

EFFECT OF TEMPERATURE ON PHOTOSYNTHESIS AND RESPIRATION IN RED AND LOBLOLLY PINES

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(WITH TWO FIGURES)

The growth of red pine (*Pinus resinosa* Ait.) planted in the Duke Forest has been very slow compared with the expected growth of this species within its natural range. Seedlings which were three years old when planted attained an average height of only 2.36 feet after eight growing seasons (8). The average height of fifteen-year-old red pine saplings on medium sites in Connecticut was about 17.5 feet (7).

There is no evidence of damage to the young trees by fungi nor by insects. The soil of the plot on which the planting was made is reasonably fertile as indicated by the good growth of slash pine (*Pinus caribaea* Morelet) and loblolly pine (*Pinus taeda* L.) on the immediately adjacent plots which have similar soil. The slash and loblolly pine trees were planted as one-year-old seedlings at the same time as the red pine and in eight growing seasons attained average heights of 12.6 and 18.2 feet, respectively. The supply of moisture is at least as favorable for the growth of trees at Durham as within the natural range of red pine, for the ratio of precipitation to evaporation is higher in North Carolina than in Connecticut during the summer. The maximum photoperiod in Connecticut is about forty minutes greater than that at Durham, but it seems unlikely that the photoperiod is an important factor, for it has been shown that the length of the growing season and the rate of growth of red pine at Durham were not modified by artificially prolonging the photoperiod (9). GUSTAFSON (4) reported that red pine seedlings must be subjected to freezing during the winter if they are to resume growth in the spring. Winters are always cold enough at Durham to insure adequate exposure to low temperature for breaking dormancy and careful observations have shown (9) that red pine resumes growth promptly in the spring. There is a consistent difference in temperature between the two regions, the mean summer temperature in Durham being higher by more than five degrees Centigrade. It is well known that temperature may have an important effect on growth and distribution of plants (11), and considering the relatively small differences between the two regions with respect to other factors, it seemed possible that the difference in temperature was of considerable importance in retarding the growth of red pine at Durham.

The most favorable temperature for apparent photosynthesis in many plants is lower than that for respiration (13). It can be expected that exposure of a plant to temperatures above the optimum for photosynthesis will result in a marked decrease in the ratio of photosynthesis to respiration (P/R), thus causing a shift of the carbohydrate balance of the plant.

For example, potato (1), tomato (16), peach, and apple (17) made more growth and usually accumulated more carbohydrates at moderate temperatures than at higher temperatures. There is evidence that the distribution of some plants is related to the effect of temperature on P/R. Baldwin apple trees accumulated less carbohydrates than Stayman trees when grown at high temperatures, and the Baldwin grows best in the cool New England region, whereas the Stayman thrives south of that region (18). HEINICKE (5) believed that one reason the Delicious apple can be grown farther south than can the McIntosh is that the Delicious has a higher rate of apparent photosynthesis at high temperatures. MÜLLER (15) suggested that high respiration during the relatively long warm summer nights of the temperate zone limits the southward extension of arctic plants. PRINTZ (19) concluded that the southern limits of *Pinus sylvestris* and *Picea excelsa* are probably determined by an unfavorable balance between photosynthesis and respiration at high temperatures.

The experimentation reported here was undertaken to discover whether there was any indication that the balance between photosynthesis and respiration in red pine was affected by high temperature in a way that might account for the retarded growth of this species in the Duke Forest. The effects of a series of temperatures on photosynthesis and respiration in red pine seedlings were measured and compared with the corresponding effects in seedlings of loblolly pine. The temperatures studied ranged from that of a relatively cool summer day to that of a relatively hot day. Loblolly pine was used for comparison because it grows well on the Duke Forest, suggesting that the effects of summer temperatures on its photosynthesis-respiration balance are probably favorable for growth. If the failure of red pine to thrive at Durham results from an unfavorable balance between photosynthesis and respiration at high temperature, then, presumably, the effect of high temperature on one or both of these processes in red pine would differ from the corresponding effect in loblolly pine, and the P/R ratio of red pine would show a greater proportional decrease at high temperature than would the P/R of loblolly pine.

