PRIMARY PRODUCTION AND ECOSYSTEM METABOLISM IN A LAKE MICHIGAN DUNE POND

By

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ABSTRACT

PRIMARY PRODUCTION AND ECOSYSTEM METABOLISM

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Estimates of the net primary productivity of phytoplankton, epipelic periphyton, and macrophytes of a small (0.25 ha.) shallow (mean depth = 41 cm.) soft water (mean alkalinity = 1.24 meq/l) pond located in the sand dunes of Lake Michigan, were independently made using *in situ* ^{14}C methods for algae and harvest techniques for macrophytes. Estimates of gross assimilation and ecosystem respiration were made within light and dark metabolic chambers (250 l. capacity) in which the CO_2 flux was measured with an infra-red gas analysis system. Laboratory measurements of photosynthesis in *Juncus balticus*, the dominant macrophyte, were used in the interpretation of diurnal and annual variations in photosynthesis observed under natural conditions.

Epipelic and planktonic algal components of the autotrophic community were qualitatively similar. Both components were dominated by the desmid, *Cosmarium* sp., mucilage secretions of which were important in maintaining a heavy algal-bacterial epipelic mat that persisted throughout the year. The macrophyte component was strongly emergent, submersed macrophytes contributing less than 0.5%

to the biomass. Floating and floating leaved macrophytes were entirely absent. Faunistically, the pond was represented by a variety of invertebrate organisms which were most abundant in the flocculent sediments.

Macrophyte production was calculated on the basis of annual changes in below ground biomass, which represented greater than 90% of total macrophyte biomass on a dry weight basis. Algal production was calculated by integrating the area under annual productivity curves with respect to time. Whereas production of phytoplankton and epipelic periphyton occurred throughout the year, production of macrophytes was limited to the growing season.

Peak net production of the phytoplankton temporally overlapped peak net production of the macrophytes, both occurring during the early summer. Net production of the periphyton increased rapidly during midsummer and was maintained at a relatively high rate through early autumn.

Total net primary productivity of the pond was 348 mg $C/m^2/day$, expressed as an annual mean daily rate. Productivity of the macrophytes (61% of total) was greater than that of the periphyton (26% of total) and that of the phytoplankton (13% of total).

During the study, the pond underwent seasonal transformations between autotrophic ($P/R > 1.0$) and heterotrophic ($P/R < 1.0$) metabolic modes. Gross photosynthesis exceeded respiration during the growing season; the reverse situation occurred during the dormant season. Annual mean daily gross productivity (547 mg $C/m^2/day$) exceeded the annual mean daily rate of ecosystem respiration

(377 mg C/m^2/day). The P/R ratio was estimated at 1.45, indicative of net accrual at the rate of 169 mg C/m^2/day, the annual mean daily rate of net ecosystem production.

Gross photosynthesis was weakly correlated with day length, efficiency, and solar energy, each treated independently. Annual efficiencies of assimilation (gross assimilation/useable solar energy) and growth (net production/gross assimilation were estimated at 0.42% and 64% respectively.

Annually, heterotrophic and autotrophic components of ecosystem respiration were comparable, each accounting for approximately half of the total respiratory activity. During the growing season, autotrophic respiration (largely attributable to macrophyte activity) represented 62% of total respiration, whereas during the dormant season, only 28% of ecosystem respiration was of an autotrophic origin.

Potential sources of inaccuracy involving methods used in this study were discussed in a general context, and more specifically within the context of this investigation. The importance of dissolved organic matter in aquatic systems was emphasized in regard to both macrophyte productivity estimates based on harvest techniques, and the interpretation of P/R ratios.

In conclusion, the dune pond is a relatively unproductive ecosystem, the net primary productivity of which falls within ranges of values cited for some of the less productive ecosystems of the world.

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INTRODUCTION

In "The Lake as a Microcosm," Forbes (1887) discussed the interdependence of plants and animals, and in so doing, conceptually described an aquatic ecosystem. Subsequently, Lindeman (1942) elucidated the functual nature of this interdependence, and Odum (1962, 1963) modified the concept, more clearly specifying the role of detritus.

Concomitant with the development of the ecosystem concept, has been an increasing interest in the process of primary productivity. To date, most estimates of aquatic primary productivity have been based on phytoplankton studies, reflecting the high degree of methodological refinement in this area. While approximating total net primary productivity of deep lakes, productivity estimates based solely on phytoplankton, underestimate total productivity of lakes with a large ratio of colonizable littoral zone to pelagic zone. Due largely to methodological constraints, in situ productivity estimates of attached algae and macrophytes have been meager. The significance of littoral producers has been demonstrated in a shallow basin (Borax Lake, Wetzel, 1964) and in a relatively deeper lake with a moderate littoral zone (Lawrence Lake, Wetzel et al., 1972). In the comprehensive Lawrence Lake study, incorporating the results of several doctoral dissertations, net primary production of the

macrophytes, periphyton, and phytoplankton respectively, accounted for 51.3%, 23.3%, and 25.4% of the total net primary production of the lake.

Community metabolism, including heterotrophic and autotrophic processes, has been studied as an extension of primary productivity investigations. Although limnologists had been measuring planktonic metabolism for years using the light-dark bottle oxygen technique (Gaarder and Gran, 1927), the notion and theoretical ramifications thereof originally arose from the energy flow diagrams and descriptive conceptualization of Odum (1956 and 1957), and have since been subsequently expanded upon by Margalef (1968).

An extension of the community metabolism concept is that of ecosystem metabolism which encompasses the integrated activity of individual communities within an ecosystem. Ecosystem metabolism studies have been implemented in terrestrial systems using CO_2 flux models (see for example, Woodwell and Whittaker, 1968; Lemon et al., 1970). Metabolic studies in lotic aquatic systems, using diurnal oxygen techniques (Odum, 1965, McDiffett et al., 1972, and others) and in lentic systems using diurnal pH models (Verduin, 1952, 1956, and others), have measured community metabolism but not the metabolism of the entire ecosystem. Cummins (1974) emphasized the heterotrophic nature of streams as processors of allochthonous organic inputs from the terrestrial watershed. As such, a stream in itself cannot be thought of as an ecosystem, and metabolic measurements within a stream are, for the most part, indicative of the metabolism of component heterotrophic communities. Similarly, studies of lentic

metabolism have generally been concerned with the activity of specific component communities, usually planktonic, and the results of these certainly cannot be extrapolated to the entire ecosystem.

Owing to conceptual and methodological advances in the areas of primary productivity and ecosystem metabolism, I have attempted to investigate the total productivity and metabolism of an entire ecosystem (a dune pond). Specifically my objectives in this study were the following:

1. The description of the dune pond ecosystem with regard to physical, chemical, and biological characteristics relevant to other aspects of the study.
2. The estimation of total net primary productivity.
3. An evaluation of the importance of the individual autotrophic components with regard to their contributions to total net primary productivity.
4. The estimation of gross primary productivity.
5. The estimation of ecosystem respiration.
6. An evaluation of the relative magnitudes of autotrophic and heterotrophic components of ecosystem respiration.
7. The estimation of net ecosystem productivity.
8. The estimation of gross photosynthetic and net photosynthetic efficiency with respect to solar energy and gross assimilation, respectively.

GENERAL DESCRIPTION OF THE STUDY AREA

The study site was a small (0.25 ha.) pond, located within the sand dunes of Lake Michigan, near the Kalamazoo River delta, Saugatuck, Allegan County, Michigan. In view of methodological considerations, this pond was selected for study over other similar ponds in this area. Detailed descriptive information on the study pond, based on 18 months of observation, is given in the results section of this text.

The existence of dune ponds, which are ubiquitous throughout the Lake Michigan sand dunes, was first cited by Cowles (1899) who conducted a descriptive survey on the vegetation and geology of the Lake Michigan sand dunes. Cowles referred to them as "ill drained inland sloughs between ridges." Shelford (1911) discussed successional aspects of animal communities and briefly described some of the floral associations within a variety of dune ponds located in the Chicago area. To my knowledge, there has been so subsequent study of the Lake Michigan dune ponds.

In the Saugatuck area, the ponds are principally located in the mid dune region, existing approximately 150 meters inland from the Lake Michigan shore line. These ponds have developed in depressions, formed by the scouring action of the wind, and they persist as aquatic habitats, dependent upon the Lake Michigan water level. Considering the reduced level of the lake at the turn of the century

(Shelford, 1911), it is unlikely that these depressions were filled at that time. However, their continual presence since the 1930's is apparent in areal photographs taken during U.S. geological surveys of the area. Dependent upon rainfall and water table fluctuations, the mean depth of the ponds is always less than 1 meter and usually less than 50 cm. Although the ponds are by no means ephemeral, the presence of remnants of fully terrestrial vegetation in shallower areas, suggests the occurrence of occasional drought periods.

In contrast to the hard water of Lake Michigan, the water of these ponds is relatively soft, suggesting a mixture of rain water and ground water. Containing high concentrations of particulate detrital material, the heavily strained water overlays a flocculent organically rich benthic substrate.

The macrophyte flora is strongly emergent and submerged life forms occur sparsely and sporadically only in locally confined deeper areas. The total absence of floating and floating-leaved macrophytes is notable. In general, the plankton is sparse and not diverse. Floristically, the plankton is strongly dominated by desmids, and faunistically, rotifers dominate. In contrast to the pelagic zone of these ponds, the benthos is well represented by various invertebrate groups, aquatic and semiaquatic insects being the most abundant metazoans. Throughout most of the year, the pond bottoms are covered by a thick mat of periphyton, consisting of a muco-bacterio-algal association. Prevailing winds seem to be quite effective in preventing the establishment of algal associations

within the emergent flora, although epiphytic associations do occur in protected areas of some of the ponds.

The presence of vertebrate macrofauna in the ponds is quite variable. Other than the potential for nutrient enrichment by migrating waterfowl, I suspect that vertebrates have very little influence on the ecology of these areas. The ponds appear to be used by the nearby Kalamazoo River marsh fauna to absorb population pressures and in turn, the relatively stable marsh area likely affords refuge when drought periods threaten the existence of the ponds. The total absence of fish is probably attributable to anoxic conditions incurred beneath the ice during severe winters.

The terrestrial environment within the Lake Michigan dune region has been the object of considerable investigation within the past century. Much of the literature in this regard has been reviewed by Mcleod, 1974, who conducted an autecological study of the establishment of the shrub, Ptelia trifoliata.

METHODS AND MATERIALS

Methods used in this study, in most cases, were selected and modified in accordance with pilot investigations. In all facets of the field studies, data were collected at least throughout an annual cycle. All portions of the pond were included in the sampling design with the exception of the water-land interface and a few hummock areas.

Net Primary Productivity of Phytoplankton

Phytoplankton productivity was estimated using the ^{14}C technique, slightly modified from that originally introduced by Steemann Nielsen (1951, 1952). Details of the modified technique have been described elsewhere (Doty and Oguri, 1959; Strickland, 1960; Wetzel, 1966; among others). In situ productivity measurements were made at two to three week intervals from the 22 March 1973 through 11 May 1974. A preliminary investigation indicated that photosynthesis varied with depth, being greater near the substrate than at the surface during the early spring, but variation was statistically insignificant between 4 bottles incubated at the same depth at different locations within the pond. Therefore a single sampling station was used during the study and photosynthesis measurements were made at two depths.

