A CHARACTERIZATION OF DAILY AND SEASONAL CARBON DIOXIDE PATTERNS IN A MID-MISSOURI, CLIMAX OAK-HICKORY FOREST [1]

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ABSTRACT

Carbon dioxide relationships were monitored daily and seasonally within a climax oak-hickory forest. Diurnal and seasonal CO_2 patterns were correlated with the state of biological activity while day-to-day variability was influenced by changes in the physical environment. Mean seasonal CO_2 concentrations were highest in the spring and lowest in the summer. The mean annual diurnal change in CO_2 concentration was 10.7% (313-344 ppm). Diurnal summer and spring variability in CO_2 concentrations correlated best with changes in net radiation and temperature, respectively, while winter and fall variability was best explained by changes in wind speed.

INTRODUCTION

The carbon dioxide content of a forest varies with changes in its biological and physical environments. Due to the influence of photosynthesis and respiration on CO_2 concentrations within a forest community, characteristic diurnal and seasonal CO_2 patterns occur (Allen et al. 1972). Day-to-day changes within a season may also be biologically influenced, with changes in the physical environment being reflected in increases or decreases in CO_2 assimilation and emission (Baumgartner 1969, Brown and Rosenberg 1970). Variability in emission and uptake in combination with the convective mixing of air masses can result in marked daily differences in CO_2 concentrations. While many studies have demonstrated such relationships in agricultural crops and coniferous forests, comparatively few recent studies have been conducted in hardwood forests (Sparling and Alt 1966, Woodwell and Dykeman 1966, Reiners and Anderson 1968, and Lemon et al. 1970). Most of these investigations were of short duration and did not encompass the yearly cycle of CO_2.

As part of a comprehensive study of the distribution of CO_2 within a climax oak-hickory forest, the objective of this study was to determine within-forest variations in CO_2 concentration both seasonally and daily.

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METHODS AND MATERIALS

Study Area

The study site is located in southeastern Boone County Missouri (38° 45′ N Lat., 92° 12′ W Long.) on variably eroded topography and is part of the Ashland Wildlife Area. The elevation varies from 175 to 245 m within the area.

All CO_2 measurements were taken over an east- and a west-facing slope covered with an overstory consisting of second-growth, relatively even-aged mixed hardwoods. The forest is dominated by white oak (*Quercus alba* L.) interspersed with black oak (*Quercus velutina* Lam.) and shagbark hickory (*Carya ovata* Mill.). Understory species consist primarily of those found in the overstory with eastern red cedar (*Juniperus virginiana* L.), flowering dogwood (*Cornus florida* L.), fragrant sumac (*Rhus aromatica* Ait.) and sassafras (*Sassafras albidum* Nutt.) being of secondary importance on the upper slopes. Sugar maple (*Acer saccharum* Marsh.) is abundant on the lower slopes and especially along the drainage separating the two slopes.

The forest is established on a Weldon silt loam soil formed from loess deposited over a cherty residuum from the Burlington limestone formation. The average height of the dominant and codominant trees is 18.3 m; crown closure occurs at approximately 14 m, while the average crown base extends down to 9 m. The average age of the overstory is 50 years and its basal area is 16.5 m^2/ha. The mean annual temperature of the area is 12.8°C and January is the only month showing a mean below freezing. The mean annual precipitation is 961 mm.

CO_2 and Environmental Data Sampling

Carbon dioxide concentration data reported herein represent 10 days each during winter and summer and 20 days each during spring and fall. The summer and winter samplings were made August 15-28 and February 27 to March 9. The fall and spring samplings include days from September 28 to October 20 and April 23 to May 20. The spring sampling covered a period during which 70% of leaf development was completed, while the fall sampling extended through the period of leaf senescence when over 60% of all leaves had dropped. Sampling in the summer and fall began at 1000 hours and continued until 0900 the next morning when the equipment was turned off for one hour for recalibration. During the winter and spring sampling was conducted from 1100 to 1000 hours.

All air samples were drawn through 4.8 mm ID polyvinyl chloride tubing (PVC) supported between two steel towers (21.3 m) by a horizontal steel cable. Six vertical sampling stations were spaced at 7.6 m intervals along the steel cable from just below the top of a west-facing slope to just below the crest of an east-facing slope. Three of the six vertical stations were sampled each day using separate strands of the PVC

tubing spaced at 3.1 m intervals to provide six separate intakes in a vertical plane at each station. The top intake consistantly held a position approximately 18.3 m above the forest floor. Each vertical station was sampled for five days during a ten-day period.

