CARBON DIOXIDE GRADIENTS IN A BEECH FOREST IN CENTRAL OHIO[1]

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Knowledge of the physical environment of biotic communities is not complete without knowledge of the carbon dioxide relations of such complexes. The present study deals with the carbon dioxide relations of a beech forest in central Ohio during late spring and early summer, 1950.

An attempt has been made to determine the daily fluctuations in concentration gradients and to suggest factors influencing these gradients. Such data not only supplement microclimatological studies such as those of Wolfe, Wareham, and Scofield (1949) but results here obtained also help to show the dynamic relationships of the integral parts of the forest habitat and how these parts are associated one with another. The true nature of these equilibria can be studied only where remnants of relatively undisturbed vegetation remain. The present study was carried out in such an area.

LOCATION AND DESCRIPTION OF THE PROBLEM AREA

The problem area is located at the western edge of a level to gently undulating Late Wisconsin till plain, between Blacklick Creek and South Fork of the Licking River. It is in northwestern Etna Township, Sec. 3, T 16 N, R 20 N, Licking County, as noted on the Thurston, Ohio U.S.G.S. quadrangle.

Elevation varies from about 1080 feet, along a slight ground swell at the western edge of the forest, to 1070 feet along an intermittent, south-flowing stream which bisects the forest. The terrain thus slopes gently east and south.

Two soil types form a mosaic in the problem area. They are Marengo silty clay loam and Bennington silt loam, both derived from glacial drift largely composed of sandstones and shales which occur in a north-south belt in the region (Stauffer *et al.*, 1911). The former develops on flat upland areas having poor internal drainage and abundant organic matter. Internal drainage of Bennington is better than that of Marengo although accumulation of organic matter is less. It occurs on undulating uplands (Wildermuth *et al.*, 1938) in the problem area chiefly on the swell at the west edge of the forest.

Beech (*Fagus grandifolia*)[2], constituting over half of the canopy, dominates the vegetation in the vicinity of the sampling area. Species of secondary importance are:

Ulmus americana
Quercus rubra
Fraxinus americana
Acer saccharum
Prunus serotina

Layer societies are those characteristic of swamp forest, in late stages of development, and include:

Small trees

Asimina triloba
Carpinus caroliniana
Carya cordiformis (saplings)
Crataegus spp.
Ostrya virginiana

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[2]The nomenclature followed here is essentially that of *Gray's Manual* (Fernald, 1950).

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Shrubs and vines

Euonymus obovatus	*Rhus radicans*
Lindera benzoin	*Sambucus canadensis*
Menispermum canadense	*Smilax glauca*
Parthenocissus quinquefolia	*Vitis* spp.

Herbs

Actea pachypoda	*I. pallida*
Anemone quinquefolia	*Mimulus ringens*
Arisaema atrorubens	*Mitchella repens*
Cardamine douglassii	*Onoclea sensibilis*
C. pensylvanica	*Ozmorhiza longistylis*
Carex spp.	*Phlox divaricata*
Circea quadrisulcata	*Phryma leptostachya*
Claytonia virginica	*Poa pretensis*
Cryptotaenia canadensis	*Podophyllum peltatum*
Dentaria laciniata	*Polemonium reptans*
Dicentra cucullaria	*Polygonatum canaliculatum*
Erythronium albidum	*Ranunculus abortivus*
E. americanum	*Sanguinaria canadensis*
Floerkea proserpinacoides	*Sanicula canadensis*
Galium aparine	*Smilacina racemosa*
G. concinnum	*Trillium grandiflorum*
G. tinctorium	*T. sessile*
G. triflorum	*Urtica dioica*
Geum canadensis	*Veronica officinalis*
G. vernum	*Viola pensylvanica*
Gratiola neglecta	*V. papilionacea*
Impatiens capensis	

On a slight rise at the west edge of the tract, the dominant vegetation is Beech-Sugar Maple.

Known disturbances of the vegetation since settlement are: (1) A strip of second growth 45–80 yards wide lies along the south border of the forest. At its closest point it is 150 yards from the sampling area. (2) In 1922 most of the ash was removed from the stand.[3] (3) Cattle from an adjoining pasture have been allowed to enter the forest since the early nineteen hundreds.[3] Effects of pasturing are slight although detectable in the Beech-Sugar Maple area.

