RELATION BETWEEN LIGHT INTENSITY AND RATE OF PHOTOSYNTHESIS OF LOBLOLLY PINE AND CERTAIN HARDWOODS

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(with two figures)

One of the most important forestry problems in the south concerns the tendency of pine stands to be succeeded by hardwoods. This occurs because pine seedlings usually fail to survive under forest canopies while the seedlings of many hardwood species survive and grow. It is often supposed that the failure of pine seedlings to grow under a forest canopy results from their high light requirements. Pine seedlings are assumed to be unable to carry on photosynthesis rapidly enough in the shade of a forest canopy to survive. Many hardwoods which presumably have lower light requirements and can therefore manufacture food more efficiently in the shade are able to grow vigorously under these conditions. Experiments of Korstian and Coile (6) indicate, however, that pine seedlings will thrive in the shade of a pine or hardwood stand if protected from the root competition of the over-story trees by trenching. Evidently pine seedlings can carry on enough photosynthesis in the shade to provide food for growth, if supplied with sufficient water.

These results raise some questions concerning the actual effect of low light intensity on the photosynthesis of pine seedlings and the importance of shade in the competition of pine with hardwoods. Few measurements of the rate of photosynthesis of tree seedlings have been made. The only comparison of American species of pines and hardwoods is based on determinations of the compensation points of several species made by Burns (1). Since no data are available for species native to the southeastern states several series of experiments were performed to determine the relative rates of photosynthesis of pine and certain competing hardwoods at various light intensities. The species studied were lobolly pine (Pinus taeda L.), eastern red oak [Quercus borealis maxima (Marsh) Ashe], white oak (Quercus alba L.) and dogwood (Cornus florida L.). It was hoped that these experiments would yield information concerning the physiological differences between lobolly pine and the hardwoods which would aid in explaining the differences in their behavior when growing under forest stands.

Methods

The plants used in these experiments were one- or two-year-old potted seedlings which had been grown out-of-doors, except the eastern red oak which was grown in a greenhouse at about half the intensity of full sunlight. The seedlings were kept in the laboratory only long enough for the actual tests, then returned to the greenhouse or out-of-doors. The plants were kept
well watered at all times because deficient soil moisture might seriously affect photosynthesis. All experiments were performed during the summer.

Apparent photosynthesis was measured by determining the difference in carbon dioxide content of an air stream before and after it was passed over the top of a seedling. The carbon dioxide content of the air was determined by passing it through a tower containing dilute sodium hydroxide and estimating the change in concentration of the alkali by titration, or in later experiments by the change in conductivity. Two seedlings were tested at the same time. The tops of the plants were enclosed in cylindrical chambers consisting of brass bases carrying covers made of cellulose acetate. The air inside the chambers was kept cool by circulating it over a coil through which flowed a stream of cold water. Two of these plant chambers were enclosed in a large rectangular chamber with a glass top over which was mounted a battery of projector-type mazda lamps. The air in this chamber was cooled by a small refrigerator unit and much of the heat from the lamps was absorbed by a one-inch layer of water flowing over the glass top of the chamber. All determinations of photosynthesis were made at approximately 30° C. Very satisfactory illumination was provided by two 300-watt and six 150-watt projector spot lights focussed on each plant chamber. This gave a light intensity of nearly 10,000 foot candles in each plant chamber. Lower light intensities were obtained by shading the plant chambers with various combinations of wire cloth and cheese cloth shades. Decker (3) has given a more complete description of the apparatus.

During the experimental runs the seedlings were maintained at a particular light intensity for one hour and a fifteen-minute adjustment period was allowed before a run was started at a new intensity. The time required for adjustment to a new intensity was found to be very short so that a fifteen-minute period was ample. The rate of air flow was such that not over 15 per cent. of the carbon dioxide was removed by the plants, thus concentration of carbon dioxide did not become a limiting factor (3). Preliminary experiments indicated that photosynthesis of oaks began to decrease rapidly after five or six hours at a high light intensity so no tree was kept in the apparatus more than four hours in any one day.

The comparison of loblolly pine with eastern red oak was the most elaborate experiment of the series. The design for this experiment was a Latin square in which seven pairs of seedlings were tested at seven different light intensities, ranging from 300 to 9,300 foot candles, and the experiment was extended over seven days. Each pair of seedlings consisted of one of each species, thus minimizing any possible day-to-day variations between species caused by weather or any other environmental factors.

The light intensities were so randomized that no two pairs received the same sequence, thus the effect of exposure to one intensity on behavior at a subsequent intensity could be eliminated. White oak was tested by itself at seven light intensities, using seven seedlings arranged in a seven by seven Latin square. Dogwood was also tested by itself. Twelve seedlings were
used, two being tested at a time in a randomized sequence of seven light intensities. The experiments on loblolly pine and eastern red oak were performed in September, 1941. The series on white oak and dogwood were performed in June and July, 1942.

