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THE COMPOSITION, QUANTITY, AND PHYSIOLOGICAL SIGNIFICANCE OF GASES IN TREE STEMS

WARREN WILLIAM CHASE[1]

INTRODUCTION

The presence of gases in the stems of woody plants has been recognized for more than two centuries. The effect of these gases upon the movements of the transpiration stream has been the cause of extended controversies for at least half of that time. Numerous investigators have studied the nature of these gases—their origin, condition, movements and function, especially within the leaves. The composition of enclosed gases, however, until very recently has attracted the attention of relatively few students in plant science. Most of these have worked only upon materials that could conveniently be brought into the laboratory, particularly twigs and fruits and leafy parts. The study of gases within the more bulky parts of plants has been neglected largely because of the inconvenience of working with them.

This investigation was carried on to determine the seasonal variations in the percentage of carbon dioxide and oxygen within the trunks of several kinds of trees, anatomically different, and indigenous to the northern part of the United States. The physiological significance of these gases in the metabolism of normal trees is of especial interest, but abnormal trees were also studied.

The data upon which this study is based were collected during the years 1931-1933 at University Farm, St. Paul, Minnesota. The analytical work was done in the plant physiology laboratory.

HISTORICAL REVIEW

Presence and Amount of Gas in Woody Tissues

A few early workers on plant anatomy recorded observations concerning the gas content of the cavities of the tubes or vessels of woody plants. Marcello Malpighi (41), in 1671, maintained that the fibrous elements of the wood were organs for water conduction and the vessels for air passage. He named the largest vessels tracheae because they closely resemble the air passages or tracheae in insects. This is not surprising, for he was more of a zoologist than a botanist. Malpighi was not certain of the origin of gas in the plant, but thought that it probably

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came up from the roots because of the abundance of tracheae in the roots and the fact that gas has a tendency to rise. Nehemiah Grew (20), in 1674, also believed that the rising sap, which he called lymph, moved upward in the lymph tubes or woody fibers. In spring the sap fills the vascular tubes of the wood, while in summer they are filled with gas.

Stephen Hales (22), about a half a century later, not only believed that the large elements are gas vessels but that gas enters plants through the surfaces of leaves and trunks. His experiments led him to believe that air moves freely through the bark of old stems but very slowly into young stems of which the "eyes" or lenticels are small. He also attempted to analyze the gases in wood, but he used heat to produce the gases and actually distilled the wood in this process.

Sachs (51), in 1887, presented definite data with regard to the amount of gas in wood. In fact he was the first to show that by determining the specific gravity and the moisture content of a definite volume of wood the space filled with gas can be computed. He stated that not all the cavities are entirely filled with water, reasoning that wood would not float if air were not present and that the crackling of fresh burning wood is due to the explosion of bubbles in the wood. His calculations on fir show that on the basis of 100 per cent fresh wood the gas in the cavities makes up 16.56 per cent. Karl Pappenheim (47), five years later, working also on fir wood, found the gas content to be 17.64 per cent by volume. According to Robert Hartig (23), heartwood contains less moisture and consequently more air than sapwood. He also pointed out that the last ten rings of sapwood are very low in air volume, averaging from 6 to 10 per cent.

In broad-leaved trees, the lumina of the tracheae are larger than the tracheid cavities of conifers and consequently there is more air present. Jones, Edson, and Morse (29) have observed that in spring maple contains gas to about one-fourth of its volume. The volume of gas, however, fluctuates, the gas and water varying inversely. According to MacDougal, Overton and Smith (38), trunks of oaks and willows contain gas to approximately one-fourth of their volume. They state further that in summer the percentage of air is higher than at other times, because of the loss of water due to transpiration and the production of gases due to respiration. During the spring and autumn water is most abundant and the gas volume is greatly reduced. This seasonal change is most pronounced in deciduous trees, because of the loss of leaves and the sudden checking of the transpiration stream in autumn and because of the beginning of the sap movement in the spring.

MacLean (39) has compiled figures, presented in the form of a graph, from which one may easily obtain the air content of a piece of wood if the moisture content and specific gravity are known. To gain an accurate knowledge of the volume of the gases within the trunk of a tree, it is necessary to know the physical conditions of the gases. The gas volume varies with temperature, atmospheric pressure, rapidity of movement of the transpiration stream, composition of the sap, composition of the gases, speed of the production and use of the gases in respiration and the rate of diffusion of these gases through the wood and bark.

Composition of Enclosed Gases

At the beginning of the nineteenth century, carbon dioxide and oxygen relations in gaseous exchanges were for the first time explained by De Saussure. At about the same time, he observed the important fact that nitrogen is not used in the gaseous state in plants but is taken up by the roots in the form of soluble compounds. Barthelemy (3), in 1874, published a summary of past analyses of internal gases. He stated that De Saussure found 9 per cent oxygen, 5 per cent carbon dioxide, and 86 per cent nitrogen in the gases drawn from an apple branch. Several decades later Boussingault repeated De Saussure's experiment and obtained the same results.

A brief resume of work done on the gas content of various plants is given by Clements (10). He states that considerable attention has been given to the study of gases drawn from marine algae, sugar beets, fruits and leaves of various land plants, but that very little work has been done on woody plants. Roots are shown to have a high carbon dioxide content and leaves to have a composition almost like that of the atmosphere. Succulent plants and fleshy fruits have a higher carbon dioxide content and a lower percentage of oxygen than the atmosphere. Devaux (14), as early as 1891, established the fact that even in the center of massive tissues oxygen is never entirely lacking. Magness (40), in 1920, found that the gases drawn from the intercellular spaces of apples, carrots, and potatoes were not free from oxygen, even tho the carbon dioxide content reached 34 per cent by volume. Herbert (25), in 1923, found that the gases within the mature coconut were high in nitrogen (99.8%), low in oxygen (0.2%), and very low in carbon dioxide, only a trace being present. Numerous other analyses have been made on the gases drawn from floating leaves and bladders. They show an almost constant nitrogen content, near that of the atmosphere, and varying amounts of oxygen and carbon dioxide. These latter gases vary inversely with each other and their sum is usually below the oxygen content of the atmosphere. Gaerlan (18) found in 1926 that the gases in the mature internodes of bamboo were composed of 5.95 per cent carbon dioxide, 13.82 per cent oxygen, and 80.26 per cent nitrogen. Bonazzi (6), in 1931, extracted gases from the basal internodes of sugar cane. He found the carbon dioxide content to be 7.73 per cent and the oxygen 14.10 per cent by volume. Clements (10) states that photosynthetic activity is credited as being the chief factor upon which the composition of the internal gas depends. This, however, was for small twigs and leafy parts of plants only. Roots in general have a high percentage of carbon dioxide and a low percentage of oxygen, while small stems and especially the green parts of stems and leaves have low percentages of carbon dioxide and high percentages of oxygen.

Faivre and Dupre (17), in 1866, working on small stems of mulberry and grape, made the first study of the seasonal composition of internal gases. They found that gases in the small stems of the mulberry were composed of the following percentages by volume at various times of the year: (leafy branches) June 15, 15.7 per cent carbon dioxide, 2.5 per cent oxygen; October 15, 3.19 per cent carbon dioxide, 13.96 per cent oxygen; January 31, 0.01 per cent carbon dioxide, 20.9 per cent oxygen.

Boehm (5), in 1878, found that gases drawn from the cells and vessels of woody branches in a winter condition contained very little oxygen, but they did contain 30 per cent or more carbon dioxide. Boehm's experimental method has been severely criticised by Pappenheim (47) and Lindner (31), who state that he allowed the frozen branches to thaw before the gas was removed and that respiration due to the increased temperature was the cause of the high carbon dioxide and low oxygen percentage. Kruticki (30), in 1889, also experimenting on small woody stems, obtained results diametrically opposite to those of Boehm. His findings show that in the winter the composition is more nearly like that of the atmosphere. It is doubtful, however, if these results are of more value than those of Boehm. Lindner is of the opinion that neither Boehm nor Kruticki took into consideration the physical factors known at that time. Altho Lindner (31), 1917, gave an extensive discussion on the theories of water and gas conduction, his results of analyses of gases were limited. He worked only on small twigs, just as workers in the past century had done. His analyses of gases drawn from these twigs showed a low carbon dioxide percentage and a very high oxygen percentage, much like that of the atmosphere. The determinations were all made in the summer and showed none of the variations due to changes in season or temperature.

Until recently, the composition of gases in large tree trunks has been unknown. Bushong (7) made the first analysis of the gases drawn from a tree. He drew gases from a large cottonwood and in 1907 reported the following percentages: Oxygen, 1.24; carbon dioxide, 7.21; methane, 60.90, and nitrogen, 30.65. No traces of ethylene, carbon monoxide, or ethane were found.

The studies of the life processes of normal tree trunks, begun by MacDougal in 1925, have led to some information concerning the gases present in the trunks of trees. From October, 1925, to November, 1927, gases were drawn from the trunks of four species of trees. The results, with brief discussions, are given by MacDougal (34, 35, 36) and MacDougal, Overton, and Smith (38).

Gases drawn from Monterey pine in the fall of 1925 were found to be composed of 4.21 per cent carbon dioxide and 15.43 per cent oxygen on October 16, and 3.80 per cent carbon dioxide and 19.90 per cent oxygen on October 19. Gases from the live oak of California had 3.03 per cent carbon dioxide and 17.84 per cent oxygen on October 6, and on October 19 the gases drawn from the walnut were found to be composed of 10.62 per cent carbon dioxide and 9.96 per cent oxygen. No further measurements were made, but in 1926 and 1927 analyses were made upon gases from four other trees.

California live oak, *Quercus agrifolia,* contained gases with the carbon dioxide percentage varying throughout the season. Active growth starts in April and extends through August. The analysis made in 1926 indicated an increased respiration in autumn after the period of growth had ended. This late resumption of activity caused high proportions of carbon dioxide to be present as late as October. On June 29 the carbon dioxide content was 9.4 per cent and on November 1, 3.6 per cent. In 1927 studies were made during a larger part of the season and the following variations were found: Starting on January 17, the carbon dioxide content was as low as 1.4 per cent; April 15, 1.5 per cent; May 26, 5.2 per cent, showing that growth had started; June 23, 11.4 per cent, and on August 3 the peak was reached, 15.1 per cent. By September 3, a decrease was noted, the carbon dioxide amounting to 8.1 per cent, and by October 22 it had dropped to 4.6 per cent.

Willow, *Salix lasiolepis,* contained gases with a carbon dioxide content of 13.1 per cent in June, 8.4 per cent in August, 12.0 per cent in October, 9.7 per cent in November, 5.2 per cent in January, 5.0 per cent in May, 8.8 per cent in June, 10.0 per cent in August, and 10.6 per cent in September. The growing season of this tree is from May until October, and it appears from the results obtained that the temperature during the dormant period is such that the process of respiration can continue throughout the year.

Gases drawn from the cottonwood, *Populus MacDougali,* were found to have a carbon dioxide content of only 1.4 to 2.4 per cent in February. By March 1 it had reached 6.0 per cent and by the end of March, 9.8 per cent. On May 8 the content of carbon dioxide was 18.2 per cent.

This tree began growth the first part of March and continued until October.

Monterey pine, *Pinus radiata,* begins growth in January and continues until July. Gases drawn from Monterey pine had a carbon dioxide content of 3.7 per cent in January, 9.1 per cent in May, 11.2 per cent in June, 11.0 per cent in August, and 12.0 per cent in October. This tree grew on the Pacific Coast at Carmel, California, where respiration continues throughout the year and the growing season lasts from January to July.

It is to be seen from MacDougal's and MacDougal, Overton, and Smith's researches that air extracted from tree trunks has a very different composition from that of the atmosphere. Altho they give no data in their last paper (1929) as to the percentages of oxygen present, they say that the proportion of the oxygen is invariably less than that of the air, and the sum of carbon dioxide and oxygen is less than in the atmosphere. The remaining gas after oxygen and carbon dioxide were removed was taken to be nitrogen. MacDougal (36), in 1927, states that this condition suggests that there may be other substances present, such as methane or carbon monoxide. Terpenes were present in the gases of pines, and they have been detected in oak, willow, and poplar gases in about one part in a thousand. Working (61), in 1931, made analyses to determine whether gases other than carbon dioxide, oxygen, nitrogen, and terpenes were present in tree trunks. No trace of carbon monoxide, hydrogen, or hydrocarbons was found. Water vapor was found to be consistently lower than the vapor pressure of pure water at the temperature of the tree when the sample was taken. Nitrogen was determined quantitatively and its ratio "to inert gas corresponded closely with that of the air, and the sum of the two accounted, within a reasonable experimental error, for all gas other than oxygen, carbon dioxide and water vapor."

It may be seen from this review of the work done on gases contained within the trunks of trees that investigations have been few and the results brief. The researches of MacDougal and his colleagues are concerned chiefly with growth, water conduction, the physical relations of the pneumatic to the hydrostatic systems and the pressure produced in each system. The composition of the gases was studied as a minor part of the study of normal tree physiology. Seasonal trends were based upon a very small amount of data, and temperature was not considered. The climate of the region in which the above researches were carried on is semi-tropical and rather arid for a large part of the year. Hence conclusions arrived at are necessarily limited to areas of similar nature.