During each measurement cycle, samples were drawn from one height across the three randomly-established vertical stations; the five remaining levels were each sampled in turn until all air intake positions in the vertical profile had been sampled. Vertical sampling stations were repositioned daily according to a randomized schedule, however, vertical sampling sequences were retained throughout a ten-day sampling cycle.

The collection tubes, plus six others used to monitor soil-evolved CO_2 (Garrett and Cox 1973), were linked to 12 separate three-way solenoid valves. Each solenoid valve was connected to an input position on a cam-operated sequential valve assembly having a common outlet for each of the 12 inlets. The valve assembly provided a means of selecting one solenoid input position for each five-minute sampling period. Air-sample selection was regulated by a valve control unit which synchronized the dual-valve system, thereby regulating the selection of each new sampling position. Air was drawn from the common outlet on the valve assembly by a small pump at a rate of 2 l/min, passed through a drying agent ($Ca\ SO_4$) and into an infrared gas analyzer (Beckman 215A). Five minutes were required for each CO_2 reading and a cycle was completed every two hours.

Net radiation, wind speed, air temperature and vapor pressure deficit were evaluated on a tower positioned on the west-facing slope. Net radiation was measured above the forest using a miniature net radiometer. Wind speed was measured with cup-type anemometers at 5.9, 12.1, 15.2 and 18.3 m. Air temperatures were measured with shielded aspirated thermistors at the same heights as wind speeds. Vapor pressure deficit determinations were made from data collected with aspirated psychrometers at 5.9 and 15.2 m and only during late spring, summer and early fall. Environmental data were collected on a continuous basis at five-minute intervals.

RESULTS AND DISCUSSION

Seasonal CO_2

The diurnal concentration patterns of forest CO_2 varied significantly ($P < 0.05$) between seasons (Fig 1). The seasonal daytime low of 288 ppm occurred at 1700 hours in the summer -- the season of most active CO_2 assimilation. The maximum daytime concentration occurred during the winter when most vegetation was dormant and assimilation was at an annual low. Spring and fall daytime concentrations were not markedly different from each other but were significantly higher ($P < 0.05$) than summer and lower than winter concentrations. Photosynthesis, an important sink for CO_2 in summer had little influence on the concentration of CO_2 in late

fall or early spring (Fig 2). Bud-burst occurred during the last week of April and leaf development was about 70% complete on May 20. Consequently, since rates of net photosynthesis usually increase from leaf emergence until full leaf expansion (Schaedle 1975), spring daytime lows did not equal those of early fall or summer. Fall photosynthesis decreased from its summer peak as a result of leaf aging, therefore, CO_2 concentrations increased from the seasonal lows established during the summer. Studies of various plant associations have revealed that sharp reductions in photosynthesis and respiration accompany leaf aging, with a reduction in leaf chlorophyll content the major limiting factor (Saeki and Nomoto 1958, Bourdeau 1959, Schaedle 1975).

