EFFECT OF DEPTH OF IMMERSION ON APPARENT PHOTOSYNTHESIS IN SUBMERSED VASCULAR AQUATICS[1]

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The influence of the depth of immersion on the rate of apparent photosynthesis in submersed aquatic plants has an important bearing on the ecological distribution of such species. Important inferences regarding the dynamics of photosynthesis, respiration, and perhaps other plant processes also can be drawn from the results of studies of this problem. Most investigations of the relation between depth of immersion and photosynthesis in submersed aquatics have been made with marine or freshwater algae. A few investigators, however, notably Ruttner ('26), Schomer ('34), Manning *et al.* ('38), and Meyer and Heritage ('41) have worked on this problem in vascular aquatics. This paper reports the results of an investigation upon five such species, several of which have not been used previously in such studies. The experimental technique employed in this work is believed to incorporate a number of improvements as compared with the procedure employed by previous investigators.

Experimental Procedure

The species used in this investigation were *Potamogeton Richardsonii* (Benn.) Rydb., *Najas flexilis* (Willd.) Rostk. & Schmidt, *Anacharis canadensis* (Michx.) Planchon, *Vallisneria americana* Michx., and *Heteranthera dubia* (Jacq.) MacM.[2] Plants were collected directly from shallow parts (depths not exceeding 1 meter) of Lake Erie in the vicinity of the Stone Laboratory at Put-in-Bay, Ohio. Collections were made in the late afternoon or evening, the plants being kept overnight in a large vessel of lake water. Six samples of plant material were used in each experiment. Selected apical portions of the plants, each about 15 cm. long, were used of all the species except *Vallisneria americana*. Each sample of this species consisted of a strip cut from the apical portion of the leaf blade about 50 cm. in length. All of the samples of plant material used in any one determination were selected carefully for close uniformity in size and configuration.

Except for the final titrations (see later), all stages in each of the experiments were conducted on a barge anchored in the mile-wide channel about midway between North Bass and Middle Bass Islands, at a point where the water was 10–12 meters deep. All experiments were carried out on clear August days in 1941 between the hours of 9:00 A.M. and 3:30 P.M. (solar time) during periods when the lake surface was relatively smooth.

The exact procedure followed was adopted only after an extensive and critical experimental study of the suitability of the methods for use in an investigation of the type described in this paper. Since the results of the investigation on the technique of measuring rates of apparent photosynthesis in submersed aquatics will be published as a separate paper no attempt will be made in the following discussion to justify or evaluate the exact procedure followed.

Pyrex culture tubes, 3 cm. in diameter and 20 cm. in length, with a capacity of 130 ± 1 ml., were employed as containers for the plants during all experiments. Each tube was provided with a tight-

[1] Paper from the Franz Theodore Stone Laboratory and the Department of Botany, No. 457, of the Ohio State University.

[2] Nomenclature follows Fassett, N. C. A manual of aquatic plants. New York. 1940.

fitting rubber stopper, hollowed on the under side to prevent accumulation of air bubbles at that point when the tube was stoppered, and a short, tapered glass plug which fitted the hole in the stopper snugly.

The tubes required for an experimental run were filled in the laboratory with Lake Erie water of reduced and uniform oxygen content, and stoppered in such a manner that no air bubbles were entrapped in the tubes. The actual oxygen content of the water as used was about half that of water at the same temperature in equilibrium with the partial pressure of oxygen in the atmosphere; expressed in usual units the oxygen content of the water used was about 4 p.p.m. or about 3 ml. per liter. The oxygen content of the water used varied slightly from one experiment to another, but all the tubes used in any one experiment were filled with water of exactly the same oxygen content. Use of water with an oxygen content less than the saturation value was necessary in order to prevent emission of gas bubbles from the plants when high rates of photosynthesis were attained. This would invalidate the method used for measurement of the oxygen content of the water, which determines dissolved oxygen only.