EQUIPMENT AND METHODS

Air samples of not less than 20 liters[4] were drawn at the rate of 40 liters per hour into four Sargent Wet Meters. The air was then pulled, by means of an electrically operated vacuum pump, into scrubber towers of the Heinecke-Hoffman (1933) type as modified by Böhning (1949) who has described the method in detail. Samples were taken 60 yards from the north edge and 100 yards from the west edge of the forest through four one-eighth inch ID plastic tubes, each at a different level above the leaf litter: three inches, three feet, 30 feet, and 41 feet. The last-named tube lay just below the lower limbs of the canopy. The tubes were connected directly to the Wet Test Meters.

Relative humidity was measured with a sling psychrometer, barometric pressure with a Taylor aneroid barometer.

Determinations were begun on April 29, 1950, and continued at more or less

[3]Personal conversation with Mr. and Mrs. H. G. Henderlick. Mr. Henderlick's father formerly owned the land.

[4]All volumes reduced to 0° C, 760 mm Hg.

regular intervals until May 25. From June 14 through June 23, and from June 29 through July 3, determinations were made at one to four hour intervals during daylight hours. Measurements were also made at two to three hour intervals between 9 P.M., June 12, and 8 A.M., June 13.

REVIEW OF THE LITERATURE

The nature of forest carbon dioxide gradients have been determined in some detail by many workers. In general, concentrations have been found to be greatest near the forest floor and show a constant decrease to some point in (Romell, 1928), or above the canopy (Gut, 1929). High concentrations nearest the substrate are attributed to diffusion of carbon dioxide from the soil, where respiratory activities of roots and micro-organisms produce considerable amounts.

Feher (1927) considered the greatest production of soil carbon dioxide to come primarily from aerobic cellulose-decomposing bacteria. Turpin (1920) found that a larger proportion of soil carbon dioxide was that released from the roots of young, rapidly growing crop plants than from soil micro-organisms. Romell (1922) stated that there is complete removal of soil air to a depth of 20 cm every hour and attributes such movement to diffusion. Such a phenomenon accounts for the evolution of 0.2–0.7 grams of carbon dioxide per square meter per hour from the soil (Romell, 1932). It then diffuses or is dispersed by wind currents to higher levels.

Meinecke (1927) found, contrary to the reports of other workers, that during daylight hours, the concentration above the canopy may be less than in the canopy although not as high as below the canopy. He assumed that most of the photosynthetic carbon dioxide has its origin in the respiratory activities of roots and micro-organisms of the soil. In this connection Lundegardh (1921), using data of his own and some of Ebermayer, calculated that 60 percent of the photosynthetic carbon dioxide of European beech forests is that which emanates from the soil.

Fuller (1948) reported that carbon dioxide gradients are usually steepest in the eight centimeters closest to the substrate. Feher (1927) found the zone of greatest concentration below four meters.

Gut (1929) measured concentrations at several levels from near the surface to 28 meters in various forests near Zurick. He found that, daily, the concentrations decreased until late morning after which there was begun a slight rise which continued until 2 A.M. the next morning. The drop in concentration was attributed to active photosynthesis in the forest while the subsequent rise was considered due to diffusion of carbon dioxide from soil organs and micro-organisms under less active photosynthetic conditions. On certain afternoons in a deciduous forest sharp increases in concentration at all levels were found. These might be explained by the accumulation of end products of photosynthesis in the leaves to the extent that the subsequent rate of photosynthesis in the leaves is reduced (Braun-Blanquet, 1932; Gut, 1929).

Night concentrations are high, being also influenced by respiration of aerial plant organs. Gut (1939) attributed decreases in concentration before sunrise to ultraviolet-induced photosynthesis. Stocker (1935) attributed low night concentrations to combination of carbon dioxide with "Kuticular Excretion der Blätter" of certain tropical forest species at Tjibodas, Java. Other tropical studies have been made (Evans, 1939; von Faber, 1935; McLean, 1919).

The lowest and most variable concentrations of forest carbon dioxide have been reported in spring while the highest concentrations are usually reached in autumn (Gut, 1929). Meinecke (1927) found concentrations increasing from April through July following which there was a gradual decline. Russell and Appleyard (1915) considered temperature the chief factor governing carbon dioxide production in the soil from November to May. Soil moisture is limiting the rest of the year. They found maximum production during late spring and autumn.