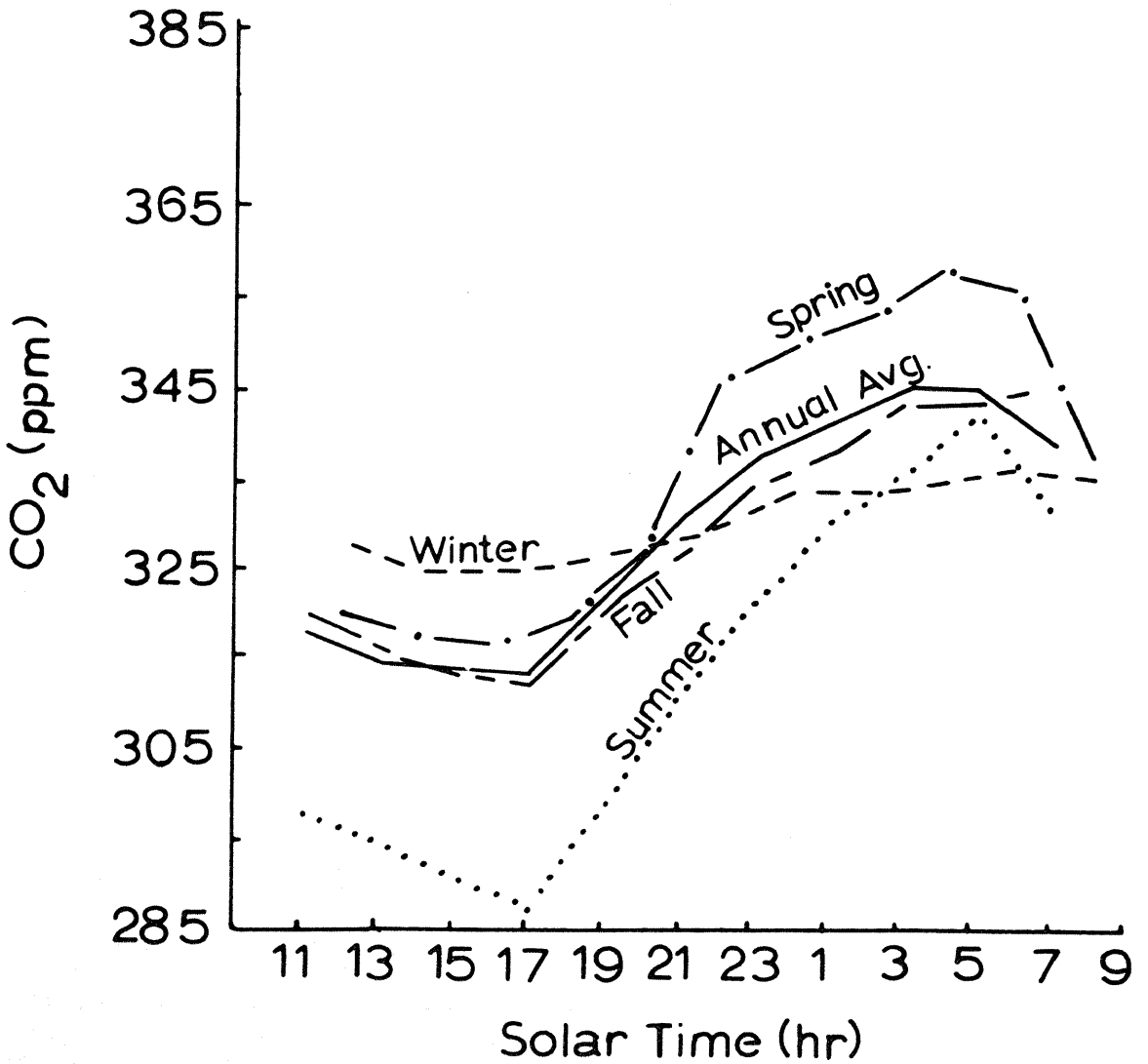


Figure 1. Mean diurnal concentrations of atmospheric CO_2 for summer (Aug. 15-28), fall (Sept. 28 to Oct. 20), winter (Feb 27 to March 9) and spring (April 23 to May 20), and the annual average.

