

PRIMARY PRODUCTIVITY, STANDING CROP AND SEASONAL
DYNAMICS OF EPIPHYTIC ALGAE IN A SOUTHERN
MANITOBA MARSH POND

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by
Nina Michelle Hooper-Reid
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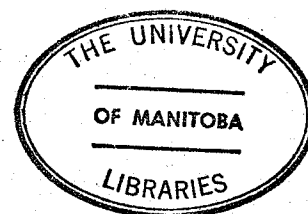
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We shall not cease from exploration
And the end of all our exploring
Will be to arrive where we started
And know the place for the first time.

T.S. Eliot
from Little Gidding

ABSTRACT

The productivity and standing crop of epiphytic algae in a marsh pond and some of the factors controlling the seasonal algal growth were investigated. The use of artificial substrates for the estimation of epiphytic algal production was evaluated. Cellulose-acetate was found to provide a convenient, reliable substrate for epiphytic algal attachment which allowed simple routine application of the C^{14} technique for productivity estimation.

The annual overall primary productivity of epiphytic algae in the marsh pond (Crescent Pond, Delta Marsh, Manitoba) was $1881 \text{ kg C yr}^{-1}$ or 26.8 g C m^{-2} pond surface area. Productivity per unit colonizable surface area was greatest on *Scirpus acutus* Muhl. ($32.3 \text{ g C m}^{-2} \text{ yr}^{-1}$) while *Potamogeton pectinatus* L. was the most significant substrate in overall pond productivity ($1700 \text{ kg C yr}^{-1}$).

Analysis of photosynthetic C uptake revealed that the photosynthesis to *in situ* light intensity relationship of the epiphytic algae was relatively constant throughout the day. A net loss during the night of 30% of C^{14} assimilated in the previous light period was detected. Apparent uptake of C^{14} by the epiphytic community was cumulative in the light for periods up to 24 hr.

Seasonal growth at two sites in the marsh pond (*Scirpus acutus* and *Potamogeton pectinatus*) was examined in detail. Productivity and standing crop of epiphytic algae were quantified in terms of C^{14} -photosynthetic uptake, cell volume, cell surface area, dry weight and chlorophyll a, protein, carbohydrate and lipid content. Standing crop and productivity increased at both sites in September and October after generally low

summer growth, with the exception of the occurrence of heterocystous blue-green algae at the *Potamogeton* site in July. Factor analysis of interrelationships among the previously mentioned parameters suggested that cell surface area was more directly related to productivity and various standing crop parameters than was cell volume.

The seasonal growth at the two sites was related to nutrient levels (N, P and Si) and to various physiological indicators of nutrient availability, including chlorophyll content, protein to carbohydrate and lipid ratio, Si debt, storage phosphate levels, alkaline phosphatase activity and nitrogenase activity. Low standing crops in June and early July coincided with indications of deficiency in terms of chlorophyll a content and protein to carbohydrate and lipid ratios at both the *Scirpus* and *Potamogeton* sites. Growth of heterocystous, N₂-fixing blue-green algae and high alkaline phosphatase activity occurred in July at the *Potamogeton* site. Increased standing crop of epiphytic algae in September and October at the *Scirpus* site coincided with higher nutrient levels and absence of deficiency symptoms. A delay in the standing crop increase at the *Potamogeton* site correlated with low nutrient levels and various physiological deficiency symptoms.

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INTRODUCTION

The necessity of a better understanding of the role of epiphytic algae in the littoral zone of freshwater lakes and ponds has become apparent with the increased recognition of the importance of this zone in overall lake productivity and cycling of organic and inorganic compounds. Wetzel (1975), in a discussion of the algae of the littoral zone states "Our lack of knowledge of the complex interactions between the sessile flora and their substrata, and their contributions to the total system productivity represents a major void in contemporary limnology that warrants intensified study."

While the significant contribution to total annual lake production that epiphytic algae may make has been documented in several studies (Allen 1971, Hickman 1971, Kowalczewski 1975), production estimates are scarce. This scarcity may reflect methodological difficulties. Furthermore, little is known about factors controlling epiphytic algal growth. The heterogenous nature of the epiphytic community, with bacterial, fungal, algal and faunal components in close proximity, and the various interactions between this community and its macrophyte substrate and aquatic medium create a complexity of factors which may influence the epiphytic algae in a multitude of ways.