Methods

The red pine seedlings were four years old and the loblolly pine seedlings two years old. All had been growing in seven-inch pots for one year preceding their use in these experiments. The red pine was obtained from the New York State College of Forestry at Syracuse, N. Y., the loblolly pine from the United States Soil Conservation Service nursery at Chapel Hill, North Carolina. The experiments were performed in July and August.

The method used in measuring photosynthesis and respiration was a modification of one which, according to SPOEHR (21), was first suggested by KREUSLER and which has been subsequently modified and used by many workers. Air is passed through a chamber containing a plant, and the change in the carbon dioxide concentration of the air is measured. A de-

crease in carbon dioxide is taken as a measure of carbon dioxide absorption by the plant, or apparent photosynthesis, and an increase in carbon dioxide concentration is taken as a measure of respiration.

The apparatus is diagrammed in figure 1. It consisted of a pair of shoot chambers (*A* and *B*)¹, a light source (*13*),¹ three air sampling and analysis units of which one is shown, and a flowmeter and valve (*18*) for regulating the flow of air through the shoot chambers. The shoot chambers consisted of circular metal bases (*5*) carrying cylindric tops (*1*) of transparent cellulose acetate film. The bases were split to allow insertion of the plant. All joints could be sealed from the outside with modeling clay making the chambers airtight except for the inlet and outlet tubes (*4*, *7*). Air temperature within a shoot chamber was maintained by circulating the air over a coil of

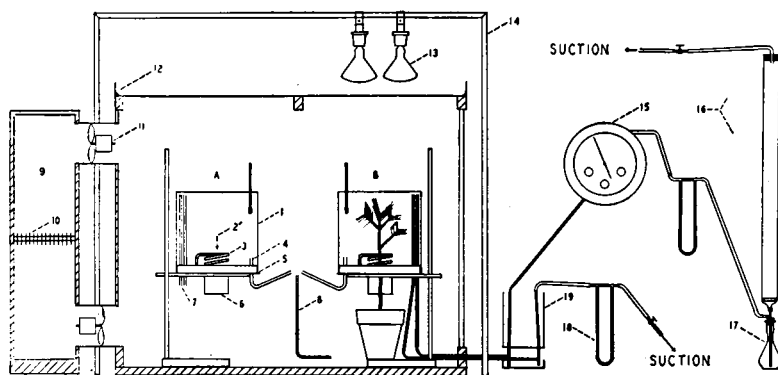


FIG. 1. Diagram of apparatus used in measuring photosynthesis and respiration under controlled conditions. Identification of numbered parts is given in the text.

tubing (*3*) through which water was pumped from a constant-temperature bath. The air was circulated by means of a small centrifugal fan (*2*) driven by an electric motor (*6*). The shoot chambers were modifications of one described by MITCHELL (*14*). They were enclosed in a large glazed chamber which was maintained at constant air temperature by circulating the air through a duct (*9*) in which it was deflected by a damper over either a refrigerated coil (*10*) or an electric heater. The damper was operated by a thermo-regulated controller. A slight positive air pressure was maintained in the chamber by means of a small electric blower which drew fresh air from out-of-doors, thus assuring a continuous supply of air of nearly constant carbon dioxide content. About one inch of cold tap water flowed over the top of the chamber and acted as a heat filter between the lights and the shoot chambers. Illumination was provided by 150-watt projector flood lamps (*13*) suspended from a metal frame (*14*) over the chamber. Eight lamps were focussed on each shoot chamber, giving an average light intensity of 4,500 foot candles as measured by a Weston Illumination Meter. In the later experiments two 300-watt and six 150-watt projector spot lamps were

¹ Letters and figures in italics refer to figure 1.

used over each shoot chamber. This combination gave an intensity of slightly more than 9,000 foot candles over the eight-inch central circle of each chamber.