Feher and Sommer (1928) concurred and stated that during winter, forest carbon dioxide concentrations sink to the level of the general atmosphere.

Lundegardh (1921, 1924, 1931) considered the chief factors influencing the carbon dioxide concentration as being the effect of season, time of day, wind strength, haze, pressure and temperature upon respiration of roots and soil micro-organisms, and respiratory and photosynthetic activity of surface vegetation. Affecting the first may be added, availability of mineral nutrients, soil texture and aggregation, moisture and aeration, organic matter, and pH (see Feher, 1927). These factors are agreed upon by most authors though data are sketchy on the relative importance of each.

Certain plant communities have been compared with respect to carbon dioxide concentration. In separate Bavarian forests of beech and pine, Ebermayer and Swappach (1878) and Ebermayer (1879, 1885) made the first attempts to measure carbon dioxide concentrations in forest communities. In the latter paper, Ebermayer reported considerably higher concentrations in a beech forest than those in pine. In spite of these apparent fluctuations he concluded that forest carbon dioxide concentrations were not unlike those of other air and, according to Gut (1929), that conclusion materially reduced the subsequent amount of research in this field. Research of the nineteenth century has been summarized by Letts and Blake (1900).

Some communities have been compared at the Hallands Vädëre Ecological Station with respect to carbon dioxide concentrations present. Johannson (1926) compared meadow and swamp communities. Others have found that concentrations averaged lower in alder than in pine or beech stands (Feher, 1927). The highest concentrations were found in a beech stand while pine was intermediate in this respect (Feher, 1927; Lundegardh, 1921).

Comparatively low concentrations have been found in forests with poorly developed layer societies as compared to multi-layered selection forests. These low concentrations are attributed to good air mixing in the former type (Gut, 1938; Meinecke, 1927). The latter author suggested that border and underplantings may reduce wind velocities enough to allow more effective utilization of carbon dioxide produced in the soils of the stand.

Harder *et al.* (1931) found fluctuations considerable even on the Sahara Desert.

A forest-grassland comparison has been made by Fuller (1948) in Illinois. He attributed higher concentrations in forest than in grassland areas to more sluggish and less extensive air movement in the former.

The effect of carbon dioxide concentration on the distribution of plant species has been little discussed in the literature. Lundegardh (1921) stated that the increased carbon dioxide supply near the ground is an important factor necessary for the existence of shade flora, *e.g. Oxalis acetosella*, in that it enables the plant to make more efficient use of sunflecks of high intensity which may cross their leaves. Such species are the so-called "carbon dioxide plants" and are said to be found on soils from which the rate of carbon dioxide evolution is high. McComb and Loomis (1944) suggested that if upland trees have roots less tolerant of carbon dioxide than prairie species, this might help to explain the failure of trees to invade grasslands, where root respiration and decay probably create a relatively high concentration. Decker (1947) stated that the diffusion of carbon dioxide into a leaf is a function of pressure rather than concentration and the pressure of carbon dioxide in the atmosphere varies directly as the total atmospheric pressure. He suggested the possible importance of carbon dioxide pressure as a factor in the altitudinal distribution of species. Daubenmire (1943) noted that high altitude is accompanied by low atmospheric pressure and a subsequent low partial pressure of carbon dioxide "which even at low altitudes is generally a limiting factor in photosynthesis." At least in the lower layer societies, light intensity is usually considered the limiting factor in photosynthesis in the forest of the type in which the writer's study was conducted. Wilson (1948) found carbon dioxide concentrations 20 to 25 percent higher on foggy than on clear mornings. The increased concentration was paralleled by an increase in apparent photosynthetic activity of plants. He observes that these facts may have an application to those regions where maximum plant growth is associated with the prevalence of fog.

RESULTS AND DISCUSSION

Spring Gradients

Few data regarding hourly fluctuations of carbon dioxide gradients before May 18, when the canopy closed, are available. Determinations made one hour apart however, usually exhibit a gradient of decreasing concentration from three inches to 41 feet.

