

**The effects of elevated soil temperatures on root and
microbial respiration in a mixed hardwood forest**

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Abstract.

To examine the belowground carbon responses to soil warming, we have been conducting a trenched and heated factorial experiment at the Harvard Forest, in Petersham, MA. In the fall of 1994, triplicate 4 m² plots of four treatments were established: (1) trenched and heated; (2) trenched and unheated; (3) untrenched and heated; (4) untrenched and unheated. CO₂ effluxes, soil temperature, and soil moisture were measured in each plot during 1996 and 1997.

A 5°C increase in soil temperature raised total soil respiration (untrenched) by 20%, microbial decomposition (trenched) by 27%, but did not appear to affect root respiration which remained constant at 20% of total soil respiration. Soil respiration increased exponentially with soil temperature ($R^2 = 0.70$) and linearly with soil moisture ($R^2 = 0.20$). Heating depressed the Q_{10} for total soil respiration from 3.1 to 2.2, while the Q_{10} for the microbial component remained constant at 2.1.

Cumulative CO₂ effluxes for all treatments and the increases due to heating were less in 1997 than in 1996. Monthly precipitation differences between 1997 and 1996 could account for 20% of the variance in the monthly CO₂ efflux. The lowered response to heating in 1997 could also be a result of a decreasing labile carbon pool due to increased microbial decomposition associated with reduced belowground litter and root inputs.

Introduction

Globally, soil respiration accounts for the release of about 60 Pg of carbon as CO₂ annually (Schimel *et al.* 1996). This figure is more than 10 times the total annual release of carbon due to anthropogenic sources (Schimel *et al.* 1996). An increase in the global mean surface temperature over the next century of approximately 2.5°C is predicted by current computer models (Houghton *et al.* 1996). This increase has the potential to substantially increase the rate of soil respiration (Raich and Schlesinger, 1992). An increase in soil respiration can lead to a positive feedback loop that would further increase global surface temperatures (Kirschbaum 1995).

To examine the potential impacts of global warming on soil respiration, a soil warming experiment was established at the Harvard Forest in central Massachusetts in 1991 (Peterjohn *et al.* 1994). This experiment has shown on average a 20% increase in annual soil respiration due to a 5°C increase in soil temperature (K. Newkirk, *personal communication*). The observed increased release of CO₂ could be a result of an increase in either microbial decomposition of soil organic matter, live root respiration, or a combination of the two (Peterjohn *et al.* 1994).

Estimating the contributions of microbial decomposition and root respiration to total soil respiration from the different belowground sources has proven difficult. In the literature, estimates of root respiration range from a low of 4% (Phillipson *et al.* 1975) to a high of 62% (Ewel *et al.* 1987) of total soil respiration. Methods (see Singh and Gupta, 1977 for a review) for assessing the relative contribution of root respiration have included physical removal of roots (Wiant 1967), measurement of CO₂ release from roots directly (Edwards and Harris 1977), and estimation of respiration indirectly using the N-budget

method (Aber *et al.* 1985; Nadelhoffer *et al.* 1985; Nadelhoffer and Raich 1992). Bowden *et al.* (1993) used an *in situ* trenching approach to estimate root and microbial contributions to soil respiration, a technique we adopt in the experiment reported here.

In this paper, we report the results from the first 2 years of the TRENched UnTrenched Heated (TRUTH) experiment, which is a part of the long-term ecological research effort at the Harvard Forest. Questions addressed in this study are: (1) What percentage of total soil respiration is attributable to microbial decomposition of soil organic matter; (2) What percentage is attributable to live root respiration; (3) How does microbial decomposition and live root respiration change as a result of a 5°C increase in soil temperature; and (4) What factors influence the rate of CO₂ evolution from each compartment?

Methods

Site description.

The 1000 m² research site is located at the Harvard Forest, Petersham, Massachusetts (43°20' N, 72°10' W) within a temperate, even-aged, mixed hardwood forest at an elevation of approximately 380 m, and is situated adjacent to the soil warming experiment (Peterjohn *et al.* 1994). Mean weekly air temperature ranges from approximately -6°C in January to a high of 20°C in July (Spurr 1957). The average annual precipitation totals 108 cm and is evenly distributed throughout the year (Spurr 1957).