Water samples collected at approximately 10 cm. below the water surface and at approximately 10 cm. above the pond bottom were placed into ground glass stoppered light and dark Pyrex bottles (125 ml.). A 1.0 ml. solution of Na_2HCO_3 containing ^{14}C tracer of known radioassay, 3.5 to 4.5 microcuries/ml. (combustion and assay in gas phase, Goldman, 1968) was injected into each bottle which was then sealed. Three bottles, two clear and one dark, were prepared and suspended at each of the two sampling depths. After a single midday 4 hr. incubation, the bottles were removed, placed in a light-free box and transported to the laboratory. The particulate content of the bottles was resuspended by gentle shaking, and 25 to 50 ml. aliquots were filtered onto membrane filters (HA Millipore Filter Corp., Bedford, Mass.) of a porosity of 0.45± .02 microns at vacuum pressures of 25-35 cm. Hg. The pore size of 0.45 microns effectively removes all of the phytoplankton (Lasker and Holmes, 1957) and furthermore molecular filters of comparable pore size have been routinely used in phytoplankton studies. The filtered phytoplankton was dried in a desiccator and radioassayed with a minimum of 2000 counts (occasionally 1000 counts for dark bottle activity during the winter) on a gasflow Geiger Muller counter (Nuclear Chicago, Model 6010, with micromil window). Prior to radioassay, all filters were decontaminated by exposure to fumes of HCl for 10 minutes (Wetzel, 1965a) although the necessity for this procedure is questionable in soft waters.

Carbon assimilation was calculated by multiplying the assayed amount of ^{14}C by the ratio between the total inorganic C of

the pond water and the total inorganic ^{14}C added to the sample bottles before incubation (see Vollenweider, 1969 for detailed outline of calculations and parameters used therein). All physical and chemical determinations, necessary for assimilation calculations and subsequently used for descriptive purposes, were made at pond side. The total inorganic C of the pond water in mg./l. was calculated from the sample temperature (YSI Telethermometer, Model 46-TUC), the total alkalinity (chemical titration, see American Public Health et al., 1971), the pH (electrometric determination, Beckman, Model G), and appropriate conversion factors (Saunders et al., 1962). An isotope descrimination factor of 6% was used in all calculations (Steemann Nielsen, 1955). Non photosynthetic carbon fixation (bacterial chemosynthesis and non bacterial heterotrophic carboxylation activity) was compensated for in all calculations of photosynthesis by subtracting the dark bottle values from those of the light. Photosynthetic assimilation was expanded from periods of incubation to entire sampling days using diurnal factors, calculated by planimetry of the solar energy curves (see Wetzel, 1964; Jassby and Goldman, 1974) from a recording Eppley pyreheliometer, operated at the Kellogg Biological Station, a distance of approximately 65 km. from the research site. Similarly, photosynthetic assimilation was estimated between sampling periods.

Data are expressed both on a volumetric (per m^3) and an areal (per m^2) basis. Data on a volumetric basis were converted to an areal basis, multiplying by the mean pond depth on respective sampling days. Annual net primary production was determined by

integrating the area under an annual productivity curve with respect to time.

Net Primary Productivity of Epipelic Periphyton

Periphyton productivity was estimated using the ^{14}C technique, slightly modified from that used in estimating phytoplankton productivity. In situ productivity measurements were made at two to three week intervals over the period from 14 April 1973 through 20 April 1974. Preliminary investigations indicated the unfeasibility of sampling from the flocculent natural benthic substrate and therefore artificial substrates were employed.

The suitability of artificial substrates for periphyton studies remains controversial. Efforts devoted to assessing qualitative and quantitative differences between artificial and natural substrates (Pieczynska and Spodniewska, 1963; Tippett, 1970) have given conflicting results. These studies dealt exclusively with epiphytic algal communities, and conclusions drawn from them are probably less applicable to benthic algae, which may colonize substrates somewhat fortuitously with a lesser regard for substrate type. Wetzel (1965b) reviewed various problems with the use of artificial substrates in productivity investigations and suggested the placement of a large number (enough for an annual study) of simulated substrates, allowing sufficient time for colonization before sampling.

Microscope slides, placed on the pond bottom in February of 1973, lacked the surface area necessary for buoyancy upon the

flocculent sediments, sank into the organic ooze and were abandoned. On 4 March 1973, 60 larger artificial substrates were positioned on the pond bottom at one meter intervals along two intersecting transects, each being 30 m. in length. These substrates worked exceptionally well, remaining flush with the natural sediments throughout the study. They were constructed of ceramic tile, 120 cm. in area, overlain with cork, and wrapped with black polyethylene film (Figure 1). The polyethylene film facilitated subsampling with a cork bore minimizing major disturbance to the rest of the tile community. Backhaus (1967) reported excellent replication of lotic epilithic periphyton on polyethylene film.

During each sampling period, four tiles were randomly selected from the transects for subsampling and then were quickly replaced on the pond bottom. Polyethylene disks, 1.5 cm. in diameter, were removed from the tiles and placed into light and dark ground glass stoppered wide mouth Pyrex bottles (125 ml.), previously filled with unfiltered and untreated pond water. A one ml. solution of Na_2HCO_3 containing the ^{14}C isotope, of identical radioassay (same lot) as that used in the phytoplankton studies, was injected into the bottles which were then sealed. Four light bottles and two dark bottles, thus prepared, were immediately positioned on the pond bottom, juxtaposed to those tiles from which their respective subsamples had been removed. In the laboratory the algal mass associated with the polyethylene disks was dislodged, the disks removed from the bottles, and any residual material wiped from the disks onto filters designated for periphyton filtration. The particulate content of

Figure 1. Artificial substrates used in periphyton study.

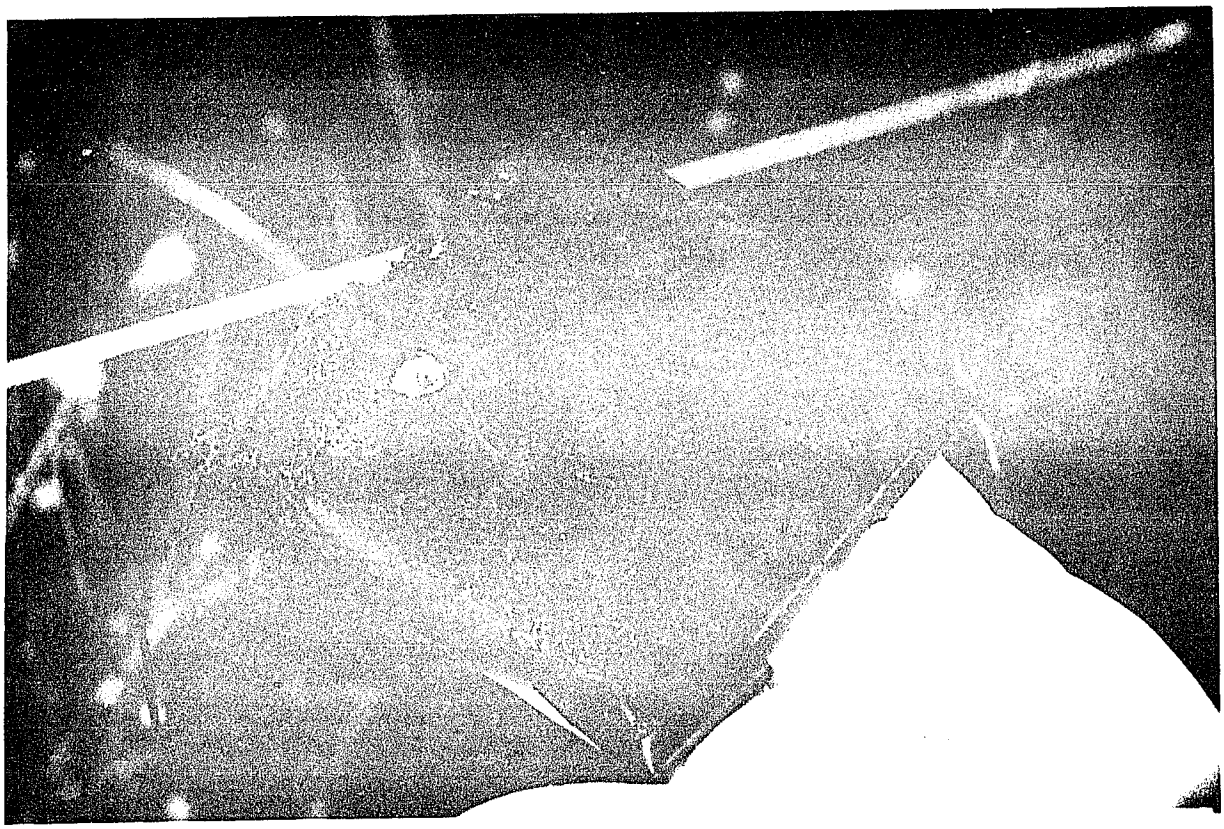

Figure 1.

the bottles was suspended by shaking and the entire contents of each passed as 25 ml. aliquots onto a series of five 0.45 micron Millipore filters. Vacuum pressures were maintained at 25-35 cm. Hg. Occasionally during the summer, it was necessary to mechanically disrupt the massive algal mat removed from the polyethylene disks in order to uniformly allocate the material, reducing self absorption difficulties. This was accomplished by pulling the mat through pipettes of decreasing volume until the algal material easily passed the 25 ml. pipette used for transfer onto the filters.

Post filtration laboratory treatment, radioassay procedures, and carbon assimilation calculations were similar to those described for the phytoplankton samples. The radioactivity exclusively associated with carbon assimilation by the periphyton was determined by subtracting the activity of the phytoplankton from the sum of the activities of the five filters used per sample. Volumes used for distribution and dilution of the algal cells were equated with the original surface area colonized and the data expressed on a per m^2 basis. Annual net primary production was determined by integrating the area under an annual productivity curve with respect to time.

Considering carbon assimilation by both the phytoplankton and the epipelic periphyton, I have assumed that the discrepancy between ^{14}C uptake rates and the true rates of algal net primary productivity are small as suggested by Ryther (1954), Antia et al. (1963), and McAllister et al. (1964). Due to the relative inaccessibility of the research site and the distance (approximately 60 km.) between it and the filtration site (Kellogg Biological Station),

unavoidable respiratory losses of labeled substrate occurred during transportation of the sample bottles in a light free box. Since the time elapsing between bottle retrieval and laboratory filtration approximated the incubation period (4 hrs.), I have chosen to treat respiratory losses during transport as a correction for night respiration (which was not measured in this study) in converting net productivity on a daylight hour basis to a daily (24 hr.) basis.

Macrophyte Biomass and Productivity

Seasonal changes in macrophyte biomass and productivity were estimated by harvesting. The harvest technique has been used extensively in aquatic systems to estimate standing crop (see review by Wetzel, 1964). Above ground productivity estimates have been previously made by expressing standing crop on a seasonal basis (Penfound, 1956; Forsberg, 1959; among others). Less frequently, due to the inherent difficulties of below ground biomass sampling (Westlake, 1968), total plant biomass estimates have been made. Productivity determinations based on total plant biomass, particularly in communities dominated by perennials with extensive rhizomal portions (eg. Westlake, 1966; Bernard, 1974), are considered the most meaningful.

Above ground biomass and litter were removed at two to three week intervals over the annual period of 14 April 1973 through 20 April 1974 with the exception of the winter months (November to February) and the 31 March 1974 sampling period during which the pond was largely ice covered. Below ground biomass was sampled at two to

three week intervals without exception over the 18 month period of 14 April 1973 through 10 October 1974. All sampling was done randomly from four transects, each being 30 m. in length, two of which ran in a north-south direction and two in an east-west direction.

Above ground living biomass and all litter was removed by clipping and raking from four 0.5 m^2 frames, one from each transect. Clipping was done as close to the substrate as possible thereby minimizing under estimates of contributions by the stubble. Immersed in a water filled basin, dead and living material was carefully cleaned and separated in the laboratory. No attempt was made to separate the plant material into taxonomic groups. Contribution to the above ground biomass by taxa other than the two dominants and with very few exceptions was minimal and usually zero (see dune pond description in results section).

