

THE EFFECT OF AIR SUPPLY ON APPARENT PHOTOSYNTHESIS

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(WITH SIX FIGURES)

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It has been recognized for a long time that the rate of absorption of CO_2 by a green plant shoot or leaf enclosed in a vessel is affected by the rate at which air is supplied. Much attention has been given to the problem of maintaining a "normal" air supply; that is, a CO_2 supply comparable to that found under natural conditions. The early literature was reviewed and discussed by HEINICKE and HOFFMAN (5), who presented results showing that the rate of photosynthesis was below normal when the air supply was less than approximately two liters per hour per square centimeter of leaf area. VERDUIN and LOOMIS (9) presented results from which they concluded that photosynthesis of corn leaves "was affected surprisingly little" by 70% depletion of the CO_2 within the leaf chambers.

BROWN and ESCOMBE (1) presented results which they interpreted as indicating an approximate proportionality between the rate of apparent photosynthesis and the mean CO_2 concentration. They pointed out that "in all cases where the illumination of the leaf was good, although the amount of intake of CO_2 into the leaf was approximately proportional to the increased partial pressure, the photosynthetic work was always somewhat in excess of what might be expected from the increased amount of CO_2 ." They were obviously expecting strict proportionality and had overlooked some of the following facts. Proportionality implies a linear relationship. General linear relationship is described by the equation $y = a + bx$; but strict proportionality exists only when $a = 0$ and $y = bx$. Apparent photosynthesis becomes zero at a measurable CO_2 concentration (the compensation point); therefore $a \neq 0$, and strict proportionality cannot exist.

The data of BROWN and ESCOMBE actually contain very little information concerning the real relationship between photosynthesis and CO_2 concentration. They made only two observations on each plant, one at high CO_2 concentration and one at low concentration. Thus only two points were established for each plant, and a linear function can be derived from any two points whether established experimentally or selected at random. Further, a variety of functions other than linear can be fitted to any two points, for example, $y = ax^n$, $y = a + 1/x$.

Data presented by DENEKE (4) indicated that the rate of photosynthesis increased with the velocity of air over the leaves and apparently approached a maximum limit at an air velocity of approximately 100 meters per minute. He circulated air over a plant in a closed system and measured the time required for a certain reduction of CO_2 content. One set of data, his figure 8, is reproduced here as figure 1. This and similar curves suggested to

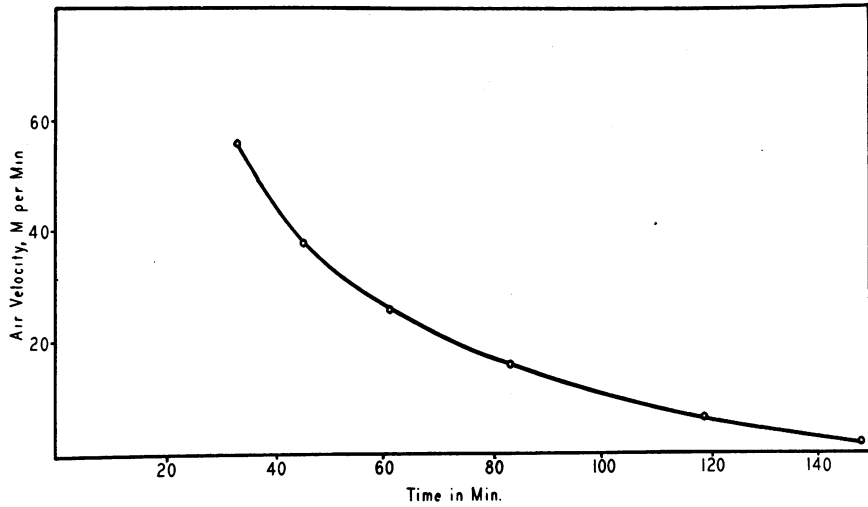


FIG. 1. Effect of air velocity on time required for a constant amount of apparent photosynthesis. Redrawn from DENEKE (4).