The dominate tree species are black oak (*Quercus velutina* Lam.), red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh.), and striped maple (*Acer*

pensylvanicum L.) (Peterjohn et al. 1994). Soils are primarily Canton series (coarse loamy over sandy or sandy skeletal, mixed, mesic Typic Dystrochrept) with a surface pH of 3.8, a subsurface pH of 4.9, and an average bulk density for the upper 15 cm of 0.64 g/cm³ (Peterjohn et al. 1994). An O horizon is present with an average depth of 2.5 cm. Historical records indicate that this site was once cultivated and the present old-field forest was established after abandonment at the turn of the century. Some cutting for firewood has occurred since the time of abandonment (Peterjohn et al. 1994).

Experimental design.

In the fall of 1994, twelve 2 × 2 m plots were randomly assigned in equal numbers to one of four treatments: (1) trenched and heated to 5°C above ambient soil temperatures (TRN05); (2) trenched and cabled but unheated (TRNDC); (3) untrenched and heated (UNT05); (4) untrenched and cabled but unheated (UNTDC) (Fig. 1). Trenching was accomplished by digging a trench around the plot to a depth of ~1 m (a few cm into the hardpan). The trench was then lined on the inside and bottom with the geotextile Grifilon™, and back-filled to form a barrier to root growth into the plot. To minimize root mass variability due to different aged trees, all plots were located between trees. All herbaceous vegetation in the trenched plots was clipped back to the soil surface and new growth was clipped regularly.

In the heated plots, we buried resistance heating cables at a depth of 10 cm in rows spaced 20 cm apart. Soil temperature is maintained at 5°C above ambient using a datalogger that compared, every five minutes, the 5 cm soil temperature of each heated plot to the mean of six control thermistors distributed evenly throughout the study site. If

the temperature difference is less than 5°C, the heating cable in that plot is turned on until the temperature difference reaches 5°C. To control for the disturbance effects of burying the heating cables, cables were also buried in the unheated plots but are not supplied with electrical power; we refer to these as disturbance control plots (DC). Peterjohn *et al.* (1994) demonstrated that the buried cables had no significant effect on soil respiration.

Field and laboratory techniques.

CO₂ flux, soil moisture, and soil temperature of each plot were measured on a weekly basis from June through October, bimonthly in April, May, and once in November of 1996 and 1997. We have been continually monitoring 5 cm soil and air temperature via thermistors connected to the datalogger since the plots were established in the fall of 1994.

CO₂ flux between the soil and atmosphere was measured using the static chamber technique (Raich *et al.* 1990, Peterjohn *et al.* 1994). A single chamber was placed over the surface of each plot and four 10 cc gas samples were drawn at 5 minute intervals for 15 minutes. Chambers are placed at fixed location in the center of each plot. Syringe samples were analyzed for CO₂ concentration using infrared gas analyzer (LICOR 6262 CO₂/H₂O analyzer). For each flux sampling date, we measured fluxes at 0600h and 1400h and calculated an average daily flux. We also measured soil temperatures at 2 and 5 cm using stem thermometers placed in-between heating cable rows adjacent to the chambers at the time of the flux measurements.

Volumetric soil water content was determined *in situ* with time domain reflectometry (Topp *et al.* 1980). Using a Tektronix 1502B cable tester, measurements

were taken daily at 1000h from June through October in 1996 and 1997, as well as at all other CO₂ flux sampling dates not within this period. Modified unbalanced 15 cm TDR probes (see Heimovaara, 1993; Zegelin and White, 1989) connected to a 5m length of RG-58U coaxial cable were placed on a 45° angle into each plot to achieve an integrated reading of the top 10 cm of the soil. TDR measurements were calibrated using a modified multi-phase mixing model (Roth *et al.* 1990).

Data analysis.

Weekly CO₂ evolution was calculated by taking the mean daily flux on a specific sampling date to be the average for that week with the sampling date as the midpoint. In this manner, we then calculated an average cumulative CO₂ evolution for each treatment throughout the sampling periods of 1996 and 1997.

