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SPATIAL AND TEMPORAL VARIATIONS IN TEMPERATE FOREST SOIL CARBON DIOXIDE DURING THE NON-GROWING SEASON

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ABSTRACT

In the Whitehall Forest of Georgia during the 1985–86 non-growing season soil CO_2 varied with soil depth, varied spatially at constant depth, and varied temporally with changing environmental conditions. Variations with depth in the upper 1·4 m of the soil were of greater magnitude than temporal variations and spatial differences at 30 cm depth were of lesser magnitude. Mean soil CO_2 in evergreen forest was higher (0·207 per cent) than in deciduous and mixed forest (0·157 per cent). There were no trends in soil CO_2 along hillslopes or with changes in soil texture, bulk density, moisture content, or temperature. Soil CO_2 did increase near trees possibly due to increased root densities and/or more numerous pockets of microbial activity. For CO_2 at 30 cm depth, two variables—the mean daily temperature range in the month before measurement and actual evapotranspiration in the week before measurement (AET7)—explained 76 per cent of the variation in mean soil CO_2. At the profile site, where soil CO_2 was measured at five depths, 66 per cent of the variability in CO_2 was explained by soil depth, AET7, and the average daily temperature range in the two months before measurement.

KEY WORDS Temperate forest Non-growing season Soil carbon dioxide

INTRODUCTION

Carbon dioxide in the soil atmosphere may be produced by root respiration, or by decomposition of organic matter by soil fauna. A knowledge of CO_2 fluctuations can give an indication of the metabolic activity of soil biota (Witkamp, 1969), and can also provide a means of constructing ecosystem carbon budgets. Carbon dioxide levels affect soil and ground water acidity, thus they play a major role in determining chemical weathering rates both within and beneath the soil zone.

In the temperate forests of eastern North America soil CO_2 is highest during the growing season and substantially lower during the rest of the year although still well above atmospheric levels (e.g. Kiefer, 1986, 1990). This is because deciduous trees cease growth during the 'non-growing' season while coniferous and broadleafed evergreens continue growth but at a reduced rate. A striking feature of this region is that three-quarters of the ground water recharge occurs during the non-growing season over much of the area (Trainer and Heath, 1976, p. 47). Thus, it is non-growing season rather than growing season CO_2 levels that determine ground water acidity, rock and soil weathering rates, and ground water chemistry. Acknowledging this, Trainer and Heath (1976) partitioned ground water recharge into that occurring during the growing and non-growing seasons, assumed 3 per cent and 1 per cent soil CO_2 levels respectively based on a survey of published soil CO_2 data, and then modelled spatial variations in denudation in carbonate areas of eastern North America.

Despite the obvious influence of non-growing season CO_2 on regional denudation and ground water chemistry characteristics, there have been few detailed studies of soil CO_2 in this season. Therefore, in

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1985–86 a study was undertaken in a temperate forest in north Georgia to examine spatial and temporal variations in soil CO_2 and the factors that might be responsible for the observed patterns. Variations in soil CO_2 with depth and the influence of hillslope position, vegetation composition, and proximity to vegetation on CO_2 were investigated. Temporal variability in CO_2 was modelled quantitatively using site temperature and moisture characteristics.

STUDY AREA AND SITES

The study was undertaken in the University of Georgia Whitehall Forest near Athens, Georgia (Figure 1). The area has a humid subtropical climate (Köppen Cfa) with a mean annual precipitation of 127 cm, and average January and July temperatures of 5·8°C and 26·2°C, respectively. Average elevation is approximately 200 m above mean sea level. The study began in late October, 1985 and continued through March, 1986, a period of 22 weeks. This time period coincides with the non-growing season in this area, as defined by the mean occurrences of the first fall freeze and the last spring freeze (Suckling, 1988). Water balance data for the Whitehall Forest and also ground water hydrograph data for eastern Tennessee in Trainer and Heath (1976, p. 44) suggest that on average 91 per cent of ground water recharge occurs between November and March—essentially the period under investigation.

Four transects were established to examine spatial and temporal variations in soil CO_2 (Figure 1). Three of these were down hillslopes in deciduous, evergreen, and mixed forest, facing northeast, west–southwest, and

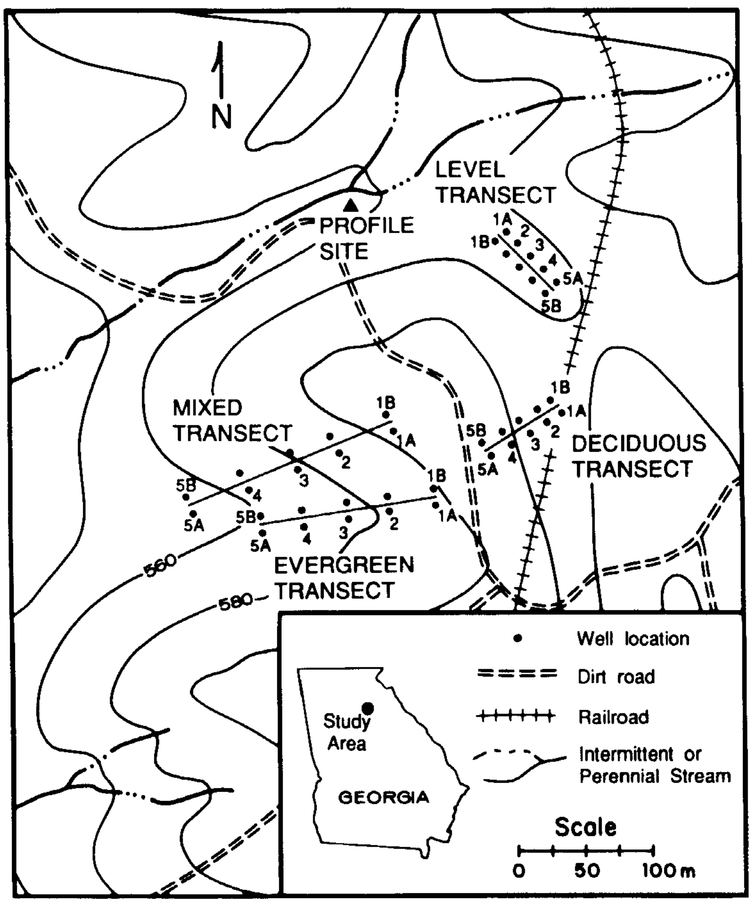

Figure 1. Location of the study area, the four transects and the profile site

southwest respectively. Slopes ranged from 10–15 per cent in the upper part of the 'deciduous transect', increasing to 25–35 per cent near the base. The vegetation consisted primarily of pignut hickory (*Carya glabra*), sweet gum (*Liquidambar styraciflua*), white oak (*Quercus alba*), and water oak (*Quercus nigra*), with little understory (nomenclature follows Harrar and Harrar (1962)). The transect in the evergreen forest (the 'evergreen transect') was located on a 15 per cent linear slope vegetated primarily with large loblolly pine (*Pinus taeda*), with some sweet gum in the understory and a few water oak at the very base of the slope. The transect in mixed forest (the 'mixed transect') was established along a relatively linear slope of 10–25 per cent. Vegetation was primarily shortleaf pine (*Pinus echinata*), pignut hickory, water oak, with white oak near the base of the slope and sweet gum near the crest. A fourth transect with a northwest orientation (the 'level transect') was established on level ground at the base of a slope in oak–hickory forest. In addition to the four transects, a fifth site (the 'profile site') was selected on level ground at the base of a slope to study variations in soil CO_2 with depth (Figure 1). Vegetation at this site was deciduous forest consisting of pignut hickory, white oak, red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*). All sites were on deep Madison sandy clay loam soils and in close proximity so as to minimize CO_2 variability due to differences in soil characteristics.