MATERIALS AND METHODS

The fact that all previous work on the composition of gases extracted from large tree trunks had been carried on in the Southwest led the present writer to attempt a determination of the seasonal changes of carbon dioxide and oxygen present in the trunks of some of the common tree species of Minnesota. The trees studied were: American elm (*Ulmus americana* Linnaeus), red oak (*Quercus borealis* Michaux f.), bur oak (*Quercus macrocarpa* Michaux), cottonwood (*Populus deltoides virginiana* [Castiglioni] Sudworth), and white pine (*Pinus strobus* Linnaeus) (57). All of these trees were large and apparently vigorous.

These trees were selected because of anatomical differences and leaf persistence. The American elm, red oak, and bur oak are ring porous; the cottonwood is diffuse porous; while the white pine is nonporous.

Bur oak has its vessels plugged with tyloses except for a part of the newer sapwood, while red oak has comparatively few tyloses even in the heartwood. Both of the oaks have their summerwood vessels in radial rows with vertical parenchyma present around the vessels and spreading out tangentially to the wood rays. The wood rays in these species are very large. American elm wood, almost lacking in tyloses, has vessels in tangential rows and wood parenchyma scattered around the tracheae. Its rays are small. Cottonwood, being diffuse porous, has numerous smaller tracheae scattered throughout the annual ring. Vertical parenchyma is terminal and the wood rays are very small. White pine is the only one of the several species selected for study with persistent leaves. The structure of the wood is homogeneous, being composed of wood tracheids only, resin canals and very small rays. Each tracheid in the white pine is a unit in itself and it is connected with those above and those below by bordered pits, whereas in the other species studied the tracheae are open at the ends making a continuous passageway up to a length of about 35 centimeters. It was thought that these structural differences might influence the amounts of carbon dioxide and oxygen within the trunks during the growing season.

The five trees used were of nearly the same size. They were measured at 40 inches above the ground level and were all from 12 to 14 inches in diameter at that height. They were not all, however, on the same site. The oaks were on high land, growing in a typical oak stand which showed evidence of damage by drouth within the last few years. The elm, cottonwood, and white pine were on a lower, less exposed site where conditions for growth were more favorable.

These five trees were bored at 3.3 feet above the ground level with a 7/16-inch bit. The holes were drilled to the approximate center of

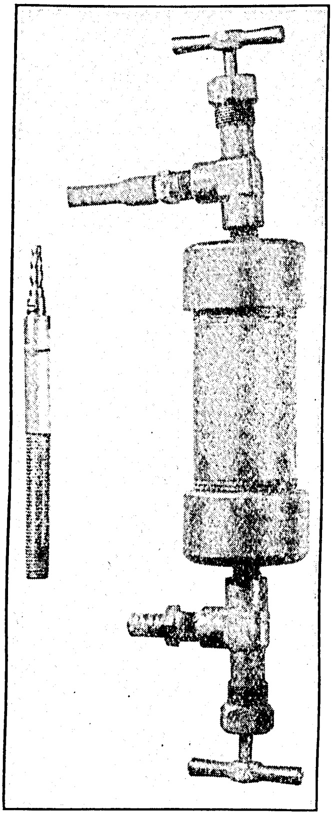


Plate I. Brass tube to be screwed into the trunk. Iron gas sampling tube fitted with all steel stopcocks and rubber connections.

the trunk. Specially-designed brass tubes were made with coarse threads on one end and a small stopcock on the other end. The tubes were six inches long and were tightly screwed into the hole in the tree for approximately three inches. Plates I and II show a tube and its attachment to the tree. As a precaution against infection, the bit and tube were dipped into absolute alcohol before they were inserted into the tree. So that a very little atmospheric air would be left in the bore and brass tube, an evacuated gas receiver was attached and most of the air was withdrawn. Samples for analysis were not withdrawn for several days in order to allow the gases in the tube and wood elements adjoining the hole to come to their normal pressure and composition.

In order to study the gases present at different heights, the same cottonwood trunk was bored at six other positions. Holes were bored and tubes inserted at the following positions on the trunk:

Height in feet	Diameter in inches
32.0	4
24.0	6
18.0	8
12.0	10
3.3	13
0.3	18

The various diameters at different heights made it undesirable to screw the tubes in very deep. At the four-inch diameter the hole was bored a little past the center of the stem and the tube screwed in to a depth of one inch. At each larger diameter the hole was bored approximately to the pith and the tubes screwed in to correspondingly greater depths, an attempt being made, of course, to tap the tree for gases as near the center as possible. At the base of the tree the tube was screwed to a depth of three inches.

To determine the difference in the composition of gases in the heartwood and sapwood, one tube was inserted into a hole bored 1.5 inches under the bark of the cottonwood tree. This was at 3.3 feet above the ground, on the side of the tree opposite the main heartwood tube described above.

Samples of the internal gases were withdrawn every ten days or two weeks for approximately one year and analyzed for carbon dioxide and oxygen. In order to take samples during the different seasons, with their consequent temperature changes, a special type of sampling tube had to be made. Glass was found to be unsuitable especially in cold weather because of the "freezing" of stopcocks when the tubes were taken out of doors. Ordinary brass tubes and stopcocks were tried, but these too were useless because of the effect of mercury upon them, and mercury was necessary in evacuating the sampling tubes and in a part of the analytical procedure. Finally all-steel tubes and stopcocks were made and these (Plate I) were entirely satisfactory. After evacuating the sampling tubes to about one atmosphere negative pressure they were attached with the aid of a clamp and short rubber tube to the rubber connection on the outer end of the tube which had been screwed into the tree trunk. The connecting stopcocks were left open until the air in the tube and in the vessels in the tree had come to equilibrium. After several preliminary trials it was found that a period of approximately 48 hours was satisfactory. This, of course, depended upon the amount of sap and air present in the tree. The sampler, after having been connected to the tree for this period of time, was removed and taken to the laboratory. After allowing the tube and gases to come to room temperature, the gas was analyzed. Duplicate analyses were made of each sample.

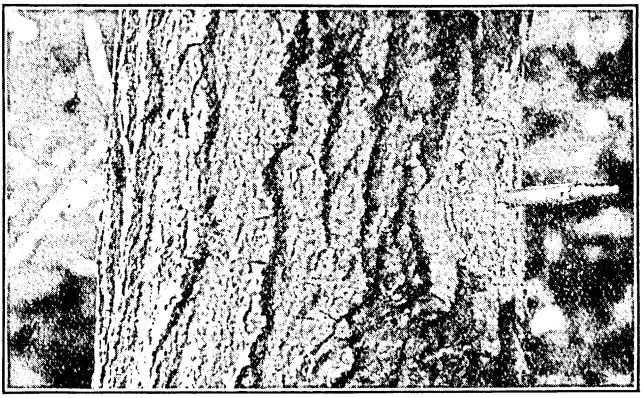


Plate II. Brass tube screwed into the trunk to a depth of three inches. The small stopcock is adjacent to the rubber connection.

The method of analysis used was volumetric, based upon the procedure given by Dennis and Nichols (13). The apparatus, as shown in Plate IV, consisted of a modified Van Slyke total nitrogen apparatus. The burette was graduated in tenths of cubic centimeters and had a total measurable volume of 40 cubic centimeters. This was surrounded by a water-jacket which aided in keeping temperature changes at a minimum during the analysis. Two Hemple absorption pipettes were connected to the burette by a three-way stopcock. One pipette contained potassium hydroxide for the removal of carbon dioxide and the other, alkaline pyrogallol for the absorption of oxygen. The concentrations of these absorbents were those suggested by Shepherd (54). These solutions were protected from the atmosphere by a layer of light mineral oil. The confining liquid was a 22 per cent sodium chloride solution. This was very satisfactory and according to Dennis and Nichols is next in accuracy to mercury for technical gas analysis. Because of its weight, mercury was used to force the gas from the sampling tube into the burette.

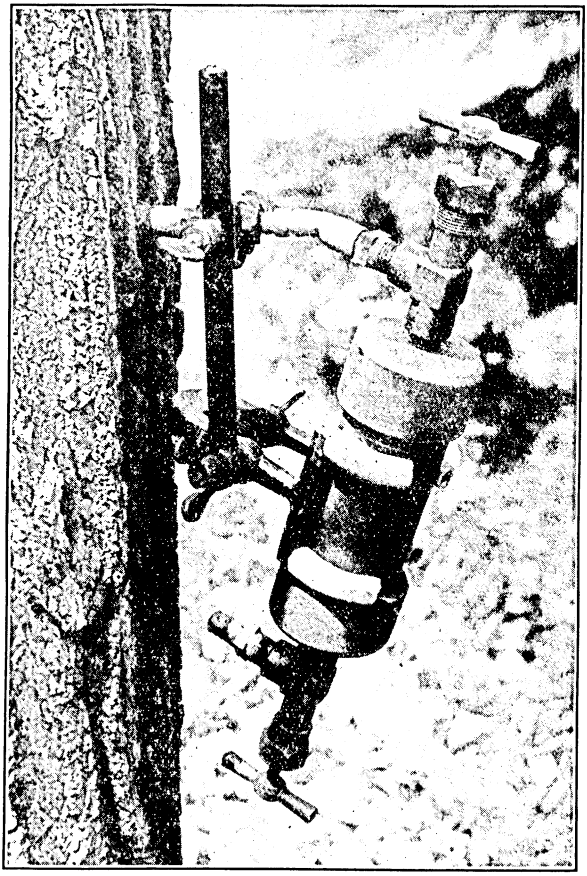


Plate III. Gas sampling tube and method of attachment to the brass tube screwed into the tree.

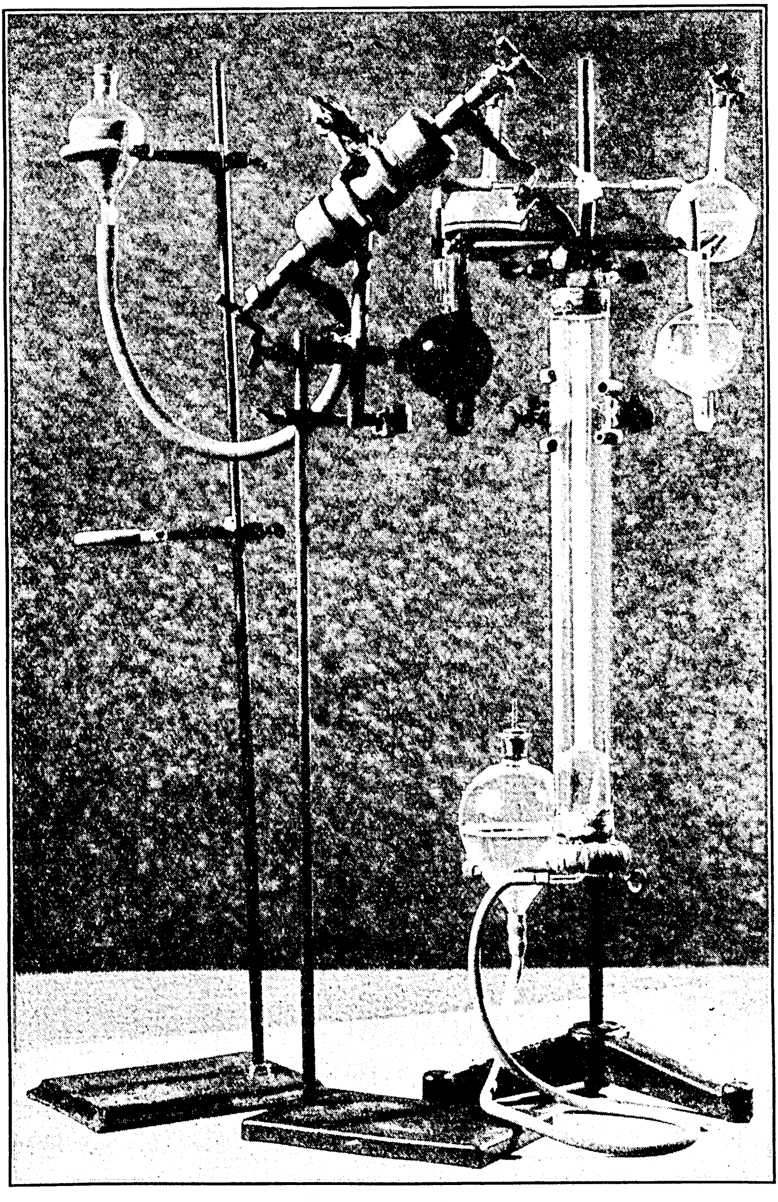


Plate IV. Gas analysis apparatus and the attachment of the iron gas sampling tube.

