laboratory, Oak Ridge, TN

Plant and Soil **206:** 85–97, 1999.

Below-ground respiratory responses of sugar maple and red maple saplings to atmospheric CO_2 enrichment and elevated air temperature

Nelson T. Edwards* and Richard J. Norby
Oak Ridge National Laboratory, Oak Ridge, TN 37831-6422, USA

Received 11 March 1998. Accepted in revised form 6 October 1998

Key words: Acer rubrum, *Acer saccharum*, CO_2 × temperature interactions, open-top chamber, root respiration

Abstract

The research described in this paper represents a part of a much broader research project with the general objective of describing the effects of elevated [CO_2] and temperature on tree growth, physiological processes, and ecosystem-level processes. The specific objective of this research was to examine the below-ground respiratory responses of sugar maple *(Acer saccharum* Marsh.) and red maple (*Acer rubrum* L.) seedlings to elevated atmospheric [CO_2] and temperature. Red maple and sugar maple seedlings were planted in the ground in each of 12 open-top chambers and exposed from 1994 through 1997 to ambient air or air enriched with 30 Pa CO_2, in combination with ambient or elevated (+4 °C) air temperatures. Carbon dioxide efflux was measured around the base of the seedlings and from root-exclusion zones at intervals during 1995 and 1996 and early 1997. The CO_2 efflux rates averaged 0.4 μmol CO_2 m^{-2} s^{-1} in the root-exclusion zones and 0.75 μmol CO_2 m^{-2} s^{-1} around the base of the seedlings. Mineral soil respiration in root-exclusion zones averaged 12% higher in the high temperature treatments than at ambient temperature, but was not affected by CO_2 treatments. The fraction of total efflux attributable to root + rhizosphere respiration ranged from 14 to 61% in measurements made around red maple plants, and from 35 to 62% around sugar maple plants. Root respiration rates ranged from 0 to 0.94 μmol CO_2 s^{-1} m^{-2} of soil surface in red maple and from 0 to 1.02 in sugar maple. In both 1995 and 1996 root respiration rates of red maple were highest in high-CO_2 treatments and lowest in high temperature treatments. Specific red maple root respiration rates of excised roots from near the soil surface in 1996 were also highest under CO_2 enrichment and lowest in high temperature treatments. In sugar maple the highest rates of CO_2 efflux were from around the base of plants exposed to both high temperature and high-CO_2, even though specific respiration rates were lowest for this species under the high temperature and CO_2 enrichment regime. In both species, patterns of response to treatments were similar in root respiration and root mass, indicating that the root respiration responses were due in part to differences in root mass. The results underscore the need for separating the processes occurring in the roots from those in the forest floor and mineral soil in order to increase our understanding of the effects of global climate change on carbon sequestration and cycling in the below-ground systems of forests.

Introduction

Responses of ecosystems to increases in atmospheric [CO_2] and increases in temperature require greater understanding if we are to accurately evaluate the impacts of current and impending global climate change. Forests in particular provide a critical feedback between the terrestrial carbon cycle and the climate system (Post et al., 1990). Increased temperature and elevated atmospheric [CO_2] are generally thought to have opposite effects on carbon storage in natural ecosystems (i.e. elevated CO_2 increases productivity and carbon sequestration while increased temperature will enhance decomposition rates and loss of carbon from soil [Kirschbaum, 1993; Raich and Schlesinger, 1992]). There are many uncertainties, however, about the magnitude and degree of interactions of these responses, especially in forest ecosystems (Vogt et al.,

* FAX No: 423 576 9939. E-mail: nte@ornl.gov

1996). Most studies of tree responses to atmospheric CO_2 enrichment have emphasized those responses that occur above the ground. This is due primarily to the difficulty of examining the below-ground system in ways that minimize disturbance and associated responses and to the fact that, in trees especially, the aboveground portions are of greater economic interest. Nevertheless, researchers now realize that an understanding of the below-ground responses of plants and soil biota to climate change are crucial to better understanding total ecosystem responses (Wullschleger et al., 1994). Also, the potential role of roots as carbon storage organs to help explain the 'missing carbon' in global climate models is receiving more attention in recent years (Norby 1994). However, below-ground respiration (an excellent integrator of below-ground processes and an essential parameter in understanding ecosystem carbon cycles) continues to be difficult to study and often even more difficult to interpret given the uncertainties associated with disturbance, measurement techniques, and quantification of CO_2 from different below-ground components. The importance of examining factors that may interact with elevated CO_2 such as drought (Tschaplinski et al., 1995) and nutrient availability (Curtis et al., 1990; BassiriRad et al., 1996; Norby et al., 1986, and others; Tingey et al. 1996) is recognized and continues to be included in many studies. Temperature is also important as an interacting variable with CO_2 because temperature is predicted to increase globally as atmospheric [CO_2] increases. The objectives of this study were: (1) to examine the below-ground respiration responses in a stand of maple seedlings growing in open-top chambers (modified for temperature control) to elevated CO_2 and temperature; and (2) to quantify differences in the root respiratory responses of red maple (*Acer rubrum* L.) and sugar maple (*Acer saccharum* Marsh.). The experiment was designed to address the hypothesis that below-ground respiration will increase in response to both enriched atmospheric CO_2 and to elevated soil temperatures, and that these responses will be additive.

Methods

Field study site and experimental setup

The research was conducted in open-top chambers at the Oak Ridge National Laboratory's Global Change Field Research Facility on the National Environmental Research Park, Oak Ridge, TN, USA. Twelve open-top chambers (Rogers et al., 1983) were constructed at the facility on soils classified as Captina silt loam (fine-silty, siliceous, mesic Typic Fragiudult) with moderate-to-medium granular structure and medium internal drainage. The chambers were 3.0 m in diameter and 2.4 m high. An additional 1.2-m panel was installed at the beginning of the third growing season to accommodate the height growth of the seedlings. The chambers were modified to operate at either ambient temperature or 4 °C above ambient, in combination with ambient or elevated (+30 Pa) atmospheric CO_2 partial pressure (Norby et al. 1997). A randomized complete block design was used with four treatments [control (C),high-CO_2(HC), high temperature (HT), and high-CO_2 and temperature (HCHT)] in each of three blocks. The temperature and CO_2 control systems were operated 24 h d^{-1} during the growing season. Temperature was regulated with thermostatically-controlled evaporative coolers and electrical resistance heaters. The system was tested from May to December 1994. During this time ambient air temperature averaged 18.5 °C, ambient chamber temperature averaged 18.9 $\pm$ 0.6 °C, and elevated temperature chambers averaged 22.2 °C $\pm$0.9 °C. Differences in soil temperatures at 10 cm depth between ambient chambers and elevated temperature chambers averaged 1.2 °C. Over the 1994 growing season the daytime (0600–1800 h) CO_2 enrichment in elevated CO_2 chambers ($\pm$ SD) was 30.1 $\pm$ 7.2 Pa in ambient temperature chambers and 30.2 $\pm$ 7.8 Pa in elevated temperature chambers. The comparable enrichment values over all 24h were $\approx$ 2 Pa higher. Similar temperature and CO_2 trends were recorded during this study which began in mid-February 1995 and continued through autumn 1997.

