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Photosynthesis in Aspen Bark During Winter Months

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BOTANY

Photosynthesis in Aspen Bark During Winter Months

Quaking aspen, *Populus tremuloides* Michx., is probably the most widely distributed tree on the North American continent. Much of its range is characterized by long winters and is generally thought of as being more suitable for evergreen conifer species which are photosynthetically active during the winter months, even at temperatures below 0° C. as indicated by Parker (1953). By use of the spectrophotometer, Pearson and Lawrence (1958) demonstrated that the green pigments in aspen bark are chlorophylls *a* and *b*. Per unit area, these pigments were more abundant in bark than in leaves during the early part of the growing season but more abundant in leaves later in the summer. Isolating regions of bark by completely removing the phloem around such regions made possible measurement of photosynthetic activity with an iodine starch test. They reported that aspen bark was photosynthetically active during the summer months. The following experiment was designed to ascertain whether or not aspen can carry on photosynthesis in its leafless condition during the winter.

MATERIALS AND METHODS

Four aspens were selected at the Cedar Creek Natural History Area in Anoka County Minnesota. The only criteria of selection were that the trees be of sufficient diameter for the purposes of the experiment and that they be relatively easily accessible; otherwise they were chosen at random from a half acre grove of aspens growing there in pure stand. On February 16 and 18, 1958, with the help of Bruce Hayward and Robert Dickerman, six regions of bark on each tree were completely isolated by removing a band of bark down to the xylem around each. These regions were in the form of squares about four inches to the side with three squares on the south side of each tree and three on the north. The three squares in each case were arranged one directly above the other with the top square six feet from the surface of the ground and with about four inches between squares. Four treatments were imposed on each of the two sides of each tree; these were: (1) a non-isolated region, above, below, or between isolated squares, exposed to full light as a control or check, (2) an isolated region exposed to full light, (3) an isolated region half covered as in the following treatment and half exposed, and (4) an isolated region fully covered with aluminum foil over black paper to prevent any light from reaching the bark. In the last two treatments, the paper used to cover the regions was held in place with cotton cord tied around the trunk of the tree. The four treatments were allocated to the four trees in the form of a latin square with independent randomization for north-facing bark and south-facing bark. Thus, for south-facing bark each of the treatments occupied the top level on one tree and only one tree, each occupied the second level on one tree, each the third, and each the lowest level; and likewise for the north-facing bark. Any differences which might conceivably be associated with distance above ground level, as well as differences due to the different trees, were therefore adequately controlled.

On February 23, 1958, two samples of bark were taken from each of three of the treatments and four samples from the partly exposed square, two from the exposed part and two from the covered part, making a total of 80 samples. As each sample was removed from the tree, a number was placed on the under side of it with a lead pencil. The squares that were covered or partly covered were immediately covered again in the same manner as before as soon as the samples were taken. Half of the bark samples were boiled in alcohol for several minutes until most of the chlorophyll was extracted and then dipped in boiling water and treated with I-KI solution to reveal the presence of starch. Independent scoring of the quantity of starch was made by each of the two investigators, scoring being an estimate of the intensity of the blue color; a deep blue typical of pure starch was scored 100 and a complete lack of blue was scored 0.

The other half of the samples were kept on ice until the following day when they were tested in the laboratory for sugar content with Fehling's solution.

On March 1, 1958, eighty more samples of bark were taken and all of these were tested for starch. At this time, the squares on two of the trees which had been exposed to light up to this time were covered and the squares which had been covered were left exposed.

On March 15, 1958, eighty samples were again taken and tested for starch. This time all treatments were left exposed.

During the period of February 16, 17, and 18, 1958, when the bark regions were being isolated, the maximum temperature was approximately —18° C with a minimum of —31° C recorded at the Lawrence cabin about 200 meters from the aspen grove. On February 18, two maximum-minimum thermometers were set up on a fifth tree in the grove and temperature readings were made at subsequent visits. One of the thermometers was placed on the south side of the tree with its bulb exposed to the rays of the sun. The other instrument was placed on the north side of the tree and its bulb was shielded with a piece of aluminum foil. The bulbs were both 67 inches above the ground. The cold snap continued until February 22 with maximum readings in Minneapolis, 35 miles away, of about minus 13° C each day. The minimum and maximum temperatures recorded in the grove for the week of Feb. 18 to Feb. 23 were —27° C and +11° C, respectively, on the north side and —27° C and +16° C on the south side. For the week of Feb. 23 to March 1, —6° C and +13° C were the minimum and maximum temperatures recorded on the north side and —6° C and +19° C on the south side. From March 1 to March 15 the north side temperatures varied from —13° C to +6° C and the south side temperatures from —13° C to +13° C. From March 15 to April 6, the temperature range was —9° C to +17° C on the north side and —10° C to +21° C on the south side.

EXPERIMENTAL RESULTS

The first starch measurements which were made on February 23 indicated almost complete absence of starch in all of the samples. The slight variation which was present was just as great within treatments as among treatments. Since the food reserves were not present in the form of starch, it was thought that differences might exist for sugar content. Fehling's solution tests for the presence of reducing sugars revealed very striking differences. There was undoubtedly more sugar present in the north-facing bark than in the south-facing bark and there appeared to be more sugar in the control treatments (non-isolated regions) at both exposures than in any of the other treatments with the same exposure, though this difference was not significant and may have been merely the result of chance variation. Variation was considerable within treatments; for instance, the sample showing the greatest amount of reducing sugar present and the sample showing the least amount were both from the same treatment, the isolated squares completely covered to exclude all light.