The change in microbial decomposition due to a 5°C increase in soil temperature was defined as [TRN05 – TRNDC] (Fig.1). Root respiration was calculated as the difference between untrenched (total soil respiration) and trenched (microbial decomposition) treatments. Thus, the change in root respiration due to heating was defined as [(UNT05 – TRN05) – (UNTDC – TRNDC)]. These data were then subjected to a two-way completely randomized analysis of variance (ANOVA) (Zar 1974) with trenching and heating as the two main factors. Both linear and multiple regression analyses were employed to determine soil temperature and soil moisture effects on CO₂ flux. Q₁₀ values were calculated based on the Arrhenius equation:

$$Q_{10} = \exp[(E_a/R)(10/T_{avg}^2)];$$

where E_a is the activation energy, R is the universal gas constant, and T_{avg} is the average temperature of the sampling period (Alberty 1983).

Results

Our heating design maintained, according to the permanent thermistors, a mean temperature difference of 5.0°C at 5 cm. One of the trenched-unheated replicates, plot #12, had to be removed from the following analyses because of highly anomalous results (missing datum was estimated following Zar (1974) for statistical measures).

Heating the soil significantly increased annual mean soil temperatures from 8.0°C in the unheated plots to 13.0°C in the heated plots (2-way ANOVA, $F = 113.42$, $P < 0.0001$, $df = 1$). Trenching had no effect ($F = 1.67$, $P = 0.20$, $df = 1$) on soil temperature. Trenching has significantly increased soil water content (2-way ANOVA, $F = 88.87$, $P < 0.0001$, $df = 1$). Average soil water contents increased from 0.19 cm³-water/cm³-soil in the untrenched treatments to 0.24 cm³-water/cm³-soil in the trenched treatments. On average, heating lowered the overall soil water contents slightly from 0.22 to 0.21 cm³-water/cm³-soil ($F = 3.94$, $P = 0.05$, $df = 1$). In 1997, the trenched unheated plots were ~20% wetter than the trenched heated plots. This trend was not observed in 1996.

CO₂ flux.

Daily CO₂ effluxes varied significantly in 1996 and 1997 among the treatments (Fig. 2). Cumulative CO₂ effluxes for the sampling period, April through mid-November, showed significant treatment effects for both trenching (2-way ANOVA, $F = 11.39$, $P = 0.01$, $df = 1$) and heating ($F = 8.28$, $P = 0.02$, $df = 1$) (Table 1). On average, total soil respiration

increased 20%, from 470 to 570 g-C·m⁻² with the 5°C increase in soil temperature. With heating, microbial decomposition increased 27% from 380 to 490 g-C·m⁻² while live root respiration, representing ~ 20% of total soil respiration, remained constant at 85 g-C·m⁻².

Cumulative CO₂ effluxes showed considerable interannual variations between 1996 and 1997 (Table 1). Both untilled treatments showed significantly higher fluxes in 1996 (2-tail paired t-test, P = 0.04 for heated and P = 0.003 for unheated plots, n = 3). The untilled heated plots had slightly higher CO₂ effluxes in 1996 (P = 0.06, n = 3), while the untilled unheated plots did not differ between years (1996 – 97, < 20 g-C·m⁻²). The percent of total soil respiration that we attribute to root respiration decreased from 27% in 1996 to 18% in 1997. Heating raised the total CO₂ effluxes (untilled) by 130 g-C·m⁻² or 27% in 1996, while in 1997 heating raised total CO₂ effluxes by 60 g-C·m⁻² or 14%.

Seasonal variations in the untilled unheated CO₂ efflux, 5cm soil temperature, and soil moisture levels were observed in both years (Fig. 3). Daily CO₂ efflux follows seasonal soil temperature with departures coinciding with periods of prolonged dry weather where soil water contents may be limiting.

Inter-annual variation in total annual CO₂ efflux is well correlated to precipitation differences between years. Degree days greater than 10°C calculated from data collected at the Harvard Forest NOAA weather station were nearly the same in 1996 and 1997, i.e. 3490 in 1996 and 3520 in 1997 (Savage *et al.* 1998). However, annual precipitation was 137 mm above the 30 year (1966 through 1996) mean in 1996 and 101 mm below normal in 1997 (Savage *et al.* 1998). We observed lower fluxes in the drier year (1997) and this correlation between below average precipitation and lowered CO₂ fluxes on a monthly

basis (Fig. 4). The 1997 vs. 1996 difference between monthly fluxes shows a significant positive trend with the same difference in the monthly total precipitation ($R^2 = 0.2$, $P = 0.01$, $n = 28$).

Soil temperature.