The procedure of running an analysis was comparatively simple. After the sampling tube containing the gases had come to room temperature, it was clamped into place on the apparatus, as shown in Plate IV. The air in the lower stopcock of the sampling tube was forced out, mercury from the leveling bulb taking its place. The upper stopcock was connected with the outlet of the burette and the air flushed out of this connection with a small amount of the gas sample. Thus the confining liquid which filled the burette was connected directly to the sample within the sampling pipette. By raising the leveling bulb containing mercury and opening the connecting stopcocks, the sample of gas was forced into the burette, displacing the confined liquid. When the gas sample filled the burette to approximately 40 cubic centimeters all stopcocks were closed. The volume of the sample was determined after being allowed to stand for about two minutes in order to let the confining liquid run down the sides of the burette. It was then forced into the absorption pipette containing potassium hydroxide. The sample was moved back and forth from the burette to the pipette three times to flush out the connections, and the absorption pipette was shaken vigorously between each flushing. After a sufficient time for complete absorption to take place—usually about three minutes—the sample was returned to the burette, allowed to stand for two minutes, and the volume read. The oxygen in the sample was removed in like manner by absorption in the pipette containing alkaline pyrogallol. The volume of each of the gases was then calculated and expressed in terms of percentage of the total volume of the sample.

The accuracy of this method of gas analysis has been tested by numerous investigators and when errors result they are due to faulty technic of operation. If the absorbing solutions are checked frequently and not allowed to become weak, and the temperature of the room is fairly constant during the analysis, there is little danger of error. Preliminary analyses of atmospheric air showed carbon dioxide to vary from 0.02 to 0.10 per cent and oxygen from 20.60 to 20.90 per cent by volume. Humphreys (28) gives 0.03 per cent carbon dioxide and 20.99 per cent oxygen as the average amounts of these components of dry air by volume.

The temperature data used in the tables and graphs for comparison with the amounts of carbon dioxide and oxygen occurring in the trunks at various times of the year were those recorded in St. Paul by the Weather Bureau, U. S. Department of Agriculture. Daily mean temperatures were averaged for the time the sample was being collected. This sampling time was in most cases a period of two days.

At the close of the experiment the tubes were removed from the tree trunks. Borings were then made with a one-inch bit to determine whether any changes had taken place in the woody material around the tubes or in the center beyond where the tubes extended. In no case was there any decomposition of the wood. There was, however, some discoloration where the brass tube came in contact with the wood. This discoloration extended only from two to three inches above and below the tube and only in those tracheids and vessels of the last year which were cut through and stopped up by the brass tube. In the inner rings, where there was no conduction of moisture, the wood was its normal color. All trees were perfectly sound to the center.

PRESENTATION OF EXPERIMENTAL RESULTS

Throughout the course of this study more than 900 individual analyses were made. Most of these determinations were made on gases drawn from the heartwood of five trees. Some were made upon gases withdrawn from the center of one tree at various heights, and some from the sapwood and heartwood at one height—all to determine if there were any differences and, if so, what they might be. The determinations are given in complete form in Tables 1-11. Data from these tables are presented graphically in Figures 1-8.

The growing season of all the trees studied extends from the last part of April and the first part of May, when the leaves are expanding, to September and October, when the leaves of the deciduous trees fall. The period of actual wood formation is of shorter duration, and altho it has not been determined by investigation for the individual species studied, it is generally believed that diameter growth takes place largely during the months of May, June, July, and a part of August. The ripening or maturing of the wood goes on all summer. The formation of buds takes place in the middle and latter part of the growing season, and the storage of food material in the parenchymatous cells continues until the leaves fall or the temperature falls too low for photosynthetic activity. Respiration uses oxygen and produces carbon dioxide within the stem, and temperature changes greatly affect this process.

From purely theoretical considerations, it would be expected that the carbon dioxide would be higher in summer than in winter, unless it diffused very rapidly outwardly, while in the case of oxygen it would be expected to fluctuate in the opposite direction. The concentration of these gases would depend then, first, upon the amount and pressure of each in the atmosphere, secondly, upon the rate of production of carbon dioxide and the consumption of oxygen within the trunk, and, thirdly, upon the rate of movement through the almost water-saturated wood, cambium and bark. The attempt to reach a state of equilibrium would be going on continuously.

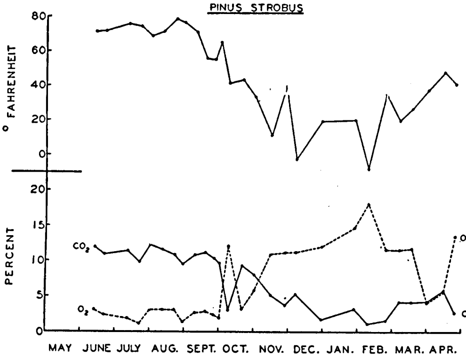
Pinus strobus

The data on white pine were collected between June 12, 1932, and April 25, 1933. Table 1 and Figure 1 show these data in tabular and graphic forms. The highest percentage of carbon dioxide present within the trunk was 12.25 on August 1 and the lowest 1.18 on February 9.

FIGURE I.

SEASONAL VARIATION OF PERCENTAGE OF CARBON DIOXIDE AND OXYGEN WITH MEAN TEMPERATURE.

PINUS STROBUS



Oxygen was lowest, 1.03 per cent, on July 22 and highest, 18.29 per cent, on February 9. Throughout the summer months, the proportion of the gases remained fairly constant. From June until the last part of September, the carbon dioxide content was between 9.52 and 12.25 per cent, and the oxygen between 1.03 and 3.14 per cent. During the autumn, when rapid temperature fluctuations were common, there were abrupt changes in the carbon dioxide and oxygen content. By October 8, carbon dioxide had dropped to 3.10 per cent and oxygen had risen to 12.10 per cent. These fluctuations lasted for only a few days following a rapid drop in temperature. On October 20 the concentration of the gases was reversed and carbon dioxide went up to 9.48 per cent and oxygen down to 3.24 per cent. This was apparently due to a slight rise in temperature. The last part of October and the first part of November brought a decrease of carbon dioxide and a steady increase of oxygen, continuing through December and January. After the lowest carbon dioxide content of the year was reached in the first part of February, there was a steady but slow increase during March and a part of April. The decrease of carbon dioxide in the last part of April indicates a slight fluctuation in the spring; this, however, was not as wide as in the autumn. Data taken after the graphs were completed show a further increase in carbon dioxide content, reaching 8.99 per cent in the first week in May. The oxygen decreased quite rapidly after reaching its highest point in February. By April 1 it had dropped to 4.18 per cent. It increased to 13.66 per cent by April 25, but it dropped again to 2.64 per cent by May 10.

Table 1

Percentage of Carbon Dioxide and Oxygen in the Trunk of *Pinus strobus*

Date	Mean air temperature, degrees F.	Percentage CO_2		Percentage O_2		Total percentage CO_2 and O_2
			Average		Average	
June 13	71.5	11.89		3.26		
“ 15		11.91	11.90	3.02	3.14	15.04
“ 21	72.0	10.89		2.50		
“ 23		11.00	10.95	2.22	2.42	13.37
July 11	76.0	11.50		1.77		
“ 13		11.33	11.42	1.94	1.84	13.26
“ 22	74.5	10.00		1.06		
“ 24		9.98	9.99	1.00	1.03	11.03
Aug. 1	69.0	12.26		3.20		
“ 3		12.24	12.25	2.94	3.07	15.32
“ 11	72.0	11.57		3.25		
“ 13		11.53	11.55	2.98	3.12	14.67
“ 22	79.0	10.83		3.12		
“ 24		10.84	10.84	2.91	3.02	13.86
“ 29	77.0	9.56		1.46		
Sept. 1		9.48	9.52	1.27	1.37	10.89
“ 10	71.5	10.90		2.55		
“ 12		10.72	10.81	2.72	2.64	13.45
“ 19	56.5	11.18		2.96		
“ 21		11.04	11.11		2.96	14.07
“ 26	56.0	10.48		2.27		
“ 28		10.35	10.41	2.48	2.37	12.78
Oct. 1	65.5	9.78		1.91		
“ 3		9.64	9.71	2.02	1.96	11.67
“ 8	42.0	3.02		12.03		
“ 10		3.17	3.10	12.12	12.10	15.20
“ 20	44.0	9.46		3.20		
“ 22		9.50	9.48	3.29	3.24	12.72
Nov. 1	34.0	8.08		5.90		
“ 3		8.12	8.10	5.98	5.94	14.04
“ 15	12.0	5.28		10.93		
“ 18		5.29	5.28	11.14	11.03	16.31
“ 28	40.0	3.70		11.28		
“ 30		3.97	3.83	11.33	11.21	15.04
Dec. 7	—2.0	5.39		11.24		
“ 10		5.37	5.38	11.31	11.27	16.65
“ 29	20.0					
Jan. 3		1.73	1.73	12.07	12.07	13.80
“ 28	20.5	3.31		14.81		
“ 30		3.27	3.29	14.98	14.89	18.18
Feb. 9	—7.0	1.23		18.15		
“ 11		1.13	1.18	18.44	18.29	19.47
“ 25	36.0	1.53		11.69		
“ 28		1.68	1.60	11.74	11.71	13.31
Mar. 7	20.3	4.28		11.59		
“ 10		4.31	4.29	11.79	11.69	15.98
“ 17	27.3	4.30		11.81		
“ 20		4.29	4.29	11.82	11.81	16.11
Apr. 1	38.3	4.46				
“ 4		4.38	4.42	4.18	4.18	8.60
“ 15	49.0	5.83		5.98		
“ 17		6.07	5.95	5.82	5.90	11.85
“ 25	42.0	2.72		13.58		
“ 27		2.68	2.70	13.74	13.66	16.36

From this study it can be seen that the carbon dioxide and oxygen contents of the tree trunk fluctuate greatly during the different seasons. The seasonal variation in general follows the mean temperature throughout the year. In most cases, when the temperature falls the carbon dioxide content decreases and the oxygen increases. This variation is present in fall, winter, and spring. But in summer, and in the case of the pine only, the carbon dioxide and oxygen fluctuations follow each other, both reaching low points the last of July, the last of August, and the last of September. They seem to follow the temperature in its monthly variations. All large temperature changes do not always produce the same effect on the amount of carbon dioxide and oxygen in the tree. Perhaps a lag will show up in daily determinations, which, however, is not shown in those taken at intervals of one week or more. One of the greatest difficulties in closely comparing these variations is that after a sample is taken from the interior of the tree the condition and composition of the enclosed gases changes. Another sample, if taken too soon, will probably be influenced by changes resulting from the previous withdrawal of gas.

The total amount of carbon dioxide and oxygen present in the gases withdrawn from the pine trunk varied from 8.60 on April 1 to 19.47 per cent on February 9. During the rest of the year it varied between 10 and 16 per cent. This is considerably lower than the total of oxygen and carbon dioxide in the atmosphere. If 21.0 per cent is taken as the normal atmospheric total of these two gases, it is seen that within the pine trunk the total carbon dioxide and oxygen percentage is only slightly more than half of that of the atmosphere. The total percentage of these gases is nearest that of the air in the winter and farthest from it in the spring after respiration has begun. The low total in the spring is due apparently to the low oxygen content in the trunk. In the last part of February and in March, with the beginning of warmer weather, the carbon dioxide content rises steadily but the oxygen content drops rapidly. This probably results from the larger need of oxygen in the newly resumed metabolic processes. To date no one has worked out the reason for this sudden drop in oxygen content.

Ulmus americana

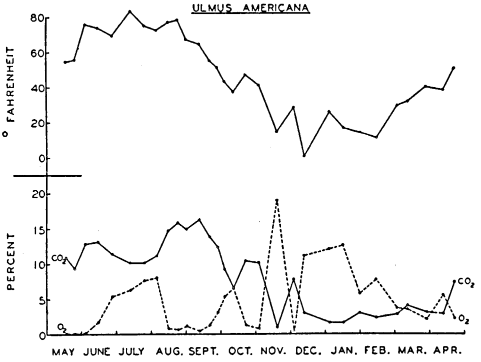
The seasonal variations of the gases found in the trunk of the American elm follow closely the trends found in the white pine. The carbon dioxide was high in summer and low in winter, while the oxygen was low in summer and high in winter. The data shown in Table 2 and the seasonal variations compared with mean temperature in Figure 2 explain the changes more readily than is possible in a description.

By May 17 the carbon dioxide content of the gas in the tree had reached 10.96 per cent. Between the 17th and the 25th, a decrease was recorded, caused presumably by the low temperatures in the middle of the month. In the first two weeks of June there was a rapid increase. Immediately following, there was a decrease which continued through

FIGURE 2

SEASONAL VARIATION OF PERCENTAGE OF CARBON DIOXIDE AND OXYGEN WITH MEAN TEMPERATURE.