FIELD AND LABORATORY METHODS

Variations in soil CO_2 along the four transects and at different soil depths at the profile site were measured using diffusion wells constructed of one-quarter inch (0·63 cm) outer diameter stainless steel tubing (Figure 2). Five pairs of wells 1 m apart inserted to 30 cm depth were spaced equally from hill crest to base along the transects in deciduous, evergreen, and mixed forest. Well pairs were spaced at 10 m intervals in the deciduous stand, 15 m in the evergreen stand, and 20 m in the mixed forest stand. In the level transect, five pairs of wells, 0·5 m apart and inserted to 30 m depth, were spaced at 2 m intervals in the 8 m separating a young white oak (19·7 cm dbh) and an older white oak (36·8 cm dbh). At the profile site, a cluster of five diffusion wells was installed to depths of 140, 100, 60, 30, and 10 cm.

Soil air samples were collected from the 45 wells at approximately two-week intervals by inserting the needle of a hyperdermic syringe through the rubber stopper of each well and withdrawing 500 μl of soil air (Figure 2). Each sample was transferred to a plain glass vacutainer for storage; laboratory analysis was carried out within two days of sample collection. Samples were always collected at 12:00 noon since soil CO_2 can vary diurnally (Witkamp and Frank, 1969).

The soil gas samples were analysed using a Carle Analytical Gas Chromatograph with a Spectra–Physics System I Computing Integrator. The vacutainers were pressurized to one atmosphere with helium to remove any vacuum, and 250 μl samples were drawn and injected into the chromatograph to obtain per cent CO_2 by volume of each sample. In calculating CO_2 levels from the chromatograph data, no corrections were made for any changes in laboratory air pressure and temperature during the study period, imposing a maximum error on CO_2 per cent determinations of about 1 per cent of the estimated value (Dyer, 1986, p. 31–32).

At the time of well installation Soiltest MC–310A soil moisture–temperature cells were installed in the four transects. These were placed at 30 cm depth midway between each well pair (Figure 2). In addition, moisture–temperature cells were installed adjacent to the battery of wells at the profile site at the same depths as the wells. Using a Soiltest MC–302 moisture–temperature meter, soil temperature and resistance were measured at the time of CO_2 sampling, the latter allowed estimation of the soil moisture content. The moisture–temperature cells were calibrated before installation (Colman, 1975).

At the beginning of the study soil samples were collected at 30 cm depth from locations close to each well pair in the four transects. Samples were collected at 10, 30, 60, 100, and 140 cm depth at the profile site. Soil bulk density, and texture (sand, silt, and clay by hydrometer), were measured in the laboratory.

At each well pair, and at the profile site, litter temperature, and air temperature and relative humidity at 1 m were measured on each sampling date. Daily temperature, precipitation, and relative humidity were obtained from a U.S. Forest Service weather station 2 km from the study area. Daily actual evapotranspiration was calculated from the weather station data using the Thornthwaite and Mather (1957) method. Environmental variables included in the analysis of temporal variations in non-growing season CO_2, and

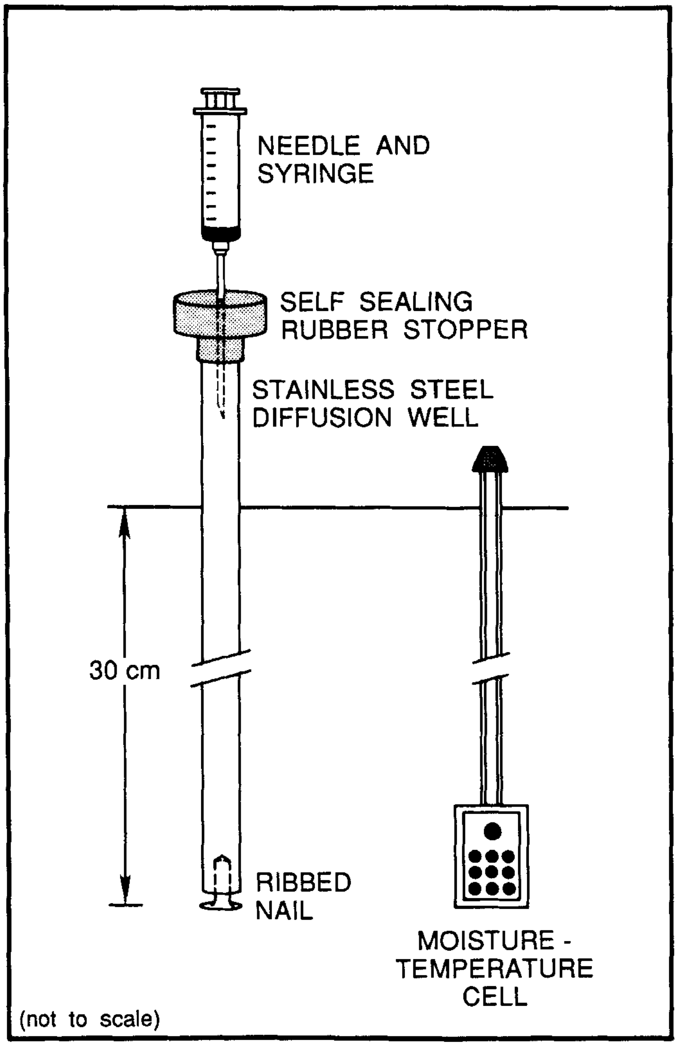

Figure 2. Soil CO_2 diffusion well and moisture–temperature cell

their possible effect on soil CO_2 levels are shown in Table I. Precipitation, actual evapotranspiration, relative humidity, and temperature values were calculated for 1, 7, 14, 28, and 56 days prior to CO_2 measurement in order to test for possible lag effects on soil CO_2.

SOIL CARBON DIOXIDE IN THE FOUR TRANSECTS

Spatial versus temporal variability

The mean soil CO_2 level measured in the four transects during the course of the study was 0·17 per cent, almost five times the atmospheric value (Table II). The standard deviation about the mean was 0·102 per cent and the coefficient of variation (CV) 60·2 per cent. The highest level of CO_2 recorded at 30 cm depth was 0·555 per cent in a level transect well on 15 March 1986. These statistics indicate considerable variability in measured soil CO_2 values during the study period. Closer examination of the data reveals that variability in CO_2 was due to both spatial and temporal differences between measured values. For example, spatial variation is reflected in the means of measured CO_2 values at individual wells, which ranged from 0·313 per cent (L1–A) to 0·076 per cent (M5–A), as well as in the coefficients of variation of site CO_2 values on each sampling date. These values ranged from 30·7 per cent on 23 November 1985 to 40·2 per cent on 29 March

Table I. Variables used in regression studies and their possible effect on soil CO_2 levels

Variable	Possible effect on soil CO_2
Dependent	
Per cent CO_2 by volume	
Independent	
*Soil temperature at well depth (°C) *Litter temperature *Air temperature 1 m above site †Maximum daily temperature †Minimum daily temperature †Average daily temperature †Daily temperature range	CO_2 concentrations should increase as soil temperature increases, due to enhanced respiration by soil biota.
*Soil moisture at well depth (%) †Precipitation (mm)	CO_2 concentrations should increase as soil moisture increases, due to stimulation of soil biota and inhibition of upward diffusion. Precipitation also has the potential to flush CO_2 through the soil.
†Actual evapotranspiration (mm) *Soil temperature × soil moisture	CO_2 concentrations should increase with increases in both temperature and moisture.
*Relative humidity 1 m above site (%) †Maximum daily relative humidity †Minimum daily relative humidity †Average daily relative humidity	CO_2 evolution should show an inverse relationship to the vapour pressure deficit.
‡Soil Bulk Density ‡Soil Texture	CO_2 concentrations should increase with an increase in bulk density and clay content, due to the inhibition of upward diffusion.