DENEKE that increasing velocity above 100 meters per minute would probably result in no further increase in the photosynthetic rate. However, it should be noted that rate is the reciprocal of time; that is, $R = K/T$ where R

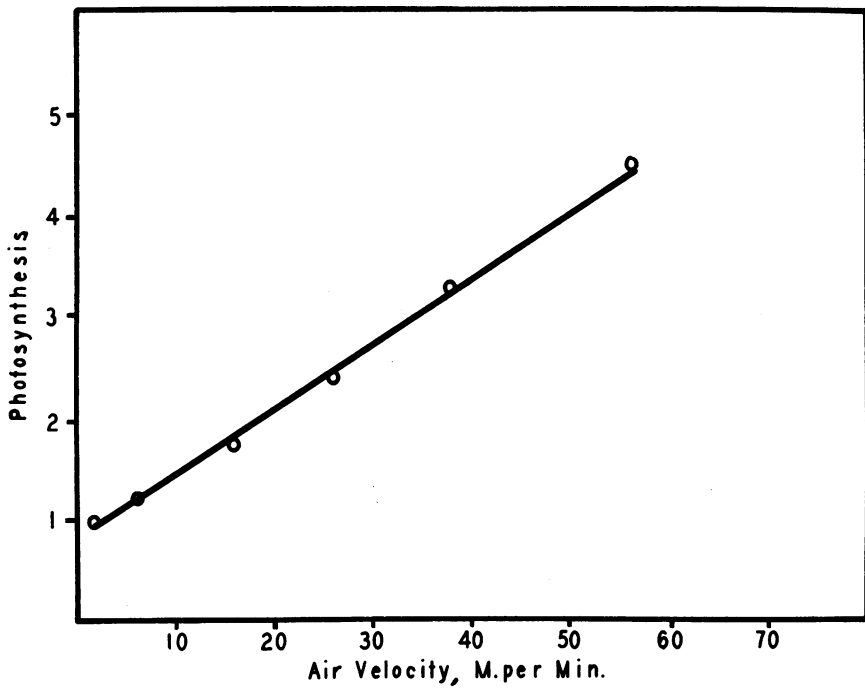


FIG. 2. Effect of air velocity on apparent photosynthesis. Recalculated from data of DENEKE (4).

is the rate of photosynthesis, and T is the time required for the absorption of a constant amount of CO_2 , K . When photosynthetic rates were calculated from DENEKE's data they were found to describe a nearly straight line in relation to air velocity as shown in figure 2. DENEKE plotted T , the reciprocal of R , and the resulting curve was hyperbolic, of course. What he has interpreted as the flattening of the curve at high velocity is merely the normal shape of a hyperbolic curve.

HEINICKE and HOFFMAN (5) presented results which they interpreted as showing that the rate of photosynthesis declined more rapidly than the mean CO_2 concentration at very low rates of air supply. This implies a curvilinear relationship between rate of photosynthesis and mean CO_2 concentration. Values for mean CO_2 concentration were calculated from the data in their table 4 using the method they described, and photosynthesis was plotted over