ULMUS AMERICANA



July. A rapid increase during August culminated in the high point of the season, on September 12, when the carbon dioxide reached 16.27 per cent. After this yearly maximum was reached, there was a sudden decrease which apparently followed the continuous drops in temperature during the autumn. By October 11, the carbon dioxide had dropped to 6.57 per cent. The autumnal temperature fluctuations now appeared to affect the gases present in the trunk. These sudden changes lasted until the first part of December. During this period, the carbon dioxide increased somewhat in the last part of October, but had dropped down to a low of 0.93 per cent by November 19. Following a change in temperature, it increased to 7.87 per cent by December 3. By the twelfth of the month, however, it dropped to 3.00 per cent. Throughout January and February the carbon dioxide content of the tree trunk remained low, fluctuating between 1.52 and 3.01 per cent. In March there was a slight increase and then a drop. By April 22, however, there was a decided increase, reaching 7.54 per cent. The fluctuations of the oxygen in the trunk of the elm were found to vary inversely with carbon dioxide—when there was a decrease in oxygen, there was an increase in carbon dioxide. These variations were present consistently throughout the year. During the middle of the summer season, the oxygen content increased to 8.03 per cent on August 5 from a low of 0.02 per cent on May 25. During the last of August and throughout September it was low, varying between 0.41 and 1.26 per cent. For the most of the autumn, it fluctuated greatly following temperature changes. When the temperature dropped suddenly, the oxygen content increased rapidly. These rapid fluctuations lasted until the period of cold weather in December, after which the oxygen content remained high throughout

Table 2

Percentage of Carbon Dioxide and Oxygen in the Trunk of *Ulmus americana*

Date	Mean air temperature, degrees F.	Percentage CO_2		Percentage O_2		Total percentage CO_2 and O_2
			Average		Average	
May 17	55.0	10.92		0.10		
" 18		11.00	10.96	0.25	0.13	11.09
" 25	56.0	9.38		0.01		
" 27		9.63	9.48	0.04	0.02	9.51
June 4	76.0	12.77		0.18		
" 6		12.91	12.85	0.02	0.09	12.95
" 14	74.0	13.16		1.66		
" 16		13.14	13.15	1.70	1.68	14.83
" 27	69.5	11.38		5.36		
" 29		11.52	11.45	5.37	5.36	16.81
July 13	83.5	10.13		6.12		
" 15		10.01	10.07	6.24	6.18	16.25
" 25	75.5	10.10		7.56		
" 27		9.92	10.01	7.67	7.61	17.62
Aug. 5	73.0	11.19		7.94		
" 7		11.15	11.17	8.12	8.03	19.20
" 15	77.5	14.62		0.81		
" 17		14.74	14.68	0.64	0.74	15.41
" 23	79.0	15.89		0.86		
" 25		15.74	15.81	0.35	0.56	16.37
Sept. 1	67.5	15.00		1.03		
" 3		14.98	14.99	1.03	1.03	16.02
" 12	65.0	16.29		0.58		
" 13		16.25	16.27	0.30	0.41	16.68
" 21	56.0	13.93		1.27		
" 23		13.79	13.86	1.25	1.26	15.12
" 28	52.0	12.24		3.19		
" 30		12.23	12.24	3.06	3.11	15.35
First frost						
Oct. 4	44.0	9.38		5.42		
" 6		9.28	9.33	5.36	5.39	14.72
" 11	38.0	6.47		6.55		
" 13		6.68	6.57	6.61	6.58	13.15
" 22	48.0	10.51		1.25		
" 24		10.46	10.48	1.35	1.30	11.78
Nov. 3	42.0	10.23		0.70		
" 5		10.15	10.19	0.73	0.71	10.90
" 19	15.5	0.83		18.95		
" 21		1.03	0.93	19.19	19.07	20.00
Dec. 3	29.0	7.88		0.42		
" 5		7.86	7.87	0.40	0.41	8.28
" 12	1.5	3.00		11.30		
" 14		2.98	3.00	11.05	11.17	14.17
Jan. 4	26.5	1.60		12.08		
" 7		1.58	1.59	12.32	12.20	13.79
" 16	18.0	1.51		12.65		
" 20		1.53	1.52	12.77	12.71	14.23
" 31	15.5	3.01		5.78		
Feb. 4		3.02	3.01	5.95	5.86	8.87
" 14	12.2	2.26		7.74		
" 18		2.31	2.28	7.99	7.86	10.14
Mar. 2	30.5	2.87		3.65		
" 6		2.92	2.90	3.78	3.71	6.61
" 11	33.0	4.10		3.55		
" 15		4.02	4.06	3.49	3.52	7.58
" 28	41.0	3.12		2.01		
" 30		3.28	3.20	2.06	2.03	5.23
Apr. 12	39.3	2.98		5.55		
" 15		3.00	2.99	5.69	5.62	8.61
" 22	51.5	7.56		2.21		
" 24		7.52	7.54	2.25	2.23	9.77

January. In the spring there was a decrease in oxygen which continued until the first part of March. As in the white pine trunk, there was a decrease in the oxygen in the trunk without a corresponding increase in the carbon dioxide. This seeming abnormality changed to the summer condition of high carbon dioxide and low oxygen during the last part of April and the first part of May, just as it did in the white pine.

Rapid temperature changes were followed closely by variations in the gases of the tree trunk. This relationship was shown for the whole year. In certain cases when the temperature changes were not rapid, there was little or no change in the carbon dioxide and oxygen content. For a closer correlation, more detailed data would have to be taken on temperature, and other factors of the environment would have to be considered.

The total percentage of oxygen and carbon dioxide present in the trunk of the elm varied during the seasons, but at all times it was less than that found in the atmosphere. The lowest value was in the spring when the buds were bursting and the leaves were beginning to expand, the lowest being 5.23 per cent on March 28. In general, in the summer, autumn, and winter, the total of the two gases remained fairly constant, averaging about 15.0 per cent. This varied from 8.28 to 20.00 per cent during the winter months, but remained almost constant from June to October, as may be seen in Table 2.

Quercus borealis

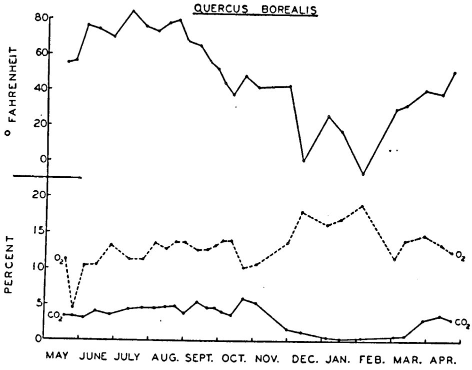
The gases drawn from red oak showed the same seasonal variations as those from the trunk of the bur oak. This is indicated in Tables 3 and 4 and Figures 3 and 4. From the middle of May, there was a steady increase in the gases throughout the summer. On May 17 the analysis of gases showed a carbon dioxide content of 3.36 per cent. By August 23 it had reached 4.81 per cent. During the months of September and October there were slight fluctuations, the highest carbon dioxide content (5.98 per cent) of the year occurring on October 22. From that date on for several months there was a steady decrease in the carbon dioxide, the lowest content (0.29 per cent) occurring January 16. Throughout February and well into March there was a very slow increase. From March 11 to the 28th, the carbon dioxide content jumped from 0.66 per cent to 3.00 per cent. By the end of April, the carbon dioxide in the trunk was at the same concentration as it was in the middle of the previous month.

The oxygen content of the red oak trunk fluctuated more than did the carbon dioxide content. This, of course, is what one would expect, because of the much greater amount of oxygen in the atmosphere. During the last part of May there was a drop in the oxygen content from

FIGURE 3

SEASONAL VARIATION OF PERCENTAGE OF CARBON DIOXIDE AND OXYGEN WITH MEAN TEMPERATURE.

QUERCUS BOREALIS



11.27 on the 17th to 4.50 per cent on the 25th. By the 4th of June, however, it again increased to 10.40 per cent. The oxygen content varied somewhat during the months of June, July, August, and September, the percentage ranging from 10.40 to 13.87. On October 11 it reached 14.07 per cent, but after that it dropped below 11.00 per cent and remained low during the whole of November. Throughout the winter, however, there was an increase in the oxygen content. Two high points were reached, one in December when 18.09 per cent was recorded, and one in February when it reached 19.12 per cent. By March 2, the concentration of oxygen had dropped to 11.61 per cent. A slight rise was shown the last of the month, followed by a decrease which lasted throughout April. The final determination was made on April 22, and the oxygen had dropped to 12.55 per cent. This was only slightly over 1.00 per cent more than it had been on the 17th of May a year before.

These seasonal fluctuations of the carbon dioxide in the trunk of the red oak followed very closely the mean temperatures recorded on the days the samples of gas were collected. As in the other trees studied, the carbon dioxide varied directly and the oxygen inversely with seasonal changes in temperature. The oxygen content, however, fluctuated more with temperature changes, undoubtedly because of the greater amount of this gas present. Rapid changes in temperature affected only slightly the carbon dioxide content of the trunk.

The total of the two gases remained below that of the atmosphere throughout the year. It was lowest on May 25, dropping to 7.80 per cent. During the two summer months of June and July the total varied between 14.53 and 16.82 per cent. In August, September, and October

Table 3

Percentage of Carbon Dioxide and Oxygen in the Trunk of *Quercus borealis*

Date	Mean air temperature, degrees F.	Percentage CO_2		Percentage O_2		Total percentage CO_2 and O_2
			Average		Average	
May 17	55.0	3.34		11.31		
“ 18		3.38	3.36	11.24	11.27	14.63
“ 25	56.0	3.30		4 47		
“ 27		3.29	3.30	4.52	4.50	7.80
June 4	76.0	3.99		10.70		
“ 6		4.27	4.13	10.10	10.40	14.53
“ 14	74.0	4.09		10.49		
“ 16		4.08	4.09	10.55	10.52	14.61
“ 27	69.5	3.56		13.28		
“ 29		3.51	3.53	13.29	13.29	16.82
July 13	83.5	4.44		11.34		
“ 15		4.47	4.45	11.31	11.32	15.77
“ 25	75.5	4.62		11.45		
“ 27		4.54	4.58	11.38	11.41	15.99
Aug. 5	73.0	4.60		13.69		
“ 7		4.57	4.58	13.67	13.68	18.26
“ 15	77.5	4.85		12.87		
“ 17		4.66	4.75	12.92	12.90	17.65
“ 23	79.0	4.87		13.73		
“ 25		4.76	4.81	14.01	13.87	18.68
Sept. 1	67.5	3.90		13.71		
“ 3		3.81	3.85	13.85	13.78	17.63
“ 12	65.0	5.49		12.65		
“ 13		5.32	5.40	12.80	12.72	18.12
“ 21	56.0	4.63		12.82		
“ 23		4.57	4.60	12.85	12.82	17.42
“ 28	52.0	4.63		13.42		
“ 30		4.68	4.65	13.47	13.44	18.09
First frost						
Oct. 4	44.0	3.96		14.07		
“ 6		4.20	4.08	14.02	14.05	18.13
“ 11	38.0	3.58		14.13		
“ 13		3.73	3.67	14.02	14.07	17.74
“ 22	48.0	5.97		10.29		
“ 24		5.98	5.98	10.29	10 29	16.27
Nov. 3	42.0	5.32		10.74		
“ 5		5.25	5.28	10.77	10.76	16.04
“ 19*						
“ 22						
“ 30	43.0	1.59		13.91		
Dec. 2		1.76	1.67	13.70	13.80	15.47
“ 12	1.5	1.21		18.02		
“ 14		1.28	1.24	18.15	18.09	19.33
Jan. 4	26.5	0.50		16.38		
“ 7		0.52	0.51	16.34	16.36	16.87
“ 16	18.0	0.27		17.11		
“ 20		0.32	0.29	17.12	17.12	17.41
“ 31*						
Feb. 3						
“ 4	—5.5	0.42		19.10		
“ 8		0.42	0.42	19.15	19.12	19.54
“ 14*						
“ 17						
Mar. 2	30.5	0.60		11.63		
“ 6		0.70	0.65	11.59	11.61	12.26
“ 11	33.0	0.60		14.16		
“ 15		0.73	0.66	14.23	14.19	14.85
“ 28	41.0	2.94		14.86		
“ 30		3.07	3.00	15.07	14.96	17.96
Apr. 12	39.3	3.65		13.43		
“ 15		3.62	3.63	13.70	13.56	17.19
“ 22	51.5	3.01		12.58		
“ 24		3.01	3.01	12.52	12.55	15.56

* Trouble with sampling. Vacuum still present after 2 days.

it remained between 16.00 and 18.00 per cent. There was a drop to 15.47 per cent during November. From December 2 to the 12th there was a gradual rise to 19.33 per cent. The highest point of the year was on February 4, when 19.54 per cent was recorded. By March 2, the total had dropped back to 12.26 per cent, increasing again, however, to 17.96 by March 28, and again decreasing to 15.56 per cent by April 22.

Quercus macrocarpa

The seasonal variations in the carbon dioxide and oxygen in the trunk of the bur oak followed in general the trends found in the pine and the elm. They corresponded closely to that of the red oak which grew on the same site. The amount of carbon dioxide remained about the same throughout the summer season, with only slight fluctuations in the autumn. The data are presented in Table 4 and Figure 4. There was a gradual rise in the carbon dioxide content from the middle of May until the first part of September. The lowest percentage of carbon dioxide was 1.68 on May 25 and the highest was 2.89 on September 1. Between these dates there was almost no fluctuation. After the autumnal variations in temperature, the amount of carbon dioxide in the trunk remained about the same throughout the winter. During December and January the percentage of this gas was between 0.40 and 1.60. In February, March, and April, however, there was an increase, the percentage of carbon dioxide reaching 2.43 on April 25.

As would be expected, the oxygen was high throughout the year. In summer, it varied inversely with the temperature, rising as the temperature fell in the autumn. After reaching a high point of 19.64 per cent in December, the oxygen content remained about the same during

FIGURE 4

SEASONAL VARIATION OF PERCENTAGE OF CARBON DIOXIDE AND OXYGEN WITH MEAN TEMPERATURE.