The plants therefore were immersed during the experiments in a water medium identical with that in which they grew in nature except that its oxygen content had been reduced to about half the usual value. The following are pertinent data [3] regarding the physical and chemical properties of Lake Erie water at a depth of 1 meter as determined in August, 1942: temperature 22.7 — 26.3° C., dissolved oxygen 8.0 — 8.2 p.p.m., free carbon dioxide 0 p.p.m., carbonate concentration 2.0 — 5.0 p.p.m. (in terms $CaCO_3$), bicarbonate concentration 79.8 — 84.0 p.p.m. (in terms $CaCO_3$), pH value 8.4 — 8.5. None of these properties of Lake Erie water in the Bass Island region show any great variation at this season from the values given for depths up to 10 meters.

At the beginning of an experimental run a sample of plant material was transferred to each of six tubes of water prepared as previously described. All of the tubes of water used in these experiments previously had been brought to the temperature of the lake water by first immersing them in the lake for a suitable period of time. The tubes were restoppered without entrapping any air bubbles within them. The plants had been kept until this time out of direct sunlight. The tubes were fastened to a specially constructed wooden float which, when placed in the water, held them in a horizontal position at a depth of 0.05 meter under the surface of the water. The purpose of this preliminary run was to allow time for the completion of the photosynthetic induction period, if any, and to bring the plants into equilibrium with the reduced oxygen concentration of the water.

At the end of 30 minutes the float was removed from the lake and the plants quickly transferred to a second set of tubes. These tubes also were attached to the float and immersed in the lake in the same manner and at the same depth as during the first run. The purpose of this "calibration run" was to determine the rate of apparent photosynthesis in all of the samples of plant material while they were exposed to identical environmental conditions.

At the end of this second 30-minute period the float was again removed from the lake and the plants transferred to the third set of tubes. These tubes were attached to a weighted wire cable in such a manner that, when the cable was lowered into the water, one of the tubes was in a horizontal position at each of the following depths below the surface: 0.05, 2, 4, 6, 8, and 10 meters. The top tube in this experimental run was at the same depth (0.05 meter) below the surface of the lake as all of the tubes in the calibration run. The duration of the experimental

[3] Analysis made by Dr. D. C. Chandler.

run was also 30 minutes. (In the experiment on *Heteranthera dubia* all three of the successive runs were 40 minutes in length instead of the usual 30 minutes.)

The complete transfer of a set of six plants from one set of tubes to the next was accomplished in about 5 minutes. No individual plant, however, was exposed to the air for more than a few seconds during such transfers. Removal or introduction of plants from or into the tubes always was accomplished with as little disturbance as possible of the enclosed water. As soon as the tubes were removed from the water at the ends of the second and third runs they were wrapped immediately in black cloths which remained in place until the plants were removed which was accomplished within a few minutes. Likewise, prior to each of these runs, as soon as the plant had been introduced into a tube, it was wrapped in a black cloth which was left in place for the few minutes which intervened before the tubes were immersed in the lake.

Immediately after removal of the plants from the tubes at the ends of the calibration and experimental runs the necessary reagents for determination of the oxygen content of the water by the Winkler method were added to each tube and to check tubes which contained samples of the water used. The procedure outlined in Standard Methods for the Analysis of Water and Sewage, 7th Ed. 1933, was followed, except that a 0.0125 N solution of sodium thiosulfate was used for the final titration. One milliliter of such a solution is equivalent to 0.07 ml. of oxygen at standard conditions. Preliminary studies indicated that it was unnecessary to use the Rideal-Stewart modification of the Winkler method in this work. Actual titrations, on 100 ml. aliquots from each tube, including the check tubes, were carried out after the tubes had been brought back to the laboratory. From these data the increase or decrease in oxygen content per 100 ml. of water could be computed for each tube in which the plants had been immersed.

The temperature of the lake water was measured at depths of 0.05 and 10 meters during each experimental run with a suitable "minimum" thermometer.