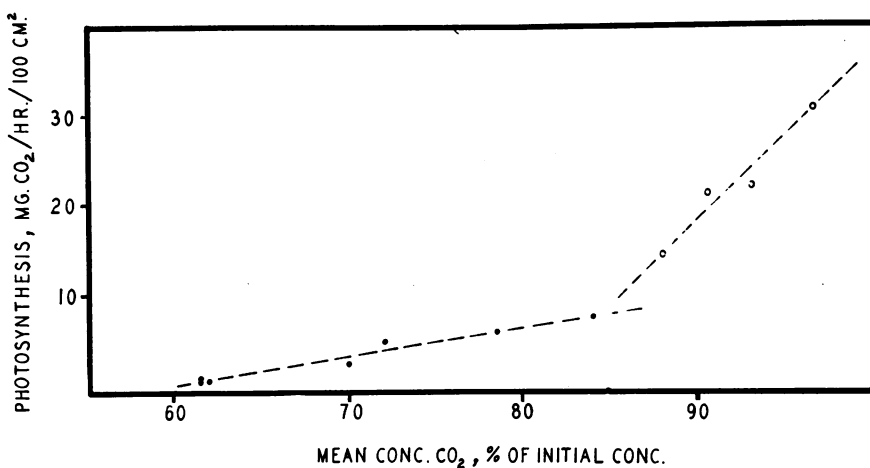


FIG. 3. Effect of CO_2 concentration on apparent photosynthesis. Data of HEINICKE and HOFFMAN (5).

mean CO_2 concentration as shown in figure 3. When the whole array is considered, a non-linear curve is suggested. It appears possible, however, that the array is composed of two sets of data describing two straight lines of different slope. It should be noted further that the four upper values were observations on single leaves and the remainder were composite measurements on many leaves. The inference of curvilinear relationship from these data is not justified.

HEINICKE and HOFFMAN stated also that the rate of photosynthesis fell rapidly when the CO_2 content was depleted more than 20%. This implies a curvilinear relationship between the rate of photosynthesis and the degree of depletion. When the data contained in their table 4 were plotted it was found, as before, that although the whole array suggested a non-linear curve, the data obviously could be separated into two groups. DECKER's (3) conclusion concerning the non-linear effect of CO_2 depletion on the photosynthetic rate of pine was based on a misinterpretation of preliminary results.

The experimentation reported here was undertaken in an attempt to clarify partially the effect of air supply on the rate of photosynthesis of the entire shoot of a tree seedling enclosed in a chamber.

Methods

The apparatus used in measuring photosynthesis was as originally described (3) except that CO₂ analysis units of the type used by WAUGH (10) were substituted. A diagram of the apparatus is shown in figure 4. The entire top of the plant was enclosed in a transparent cylindrical chamber and was illuminated from above by a battery of electric lights. Air was drawn through the chamber at a known rate, and the difference between the amounts of CO₂ entering and leaving the chamber was taken as a measure of apparent photosynthesis. A small radial-flow fan (2) circulated the air rapidly within the chamber. A simple test with smoke showed that the turbulence caused by the fan was very much greater than that caused by the flow of air from inlet to outlet. It is presumed, therefore, that the rate of air movement within the chamber and over the leaves was essentially constant at the different rates of air supply. Air temperature in the shoot chambers was maintained at $25^{\circ} \pm 1^{\circ}$ C.

The arrangement of the CO₂ analysis units for direct sampling was similar to that described by WILSON (12). For simplicity only one of the units is shown in figure 4. Another was connected to the blank sampling tube (8) and a third to the other shoot chamber (7). The three units were arranged in a suitable thermostatic water bath. The sample was metered (14) through the absorption tower (15) which was charged with 50 ml. of 0.0055 N NaOH solution. The change in concentration of the NaOH was measured by the change in electrical resistance of the solution. The operating routine was as follows. The tower was charged with fresh solution and was stirred for five minutes by passing the CO₂-free air stream through it. The air stream was made CO₂-free by passing it through soda-lime (17). The tower was then by-passed and the initial resistance reading was made. The tower was again switched into the air stream and the soda-lime tube was by-passed for exactly fifteen minutes. The CO₂-free stream was then allowed to pass through the system for an additional three minutes to sweep the remaining CO₂ into the tower, the tower was by-passed, and the final resistance reading was made. At a CO₂ concentration of 0.55 mg./l. and an air flow of 0.55 l./min. a run of 15 minutes gave a resistance change of approximately 100 ohms. An Industrial Instruments Model RC-1B bridge was used, and with a decade variable resistance coupled in series it was possible to make readings to the nearest 0.5 ohm with considerable ease and speed. Replicated tests with the three units sampling a common source of air revealed an average discrepancy between units of approximately 1%.