During a measurement of photosynthesis or respiration air samples were drawn at a constant rate from the shoot chambers and the large chamber through a condenser (19) to remove water vapor and then into the analysis units. To simplify the diagram only one of the three analysis units is shown in figure 1. It consisted of a wet-test gas meter (15) and a carbon dioxide absorption tower (16). Similar units were connected with the outlet tube of the other shoot chamber and with the blank sampling tube (8). The volume of the air sample was registered on the gas meter, the air bubbled through a special carbon dioxide absorption tube charged with dilute sodium hydroxide solution, and the carbon dioxide content was then measured by titration of the absorbent solution. The difference in carbon dioxide concentration between the blank sample and the sample from the shoot chamber, multiplied by the total volume of air which had passed through the shoot chamber, gave the total amount of carbon dioxide absorbed or liberated by the plant. The method used in analyzing air samples was essentially similar to that described by HEINICKE and HOFFMAN (6). A small amount of n-butyl alcohol was added to the absorbent solution to decrease surface tension and accelerate absorption (22), and the reservoir for the absorbent solution was a special 250-ml. volumetric flask (17) which simplified the dilution of the absorbent solution for titration.

The routine procedure used in making measurements of photosynthesis and respiration was as follows. The seedlings were sealed in the shoot chamber and left for one hour under the desired conditions to allow the rate of photosynthesis to become stable. During this time the air sampling apparatus was operated with the absorption towers by-passed. Air samples were then drawn through the towers continuously for one hour. At the end of the photosynthesis measurement the shoot chamber was darkened, fifteen minutes were allowed for the respiration rate to become stable and respiration was measured for a one-hour period. The shoot chambers were again illuminated and the controls reset for the second temperature. Thirty to sixty minutes were required to attain the desired temperatures and thirty minutes at this temperature were allowed before the measurement of photosynthesis was made. This was followed by a measurement of respiration at the same temperature. The routine was repeated for the third temperature.

Preliminary tests showed that the rate of photosynthesis remained unchanged for at least six hours at each of the experimental temperatures. It seems therefore that measurements made according to the procedure outlined above should be fairly representative of the activity of the plant for at least six hours at that temperature. Similar tests were made for respiration measurements, and it was found that the respiration rate remained constant for at least three to six hours in darkness. These results are similar

to those of MCALISTER (12) who found that the respiration rate of wheat seedlings was the same immediately after they were darkened as after ten hours of darkness.

Another series of preliminary tests was made to determine the effect of air supply on photosynthesis. HEINICKE and HOFFMAN (6) found that photosynthesis was retarded markedly in apple leaves when air was supplied at a rate so low that more than 15 to 20 per cent. of the carbon dioxide was removed. Photosynthesis in pine was found to be affected similarly. In all the following experiments the air supply was so adjusted that the carbon dioxide content of the air was reduced 15 per cent. or less. The air sampling apparatus drew air through the shoot chambers at about four cubic feet per hour. When a greater flow of air was required, additional air was drawn through by a system consisting of a flow meter (18), a vacuum pump and the necessary connections. One such system was connected to each shoot chamber. The flow meters were of the type described by GILBERT and SHIVE (3).

No attempt was made to control humidity, for it is unlikely that moderate variations in humidity have any direct effect on photosynthesis in pine seedlings. MITCHELL (14) and MCALISTER (12) have shown that ordinary variations in humidity have no direct effect on photosynthesis in certain herbaceous plants. The photosynthetic rate might be expected to decline if the plants were to become desiccated (20), but preliminary tests showed that the time required for the experimental measurements was not sufficient to produce desiccation.

Eighteen pairs of plants were used. A pair consisted of one plant of each species, and the pairing was randomized. The plants remained out-of-doors until immediately before use in the experiments. It was expected that the behavior of a plant on any day might be affected slightly by the weather conditions of the previous day, and pairing would tend to distribute any such effect uniformly over the two species.