Below ground biomass samples were obtained with a coring auger, having a cross sectional area of 50 $cm.^2$, and capable of removing a core, 21 cm. in length. Due to the nature of the pond bottom and the mode of growth of the rhizomal and rooted portions of the plants, this method was very effective. Below ground plant material grew laterally, rarely exceeding 15 cm. of depth in the tightly compacted sand soil. Cutting cleanly through the extensive rhizomal mat, the auger encountered the underlying compacted layer of sand which effectively sealed the plant sample within the auger, thereby preventing losses upon retrieval. Eight 100 $cm.^2$ samples (two from each transect), each consisting of two cores, were taken

during each sampling period. In the laboratory, the samples, contained within a wire mesh straining seive, were vigorously cleaned of the sand and associated organic debris. No attempt was made to separate dead from living below ground material. Indeed the absence of metabolic activity in a submerged organ in no way precludes its usefulness to the plant (Westlake, 1965). Such organs may be important as supportive structures and may also function in a storage capacity. Therefore all below ground portions that were strong enough to remain intact after the washing process were treated as biomass.

To obtain dry weight estimates, all macrophyte samples (above and below ground) and the litter were dried for a minimum of 24 hours in a forced air oven at 100°C and weighted on a triple beam balance. These samples were then powdered in a Wiley mill, subsampled, combusted in a muffle furnace at 550°C and reweighed on a torsion balance to obtain ash free dry weight (organic weight) estimates. Using appropriate areal conversion factors, macrophyte biomass was calculated and is given as dry weight per m^2. Converting from organic weight to carbon weight using the factor of 0.465 (Westlake, 1965), macrophyte productivity is expressed as mgC/m^2 on daily and annual bases so that it may be compared to the algae in determining relative contributions of individual autotrophic components to the total net primary productivity of the dune pond ecosystem.

Ecosystem Metabolism

In situ estimates of gross productivity and ecosystem respiration were made using a gas analysis technique based on carbon dioxide exchange measured with an infra-red gas analyzer (Beckman, Model 215 A). Bordeau and Woodwell (1965) have reviewed infra-red absorption techniques for measuring rates of CO_2 exchange. This technique for measuring CO_2 concentrations was selected over chemical methods because of its accuracy (Heath, 1969).

Two portable metabolic chambers, constructed of 1/8 inch clear Plexiglas (Figure 2) were used in the study to enclose portions of the pond for analysis of ecosystem gas exchange. These chambers were identical in their dimensions, being one meter tall, 1/4 m^2 in cross sectional area (50 cm. x 50 cm.), and each having a volume of 250 liters. One of the chambers (hence referred to as the dark chamber) was wrapped with five layers of black polyethylene plastic, excluding all light. Both were equipped with 1/4 inch inlet and outlet ports, positioned opposite each other, at 25 and 75 cm. distances from the base. The upper ports were used for gas withdrawal and the lower for water circulation.

Due to the technical difficulties involved in field applications of the infra-red analysis technique (Mooney et al., 1971), particularly in aquatic systems, gas samples were transported in gas collecting vessels to the laboratory for analysis. A number of gas collecting vessels were constructed for field use from 500 ml. glass side arm flasks, gum tubing, and compressor clamps. These vessels were routinely autoclaved and oven dried to prevent colonization of

Figure 2. Metabolic chambers used in gas exchange study.

Figure 2.

the inner surfaces by microbial organisms which, owing to their own metabolic activity, would likely affect the analyses. A check on the integrity of these collecting vessels in terms of their ability to retain qualitatively unchanged gas samples was performed by filling them with calibration mixtures of 155, 309, and 455 ppm CO_2 (balance nitrogen). The quality (with respect to CO_2 concentration) of these samples remained statistically (α = .05) unchanged for a minimum of 28 hours after which they slowly approached the ambient (room) concentration, undoubtedly through diffusive exchange via the tubing inlet-outlet ports. During the course of this study, the time lag between gas sampling and analysis rarely exceed 15 hours with the exception of three sampling periods in the summer of 1973 during which diurnal changes in ecosystem respiration were monitored.

Determinations of ecosystem metabolism were made at 3 to 4 week intervals (with few exceptions) over the 15 month period of 6 July 1973 to 10 October 1974. In order to avoid disturbed areas of the pond, as well as the artificial substrates used for periphyton sampling, the light and dark metabolic chambers were non randomly positioned during each incubation period. The two were always situated adjacent to one another thereby insuring reasonable biological and physical homogeneity between them at a particular site. The water level in the chambers rarely exceeded 40 cm.; and the volume of the chambers occupied by water was generally less than 1/3 of the total volume.

Measurement of carbon dioxide in a closed system has the disadvantage that this gas is the substrate used in forming

carbohydrates in photosynthesis. Furthermore, in reacting with water, CO_2 forms a weak acid (H_2CO_3) which in a closed system may create a pH change inconsistant with normal biological function. In attempting to minimize the potential inhibitory effects of very high and very low CO_2 concentrations in the dark and light chambers respectively, incubation periods, ranging from 1/2 hour during the early summer and 6 hours during the winter, were inversely adjusted to the metabolic activity of the pond.

Normally the chambers were positioned for incubation purposes at 3 to 5 different positions throughout the pond between 08:00 and 20:00 during a sampling day. At the beginning of this study, incubations were performed diurnally with at least one night time measurement. Subsequent statistical analysis of ecosystem respiration rates (Table 1) failed to demonstrate any differences between day and night respiratory activity; therefore night time metabolic measurements were discontinued for the remainder of the study.

During each incubation, air and water temperature within both chambers was monitored at intervals of 15 to 30 minutes using a six channel telethermometer (Yellow Springs, Model 46-TUC). Determinations of ambient air and water temperatures were similarly made. Using a pressure-vacuum handpump (850 ml. capacity), connected in series to the lower chamber portals, the aqueous volume of the two chambers was periodically circulated to minimize artifactually induced stratification potentially inhibiting CO_2 diffusive exchange during longer incubation periods. Using another handpump, of

Table 1. Analysis of Diurnal Variation In Ecosystem Respiration Rates.

Date	Morning Resp. $mgC/m^2/hr.$	Noon Resp. $mgC/m^2/hr.$	Evening Resp. $mgC/m^2/hr.$	Night Resp. $mgC/m^2/hr.$
3 August 73	30.4	20.0	31.1	22.7
25 August 73	25.2	22.4	17.6	25.6
12 September 73	25.6	19.1	30.9	30.9
Average	27.0	20.5	26.5	26.4

Tukey's (LSR) Multiple Range Test[1]

	27.044	26.546	26.432	20.466
20.466	6.578	6.080	5.966	
26.432	0.612	0.114		
26.546	0.498			
27.044				

[1] $LSR_{(.05)} = Q_{(4.8)} \times 2.74 = 12.41$

No differences between collumn averages are significant at 5% level.

identical design, gas samples were withdrawn in duplicate from the chambers into gas collecting vessels at the commencement and at the end of each incubation. To avoid the possibility of promoting microbial activity under humid conditions, gas samples were dried by passing them through a drierite column before introduction into collecting vessels. Both the collecting vessels and the drierite column were connected in series with the handpump to the upper chamber portals. Gas collecting vessels were not disengaged from the series until the entire sampling system was brought into qualitative equilibrium with the chamber sampled. Usually, 30 to 40 liters of gas (50 depressions of the handpump) were circulated through the sampling system before sample removal. At the end of each sampling day, the gas collecting vessels were transported immediately to the laboratory for CO_2 analysis.

The infra-red gas analyzer, coupled to a strip chart recorder (Honeywell, Model 193), was calibrated using reference gases of 0, 155, 309, 455, and occasionally 600 ppm CO_2 (balance nitrogen). By high amplification of the analysis system, great sensitivity (approximately 4 ppm CO_2) was attained. Reference and sample gases were introduced into the analyzer in aliquots of 20 cc., using a gas tight hypodermic syringe. In response to the introduction of these gases, a series of normal curves were generated (Figure 3), the areas of which were linearly proportional to the CO_2 concentration of the reference gases administered. Using the recorder curves associated with the reference gases, the areas beneath them (determined by planimetry) were regressed on their respective CO_2

Figure 3. Infra-red gas analysis determination of carbon dioxide flux in light and dark chambers.

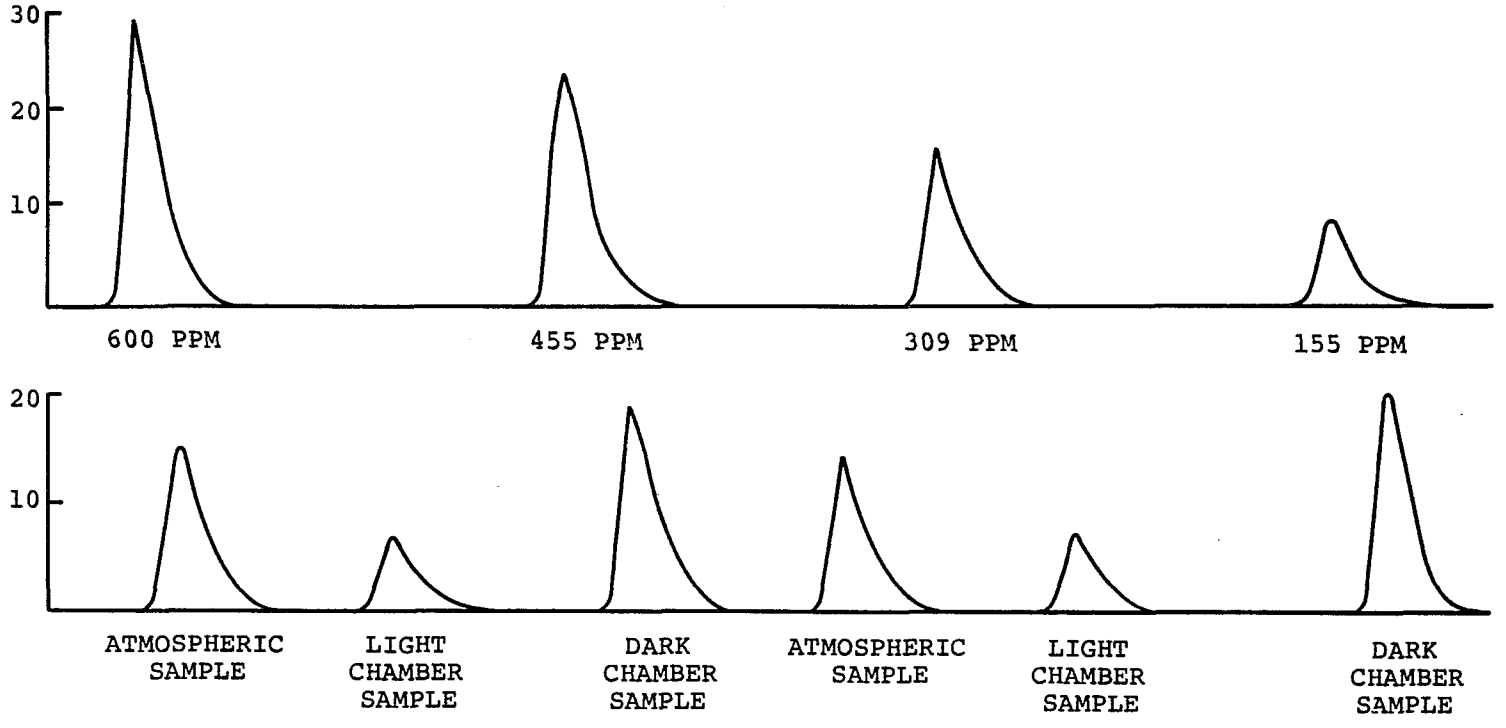
30
20
10
600 PPM
455 PPM
309 PPM
155 PPM
20
10
ATMOSPHERIC SAMPLE
LIGHT CHAMBER SAMPLE
DARK CHAMBER SAMPLE
ATMOSPHERIC SAMPLE
LIGHT CHAMBER SAMPLE
DARK CHAMBER SAMPLE

FIGURE 3

concentrations in developing linear prediction equations ($y = mx + b$), used to calculate the CO_2 concentration (in ppm) of the sample gases.