The sampling unit drew air from the shoot chamber at a constant rate of 0.55 l./min. The total flow through the chamber was controlled by means of another air line and flowmeter (18) which was calibrated over the range 0.5

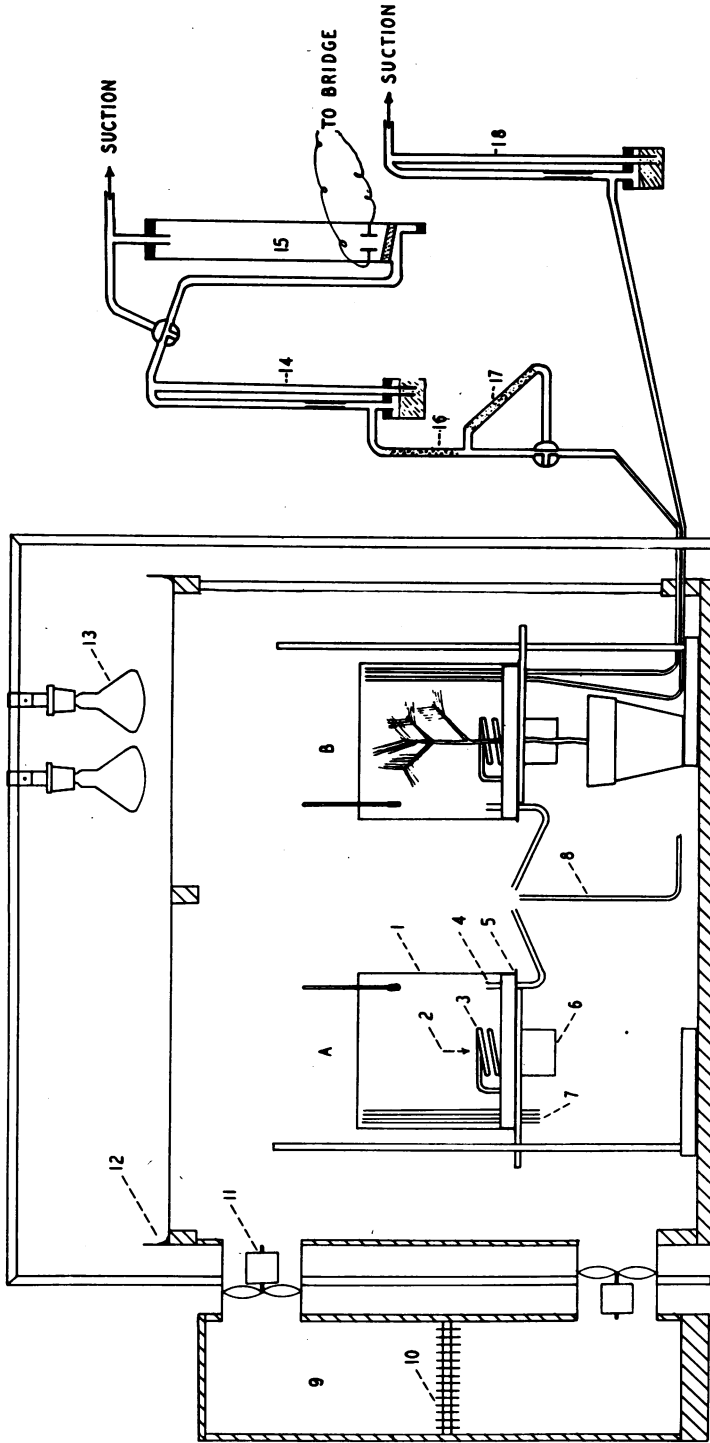


FIG. 4. Apparatus used to measure apparent photosynthesis of entire shoots under controlled conditions. Letters and numerals refer to descriptions in the text.

to 10.0 l./min. The desired rate of supply was established 20–25 minutes before a measurement was begun. Preliminary tests made at the lowest rate of air supply showed no difference between measurements begun 20–25 minutes after a change in rate of supply and those begun 45–50 minutes after the change.