Measurements of light intensity, incident on a horizontal surface, were made with the degree of accuracy obtainable with a Weston "Photronic" cell when used in lacustrine habitats. The cell was mounted in a metal case and provided with an opal glass filter according to the specifications of Atkins *et al.* ('38). The electrical circuit from the photocell to suitable milli- and microammeters was completed through a heavy waterproof cable which also served as a support for the instrument while it was suspended in the water. Although instruments of this type are being used rather widely for measuring the penetration of light into water, not more than a roughly quantitative significance should be attached to results obtained with them. This is particularly likely to be true in bodies of water in which rapidly fluctuating turbidities are often encountered. This is the situation in that part of Lake Erie in which these investigations were conducted. Photocells of the rectifier type are all selective detectors of radiant energy, and since both quality and intensity of light vary with depth of immersion, strictly quantitative relations between the intensity of light prevailing at a given depth under the water and the current developed by the cell are not to be expected.

The light intensity measurements recorded in this paper were all made during the "experimental run" of each series of determinations. The highest value of any reading recorded was 735 microamperes for the reading in air on August 7, at 10:45 A.M.; the corresponding reading obtained with the recording pyrheliometer located at the Stone Laboratory about one and one-half miles distant was 1.23 g.-cal. per cm.^{2} per minute. This reading was given an arbitrary value of 100 and all light intensities are expressed

TABLE I. *Apparent photosynthesis in* Anacharis canadensis *at different depths*

August 21, 1941 — Water temperature, 21° C.

Plant no.	Calibration run 9:19–9:49 A.M.	Experimental run 9:53–10:23 A.M.		Relative light intensity.	Expt. run as per cent of calib. run
	Gain O_2, ml. per 100 ml. solution	Depth of tubes, meters	Gain or loss O_2, ml. per 100 ml. solution	Air, 97	
1	0.198	0.05	0.171	89	87
2	0.209	2	0.141	38	68
3	0.238	4	0.050	12	21
4	0.213	6	0.029	3.5	14
5	0.246	8	0.019	1.0	8
6	0.140	10	−0.019	0.27	−14

on a relative basis with reference to this as a standard.

Results and Discussion

Two or more experiments were performed with plants of each of the five species reported on in this paper. Closely similar results were obtained in all of the determinations on a given species; hence the one set of data presented for each species may be regarded as representative.

If six similar portions of plants of the same species are suspended at different depths beneath the surface of a body of water and their measured rates of apparent photosynthesis found to be different there is no way of ascertaining to what extent differences in the observed rates result from differences in environmental conditions and to what extent they arise from intrinsic differences in the photosynthetic capacity of the several samples of plant material. For this reason the photosynthetic rates of all the plants used in a given experiment first were measured under identical environmental conditions in the calibration run before their rates of apparent photosynthesis were measured at different depths. "Calibration" of plants in this manner gave a quantitative measurement of their inherent differences in photosynthetic capacity. In other experiments we have found that the rate of apparent photosynthesis in several species of submersed aquatics remains virtually constant for periods of at least several hours under constant environmental conditions as favorable to photosynthesis as any likely to be encountered in Lake Erie. Gessner ('37) obtained similar results with *Ceratophyllum demersum*. Hence it is a valid inference that differences in the rate of apparent photosynthesis exhibited by the plants in the experimental as compared to the calibration run result from differences in

TABLE II. *Apparent photosynthesis in* Najas flexilis *at different depths*

August 2, 1941 — Water temperature, 25° C.

Plant no.	Calibration run 2:25–2:55 P.M.	Experimental run 3:01–3:31 P.M.		Relative light intensity.	Expt. run as per cent of calib. run
	Gain O_2, ml. per 100 ml. solution	Depth of tubes, meters	Gain or loss O_2, ml. per 100 ml. solution	Air, 94	
1	0.173	0.05	0.152.	87	87
2	0.160	2	0.105	57	66
3	0.139	4	0.054	26	39
4	0.209	6	0.020	8.4	10
5	0.134	8	0.006	2.8	4
6	0.114	10	−0.030	0.82	−26

the environmental conditions at the different depths. In order to obtain comparable indices of the rate of apparent photosynthesis (photosynthesis minus respiration) the oxygen evolution for each plant during the experimental run has been expressed as the percentage of the oxygen evolution during its calibration run.