CO_2 flux within the total volume of the chambers during incubation was calculated from empirically determined changes in the CO_2 partial pressure of the gaseous volume (VG). The CO_2 flux within VG was calculated in mgC using equation 1.

$$\text{Equation 1:} \quad \Delta \text{ mgC/VG} = \text{VG} \times \frac{537.714 \text{ mgC}}{\text{Liter } (10^6 \text{ppm})} \times \left[\left(\text{ppm } CO_{2(2)} \times \frac{273°K}{TG_{(2)}} \right) - \left(\text{ppm } CO_{2(1)} \times \frac{273°K}{TG_{(1)}} \right) \right]$$

Where: 537.714 = molecular wt. of carbon (mg) in one liter of pure (10^6 ppm) CO_2.

ppm $CO_{2(1)}$ = initial CO_2 partial pressure.

ppm $CO_{2(2)}$ = CO_2 partial pressure at the end of incubation.

$TG_{(1)}$ = initial temperature (°K) of VG.

$TG_{(2)}$ = temperature (°K) at the end of incubation.

Considering the dynamic equilibrium existing between aqueous and gaseous CO_2 concentrations, the temperature dependent CO_2 flux rate (in mgC) within the aqueous volume (VA), was calculated (equation 2) knowing the gaseous flux rate.

$$\text{Equation 2:} \quad \Delta \text{ mgC/VA} = (\Delta \text{ mgC/VG}) \times \frac{\text{VA}}{\text{VG}} \times \text{AC factor}$$

In equation 2, AC factor represents a ratio of Bunsen absorption coefficients, which adjusts the estimate of aqueous CO_2 flux in

accordance with temperature dependent changes in the degree of CO_2 solubility during incubation. When respiration exceeds photosynthesis (i.e., dark chamber), AC factor = (AC at incubation end/AC at incubation initiation). When photosynthesis exceeds respiration (i.e., light chamber), AC factor = (AC at incubation initiation/AC at incubation end). CO_2 flux within the total volume (VT) of the chambers was calculated in mgC using equation 3.

Equation 3: Δ mgC/VT = (Δ mgC/VG) + (Δ mgC/VA)

After this summation, carbon flux was converted from a volumetric basis (per 250 L.) to an areal basis (per m^2), using appropriate conversion factors. Carbon flux was positive with respect to ambient concentration when respiration exceeded photosynthesis (i.e., dark chamber) and negative with respect to ambient concentration when photosynthesis exceeded respiration (i.e., light chamber).

Generally, this method was used to provide a static (2 reference points) appraisal of the metabolically mediated CO_2 flux occurring within the ecosystem under natural conditions. Occasionally, incubation periods were extended and gas samples removed intermittently as well as at the commencement and completion of incubation, in order to determine CO_2 compensation characteristics of the ecosystem. The calculations of gross productivity and ecosystem respiration were essentially the same as those commonly employed in oxygen light and dark bottle determinations of phytoplankton community metabolism. Differential changes in the carbon concentration within the light and dark chambers during incubation were treated as

net ecosystem productivity and ecosystem respiration respectively. Gross productivity was calculated from the carbon differential established between the light and dark chambers during incubation.

Metabolic data are expressed as means in mgC/m^2 on hourly, daily, growing season, and annual bases. No relationship was found between solar energy and photosynthetic assimilation (see results section of this text), therefore mean hourly rates of gross photosynthesis were expanded to daily rates, multiplying by the number of hours between sun-up and sun-set. Annual mean rates of gross production and ecosystem respiration were determined by integrating the area under annual curves with respect to time. Annual mean net ecosystem productivity was calculated as the difference between the integrated rates of gross production and ecosystem respiration. Growing season means were similarly determined.

Laboratory Determination of Light Response Characteristics of Juncus balticus

Photosynthetic rate in Juncus balticus, the dominant emergent, was estimated using a closed Plexiglas gas exchange system with a volume of 12 liters. The CO_2 flux within the system was continuously monitored using the same infra-red gas analysis and recording equipment used in analyzing gas samples collected during in situ investigations. The analyzer was calibrated using gases of 309, 155, and 0 ppm CO_2 (balance nitrogen).

Artificial light was provided by a bank of two 500 watt metal halide full spectrum bulbs and light intensities were measured with a Weston Electric Corp. foot candle meter at distances of

10, 20, 30, and 40 cm. within a 60 cm. high cylindrical metabolic chamber (Figure 4). Changes in illumination were facilitated using a varying rheostat connected in series with a Stabline voltage regulator to the light bank. The gas exchange system was cooled by suspending the light source in a water filled Plexiglas basin through which cold tap water was circulated. Temperature (telethermometer determinations) within the photosynthetic chamber ranged from 22.0°C at the lowest light intensity to 26.0°C at the highest. Gas flow through the system was maintained at the rate of 20 S.C.F.H. by regulating the output of an air tight pressure vacuum pump.

Several clones of Juncus balticus were removed from the dune pond on the evening before the day of the experimentation. These were carefully excavated in their entirety (roots and rhizomes intact), placed in pond water filled buckets and transported to the laboratory. To avoid curling and breakage of the apical tips in the metabolic chamber, only the upper 60 cm. of the stems were used in these experiments. The excision of the upper 60 cm. portion of the stems and their placement into a flask of distilled water, was done immediately preceeding analysis. In control experiments, McNaughton (1973) has shown that stem preparation as just described has minimal effect on both photosynthesis and transpiration. Analyses at nine different light intensities were performed once on 30 arbitrarily classified older stems and once on 40 arbitrarily classified younger stems. Wet weights of plant material were essentially equal with respect to age categories analyzed.

Figure 4. Metabolic chamber used in laboratory determinations of net photosynthesis in Juncus balticus.

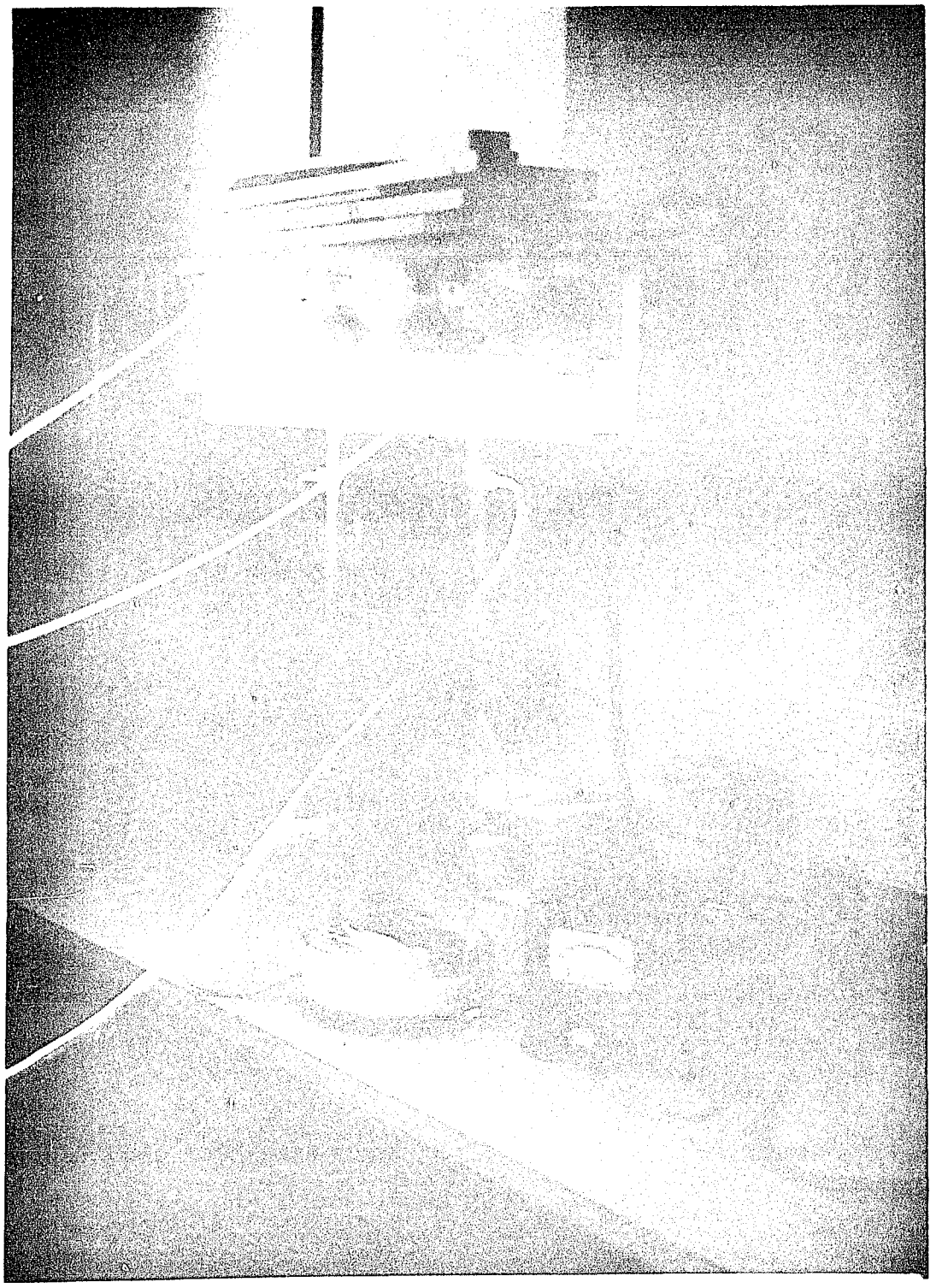

Figure 4.

Net photosynthetic rate determinations as ppm CO_2 $hr.^{-1}$, determined from the recorder output and a calibration curve, were converted to $mgCO_2$ $hr.^{-1}$ using the following expression:

$$mgCO_2hr^{-1} = \text{ppm } CO_2hr^{-1} \times 12 \text{ liters} \times \frac{1964.28 mgCO_2}{\text{liter}(10^6 \text{ppm})} \times \frac{273°K}{\text{chamber atmos. temp. } °K}$$

In this expression, 1964.28 represents the molecular weight of CO_2 (as mg.) in one liter of pure (10^6ppm) CO_2 at S.T.P.

All rates of net photosynthesis are given as mg CO_2 hr^{-1} and are expressed on a dry weight basis (stems dried at 100°C for minimum of 24 hours). CO_2 compensation point determinations, graphically derived from the calibration curve, are expressed as ppm CO_2. Light compensation points, determined graphically from light response curves (see results), are expressed in foot candles and in lux.

RESULTS

Description of the Study Pond

During the study, solar flux at normal incidence (Table 2) was approximately 50% of the potential solar input (Kondratyev, 1969) at this latitude. Light measurements within the water column were not taken, and the extent of qualitative and quantitative attenuation of light therein is not known. Judging from its stained appearance, the pond water is probably bog-like with respect to its light extinction characteristics (See The Fate of Solar Radiation, in: Ruttner, 1952). Observed annual and diurnal variations in measured physical and chemical parameters are shown in Tables 3 and 4. These data as well as subsequently described biological features pertain to the study pond (hereafter referred to as "the pond"), and can probably be extrapolated to some of the nearby ponds, many of which differ only slightly in morphometry, age, etc.