QUERCUS MACROCARPA

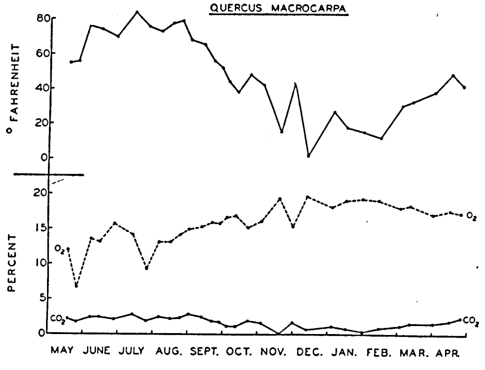


Table 4

Percentage of Carbon Dioxide and Oxygen in the Trunk of *Quercus macrocarpa*

Date	Mean air temperature, degrees F.	Percentage CO_2		Percentage O_2		Total percentage CO_2 and O_2
			Average		Average	
May 17	55.0	2.23		12.04		
“ 18		2.14	2.19	11.92	11.96	14.15
“ 25	56.0	1.62		6.73		
“ 27		1.74	1.68	6.70	6.71	8.39
June 4	76.0	2.48		13.51		
“ 6		2.46	2.47	13.52	13.51	15.98
“ 14	74.0	2.42		12.95		
“ 16		2.52	2.47	13.12	13.04	15.51
“ 27	69.5	2.08		15.58		
“ 29		2.10	2.09	15.67	15.62	17.71
July 13	83.5	2.80		14.03		
“ 15		2.84	2.82	14.05	14.04	16.86
“ 25	75.5	1.83		9.32		
“ 27		1.78	1.80	9.25	9.28	11.08
Aug. 5	73.0	2.51		13.04		
“ 7		2.43	2.47	13.02	13.03	15.50
“ 15	77.5	2.27				
“ 17		2.11	2.19	13.11	13.11	15.30
“ 23	79.0	2.31		14.20		
“ 25		2.36	2.32	14.06	14.13	16.45
Sept. 1	67.5	2.95		14.88		
“ 3		2.84	2.89	14.92	14.90	17.79
“ 12	65.0	2.36		15.28		
“ 13		2.47	2.41	15.24	15.26	17.67
“ 21	56.0	1.82		15.86		
“ 23		1.80	1.81	15.88	15.87	17.68
“ 28	52.0	1.71		15.68		
“ 30		1.63	1.67	15.76	15.72	17.39
First frost						
Oct. 4	44.0	1.27		16.67		
“ 6		1.03	1.15	16.57	16.62	17.77
“ 11	38.0	1.05		16.97		
“ 13		1.10	1.10	16.89	16.93	18.03
“ 22	48.0	1.91		15.19		
“ 24		1.79	1.85	15.13	15.16	17.01
Nov. 3	42.0	1.56		16.01		
“ 5		1.53	1.54	16.07	16.04	17.58
“ 19	15.5	0.03		19.45		
“ 21		0.05	0.04	19.26	19.35	19.39
“ 30	43.0	1.69		15.29		
Dec. 2		1.52	1.60	15.29	15.29	16.89
“ 12	1.5	0.65		19.65		
“ 14		0.65	0.65	19.63	19.64	20.29
Jan. 4	26.5	1.05		18.15		
“ 7		1.05	1.05	18.14	18.15	19.20
“ 16	18.0	0.77		19.06		
“ 20		0.75	0.76	18.97	19.01	19.77
“ 31	15.5	0.35		19.38		
Feb. 4		0.45	0.40	19.35	19.36	19.76
“ 14	12.2	0.83		19.00		
“ 18		0.95	0.89	19.26	19.13	20.02
Mar. 2	30.5	1.26		17.92		
“ 6		1.18	1.22	18.16	18.04	19.26
“ 11	33.0	1.56		18.41		
“ 15		1.53	1.54	18.47	18.44	19.98
Apr. 1	38.3	1.58		16.99		
“ 4		1.53	1.55	17.09	17.04	18.59
“ 15	49.0	2.02		17.65		
“ 17		1.84	1.93	17.62	17.63	19.56
“ 25	42.0	2.46		17.29		
“ 27		2.41	2.43	17.33	17.31	19.74

the winter. It slowly decreased in the spring months, but it did not drop below 17.04 per cent by the end of April.

The effect of temperature changes upon the internal gases of tree trunks is well shown in the results on bur oak. The curve for carbon dioxide follows the temperature changes directly, the variations being greatest when the temperature changes were most rapid. Variations in oxygen content followed temperature changes inversely, and for almost every difference in temperature a corresponding difference was shown in the amount of oxygen present in the trunk.

The total percentage of oxygen and carbon dioxide in the trunk was higher than in either the pine or the elm. In spring and summer it was lowest, varying from 8.39 in May to over 17.0 per cent in the autumn months. As the season advanced from autumn to winter it fluctuated somewhat, reaching a high point of 20.29 per cent on December 12. Throughout the winter it was higher than in the summer, continuing above 19.0 per cent throughout April. Bur oak did not show the rapid drop in oxygen in the spring that was shown in the trees previously described. From the high point in oxygen content in December and January, it slowly decreased in the beginning of the growing season. The high totals of the two gases are definitely correlated with the changes in temperature. In both cases, when the total of carbon dioxide and oxygen reached almost the atmospheric average, the temperatures were lowest and the temperature change was the most abrupt, as noted in Figure 4.

Populus deltoides virginiana

The gases present in the trunk of the cottonwood tree showed greater seasonal fluctuations than any of the other four trees studied. Seasonal amounts of carbon dioxide and oxygen changed abruptly in November and March. (See Figure 5, and Table 5.) During the first part of the summer carbon dioxide remained between 5.0 and 10.0 per cent. By the 4th of August it had increased to 18.89 per cent. During the remainder of the summer and fall it fluctuated between 12.21 and 20.52 per cent, reaching the highest point on September 19. By the end of November the autumnal changes had ceased and there was a sudden decrease in the percentage of carbon dioxide. By December 7 it had decreased to 6.07 per cent and by the 15th to 1.51 per cent. During the next two months considerable trouble with sampling was encountered, but several satisfactory samples were obtained and the analysis showed a carbon dioxide content of 0.82 per cent on January 21, and 1.20 and 1.02 per cent on February 18 and 25, respectively. By March 7 there was an increase, the concentration being 4.18 per cent. During the remainder of March and the first week in April some spring fluctuations appeared. These were followed by a steady rise from 2.19 per cent on

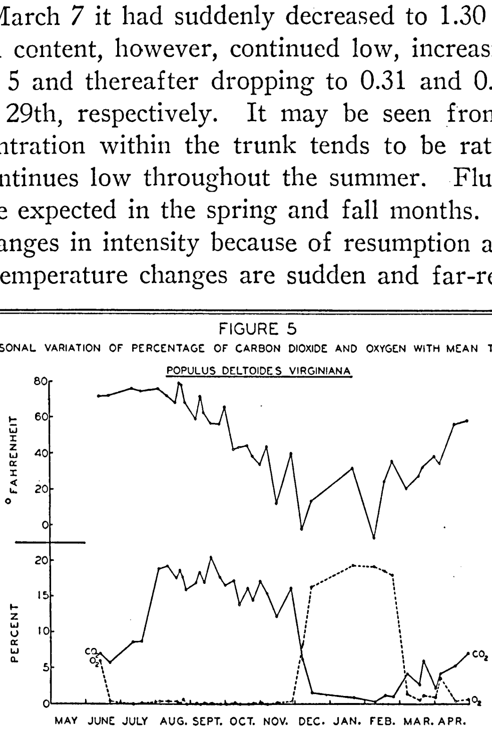
April 1 to 6.90 per cent on April 29. Eleven months before, when work was begun on this tree, the concentration of carbon dioxide in the trunk was 6.88 per cent.

The oxygen concentration in this portion of the cottonwood trunk was extremely low in summer and very high in winter. After the first determination, which showed 5.84 per cent on June 13, the oxygen content dropped to 0.42 per cent and remained below 1.00 per cent through the summer and autumn. On November 28 the oxygen content was 0.40 per cent. By December 7 it had increased to 8.26 per cent and by the 15th to 16.26 per cent. On January 21 it was 19.40 per cent, the highest point of the season. Throughout February it remained above 17.00 per cent, but by March 7 it had suddenly decreased to 1.30 per cent. The spring oxygen content, however, continued low, increasing to 3.67 per cent on April 5 and thereafter dropping to 0.31 and 0.52 per cent on the 18th and 29th, respectively. It may be seen from this that the oxygen concentration within the trunk tends to be rather low in the spring and continues low throughout the summer. Fluctuations, however, are to be expected in the spring and fall months. It is then that respiration changes in intensity because of resumption and cessation of growth, and temperature changes are sudden and far-reaching.

FIGURE 5

SEASONAL VARIATION OF PERCENTAGE OF CARBON DIOXIDE AND OXYGEN WITH MEAN TEMPERATURE.

POPULUS DELTOIDES VIRGINIANA



In general, the carbon dioxide content is directly proportional to the mean temperature of the days on which the samples were collected. This does not hold in all cases, but for the seasonal variations it is certainly true. Slight changes in temperature are not always followed by corresponding carbon dioxide changes, but sudden changes which last for several days tend to change the concentration of carbon dioxide considerably. This does not hold for the winter months, however, when all activity is at a standstill. Oxygen, in the case of the cottonwood, fluctuated very little with temperature. The small variations that occurred in winter and spring were inversely proportional to the mean temperature.

Table 5

Percentage of Carbon Dioxide and Oxygen in the Trunk of *Populus deltoides virginiana*

Date	Mean air temperature, degrees F.	Percentage CO_2		Percentage O_2		Total percentage CO_2 and O_2
			Average		Average	
June 13	71.5	6.91		5.88		
“ 15		6.86	6.88	5.80	5.84	12.72
“ 21	72.0	6.31		0.15		
“ 23		5.07	5.68	0.70	0.42	6.10
July 11	76.0	8.63		0.00		
“ 13		8.40	8.51	0.00	0.00	8.51
“ 22	74.5	8.86		0.10		
“ 24		8.50	8.68	0.10	0.10	8.78
Aug. 1	69.0	25.22		0.88		
“ 3*			25.33		0.88	26.10
“ 4	76.0	18.89		0.30		
“ 6*			18.89		0.30	19.19
“ 11	72.0	19.49		0.53		
“ 13		19.12	19.30	0.15	0.34	19.64
“ 19	68.0	17.70		0.45		
“ 21		17.46	17.58	0.25	0.35	17.93
“ 22	79.0	18.66		0.10		
“ 24		18.55	18.60	0.07	0.08	18.68
“ 24	78.0	17.87		0.37		
“ 25		17.61	17.74	0.22	0.30	18.04
“ 27	68.0	16.12		0.05		
“ 28		15.68	15.90	0.00	0.02	15.92
Sept. 6	59.0	17.08		0.05		
“ 7		16.67	16.87	0.20	0.12	17.00
“ 10	71.5	18.30		trace		
“ 12		18.24	18.27	trace		18.27
“ 13	62.5	17.01		0.15		
“ 15		16.81	16.91	0.12	0.13	17.04
“ 19	56.5	20.53		0.07		
“ 21		20.52	20.52	trace	0.07	20.60
“ 26	56.0	17.67		trace		
“ 28		17.59	17.63	trace		17.63
Oct. 1	65.5	16.50				
“ 3		16.46	16.48			16.48
“ 8	42.0	17.30		0.22		
“ 10		17.22	17.26	0.07	0.15	17.41
“ 13	43.0	14.06				
“ 14		13.88	13.97			13.97
“ 20	44.0	16.01		trace		
“ 22		16.13	16.07	trace		16.07
“ 25	38.5	14.68		0.07		
“ 28		14.48	14.58	0.05	0.06	14.64
Nov. 1	34.0	17.30		0.25		
“ 3		17.06	17.18	0.20	0.22	17.40
“ 7	43.6	15.35		trace		
“ 10		15.43	15.39	trace		15.39
“ 15	12.0	12.29		0.22		
“ 18		12.13	12.21	0.15	0.18	12.39
“ 28	40.0	16.08		0.50		
“ 30		15.96	16.02	0.30	0.40	16.42
Dec. 7	—2.0	6.10		8.36		
“ 10		6.04	6.07	8.17	8.26	14.29
“ 15	13.5	1.54		16.18		
“ 21		1.48	1.51	16.35	16.26	17.77
“ 29*	20.0					

Table 5—Continued

Date	Mean air temperature, degrees F.	Percentage CO_2		Percentage O_2		Total percentage CO_2 and O_2
Jan. 3						
“ 21	32.0	0.85		19.24		
“ 23		0.80	0.82	19.57	19.40	20.22
“ 28†	20.5	8.90		5.79		14.69
“ 30						
Feb. 9†	−7.0	0.27		19.22		19.49
“ 11						
“ 18	24.3	1.25		18.42		
“ 21		1.16	1.20	18.59	18.50	19.70
“ 25	36.0	1.01		17.89		
“ 28		1.03	1.02	17.97	17.93	18.95
Mar. 7	20.3	4.18		1.35		
“ 10		4.18	4.18	1.27	1.30	5.48
“ 17	27.3	2.78		0.65		
“ 20		2.59	2.68	0.52	0.58	3.26
“ 21	32.3	5.89		1.26		
“ 24		5.88	5.88	1.25	1.26	7.14
Apr. 1	38.3	2.19		0.90		
“ 4		2.19	2.19	0.90	0.90	3.09
“ 5	34.5	4.24		3.69		
“ 7		4.04	4.14	3.62	3.67	7.81
“ 18	56.0	5.09		0.45		
“ 20		5.31	5.20	0.17	0.31	5.51
“ 29	58.0	6.85		0.67		
May 1		6.95	6.90	0.37	0.52	7.42

* Trouble with sampling. Vacuum still present after 4 days.
† Partial vacuum present in tube at time of analysis.