Moreover, considerably more variability is exhibited before than after canopy closure, *e.g.* the morning of May 8 was preceded by minimum temperatures of 1° C at 20 feet and 4° C under the leaf litter.[5] Such low temperatures may have reduced the rates of respiration of soil micro-organisms, roots, and surface vegetation to a degree low enough to account for a concentration of 0.025 at three inches and 0.023 volume percent at higher levels. These are minimum concentrations found for the spring season. The effect of a high water table upon the metabolic activity of soil microflora must also have been considerable. It is noted that pools of water persisted on the forest floor until the end of April.

Maximum concentrations for the spring season at three inches is 0.04 volume percent; three and 30 feet, 0.034; and 41 feet, 0.031. Spring concentrations average, 8 A.M. to 6:30 P.M., 0.030 volume percent.

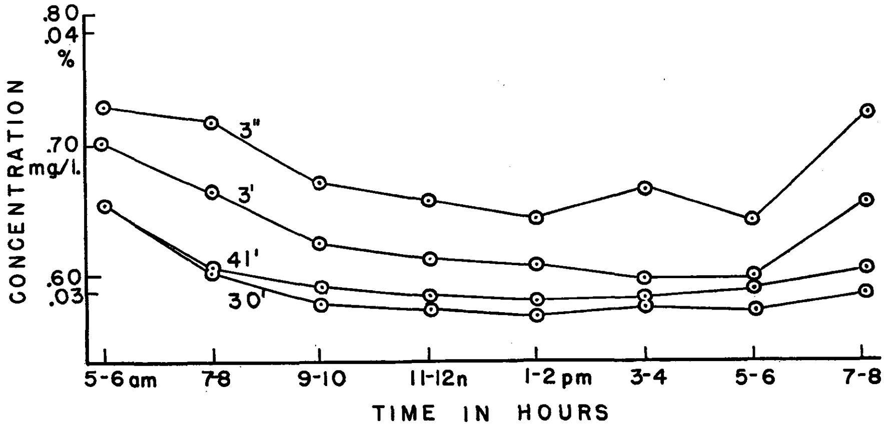

FIGURE 1. Average early summer gradients. In the vertical axis, carbon dioxide concentrations are given in percent and in mg/liter. Points determined by averaging values for 5 and 6 A. M., 7 and 8 A. M., etc.

Summer Gradients

Determinations made after May 18 were simultaneous at the four levels previously described. The data have been averaged and are represented diagramatically in figure 1. While averaging such values may obscure many phenomena, especially maximum and minimum concentrations, the general relation of time and strata to concentration is apparent by inspection.

[5]Christy (1952) has described certain temperature phenomena in this forest, April through December, 1950.

As in spring, concentrations at three inches were higher than at any other level. This is undoubtedly due to its proximity to the soil. Also important is the fact that herbs and shrubs at this level reduce wind velocities and mixing of carbon dioxide with air at higher levels does not occur. The slight ground swell to the west of the station also shelters the three inch level at this point when winds are from that direction (during about 60 percent of the sampling periods).