Except for occasional short periods the portion of Lake Erie in the vicinity of the Bass Islands is virtually an isothermal body of water. Actual measurements during the course of these experiments never showed a temperature differential of more than 1° C. between the 0.05 and 10 meter depths, and usually less than this. Any differences found in the rate of apparent photosynthesis at different depths cannot, therefore, be ascribed to the temperature factor. This essentially isothermal condition of the lake simplifies interpretation of the results of an investigation of this type.

The conditions under which these experiments were performed were such that any differences found in the rate of apparent photosynthesis at one depth as compared with another must result principally and probably entirely from differences in the light conditions at the different depths. As is well known, both the intensity and quality of light vary with depth of penetration into water. No attempt was made in this investigation to evaluate effects of differences in light quality at different depths upon the rate of apparent photosynthesis. Even the measurements of light intensity, recorded in connection with the measurements of photosynthesis, can be accepted only with certain qualifications, as pointed out previously.

The results obtained with *Anacharis canadensis* (table I) indicate that there is a consistent decrease in rate of apparent photosynthesis with increase in depth. The compensation point was attained in this species under the prevailing environmental conditions at a depth of between 8 and 10 meters.

Results obtained with *Najas flexilis* (table II) are, in general, similar to those obtained with *Anacharis canadensis.* The light intensities at all except the 0.05 meter depth were greater in this series than in any other. This was correlated with the lesser turbidity of the water on this date than on other days on which experiments were performed. The compensation point for this species appears to be slightly higher than for any of the other species investigated.

The results obtained with *Potamogeton Richardsonii* (table III) were similar to those found with *Anacharis canadensis* and *Najas flexilis.* In general, rate of apparent photosynthesis decreased consistently with increase in depth of immersion of the plants. The compensation point was closely approached, although not quite reached at the depth of 10 meters. Light intensities at the different depths in this experiment were closely compar-

TABLE III. *Apparent photosynthesis in* Potamogeton Richardsonii *at different depths*

August 20, 1941 — Water temperature, 22° C.

Plant no.	Calibration run 2:19–2:49 P.M. Gain O_2, ml. per 100 ml. solution	Experimental run 2:55–3:25 P.M. Depth of tubes, meters	Experimental run Gain or loss O_2, ml. per 100 ml. solution	Relative light intensity. Air, 92	Expt. run as per cent of calib. run
1	0.393	0.05	0.317	81	81
2	0.367	2	0.233	36	64
3	0.428	4	0.138	10	32
4	0.346	6	0.077	2.5	22
5	0.361	8	0.068	0.95	19
6	0.368	10	0.040	0.41	11

TABLE IV. *Apparent photosynthesis in* Vallisneria americana *at different depths*

August 23, 1941 — Water temperature, 22.5° C.

Plant no.	Calibration run 2:11–2:41 P.M. Gain O_2, ml. per 100 ml. solution	Experimental run 2:46–3:24 P.M.		Relative light intensity. Air, 91	Expt. run as per cent of calib. run
		Depth of tubes, meters	Gain or loss, O_2, ml. per 100 ml. solution		
1	0.191	0.05	0.191	83	100
2	0.183	2	0.136	33	74
3	0.225	4	0.115	13	51
4	0.207	6	0.081	4.1	39
5	0.154	8	0.048	1.4	31
6	0.186	10	0.047	0.54	25

able with those prevailing during the experiment with *Anacharis canadensis.*

The relation between depth of immersion and rate of apparent photosynthesis was distinctly different in *Vallisneria americana* (table IV) than in the other species studied. Although there was a consistent decrease in rate of apparent photosynthesis with increase in depth of immersion a very appreciable rate (25 per cent of that at the surface) was maintained at a depth of 10 meters, although the prevailing light intensity was only of the order of 0.5 per cent of that at the surface on the clearest days.