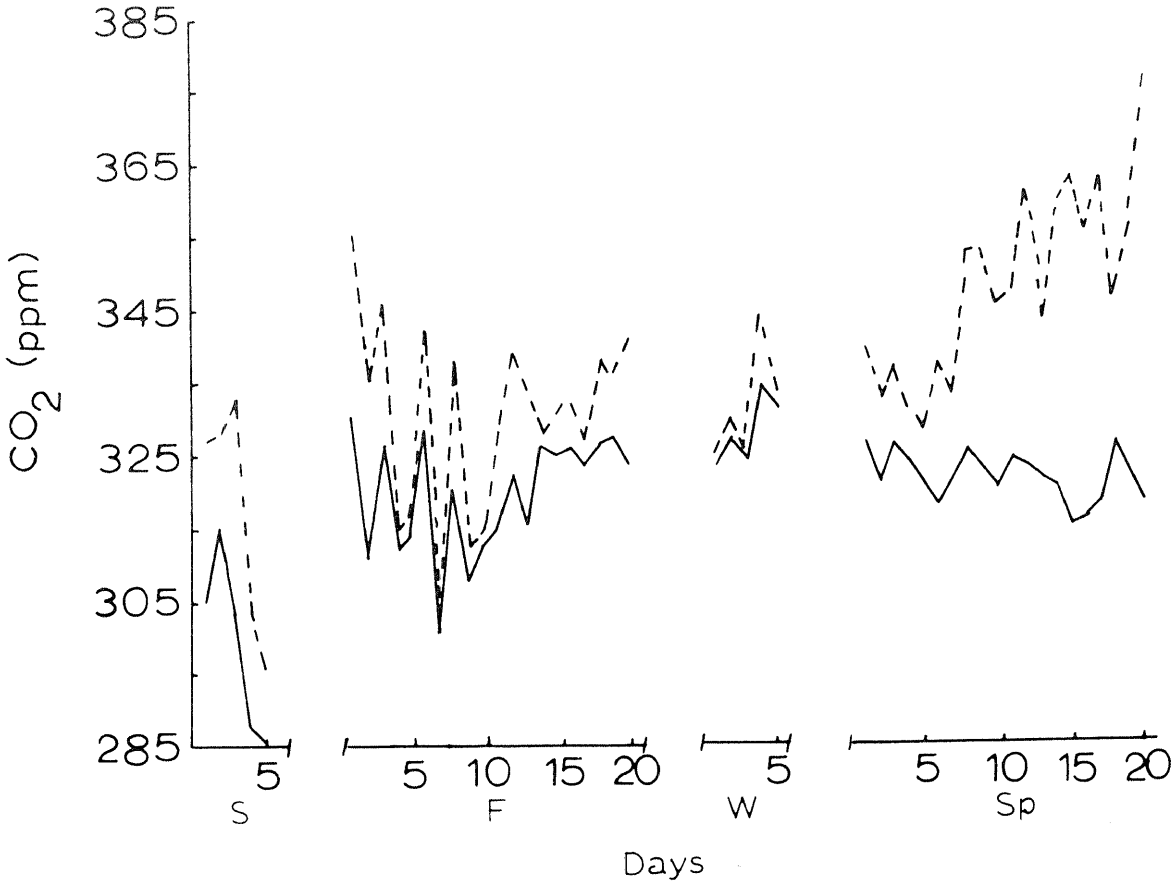


Figure 2. Mean daytime (——) and nighttime (----) CO_2 concentrations for summer (Aug. 15-28), fall (Sept. 28 to Oct. 20), winter (Feb. 27 to March 9), and spring (April 23 to May 20) days.

Nocturnal concentrations of CO_2 reached a seasonal high (359 ppm) in the spring when flower, leaf and stem respiration were at a peak and were contributing large quantities of CO_2 to the forest environment. The spring high is also in part attributed to low assimilation of CO_2 during daylight hours which resulted in maintaining high daytime CO_2 levels. Minimum nighttime concentrations were recorded during winter corresponding to the season of minimum respiration.

The greatest amplitude of diurnal fluctuation in CO_2 concentration was measured during the summer. A diurnal change of 19% occurred when CO_2 levels increased from 288 ppm at 1700 to 343 at 0500. In spring a 12.9% change was recorded, followed respectively by a 10.7 and a 3.6% change during fall and winter. Although diurnal variations of only 12 ppm (325-337) were recorded during the winter, nighttime seasonal CO_2 was again higher than daytime CO_2. It is significant that the seasonal order of amplitude of diurnal change in this forest is similar to the seasonal order for soil-evolved CO_2. The highest mean evolution rates

occurred during the summer (0.90 g/m^2 per hr) followed by fall (0.38 g/m^2 per hr), spring (0.31 g/m^2 per hr) and winter (0.11 g/m^2 per hr) (Garrett and Cox 1973).

While many investigators have attributed nighttime increases during winter to the consumption of fossil fuels and CO_2 release, such a possibility is remote in this study. Only Jefferson City which is located 22 km south of the research area, or Columbia, 26 km to the northwest, are positioned close enough to influence CO_2 levels in the Ashland Wildlife Area and neither is industrialized. We therefore conclude that the primary source of CO_2 is respiration and that build-ups resulted from reduced nighttime wind speeds. Woodwell and Botkin (1970) have demonstrated the release of significant amounts of CO_2 by various components of oak trees during the winter, and Allen (1971) attributed CO_2 build-up over an agricultural field in upper New York to winter respiration.