Ten bare root 1-y-old seedlings each of red maple (*Acer rubrum* L.) and sugar maple (*Acer saccharum* Marsh.) were planted in the ground in each of the 12 chambers in February 1994. Seedlings that did not survive the first year were replaced in late winter of 1995.

Measurements of soil and root respiration in situ

Two root-exclusions zones were established in each chamber with 24 dm^3 bottomless plastic pots. Round holes were dug slightly larger in diameter than the bottomless pots. The pots were then inserted into the holes so that about 30 cm of the pot extended below ground and the top rim of the pot extended about 4 cm above the soil surface. Soil was placed back in the pot in reverse order of removal. Left over soil was placed in the pots as the soil compacted during the following month. Soil cores taken from each root-exclusion zone during 1996 confirmed the apparent absence of roots in the exclusion zones; however, when all of the soil in each exclusion zone was examined at the end of the study, nearly half of the exclusion zones were found to have roots growing in them, mainly around the inside edges of walls of the exclusion zones. The roots had grown into the exclusion zones from the bottom. Exclusion zones containing roots were found to have higher than average CO_2 efflux rates and these data were discarded.

All bare soil in the chambers was covered with synthetic mulch cloth to control weeds without restricting air or water and to prevent introducing exogenous organic carbon to the soil. The sides and tops of the open-top chambers were covered with 73% shade cloth to approximate the reduced light conditions under which maple saplings usually grow. Soil moisture was measured periodically in 1995 and 1996 at two positions in each chamber (0–23 cm depth) using a time domain reflectometer (TDR) following the procedure of Topp and Davis (1985). The TDR waveguides were permanently installed vertically to a depth of 23 cm. During one period in August 1997, after 3 weeks without rainfall, soil moisture was also determined with TDR rods temporarily inserted into the soil to a depth of 15 cm. Soil moisture was gravimetrically determined at 0–4 cm depth on two occasions, once in July 1997 one week after a saturating rainfall event and again in August following three weeks without rainfall. Gravimetrically determined moisture values were converted to volumetric values (bulk density = 1.5).

Below-ground respiration was measured in the root-exclusion zones and around the base of four saplings of each species in each chamber. Selection of saplings for respiration measurements was based on logistics within the open-top chambers (i.e. saplings selected were positioned away from monitoring devices). Measurements were made at about monthly intervals throughout the 1995 and 1996 growing seasons and once during dormancy in February 1997 with a modified Li-Cor 6250 infrared gas analyzer (Li-Cor, Lincoln, Nebraska). The modification involved changing the Li-Cor software to allow us to measure soil temperature with a soil temperature probe while using the leaf temperature channel. We used a closed loop system with air pumped from the analyzer through an aluminum chamber, inserted over the soil surface, and back to the analyzer. The chamber was equipped with an air-delivery manifold on one side and an air-return manifold on the other to provide proper mixing of the air without the use of a fan. The use of a fan in chambers designed to measure CO_2 efflux from soil has been shown to disturb the boundary layer and cause unusually high rates of CO_2 efflux (Hanson et al., 1993). Air flow rates to and from the chamber were equal indicating no difference in air pressure between the inside and outside of the chamber. The cylindrical shaped chamber is 8 cm deep and 25 cm in diameter with a 5 cm wide slot in one side to permit placement of the chamber around the base of seedlings. A 3 cm thick closed foam gasket placed between the chamber base and the soil and a 12 kg weight placed on top of the chamber prevented leakage between chamber air and outside air.

Six 20-s measurements were taken at the base of each seedling and on the surface of each root-exclusion zone. One set of three measurements was taken on one side of each seedling and exclusion zone and another set of three was taken 180° from the first set. Measurements were begun at the approximate CO_2 concentration existing in the open-top chamber at the time of measurement (i.e. 35–40 Pa in ambient chambers and 65–70 Pa in the CO_2 enriched chambers). The mulch cloth was left in place during the measurements. Measurements were made between about 900 h and 1500 h over a 3-d period (one block per day). Soil temperature at 10 cm depth was recorded during each respiration measurement. During a single set of measurements soil temperature would often vary as much as 5 °C or about five-fold greater than temperature treatment differences. Therefore, it was necessary to normalize each respiration rate to the mean temperature for each sample period. Even though this procedure allowed us to see only indirect temperature treatment effects on total CO_2 efflux from around the saplings, without Q_{10} normalization respiration responses to the CO_2 treatment could have been obscured. We would expect direct temperature treatment effects on below-ground res-

piration to be extremely small given that the soil in the high temperature chambers averaged only 1.2 °C higher than in the ambient temperature chambers.

The average CO_2 efflux rate from root-exclusion zones was subtracted from measurements made around the base of each sapling for an estimate of root respiration. Both root-exclusion zone rates and rates from around the base of saplings were normalized to the average soil temperature for the sample period using a Q_{10} of 2. Root respiration in this study includes (1) live root growth and maintenance respiration, (2) respiratory activity outside the root that might be directly influenced by the root (e.g. microbial metabolism of root exudates and mycorrhizal activity), and (3) dead root decomposition. A chamber mean total (roots plus soil) CO_2 efflux rate and a root respiration rate were calculated for each species per m^2 soil surface.

Roots immediately beneath half of the respiration chamber positions were excavated to a depth of 30 cm during the fall of 1997. A cylinder of soil having the same diameter as the respiration chambers and containing the stump of the seedling was removed with a shovel. Most of the roots were removed by hand by crumbling the soil away from the roots. Very fine roots were removed from the crumbled soil by placing it on a fine mesh screen and washing with a strong jet of warm water. Finally all roots were thoroughly washed, separated into stump, coarse (>1 mm dia.), and fine roots (<1 mm dia.), dried, and weighed. Root systems of 24 red maple and 24 sugar maple saplings (two of each species per open top chamber) were processed.

Respiration measurements on isolated root segments

Specific root respiration rates were determined on a single set of root samples (1 sample per species per open-top chamber) collected in early September 1997. A block of soil (13 cm × 6.5 cm × 4 cm deep) was removed from near the stem base of the saplings. All soil blocks were collected, covered with cloth to reduce moisture loss, then taken intact to an adjacent field laboratory. Roots were carefully removed by hand from each soil block, separated into coarse roots (1 to 5 mm dia.) and fine roots (< 1 mm dia.), and immediately placed in a metal respiration chamber (500 cm^3 volume). The chamber was sealed and respiration rates were measured in the closed system with the same CO_2 analyzer used for field measurements. Three 20 s measurements were made on each root sample. Measurements were performed over a 8 h period in a field laboratory where the temperature ranged from 17 and 27 °C. During the measurement period soil blocks not being measured were covered with cloth to reduce moisture loss. To reduce sampling bias, a set of samples representing each species and treatment were measured in sequence before measuring succeeding sets of the same species and treatment combinations. All root samples were later dried and weighed. The very small sample size of the fine roots (generally < 0.05 g) and thus the extremely low CO_2 efflux rates into a relatively large respiration chamber made these measurements unreliable and therefore the fine root specific root respiration data are not included here. Most (95%) of the root mass was in the coarse root fraction (< 0.2 g $sample^{-1}$) with an average diameter of about 2 mm. It was necessary to normalize all the respiration data to a constant temperature. Average respiration rates across treatments over a range of temperatures were plotted against temperature and from these a Q_{10} of 2 was determined for coarse roots. These Q_{10} values were then used to normalize all specific root respiration rates to 25 °C.