The annual mean depth of the pond during the period of April 1973 through March 1974 was 41 cm. During the summer of 1974, the mean depth was 11% less than that of the summer, 1973. Depth maxima and minima occurred during the summer and winter months respectively, and directly correlate with fluctuations in the Lake Michigan water level (USCOMM-NOAA-DC Lake Survey, 1974).

With few exceptions, the pond was not thermally stratified. Occasionally during windless mornings, particularly on very hot

Table 2. Actual[1] And Potential[2] Solar Energy At Normal Incidence In Southern Michigan.

	April 73 through March 74[3]	October 73 through September 74[4]
Potential Energy	187.9 kcal/cm^2/year	187.9 kcal/cm^2/year
Actual Energy	94.8 kcal/cm^2/year	97.0 kcal/cm^2/year
Percent (Actual/Potential)	50.5%	51.6%

[1] Estimated with an Eppley pyrheliometer.

[2] Calculated from global radiation data (K. Ya. Kondratyev, 1969).

[3] Period during which annual net primary productivity was estimated.

[4] Period during which annual gross primary productivity was estimated.

Table 3. Seasonal Variation[1] In Depth, Water Temperature, pH, and Alkalinity.

Date	Mean Depth[2](cm.)	Water Temp.(°C)	pH	Alkalinity (meq/l.)
14 April 73	38.0	13.0	6.85	0.83
5 May 73	46.0	14.5	7.00	0.87
25 May 73	50.0	19.0	7.20	0.97
14 June 73	47.5	23.0	7.10	1.32
3 July 73	51.5	25.0	7.50	1.45
20 July 73	43.0	26.0	7.30	1.81
7 August 73	45.0	26.0	7.50	2.12
21 August 73	55.0	24.0	7.55	1.72
11 September 73	42.0	22.0	7.55	1.94
29 September 73	43.5	19.0	7.60	1.80
20 October 73	43.5	13.0	7.55	1.54
10 November 73	39.0 (0.5)	2.0	7.50	1.50
6 December 73	45.0 (2.0)	1.0	7.50	1.02
3 January 74	38.0 (16.0)	0.5	7.00	1.18
24 January 74	44.0 (10.0)	0.5	6.55	0.33
14 February 74	33.0 (10.0)	0.5	6.55	0.86
7 March 74	35.0	12.0	7.30	0.56
31 March 74	39.0	5.0	7.40	0.52
20 April 74	39.0	12.5	7.50	0.70
11 May 74	38.0	13.5	7.50	0.86
30 May 74	45.0	20.0	7.10	0.98
13 June 74	46.0	19.0	7.55	1.02
30 June 74	46.0	24.0	7.65	1.43
22 July 74	39.5	21.5	7.05	1.99
12 August 74	43.5	25.0	7.60	1.82
5 September 74	34.0	19.0	7.70	2.10
10 October 74	35.0	15.0	7.50	1.60

[1]Determinations made at approximately noon during each sampling day.

[2]Numbers in parentheses represent ice thickness during winter months.

Table 4. Diurnal Variation[1] In Air Temperature, Water Temperature, and pH.

Time	Air Temperature(°C)	Water Temperature(°C)	pH
08:00	12.0	17.5	7.40
10:00		19.0	7.50
12:00	24.0	20.0	7.50
14:00		22.5	7.60
16:00	28.0	24.5	7.65
18:00		25.0	7.90
20:00	12.0	24.0	7.55
22:00		22.0	7.50

[1]Data from 12 September 73, a clear day exemplifying observed ranges of diurnal temperature and pH flux.

summer days, the upper water stratum would warm more quickly than the lower, creating a 2° to 3°C temperature gradient. Such gradients were quickly dissipated by a slight breeze, and normally were no longer detectable by 10:00. Diurnal water temperature fluctuations, non existant during the winter, and most notable during the spring and fall, were generally on the order of 5° to 10°C. Maximum observed ice thickness (16.0 cm.) was observed in January during a period of nearly continual ice cover (November 1973 through February 1974). Temporary thawing occurred at least twice during the winter prior to the spring thaw in mid March.

During the annual period of April 1973 through March 1974, the mean alkalinity of the pond water was 1.24 meq/l. Mean alkalinities during the summer of 1973 and 1974 were comparable, being 1.48 and 1.39 meq/l. respectively. Annually, the alkalinity changed significantly, ranging between winter minima and summer maxima,

observed maximal and minimal alkalinities being 2.12 and 0.33 meq.l. respectively. Variation in alkalinity appeared to be associated with changes in the level of the ground water table, caused by fluctuations in the level of Lake Michigan.

To determine the inorganic carbon binding capacity of the pond water relative to that of distilled water, a laboratory check was made by subjecting water samples of increasing alkalinity (equilibrated with the atmosphere at a constant temperature) to a nitrogen purge, measuring the amount of CO_2 evolved with an infrared gas analysis system. Pond water samples of alkalinities up to approximately 1.60 meq/l. were not significantly ($\alpha = .05$) different from distilled water in terms of their inorganic carbon binding capacity.

Maxima and minima of pH followed an annual pattern identical to that described for water depth and alkalinity. Observed midday pH values ranged from a winter minimum of 6.50 to a summer maximum of 7.70. Diurnal fluctuations in pH generally on the order of 0.2 to 0.5 units during the summer, were not observed during the winter. Both annual and diurnal variations in pH appeared to be strongly related to water temperature change.

Observed atmospheric CO_2 partial pressure during daylight hours ranged from a minimal summer value of 285 ppm to a winter maximum of 383 ppm. Atmospheric CO_2 concentrations were consistantly higher during the night than during the day. The annual mean, estimated from measurements during the day, was 336 ppm. Dissolved CO_2 approximations (calculated from total alkalinity, pH, and temperature

data; see Ruttner, 1959) indicated annual supersaturation of the pond water with CO_2 on the order of 5 to 15 times atmospheric CO_2 concentrations, suggesting higher rates of respiration relative to photosynthesis within the water of the pond.

The biological structure of the pond can be outlined as follows:

A. Autotrophic community
    1. Macrophytes
        a. Emergent
        b. Submerged
    2. Epipelic periphyton
    3. Phytoplankton
B. Heterotrophic community
    1. Invertebrates
        a. Benthic
        b. Planktonic
    2. Semiaquatic vertebrates

The emergent macrophyte flora, homogeneously distributed throughout the pond, was represented by Juncus balticus and Cladium mariscoides, collectively comprising 100% of the emergent vegetation sampled during the study. Potential contributions by Carex sp. and Eleocharis sp., intermixed with terrestrial representatives along the shore-water interface, were excluded by the sampling design as previously discussed. Juncus balticus and Cladium mariscoides, exceedingly difficult to distinguish from one another vegetatively, are separable by floral and subtle rhizomal differences (Fassett, 1957).

Primarily on the basis of rhizomal differences, since so few of these plants ever formed inflorescences during the study, I estimate that greater than 90% of the emergent plant biomass was J. balticus. Dominance by this species in similar Lake Michigan dune ponds has been cited by Cowles (1899) and Shelford (1911).

The tendency of emergent plants to form pure closed communities inhibiting colonization by potential competitors has been discussed by Sculthorpe (1967). In this regard, plants which vigorously spread by means of rhizomes, such as J. balticus, may readily realize a dominant role where conditions favor their existence.

The submerged macrophyte flora was diminuitively represented by Ultricularia sp., Chara sp., Fontinalis sp., and Potomageton sp. Reiffer and Kleinsmith (1973), conducting a descriptive survey of the pond as a class project, estimated the contribution of these plants to the total standing crop at less than 0.5%. Rarely measureable in those few samples in which they occurred, these plants contributed very little to the biomass in this study, and were treated with the emergent flora as previously discussed.

Dominant algal genera appeared to be represented in both pelagic and benthic regions of the pond. The algal community, strongly dominated by Desmidacean representatives, including Cosmarium sp., Staurastrum sp., Micrasterias sp., and Desmidium sp., was subject to late summer invasion by Cyanophycean representatives, including Anabaena sp. and Oscillatoria sp. Bacillariophycean genera, infra-abundant throughout the season, assumed a very minor importance in terms of algal biomass and, I suspect, productivity. The

bacterio-algal periphyton association, epipelic in nature for reasons previously discussed, was structurally dependent upon the copius mucilage secretion of Cosmarium sp., the dominant alga within the pond.

Grazing and detrital food processing pathways were completely dominated by invertebrate organisms, as is commonly the case. Observations on these invertebrate communities of the pond indicated high diversity in stark contrast to the floral uniformity.

Holotrich citiates, the dominant protozoan representatives, were complemented by the less abundant peritrichs, both of which were principally associated with the rich organic benthic substrate. Mastigophoran and sarodinian protozoans were found rather infrequently. Rotifers, equally abundant both upon the pond bottom and within the plankton, dominated the zooplankton community. Oligochaete annelids occurred abundantly in the sediments, yet hirudinean representatives were totally absent from the pond, perhaps reflecting the paucicity of potential vertebrate hosts. The phylum Arthropoda was meagerly represented by planktonically occurring cladocerans and copepods, yet was abundantly represented by various taxa of aquatic and semiaquatic insects, including: Odonata, Coleoptera, Diptera, Hemiptera.

The most frequently encountered vertebrates were frogs, several species of which inhabited the shoreline region. During the spring of 1974, a few previously unencountered mud turtles established residence in the pond. Occasionally, particularly on stormy days, migrating ducks moved in from Lake Michigan, seeking temporary refuge

in the dune ponds and in the nearby Kalamazoo river marsh. Located on the eastern shoreline, a single lodge, housed at least one muscrat pair whose activities were largely restricted to an adjacent much shallower swale where they browsed on the younger shoots of Carex and Eleocharis. There were no fish in the pond, and I found no evidence indicating that any had ever been present. Possible reasons for this have already been discussed.

Algal Net Primary Productivity

Seasonal patterns of net primary productivity of phytoplankton and epipelic periphyton are presented in Figure 5. Annual mean daily rates of net production of phytoplankton and periphyton were 46.6 $mgC/m^2/day$ and 88.7 $mgC/m^2/day$ respectively. The productivity of the phytoplankton ranged from 1.6 $mgC/m^2/day$ in mid winter to 239.3 $mgC/m^2/day$ in early summer and that of the periphyton from 4.3 $mgC/m^2/day$ in mid winter to 262.4 $mgC/m^2/day$ in late summer. Although the ranges of productivity values of the periphyton and phytoplankton were similar, the duration of peak periphyton productivity was considerably greater than that of the phytoplankton, which on an annual basis, was only 52.5% as productive as the periphyton.

Differences in rates of carbon assimilation by the phytoplankton, insignificant between bottles incubated at the same depth, were significant ($\alpha = .05$) between bottles incubated at different depths. During the period of May through October, assimilation within the upper water stratum averaged 48% greater than that within

Figure 5. The net primary productivity of algae is presented for the period of March 1973 through March 1974. Monthly designations (abscissa) identify mid month dates. Points represent the net primary productivity of phytoplankton (●) and epipelic periphyton (▲).