The average annual diurnal change in CO_2 for this forest was 10.7% ranging from a low of 313 to a high of 344 ppm (Fig 1). Similar diurnal patterns in hardwood forests have been reported by other investigators. Sukachev and Dylis (1964) reported diurnal CO_2 changes as great as 43% occurring in oak stands with daytime concentrations falling below 250 ppm during periods of active photosynthesis. Midday concentrations of 250 ppm have also been reported for tropical rain forests with nighttime levels reaching highs of 330 ppm (Lemon et al. 1970).

Daily CO_2

A regression analysis was conducted for each season in an attempt to evaluate some of the effects of environmental variables on CO_2 concentration. Independent environmental variables were net radiation (daytime only), mean air temperature, mean wind speed and mean vapor pressure deficit, while the dependent measurement was CO_2 concentration subdivided into daytime and nighttime levels. The greatest share of the annual variance in daily concentrations was associated with changes in mean wind speed. As a rule, increases in wind speed resulted in decreases in mean CO_2 levels. However, due to the interactions between biological and physical components of the forest environment, the coefficient of determination as well as the response function for most of the independent variables changed diurnally and seasonally (Table 1).

During summer daylight hours CO_2 concentration was markedly influenced by variations in net radiation, temperature and vapor pressure deficit (Table 1). Seventy-seven percent of the variability in CO_2 levels was accounted for in a regression equation using these three measurements, with changes in net radiation showing the highest coefficient of determination. The lowest CO_2 concentrations were associated with the highest net radiation levels. Geis et al. (1971) demonstrated that peak net assimilation rates for oak species correspond to peak rates of total solar radiation. Increases in CO_2 concentrations were also associated with increases in both temperature and vapor pressure deficit.

While the effect of wind speed on CO_2 concentrations was not nearly so pronounced in summer as during the other seasons, increases in daytime wind speed were associated with increases in CO_2 concentration. Increases were attributed to the influx of air from above the stand. Other investigators have demonstrated that this can occur during periods of high photosynthesis when CO_2 levels above vegetation are greater than those within (Brown and Rosenberg 1970).

Simple linear regression equations accounted for only a small portion of the variance in summer nocturnal CO_2 concentrations (Table 1). However, through multiple regression, 46% of the variability was attributed to vapor pressure deficit, temperature and their interaction. In contrast to the effects of daytime wind speeds, increased nighttime wind levels were associated with decreased CO_2 concentrations, although the effect was not significant. The overall reduced effect of wind on CO_2 concentrations during the summer would seem to result from the presence of a fully leafed canopy. While wind shear extending deep into the stand during fall, winter and spring results in strong mixing, this effect is somewhat reduced during the summer.

With the approach of photosynthetic decline in the fall (1st frost Oct. 3, killing frost Oct. 13) and the onset of winter, daily variability in CO_2 concentration became more highly correlated with the physical environment. Consequently, daytime and nighttime concentrations during the fall and winter were significantly correlated with changes in wind speed (Table 1). During the fall, temperature and vapor pressure deficit continued to influence CO_2 levels. However, it is significant that the effect of temperature in fall and winter was opposite to that observed during summer and spring. Increases in temperature were associated with decreases in CO_2 levels during both fall and winter. This is believed to be the result of temperatures which are warmer within the forest than above it causing turbulence and CO_2 advection from the stand. This could in part explain why CO_2 build-ups were not found within the forest on every night of the winter sampling period.

Data for September 28 and October 2 illustrate the effects of wind speed and turbulence on fall CO_2 levels (Fig 3). Both days were clear with similar temperature and net radiation levels. Vapor pressure deficits differed during daylight hours but were similar at night. However, major differences in wind speed were recorded throughout the 24-hour periods and a moderate thermal inversion existed within the forest on September 28 but not on October 2. Nocturnal temperatures in the forest canopy averaged 2-3°C higher than those within 5 m of the forest floor on this date. Consequently, due to decreased vertical motion and turbulence resulting from the inversion (Allen _et al_. 1972), CO_2 concentration increased from a daytime low of 311 to a nighttime high of 396 ppm on September 28. On October 2, wind speeds consistently exceeded 0.60 m/sec throughout the day and peaked at velocities in excess of 1.0 m/sec at night resulting in a high of only 321 ppm. Thermal inversions are not uncommon and can result in differences between daylight and dark CO_2 concentrations which can exceed 200 ppm (Woodwell _et al_. 1973).