Data analysis

Chamber mean respiration values (n = 3) were analyzed with a split plot analysis of variance to test treatment differences, block effects, and species by treatment interactions. Since this test indicated species by treatment interactions on 7 of the 13 sample dates, a general two-way analysis of variance (ANOVA) was used on data from each individual species for each sample date and on annual mean values to test for CO_2 effect, temperature effect, and CO_2 × temperature interactions using CO_2 × block, temperature × block, and CO_2 × temperature x block as error terms. Root respiration rates by treatment were calculated by subtracting the pooled mean from root-exclusion zones across species and treatments from the mean of total CO_2 efflux in each treatment. Standard errors for root respiration incorporated both standard errors of total CO_2 efflux and CO_2 efflux from root-exclusion zones.

Results

Both total CO_2 efflux rates and calculated root respiration (averaged across all treatments and both species) fluctuated with the seasonal trend of soil temperature (Figure 1).

When separated by species and treatment and averaged for each growing season (Table 1) total CO_2 ef-

Table 1. Total CO_2 efflux rates by species and treatment for each sample date. Values are means ±1 standard error (n = 3). Numbers under CO_2 effects and temperature effects table headings are p values. Plus (+) indicates higher respiration rates and minus (–) indicates lower respiration rates compared to the control (C) treatment. An asterisk (*) after a date indicates dormant season. No significant treatment interactions were observed

Date	Species	CO_2 Efflux Rates by Treatment and Date (μmole CO_2 m^{-2} s^{-1})				CO_2 effect	Temperature effect
		C	HC	HT	HCHT		
5 June 95	Red Maple	0.79±0.13	0.89±0.15	0.69±0.10	0.98±0.20		
6 July 95		0.85±0.03	1.23±0.16	0.51±0.14	0.86±0.15	0.033 (+)	0.10 (–)
24 July 95		0.82±0.14	0.97±0.11	0.54±0.09	0.79±0.18		
8 Aug 95		0.69±0.08	0.82±0.09	0.48±0.07	0.56±0.08	0.10 (–)	
27 Sept 95		0.49±0.03	0.62±0.10	0.35±0.06	0.50±0.07		
3 Apr 96		0.37±0.13	0.77±0.11	0.26±0.05	0.54±0.03	0.031 (+)	
20 May 96		0.89±0.05	0.91±0.12	0.84±0.19	1.03±0.05		
12 June 96		0.52±0.05	0.66±0.39	0.52±0.10	0.66±0.23		
1 July 96		0.88±0.09	1.23±0.33	0.79±0.11	1.19±0.24		
23 July 96		0.85±0.14	1.04±0.02	0.82±0.08	1.44±0.13	0.044 (+)	
10 Sept 96		0.94±0.21	1.10±0.17	0.82±0.09	0.99±0.33		
9 Oct96*		0.66±0.06	0.95±0.10	0.53±0.10	0.73±0.02 0.01 (+)	0.062 (–)	
19 Feb97*		0.31±0.03	0.30±0.04	0.27±0.03	0.45±0.08		
ANNUAL AVERAGES							
1995		0.73±0.09	0.91±0.12	0.51±0.09	0.74±0.15		0.057 (–)
1996		0.73±0.12	0.95±0.16	0.66±0.11	0.94±0.18	0.012 (+)	0.022 (–)
5 June 95	Sugar Maple	0.78±0.02	0.77±0.12	1.00±0.05	0.89±0.09		0.10 (+)
6 July 95		0.90±0.05	0.77±0.16	0.82±0.01	1.19±0.43		
24 July 95		0.68±0.09	0.84±0.08	0.74±0.12	0.74±0.09		
8 Aug 95		0.62±0.09	0.55±0.10	0.79±0.06	0.64±0.09	0.092 (–)	
27 Sept 95		0.51±0.04	0.44±0.08	0.48±0.14	0.64±0.05		
3 Apr 96		0.41±0.11	0.61±0.03	0.32±0.05	0.52±0.03	0.10 (+)	
20 May 96		1.02±0.02	1.27±0.12	1.00±0.10	1.40±0.10		
12 June 96		0.46±0.10	0.56±0.01	0.62±0.19	0.68±0.26	0.066 (+)	
1 July 96		0.92±0.18	0.80±0.14	0.87±0.21	1.04±0.02		
23 July 96		0.88±0.19	1.00±0.09	1.08±0.07	1.28±0.04	0.10 (+)	
10 Sept 96		0.85±0.15	0.91±0.24	1.03±0.12	1.43±0.08		
9 Oct 96*		0.72±0.02	0.70±0.04	0.67±0.11	0.74±0.10		
27 Feb 97*		0.35±0.01	0.46± 0.02	0.43±0.01	0.41±0.02	0.067 (+)	
ANNUAL AVERAGES							
1995		0.70±0.06	0.68±0.11	0.77±0.07	0.82±0.21		0.022 (+)
1996		0.75±0.13	0.84±0.12	0.80±0.11	1.01±.0.12	0.024 (+)	0.011 (+)

flux was highest around red maple saplings in the HC treatment (0.91 and 0.95 μmol m^{-2} s^{-1} in 1995 and 1996, respectively) and around sugar maple saplings in the HCHT treatment (0.82 and 1.01 μmol m^{-2} s^{-1}). The lowest averages in red maple were in the HT treatment (0.51 and 0.66 μmol m^{-2} s^{-1}, in 1995 and 1996, respectively). The lowest averages in sugar maple were in the HC and C treatments in 1995 (0.68 and 0.70 μmol m^{-2} s^{-1}) and in the C treatment in 1996 (0.75 μmol m^{-2} s^{-1}).