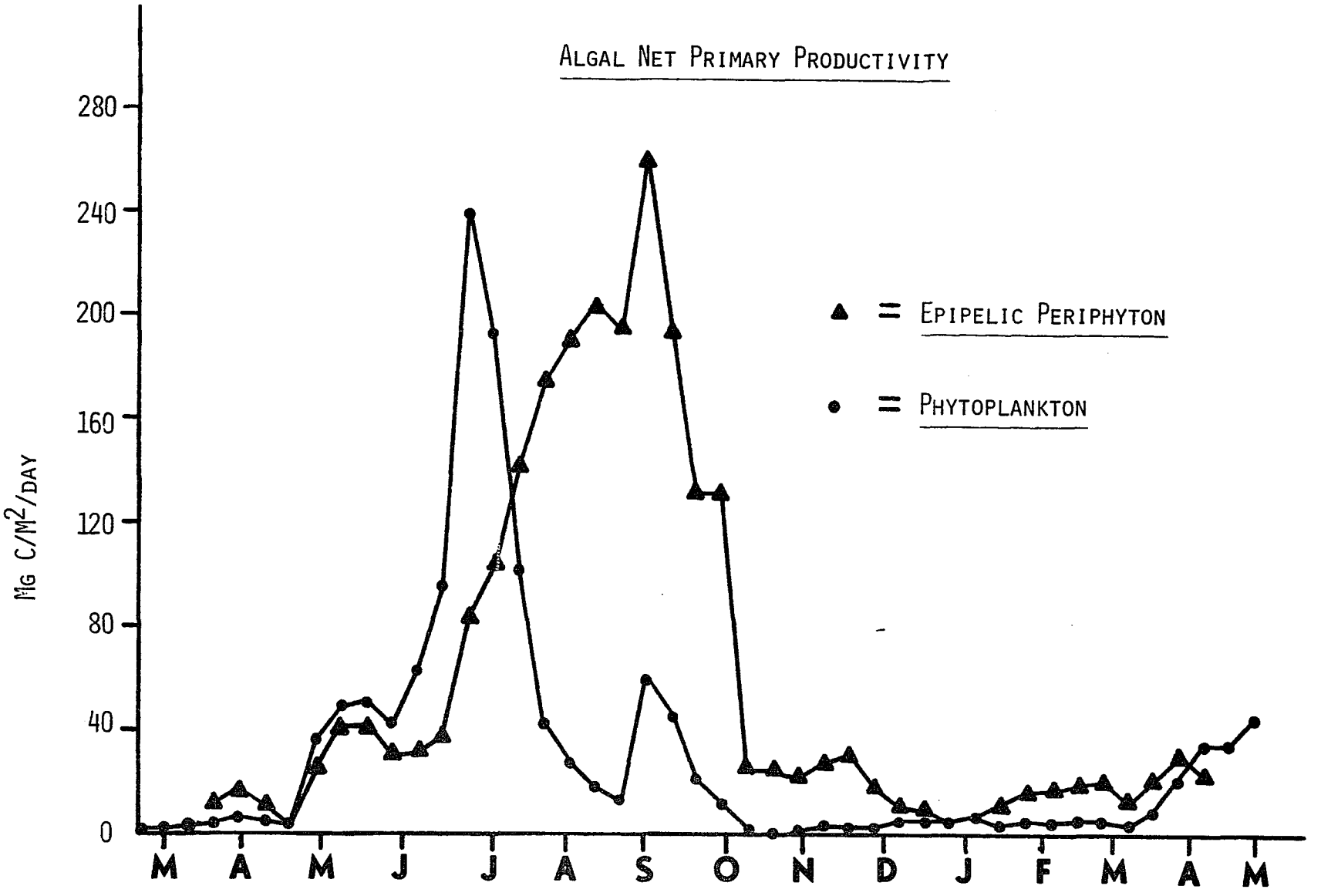
ALGAL NET PRIMARY PRODUCTIVITY
280
240
200
160
120
80
40
0
MG C/M2/DAY
▲ = EPIPELIC PERIPHYTON
● = PHYTOPLANKTON
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M

FIGURE 5

the lower. Conversely, the opposite effect occurred without exception during the period of October through May, when assimilation by phytoplankton within the lower water stratum was 74% greater than that within the upper. Variations in rates of carbon assimilation between replicate periphyton samples demonstrated no pattern. On an annual basis, the coefficient of variability (S.D./$\bar{x}$ as a percentage) averaged 27.2% ranging from 11.5% to 64.9%.

Annual patterns of benthic and planktonic dark fixation mimiced patterns of light fixation by the periphyton and phytoplankton. Chemosynthetic rates of dark fixation (Table 5), interpreted as secondary productivity (see Sorokin, 1965) represented 4.2% and 13.1% of the annual mean light fixation within the planktonic and benthic communities respectively.

Table 5. Chemosynthetic Rates of Dark Fixation.

	Annual Mean $mgC/m^2/day$	% of Carbon Fixation in Light
Benthic	11.6	13.1
Pelagic	2.0	4.2

Biomass and Net Primary Productivity of the Macrophytes

Distributions of above and below ground biomass and litter are given in Figure 6. The below ground vegetation annually represented between 90.4% and 96.6% of the total macrophyte biomass

Figure 6. Distributions of macrophyte biomass and litter are presented for the period of April 1973 through October 1974. Monthly designations (abscissa) identify mid month dates. Vertical bars represent one standard error of the mean values.

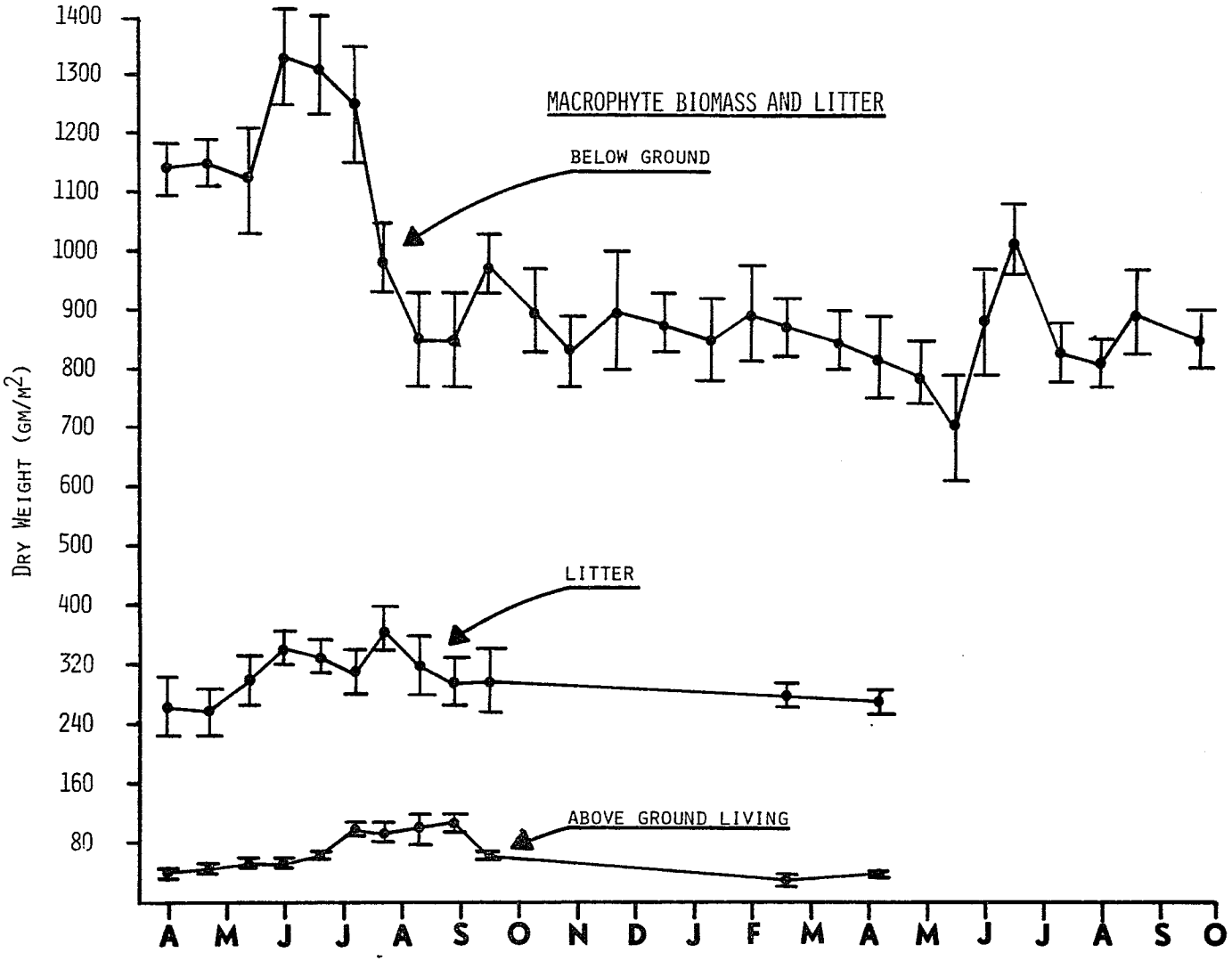
MACROPHYTE BIOMASS AND LITTER
BELOW GROUND
LITTER
ABOVE GROUND LIVING
DRY WEIGHT (GM/M2)
1400
1300
1200
1100
1000
900
800
700
600
500
400
320
240
160
80
A M J J A S O N D J F M A M J J A S O

FIGURE 6

(Table 6). Litter was continually present, remaining at least three times more abundant than above ground living vegetation throughout the study.

Table 6. Seasonal[1] Changes In Below Ground Proportion of Total Macrophyte Biomass.

	Below Ground Biomass (% of total)
April 73	96.6
May 73	96.0
June 73	96.5
July 73	94.1
August 73	90.4
September 73	91.3
October 73	-
November 73	-
December 73	-
January 74	-
February 74	-
March 74	96.2

[1]Above ground biomass harvesting discontinued between October 1973 and February 1974.

During the 1973 growing season, above ground biomass, litter-mass, and below ground biomass maxima of 109 gm., 363 gm., and 1328 gm. per m^2(dry wt.) respectively, were estimated. Periods of above and below ground biomass accrual did not correspond temporally; the above ground accrual, occurring in mid to late summer, lagged behind that

of the below ground which occurred in late spring to early summer. Litter mass increased slightly during mid summer.

Pre-growing season measurements of above ground biomass, as well as litter, were not statistically ($\alpha = .05$) different in 1973 and 1974. April measurements, expressed as dry wt./m^2, showed 40 gm. in 1973 and 38 gm. in 1974 present as above ground biomass, and 263 gm. and 268 gm. present as litter mass during the same periods. Below ground biomass baselines differed significantly however between 1973 and 1974, decreasing 35% from a mean value (May data, 1973) of 1139 gm. dry wt./m^2 to a mean value of 742 gm. dry wt./m^2 calculated during the same period in 1974.

Coefficients of variability (S.D./$\bar{x}$ as a percentage) were calculated for biomass and litter determinations. Annually, C.V. values per sampling period averaged 18.9% for below ground biomass, ranging from 7.3% to 31.1%; 19.9% for above ground biomass, ranging from 5.2% to 38.6%; 20.5% for litter, ranging from 12.4% to 35.3%. Distributions of C.V. values showed no pattern, inasmuch as the magnitudes of the values appeared to be seasonally independent.

Seasonal changes in the ash content of above and below ground biomass and litter are given in Table 7. The ash contents of the above ground biomass and litter remained relatively constant at 2% and 4% respectively. The ash content of the below ground biomass exhibited a seasonal pattern of change, ranging from 8% during the summer and fall months to as high as 15% during the spring.

As pointed out by Westlake (1966), combustion of plant biomass provides a check on the adequacy of root washing. It is

Table 7. Seasonal Changes In Ash Content[1] Of Macrophyte Biomass And Litter.