Ten potted loblolly pine (*Pinus taeda* L.) seedlings which had completed the initial growth of their second growing season were used. Throughout the season they had been exposed to normal light in a greenhouse. The experiment was arranged as a 5 × 5 Latin square in which columns represented hours of the day, rows represented pairs of plants and days, and the five rates of flow were distributed within the square. To allow separation of any differential effect of light intensity, one plant of each pair was exposed to a light intensity of 10,000 foot candles and the other to 2,200 fc. throughout the

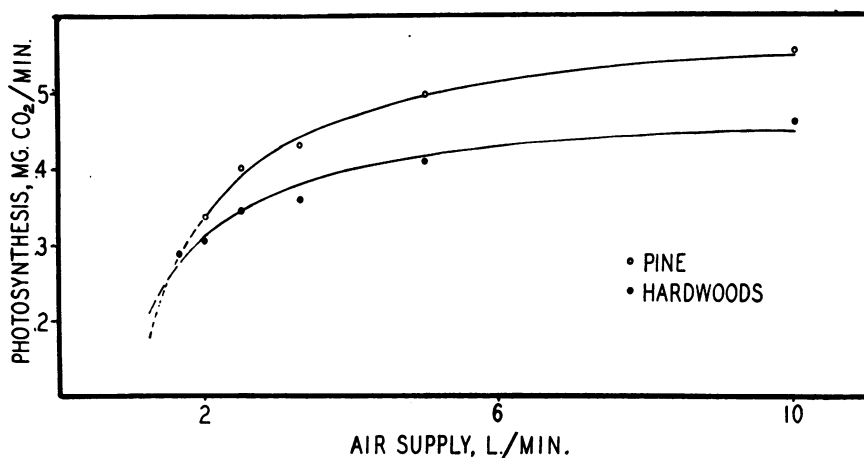


FIG. 5. Effect of air supply on apparent photosynthesis of entire shoots of tree seedlings. Data of table II.

series of flows. The Latin square design was chosen because it would reduce the chance of having the decline of the CO₂ content of air from out-of-doors through the day confounded with the effect of air supply. All plants were exposed to all rates of supply and thus the amount of tissue involved was a constant whose effect did not appear in differences between rates of supply.

The results of HEINICKE and HOFFMAN indicated that the rate of photosynthesis could probably be expected to vary hyperbolically with the rate of air supply and therefore linearly with the reciprocal of air supply. The rates of supply which were used (2.0, 2.5, 3.3, 5.0, 10.0 liters per minute) were chosen because the reciprocals were convenient values.

A second series was run using six dogwood (*Cornus florida* L.) seedlings and six tulip poplar (*Liriodendron tulipifera* L.) seedlings. These plants were in their third growing season and were kept in the greenhouse near the pine seedlings. A design similar to the previous one was used, with a 6 × 6 square, one plant of each species in a pair, and a sixth rate of supply of 1.67 l./min. Only one light intensity, 10,000 fc., was used in this series.

TABLE I

APPARENT PHOTOSYNTHESIS OF ENTIRE SHOOTS AT DIFFERENT RATES OF AIR SUPPLY.
MG. CO₂/MIN./SHOOT

SPECIES	LIGHT INTENSITY	AIR SUPPLY, L./MIN.					
		10	5	3.3	2.5	2.0	1.67
	<i>fc.</i>						
Loblolly pine*	10,000	.579	.531	.464	.441	.366
“ “ *	2,200	.530	.470	.401	.361	.309
Dogwood†	10,000	.414	.371	.318	.310	.282	.260
Tulip poplar†	10,000	.519	.455	.409	.383	.333	.318

* Values are means of 5.

† Values are means of 6.

Results

Results are summarized in tables I and II. Values for mean CO₂ concentration and degree of depletion were calculated from the mean initial and final concentrations within each air supply group.

There is an obvious difference between the values for the two light intensities with pine; however, an analysis of variance (table III) revealed no differential effect of air supply with light intensity, and the two sets of data were combined for all further considerations. Similarly, no differential effect of air supply with the two hardwood species was found, and the data for the two species were combined. The statistical significance of row and column effects indicates that the Latin square design gave a real increase in precision.