The present study was initiated to quantify epiphytic algal growth in a marsh pond and to examine some factors which may influence seasonal growth. Four areas of investigation can be identified. Initial investigation involved the estimation of primary productivity of epiphytic algae, with necessary evaluation of methodology. In the second area of

investigation, the diurnal pattern of carbon fixation and loss by the epiphytic community was examined. The third area was concerned with the seasonal measurement of various standing crop and productivity parameters and their inter-relationships. The final area of investigation focused on the role of certain nutrients in seasonal growth and community composition of epiphytic algae at two macrophyte sites in the marsh pond. Various physiological indicators of nutrient deficiency were incorporated into the investigation.

CHAPTER 1

LITERATURE REVIEW

LITERATURE REVIEW

Terminology

Terminology pertaining to attached algae is complex and confusing, with numerous synonymous and redefined terms. Since the history of the various terms has been well reviewed (Young 1945; Cooke 1956; Sladeckova 1962; Round 1964; Wetzel 1964; Hutchinson 1967) current terminology will be emphasized in this review.

The term "periphyton" is a collective term commonly used in reference to microfloral growth upon various submerged substrates, especially in studies of algal substrates in lotic environments (e.g. Hansmann and Phinney 1973; Brettum 1974; Dickman 1974). "Aufwuchs" is generally considered to be synonymous with "periphyton" although the term is now used infrequently. However, Woelkerling (1976) followed the classification scheme of Krieger (1933) for desmid populations and restricted the use of "Aufwuchs" to algae associated with a "biological" substrate only.

Moss (1968) and Moore (1974) considered "benthic algae" to be algae associated with interfaces of either sediment and water or attachment surfaces and water, in accord with terminology proposed by Round (1964). Round subdivided the benthic community into "epipellic" (associated with sediments), "epilithic" (with rocks and stones) and "epiphytic" (with macrophytic plants). Moss (1968) recognized three groups within the benthic algae; "epipellic", "attached" (composed of epilithic, episammic and epiphytic) and "mat-forming". Hutchinson (1975) recognized "algal haptobenthos", growing on solid substratum and "algal herpobenthos", growing on or in mud. "Algal herpobenthos" is synonymous with Moss's "epipellic benthic algae", while "algal haptobenthos" corresponds to the "attached benthic algae".

Most recent papers refer to attached algae in terms of the attachment substrata (e.g. epiphytic or epilithic algae). These terms have been used for algae colonizing artificial substrates considered representative of the natural substrate as well as for algae colonizing the actual natural substrate (e.g. Allen 1971). Foerster and Schlichting (1965) used the term "phyco-periphyton" in a sense synonymous with "epiphytic algae".

"Periphyton" or "periphytic algae" seems to be the least confusing collective term for attached and for the most part submerged algae. Specific algal-attachment substrate relationships of periphyton can then be recognized: epiphytic, epilithic, episammic and epipellic. Use of the term "benthic" implies an association with the bottom substrate, which does not occur in the case of epiphytic algae.

Methodology

In the examination of epiphytic algae on natural substrates it has generally been necessary to first remove the algae from the macrophyte surface, although in some cases where leaves were thin and could be cleared by chlorophyll extraction, the epiphytic algae on the leaf surface have been examined directly (Rehbronn 1937) in Sladeckova (1962). Various techniques used for the removal of epiphytic algae from natural substrates have included scraping (Godward 1937; Young 1945; Tai and Hogdkiss 1975), washing with water jets followed by agitation (Hickman 1971), grinding (Douglas 1958) and agitation (Knudson 1957; Foerster and Schlichting 1965; Gough and Woelkerling 1976). Foerster and Schlichting (1965) estimated up to 30% of algal cells were retained on *Myriophyllum* after their agitation procedure, while Gough and Woelkerling (1976) achieved a removal efficiency of 98% from five hosts of widely differing morphology using a method involving agitation and acid hydrolysis.

Once removed from the macrophyte surface and suspended in water, the epiphytic algae have been examined qualitatively and quantitatively by a number of techniques commonly employed for phytoplankton analysis. These have included cell counts, cell volume estimation, dry weight and chlorophyll determinations. Results have generally been expressed in terms of unit area plant surface or total plant surface per unit area of littoral zone, although Gough and Woelkerling (1976) expressed results in terms of cells per unit macrophyte dry weight. The authors stated that results expressed in these terms were of limited value since macrophyte dry weight to surface area ratios were highly variable. Macrophyte surface area has been estimated by mathematical approximation and, in the case of macrophytes with finely dissected leaves, by the use of a surfactant (Harrod and Hall 1962).