Mean daily CO₂ efflux increased exponentially with soil temperature (Fig. 5) and a logarithmic regression model explained 52 to 72% of the variability (Table 2). The average Q₁₀ value for unheated total-soil respiration was 3.1, for microbial decomposition the Q₁₀ was 2.1, and for “root” respiration we estimate the Q₁₀ to be 4.0 (Table 1). Activation energies ranged from 50 to 96 kJ/mol for these unheated treatments. Heating depressed the Q₁₀ for total soil respiration from 3.1 to 2.2; the Q₁₀ for the microbial component remained constant at 2.1; and heating increased the Q₁₀ for root respiration from 4.0 to 6.4. Since root respiration is calculated and not actually measured from live roots per se, our confidence in this number is limited. The Q₁₀ values also showed inter-annual variability, especially in the root respiration estimate (Table 1).

Soil moisture.

Soil water contents follow a general seasonal trend in temperate regions – wetter in the winter months when evapotranspiration is low and drier in the warm summer months (Fig. 3). We attempted to remove the seasonal influence of temperature on the relationship between CO₂ efflux and soil moisture, by looking at the relationship of CO₂ efflux and soil moisture for June through September only, when soil temperatures were consistently over 15°C. In these months, there was a significant linear increase in CO₂

flux with soil moisture for all four treatments (Fig. 6). This relationship accounted for 9 to 20% of the variance in the daily average flux (Table 2).

Discussion.

Estimating root respiration.

Our estimate for root respiration at 20% of total soil respiration is lower than values reported for other temperate forests. Edwards and Harris (1977) estimated root respiration at 35% by direct measurement of roots removed from a 50-year-old tulip-tree forest in Tennessee and Ewel *et al.* (1987) reported 62% using a trenching technique along with root decomposition estimates in a 29-year-old slash pine plantation in Florida. Bowden *et al.* (1993) reported that root respiration contributed 33% to total soil respiration using the same trenching technique as our study at a separate mixed hardwood stand at the Harvard Forest. Although, the Bowden *et al.* (1993) study was located within 2 km of our study, there are numerous site differences (J. Sanderman, *personal observation*) that must be considered when comparing the root respiration estimates.

Central to our experimental design is the assumption that contributions to the CO₂ efflux from the trenched plots do not include respiration from the decomposition of the severed roots. If this assumption is untrue, then we have underestimated the root contribution to total soil respiration. However, several previous studies suggest that this is not likely. Fahey *et al.* (1988) working in a mixed hardwood forest in New Hampshire, Ewel *et al.* (1987) in a pine plantation in Florida, and Bowden *et al.* (1993) all found that root decomposition stabilized to negligible levels within 6 months of trenching. We

completed trenching in July of 1994, this gave the roots at least 20 months to decompose before the first reported data in April 1996.

Effects of heating.

Our reported 20% increase in soil respiration in response to heating agrees with values reported by Peterjohn *et al.* (1994). Heating had a greater effect on increasing soil respiration in 1996 than in 1997 (Table 1). This declining impact of warming during successive years has been observed at the previous soil warming experiment at the Harvard Forest (Peterjohn *et al.* 1994). By heating the soil, the labile C-pool may have been metabolized faster than it could be replenished by fresh litter and fine root inputs. Kirschbaum (1995) reached the same conclusion in a review of laboratory-based CO₂ efflux experiments.

The data from this study indicate that the microbial component of soil respiration increases with heating, while root respiration remains constant. Microbial decomposition is a highly temperature-dependent process, thus an increase in soil temperature is expected to lead to increased microbial activity and higher respiration rates. The fact that root respiration did not change due to elevated soil temperatures indicates that the vegetative response to global warming with respect to carbon may be dependent upon aboveground conditions (i.e. air temperature and CO₂ concentration).

Factors controlling CO₂ efflux.

Our results provide further evidence that soil temperature and soil moisture are the two major abiotic factors influencing soil respiration. Soil respiration increased exponentially

with soil temperature and the slopes of the lognormal regression analysis for all four treatments were nearly identical (Table 2) lending support to the conclusion that only the microbial component of soil respiration increases with heating. The additional respiration due to roots roughly shifts the regression lines 20% higher (Fig. 5). The Q_{10} values for the unheated treatments are in agreement with values reported for a similar site with the same trenching technique (Boone et al. 1998). Additionally, the observed decrease in Q_{10} values with heating for total soil respiration is consistent with previous studies (see Kirchbaum, 1995) and with observations of the data at the original soil warming experiment (K. Newkirk, *personal communication*).