Table 1. Coefficients of Determination for Daytime and Nighttime CO_2 (Concentrations by Seasons)

Independent Variable	Coefficient of Determination							
	Summer CO_2		Fall CO_2		Winter CO_2		Spring CO_2	
	Day	Night	Day	Night	Day	Night	Day	Night
1/Net Radiation	.40*	---	.05**	---	---	---	.15*	---
Wind	.11*	---	---	---	---	---	---	---
1/Wind	---	.05	.55*	.75*	.75*	.40*	.30*	.20*
Temperature	.20*	.06	---	---	---	---	.52*	.60*
1/Temperature	---	---	.50*	.30*	.05	.13*	---	---
Vapor Pressure Deficit	.24*	---	.10	.30*	---	---	.06	.27
1/VPD	---	.18	---	---	---	---	---	---

* Significant at the 0.10 percent level.
** Coefficients of less than 0.05 are not presented.

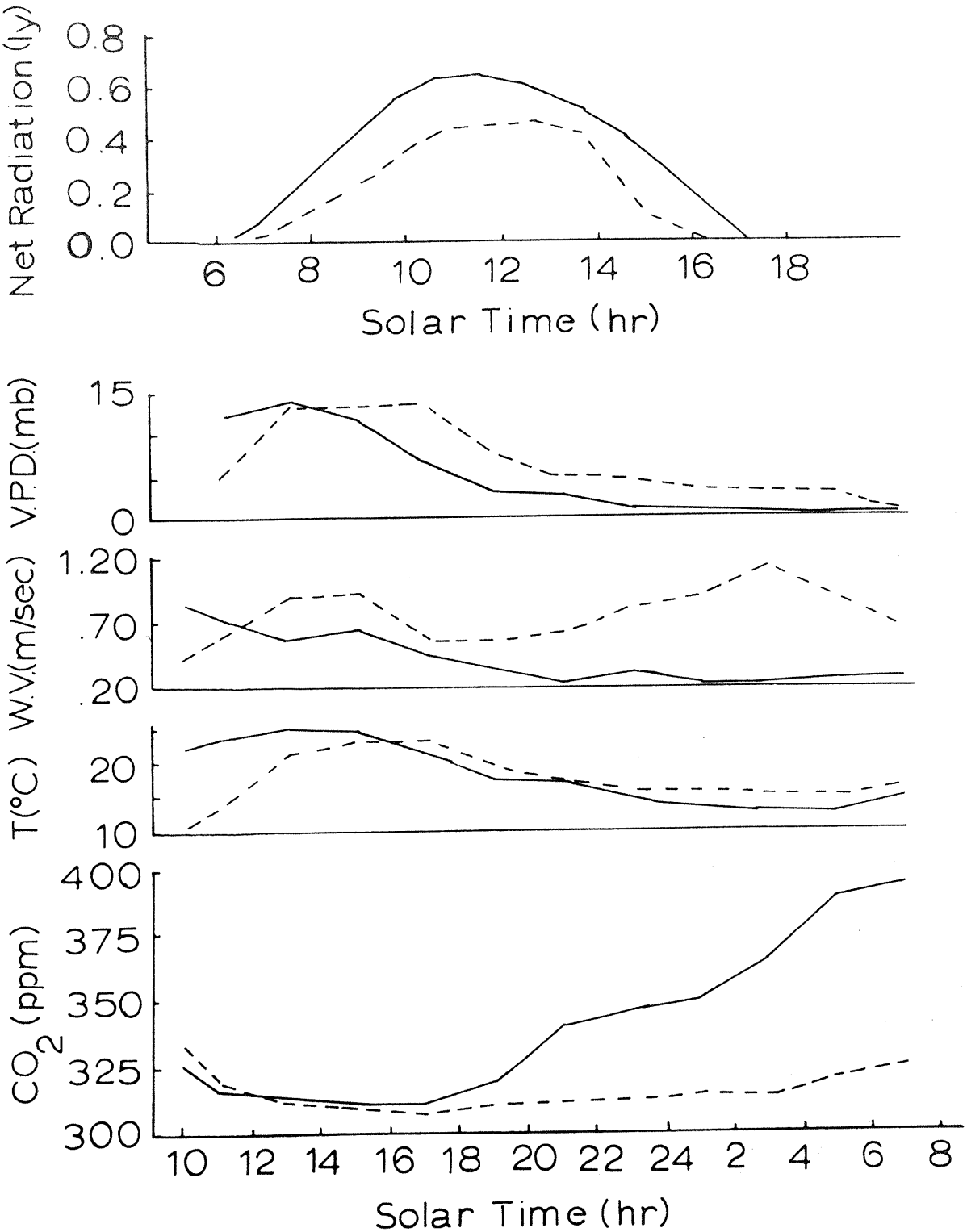


Figure 3. Net radiation, vapor pressure deficit, wind speed, temperature and CO_2 concentration for two fall days, Sept. 28 (——) and Oct. 2 (----).