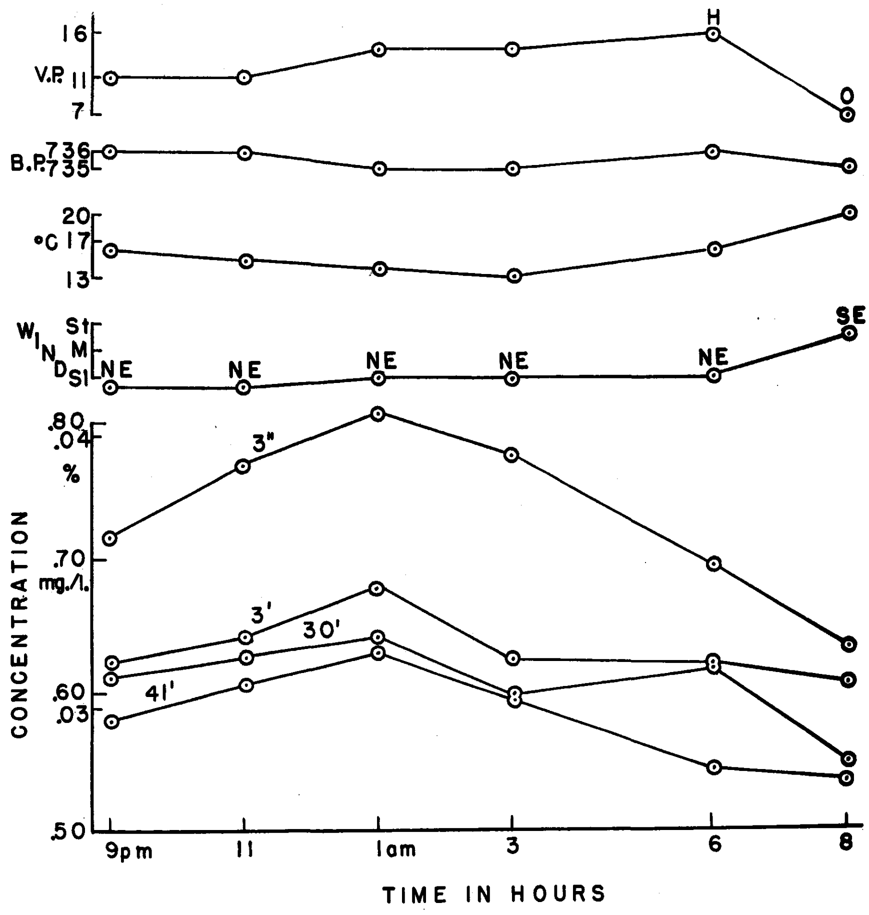

FIGURE 2. Night concentrations of carbon dioxide. In this figure, and those that follow, V.P. refers to vapor pressure in mm of Hg; over the vapor pressure curve are symbols indicating character of the atmosphere: O = overcast; H = hazy; no letter = clear. Also indicated: B.P. for barometric pressure; °C = temperature at three feet; wind: M = moderate, St = strong, Sl = slight.

The decline in concentration until early afternoon is probably due to better air mixing associated with higher wind velocities than those in the morning, increased number and strength of convection currents caused by heating of the substrate by sunflecks, and photosynthesis in the forest and surrounding areas. Increases in concentration in the late afternoon parallel lessened photosynthetic activity though emanation of carbon dioxide from the soil is undiminished.

As indicated by the high concentrations in the early morning and late evening, those at night are usually higher than during the day (fig. 2).

Concentrations at the three foot level are always lower than at three inches, though the daily trend is the same. The effect of greater air mixing is evident.

As has been stated, the sampling tubes were about 100 yards from the west edge of the forest. Pasturing has somewhat reduced the number of shrubs and small trees between the forest edge and the intake tubes, hence wind at that level, from the west and southwest had little to impede its progress into the forest. While the three inch and three foot levels were somewhat sheltered, the 30 foot level was exposed, on over half of the measurements, to a current of well-mixed "outside air." This fact may account for the low concentrations indicated in figure 1. In an unbroken forest this probably does not occur.