Results of the experiments on *Heteranthera dubia* (table V) were also somewhat distinctive. The rate of apparent photosynthesis is the same at the 2-meter depth as at the surface, but there is an abrupt and marked diminution in rate between the 2 and 4 meter depths. Rates were essentially the same at the 4, 6, and 8 meter depths although this vertical range corresponds to a considerable range of light intensities. The compensation point was attained between the depths of 8 and 10 meters.

In all five of the species studied the rate of apparent photosynthesis decreases less rapidly with depth of immersion than does the light intensity. This is in accord with the principle, apparently valid for all species of plants, that maximum photosynthesis per unit of leaf area is attained at light intensities which are considerably less than that of full sunlight.

For all the species studied, except *Najas flexilis,* the compensation point is less than 2 per cent of full sunlight on clear August days. The compensation point for *Najas flexilis* apparently falls between 2 and 3 per cent of full sunlight. In an analogous investigation with *Ceratophyllum demersum,* in which similar experimental methods were used, it was found by Meyer and Heritage ('41) that in this species also there is a consistent decrease in the rate of apparent photosynthesis with increase in depth, and that the compensation point had a value of less than 2 per cent of full sunlight intensity in August. The compensation points found for these aquatic species are considerably lower than the values which have been recorded for most species of terrestrial plants with the exception of a few pronounced "shade" species.

The depth of penetration of sunlight into the water during the period of this investigation approached closely to the maximum values which have been recorded for Lake Erie water in the Bass Island region (Chandler, '42). Hence some approximate predictions can be made regarding the depth to which the several species investigated might be expected to survive. No species will survive at a light intensity corresponding to the compensation point, because under such conditions sufficient photosynthesis occurs to compensate for respiration only during the period of illumination. Bare survival should be possible, however, at

TABLE V. *Apparent photosynthesis in* Heteranthera dubia *at different depths*

August 7, 1941 — Water temperature, 24° C.

Plant no.	Calibration run 9:13–9:53 A.M. Gain O_2, ml. per 100 ml. solution	Experimental run 9:57–10:37 A.M. Depth of tubes, meters	Experimental run 9:57–10:37 A.M. Gain or loss O_2, ml. per 100 ml. solution	Relative light intensity. Air, 100	Expt. run as per cent of calib. run
1	0.238	0.05	0.240	93	101
2	0.268	2	0.279	51	104
3	0.252	4	0.038	18	15
4	0.273	6	0.034	5.7	12
5	0.244	8	0.035	1.8	14
6	0.307	10	−0.030	0.68	−10

light intensities not greatly exceeding the compensation point, although still greater intensities would be required if the plant is to thrive and grow. Examination of the data in tables I–V suggests that all the species except possibly *Najas flexilis* could survive, although not necessarily grow, at depths down to about 8 meters, under conditions permitting approximately maximum penetration of light into the waters of western Lake Erie. It also seems probable, judging from the results with this species, that *Vallisneria americana* could survive at somewhat greater depths than the other four species investigated. The results suggest that this species falls into a somewhat different category ecologically than the other four.

Because of season to season and often day to day variations in turbidity, light penetration into Lake Erie water is often quantitatively much less than during the period of this investigation. Actually, therefore, the limiting effect of such periods of lower light intensity would make survival of these species unachievable at as great a depth as might be possible were light penetration to be maintained consistently at the values which prevailed during this investigation.

SUMMARY

A study has been made of the relative rates of apparent photosynthesis in *Potamogeton Richardsonii, Najas flexilis, Anacharis canadensis, Vallisneria americana,* and *Heteranthera dubia* when immersed at a series of depths ranging to 10 meters in Lake Erie. In all five species the rate of apparent photosynthesis decreases less rapidly with depth of immersion than does the light intensity. In all of these species except *Najas flexilis,* for which the value is slightly higher, the compensation point is less than 2 per cent of the sunlight intensity on clear summer days. The results indicate that *Vallisneria americana* can survive at lower light intensities than any of the other four species.

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