* Measured at site on each sampling date.
† From weather data for a U.S. Forest Service weather station 2 km from the study area. Estimates of these variables were made for 1, 7, 14, 28 and 56 days prior to soil CO_2 measurements.
‡ Measured at site prior to sampling initiation.

Table II. Variations in transect soil CO_2 during the study period

Transect	Mean soil CO_2* (%)	Standard deviation (%)	Coefficient of variation (%)	Number of measurements
Level	0·175	0·114	65·4	109
Deciduous	0·158	0·097	61·5	107
Mixed	0·139	0·085	61·3	102
Evergreen	0·207	0·095	45·9	107
All transect data	0·170	0·102	60·2	425

* Estimates are based on measurements at individual wells.

1986 (Tables III and IV). Temporal variability is reflected in the values of soil CO_2 averaged by sampling date, which ranged from 0·301 per cent on 23 November 1985 to 0·110 per cent on 26 October 1985, and also in the large coefficients of variation about individual well means. These values ranged from 61·1 per cent (L3–B) to 31·0 per cent (M2–B) (Tables III and IV).

Based on their work in New Zealand, Gunn and Trudgill (1982) have argued that soil CO_2 concentrations at any particular point in space and time depend as much on local factors controlling soil gas diffusivity as on weather patterns which control production rates. Therefore, they suggest that spatial variations in measured CO_2 may be large enough to mask temporal variations induced by changing environmental conditions. Our non-growing season CO_2 data provided a rigorous test of this argument as CO_2 levels and temporal fluctuations in this season are of much lower magnitude than is typical of the spring and summer months.

The test was conducted by a one-way analysis of variance for both the entire data set (425 well measurements) and for each of the four transects separately. Data were partitioned into eleven groups by

Table III. Well and site soil CO_2 characteristics in the level, deciduous, mixed, and evergreen transects

Transect and site	Site data*		Well A		Well B		Difference between wells A and B	
	Mean (%)	CV (%)	Mean (%)	CV (%)	Mean (%)	CV (%)	Largest (%)	Mean (%)
Level transect								
L1	0·306	41·8	0·313	42·9	0·298	46·0	0·169	0·063
L2	0·125	58·9	0·122	63·3	0·129	57·3	0·095	0·018
L3	0·145	60·6	0·136	60·9	0·155	61·1	0·057	0·024
L4	0·138	54·3	0·135	55·9	0·133	59·2	0·116	0·025
L5	0·164	51·9	0·180	50·8	0·148	54·2	0·069	0·031
Deciduous transect								
D1	0·189	48·9	0·186	47·2	0·192	51·4	0·080	0·015
D2	0·111	49·9	0·113	51·8	0·110	49·0	0·040	0·011
D3	0·109	42·7	0·081	48·8	0·133	48·5	0·121	0·063
D4	0·139	47·3	0·117	48·0	0·160	49·0	0·107	0·048
D5	0·245	42·9	0·249	49·6	0·242	41·6	0·127	0·043
Mixed transect								
M1	0·123	32·8	0·139	39·0	0·107	38·9	0·145	0·064
M2	0·160	30·4	0·158	32·7	0·163	31·0	0·078	0·028
M3	0·225	42·4	0·219	37·4	0·220	49·6	0·095	0·032
M4	0·088	40·3	0·099	39·6	0·077	48·1	0·061	0·020
M5	0·087	38·7	0·076	45·8	0·102	50·1	0·114	0·047
Evergreen transect								
E1	0·221	32·4	0·258	33·1	0·184	39·9	0·257	0·078
E2	0·161	33·5	0·155	34·4	0·166	38·0	0·131	0·029
E3	0·166	37·0	0·199	36·7	0·128	46·9	0·182	0·072
E4	0·250	29·1	0·244	31·7	0·256	35·7	0·223	0·053
E5	0·246	42·4	0·225	54·2	0·247	37·7	0·071	0·033

* Site values are averages of Wells A and B.

Table IV. Temporal and spatial variability in transect site soil CO_2 values

Sampling date	Level transect*		Deciduous transect*		Mixed transect*		Evergreen transect*		All data†	
	Mean (%)	CV (%)	Mean (%)	CV (%)	Mean (%)	CV (%)	Mean (%)	CV (%)	Mean (%)	CV (%)
26 Oct. 1985	0·083	38·9	0·124	28·6	0·097	46·2	0·138	28·6	0·110	37·6
9 Nov. 1985	0·229	26·0	0·243	36·6	0·166	47·1	0·300	15·8	0·234	34·5
23 Nov. 1985	0·306	25·0	0·296	39·0	0·251	41·8	0·349	18·8	0·301	30·7
7 Dec. 1985	0·269	48·3	0·240	38·2	0·140	41·5	0·258	34·4	0·227	45·1
7 Jan. 1986	0·128	66·9	0·103	40·8	0·104	45·5	0·157	23·1	0·123	45·8
18 Jan. 1986	0·104	46·9	0·102	36·8	0·112	37·7	0·186	14·8	0·126	40·7
1 Feb. 1986	0·122	67·8	0·089	48·1	0·090	39·4	0·155	17·0	0·114	48·1
15 Feb. 1986	0·119	67·2	0·103	43·4	0·105	50·6	0·143	31·0	0·117	47·0
1 Mar. 1986	0·103	40·8	0·121	36·1	0·121	44·1	0·170	22·6	0·129	37·5
15 Mar. 1986	0·290	38·2	0·176	31·5	0·144	50·1	0·219	26·6	0·208	43·6
29 Mar. 1986	0·178	69·0	0·149	44·0	0·171	56·2	0·222	32·0	0·180	49·2
Average‡	0·175	48·6	0·159	38·5	0·136	45·5	0·209	24·1	0·170	37·6

* Means and CV values calculated from five averages (i.e. from averages of the two well values).
† Means and CVs calculated from 20 site averages.
‡ Calculated by averaging values given in the table.

sampling date. The analysis of variance attempted to determine if 'between' group variance, that is temporal variability in soil CO_2, exceeded 'within' group variance, or the spatial variability in soil CO_2 on each sampling date. For the entire data set, and for each of the four transects, the analyses showed much greater temporal than spatial variability in CO_2, the differences being significant statistically at the 0·0001 confidence level. This is an important result because it suggests that even in the non-growing season the greatest variability in CO_2 occurs in response to temporal changes in production rates influenced by environmental conditions.

Spatial variations in soil CO_2

Although some previous studies of soil CO_2 have shown consistent relationships with hillslope position (e.g. de Jong, 1981; Garrett and Cox, 1973) our results showed no statistically significant relationship with this environmental variable in the three transects located on slopes. Marked differences in soil CO_2 over distances of 0·5–20 m and broad differences in CO_2 between transects were apparent, however. These differences will now be examined in more detail.