For the range of soil water content observed in the warmest months (0.08 to 0.36 $\text{cm}^3\text{-water/cm}^3\text{-soil}$), we report a small but significant linear increase in soil respiration (Fig. 6). Other studies (see Singh and Gupta, 1977) have shown that soil respiration will increase up to an optimal water content and then decrease as soil moisture increases beyond this point. In restricting our analysis to the period June through September, we did not observe any prolonged periods of very wet conditions that would result in decreased soil respiration. Multiple regression with soil temperature and soil moisture could not improve our prediction of soil respiration with soil temperature alone because of the complex interactions between temperature, soil moisture and seasonal factors.

Besides the possible change in the labile C-pool resulting in decreased CO_2 effluxes in the heated plots, much of the interannual variability can best be explained by meteorological patterns resulting in differing soil conditions between years. Our result that monthly CO_2 effluxes positively correlate to precipitation totals (Fig. 4) agrees with a similar analysis by Savage et al. (1998).

This positive relationship between soil respiration and precipitation is consistent with the positive relationship found between respiration and soil moisture (Fig. 6). However, the relationship with soil moisture cannot account for the residual variance (actual CO₂ value - expected CO₂ values based on soil temperature alone) between CO₂ efflux and soil temperature, which would be expected if temperature and soil moisture were the only two factors influencing soil respiration. There is a strong seasonal pattern to the residuals (Fig. 7). In the winter and early spring, soil respiration is close to predicted with the heated plots showing slightly higher values than predicted as plant growth starts earlier in these plots (Farnsworth *et al.* 1995). As the soil heats up, the biological community lags behind creating negative residuals. Once leaf-out occurs and the growing season progresses, soil respiration is higher than predicted. As summer progresses into fall, growth senesces and soil respiration falls back in line with what would be predicted by temperature alone.

This experiment was framed in the context of global change. Our results indicate that when soil temperatures are increased, it is the microbial component of soil respiration that increases and not the live root component. However, because we have decoupled aboveground from belowground processes it is hard to draw conclusions regarding the ultimate response of terrestrial ecosystems to proposed global warming. Warmer global temperatures coupled with increased atmospheric CO₂ may increase plant productivity faster than our reported increase in soil respiration and the terrestrial C-pool may in turn act as a sink. Increased photosynthesis will lead to a decrease in atmospheric CO₂ if the newly fixed C is stored away in a long-term C-pool. Several recent CO₂-

enrichment experiments (Hungate *et al.* 1997; Bernston and Bazzaz, 1996, 1997) have shown that plant productivity increases substantially, but that most of the C is allocated to the labile C-pool that ends up being respired right back to the atmosphere resulting in little net storage. If these observations are confirmed by further studies, then the terrestrial C-pool will likely act as an additional source of atmospheric CO₂, creating a positive feedback to the global C cycle. Regardless of the final impact on terrestrial ecosystems, our results are intended to help to further refine the below-ground response to global change in ecosystem models (e.g., Rastetter *et al.* 1991).