Estimation of primary productivity of epiphytic algae attached to natural macrophyte substrates is complicated by interference from the photosynthetic activity of the macrophytes. Assman (1951,1953) in Wetzel (1975), estimated the productivity of *Equisetum* and its associated epiphytic algae by enclosing both in casings and following changes in oxygen concentration. Hickman (1971) and Hickman and Klarer (1973) measured the primary productivity of epiphytic algae from stems of *Equisetum* and *Scirpus* respectively using $C^{14}O_2$ uptake. Prior to incubation, epiphytic algae were scraped from the stem surface and suspended in filtered pond water. Sheldon and Boylen (1975) determined the productivity, on the basis of $C^{14}O_2$ uptake, of *Potamogeton* leaves washed free of epiphytes, the epiphytes alone and the intact macrophyte-epiphyte system.

Many studies of periphytic algae have employed artificial substrates for algal colonization. The artificial substrates provide a uniform attachment substrate which has been submerged for a specific time interval and is readily removable. The historical development of techniques employed for examining periphytic algal growth on artificial substrates has been well reviewed (Cooke 1956; Castenholz 1960; Sladeckova 1962; Wetzel 1964; Hutchinson 1975). While a wide range of substrates have been proposed, glass slides have been used most frequently. Numerous comparisons of periphytic algal growth on natural and artificial substrates have been carried out. Results, especially with regards to epiphytic algae, have been confusing.

Castenholz (1960) used glass plates placed in close proximity to natural rock substrates to study changes in attached algae in a number of freshwater and saline lakes. He concluded that the glass plates were not unduly selective. All periphytic algal species found on natural substrates

were observed on artificial substrates, although some blue-green algae such as *Calothrix* did not occur commonly on the glass slides until 6 weeks of exposure. Peters, Ball and Kevern (1968), using Plexiglas plates, found the same dominant algae occurred on both the natural and artificial substrates. Evans and Stockner (1972) observed that the composition of attached algae on reefs and rock outcrops was similar to that encountered on navigational buoys exposed for 145 days in Lake Winnipeg. These three studies indicate little discrepancy between algal growth on natural inert substrates and artificial substrates. However, studies comparing algae on natural macrophyte and artificial substrates have shown no such agreement in results.

Godward (1937) compared periphytic algal species on stones, macrophytes, mud and horizontally suspended glass slides in Lake Windermere. She concluded that the glass slides were colonized only by algae associated with macrophyte substrates. Certain blue-greens, found only on stones, did not occur on the glass slides.

Foerster and Schlichting (1965) compared algae colonizing glass lantern slides with colonization on *Vallisneria*, *Myriophyllum* and *Sagittaria* as well as on screened *Vallisneria*. Little information was given as to the exposure period or to the placement method for the glass slides within the aquatic vegetation. The authors, in comparing growth on artificial and natural substrates state, "the artificial barren surface gave a false indication of the true productivity trends and indicated only some of the significant genera in the ecosystem". In later discussion, they suggest that the glass slides showed colonization of a barren substrate, comparable to colonization occurring when the wire screen was removed from around the *Vallisneria*. This study has been cited (e.g. Hickman and Klarer

1973) as evidence of discrepancies between natural and artificial substrate algal populations. On the basis of insufficient information on substrate exposure, such interpretation appears unfounded. Rather, results suggest that similar standing crops occurred on recently exposed natural and artificial substrates.

Another frequently cited study of Tippet (1970) supposedly "shows differences between natural epiphytic diatom populations and those found on glass slides" (Hickman and Klarer 1973). Yet, the study involved comparison of glass slides exposed from 2 to 4 weeks with macrophytes exposed for undefined time periods. Part of the apparent discrepancy may have been related to differences in colonization times of the substrates.

Allen (1971) compared productivity of epiphytic algae on artificial and natural macrophyte substrates with similar exposure times using the $C^{14}O_2$ uptake technique. He found similar photosynthetic rates on both substrates.

Mason and Bryant (1975) compared algae on glass rods, exposed in February, with algae on *Typha* stems from the previous year's growth. In the April to December study period, they reported that species of algae on the glass rods were similar to those on stems. The times of peak standing crop coincided for the two substrates, although subsequent changes in standing crop differed. The authors suggested that a better comparison with the glass rods might have been made with *Typha* stems emerging in the spring. Both substrates would then have had equal exposure periods.