One pair of plants was placed in the apparatus, runs were made at the three temperatures, and the plants were removed and set aside. It seemed possible that the sequence of temperatures might be important. For example, the effect of exposure to 40° might vary slightly according to whether it preceded or followed exposure to the other temperatures. To exclude any such effect from the main effect of temperature an arrangement was made whereby each of the six possible sequences was used three times. All temperatures thus appeared a uniform number of times at all sequence positions, and presumably any possible sequence effect was distributed uniformly for all temperatures and does not appear, therefore, in comparisons between temperatures. The differential response of the species to temperature was the comparison of most interest. It was based on successive measurements on the same plant, because they were expected to be the most precise measurements available with the present apparatus. The direct effects of extraneous factors, such as variations in size or chlorophyll content of indi-

viduals or differences in previous treatment, do not enter into this comparison.

Results and discussion

The results of much of the past research in photosynthesis have been expressed in terms of the amount of carbon dioxide absorbed per unit leaf surface, dry or fresh weight, leaf volume, or other estimate of the amount of active tissue involved. This method was considered undesirable in the present experimentation because direct comparisons between species on such a basis require the assumption that a unit of tissue of one species is the physiological equivalent of a unit of tissue of the other species. It was simpler to make the measurements on the basis of individual plants and subject the data to an analysis of variance according to the method of FISHER (2), testing for a differential response of the species to temperature. This comparison is based on the effects of the temperatures within each species. These effects are independent of the amount of tissue involved, because the same seedlings were used for all tests and thus the amount of tissue was constant within each species.

The results shown in table I and figure 2 are expressed as milligrams

TABLE I

EFFECT OF TEMPERATURE ON THE RATE OF CARBON DIOXIDE EXCHANGE IN RED AND LOBLOLLY PINES. EACH VALUE IS THE MEAN OF EIGHTEEN OBSERVATIONS AND REPRESENTS MILLIGRAMS OF CARBON DIOXIDE ABSORBED OR LIBERATED PER SHOOT PER HOUR. PHOTOSYNTHESIS WAS MEASURED AT A LIGHT INTENSITY OF 4500 FOOT CANDLES

MEASUREMENTS	RED PINE			LOBLOLLY PINE		
	20° C.	30° C.	40° C.	20° C.	30° C.	40° C.
Apparent photosynthesis	30.7	30.1	17.2	30.6	32.3	16.7
Respiration	2.4	5.2	8.2	2.4	5.4	8.3
Actual photosynthesis	33.1	35.2	25.4	33.0	37.7	25.0
Ratio of photosynthesis to respiration	13.7	6.7	3.1	13.7	6.9	3.0

of carbon dioxide exchanged per hour by the entire shoot, and each value represents the mean of separate observations on eighteen plants. Actual photosynthesis was calculated by adding the value for apparent photosynthesis to the corresponding value for respiration. The analysis of variance revealed no significant difference between the reactions of the two species with respect to either photosynthesis or respiration. The similarity between the reactions of the two species is apparent from the data of table I and perhaps is shown most clearly by the P/R ratios, which are essentially the same at each temperature. In both species the apparent photosynthetic rate was about the same at 30° as at 20° and was about 45 per cent. lower at 40° C. Respiration increased with temperature up to 40°. A part of the decrease in the apparent photosynthetic rate at 40° seems to have been caused by the increased rate of respiration and a larger part by decrease in the actual photosynthetic rate.

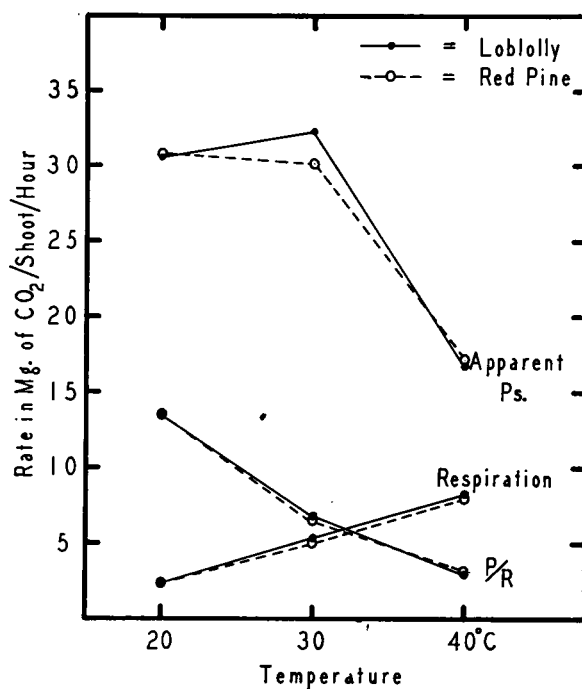


FIG. 2. Graph showing apparent photosynthesis and respiration of loblolly and red pine seedlings at moderate to high air temperatures.