Results

The results of these experiments are shown graphically in figures 1 and 2. In figure 1 the results are expressed as milligrams of carbon dioxide per 100 square centimeters of stomate-bearing leaf surface. Loblolly pine has stomates on all three surfaces of its needles, while the deciduous species have stomates only on the under surfaces. The leaf areas of the deciduous species were determined with a photoelectric leaf area device while those of the pines were calculated by the method described by Kozlowski and Schumacher (7). In figure 2 all rates of photosynthesis for each species are expressed as percentages of the rate for the light intensity at which that species showed maximum photosynthetic activity.

Choice of a satisfactory basis for comparing the photosynthetic activity of different species is somewhat difficult. In most previous research the results have been expressed as the rate of carbon dioxide absorption per unit of leaf tissue, usually per unit of leaf surface. Uhl (14) investigated the relation between photosynthetic activity in various species of pine and several different methods of estimating active leaf tissue. He found the
rate of photosynthesis was more closely related to the area of illuminated leaf surface than to total leaf surface, internal volume, chlorophyll content, or stomatal opening. In passing it should be stated that UHL followed stomatal opening by infiltration with ether which, according to SCHORN (12), probably is not a reliable method. The results of Pickett (10) suggest that the rate of photosynthesis may be closely related to the area of internal exposed surface. The difficulties of measuring the internal surface prevent its extensive use. Any comparison based on units of leaf tissue assume that

![Diagram of Photosynthesis Rates](image)

Fig. 2. Photosynthesis of tree seedlings expressed as percentages of maximum observed rates. These curves are plotted from the same data as the curves in figure 1.

a unit of tissue of one species is physiologically similar to a unit of tissue of another species. This has not been demonstrated, especially for such dissimilar tissue as pine and hardwood leaves. It is therefore simpler and more satisfactory to base the comparisons between species on the observed maximum rates of photosynthesis and to express all observations directly in terms of the observed maxima, as done in figure 2. Such comparisons require the assumption that the maxima have similar significance for the growth of the species being compared. For example, the maximum photosynthetic rate of pine is assumed to have the same significance for the growth
of pine seedlings that the maximum photosynthetic rate of oak has for the
growth of oak. This assumption seems reasonable, but has not been tested
experimentally.

It should be remembered that the method used in this study measures
apparent photosynthesis; that is, photosynthesis minus respiration. This is
because it measures only the carbon dioxide absorbed from the surrounding
air, while the actual rate of photosynthesis in terms of carbon dioxide used
includes both the carbon dioxide absorbed from the surrounding air and
that produced in respiration. As the rates of respiration of loblolly pine
and eastern red oak were determined, the actual rates of photosynthesis of
these species could have been calculated by adding the rate of respiration
to the rate of photosynthesis, but for our purposes there was no advantage
in using the actual rates.

Inspection of the curves in figures 1 and 2 show certain similarities as
well as important differences among the four species studied. All four
species show a rapid rise in rate of photosynthesis with increase in light
intensity at the lower intensities. This is said by LUNDEGARDH (8) to be
characteristic of most species and is quite apparent in the curves for various
species published by him. The difference between the behavior of loblolly
pine and that of the three hardwood species is very striking and is best seen
in figure 2. Photosynthesis of loblolly pine increased with increasing light
intensity up to the maximum intensity available, which was over 90 per cent.
of full sunlight. Statistical analysis of the data indicates that the increase
in photosynthesis from half to full light intensity was significant; that is,
such an increase would occur by chance less than once in twenty experimen-
tials. The relation of rate of photosynthesis to light intensity was similar
in all three hardwoods, the maximum rate being attained at one-third or less
of full light intensity and further increase in light intensity producing no
further increase in photosynthesis. There is some indication that photo-
synthesis of the hardwoods might have decreased slightly at the higher light
intensities, but statistical analysis showed that the observed decrease might
have occurred by chance more than once in twenty experiments. LUNDE-
GARDH (8) shows a curve for the shade fern *Dryopteris austriaca* with a
marked decrease in photosynthesis at high light intensities. He also shows
a curve for photosynthesis of *Pinus sylvestris* at various light intensities
which is very similar in shape to our curve for loblolly pine.

It would be interesting to compare the rates of photosynthesis obtained
in this experiment with those obtained by other investigators. Unfortu-
nately this is difficult because of the various bases upon which results have
been calculated and the lack of definite information concerning methods
used. UHL’s data (14) on photosynthesis of various species of pine, for
example, are based on fresh weight of leaves and therefore cannot be com-
pared with our data. HEINICKE and CHILDERS (5) reported that the average
rate of photosynthesis of an apple tree for the entire season was 4.5 mg. of
carbon dioxide per 100 square centimeters of leaf area. For the best ten
days of the season the average rate was about 6.6 mg. of carbon dioxide per 100 square centimeters of leaf area. Much higher rates were obtained with single leaves fully exposed to bright light. In our experiments the maximum rates of photosynthesis per 100 sq. cm. of leaf area per hour were: loblolly pine, 3.59; eastern red oak, 6.04; white oak, 5.33; dogwood, 3.06. The rates of photosynthesis of the forest trees studied seem at least to be of the same order of magnitude as that of apple.