The average percentage contribution by roots to total CO_2 efflux provides interesting treatment comparisons. The highest growing season percentage contribution by red maple roots to total CO_2 efflux was in the HC treatment (52 and 59% in 1995 and 1996, respectively), while in sugar maple the highest per-

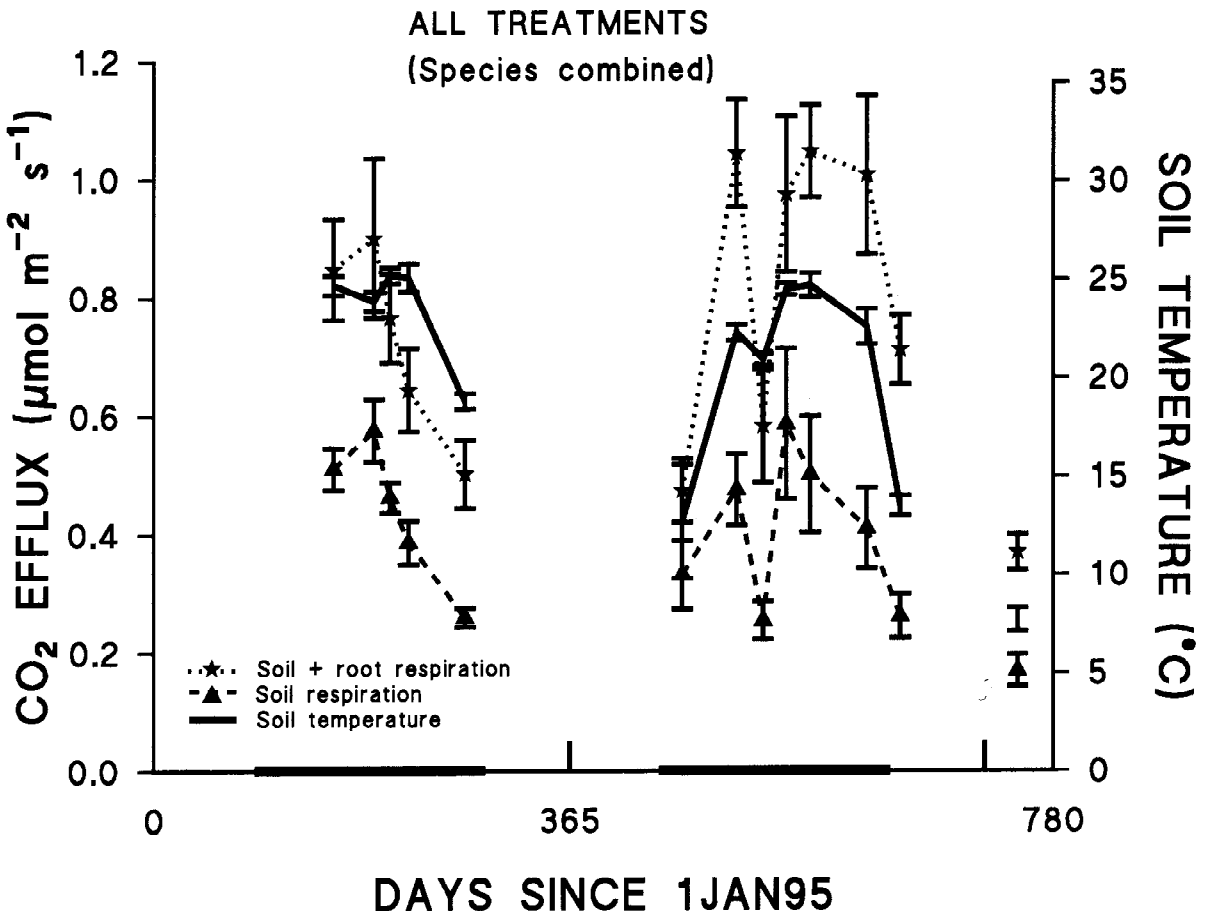

Figure 1. Seasonal patterns of CO_2 efflux rates and soil temperatures (10 cm depth). Values are means ± 1 standard error across treatments and species (n = 12 for roots + soil; n = 9 for soil only). Horizontal bars on the x-axis denote the 1995 and 1996 growing seasons.

centage due to root respiration was in the HCHT treatment (46 and 58% in 1995 and 1996). Percentage contribution by red maple root respiration was lowest in the HT treatment, accounting for only 14% of total CO_2 efflux in 1995 and only 33% in 1996. Percentage contribution by sugar maple root respiration was lowest in HC in 1995 (35%) and in HT and C in 1996 (45%).

Soil respiration rates in root-exclusion zones were not affected by elevated CO_2, but were stimulated by elevated soil temperatures. Soil temperatures at a depth of 10 cm and at the time measurements were made averaged 0.5 °C higher in the high temperature treatments than in the ambient temperature treatments. Without normalization of the data, CO_2 efflux within the root-exclusion zones over the course of the study ranged from 0.13 to 0.62 μmol m^{-2} s^{-1} in the ambient temperature chambers and from 0.17 to 0.79 μmol m^{-2} s^{-1} in the high temperature chambers. The overall average soil respiration rate was 12% higher in elevated temperatures (0.46 μmol m^{-2} s^{-1}) than in ambient temperatures (0.41 μmol m^{-2} s^{-1}). As expected, there were no differences in CO_2 efflux by temperature treatments when the data were normalized to an average soil temperature using a Q_{10} of 2. This means that no indirect effects of the temperature treatments on soil respiration in root exclusion zones were observed during this study.

Soil moisture tended to be slightly higher in ambient temperatures than in elevated temperatures in both rooting zones and root-exclusion zones, with highest moisture levels in root-exclusion zones. In rooting zones, moisture integrated over the top 23 cm of soil ranged from 21% in elevated temperatures and 25% in ambient temperatures during the driest portions of each growing season to 40% in both tempera-