The total of carbon dioxide and oxygen present in the tree trunk was less than atmospheric. One exception on August 1 should not be considered, as the sampling tube was half-filled with sap and apparently had not come to equilibrium with the gases in the trunk. The total percentage, as seen in Table 5, was low in the early summer, varying from 6.10 to 12.72 per cent. During August and September it was higher, from 15.92 to 20.60 per cent. In October, November, and December there was a variation of 12.39 to 17.77 per cent, while in January and February there was an increase up to 20.22 per cent. Throughout March and April, the total was considerably lower than in the winter, varying from 3.09 to 7.81 per cent.

The cottonwood was the only tree of the five studied that contained any gases of an inflammable nature. Further work should be done upon this and related species to determine whether combustible gases are present naturally or are produced by the break-down of cellulose by foreign organisms. Bushong (7) found a high percentage of methane in a cottonwood trunk. MacDougal (36), on the other hand, is of the opinion that there are no gases present in normal tree trunks other than carbon dioxide, oxygen, nitrogen, and a trace of terpenes.

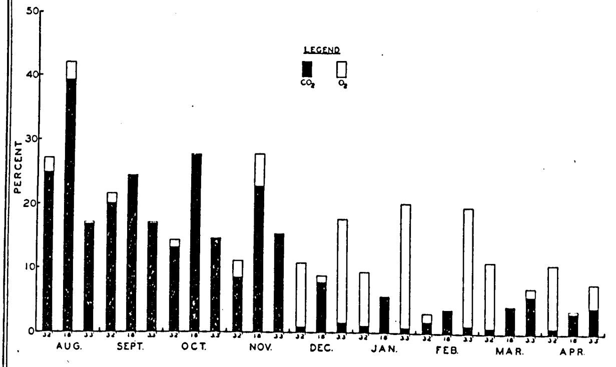
Gases at different heights above the ground.—Much the same seasonal variation was shown in the study of gases at various heights above the ground in the cottonwood tree as was shown at the 3.3-foot height of the five trees studied. Carbon dioxide was very high and oxygen low in summer, while the opposite condition existed in the winter periods. The total of both carbon dioxide and oxygen was highest in the summer and lowest in the early spring. These data are given in detail in Tables 5, 7, 8, 9, 10, and 11. Monthly averages presented in graphic form in Figures 6 and 7 show comparisons of the gases at the different heights and their seasonal trends. Figure 6 presents the results obtained from the analyses of gases withdrawn simultaneously from the 32-, 18-, and 3.3-foot levels, and Figure 7 the results from the alternate heights of 24, 12, and 0.3 feet. It was impossible to get experimental data at some of the heights for a part of the winter, because of the great volume of sap which flowed into the sampling tubes.

An inflammable gas, presumably methane, was present during the summer and autumn. This foreign gas was not observed during the winter. Possibly it was a product of the decay of the wood at or near the place of collection, but no trace of the breakdown of cellulose was discovered when the holes were opened and rebored at the end of the experiment.

FIGURE 6

SEASONAL VARIATION OF PERCENTAGE OF CARBON DIOXIDE AND OXYGEN AT DIFFERENT HEIGHTS ABOVE THE GROUND.

POPULUS DELTOIDES VIRGINIANA



The extremely high concentrations of carbon dioxide during the summer were associated with a high sap content in the sampling tubes and probably do not represent the true concentration of this gas as nearly as those in which the sap did not interfere with the volume of gas sampled. When the carbon dioxide content was very high—more than 20 per cent of the sample, it was invariably found that there was only enough gas present for one analysis, the sap filling the remainder of the sampling tubes.

During the summer months the highest total concentration of carbon dioxide and oxygen was in the central portion of the tree trunk, at 12 and 18 feet above the ground. The highest portion at 32 and 24 feet was next, and at the base of the tree the concentration was lowest. The carbon dioxide percentage remained highest at the medium heights until March and in both cases, at 12 and 18 feet, there was almost no oxygen present. At the other heights there were variable amounts of oxygen, but it was lowest near the top of the tree and highest at the base.

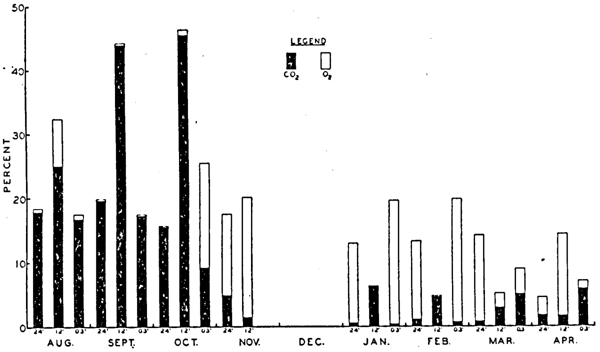


FIGURE 7

SEASONAL VARIATION OF PERCENTAGE OF CARBON DIOXIDE AND OXYGEN AT DIFFERENT HEIGHTS ABOVE THE GROUND.

POPULUS DELTOIDES VIRGINIANA

Beginning in March, this relationship changed and remained so during April. Then the carbon dioxide was highest at the base of the tree and lowest at the top. The oxygen was high at the top and low at the base, except in the case of the 12-foot level, which showed the highest oxygen percentage during the spring period.

The value of these results on the concentration of gases at various heights above the ground is rather doubtful. Data for the summer and fall periods were apparently influenced by some factor which greatly increased the amounts of carbon dioxide, especially at the middle heights. During the spring period the results at different heights were more nearly what one might expect. According to Nicolas (43), who worked on the variation of respiration with the age of the plant, the younger, more vigorous parts produce the most carbon dioxide. But, on the other hand, the smaller the stem the more rapid is the gaseous exchange, and the larger the stem the slower the movement. Therefore the more bulky portion of the trunk has the greatest concentration. This condition is shown during March and April. So far as the present writer is aware, this is the only work that has been attempted upon the seasonal variations of carbon dioxide and oxygen at different heights above the ground. It is recognized that more data are needed, based upon a number of trees of the same species growing on various habitats, before any definite conclusions can be reached concerning the concentrations of these gases at different heights above the ground.

Table 6

Percentage of Carbon Dioxide and Oxygen at a Depth of 1.5 Inches Under the Bark of *Populus deltoides virginiana*

Date	Mean air temperature, degrees F.	Percentage CO_2		Percentage O_2		Total percentage CO_2 and O_2
			Average		Average	
Aug. 1	69.0	9.49		8.78		
" 3		9.45	9.47	8.82	8.80	18.27
" 11	72.0	7.24		9.68		
" 13		7.11	7.17	9.85	9.74	16.91
" 19	66.0	2.82		15.91		
" 21		2.85	2.84	16.00	15.95	18.79
" 22	79.0	2.46		15.33		
" 24		2.42	2.44	15.59	15.46	17.90
" 29	77.0	4.98		13.42		
Sept. 1		4.73	4.85	13.56	13.49	18.34
" 10	71.5	8.80		13.06		
" 12			8.80		13.06	21.86
" 19*	60.0					
" 20						
" 26*	58.0					
" 27						
Oct. 1*	65.5					
" 3						
" 8*	42.0					
" 10						
" 20	44.0	3.18		17.88		
" 22		3.25	3.21	18.10	17.99	21.20
Nov. 1*	34.0					
" 3						
" 15	12.0	1.05		17.75		
" 18		1.13	1.17	17.87	17.79	18.96
Dec. 3	29.0	2.44		17.25		
" 5			2.44		17.25	19.69
" 29	20.0	1.02		17.81		
Jan. 3		1.12	1.07	17.91	17.86	18.93
" 28	20.5	0.50		19.77		
" 30		0.50	0.50	19.92	19.84	20.30
Feb. 9	—7.0	0.45		20.02		
" 11		0.32	0.35	20.03	20.03	20.38
" 25	36.0	0.05		11.01		
" 28		0.25	0.15	10.91	10.96	11.11
Mar. 7	20.3	0.52		17.31		
" 10		0.47	0.50	17.30	17.30	17.80
" 17	27.3	0.80		19.46		
" 20		0.83	0.81	19.83	19.65	20.46
Apr. 18	56.0	1.76		17.33		
" 20		1.71	1.73	17.56	17.45	19.18
" 29	58.0	1.25		16.22		
May 1		1.25	1.25	16.28	16.25	17.50

* Moisture content of sapwood high. Sampling tube either filled with sap or vacuum still present.

Gases in the sapwood and heartwood.—The seasonal variations of the percentages of carbon dioxide and oxygen in the sapwood and heartwood of the cottonwood trunk are shown in Figure 8. The data

Table 7

Percentage of Carbon Dioxide and Oxygen in the Trunk of *Populus deltoides virginiana* at a Height of 32 Feet

Date	Mean air temperature, degrees F.	Percentage CO_2		Percentage O_2		Total percentage CO_2 and O_2
			Average		Average	
Aug. 2	72.0	16.82	16.78	1.17	1.14	17.92
" 3		16.75		1.11		
" 17*	70.0					
" 18						
" 18*	77.8					
" 19						
" 19	66.0	20.03	19.69	2.28	2.25	21.94
" 21		19.28		2.22		
" 24	78.0	30.20	30.20	3.93	3.93	34.13
" 25						
" 27	68.0	20.03	19.74	0.25	0.20	19.94
" 28		19.46		0.15		
Sept. 6	59.0	20.47	20.10	1.18	1.32	21.42
" 7		19.74		1.47		
" 13	62.0	20.39	20.04	2.01	1.83	21.12
" 14		19.70		1.66		
Oct. 13	43.0	1.85	1.85	16.55	16.60	18.45
" 14		1.86		16.66		
" 25	38.0	13.73	13.37	0.97	1.03	14.40
" 28		13.02		1.10		
Nov. 7	43.6	8.55	8.53	2.58	2.56	11.09
" 10		8.52		2.55		
Dec. 15	13.5	0.77	0.85	10.00	10.08	10.93
" 21		0.93		10.17		
Jan. 21	32.0	1.05	1.05	8.31	8.45	9.09
" 23		1.05		8.58		
Feb. 18	24.3	1.76	1.77	1.35	1.34	3.11
" 21		1.78		1.33		
Mar. 21	32.3	0.95	0.90	10.16	10.22	11.12
" 24		0.85		10.28		
Apr. 5	34.5	0.98	0.98	10.84	10.81	11.79
" 7		0.98		10.78		

* Tube on tree plugged. Hole cleaned out with wire.

upon which this graph is based are given in detail in Tables 5[2] and 6. In general, the heartwood had a high carbon dioxide and a low oxygen content during the summer period, a reversal in the winter, and a change back toward the summer trend during the spring months. The gases of the sapwood, on the other hand, were composed of small amounts of carbon dioxide and relatively large amounts of oxygen during the whole year. In the summer the carbon dioxide content was higher and the oxygen lower than in the winter. The sapwood gases remained much nearer the normal atmospheric contents than did those of the heartwood. Oxygen and carbon dioxide both showed decided fluctuations in the fall and spring months. The sapwood gases, however, changed more during the early fall than in the spring months, while, in comparison, the gases of the heartwood showed more decided movements in the spring.

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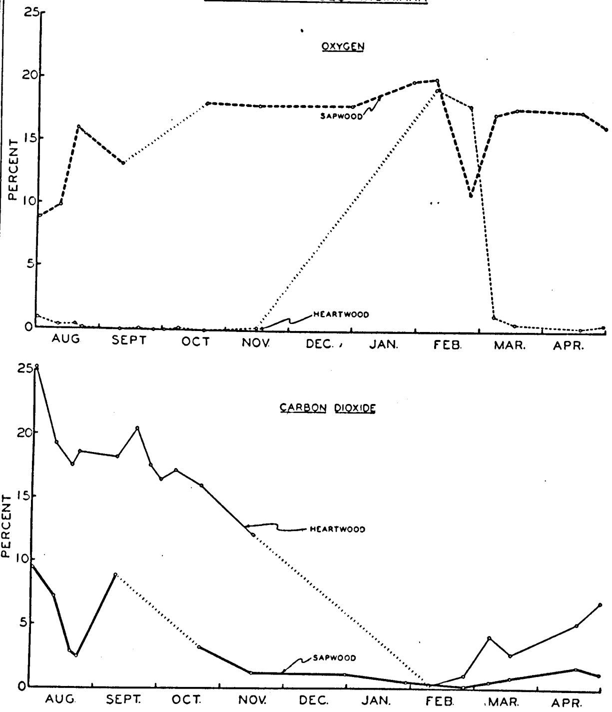
[2] For this section, only those data in Table 5 corresponding to the dates in Table 6 are comparable.