The data in table I suggested a possibility of the apparent photosynthetic rate of loblolly pine trending upward to 30° and of the apparent photosynthetic rate of red pine trending upward to 20°. Although the analysis of variance indicated that these suggested trends were probably entirely fortuitous it was decided to make further tests. The light intensity used in the first experiments was about 4,500 foot candles, which was sub-optimal (10). Changes in the apparatus produced a light intensity of about 9,000 foot candles and a minimum temperature of 19° C. It was thought that if there were actual but very small trends toward differences between the species under the conditions of the first experiment these trends might become more pronounced if the light intensity were increased and the tem-

TABLE II

EFFECT OF TEMPERATURE ON THE APPARENT PHOTOSYNTHETIC RATE OF RED AND LOBLOLLY PINES AT A LIGHT INTENSITY OF 9300 FOOT CANDLES. EACH VALUE IS THE MEAN OF TWELVE OBSERVATIONS AND REPRESENTS MILLIGRAMS OF CARBON DIOXIDE ABSORBED PER SHOOT PER HOUR

SPECIES	19° C.	32° C.
Red pine	33.7	30.8
Loblolly pine	36.3	30.7

perature range expanded. In the second series of experiments twelve pairs of trees were used and photosynthesis was measured at 19° C. and 32° C. Respiration rates were not measured, because no differences were suggested by the data of the first experiment. Otherwise the procedure was the same. A summary of the results is given in table II. An analysis of variance showed that the small difference in the reactions of the species could be expected to occur fortuitously once in five trials. It cannot, therefore, be regarded as real.

Neither series of measurements gave any indication that the effect of high temperature on photosynthesis and respiration differed with the two species. It seems unlikely, therefore, that the failure of red pine to grow in the Duke Forest results from a disturbance of the photosynthetic-respiratory balance at the higher temperatures which prevail in that region. Only the direct effects of temperature were considered in this work. It is conceivable that there are important interactions among temperature and other factors. It is conceivable also that the comparison with loblolly pine is not a sufficiently delicate test to reveal the minimum shift in carbon dioxide exchange which affects the growth rate of red pine.

Summary

Apparent photosynthesis and respiration were measured in seedlings of loblolly and red pine at 20°, 30° and 40° C. A light intensity of 4500 foot candles was used for the measurement of photosynthesis. The rates of apparent photosynthesis of the two species were approximately the same at 30° as at 20° C., but decreased about 45 per cent. when the temperature was increased from 30 to 40° C. The rate of respiration of both species doubled when the temperature was increased from 20° C. to 30° C. and increased about 50 per cent. from 30 to 40° C. The ratio of photosynthesis to respiration for both species was about 13 at 20°, 6.8 at 30° and only 3 at 40° C. Supplementary measurements of photosynthesis at a light intensity of 9300 foot candles and temperatures of 19° and 32° C. showed no significant difference in the behavior of the two species. The ratios of photosynthesis to respiration showed the same proportional decrease with increasing temperature in both species. There was no indication of a gross disturbance of the photosynthetic-respiratory balance of red pine at high temperature that might explain the retarded growth of this species south of its normal range.

The writer is now Captain, Air Corps, on active service with the United States Army Air Force. This work was done at the Department of Botany, Duke University, before entering the military service. The assistance and encouragement of Dr. PAUL J. KRAMER, on all phases of the work, the co-operation of Mr. LLOYD ROOF of the Soil Conservation Service Nursery, Chapel Hill, N. C., and of Professor R. P. PRICHARD of the New York State College of Forestry, in supplying the seedlings, and the assistance of Mr.

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