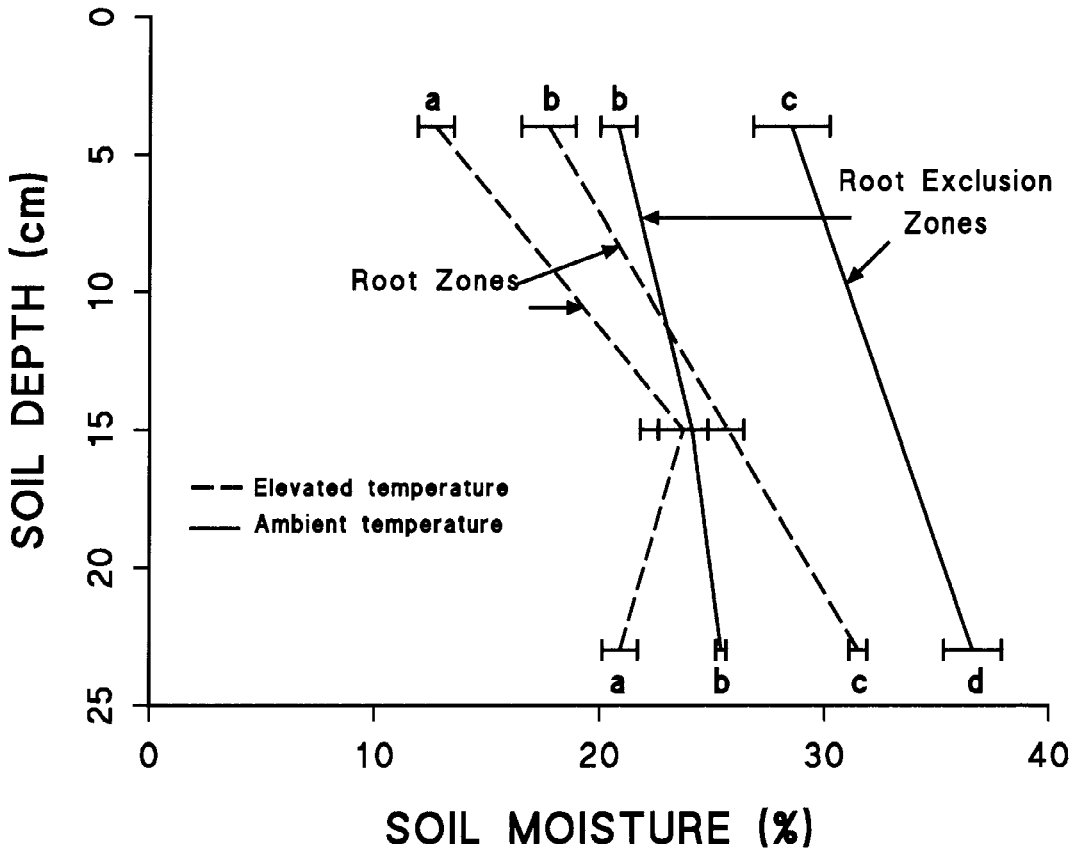

Figure 2. Soil moisture (v/v) in root-exclusion zones and root zones under ambient and elevated temperatures. Measurements were made during a dry period in August 1997. The values at 15 and 25 cm depths are based on TDR measurements and the values at the 4 cm depth were determined gravimetrically. Gravimetric values were converted to volumetric values (soil bulk density = 1.5). Values are means ± 1 standard error (n = 3). Dissimilar superscripts denote significant differences at each depth (ANOVA, $P < 0.05$).

ture regimes during the dormant seasons. The highest range of soil moisture levels were recorded in August 1997 near the end of a 3 week period without rainfall (Figure 2). During this period moisture levels near the soil surface (0–4 cm depth) ranged from 12% in elevated temperatures in the rooting zone to 29% in ambient temperatures in the root-exclusion zone. Soil moisture at 0–23 cm ranged from 20% in elevated temperature in the rooting zone to 35% in the root-exclusion zone in ambient temperature. A few weeks earlier (July 9) soil moisture in the rooting zone (0–4 cm depth) dropped to 17% in elevated temperatures after one week without rainfall compared to 21% in ambient temperature.

Temporal changes in root respiration rates by species and treatment are graphically depicted in Figure 3a and 3b. A trend of higher root respiration in response to the HC treatment is evident for red maple. In red maple root respiration averaged over each growing season was 68% and 70% higher in HC than in C in 1995 and 1996, respectively. However, no differences by treatment were observed during the dormant season measurement of red maple root respiration. In sugar maple there was no clear response to elevated CO_2 during the 1995 and 1996 growing seasons. During the one measurement in the 1997 dormant season, however, sugar maple root respiration was higher in HC than in C (61% higher in HC than C). Root respiration response to temperature is different for the two species. In red maple HT root respiration was 25%, 69%, and 69% of C root respiration in 1995, 1996, and 1997, respectively. Conversely, sugar maple root respiration responses to HT were not evident. However, the combined treatments of elevated CO_2 and high temperature (HCHT) in 1996 resulted in 50% higher sugar maple root respiration in HCHT than in C. The response in sugar maple root respiration to HT and HC

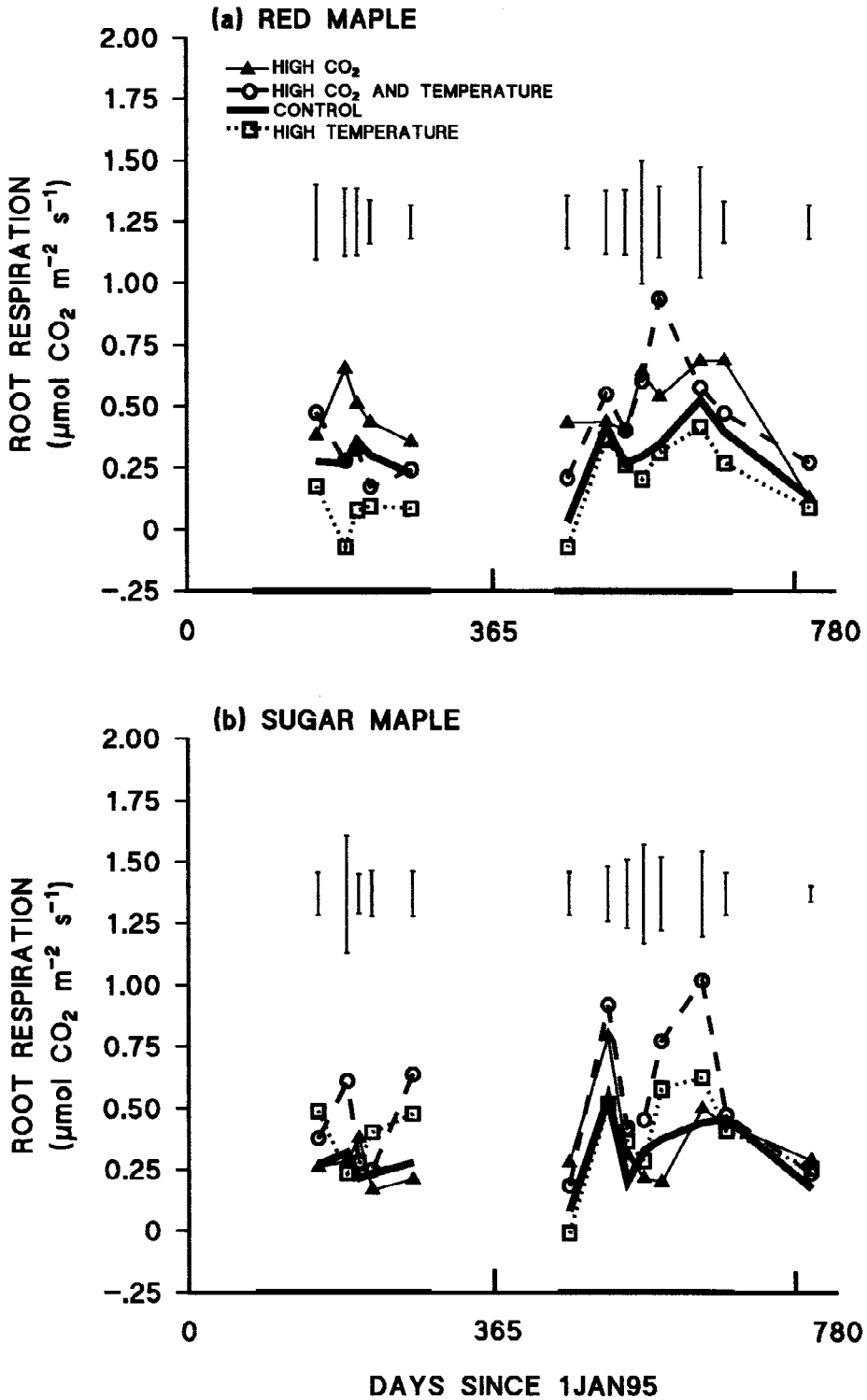

Figure 3. Seasonal patterns of calculated root respiration under different treatment regimes for (a) red maple and (b) sugar maple saplings. Values were calculated by subtracting CO_2 efflux rates in root-exclusion zones from CO_2 efflux rates measured around the base of individual trees (4 trees of each species per chamber). Values are means of individual open top chamber treatments ($n = 3$). Vertical bars represent standard errors (pooled across treatments). Horizontal bars on the x-axis denote the 1995 and 1996 growing seasons.