	Above Ground	Litter	Below Ground
April 73	2%	4%	15%
May 73	2%	4%	9%
June 73	3%	4%	8%
July 73	4%	4%	8%
August 73	2%	4%	8%
September 73	2%	4%	8%
October 73	-	-	8%
November 73	-	-	8%
December 73	-	-	8%
January 74	-	-	10%
February 74	-	-	10%
March 74	2%	5%	13%
April 74	2%	4%	14%

[1]Ash content represented as percentage of oven dry weight.

felt that contamination of below ground biomass samples by soil particles (sand) was negligible in this study because the values for ash content conform with similar estimates cited in the literature (see discussion).

Estimating the productivity of perennial macrophytes from biomass statistics is often problematical (see application of various techniques by Rich et al., 1971). Generally applicable models for such estimates unfortunately do not exist.

In calculating the macrophyte productivity of the dune pond, several assumptions were made regarding the pattern of macrophyte growth during this study.

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October 73	-	-	8%
November 73	-	-	8%
December 73	-	-	8%
January 74	-	-	10%
February 74	-	-	10%
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Estimating the productivity of perennial macrophytes from biomass statistics is often problematical (see application of various techniques by Rich et al., 1971). Generally applicable models for such estimates unfortunately do not exist.

In calculating the macrophyte productivity of the dune pond, several assumptions were made regarding the pattern of macrophyte growth during this study.

1. Net photosynthetic accrual, as evidenced by the rapid and significant increase in below ground biomass, occurs almost exclusively during the early summer. This was substantiated by in situ and laboratory measurements of photosynthesis (discussed in a later section of this test).
2. Losses due to grazing, damage, and mortality during this brief period of early summer production are negligible.
3. The mid to late summer increase in above ground biomass is not an additional accumulation of net primary production. This accumulation, representing previously assimilated photosynthate, reflects the translocation of materials from storage organs which provide a highly labile pool for growth and stem replacement following damage and mortality. Furthermore, this pool is used as a supplementary substrate for the increased respiratory demands associated with senescence. This assumption is supported by the mid to late summer pattern of below ground biomass depletion which temporally corresponds with increased above ground biomass production and litter accumulation. Furthermore, this period of depletion can be associated with increased respiratory activity by the macrophytes (discussed in a later section).

To check the general pattern of below ground biomass change observed in 1973, biomass determinations were continued through the 1974 growing season. Aside from the fact that the mid summer

depletion of stored reserves from submerged organs was less pronounced in 1974, the overall pattern repeated itself. Macrophyte net productivity was calculated on the basis of below ground biomass change, incorporating factors for organic content (ash wt. determinations) and organic carbon content (0.465 recommended by Westlake, 1965). Productivity in 1974 was comparable to that in 1973, being 239.3 $mgC/m^2/day$ and 212.1 $mgC/m^2/day$ respectively.

Total Net Primary Productivity of the Dune Pond

The net primary productivity (NPP) of the three autotrophic components within the pond are compared in Table 8. To be temporally consistant with algal productivity estimates, macrophyte productivity (as listed in Table 8) is based on data collected during the 1973 growing season. The total annual mean daily NPP of the pond was 347.4 $mgC/m^2/day$ and production by the macrophytes accounted for 61.1% of that total. Of secondary importance were the algal components, periphyton accounting for 25.5% and phytoplankton for 13.4% of the total. 93.1% of total annual net production occurred during the "growing season," a period of approximately 160 days between mid May and mid October. The "growing season," as referred to in this study, corresponds with the period of net ecosystem production (subsequently discussed). Acknowledging the continued net production of algae during the "dormant season," the designation of these two seasons does not imply the contrary. Growing season mean daily rates of net primary production for all autotrophic components were approximately twice annual mean daily rates.

Table 8. Net Primary Productivity (NPP): Comparison of autotrophic communities in terms of their individual contributions to the total net primary productivity (TNPP) of the dune pond.

	Annual Mean Daily Rate[1] $mgC/m^2/day$	% TNPP	Growing Season Mean Daily Rate[2] $mgC/m^2/day$	% TNPP	$\frac{\text{Growing Season Prod.}}{\text{Annual Production}} \times 100$
Macrophytes	212.4	61.1	483.9	65.6	100.0
Epipelic Periphyton	88.7	25.5	161.5	21.9	79.8
Phytoplankton	46.6	13.4	92.3	12.5	86.9
TNPP	347.4	100.0	737.7	100.0	93.0

[1] 365 day period (April 1973 through March 1974).

[2] 160 day period (May 1973 through October 1973).

Ecosystem Metabolism

Patterns of gross photosynthesis and ecosystem respiration are presented in Figure 7 for the 15 month period of 6 July 1973 through 10 October 1974. Annual mean daily rates of gross photosynthesis, and ecosystem respiration, 546.7 $mgC/m^2/day$ and 377.3 $mgC/m^2/day$ respectively, were calculated for the 365 day period of mid October 1973 through mid October 1974. The annual mean daily rate of net ecosystem production during the same period, calculated as the integrated difference between rates of gross photosynthesis and ecosystem respiration, was 169.4 $mgC/m^2/day$. Annual net ecosystem production (61.8 gmC/m^2) was 22.7% less than the growing season accrual of 80.0 gmC/m^2.

During the study, the pond underwent seasonal transformations between autotrophic ($P/R > 1.0$) and heterotrophic ($P/R < 1.0$) metabolic modes, periods of autotrophy and heterotrophy being quite distinct. Autotrophic processes dominated between mid May and mid October, the growing season, and heterotrophic processes between mid October and mid May, the dormant season. The mid October conversion from autotrophy to heterotrophy occurred within approximately one week of the same conversion in 1973. Since no gas exchange determinations were made during the spring and early summer of 1973, I can only speculate on the temporal repeatability of the alternate conversion (heterotrophy to autotrophy) which occurred in mid May 1974. Judging from previously discussed patterns of net photosynthesis however, it is likely that this conversion similarly occurred sometime during May of 1973.

Figure 7. Ecosystem metabolism is presented for the period of July 1973 through October 1974. Monthly designations (abscissa) identify mid month dates. Points represent rates of gross photosynthesis (●) and ecosystem respiration (▲).

ECOSYSTEM METABOLISM

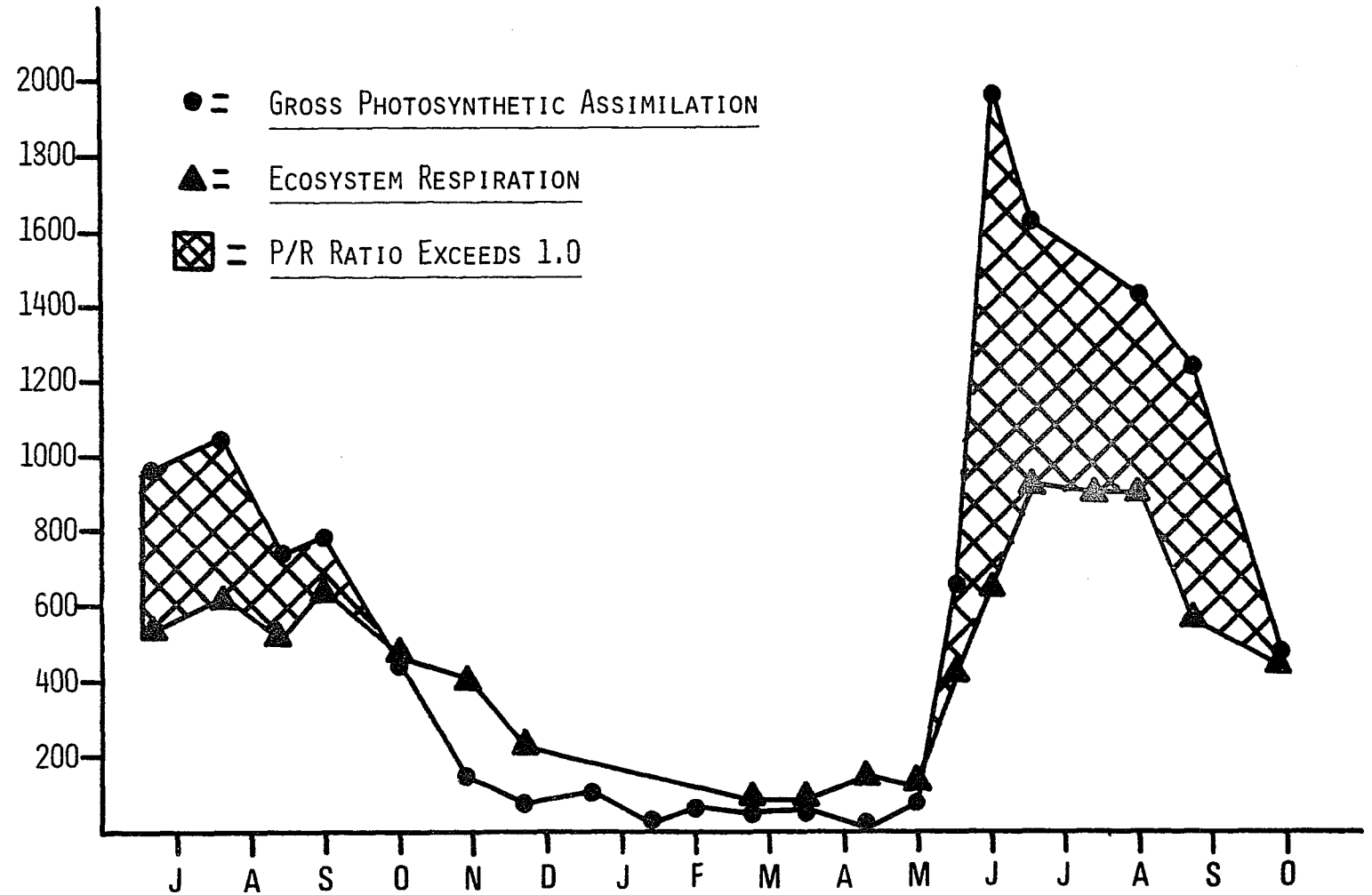

FIGURE 7

Peak photosynthetic activity, occurring during the early summer, temporally correlates with the rapid below ground biomass accrual observed in June of 1974. Respiration activity lagged photosynthetic activity and peaked in mid July. Whereas ecosystem respiration was maintained throughout mid summer at a somewhat constant rate, the rate of gross photosynthesis was gradually attenuated. Rapid reduction in rates of both respiration and gross photosynthesis were observed in mid September, as the two processes approached equivalence in mid October. Gas exchange measurements during the period of winter ice cover were complicated by conditions of reduced gaseous exchange with the atmosphere. As a result of the ice cover, impeding equilibrium, CO_2 supersaturation of the pond water became relatively extreme compared to that occurring during ice free periods. The CO_2 released into the metabolic chambers, positioned in holes chopped through the ice, accumulated at rates on the order of 2 to 3 times maximal observed respiratory rates. As a result of these conditions, respiratory estimates made during three mid winter sampling periods were discarded and are not presented in Figure 7. Assuming that this phenomenon occurred similarly within both light and dark metabolic chambers, estimates of gross photosynthesis, made under these conditions, were not affected.

Gas exchange measurements made during the summer of 1973 (not used in annual or growing season metabolic rate calculations) are believed to be underestimates caused by the extended incubation periods (2 to 3 hours) used at that time. It is apparent (Table 9) that photosynthetic rate was inversely related to the duration of

Table 9. In Situ Determination[1] Of The Carbon Dioxide Compensation Point For The Dune Pond.