Brown (1976) compared colonization of recently submerged *Eleocharis* and glass slides suspended within a bottomless wooden box in the limnetic and littoral zone of a lake. In the limnetic area, the majority of species were chlorophytes with many of the same species appearing on both the slides

and plants. Desmids, filamentous chlorophytes, and cyanophytes formed a larger proportion of the total periphyton on the macrophyte than on the glass slide. In the littoral zone, similar species occurred on both substrates but in different proportions. Genera such as *Coleochaete* and *Protoderma* were more common on artificial than on natural substrates.

These preceding studies illustrate the confusion regarding the reliability of artificial substrates and some of the causes of this confusion. Insufficient attention has been paid to equating exposure periods of substrates and to locating artificial substrates in close proximity to natural substrates. Most studies showing discrepancies between algae on macrophyte and artificial substrates can be criticized for improper artificial substrate exposure. However, it should be recognized that part of the above confusion may be related to real differences in macrophytes and localities.

Algae have generally been scraped from the artificial substrates and methods of quantitative and qualitative analysis similar to those used for algae from natural substrates have generally been employed. Few studies of primary productivity have been carried out. Allen (1971), using $C^{14}O_2$ uptake, incubated Plexiglas slides colonized with epiphytic algae. After incubation, algae were removed by gentle rubbing, redistributed in filtered water and filtered through membrane filters. The filters were dried and radioactivity was determined with a gas-flow Geiger-Mueller counter. Rosemarin (1975), in an examination of periphyton in the Ottawa River, modified this method by placing small pieces of colonized Plexiglas directly into scintillation fluor after incubation with C^{14} and subsequent gentle rinsing.

Standing Crop and Productivity

In any comparison of epiphytic algal standing crop and productivity, the units of expression must be carefully considered. Results may be expressed on the basis of unit area of (1) macrophyte surface, (2) artificial substrate surface, (3) littoral zone colonized by a particular macrophyte, (4) total littoral zone, or (5) total pond or lake area. Total production of epiphytic algae may largely be limited by available colonizable substrate. Results expressed on the basis of either macrophyte surface area or artificial substrate surface area give the best indication of relative standing crop and productivity of the epiphytic algae independent of macrophyte growth.

Studies of seasonal standing crop and productivity of epiphytic algae, summarized in Table 1-1, are reviewed below.

Allen (1971) measured primary productivity and chlorophyll content of epiphytic algae colonizing Plexiglas slides at *Scirpus* and *Najas-Chara* sites in Lawrence Lake, Michigan. Productivity at the *Scirpus* site reached an initial peak in June, decreased in late June, reached maximum levels in July and August, then decreased to winter levels by November. A similar trend was noted at the *Najas-Chara* site, with a third, low peak in productivity in November. Between April and November chlorophyll a levels generally correlated with primary productivity. However, the highest observed level of chlorophyll a, at the *Najas-Chara* site in January, coincided with the lowest observed rate of photosynthesis. According to Allen, the epiphytic algae were responsible for 31.3% of the total annual littoral production, including macrophytes, and 21.4% of the total annual lake production.

Hickman (1971) measured standing crop and primary productivity of

Table 1-1. Standing crop and primary productivity of epiphytic algae on various substrates from several sites.

Lake	Substrate	m ⁻² coloni- zed area	m ⁻² littor- al zone
Lawrence L., Michigan (Allen, 1971)	Plexiglas at <i>Scirpus</i> site		
	Chlorophyll <u>a</u> maximum	650 mg	383 mg
	Productivity (day ⁻¹)		
	maximum	2,000 mg C	1,400 mg C
	average	336 mg C	145 mg C
	Plexiglas at <i>Najas-Chara</i> site		
Priddy Pool, England (Hickman, 1971)	Chlorophyll <u>a</u> maximum	850 mg	7,300 mg
	Productivity (day ⁻¹)		
	maximum	1,600 mg C	14,000 mg C
	average	258 mg C	1,807 mg C
Langford Spring, England (Hickman, 1974)	<i>Equisetum</i> Chlorophyll <u>a</u> maximum	250 mg	85 mg
	median range	50-100 mg	20-40 mg
	Cell number		
	maximum	48 x 10 ⁹	12 x 10 ⁹
	median range	10-20 x 10 ⁹	4-8 x 10 ⁹
	Productivity (h ⁻¹)		
Langford Spring, England (Hickman, 1974)	maximum	200 mg C	140 mg C
	median range	40-80 mg C	30-50 mg C
	<i>Chiloscyphus</i> Cell number		
maximum		20 x 10 ⁷	
median range		3-7 x 10 ⁷	
Langford Spring, England (Hickman, 1974)	Productivity (h ⁻¹)		
	maximum		16.3 mg C
	median range		3-7 mg C