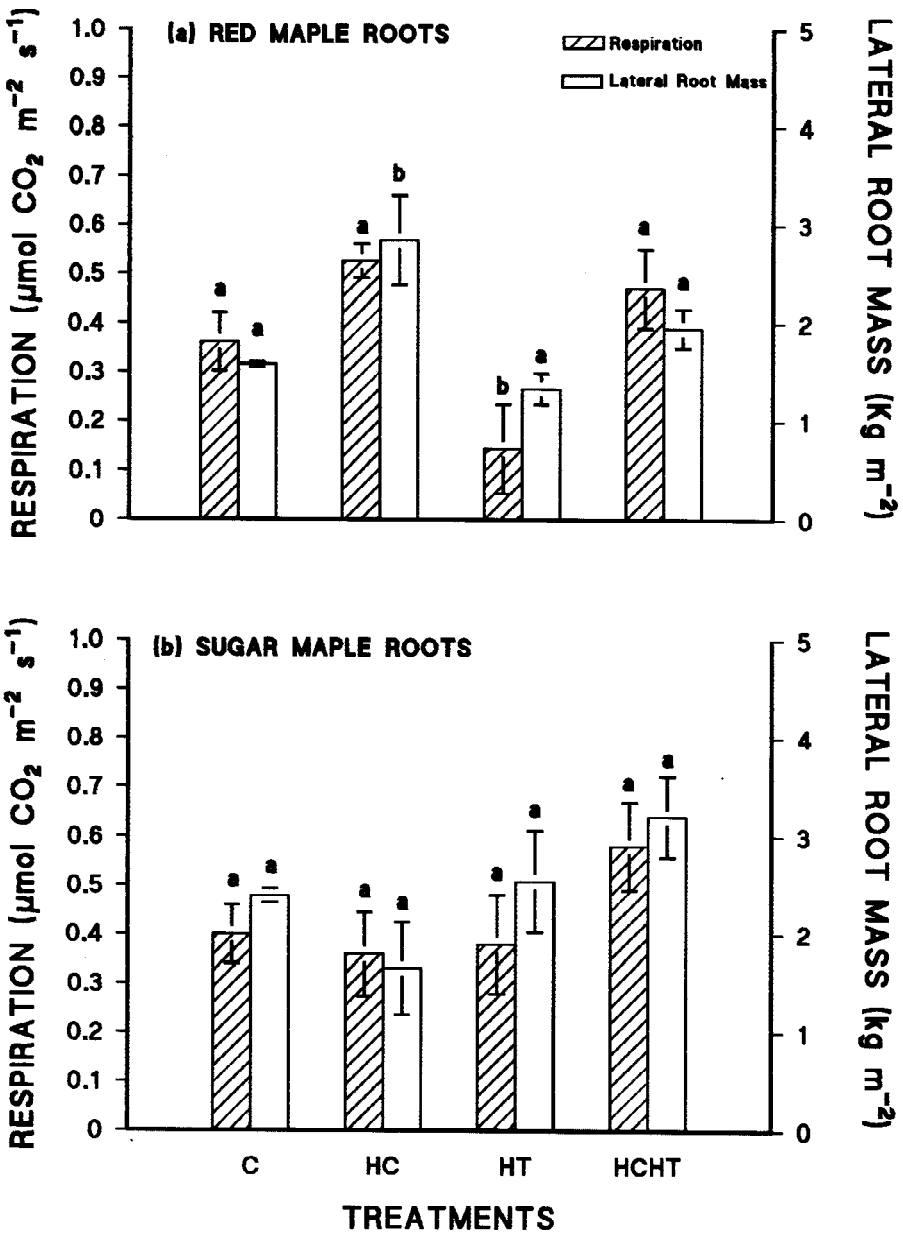

Figure 4. Calculated average CO_2 efflux rates from roots in 1996 with comparisons to lateral root mass beneath the chambers used in the measurements of CO_2 efflux. Roots were harvested at the end of the study (September 1997). Root mass values are for all roots (but not including stumps) to a depth of 30 cm. All values are means ± 1 standard error (n = 3). Dissimilar superscripts denote significant differences in root respiration or mass between treatments (ANOVA, $P < 0.05$).

appears to be additive on a number of sample dates and annually.

Root mass below the respiration chambers followed similar response patterns to the treatments as did 1996 root respiration (Figure 4). For example, in red maple both root respiration and root mass were highest in the HC treatment (P = 0.09 for mass, not significant for respiration) and lowest in the HT treatment (P = 0.006 for respiration, not significant for mass). However, in sugar maple both root respiration and root mass were highest in the HCHT treatment (not significant for respiration or for mass) with little difference between the other three treatments. Coarse root mass averaged 95% of the total root mass in both

species and the proportion of coarse root to fine root mass did not vary with treatment, with the contribution by coarse roots ranging from 93 to 96%.

Specific respiration rates of red maple coarse roots were highest in HC and lowest in HT (Figure 5). Rates in HC were 120% higher than in C (P = 0.041) and rates in HT were only 50% of the rates in C (P = 0.049), 30% of the HCHT rates (not significant), and 22% of the rates in HC (P = 0.01). Specific respiration rates in sugar maple followed the same trend except that in red maple CO_2 enrichment tended to offset the effects of high temperature, while in sugar maple the lowest respiration rates were observed with both high temperatures and CO_2 enrichment. In fact sugar maple specific root respiration rates in the HCHT treatment were only 20% of the rates in the HC treatment. Sugar maple root respiration was 191% greater in HC than in C (P = 0.071). None of the other treatment differences in sugar maple specific root respiration were statistically significant.

Discussion

The results reported here as root respiration must in fact be considered as the integrated responses of the root system and its associated rhizosphere. We must also caution that differences in species responses to the treatments requires further study because measurements of the below-ground system of one species did not completely exclude the root system of the other species. However since the respiration chamber used in the study fit around the base of the saplings most of the roots directly under the chamber probably belonged to that seedling. Observations during harvest at the end of the study confirmed that most of the roots (95% estimated) under the area where respiration was measured belonged to the saplings adjacent to the area. Also, the greater the invasion of the soil beneath a seedling by roots from a different species the less likely we would have observed the species differences reported here. Therefore, the evidence is relatively strong that the rhizospheres of red maple and sugar maple behave differently to increased temperature and CO_2 enrichment.