Differences between transects. Mean CO_2 measured in the level, deciduous, evergreen, and mixed transects was 0·175, 0·158, 0·207, and 0·139 per cent, respectively, and the average coefficient of variation by sampling date was 48·6, 38·5, 24·1, and 45·5 per cent (Tables II and IV). Significantly, the highest mean CO_2 value and the lowest observed variability was in the evergreen transect which had the highest mean CO_2 on every sampling date but two (7 December 1985 and 15 March 1986) when the highest values occurred in the level transect (Table IV). Also, the evergreen transect had the largest measured difference between wells in well pairs (0·223 per cent compared with 0·169, 0·127, and 0·145 per cent for the level, deciduous, and mixed transects, respectively), as well as the highest mean difference between well pairs (0·053 per cent compared to 0·032, 0·036, and 0·038 per cent for the level, deciduous, and mixed transects, respectively) (Table III).

A one-way analysis of variance was conducted (Tukey's studentized range test) to determine if differences in soil CO_2, moisture, temperature, and bulk density between the evergreen and the other three transects (made up largely of deciduous trees) were statistically significant. It was found that soil CO_2 was significantly higher in the evergreen transect at the 0·05 significance level. Soil moisture was significantly lower and soil temperature was significantly higher at the 0·05 level. Differences in bulk density were not statistically significant.

The higher soil CO_2 in the evergreen transect is attributed to the continued growth activity of the evergreen trees during the 'non-growing' season. Generally, the largest differences between the evergreen and deciduous stands occurred towards the middle of the non-growing season. Presumably at this time, the deciduous trees had essentially terminated root respiration, while the evergreen stand continued to be active. Early in the non-growing season, and as the growing season was approaching, the difference in soil CO_2 between the stands was less pronounced, because both stands were actively respiring CO_2 into the soil. Continued respiration of CO_2 in the evergreen transect would raise soil CO_2 levels near roots, increasing differences between closely-spaced sites (e.g. individual wells in well pairs). The forest floor in the evergreen transect generally received greater insolation than the other transects due to its aspect and canopy density. This accounts for the higher soil temperatures in this transect. The higher temperatures, coupled with increased transpiration could account for the lower soil moisture levels.

Differences in CO_2 over distances of 0·5 *to* 20 *m.* Well pairs were spaced 2, 10, 15, and 20 m apart in the level, deciduous, evergreen, and mixed transects, respectively. The wells in each pair were 1·0 m apart in the deciduous, mixed, and evergreen transects, and 0·5 m apart in the level transect. This spacing provided a means of assessing spatial variations in CO_2 at distances of 0·5 to 20 m. Mean differences in CO_2 between adjacent well pairs in the level, deciduous, evergreen, and mixed transects were 0·064, 0·059, 0·053, and 0·067 per cent, respectively, and the largest differences measured were 0·142, 0·127, 0·069, and 0·118 per cent. Mean differences in CO_2 measured in individual wells of well pairs were 0·032, 0·035, 0·054, and 0·036 per cent in the level, deciduous, evergreen, and mixed transects, respectively, and the largest differences measured were 0·169, 0·127, 0·257 and 0·145 per cent. Most of the mean differences were greater than the atmospheric CO_2 level and the largest difference measured (0·257 per cent) was almost seven times this value (Table III).

Such spatial variations in soil CO_2 could be due to differences in soil texture and bulk density which affect gas diffusivity from the soil, or to differences in soil moisture or soil temperature which affect both production and loss of CO_2 from the soil. Measured differences may also reflect the fact that some wells are closer to plant roots or pockets of microbial activity, both of which are centres of CO_2 production.

The effects of soil texture, bulk density, and soil temperature and moisture at 30 cm on site CO_2 values (averages of wells in each well pair) were examined. This was done for each of the four transects separately, and also for these data combined. Transect data were examined separately because CO_2 in the evergreen forest was found to be significantly higher than in the other forest types and this was attributed to the continued activity of the evergreen trees during the 'non-growing' season. Correlation analysis revealed no statistically significant relationships between soil CO_2 and any of the variables examined.

Data from the level transect provided an opportunity to assess the possible effects of tree root systems (and associated pockets of microbial activity) on soil CO_2. In the level transect five well pairs (L1 to L5) were installed 2 m apart from the base of a white oak 36·8 cm in diameter (dbh) to the base of a second younger white oak 19·7 cm in diameter. Individual wells of each pair were 0·5 m apart (Figure 3). Significantly, the well pair nearest to the large white oak (L1) had the highest mean CO_2 (0·306 per cent) and the lowest coefficient of variation (41·8 per cent) of the well pairs. The well pair nearest the smaller oak (L5) had the next highest mean CO_2 (0·164 per cent) and the second lowest coefficient of variation (51·9 per cent). The other three well pairs had lower average CO_2 and higher variability (Table III, Figure 3).

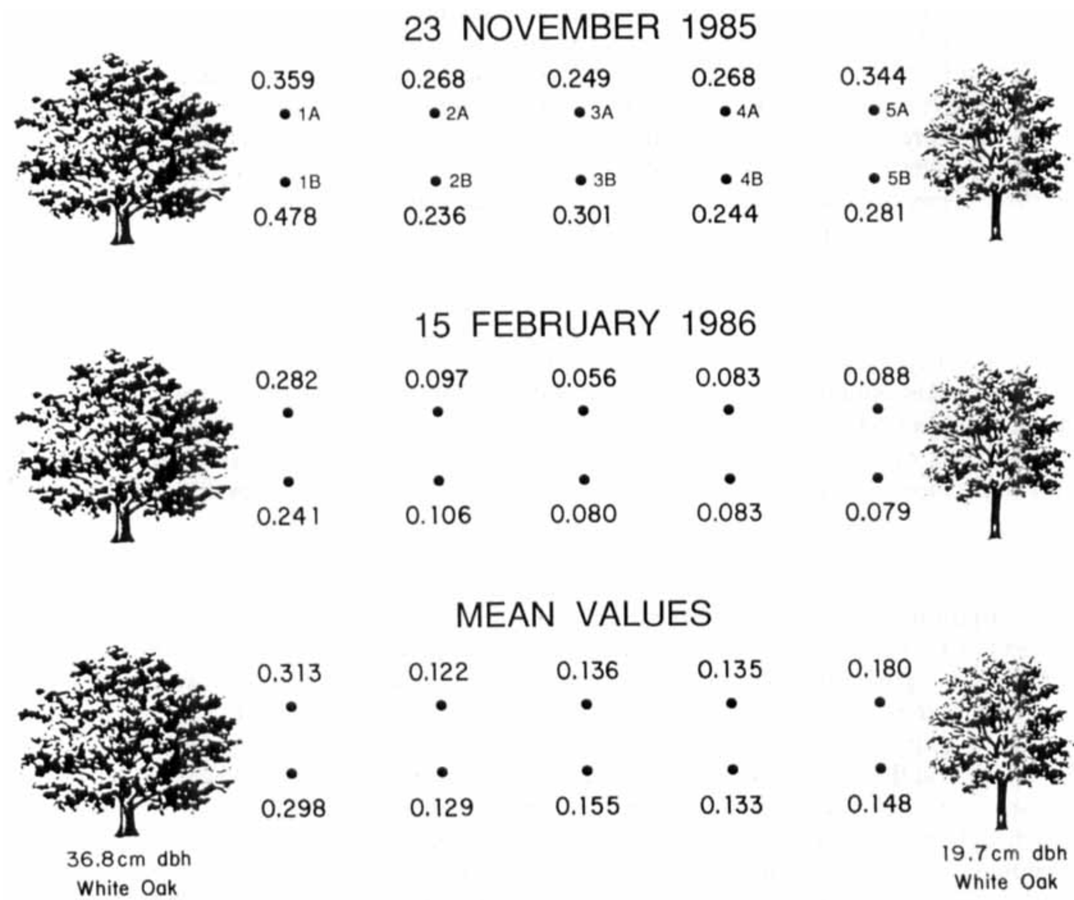

Figure 3. Soil CO_2 percentages in level transect wells 23 November, 1985, 15 February, 1986 and mean values