During the spring, CO_2 concentrations were again influenced by changes in rates of metabolic activity. Even as early as April 23 (Day 1, Fig 2), the forest was characterized by a significant difference ($P < 0.05$) between daytime and nighttime CO_2 levels although leaf emergence did not occur until April 26-27. Throughout this period of rapid growth and development, respiration contributes heavily to the CO_2 in the air. During the period of early leaf expansion net assimilation rates may be negative with the rate of respiration exceeding photosynthesis for periods of several weeks (Schaedle 1975).

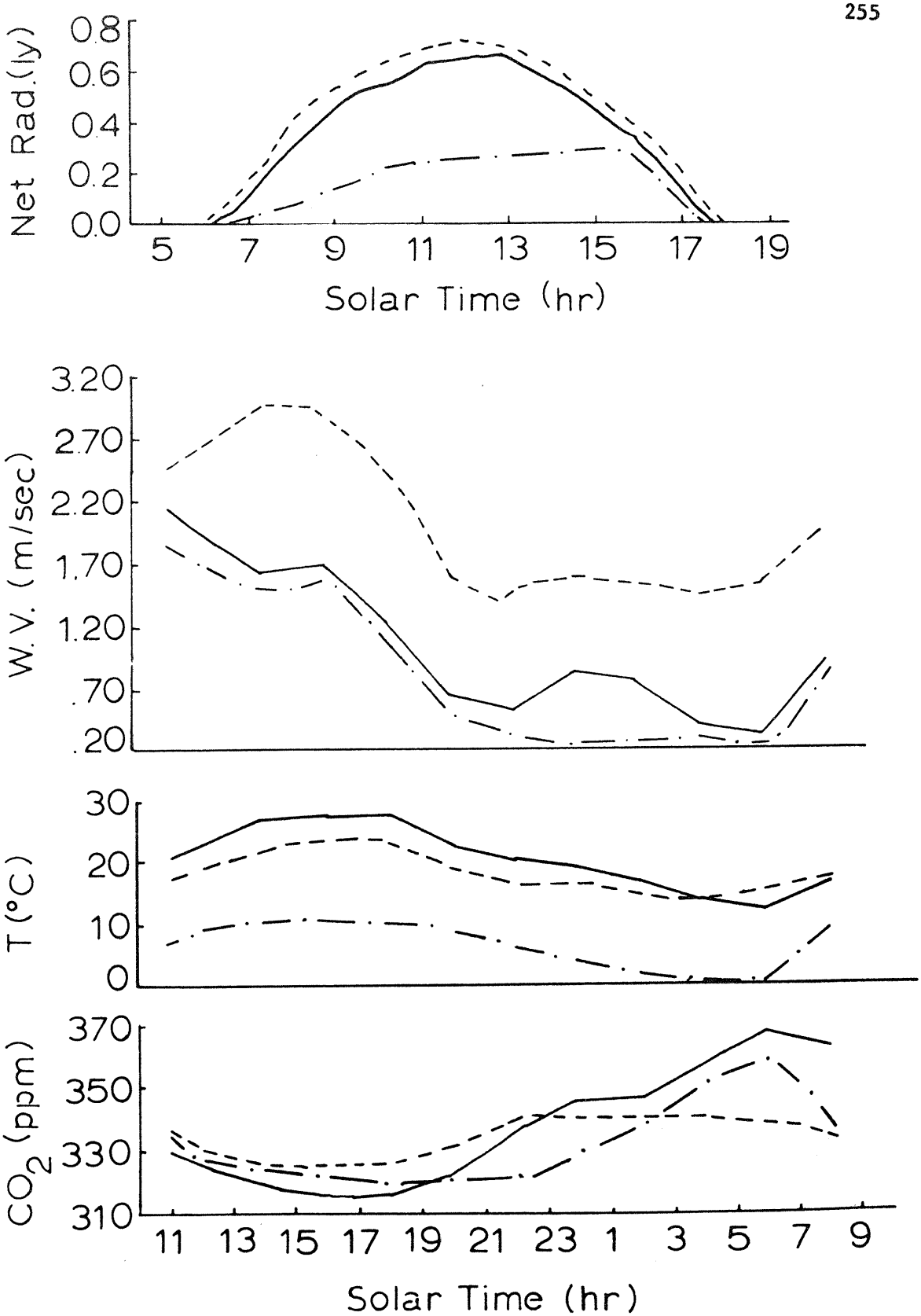
The dominance of respiration over photosynthesis during this 20-day spring period is demonstrated by an 11% increase in levels of nighttime CO_2 (339-376 ppm) and only a 3% decrease (327-317 ppm) in daytime levels (Fig 2). A decided shift in nighttime CO_2 concentration on May 2 (Day 8, Fig 2) is especially significant as it follows leaf emergence by 4-5 days and is probably the result of bud burst.