The samples taken March 1, 1958 showed extreme differences in quantity of starch present. At this time there was considerably more starch present in the regions exposed to light than in the darkened regions. Comparing the two halves of the regions half exposed and half covered, there seemed to be very little movement of food within the isolated regions from lighted to darkened sections. The difference between the well-lighted south-facing bark and the poorly-lighted north-facing bark was also very striking. These data are summarized in Table 1.

TABLE 1.—*Relative starch content of light-exposed and darkened areas of aspen bark eleven days after isolation by removal of the phloem. Values are given as the color intensity of the samples expressed as a per cent of the intensity of a pure starch-iodine complex.*

Treatment	AVG. OF 8 SAMPLES FROM 4 TREES South-facing bark	North-facing bark
1. Control. Non-isolated regions of bark completely exposed to light	79%	47%
2. Isolated region completely exposed to light	81%	48%
3. Isolated region half exposed and half covered; Exposed half	74%	43%
4. Isolated region half exposed and half covered; Covered half	45%	48%
5. Isolated region completely covered with aluminum foil over black paper	37%	37%
LSD, 5% level of probability	10%	10%

On March 15, there were also distinct differences noted among samples although some of the samples were difficult to evaluate because of necrotic areas in the bark. In general, the differences became more pronounced for the treatments which were continued for the full 25 days. In the other treatments, there was a tendency for the regions which were low in starch on March 1, as a result

TABLE 2.—*Relative starch content of light-exposed and darkened areas of aspen bark twenty-five days after isolation by removal of the phloem. Values are given as the color intensity of the samples expressed as a percent of the intensity of a pure starch-iodine complex.*

	SOUTH SIDE (Avg of 2 to 8 samples)			NORTH SIDE (Avg of 8 samples)
Treatment	March 1	March 15	Net Change	March 15
1. Control. Non-isolated region completely exposed to light	79%	76%	— 3%	31%
2. Isolated regoin exposed to light for 25 days	74%	85%	+11%	36%
3. Isolated region darkened for 11 days and then exposed to light for 14 days	30%	65%	+35%**	..
4. Isolated region exposed to light for 11 days and then darkened for 14	88%	71%	—17%*	..
5. Half of isolated region half exposed and half covered; exposed for 25 days	71%	63%	— 8%	32%
6. Half of isolated region half exposed and half darkened; Covered for 11 days and then exposed for 14	45%	41%	— 4%	..
7. Half of isolated region half exposed and half darkened; exposed for 11 days and then darkened for 14	85%	82%	— 3%	..
8. Half of isolated region half exposed and half darkened; Darkened for 25 days	45%	25%	—20%*	22%
9. Isolated region covered for 25 days	44%	30%	—14%	29%
LSD, 5% Probability		16%	..	11%

*Net change greater than would be expected by chance, 5% level.
**Net change greater than would be expected by chance, 1% level.

of having been covered, to increase in starch content after the covering was removed and likewise for the starch content to decrease in those regions which were exposed until March 1 and then covered. However, the variation within treatments was considerably greater on March 15 than it had been on March 1. The results of this second reading are shown in Table 2.

DISCUSSION

The ability of aspen bark to produce starch even at low temperatures when exposed to light seems well established from data gathered March 1 (Table 1). It might be argued, however, that the starch was produced not by the stimulation of light energy as a photosynthetic process but by the stimulation of heat energy as a hydrolytic reaction from sugar already present in the bark. It certainly seems likely that different temperatures prevailed in the light exposed and the darkened regions as well as light differences. The data obtained March 15, however, make it appear more likely that the response was due to light differences inasmuch as the isolated regions which were darkened first, increased in starch content following subsequent exposure to light and the regions which were exposed first, decreased in starch content after being darkened (Table 2, treatments 3 and 4, respectively). The ability of aspen bark to take advantage of solar energy during the long winter season in much the same way that the leaves of evergreens do would increase the efficiency of this species and could explain in part its ability to thrive in what is generally thought of as a coniferous evergreen environment.

Methods of measuring CO_2 utilization were employed by Parker (1953) in studying photosynthesis in the leaves of *Picea excelsa* and by Chapman and Loomis (1953) in studying photosynthesis in the leaves of the potato, *Solanum tuberosum*. These methods have some advantages over the starch-iodine method used in this study: they measure a direct reactant (CO_2) rather than a secondary reactant (starch, a product of polymerization of the photosynthetically produced sugars), they enable measurements to be made over a period of a few minutes rather than demanding several days, and in the case of Parker's method automatic recording can be utilized to give a continuous record. However, the difficulties in adapting these methods which work so well on leaves in or near a laboratory to measuring photosynthesis in the bark of aspen trees under forest conditions are great and have not as yet been satisfactorily solved.

The rapid development of necrosis in much of the bark tissue by the end of the second week of the experiment point up the necessity in experiments of this type in which drastic treatments are imposed upon plants otherwise in their native habitat of obtaining all the data needed as rapidly as possible. In addition to the necrosis noted, it was observed that yeasts were very abundant on some of the covered regions by the end of the experimentation period. What effect these organisms may have had on the final results is not known.

SUMMARY

Isolating square regions of bark by completely removing the phloem around them made possible measurement of photosynthetic activity with an iodine starch test. It was ascertained that the chlorophyll in aspen bark is active during winter months as well as during the growing season. It is suggested that this ability of aspen to carry on photosynthesis in its bark might in part account for the ability of this species to thrive in regions of long winter which are otherwise generally thought of as being more suitable for evergreen conifer species.

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