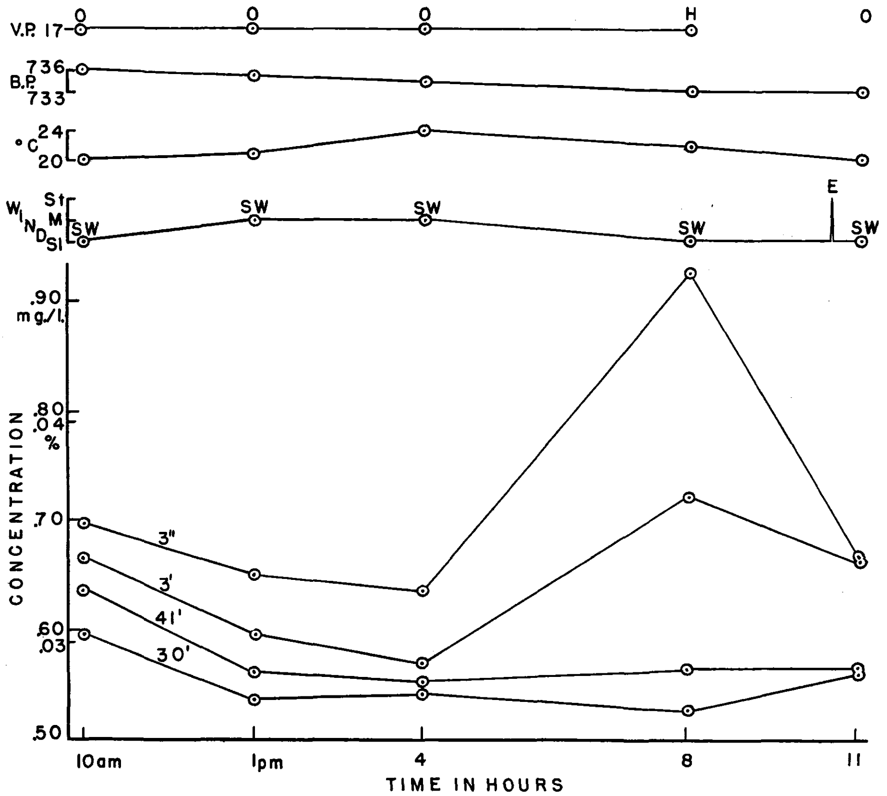

FIGURE 3. Effect of wind on carbon dioxide gradients at lower levels.

The intake at the 41 foot level, located just below the lower branches of the canopy, is thus more sheltered than the 30 foot level. Concentrations at this level were usually not lower than those of the "outside air" as reported in the canopy by other authors. Daily patterns of concentrations are closely associated with the 30 foot level, though occasionally they are more nearly like those at three feet (fig. 4).

The average summer concentration, 5 A.M. to 8 P.M. at three inches is 0.035 volume percent; three feet, 0.032; 30 feet, 0.030; and at 41 feet, 0.031. Discounting strata, the total average daytime concentration value is 0.032. The daytime minimum and maximum concentrations at three inches are 0.029 and 0.047 volume percent respectively; three feet, 0.0275 and 0.040; 30 feet, 0.026 and 0.036; and at

41 feet, 0.027 and 0.036. Most minimums occurred after 1 P.M., while most maximum concentrations occurred between 5 and 6 A.M.

The effect of the respiration of plant organs and micro-organisms at night is demonstrated in figure 2. The measurement of gradients was begun at 9 P.M., June 13, and ended at 8 A.M., June 14. During this interval concentrations at all levels increased until 1 A.M. following which there was a decrease which continued until determinations were ended. The increase is attributed to respiratory activity