Mean values of CO_2 for the ten wells in the level transect as well as values for 23 November 1985 when average transect CO_2 levels were high, and for 15 February 1986 when these values were low are shown in Figure 3. Well L1–A had the highest mean CO_2 during the study period (0·313 per cent) followed by L1–B (0·298 per cent) and L5–A (0·180 per cent). Well L5–B had the fifth highest mean value. At times of high or low CO_2, and indeed on every sampling date, CO_2 in wells L1–A and L1–B was higher than in other wells in the transect, and wells L5–A and L5–B showed consistently high values compared to wells L2, L3, and L4. These findings indicate that soil CO_2 was generally higher closest to the two trees and lower away from them throughout the non-growing season.

In fact, wells L1–A and L1–B, sited at the base of a deciduous tree dormant for much of the study period, had some of the highest CO_2 values recorded at any site during the study. During the non-growing season, respiration of CO_2 may have virtually ceased from the white oak. It is possible, however, that the extensive root system of the large tree, and to a lesser extent that of the younger white oak, fostered 'pockets' of microbial activity within the soil which continued to produce CO_2 even in the absence of root respiration. If this was so, it is apparent that proximity to vegetation may play a major role in controlling spatial variations in soil CO_2 in the non-growing season and perhaps also at other times of the year. In the non-growing season both root respiration and microbial activity in evergreen forest may produce spatial differences in soil CO_2, in deciduous forest microbial activity alone may be responsible for observed spatial variations.

In conclusion, it appears from the data presented that, at least in the Whitehall Forest of Georgia during the non-growing season, marked spatial variations in soil CO_2 are not due to hillslope position or to differences in soil properties (texture, bulk density, temperature, moisture) but appear to be due to the nearness and abundance of sources of CO_2—particularly plant roots and pockets of microbial activity.

Temporal variations in soil CO_2

As Figure 4 shows, well pair averages for each sampling period varied considerably from site to site in each of the four transects. However, temporal trends in site means were generally similar, with site CO_2 trend lines being essentially parallel to one another. Previous analysis demonstrated that the intersite differences in CO_2 could not be explained in terms of soil properties. Therefore, it is clear that no single model can be expected to explain variations in CO_2 levels at every site monitored. To overcome this problem mean CO_2 values for the study area were calculated for each sampling date and these values were used in the analysis of temporal trends.

Temporal variations in transect means and in data set means are shown in Figure 5 along with data on selected environmental variables. Precipitation was 2·8 cm and 6·3 cm above normal and average monthly temperatures 2·4°C and 5·3°C above normal in October and November, respectively. The rest of the study period was characterized by temperatures just slightly below normal, however, precipitation between December and March was 26·7 cm below normal. It is noteworthy that the two peaks seen in the CO_2 record (23 November 1985 and 15 March 1986) occurred when a significant precipitation event occurred in the two days before CO_2 sampling (5·2 cm and 3·4 cm total, respectively). These precipitation events may have facilitated soil respiration and inhibited diffusion losses of CO_2, but perhaps more likely the precipitation acted to flush CO_2 downwards from higher in the profile.

To explain the observed temporal variations in soil CO_2, mean values were analysed against the environmental variables listed in Table I using multiple linear regression. It was realized that CO_2 might not demonstrate a linear relationship with the environmental variables. Indeed, a logistic or 'S' curve, which is characteristic of many biologically based responses might be expected, as initial low levels of CO_2 increase sharply with a rapid response to environmental stimuli, eventually reaching some upper limit. Soil CO_2 levels showed no signs of reaching an upper limit during this study. This was to be expected since CO_2 levels are relatively low throughout the non-growing season as biotic activity is depressed. The data acquired during this study apparently represent the linear segment of a probable non-linear relationship. Scatter diagrams revealed essentially linear relationships between CO_2 percentages and the various independent variables in Table I, so CO_2 percentages were not transformed when used in regression analysis.

Mean CO_2 concentrations across all sites were analysed first. The variable which emerged as the best predictor of these values was the average difference between the daily high and low temperatures for the 28