Regressions were fitted to the two sets of data using 1/R (where R is the rate of air supply) as the independent variable and rate of CO₂ absorption as the dependent variable. Both were found to be linear. The analyses of variance are given in table III. The linear curves became hyperbolic, of course, when transformed from the reciprocal scale to the normal scale as shown in figure 5.

TABLE II

APPARENT PHOTOSYNTHESIS, MEAN CO₂ CONCENTRATION AND DEGREE OF DEPLETION OF CO₂ AT DIFFERENT RATES OF AIR SUPPLY

		AIR SUPPLY, L./MIN.					
		10	5	3.3	2.5	2.0	1.67
Pine	Photosynthesis (mg. CO ₂ /min.)	0.555	0.501	0.432	0.401	0.337
	Mean CO ₂ conc. (mg./l.)	0.520	0.495	0.479	0.465	0.456
	% depletion	10.2	18.4	23.8	29.4	31.2
Hardwoods†	Photosynthesis	0.466	0.413	0.363	0.346	0.307	0.289
	Mean CO ₂ conc.	0.508	0.494	0.473	0.463	0.453	0.448
	% depletion	8.8	15.1	20.9	26.3	29.3	31.9

* Values are means of 10.

† Values are means of 12.

TABLE III
ANALYSIS OF VARIANCE

PINE			HARDWOODS		
SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE
Rows	4	.077205	Rows	5	.002735
Columns	4	.001496	Columns	5	.022684
Flows	4	.072026	Flows	5	.052861
Error	12	.002782	Error	20	.003940
Total	24		Total	35	
Light	1	.047678	Species	1	.106650
Light-Flow	4	.000305	Species-Flow	5	.001221
Error	20	.009930	Error	30	.002864
Total	49		Total	71	
Regression*	1	.028569	Regression*	1	.021260
Residuals	3	.000081	Residuals	4	.000195
Total	4		Total	5	
$b = -.54 \pm .09 \dagger$			$b = -.35 \pm .09 \dagger$		

* Regression tables are based on means of 10 and 12 observations respectively.

† Standard error of b multiplied by 5% t .

The curves of apparent photosynthetic rate plotted over the degree of depletion (not shown) appeared to be linear with essentially the same dispersion of points shown in figure 6.

Discussion

These data are in general agreement with the conclusion of HEINICKE and HOFFMAN that the effect of air supply on CO_2 absorption is curvilinear

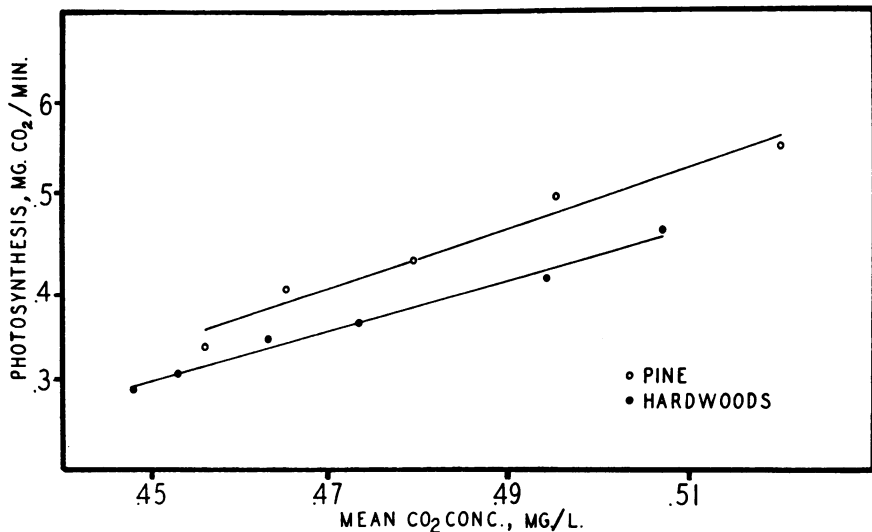


FIG. 6. Effect of CO_2 concentration on apparent photosynthesis of entire shoots of tree seedlings. Data of table II.