Table 1-1. continued

Mikolajskie L., Poland (Kowalewski, 1975)	<i>Elodea, Myriophyllum,</i> <i>Potamogeton</i>	Chlorophyll <u>a</u>			
		maximum	33.4 mg		
		average	8 mg	51 mg	
		Dry weight			
		average	37 g		
Alderfen Broad, England (Mason and Bryant, 1975)	Glass rods in <i>Typha</i> stand	Dry weight			
		maximum	19.3 g		
	Dead <i>Typha</i> stems	Dry weight			
		maximum	18.0 g		
Lake George, New York (Sheldon and Boylan, 1975)	<i>Potamogeton</i>	Productivity (h^{-1})			
		maximum	.63 mg C		
		median range	0.2-.3 mg C		
	Dry weight	maximum	2.2 g		
		median range	0.5-1.5 g		
	Diatom cell number	range	$3 \times 10^6 -$ 1.4×10^8		
Plover Cove Reservoir, Hong Kong (Tai and Hodgkiss, 1975)	Wood	Chlorophyll <u>a</u>			
		maximum	1,870 mg		
		median range	700-900 mg		
	Diatom cell number	maximum	18.6×10^7		
		median range	$4-6 \times 10^7$		

epiphytic algae attached to *Equisetum* over a two-year period in Priddy Pond, North Somerset. Seasonal productivity rates and standing crop levels, expressed on a macrophyte surface area basis, fluctuated considerably over the two-year period with no consistent seasonal trends, with the exception of highest chlorophyll a levels generally occurring in January and February. Maximum values of chlorophyll a (Table 1-1) were considerably lower than those determined by Allen (1971). Hickman estimated that the yearly standing crop of epiphyton was approximately 27 times that of either phytoplankton or epipelon in Priddy Pond, while primary productivity was approximately 40 times that of the other algal components.

The epiphytic algae attached to *Chiloscyphus*, a liverwort, were examined by Hickman (1973). Productivity and standing crop were closely related, with maxima in both occurring in late April, mid-July and mid-August. A fourth peak occurred in primary productivity in early December and in standing crop in January.

Epiphytic algae on submerged macrophytes were investigated by Kowalczewski (1975). Photosynthetic activity per unit chlorophyll was 5 times higher for phytoplankton than for periphyton. At various sites, the epiphytic algal gross production ranged from 0 - 100% of the total epiphytic and planktonic algal production.

Mason and Bryant (1975) estimated standing crop on the previous year's stems of *Typha*. Standing crop fell from a maximum in April to almost zero by November. Epiphytic algae on glass rods, exposed in spring, reached maximum values in May and declined slightly to a stable level which lasted until the end of the study in December.

Epiphytic algae on *Potamogeton* in an oligotrophic lake were examined

from May to October (Sheldon and Boylen 1975). Maximum photosynthesis and standing crop occurred in July and August. Productivity of epiphytes from lower leaves was ten-fold greater than that from upper leaves. The epiphytic algae assimilated approximately 5% (0.07 - 10.84%) as much inorganic C as the leaves of *Potamogeton amplifolius* from which they were taken.

Tai and Hodgkiss (1975) followed seasonal changes in attached algae on wood in Plover Cove Reservoir, Hong Kong. Chlorophyll a and cell counts followed similar seasonal trends, with maximum growth in winter, moderate spring and autumn growth and low summer growth.

Community Composition

Numerous lists indicating the wide range of algal species which occur in the epiphytic habitat have been published. Among the most comprehensive lists are those of Godward (1937) and Young (1945). Godward recorded a large number of green, blue-green and especially diatom species growing on plants in Lake Windermere. Young (1945) compiled an extensive list of epiphytic species on *Scirpus* culms. As well as the dominant pennate diatoms, members of the Tetrasporales, Ulotrichales, Oedogoniales, Zygnemetales, Chlorococcales, Hormogoniales, Chroococcales and Centrales were reported. Other organisms present on the culms included invertebrate species, bacteria and fungi.

Hodgkiss and Tai (1976) presented additional evidence to support the generalization of Round (1964) that the epilithic and epiphytic communities are similar in species composition. Hodgkiss and Tai (1976) compared four periphytic communities in Plover Cove Reservoir, Hong Kong. Of a total of 61 species, 54 occurred in the epiphytic community, 46 in the epilithic,