Another potentially complicating factor in this study involves the differences in the soil moisture levels in the root-exclusion zones vs. the moisture levels in the rooting zone. Moisture levels in the root-exclusion zones were generally higher than in the rooting zone and therefore mineral soil respiration rates may have been higher in the root-exclusion zones than the mineral soil rates in rooting zones, especially during dry periods. This would underestimate root respiration in our calculations. However, the opposite could be true under extremely wet conditions (e.g., anaerobic conditions immediately following heavy rain would persist longer in root-exclusion zones). We expect these discrepancies to be negligible because it has been shown that forest soil respiration is influenced little over a relatively wide range of moisture conditions in eastern deciduous forest soils (Edwards, 1975; Hanson et al., 1993). Another complicating factor that could have resulted in overestimates of root respiration is the fact that there were no carbon inputs (e.g., root exudates and dying roots) to the root-exclusion zone. We, therefore caution that our estimates of root respiration include roots and all carbon sources traceable back to the root systems.

Specific respiration rates suffer from the fact the roots were not intact and disturbance factors (e.g., realistic CO_2 and O_2 concentrations in the root atmosphere) result in inaccurate measurements of absolute specific respiration rates. For example, Steinbeck and McAlpine (1966) reported specific respiration rates of 41 to 57 nmol CO_2 g^{-1} s^{-1} at 25 °C in excised red maple root tips, while Ewel et al., (1986) reported rates of only 0.44 nmol g^{-1} s^{-1} at field temperatures in intact roots at of 9-y-old slash pine saplings. The rates reported in this study (1.5 to 6 nmol g^{-1} s^{-1} at 25 EC) fall between those two extremes and are comparable to rates (1.8 nmol g^{-1} s^{-1} at 20 EC) in tulip poplar roots of the same size class reported by Edwards and Harris (1977). Therefore, while this study does not profess to provide highly accurate absolute rates of specific root respiration, the comparative rates of specific root respiration as affected by the treatments (all of which have the same potential biases) are defensible.

The similarity in treatment response patterns of CO_2 efflux from roots and root mass in the respiration measurement zone strongly suggest that the respiratory responses to treatment are due in part to differences in root mass. Johnson et al., (1994) observed an increase in both below-ground respiration and root biomass in ponderosa pine seedlings exposed to elevated CO_2. Tingey et al., (1996) found increased fine root density in ponderosa pine and Norby (1996) found increased fine root density in white oak saplings grown in elevated CO_2. We observed decreased specific respiration in coarse roots of red maple in response to elevated temperature and increased specific coarse

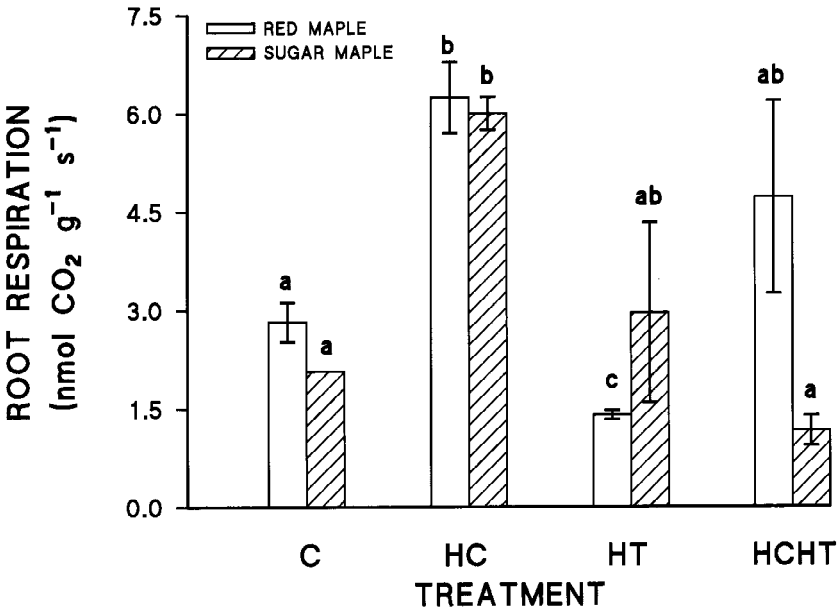

Figure 5. Specific root respiration rates in coarse (> 1mm dia. and generally not greater than 2 mm dia.) roots of red maple or sugar maple in different treatment regimes. Measurements were made in early September 1997 on excised roots collected from upper 5 cm of soil (one sample per open-top chamber per species). Values are means ± 1 standard error (n = 3). Dissimilar superscripts denote significant differences by species between treatments (ANOVA, $P < 0.1$).

root respiration rates in response to CO_2 enrichment. Conversely, Norby (1996) reported reduced specific fine root respiration in white oak CO_2 enrichment even though total CO_2 efflux from around the base of the white oak saplings increased. Also, BassiriRad et al., (1996) reported that despite increased carbohydrate concentrations in roots of tussock sedge exposed to elevated [CO_2], specific root respiration decreased.

Our data suggest that in red maple both specific coarse root respiration and root mass are reduced under high temperatures. Reduced specific respiration in coarse roots becomes highly significant in terms of total CO_2 efflux from the roots when we consider that 95% of the root mass beneath the respiration chambers was coarse roots. Given that soil temperatures during the time our field measurements were made averaged only about 0.5 °C warmer at 10 cm depth in the high temperature treatments than in ambient temperature treatments, it is unlikely that temperature had a great enough effect on specific root respiration to have been detectable in our field measurements of CO_2 efflux. We calculated (using a Q_{10} value of 2) that a 0.5 °C difference in soil temperature between the high temperature and ambient temperature treatments would have resulted in 3.5% increase in field determined root respiration rates, assuming that no acclimation to temperature occurred, or less, assuming that acclimation to temperature did occur. Lambers et al., (1991) reported that researchers have found acclimation of root respiration to growth temperatures in some species, but not in others. Our data did not allow us to address this issue. We recorded a decrease (not an increase) in respiration, under higher temperatures,. Therefore, the lower respiration rates in the high temperature treatment cannot be explained by a direct temperature effect on root respiration.

If soil temperature does not explain the observed decrease in specific root respiration, the next logical question would address the possible indirect effect of temperature on soil moisture, because we did observe significantly drier soil in the high temperature treatments, especially near the surface during a very dry period in late summer. All of the roots used for specific root respiration in this study were removed during this dry period from the top 5 cm of soil. The drier surface soil in the high temperature treatments may have reduced metabolic activity in those roots resulting in lower respiration rates. Bryla et al., (1997) reported that fine roots of citrus seedlings remained alive in very dry soil but respiration rates decreased.

Another possible explanation for reduced specific respiration of red maple roots in the HT treatment, is the possibility of a reduced carbohydrate supply to the roots. Net photosynthetic rates in these red maple

saplings were significantly lower (29%) in HT than C, and this reduction in photosynthesis was less under CO_2 enrichment than in ambient CO_2 (Gunderson et al., 1996). This was not observed in the sugar maple saplings. According to Lambers et al. (1991), from eight to fifty-two percent of all carbohydrates produced per day in photosynthesis are respired in the roots during the same time period. Thus, our observations on root respiration responses to the HT and the HCHT treatments are in line with Gunderson's observations of net photosynthesis, if we assume that net photosynthesis rates influence the carbohydrate supply to the roots.