over the known range. There is apparent disagreement with DENEKE's data, which showed a linear relationship; however, the technique used by DENEKE differed from that used in the present study. DENEKE measured the time required for a standard depletion of the CO₂ content of a fixed volume of air in a closed system, thus the mean CO₂ content was constant for all air velocities. It appears that he measured directly the simple effect of air velocity over the leaf. In the present study the air velocity was held essentially constant and the mean CO₂ content was varied.

Considerable attention has been given in past studies of photosynthesis to the problem of maintaining a "normal" or at least known CO₂ supply. A frequent practice has been to maintain an air supply such that the CO₂ content was reduced not more than 15-20%. This practice is subject to question because it has been based on the conclusion of HEINICKE and HOFFMAN that the effect of depletion on the photosynthetic rate increases rapidly at depletions greater than 20%. There is another objection to the use of degree of depletion in attempting to evaluate or control the effect of CO₂ supply. Degree of depletion is a relative value and does not take into account the actual CO₂ pressure, thus 20% depletion when the initial concentration was 0.6 mg./l. is different from 20% depletion when the initial concentration was 0.4 mg./l. The mean CO₂ content of air as used by BROWN and ESCOMBE, that is, the arithmetic average of the affluent and effluent air, is probably a more useful value. The relationship between rate of photosynthesis and mean CO₂ concentration found in the present experimentation is shown in figure 6. It is proposed that for a given set of experimental plants a similar regression could be established, by means of which all further experimental measurements of photosynthesis could be corrected to a selected mean CO₂ concentration. The effect of CO₂ supply could thus be eliminated from comparisons between measurements. In such a regression proper account should be taken of the fact that the independent variable, *x*, is subject to considerable sampling error.

Apparently it is generally supposed that, because the volume percentage concentration of CO₂ in air is essentially constant at all altitudes, CO₂ is not one of the determinative factors in the altitudinal distribution of species. The writer has been unable to discover any direct evidence supporting this supposition. LUNDEGARDH (6) discussed CO₂ as an ecological factor but made no mention of it in relation to altitude. WEAVER and CLEMENTS (11) did not mention it. MEYER and ANDERSON (7) stated that because CO₂ concentration is nearly constant it seldom need be considered a variable in interpreting the developmental behavior of plants under natural conditions. However, the diffusion of CO₂ into a leaf is a function of CO₂ pressure rather than concentration, and the pressure of CO₂ in the atmosphere varies directly as the total atmospheric pressure. The normal pressure of atmospheric CO₂ is approximately 22.8 mm. Hg at sea level and 13.0 mm. Hg at 15,000 feet altitude. DAUBENMIRE (2) recognized that the partial pressure of CO₂ varies with atmospheric pressure and stated that its effect on plant growth is indirect.

From the relationship between photosynthesis and CO₂ concentration shown in figure 6 a similar relationship between photosynthesis and CO₂ pressure may be deduced, for CO₂ pressure is a direct function of CO₂ concentration at constant total pressure. These data indicate a possible differential response to CO₂ pressure of the photosynthetic mechanisms of species normally growing at the same altitude.

In general, the natural distribution of vegetation is determined by the differential responses of species to gradients in one or more environmental factors. It seems reasonable to expect, therefore, that some species characteristic of different altitudes may exhibit differential responses to CO₂ pressure which are related to distribution, and thus at times the gradient in CO₂ pressure might be one of the significant factors of the determinative complex.

Summary

The apparent photosynthetic rate of the entire shoots of tree seedlings was found to vary hyperbolically with the rate of air supply and linearly with mean CO₂ concentration over the range 0.52 to 0.45 mg./l. The possible importance of CO₂ pressure as a factor in altitudinal distribution of species is suggested.

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