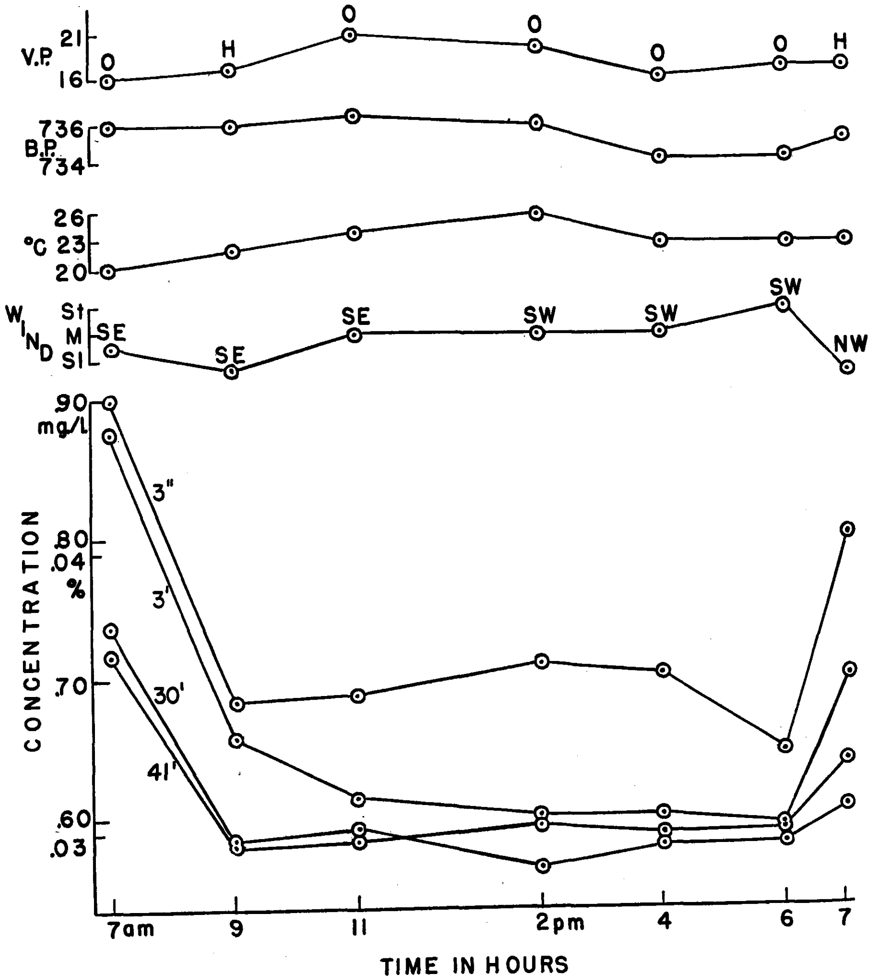

FIGURE 4. Effect of wind direction and velocity on carbon dioxide gradients.

of plant cells both in and above the substrate. The decline in concentration was preceded by a slight increase in wind velocity which initiated replacement of forest air with that from the outside in which the concentration was lower. This replacement proceeded at a faster rate than the concentration was rebuilt by respiration.

It is noted that the gradient from soil to canopy is constant, that is, the 30 foot level had a higher concentration than that at 41 feet. This is thought to be a consequence of poorer air mixing at 30 than at 41 feet due to the reduction of wind velocities by a well developed understory characteristic of the northeastern part of this stand.

Other workers have attributed high concentrations in the canopy during the night to the large respiring surface there. The gradual decline in the difference in concentration between the 30 and 41 foot levels may be due to the proximity of the higher sampling inlet to the canopy.

By 8 A.M. light intensity was only 40 foot candles at a point five inches above the substrate. Though intensities were perhaps several times greater in the canopy,

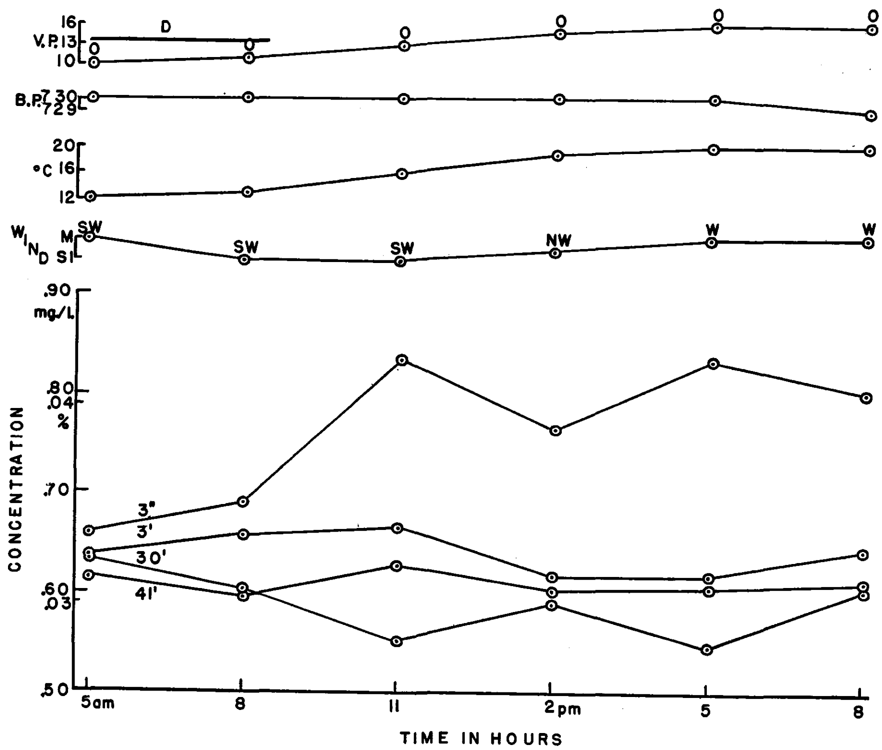

FIGURE 5. Effect of rain on carbon dioxide gradients. D = drizzle type rain; underscore indicates its duration.

it is doubtful if even the compensation point had been reached in beech until after 8 A.M.