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References

- Aber, J.D., J.M. Melillo, K.J. Nadelhoffer, C.A. McCaugherty and J.D. Pastor. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of methods. *Oecologia*. 66: 317-321.
- Alberty, R.A. 1983. *Physical Chemistry*, 6th edition. John Wiley & Sons: New York. pp. 617-620.
- Bernston, G.M. and F.A. Bazzaz. 1996. Belowground positive and negative feedbacks on CO₂ growth enhancement. *Plant & Soil* 187: 119-131.
- Bernston, G.M. and F.A. Bazzaz. 1997. Elevated CO₂ and the magnitude and seasonal dynamics of root production and loss in *Betula papyrifera*. *Plant & Soil* 190: 211-216.
- Boone, R., K. Nadelhoffer, J. Canary, and J. Kaye. 1998. Controls on the temperature sensitivity of soil respiration. *Abstracts from the 9th annual Harvard Forest ecology symposium*, March 11, 1998.
- Bowden, R.D., K.J. Nadelhoffer, R.D. Boone, J.M. Melillo and J.B. Garrison. 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Can. J. For. Res.* 23: 1402-1407.
- Edwards, N.T. and W.F. Harris. 1977. Carbon cycling in a mixed deciduous forest floor. *Ecology*. 58: 431-437.
- Ewel, K.C., W.P. Cropper Jr. and H.L. Gholz. 1987. Soil CO₂ evolution in Florida slash pine plantations. II. Importance of root respiration. *Can. J. For. Res.* 17: 330-333.
- Fahey, T.J., J.W. Hughes, M. Pu and M.A. Arthur. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. *Can. J. For. Sci.* 34: 744-768.
- Farnsworth, E.J., J. Nunez-Farfan, S.A. Careaga and F.A. Bazzaz. 1995. Phenology and growth of the temperate forest life forms in response to artificial soil warming. *J. of Ecology* 83: 967-977.
- Heimovaara, T.J. 1993. Design of triple-wire time domain reflectometry probes in practice and theory. *Soil Sci. Soc. Am. J.* 57: 1410-1417.
- Houghton, J.T., L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattenberg and K. Maskell. 1995. *Climate change 1995: the science of climate change*. Cambridge University Press, Cambridge.
- Kirschbaum, M.U.F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic storage. *Soil Biol. Biochem.* 27(6): 753-760.
- Hungate, B.A., E.A. Holland, R.B. Jackson, F.S. Chapin III, H.A. Mooney and C.B. Field. 1997. The fate of carbon in grasslands under carbon dioxide enrichment. *Nature* 388: 576-579.
- Nadelhoffer, K.J. and J.W. Raich. 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. *Ecology*. 73: 1139-1147.
- Nadelhoffer, K.J., J.D. Aber and J.M. Melillo. 1985. Fine root production in relation to net primary production along a nitrogen availability gradient in temperate forests: a new hypothesis. *Ecology*. 66: 1377-1390.

- Peterjohn, W.T., J.M. Melillo, P.A. Steudler, K.M. Newkirk, F.P. Bowles, and J.D. Aber. 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecological Applications*. 4(3): 616-625.
- Phillipson, J., R.J. Putman, J. Steel and S.R.J. Woodell. 1975. Litter input, litter decomposition, and the evolution of carbon dioxide in a beech woodland – Wytham Woods, Oxford. *Oecologia*. 20: 203-217.
- Raich, J.W. and W.H. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus*, 44B: 81-99.
- Raich, J.W., R.D. Bowden and P.A. Steudler. 1990. Comparison of two static chamber techniques for determining carbon dioxide efflux from forest soils. *Soil Sci. Soc. Am. J.* 54: 1754-1757.
- Rastetter, E.B., M.G. Ryan, G.R. Shaver, J.M. Melillo, K.J. Nadelhoffer, J.E. Hobbie and J.D. Aber. 1991. A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO₂, climate, and N deposition. *Tree Physiology* 9: 101-126.
- Roth, K., R. Schulin, H. Fluhler, and W. Attinger. 1990. Calibration of time domain reflectometry for water content measurements using a composite dielectric approach. *Water Resour. Res.* 26(10): 2267-2273.
- Savage, K., E. Davidson and E. Belk. 1998. Interannual variation in soil respiration rates at Harvard Forest. *Abstracts from the 9th annual Harvard Forest ecology symposium*, March 11, 1998.
- Schimel, D., D. Alves, I. Enting, M. Heimann, F. Joos, D. Raynaud, T. Wigley. 1995. Radiative forcing of climate change. In *Climate change: the science of climate change*. Edited by Houghton, J.T., L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattenberg and K. Maskell. Cambridge University Press, Cambridge. pp. 1-40.
- Singh, J.S. and S.R. Gupta. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. *The Botanical Review*. 43: 449-528.
- Spurr, S.H. 1957. Local climate in the Harvard Forest. *Ecology*. 38: 37-46.
- Topp, G.C., J.L. Davis, and A.P. Annan. 1980. Electromagnetic determination of soil water content: measurements in coaxial transmission lines. *Water Resour. Res.* 16(3): 574-582.
- Wiant, H.V., Jr. 1967. Contribution of roots to forest “soil respiration.” *Adv. Front. Plant Sci.* 18: 163-167.
- Zar, J.H. 1974. *Biostatistical Analysis*. Prentice-Hall, New Jersey, USA.
- Zegelin, S.J. and I. White. 1989. Improved field probes for soil water content and electrical conductivity measurement using time domain reflectometry. *Water Resour. Res.* 25(11): 2367-2376.