In summary, we found that total CO_2 efflux from the soil surface around the base of both species emulated the seasonal pattern of soil temperature. Our data suggest that CO_2 enrichment results in increased root mass in red maple saplings and that the increased biomass is reflected in increased CO_2 efflux from the root system of red maple. We also found evidence of increased specific root respiration in both species in response to CO_2 enrichment. In red maple both coarse root biomass and coarse root specific respiration decreased in elevated temperature, while in sugar maple the temperature treatment had no significant effect on specific root respiration.

Our data also demonstrate that a small increase in soil temperature resulted in an increase in mineral soil respiration, but that CO_2 enrichment had no effect on mineral soil respiration.

We reject our original hypothesis that both elevated [CO_2] and increased temperatures will result in increased CO_2 efflux from below-ground. Given that the two species are of the same genus, these results highlight the difficulty of predicting the responses of the complex eastern deciduous forest ecosystem to global climate change. The results also underscore the need for separating the processes occurring in the roots from those in the forest floor and mineral soil in order to increase our understanding of the effects of global climate change on carbon sequestration and cycling in the below-ground systems of forests. This separation becomes even more important in mature forest stands, with very large amounts of carbon stored in both soil detritus and in roots. We must caution that these results should not be considered unconditionally extrapolative to mature forest stands because of the diversity of species, the larger carbon pools in both living tissue and soil detritus, and especially because the root systems (which may already fully occupy the soil in a closed canopy forest) may respond differently.

Acknowledgments

We thank Joshua Johnson for technical help in collecting the data. The research was sponsored by the Global Change Research Program of the Environmental Sciences Division, Office of Health and Environmental Research, US Department of Energy under contract No. DE-ACO5-96OR22464 Lockheed Martin Energy Research Corp. Publication #4815, Environmental Sciences Division, Oak Ridge National Laboratory. This work contributes to the Global Change and Terrestrial Ecosystems Core Research Programme, a core project of the International Geosphere-Biosphere Programme.

References

BassiriRad H, Harmoz B, Griffin K L Strain B R and Reynolds J F 1996 Effects of CO_2 enrichment on growth and root $^{15}NH_4^+$ uptake rate of loblolly pine and ponderosa pine seedlings. Tree Physiol. 16, 957–962.

BassiriRad H, Tissue D T, Reynolds J F and Chapin F S III. 1996 Response of *Eriophorum vaginatum* to CO_2 enrichment at different soil temperatures: effects on growth, root respiration and PO_4^{3-} uptake kinetics. New Phytol. 133, 423-430.

Bryla D R, Bouma T J and Eissenstat D M 1997 Root respiration in citrus acclimates to temperature and slows during drought. Plant Cell Environ. 20, 1411–1420.

Curtis P S, Balduman L M, Drake B G and Whigham D F 1990 Elevated atmospheric CO_2 effects on below-ground processes in C_3 and C_4 estuarine marsh communities. Ecology 71, 2001–2006.

Edwards N T 1975 Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. Soil Sci. Soc. Am. 39, 361–365.

Edwards N T and Harris W F 1977 Carbon cycling in a mixed deciduous forest floor. Ecology 58, 431–437.

Ewel K C, Cropper W P and Gholz, HL 1987 Soil CO_2 evolution in Florida slash pine plantations. II. Importance of root respiration. Can. J. For. Res. 17, 330–333.

Gunderson C A, Wullschleger S D and Norby R J 1996 Temperature effects on gas exchange responses to elevated CO_2 in two maples. Supplement to Bull. Ecol. Soc. of Am. 77, 175.

Hanson P J, Wullschleger S D, Bohlman S A and Todd D E 1993 Seasonal and topographic patterns of forest floor CO_2 efflux from an upland oak forest. Tree Physiol. 13, 1–15.

Johnson D, Geisinger D, Walker R, Newman J, Vose J, Elliot K and Ball T 1994 Soil pCO_2, soil respiration, and root activity in CO_2-fumigated and nitrogen-fertilized ponderosa pine. Plant Soil 165, 129–138.

Kirschbaum M U F 1993 A modeling study of the effects of changes in atmospheric CO_2 concentration, temperature and atmospheric nitrogen input on soil organic carbon storage. Tellus 45B, 321–334.

Lambers H, Atkin O K and Scheurwater I 1991. Respiratory patterns in roots in relation to their functioning. *In* Plant Roots: The Hidden Half. Second edition. Eds. Y Waisel, A Eshel and U Kafdafi. pp 323–362. Marcel Dekker Inc., New York.

Lambers H, Stulen I and A van der Werf 1996 Carbon use in root respiration as affected by elevated atmospheric CO_2. Plant Soil 187, 251–263.

Norby R J, O'Neill E G and Luxmoore R J 1986 Effects of atmospheric CO_2 enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. Plant Physiol. 82, 83–89.

Norby R J, O'Neill E G, Hood W G, and Luxmoore R J 1987. Carbon allocation, root exudation and mycorrhizal colonization of *Pinus echinata* seedlings grown under CO_2 enrichment. Tree Physiol. 3, 203–210.

Norby R J 1994 Issues and perspectives for investigating root responses to elevated atmospheric carbon dioxide. Plant Soil 165, 9–20.

Norby R J 1996 Oak in a high-CO_2 world. Ann Sci For 53, 413–429.

Norby R J, Edwards N T, Riggs J S, Abner C H, Wullschleger S D and Gunderson C A 1997 Temperature-controlled open-top chambers for global change research. Global Change Biol. 3, 259–268.

Post W M, Peng T H, Emanuel W R, King A W, Dale V H and DeAngelis D L 1990 The global carbon cycle. Am. Sci. 78, 310–326.

Rogers H H, Heck W W and Heagle A S 1983 A field technique for the study of plant responses to elevated carbon dioxide concentrations. J. Air Pol. Cont. Assoc. 33, 42–44.

Raich J W and Schlesinger W H 1992 The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B, 81–99.

Steinbeck K and McAlpine R G 1966 Inter- and Intra-specific differences in root respiration rates of four hardwood species. For. Sci. 12, 473–476.

Tingey D T, Johnson M G, Phillips D L, Johnson D W and Ball J T 1996 Effects of elevated CO_2 and nitrogen on the synchrony of shoot and root growth in ponderosa pine. Tree Physiol. 16, 905–914.

Topp, G C and Davis, J L 1985. Measurement of soil water content using time domain reflectometry (TDR): a field evaluation. Soil Sci. Soc. Amer. J. 49, 19–24.

Tschaplinski T J, Stewart D B, Hanson P J and Norby R J 1995 Interactions between drought and elevated CO_2 on growth and gas exchange of seedlings of three deciduous tree species. New Phytol. 129, 63–71.

Vogt K A, Vogt D J, Palmiotto P A, Boon P, O'Hara J and Asbjornsen H 1996 Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187, 159–219.

Wullschleger S D, Lynch J P and Berntson G M 1994 Modeling the belowground responses of plants and soil biota to edaphic and climatic change – What can we expect to gain? Plant Soil 165, 149–160.

Section editor: H Lambers