In considering these data it should be remembered that temperature was maintained at about 30° C. regardless of light intensity while in nature temperature would usually vary considerably with changing light intensity. The natural fluctuations in temperature might have considerable effect on the rate of apparent photosynthesis through changes in the rate of respiration. Decker (3) found the apparent photosynthesis of loblolly pine to be nearly twice as high at 30° as at 40° C. and the rate of respiration to be over 50 per cent. higher at 40° than at 30° C. Although no data are available it is likely that respiration of oak is likewise affected materially by temperature. It should also be remembered that the seedlings were never exposed to any given light intensity for more than an hour and a quarter whereas in nature they might be exposed to a high intensity for several hours. According to Uhl (14) several species of pine often show a mid-day decrease in photosynthesis and NUTMAN (9) states that Coffea arabica shows a decrease in photosynthesis at high light intensities because of closure of stomata.

The closely grouped pine needles undoubtedly shaded each other more than the oak leaves, and the dogwood leaves may also have shaded each other more than the oak leaves. Probably differences in mutual shading of leaves by one another is an important factor in the differences in rates of photosynthesis of different species. The greater the extent of mutual shading the higher the light intensity required for maximum photosynthesis. Since photosynthesis of the entire tops of these seedlings was measured, mutual shading was a much more important factor than if photosynthesis had been measured on individual, well-exposed leaves. Heinicke and Childers (5) state that although individual apple leaves exposed to full light may reach their maximum rate of photosynthesis at one-fourth or one-third of full sunlight the rate of photosynthesis of the entire tree increases up to full sunlight. This, they state, is because a large part of the foliage is normally shaded and receives enough light for rapid photosynthesis only in the brightest sunlight.

Discussion

The results of these experiments aid materially in explaining why loblolly pine seedlings are unable to survive under pine and hardwood stands where hardwood seedlings thrive. According to Korstian and Coile (6) the average light intensity on a sunny day under a 31-year-old loblolly pine stand is about 4,500 foot candles and under a hardwood stand composed
chiefly of oaks it is only about 1,900 foot candles. Reference to figure 2 shows that pine seedlings would attain about 75 per cent. of their maximum photosynthesis under such a pine stand and only 60 per cent. of their maximum rate under the hardwood stand. All three species of hardwood seedlings would attain approximately their maximum rate of photosynthesis even under the hardwoods. As shown by the results of the trench plot experiments pines are able to survive in this much shade if provided with adequate water, but the difference in rates of photosynthesis undoubtedly results in the hardwoods having more food available for growth. COILE (2) found year-old seedlings of white oak grown under forest stands to have more extensive and deeper root systems than pine seedlings from similar sites. The more extensive root systems and presumably more adequate food reserves may have some connection with the marked tendency of many hardwoods to sprout from the roots after they have been cut or killed back. This ability to sprout is doubtless one reason for the survival of hardwoods. COILE also found that loblolly pine seedlings grown under pine and hardwood stands consistently had smaller, less extensive root systems than seedlings grown during a season with unusually high rainfall, so soil moisture could scarcely have been limiting in either site. HAIG (4) likewise reported very poor root systems on several western species of conifers when grown in the shade. It seems probable that the root systems are smaller on pine seedlings grown in the shade because they are unable to synthesize enough food for the growth of extensive root systems. So long as soil moisture is relatively abundant the less extensive root systems of pine are no hindrance to survival, but during periods of deficient soil moisture pine seedlings are at a disadvantage as compared to hardwood seedlings with their more extensive root systems. Of course it has not been proved that the death of the pine seedlings is directly caused by desiccation, probable as this seems. It has been demonstrated that deficient soil moisture greatly reduces photosynthesis of apple (11) so it is possible that starvation is also a factor in bringing about death of pine seedlings during a drought.

Several aspects of this problem deserve further attention. It is hoped that studies can be made of the effects of light intensity, soil moisture, and mineral nutrition on the rate of photosynthesis and growth of pine and hardwood species. In the light of our present knowledge, however, it seems possible that pine seedlings are unable to survive under forest stands because they are unable to manufacture enough food to grow sufficiently extensive root systems for the absorption of adequate water and minerals during periods of deficient soil moisture.

Summary

Rates of photosynthesis of loblolly pine, eastern red oak, white oak, and dogwood were determined for one-hour periods at approximately 30° C. at various light intensities from 300 up to nearly 10,000 foot candles.
Photosynthesis of loblolly pine increased with light intensity up to the highest light intensity used which is almost that of full sun. Photosynthesis of the three hardwood species reached its maximum at one-third or less of full sunlight and showed slight, but statistically insignificant, decreases at higher light intensities.

These results indicate that lack of sufficient light for maximum photosynthesis may be a significant factor in the failure of pine seedlings to become established under forest stands. Pine seedlings are probably unable to manufacture enough food in the shade to develop sufficiently extensive root systems for the absorption of adequate water during periods of drought. Certain species of hardwood seedlings, on the other hand, are able to carry on relatively more photosynthesis in the shade and therefore can develop more extensive root systems, probably thus enabling them to survive droughts which are fatal to pine seedlings.

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**LITERATURE CITED**

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