EFFECT OF AGE OF LEAVES UPON THE RATE OF PHOTOSYNTHESIS IN SOME CONIFERS

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(WITH ONE FIGURE)

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Introduction

Information regarding the relationship between photosynthesis and the complex of internal factors encompassed by the term, age, may be of interest either from the point of view of basic science or of practical application. The literature on this subject appears to be rather meager. Singh and Lal (2) working with different aged leaves of flax, sugar cane, and wheat found that the rates of photosynthesis were slow for young leaves, increased to a maximum for mature leaves, and then decreased with increasing age. From studies on aging effects in Chlorella cultures, Winokur (5) reported that the rate of photosynthesis, expressed either per unit number of cells or per unit dry weight, increased during the first few days of a culture and then declined with increasing age of the culture. It would appear that those conifers which maintain their leaves for several years would be especially appropriate for the study of the effects of aging on processes in the leaves. Stålfelt (3) investigated the rates of photosynthesis in spruce and pine with respect to age of needles and light intensity. He concluded for spruce that the rate of photosynthesis, when calculated per gram of fresh weight of needles, appeared to decrease with increasing age of the needles only because the weight of the needles increased with age; whereas actually the rate per unit number of leaves increased with increasing age for five years before declining. The results were most marked at about 30% of full sunlight but were quite evident both below and above this light intensity. For pine, in 30% of full sunlight, he found a similar increase in the amount of photosynthesis per unit number of leaves with increasing age up to three years, the oldest used; but in full sunlight the rate was approximately the same for leaves of all ages.

From this review of literature, one may conclude that for some plants the peak photosynthetic capacity is reached at the time of maturity of the photosynthetic organ or structure, but in conifers the peak is not reached until the leaves are several years old. The purpose of the research reported in this paper was to obtain further data regarding the rates of photosynthesis in conifer leaves of varying age.

Methods and materials

The experimental plants used were Scotch pine, Pinus sylvestris L.; white pine, Pinus strobus L.; Austrian pine, Pinus nigra Arnold; western yellow...
pine, *Pinus ponderosa* Laws.; white fir, *Abies concolor* Lindl. and Gord.; and Colorado blue spruce, *Picea pungens* Engelm. These plants were all young trees about fifteen feet tall, spaced widely as in specimen planting, and growing on or near the University campus. All experiments were performed from July through October after the leaves on the current year of growth were apparently mature. After a suitable branch was selected on a tree, it was cut into separate annual segments with the leaves intact. None of the trees had stem segments four or more years old with leaves in sufficient number or state of preservation for investigation; so leafy stems one (current), two, and three years old were employed in the study. In the laboratory, the basal end of each stem segment was cut off under water. The leafy stem sections were then placed in glass cylinders, 6 cm. × 30 cm., with the basal end of each stem in shallow water at the bottom of the container. Each cylinder contained leaves of a particular age. The cylinders were placed vertically in a constant temperature bath which was illuminated from one side by a combination of incandescent and fluorescent lights which gave a light intensity of 2200 foot-candles on the plants. In some experiments, especially with pines, the needles were removed from the more shaded portions of each stem to prevent excessive crowding and shading. The top of each cylinder was fitted with inlet and outlet tubes, the latter reaching nearly to the bottom, through which metered air was passed over the leaves at the rate of six liters per hour. The bath temperature was kept at 24° C.

Apparent photosynthesis was measured by determining the difference between the carbon dioxide content of the air before and after it passed over the plants. Carbon dioxide in the air was determined by the method described by Waugh (4) which consists of measuring the changes in electrical resistance, at a constant temperature, of a dilute solution of KOH in a gas absorption bottle through which the air is passed. By repeated and simultaneous analysis of air from the same source with the four gas absorption towers used in this research, it was established that carbon dioxide in milliliters per liter of air at 24° C could be determined with a standard error of ± 0.007 which amounted to a maximum calculated discrepancy between the towers of less than 2%. At the close of each experiment, all leaves were removed from each annual stem segment for counting and volume and weight determinations.

**Results and discussion**

The common practice of expressing the rate of photosynthesis per unit area of leaf is not practical for the needle-shaped leaves of the gymnosperms used in this study. One is left with a choice between calculating the rate per unit volume, unit weight, or unit number of leaves, all of which can be easily and accurately determined. As noted earlier, Stålfelt concluded that both the fresh and dry weights of pine and spruce needles increased with age and that the rates of photosynthesis for leaves of different ages
expressed on this basis presented an erroneous picture, whereas calculation of the rates per unit number of leaves presented a different but true picture.

A preliminary survey of several conifers based upon samples of 400 to 500 leaves per year for leaves from one to four years old seemed to verify Stålfelt's conclusion that the fresh and dry weights of such leaves do increase with age. The volume was also found to increase in a similar manner. Occasionally, apparent exceptions were found but the over-all aspect was one of a measurable increase in weight and volume with an increase in age of the needles. Consequently, it was decided to calculate the rates of apparent photosynthesis simply on the basis of a unit number of leaves. It is from this point of view that all of the results pertaining to the rates of apparent photosynthesis with respect to age of leaves of various conifers are presented in tables I and II and figure 1.

![Graph showing apparent photosynthesis in conifers with respect to age of leaves.](image)

Fig. 1. Apparent photosynthesis in conifers with respect to age of leaves.