FIGURE 8

SEASONAL VARIATION OF PERCENTAGE OF CARBON DIOXIDE AND OXYGEN IN THE SAPWOOD AND HEARTWOOD.

POPULUS DELTOIDES VIRGINIANA



It was impossible during parts of the fall and winter to gather data for comparison. The fine broken lines in Figure 8 indicate the periods when sufficient samples for analyses could not be secured. The lack of gas volume resulted from the abundance of moisture present within the wood. It has been mentioned previously that during the fall and winter there is more sap present and consequently less gas than during the summer period. And, as the leaves drop off during September and October, it would be expected that the sapwood, which conducts the transpiration stream, would be filled with water before the dead heartwood. These data indicate that this very thing happened. It is assumed that the sapwood, after having been oversupplied with moisture during the autumn, began to lose its water to the drier heartwood. And apparently enough sap was transferred so that it caused much trouble in sampling, and no adequate samples of gas were obtained during the winter for this part of the experiment. The importance of this moisture increase is discussed in detail in the section on Physiological Significance.

Table 8

Percentage of Carbon Dioxide and Oxygen in the Trunk of *Populus deltoides virginiana* at a Height of 24 Feet

Date	Mean air temperature, degrees F.	Percentage CO_2		Percentage O_2		Total percentage CO_2 and O_2
			Average		Average	
Aug. 4	76.0	17.71		1.28		
" 6		17.80	17.76	1.25	1.26	19.02
" 18	63.0	17.26		0.25		
" 19		17.10	17.18	0.22	0.24	17.42
" 25	69.0	18.99		0.05		
" 27		18.74	18.86	0.10	0.07	18.93
Sept. 8	68.0	18.89		0.05		
" 9		19.03	18.96	0.02	0.03	19.33
" 15	62.0	20.21				
" 17		20.08	20.14			20.14
Oct. 15	57.0	15.86		0.15		
" 17		15.81	15.83	0.15	0.15	15.98
" 28	41.0	15.10		0.05		
" 30		15.03	15.07	0.05	0.05	15.12
Nov. 11	25.5	4.94		12.50		
" 13		4.95	4.94	12.56	12.53	17.47
Jan. 24	31.6	0.57		12.32		
" 27		0.52	0.55	12.32	12.32	12.87
Feb. 21	29.3	1.03		12.20		
" 24		1.03	1.03	12.22	12.21	13.24
Mar. 25	34.0	0.75		13.38		
" 27		0.68	0.71	13.46	13.42	14.13
Apr. 8	37.5	1.71		2.64		
" 11		1.74	1.72	3.02	2.83	4.55

Table 9

Percentage of Carbon Dioxide and Oxygen in the Trunk of *Populus deltoides virginiana* at a Height of 18 Feet

Date	Mean air temperature, degrees F.	Percentage CO_2		Percentage O_2		Total percentage CO_2 and O_2
			Average		Average	
Aug. 2	72.0	24.37		1.81		
" 3			24.37		1.81	26.18
" 17	70.0	4.42		16.00		
" 18		4.25	4.33	15.98	15.99	20.32
" 24	78.0	42.55		4.25		
" 25			42.55		4.25	46.80
" 27	68.0	36.20		1.11		
" 28			36.20		1.11	37.31
Sept. 6	59.0	22.28		0.12		
" 7		21.61	21.84	0.10	0.11	21.95
" 13	62.0	27.80		trace		
" 14		26.39	27.09	trace		27.09
Oct. 13	43.0	31.01		0.35		
" 14			31.01		0.35	31.36
" 25	38.5	28.30		0.15		
" 28		26.72	27.56	0.09	0.12	27.68
Nov. 7	43.6	23.15		5.06		
" 10		22.66	22.90	4.96	5.01	27.91
Dec. 15	13.5	8.00		0.95		
" 21		7.91	7.95	0.82	0.88	8.83
Jan. 21	32.0	5.58		0.02		
" 23		5.48	5.53	trace	0.02	5.55
Feb. 18	24.3	3.77				
" 21		3.69	3.73			3.73
Mar. 21	32.3	4.26		0.12		
" 24		4.14	4.20	0.10	0.11	4.31
Apr. 5	34.5	3.24		0.45		
" 7		3.26	3.25	0.27	0.36	3.61

Table 10

Percentage of Carbon Dioxide and Oxygen in the Trunk of *Populus deltoides virginiana* at a Height of 12 Feet

Date	Mean air temperature, degrees F.	Percentage CO_2		Percentage O_2		Total percentage CO_2 and O_2
			Average		Average	
Aug. 4	76.0	18.00		9.49		
" 6*			18.00		9.49	27.49
" 18	63.0	17.35		10.92		
" 19*			17.35		10.92	28.27
" 25	69.0	39.60		1.79		
" 27*			39.60		1.79	41.39
Sept. 8	68.0	37.73		0.15		
" 9			37.73		0.15	37.88
" 15	62.0	50.00		0.27		
" 17*			50.00		0.27	50.27
Oct. 15	57.0	47.30		0.41		
" 17*			47.30		0.41	47.71
" 28	41.0	43.34		1.32		
" 30*			43.34		1.32	44.66
Nov. 11	25.5	1.49		18.57		
" 13		1.43	1.46	18.52	18.54	20.00
Jan. 24	31.6	6.37		0.02		
" 27		6.06	6.20	trace	0.02	6.22
Feb. 21	29.3	4.69		0.30		
" 24		4.54	4.61	0.02	0.16	4.77
Mar. 25	34.0	2.90		2.34		
" 27		3.00	2.95	2.02	2.18	5.13
Apr. 8	37.5	1.57		12.86		
" 11		1.60	1.58	12.66	12.76	14.31

* Sampling tube half-filled with sap.

Table 11

Percentage of Carbon Dioxide and Oxygen in the Trunk of *Populus deltoides virginiana* at a Height of 0.3 Feet

Date	Mean air temperature, degrees F.	Percentage CO_2		Percentage O_2.		Total percentage CO_2 and O_2
			Average		Average	
Aug. 2	72.0	17.78		2.13		
" 3			17.78		2.13	19.91
" 17	70.0	18.01		0.63		
" 18			18.01		0.63	18.64
" 25	69.0	17.70		trace		
" 27		16.69	17.20	0.24	0.24	17.44
" 29	77.0	13.85		0.35		
Sept. 1		13.44	13.64	0.04	0.20	13.84
" 8	68.0	16.63		0.05		
" 9		16.31	16.47	0.07	0.06	17.09
" 15	62.0	18.01		0.10		
" 17		17.53	17.77	0.05	0.07	17.84
Oct. 15	57.0	16.04				
" 17		15.80	15.92			15.92
" 28	41.0	2.45		15.96		
" 30		2.47	2.46	16.21	16.08	18.54
Nov. 11*	25.5					
" 13						
Jan. 24	31.6	0.37		18.68		
" 27		0.30	0.33	19.01	19.17	19.50
Feb. 21	29.3	0.68		19.07		
" 24		0.58	0.63	19.14	19.10	19.73
Mar. 25	34.0	4.99		3.94		
" 27		5.07	5.03	4.04	3.99	9.32
Apr. 8	37.5	5.92		1.21		
" 11		5.96	5.94	1.11	1.16	7.10

* Tube opened and partly torn off tree.

PHYSIOLOGICAL SIGNIFICANCE

There is a definite seasonal variation in the amounts of carbon dioxide and oxygen in the trunks of trees. This indicates that there is a definite relationship between the amounts of these gases present in the trunk and the life processes of the tree. In other words, these gases play a part in the complicated metabolic processes of the tree. The part they play is largely a matter of speculation based upon what is known in general about the metabolism of both plant and animal tissues.

In any problem dealing with the physiology of the interior of a large woody stem the transpiration stream is of importance since the movement of water from the roots to the leaves affects the gases present—MacDougal (33). Numerous theories have been advanced to account for water movement in trees. Evidence that the path of the transpiration stream is through the xylem has been abundant since the work of Stephen Hales. With the aid of dyes it has been shown that regardless of the energy source, the liquid from the roots moves upward in the xylem and not through the pith, phloem, or cortex. It has been shown that if the xylem elements are blocked or severed insufficient water is supplied to the leaves, and, also, that a ringed tree will continue to transpire for a long time.

It has not been easy to demonstrate the specific portions of the xylem which conduct water. This was complicated considerably by the knowledge that gases were present in parts of each annual ring. It is now generally agreed that the outer rings of the xylem carry most of the water. This was proved definitely by Strasburger (56) with the aid of dyes. The fact that the leaves of any given year are connected to the annual ring of the previous year was considered by MacDougal, Overton and Smith (38) as evidence that a few rings only are necessary for direct communication with even the oldest persistent leaves of conifers.

Within the individual annual rings it has been found that there is a marked localization, water being present in a portion of the annual ring while gas fills the other part. This has not been stressed by any observer previous to MacDougal, Overton and Smith (38) altho they state that Strasburger observed this localization but did not see the significance of it. These workers state that there is a zonation in the relatively few annual rings that conduct water. In willow, alder, and walnut growing in California this zonation varied. Movement of water in the willow was in the late summerwood, in alder through the springwood only, and in walnut through the early springwood and late summerwood. In young pine trees no zonation was found. The outer four rings were found to conduct water most rapidly, but there was some conduction at greater depths. Overton (45) continued this work in Wisconsin to ascertain if the zonation would remain constant with the various genera in an entirely different climate. He found that for northern willow and alder the zonations in the summer season were the same as in the California species. Overton (45) states that as the season advances and transpiration is reduced toward winter, the gas-filled portion of each annual layer becomes narrower and by spring is almost or completely filled with water. For willow and alder, however, some gas was present throughout the year. This is very likely true for other trees, tho it has as yet not been proved experimentally.

MacDougal (33) states that generally three or four, or fifteen or twenty at the most, of the outermost layers of wood cells retain their plasmatic material for any length of time. These cells, however, mature quickly and are then available for conduction.

The relative amounts of water and gas present in the conducting elements vary considerably with the time of day and the season of the year. Gases fluctuate inversely with the amount of water present, since the latter is high at night and low during the day, when transpiration is at its maximum. MacDougal, Overton and Smith (38) state that the water content of the xylem is higher during the autumn, winter, and spring than during the season of active growth.

Numerous theories have been advanced to account for the ascent of sap. Such physical phenomena as atmospheric pressure, capillarity, root pressure, imbibition, and evaporation have been suggested to explain this movement. Vital theories have also been used to explain sap movement and certain workers are of the opinion that the living cells of the xylem have a pumping action which forces the water upward. Strasburger (56) showed with the use of poison dyes that living cells were not necessary for the movement of liquids to the tops of trees. There are still supporters of the vital theory, altho Strasburger (56), Dixon (16), MacDougal (33, 35) and MacDougal, Overton and Smith (38) have shown that living cells are not necessary for conduction. The cohesion theory as presented by Dixon accounts for the rise of water in the stem by assuming that the sap in the conducting cells is under a state of tension due to evaporation of water from the surfaces of the living cells of the leaves. The greatest criticism of this theory is that if a bubble of air were present in the conducting tract, the column would lose its lifting force of cohesion. Dixon states that the bubbles present will congregate in a few tracheids and not interfere with the transpiration stream. MacDougal, Overton and Smith (38) have made a more complete study of the relations of air and water in the wood and they state that there are both gas and water systems in definite parts of the annual rings and that these systems are interchangeable. The amounts of each will vary at different times due to differences in temperature, tension, and root pressure. Living cells affect the amounts of gas produced and water used but do not aid in the movement of water up the stem. Altho many plant physiologists believe the cohesion tension theory to be the most acceptable so far advanced, it is still open to various objections. Barton-Wright (4) states that there is at this time no entirely adequate explanation of the rise of sap, " . . . and although the cohesion of water possibly plays a considerable part in the matter, it is probably only a portion of the whole truth."

Aside from that important portion of the tree, the sapwood, and especially the outer rings where most of the conduction takes place, there is a large central portion in large trunks called the heartwood. This inner part is lower in moisture and consequently higher in gas volume than the sapwood.

The carbon dioxide within the sapwood and heartwood of a tree originates chiefly from the respiration of the living cells of the wood rays, vertical parenchyma, and cambium. During the summer months these cells are very active and oxygen is low and carbon dioxide high. Nitrogen, however, is the principal constituent of the internal atmosphere of trees. It is very likely that some oxygen and carbon dioxide enter the roots dissolved in the water of the sap stream. MacDougal, Overton and Smith (38) state that some oxygen and more carbon dioxide probably do enter the plant in this manner. Another means of entrance of gases into the trunk is by the stomata of the leaves. Carbon dioxide enters the leaves and is used in photosynthesis, and oxygen is given off and escapes to the atmosphere. So far as is known, no work has been done on movements of gases downward from the leaves. It seems very likely that the transpiration stream would prevent such movement. Gases may enter through the lenticels of the bark into the intercellular spaces of the cortex and phloem. Oxygen probably enters because of the difference in its partial pressures inside and outside the trunk. The writer has found that oxygen is lower in concentration within the trunk and higher outside most of the year, while the concentration of carbon dioxide is definitely higher inside than outside for the whole year. Thus the carbon dioxide always diffuses outwardly.