Figure 3 shows the effect of a single gust of wind on the carbon dioxide concentration at the three inch and three foot levels at night. During the day the concentrations followed the usual downward trend until at least 4 P.M. Between 4 and 8 P.M., wind velocities declined, photosynthesis had become negligible and concentrations at the lower levels had reached sizeable proportions. At 10:30 P.M., however, the air was replaced with air from outside the forest containing a considerably lower concentration. This replacement was accomplished by a strong northeasterly wind of only a minute's duration.

June 15 exemplifies a day when respiration by soil organs and micro-organisms was intensive but moderate southeast and southwest winds reduced concentrations at higher levels (fig. 4). Until noon the gradient is constant and the concentration at the 30 foot level did not drop below that at 41 feet until the wind direction had shifted from southeast to southwest. To the southeast, as to the northeast, there is a considerable area of dense vegetation, well developed in all layer societies. The impedance of wind speed at 30 feet by vegetation is apparent.

The 5 A.M. measurements on June 19 (fig. 5) were preceded by gusty south winds accompanied by rain. Again the gradient was constant under the influence of wind direction. With a shift to the southwest, however, the typical inversion appeared, was partially destroyed by northwest winds, and reappeared with westerlies. The formation of constant gradients under the influence of northwest winds was a regular occurrence and related not only to the density of the forest vegetation but also the presence of overgrown fencerows in that direction.

The close grouping of concentrations at 5 A.M. accompanies good mixing associated with moderate winds.

Following rain, the concentration of carbon dioxide is generally increased. The explanations of such a phenomenon are various: replacement of soil air with water, increased activity of soil micro-organisms under the accelerating effect of moisture or dissolved oxygen, and accompanying low pressures "sucking out" the soil air. Early morning determinations on June 16 were taken during a thunderstorm. The average concentration for the day was 0.034 while at the three inch level it was 0.038. Individual measurements were as much as 20 percent higher than average for that two hour period. Such high concentrations are not evident the next day.

SUMMARY

The concentration of atmospheric carbon dioxide effects the rates of both photosynthesis and respiration in green plants. Since the relative rates of these processes may determine whether or not a plant survives in an environment, a study of the factors influencing these rates is necessary for an understanding of the habitat and its biota.

Indeed some relationships are reciprocal: the activities of plants are not only in part controlled by their environment, but they control or at least modify that environment. These environmental relationships are cyclic and interdependent.

The ecological relations of the daily periodicity of atmospheric carbon dioxide gradients in spring and early summer found as a result of this study are:

1. Average spring and summer concentrations (8 A.M. to 6:30 P.M.) are 0.030 and 0.031 volume percent respectively.
2. Spring concentrations at all levels exhibit greater day to day variation than do those of summer.
3. Concentrations in spring at all levels are usually lower than those in summer.
4. Spring gradients are regularly constant from soil to the unopened canopy.
5. Average summer concentration (5 A.M. to 8 P.M.) is 0.032 volume percent.
6. Although gradients are not always constant, much of the photosynthetic carbon dioxide in summer also emanates from the soil level.
7. Average summer daytime concentrations are: at three inches, 0.035 volume percent; three feet, 0.032; 30 feet, 0.030; 41 feet, 0.031.
8. Absolute maximum and minimum concentrations (5 A.M. to 8 P.M.) during early summer at three inches are 0.047 and 0.029 volume percent respectively; at three feet, 0.040 and 0.0275; at 30 feet, 0.036 and 0.026; and at 41 feet, 0.036 and 0.027.
9. Wind direction, *per se*, has no apparent effect on carbon dioxide concentration. Its effect in summer lies in its relation to air mixing especially at the 30 and 41 foot levels. Winds from the west and southwest result here in a reduction in concentration at the 30 foot level. Constant gradients from three inches to 41 feet are formed when winds are from other directions.

10. Rain increases the carbon dioxide concentration. These increases are not evident the following day.

11. Early summer concentrations are usually higher during the early morning, and late afternoon and evening hours than during other parts of the day. These hourly differences are probably due to increased wind movement and higher rates of photosynthesis of adjacent vegetation accompanying increased light intensity.

12. Concentrations at night are higher than those during the day unless influenced by considerable air mixing.

13. Maximum rates of change in concentrations usually occur in the early morning and late evening. Minimum rates occur in the late morning and afternoon.

14. Herbs, shrubs, and saplings are subject to higher concentrations than are individuals with leaves at higher levels.

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