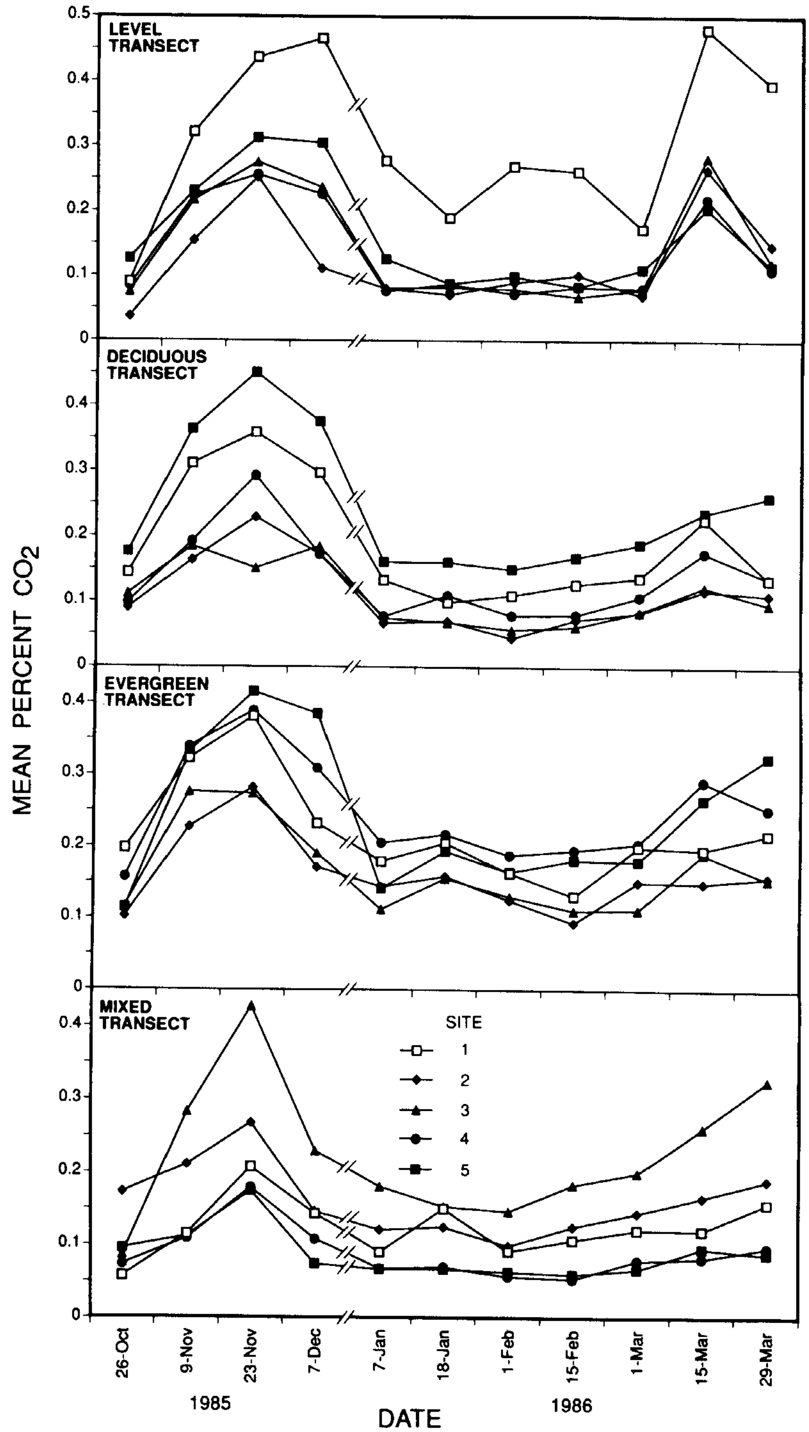

Figure 4. Temporal variations in transect well-pair CO_2 averages

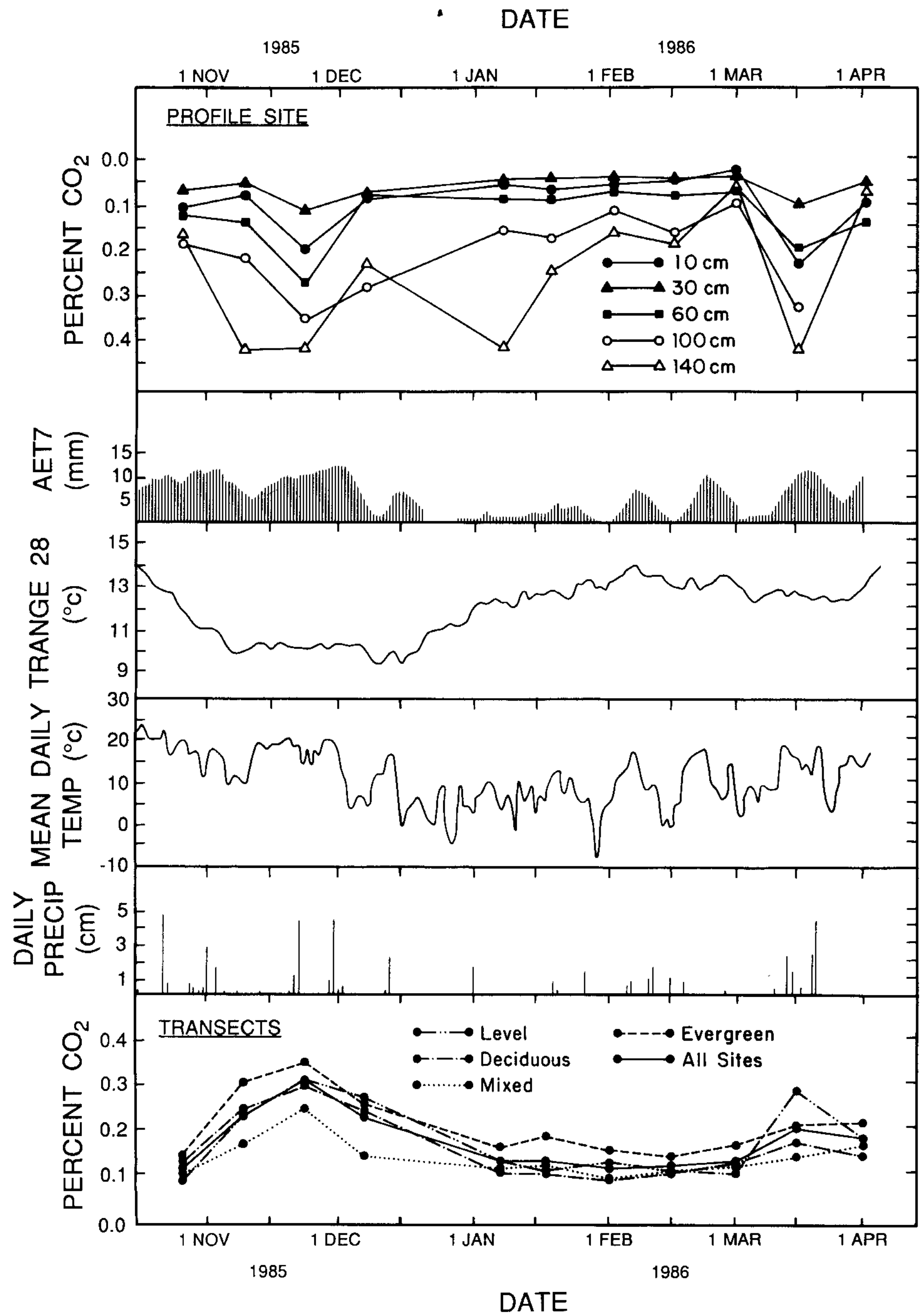

Figure 5. Temporal variations in measured soil CO_2 and in selected climatic variables

days prior to sampling (TRANGE28), which accounted for 58 per cent of the variability in mean CO_2 concentration. The best two-variable model included TRANGE28, as well as actual evapotranspiration during the week prior to sampling (AET7). The model which provided the highest level of explanatory power was:

$$\mathrm{MEANCO_2} = 0{\cdot}445 - 0{\cdot}026\,(\mathrm{TRANGE28}) + 0{\cdot}008\,(\mathrm{AET7}) \qquad R^2 = 0{\cdot}76$$

where $MEANCO_2$ is in per cent by volume, TRANGE28 is in degrees celsius, and AET7 is in millimetres (Figures 5 and 6). All regression coefficients were significant at the 0·05 level.

In an attempt to determine if the controlling factors on CO_2 concentrations were uniform between forest types, the data from the deciduous and the evergreen stands, the two end members of the vegetation types under investigation, were analysed separately. The sample size remained 11 for each subset, one value for each sampling date. Each of these values consisted of the mean value of all five well pairs within each forest type (i.e. 10 wells averaged over each sampling period).

When one-variable regression models were generated, TRANGE28 again emerged as the variable accounting for the greatest amount of variability in both the deciduous and evergreen stands (accounting for 76 per cent and 59 per cent, respectively). The best two-variable model also included TRANGE28 and AET7 for both forest types, again with a greater amount of variability in mean soil CO_2 being accounted for in the deciduous stand compared to the evergreen stand (89 per cent and 71 per cent, respectively). The difference in predictive power between the two stands may be attributable to the greater variability in the response of non-dormant evergreen trees. The emergence of the same environmental variables in the regression analysis attests to the importance of temperature and moisture in influencing soil CO_2 concentrations, and also indicates that the response of soil CO_2 to changes in these variables is lagged.

SOIL CO_2 VARIATIONS AT THE PROFILE SITE

The mean soil CO_2 measured at the profile site was 0·140 per cent over 52 measurements. Average values over the study period increased from 0·054 per cent at 10 cm depth to 0·247 per cent at 140 cm depth (Table V). The three lowest values measured were close to atmospheric (0·028, 0·032, and 0·034 per cent) and all at 10 cm depth reflecting diffusion losses to the atmosphere close to the soil surface. The three highest values (0·417, 0·415, and 0·415 per cent) were all at 140 cm depth. Over the period of study averages of the five measurements (where all five were successful) varied from 0·268 per cent on 23 November 1985 to 0·096 per cent on 15 February 1986.