The pressure of the gases, as well as their composition, plays an important part in determining the direction of movement of the interior gases. The loss of water from the leaves causes a tension in the transpiration stream. When transpiration is very active there is a loss of water in the parts of the rings that transport the water, and gases in solution are drawn toward the leaves. The resulting condition in the trunk is one of negative pressure. Hales (22) mentioned the existence of rarified air in plants as early as 1727. Von Höhnel (26), in 1879, cut twigs under mercury and found a condition of negative pressure. Pfeffer (48) has recorded that Schwendener by the same method found the internal air to be one-half to one-third of an atmosphere of pressure. Scheit (53), in 1885, thought that a complete vacuum was formed. According to Claussen (9), the air of the vessels fluctuates from 0.5 to 0.9 of an atmosphere. MacDougal, Overton and Smith (38) state that tensions in the pneumatic system vary from under one-half atmosphere to almost two atmospheres. It is of interest to note that Sachs (51), Pappenheim (47), Noll (44), and Deveaux (15) discussed in some detail the rarifaction of tracheal air. Each stated that this condition is caused by rapid transpiration. Palladin (46) gives credit to von Höhnel (26) for showing that air in the cortex and in the wood are not continuous. The intercellular spaces hold the air in the cortex and these are indirectly connected to the atmosphere by the lenticels. Therefore, the pressures of the gases in the cortex are the same as in the atmosphere. The aeration system of the wood is partially a closed system and usually has a pressure either reduced or positive. Negative pressures tend to disappear gradually when transpiration ceases. This is rather slow because of the lack of rapidity with which gases diffuse through the cambium and wood. Positive pressures are due to a release of carbon dioxide, a slowing down of transpiration, and are probably affected by temperature. Jones, Edson and Morse (29) state that the highest positive pressures occur in the early spring, as evidenced by the sap flow from maple trees. Temperature effects are partly responsible for this pressure, the gases present expanding sufficiently to force out great quantities of sap. They found the greatest sugar concentration in spring, followed by a dilution of sugars throughout the remainder of the spring and summer. Positive gas pressures have been noted by field men in their collection of growth data with the aid of increment borers. Abell and Hursh (1), Gates (19), Haasis (21), and Reynolds (50) have given evidence that enormous positive pressures are present at various times during the summer months. This condition has been observed mostly in trees growing on damp sites and is most common in the early morning hours when the air temperatures are rapidly rising. The writer thinks this is caused by the expansion of gases due to an increase in the temperature. Later in the day, because of increased transpiration and closer equalization of internal and external temperatures, negative pressures replace the positive pressures of the morning hours.

Movements of gases in various directions in tree trunks are not well understood. Wiesner (58), in 1879, stated that movement is very fast in a longitudinal direction when aided by transpiration, but is slow in the tangential and still slower in the radial direction because it can pass only through the membranes. He also stated erroneously that the drier the wood, the faster the air will move. Claussen (9) found that wood membranes behave as other membranes in relation to their permeability to air—that they are more permeable to gas with an increase in moisture content. He stated also that the works of Wiesner (58) and Wiesner and Molisch (59) must be partly discounted because dry membranes are not found in nature. MacDougal, Overton and Smith (38) found—just as did Wiesner—that gases could pass freely in a vertical direction many times the length of the vessels and also that tangential movement was very slow but not as slow as radial movement. According to MacDougal (32), the vessels and tracheids which usually contain gases in mature plants have no direct connection with the air in the intercellular spaces. Any exchange with them must take place by osmosis through one or more membranes, since it is possible to force gas through a membrane by pressure as a liquid might be transmitted. The withdrawal of water from cells by drying out, or diffusion, may reduce the pressure below that of the atmosphere, and in some instances results in an almost perfect vacuum, since the air may not penetrate the wall except by diffusion unless actual openings are present. It is to these causes that the negative pressure of shoots and branches of large woody plants is principally due. The unequal diffusibility of the atmospheric gases also causes variations in the composition of the air enclosed in the closed vessels of a plant. Bailey (2), working on the pit perforations of conifers, found that it took one to six atmospheres to pull gas through the perforations in bordered pits of Larix. The force necessary, of course, depends upon the size of the perforations.

Gas movement through the cambium has been investigated by MacDougal (37). He states that the microscope has shown no openings in the cambium through which gases might pass by streaming. He believes, however, that such passages do exist. Experimenting on live oak, he found suctions of 80 to 100 mm. of mercury to cause a movement of 0.010 c.c. per square cm. per hour. When the suction was reduced one-half, the rate fell to 0.003-0.004 c.c. per hour. Based upon this, he conjectures that the natural rate of streaming is near 0.001 c.c. per square cm. per hour. The air in a tree is thus seen to be enclosed in a cylinder of living cells, the cambium, which does not "leak" under this minimum pressure (10-20 mm. Hg.) but does so at higher pressures.

Zimmerman, Hitchcock and Crocker (62) in their report on the movement of ethylene gas through the tissues of seven different plants, found ethylene to move rapidly in all directions, spreading throughout the plant body very quickly. If other gases pass through tissues as readily as ethylene, the plant has an effective aerating system.

With regard to the effects of the gases upon the plant itself we have surprisingly little specific data. The purpose which the carbon dioxide and oxygen serve is of inestimable value to physiologists seeking a more complete knowledge of the metabolism of interior tissues. Carbon dioxide is known definitely to be a result of respiration. It is not used in the tissues of the stem. Oxygen has for its purpose the oxidation of materials within the living cells. It is possible that these gases associated with nitrogen in the pneumatic system may have some influence upon the transpiration stream.

MacDougal, Overton and Smith (38) found no consistent response in the hydrostatic system to variations of tension in the pneumatic system. Harvey (24) devised an apparatus for measuring the relationship between the two systems and he states that the pneumatic system can aid the water system under certain conditions. He says that the pneumatic units of a stem, being relatively more in communication than the corresponding hydrostatic units, can transmit a negative tension from one hydrostatic-pneumatic unit to another and as a consequence cause work to be performed in other, perhaps distant, hydrostatic units. No other investigator has expressed a similar belief, altho Lindner (31) stated that he believed the transpiration stream to be greater because of the large amount of carbon dioxide present. This, however, was purely speculation.

It is altogether possible that the transpiration stream carries large quantities of carbon dioxide in solution and that this gas is used in photosynthesis. The transport of this gas depends upon the amount present and its solubility in the transpiration stream. Its importance to photosynthesis has yet to be determined. Lindner (31) believed there is self-regulation of photosynthesis and respiration owing to this supposed availability of carbon dioxide in the sap stream. MacDougal, Overton and Smith (38) state that its importance is not known. Oxygen and nitrogen may also be transported upward to the leaves. Oxygen is used in respiration wherever it is needed, but there is no reason to believe that the inward diffusion of oxygen from the atmosphere is not sufficient to fulfill this need. Gaseous nitrogen is not used in metabolism but is present because of its high partial pressure in the atmosphere and its capacity for diffusion. There is also the possibility that the gases present may move downward from the lower part of the stem into the roots and finally into the soil. Cannon (8) found that oxygen moved from the shoot and roots of a small willow tree into an oxygen-free soil solution. The movement of carbon dioxide in this direction has not been determined.

Numerous investigators have speculated upon the cause of heartwood formation. It has been suggested that the large amount of carbon dioxide and relatively small amount of oxygen present in the center of the trunk is responsible for this change from a living to a dead condition. Priestley (49) stated that heartwood would appear to be the result of such an accumulation of air in closed vessel systems, with its consequent effect upon the permanent water content of the wood, which brings in its train secondary changes in the secretions from the living parenchyma cells. Sledge (55), discussing Priestley's suggestions, said that in the older shoots the water tension in the current year's wood results in the withdrawal of water from the older xylem. As a consequence air gradually replaces water, appearing first in the inner layers of the wood and subsequently working outwards. Just how this change increases the durability of the heartwood of most trees is unknown.

With regard to insect infestations, their tunnels are sufficient for a ready access of air, the oxygen content of which is more than is needed for their further development and growth. Graham[3] believes that diffusion through the wood would probably be sufficient to provide borers with an adequate supply of oxygen since the metabolic rate of these insects is very low. Furthermore, insects have an effective mechanism for bringing oxygen into contact with the living tissues so that they can make effective use of the oxygen that is present. Dendy (12), working with grain weevils, reported that the insects became sluggish when the amount of carbon dioxide reached about 18 or 19 per cent of the total volume of air. Further experiments showed that the insects succumbed as soon as the oxygen supply was exhausted. Insects placed with wheat in sealed tubes at 20-22° C. died when the carbon dioxide content reached 15.05 per cent and the oxygen 0.10 per cent. Almost all oxygen was used up when there was a very low per cent of carbon dioxide, but the higher the carbon dioxide percentage the sooner the weevils died without using much of the available oxygen. With 78 per cent carbon dioxide and 21 per cent oxygen, weevils died in a few minutes, while in an atmosphere of 14.08 per cent carbon dioxide and 23.60 per cent oxygen they lived for approximately 250 hours. It appears, then, from the above evidence and from the data given in Table 6 (which shows a carbon dioxide content of 2.44 to 9.47 per cent and an oxygen content of 8.80 to 15.95 per cent in the sapwood during the growing season) that there would be sufficient oxygen for growth even tho there were no tunnels present. Insect passageways would allow a ready exchange of air between the heartwood and the atmosphere, which would allow insect activity in the center of the tree if other conditions were favorable.

Fungi present a somewhat different condition in their air relationships within the wood. The hyphae of these organisms usually grow in tissues where diffusion of air could not take place except through membranes. It is, of course, altogether possible that the hyphae are

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[3] Letter written by Dr. S. A. Graham, August 27, 1931, in response to a request from the writer.

more or less adapted to the percentages of gases present. Also, they may change conditions within the wood with results more favorable for themselves. Nelson (42) stated that the gases produced by hyphae may fill the conducting elements with bubbles to such an extent that conduction is seriously interferred with and the moisture content of the wood lowered. This in itself would make a more favorable condition for growth in the sapwood, where moisture is often too abundant for the best development of hyphae. Hubert (27) states that the part the anatomical structures of the host, its water-air balance, and its chemical constituents, may play in the infection and establishment of disease organisms should be determined. Gases in the central part of the trunk may also be a factor of some importance in the growth of fungi. There is no direct evidence for this assumption, but it seems reasonable because the carbon dioxide is much higher and the oxygen lower in these tissues than in those nearer the bark. Before these points can be settled definitely, however, a large amount of information will have to be gathered on the life processes of both host and parasite.

A definite relationship is evident between the percentage of carbon dioxide in the trunk and the rate of diameter growth for the trees studied. The average percentage of carbon dioxide in the trunk of each tree averaged for the summer season compared with the annual increment shows the following relationship: Cottonwood, with a percentage of carbon dioxide of 14.82, had a ring width of 7 mm.; American elm had 12.39 per cent carbon dioxide and a ring width of 2.5 mm.; red oak had 4.36 per cent carbon dioxide and a ring width of 1.0 mm.; bur oak had 2.33 per cent carbon dioxide and a ring width of 0.2 mm.; white pine had a carbon dioxide content of 11.05 per cent and a ring width of 1.0 mm. Of the Angiosperms, the cottonwood had the greatest growth and the highest percentage of carbon dioxide. Bur oak, with the narrowest ring width, had the smallest percentage of carbon dioxide. White pine, the only conifer studied, seems to differ considerably from the other trees in its carbon-dioxide growth relationship. It had the same growth as red oak but its carbon dioxide percentage was very high in comparison.

The proportions of carbon dioxide and oxygen in tree trunks are believed to be the result of respiration and the rate of diffusion through the cambium. The high percentage of carbon dioxide in the trunk apparently does not have any inhibiting effect upon cell activity in or near the cambium. Oxygen seems to be present in sufficient amounts to supply the needs of the living cells of the xylem. It appears that the varying proportions of these gases in the trunk are a result of metabolism and probably have slight influence upon internal life processes.

SUMMARY AND CONCLUSIONS

A study of the composition of gases drawn from the trunks of four Angiosperm trees and one Gymnosperm tree has resulted in the following relationships:

1. The percentage of carbon dioxide is highest during the growing season. It fluctuates somewhat during the autumn and spring and is lowest in winter.
2. The percentage of oxygen is lowest in summer and highest in winter. It varies inversely with the percentage of carbon dioxide throughout the year.
3. The sum of carbon dioxide and oxygen is less than the total of these gases in the atmosphere. This relationship is present throughout the year, but is less pronounced during the dormant season.
4. The percentage of carbon dioxide is very low during the growing season for the Angiospermous species which produce narrow annual rings, and higher for those which grow more rapidly.
5. Gases drawn from the outer rings of the sapwood are lower in carbon dioxide and higher in oxygen than those drawn from the heartwood.
6. There is no apparent relationship between the percentage of carbon dioxide and oxygen at different heights above the ground.

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