From these data, the leaves of all of the species investigated attained a rate of photosynthesis which was at or near the maximum by the time of apparent leaf maturity during the first season of growth. Since there are no data for the spring or early summer, it is not possible to establish precisely when the peak is reached. It is evident, however, that the photosynthetic capacity of the leaves decreases with increasing age beginning during the second year. These data are in accord with those published by Singh and Lal (2) who reported that the maximum photosynthetic capacity was attained in some angiosperms at the time of apparent leaf maturity. The results do not confirm the conclusion of Stålfelt (3) that the rate of photosynthesis increases with increasing age of needles up to three and five years for pine and spruce, respectively. Perhaps this discrepancy is more apparent than real since it does not appear that Stålfelt controlled temperature
or made any correction for this factor whereas the data in this report were obtained under uniform conditions with respect to light, temperature, and concentration of carbon dioxide. The rates of photosynthesis of leaves of different ages for each species reported in the present paper were determined simultaneously which insured that in each experiment the previous environment was approximately the same for all of the leaves under consideration. Such uniformity was apparently not the case in Stålffelt’s experiments. It should also be stated that Stålffelt noted some exceptions, especially in spruce, to the general conclusion that photosynthesis increases with increasing age of needles to five years. However, it is obvious both from the data in this report and those obtained by Stålffelt that the rate of photosynthesis in the leaves of certain gymnosperms may remain quite high for a period of two to three years.

In handling the needles of the various conifers throughout the course of the experiments, it was noted that the older ones particularly were often quite dark and dirty. It was thought that possibly the apparent differences between the results reported in this paper and those of Stålffelt might be due to the accumulation of soot and other dirt on the leaves. Several experiments were performed to test this hypothesis. The rates of photosynthesis

**TABLE II**

**APPARENT PHOTOSYNTHESIS IN LEAVES OF CONIFERS BEFORE AND AFTER DIRT WAS REMOVED FROM THE LEAVES.**

<table>
<thead>
<tr>
<th>Plant</th>
<th>Condition of leaf surface</th>
<th>Photosynthesis in leaves</th>
<th>mg. CO₂/100 leaves/hr.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>One year old</td>
<td>Two years old</td>
</tr>
<tr>
<td>White fir</td>
<td>Uncleaned</td>
<td>0.7</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>Cleaned</td>
<td>0.6</td>
<td>0.3</td>
</tr>
<tr>
<td>Spruce</td>
<td>Uncleaned</td>
<td>0.5</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Cleaned</td>
<td>0.6</td>
<td>0.4</td>
</tr>
<tr>
<td>Austrian pine</td>
<td>Uncleaned</td>
<td>1.3</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td>Cleaned</td>
<td>1.4</td>
<td>1.1</td>
</tr>
</tbody>
</table>
were first determined as usual; then the leafy branches were removed from the cylinders and the leaves were carefully, but thoroughly, scrubbed with a soft bristle brush and a dilute solution of either a detergent or soap. After scrubbing, the branches were rinsed in tap water and replaced in their respective containers for a second determination of photosynthesis. Since the results of all of these experiments follow the same trend, only representative samples are presented in table II. Examination of many of the leaves, both superficially and under a dissecting microscope, indicated that washing of the leaves was rather effective in removing the dirt. Nevertheless, the washing had no marked effects upon the order or magnitude of the rates of photosynthesis in the leaves of various ages. Therefore, it seems that the decrease in the rate of photosynthesis in conifer leaves, beginning during the second year, cannot be explained solely on the basis of the presence of dirt on the surface of the leaves at the moment. There is still a possibility that the accumulation of dirt on the leaves over an extended period of time may have induced secondary changes in the leaves which in turn may have resulted in a decrease in photosynthetic capacity. In view of the work by Clendenning and Gorham (1) with respect to the effects of leaf ontogeny on the photochemical activity (Hill Reaction) of isolated chloroplasts, it seems likely that the decrease in photosynthesis with increasing age of leaves of conifers is due to internal cellular changes which occur normally with age. Clendenning and Gorham did not obtain active chloroplast suspensions from any of the four gymnosperms tried, but in using spinach and wheat they found that the photochemical activity of the chloroplasts increased as the leaves enlarged and matured and then decreased as the leaves became older. They reported that the order of activity of chloroplasts from young and mature spinach leaves was not altered by suspending the chloroplasts in the cell sap-cytoplasm from mature and young leaves, respectively, and therefore that changes in activity associated with age of leaf must be due to changes in the chloroplasts. If these conclusions should be found to hold true for gymnosperms, there would still be the problem of what change occurs in the chloroplasts which leads to an increase in photosynthetic capacity up to the maturity of the leaves, followed by a decrease in rate with further aging.

It is of interest, from the practical point of view, to know that the older leaves of conifers do have considerable photosynthetic capacity, even though it is less than in the leaves recently matured. Therefore, it seems safe to predict that pruning of conifers for shaping or other purposes will ordinarily not seriously impair the available supply of photosyntate in a branch or tree so long as no more than the youngest growth of the current season is removed.

Summary

The rates of apparent photosynthesis were determined for leaves of different age on the following conifers: Pinus sylvestris L., Pinus strobus L.,
Pinus nigra Arnold, Pinus ponderosa Laws., Abies concolor Lindl. and Gord., and Picea pungens Engelm. The leaves of all of the species investigated attained their maximum photosynthetic capacity approximately at the time of apparent leaf maturity during the first season of growth. Beginning during the second year of age, the rate of photosynthesis decreases slowly with increasing age of the leaves. The data indicate that the decrease in rate with increase in age is not due to the presence of dirt on the leaf surfaces. In spite of the decrease in rate with increasing age, conifer leaves three years old still have an appreciable photosynthetic capacity.

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LITERATURE CITED