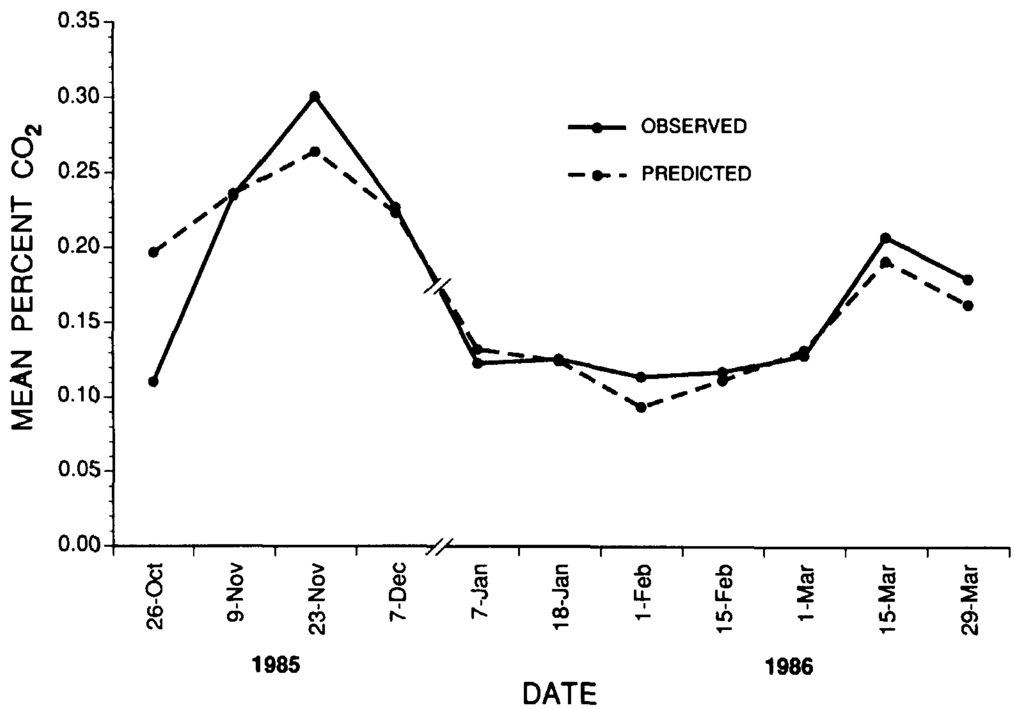

Figure 6. Temporal trends in measured and predicted mean transect CO_2

Table V. Variations in soil carbon dioxide with depth at the profile site

Date	Soil CO_2 (%) 10 cm	30 cm	60 cm	100 cm	140 cm	Mean
26 Oct. 1985	0·062	0·102	0·110	0·175	0·161	0·122
9 Nov. 1985	0·045	0·073	0·132	0·201	0·417	0·174
23 Nov. 1985	0·109	0·196	0·269	0·353	0·415	0·268
7 Dec. 1985	0·065	0·077	0·070	0·279	0·226	0·143
7 Jan. 1986	0·038	0·039	0·074	0·144	0·410	0·141
18 Jan. 1986	0·034	0·060	0·073	0·163	0·235	0·113
1 Feb. 1986	0·028	0·043	0·059	0·104	0·151	0·077
15 Feb. 1986	0·032	0·035	0·072	0·164	0·178	0·096
1 Mar. 1986	—	—	0·055	0·084	0·043	—
15 Mar. 1986	0·091	0·225	0·187	0·321	0·415	0·248
29 Mar. 1986	0·039	0·090	0·128	—	0·062	—
Mean	0·054	0·094	0·112	0·199	0·247	0·140

Variations in soil temperature, soil moisture, and soil CO_2 with depth on the eleven sampling dates in 1985–86 are shown in Figure 7. Measured CO_2 percentages are presented in Table V. The data clearly show an increase in soil CO_2 with depth over the study period, and except for soil moisture on 26 October 1985 and 9 November 1985, increasing soil temperature and soil moisture with depth is also indicated. Regression modelling of soil CO_2 in terms of soil moisture and soil temperature did not, however, produce statistically significant relationships, suggesting that the observed increase in soil CO_2 with depth may be due largely to the gradual diffusion of CO_2 from the soil into the atmosphere at a rate largely determined by soil properties.

However, as Table V shows, mean CO_2 of the five wells varied considerably with sampling date, suggesting that in addition to a depth control on CO_2 there were also temporal environmental controls. To determine which environmental factors were most influencing the input of CO_2 to the soil at the profile site, correlation and regression procedures were used with soil CO_2 as the dependent variable and soil depth and the environmental variables listed in Table I as the independent variables.

The variable DEPTH was found to explain the highest percentage of soil CO_2 variability at the profile site. Indeed, when mean CO_2 was regressed against well depth, the following model resulted:

$$\mathrm{MEANCO_2} = 0{\cdot}035 + 0{\cdot}0015(\mathrm{DEPTH}) \qquad R^2 = 0{\cdot}99$$

where $\mathrm{MEANCO_2}$ is mean per cent CO_2 by volume, and DEPTH is depth below the soil surface in centimetres. The regression coefficient was significant at the 0·0005 level. The model correctly predicts that CO_2 at the soil surface (DEPTH = 0) is essentially the atmospheric level (model predicts 0·035 per cent). This result suggests that during the non-growing season variations in CO_2 with depth (to 140 cm) are of greater magnitude than temporal variations induced by changing environmental conditions.

When temporally-varying environmental variables were entered into the analysis, the following model emerged as the best predictor of soil CO_2:

$$CO_2 = 0{\cdot}291 + 0{\cdot}0015\,(\mathrm{DEPTH}) + 0{\cdot}0126\,(\mathrm{AET7}) - 0{\cdot}0262\,(\mathrm{TRANGE56}) \qquad R^2 = 0{\cdot}66$$

where TRANGE56 is the average daily temperature range in the eight weeks prior to sampling. Regression coefficients were significant at the 0·005 level.

DISCUSSION

In the Whitehall Forest of Georgia during the period 26 October 1985 to 29 March 1986 soil CO_2 varied with soil depth, varied spatially at constant depth, and varied temporally with changing environmental conditions. Variations with depth in the upper 1·4 m of the soil profile were of greater magnitude than temporal variations, and spatial variations at 30 cm depth were of lesser magnitude than temporal variations.