As the result of a strong correlation between temperature and respiration, the highest daytime and nighttime coefficients of determination during the spring were associated with temperature (Table 1). Increases in temperature resulted in increases in CO_2 concentration. Relatively high correlations were also obtained with the reciprocal of wind.

The effects of temperature and wind speed on CO_2 concentrations are shown for three spring days in figure 4. April 24 and April 30 had very similar wind speeds with highly dissimilar diurnal temperatures. Low temperatures on April 24 were in part due to a reduced radiation load but were primarily the result of a cool air mass which had moved into the area late the preceding night. The impact of the low temperatures caused a reduction in respiration and low CO_2 concentrations in the forest. While CO_2 levels continued to increase during the night they did not reach the levels recorded for April 23 (Day 1, Fig 2), or April 30 (Fig 2 and 4), both warm days.

April 29 and 30 experienced similar light and temperature conditions but wind speeds were quite different. On April 29 nocturnal wind speeds of 1.5 m/sec or greater were common and the concentration of CO_2 was only slightly higher than the daytime concentration. On April 30, a lack of strong winds resulted in a build-up of CO_2 within the forest. Mean wind speeds less than 0.8 m/sec appeared critical for nighttime CO_2 build-up. A discernible reduction in the progressive increase of nighttime CO_2 at 2400 hours on April 30 was associated with increases in wind speeds to 0.8 m/sec. A decrease in wind speeds beyond 0200 hours resulted in a continuation of CO_2 increases. A similar effect of wind speeds on nocturnal CO_2 levels is shown in figure 3.

Figure 4. Net radiation, wind speed, temperature and CO_2 concentration for three spring days, April 24, (——· ——), April 29 (----) and April 30 (——).


Net Rad.(ly)
0.8
0.6
0.4
0.2
0.0
5
7
9
11
13
15
17
19
Solar Time (hr)
W.V. (m/sec)
3.20
2.70
2.20
1.70
1.20
.70
.20
T (°C)
30
20
10
0
CO_2 (ppm)
370
350
330
310
11
13
15
17
19
21
23
1
3
5
7
9
Solar Time (hr)

CONCLUDING REMARKS

The concentration of CO_2 was influenced by assimilation and respiration of vegetation and the soil, and by vertical and horizontal mixing of the air. Concentrations varied seasonally as much as 71 ppm from a spring maximum (359 ppm) to a late summer minimum (288 ppm). A characteristic diurnal CO_2 pattern existed for all seasons with a daytime low occurring between 1400 and 1700 hours True Solar Time, while a nighttime high was noted between 0400 and 0700 hours. Observed nighttime increases during winter, the season of least biological activity, primarily resulted from respiration.

Day-to-day variability was significant ($P < 0.05$) and was a function of the interaction between biological and physical components of the forest environment. During summer and spring when photosynthesis and respiration were at their peaks, CO_2 concentrations were most strongly influenced by variations in net radiation and temperature. During fall, and winter when biological activity was declining or at its annual low, changes in CO_2 concentrations correlated best with changes in wind speed.

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