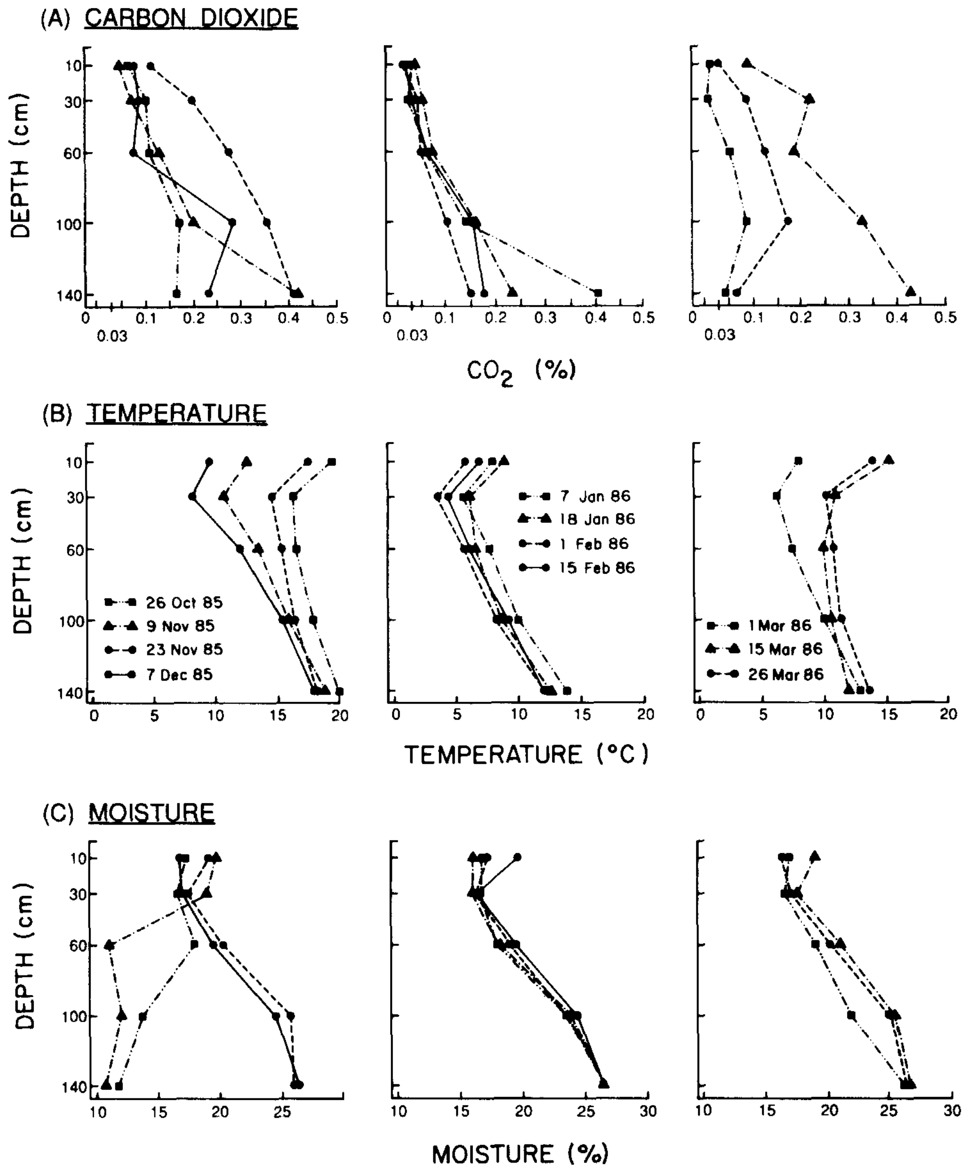

Figure 7. Variations in soil CO_2, soil temperature, and soil moisture with depth at the profile site

At the profile site the average increase in CO_2 with depth was 0·15 per cent per 100 cm to 1·4 m. The measured gradient is believed to reflect the balance between the gas diffusivity of the soil, and the production of CO_2 by plant respiration and microbial activity. The observed CO_2-depth relationship suggests that even during the non-growing season CO_2 levels at depths of more than about 2 m are likely to be more than ten times the atmospheric level. Assuming that the observed linear increase in CO_2 with depth continues beyond 1·4 m, a level of 1·0 per cent CO_2 should be reached at 6·4 m. As diffuse ground water recharge in carbonate areas often penetrates deep, soil-filled, karstic fissures on its way to the ground water body, the assumption of a non-growing season CO_2 level of 1·0 per cent by Trainer and Heath (1976) does not seem unreasonable.

In the Whitehall Forest, forest type was found to be an important determinant of non-growing season soil CO_2. CO_2 levels were much higher in evergreen coniferous forest, which remains active in the 'non-growing' season, than they were in deciduous and mixed forest where the majority of trees are dormant during this time. Mean measured soil CO_2 in evergreen forest was 0·207 per cent, in deciduous and mixed forests it averaged 0·157 per cent.

No trends in soil CO_2 were observed along hillslopes, nor were there statistically significant spatial relationships between soil CO_2 and soil texture, bulk density, moisture content, and temperature on any of the sampling dates or for the entire study period. A positive relationship between soil CO_2 and proximity to vegetation in the level transect, however, suggests that much of the non-growing season spatial variation in soil CO_2 over distances from 0·5 to 20 m may be due to the proximity and density of roots that respire CO_2 or to pockets of microbial activity which may also be more common within plant root systems.

At 30 cm depth in the four transects and at various depths at the profile site, soil CO_2 was found to vary significantly over time with changing temperature and moisture conditions. At 30 cm depth the two variables TRANGE28 and AET7 explained 76 per cent of the variation in sampling date mean CO_2 values while at the profile site 66 per cent of CO_2 variability was explained by DEPTH, AET7, and TRANGE56. In both cases actual evapotranspiration in the week prior to sampling provided a statistically significant degree of explanation of soil CO_2 levels. This is not surprising for this variable is derived from precipitation, soil moisture, and temperature data and is thus a measure of the interactive effect of temperature and moisture on biogenic activity (Brook *et al.*, 1983; Kiefer, 1990).

The emergence of temperature range as a significant predictor of soil CO_2 was not as intuitive. It appears that the positive influence of higher temperatures on biogenic CO_2 production—as reflected in high AET7 values—is conditioned by the inhibitory effect that low temperatures have on the respiring soil biota. High daytime temperatures stimulate photosynthesis and increase root respiration; when evening temperatures are also high (the daily temperature range is small) CO_2 continues to enter the soil via the roots. If evening temperatures are cool, however (the daily temperature range is large), metabolism and consequently respiration is reduced resulting in lower soil CO_2 levels.

Soil CO_2 at the profile site to depths of 1·4 m was influenced by the temperature range in the 56 day period before measurement (TRANGE56); in the four transects CO_2 at 30 cm depth was affected by the temperature range only in the 28 days before measurement (TRANGE28). This difference may be due to the fact that temperature conditions deeper in the soil profile respond to ambient temperatures with greater lags. For example, at the profile site soil temperatures at 10 and 30 cm depth were strongly related to average daily temperatures during the previous week ($r = 0{\cdot}96$ and $r = 0{\cdot}98$ respectively), while temperatures at 60 cm correlated best with mean daily temperatures during the previous four weeks ($r = 0{\cdot}95$) and temperatures at 100 and 140 cm with air temperatures during the previous eight weeks ($r = 0{\cdot}99$ and $r = 0{\cdot}98$ respectively). Since the model developed for CO_2 at the profile site included CO_2 data to 1·4 m depth, it is to be expected that the temperature variable in the model would be more lagged than that in the model developed using transect data for conditions at 30 cm depth.

In conclusion, soil CO_2 in the Whitehall Forest of Georgia during the non-growing season appears to depend on depth below the surface, on vegetation type, on the environmental variables actual evapotranspiration and temperature range, and possibly also on proximity to sources of CO_2 production (roots and pockets of microbial activity). Regression modelling indicates that temporal changes in average CO_2 for an area can be predicted using climatic/water balance variables but that spatial variations controlled by soil biogenic activity cannot be predicted accurately because of the difficulty of acquiring data on plant root and soil microbe locations and densities.

Our finding that temperature range is an important control of non-growing season soil CO_2 production suggests that different climatic variables may affect soil CO_2 in different seasons. Temperature range may affect CO_2 production during the cold season in temperate regions when daily temperature minima are sufficiently low to inhibit biogenic processes. In the warm season this may not be the case, and daily temperature averages or maxima may exert stronger control on soil CO_2 levels.

The finding that soil CO_2 levels beneath evergreen forest were higher than beneath deciduous forest throughout the non-growing season suggests that ground waters and soil water recharge from these stands should be more acid and therefore more capable of chemical weathering and solutional denudation than recharge waters from areas of deciduous forest. Further studies are needed to explore the possibility of more rapid landform development under evergreen forest in eastern North America.

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