	Light Chamber		Dark Chamber	
Time	$\lvert CO_2 \rvert$ in ppm	$\Delta \lvert CO_2 \rvert$ in ppm/hr	$\lvert CO_2 \rvert$ in ppm	$\Delta \lvert CO_2 \rvert$ in ppm/hr
10:30	311	-	311	-
11:00	217	188	347	72
11:30	161	112	429	87
12:30	105	28	515	89
13:30	105	0	592	77

[1]Data from 30 June 74. Chambers placed in a single position at 10:30. Gas removal at half hour and one hour intervals during a 3 hour period.

incubation, CO_2 compensation achieved within 2 to 3 hours during periods of active photosynthesis. Although respiratory rate was little affected by the duration of incubation, extremely high dark-chamber CO_2 concentrations, associated with extended incubation during mid to late summer periods of increased respiratory activity, produced a potential for inaccuracy in the analysis of subsamples, the CO_2 concentrations of which were too high (> 600 ppm) to accurately measure with the analysis system.

Diurnal patterns of gross photosynthesis and the efficiency of gross photosynthesis in relation to solar energy are presented in Table 10 for selected clear to partly cloudy sampling days during the summer of 1973 and 1974. Gross photosynthesis and, more strongly, the efficiency of gross photosynthesis demonstrated morning and evening maxima, the morning maxima being more pronounced than that

Table 10. Diurnal Variability In Rates Of Gross Photosynthesis And Gross Photosynthetic Efficiency On Fair Days.[1]

Date	Time of Day	Gross Photosynthesis $mgC/m^2/hr$	Solar Energy $gm\ cal/cm^2/hr$	Efficiency Index[2]
13 June 74	10:00	176	27	6.46
	12:00	126	27	4.65
	14:00	114	35	3.24
	16:00	98	35	2.79
30 June 74	09:00	138	24	5.68
	11:00	121	42	2.90
	14:00	100	64	1.55
	15:00	63	65	0.97
23 August 73	08:00	48	10	4.67
	11:00	57	50	1.16
	13:00	59	49	1.20
	19:00	51	18	2.88
12 September 73	09:00	72	23	3.13
	13:00	59	59	1.01
	18:00	64	29	2.21

[1] Data selected from clear to partly cloudy sampling days during the summers of 1973 and 1974.

[2] $(mgC/m^2/day)$ per $(gm\ cal/cm^2/day)$ = gross photosynthesis/solar energy.

of the evening. Gross photosynthesis and the efficiency thereof appeared to be inversely related to solar energy during these sampling periods. On heavily overcast days, represented by 22 July 1974 (Table 11), temporally related diurnal patterns of gross photosynthesis and gross photosynthetic efficiency were no longer evident, as increased photosynthesis became more strongly dependent upon solar energy availability.

Table 11. Diurnal Variability In Rates Of Gross Photosynthesis And Gross Photosynthetic Efficiency On An Overcast Day In July.(1)

Time of Day	Gross Photosynthesis $mgC/m^2/hr$	Solar Energy $gm\ cal/cm^2/hr$	Efficiency Index(2)
10:00	76	19	3.99
12:00	77	9	8.18
13:00	58	7	8.14
14:00	42	4	10.58

(1) Extremely heavy cloud cover and rain throughout the day (22 July 1974).

(2) $(mgC/m^2/day)$ per $(gm\ cal/cm^2/day)$ = Gross photosynthesis/solar energy.

Annual interrelationships between gross photosynthesis, gross photosynthetic efficiency, solar energy, and day length, are given in Table 12 for sampling periods between 13 October 1973 and 10 October 1974. The distribution of solar energy was generally related to that of day length. However, because the sampling schedule was implemented, in most cases, irrespective of weather conditions,

Table 12. Seasonal Interrelationships Between Gross Photosynthesis, Indices of Gross Photosynthetic Efficiency, Solar Energy, And Daylength.

Date	Gross Photosynthesis[2] $mgC/m^2/day$	Solar Energy $gm\ cal/cm^2/day$	Efficiency Index[3]	Daylength(4)
13 October 73	437	100	4.37	11.00
11 November 73	148	61	2.42	9.92
6 December 73	74	75	0.99	8.07
3 January 74	105	78	1.35	9.08
24 January 74	24	221	0.11	9.80
14 February 74	67	250	0.27	10.50
7 March 74	45	380	0.12	11.50
31 March 74	68	323	0.21	12.67
20 April 74	0	543	0.00	13.60
11 May 74	82	159	0.52	14.50
30 May 74	655	252	2.60	15.10
13 June 74	1967	445	4.42	15.32
30 June 74	1614	572	2.82	15.30
22 July 74	1007	104	9.68	14.85
12 August 74	1407	473	2.97	14.08
5 September 74	1240	380	3.26	13.00
10 October 74	466	235	1.98	11.00

(1) Gas exchange sampling dates.

(2) Calculated by multiplying mean uptake by daylength.

(3) $(mgC/m^2/day)$ per $(gm\ cal/cm^2/day)$ = gross photosynthesis/solar energy.

(4) Hours between sunrise and sunset.

gas exchange measurements were made under a variety of solar energy conditions. Gross photosynthetic efficiency was greatest during the growing season and least during the dormant season, being gradually attenuated during the fall months to winter values an order of magnitude lower than those of the summer. An analysis of possible correlative factors affecting gross photosynthesis (Table 13) revealed weak relationships between it and day length, efficiency, and solar energy, each treated independently. Gross photosynthesis was best correlated with day length and least correlated with solar energy.

Table 13. Analysis[1] Of Possible Correlative Factors Affecting Gross Photosynthesis.

Correlation	Correlation Coefficient (r)
Gross Photosynthesis[2] and Daylength[3]	0.66
Gross Photosynthesis and Efficiency Indices[4]	0.57
Gross Photosynthesis and Solar Energy[5]	0.39

[1] Linear regression analyses.

[2] $mgC/m^2/day$.

[3] Hours between sunrise and sunset.

[4] $(mgC/m^2/day)$ per $(gm\ cal/cm^2/day)$ = Gross photosynthesis/solar energy.

[5] $gm\ cal/cm^2/day$.

To examine the effect of above ground macrophyte biomass removal on ecosystem metabolism, gas exchange determinations were made on harvested sites (Table 14) at intervals of approximately 4 months

Table 14. Gross Photosynthesis And Ecosystem Respiration On Harvested[1] And Non Harvested[2] Plots.

	Gross Photosynthesis $mgC/m^2/day$	Ecosystem Respiration $mgC/m^2/day$
9 September 73		
Nonharvested	777	639
Harvested	81	694
13 October 73		
Nonharvested	437	455
Harvested	65	414
12 August 74		
Nonharvested	1405	902
Harvested	11	170
5 September 74		
Nonharvested	1240	556
Harvested	1	118

[1]"Harvested" refers to those plots which were disturbed by the complete removal of macrophyte above ground biomass and litter in June and July 1973.

[2]"Non harvested" plots contained intact communities.

and 15 months after removal during June and July of 1973. Ecosystem respiration approximately 4 months after removal, appeared to be unaffected, implicating the remaining below ground biomass, associated stubble and the decomposition thereof in the maintenance of continued respiratory activity. Approximately 15 months after removal however, the harvested plots were totally devoid of stubble and respiratory activity had been reduced to 20% of that measured within undisturbed

portions of the pond. The periphyton, perhaps dependent upon microbially mediated nutrient release from the litter, never effectively recolonized sites which had been cleared of nearly all litter during the harvesting process. Gross photosynthesis on the harvested sites was drastically curtailed, being almost immeasureable after 15 months, again reflecting the importance of the macrophytes and periphyton in the productivity of the pond.

Annual and growing season mean daily rates of carbohydrate production and degradation are summarized in Table 15, where autotrophic and heterotrophic components of ecosystem respiration are independently presented. Autotrophic respiratory rates were calculated by subtracting total net primary productivity from gross primary productivity and heterotrophic rates by subtracting autotrophic respiration rates from ecosystem respiration rates. As previously intimated by demonstrated seasonal patterns of net photosynthesis, autotrophic metabolism appears to be largely limited to the growing season, 90.2% of annual gross photosynthesis and 85.3% of annual autotrophic respiration occurring during this period. In contrast, only 58.6% of annual heterotrophic respiration takes place at this time. Consistent with the arbitrary designation of "growing season," 100% of net ecosystem production occurs then.

Metabolic Indices (Table 16) were calculated from photosynthesis, respiration, and solar energy data. It was assumed that 50% of the total insolation, wavelengths between 390 and 760 nanometers, can be used in photosynthesis (Bray, 1961; Talling, 1961). Gross primary production was converted into its caloric equivalent

Table 15. Ecosystem Metabolism: Carbohydrate production and degradation within the dune pond.

	Annual Mean Daily Rate[1] $mgC/m^2/day$	Growing Season Mean Daily Rate[2] $mgC/m^2/day$	Growing Season Prod. or Loss / Annual Production or Loss x 100
Gross Productivity	546.7	1125.4	90.2
Net Ecosystem Productivity	169.4	500.0	100.0
Ecosystem Respiration	377.3	625.4	72.7
Autotrophic Respiration	199.3	387.7	85.3
Heterotrophic Respiration	178.0	237.7	58.6

[1] 365 day period (October 1973 to October 1974).

[2] 160 day period (May 1974 to October 1974).

Table 16. Ecosystem Metabolic Indices: Seasonal changes in indices of carbohydrate production and degradation in the dune pond.
L = available solar energy; GPP = gross primary productivity;
NPP = net primary productivity; NEP = net ecosystem productivity;
ER = ecosystem respiration; AR = autotrophic respiration;
HR = heterotrophic respiration.

	Annual Basis[1]	Growing Season Basis[2]	Dormant Season Basis[3]
GPP/L	0.0042	0.0147	0.0018
NPP/GPP[4]	0.64	0.66	0.45
GPP/ER	1.45	1.80	0.52
AR/ER	0.53	0.62	0.28
HR/ER	0.47	0.38	0.72

[1] 365 day period (October 1973 through October 1974).

[2] 160 day period (May 1974 through October 1974).

[3] 205 day period (October 1973 through May 1974).

[4] It is assumed that NPP during the 1973 growing season approximates NPP during the 1974 growing season.

using 4775 cal/gm. organic wt., a compromise between values of 4770 and 4780 suggested by Cummins and Wuycheck (1971), for aquatic monocots and green algae respectively. Efficiency indices were calculated relating gross production to available solar energy at the pond surface (GPP/L), and total net primary production to gross primary production (NPP/GPP). Indices of GPP/L and NPP/GPP have been termed "assimilation efficiency" and "growth efficiency" respectively by Clarke (1946) and others. Assimilation efficiency was 0.42% annually, varying between dormant and growing season values of 0.18% and 1.47% respectively. Growth efficiency, 64% annually, varied between dormant and growing season values of 45% and 66% respectively. The ratio of gross production to ecosystem respiration (GPP/ER) is commonly termed the "P/R ratio" (Odum, 1956). Annually, the P/R ratio was 1.45 varying between dormant and growing season values of 0.52 and 1.80 respectively. Expressed as percentages of ecosystem respiration (ER) autotrophic respiration (AR) and heterotrophic respiration (HR) were quite similar annually, being 53% and 47% respectively. The dominant component (62%) of ER during the growing season was AR while HR dominated (72% of ER) during the dormant season.

Light Response Characteristics of Juncus balticus

As previously discussed, Juncus balticus was the dominant macrophyte within the dune pond. Considering the demonstrated importance of the macrophytes in terms of contribution to the metabolism of this ecosystem, it is felt that photosynthetic characteristics

of this species may be somewhat representative of the ecosystem itself during the growing season.

The response of each of the two age categories of stems (young and old) to increasing illumination (Figure 8) was similar, yet the net photosynthetic rate of the younger age category was consistently greater than that of the older at all levels of illumination.

Unlike typical light saturation curves (Ribinowitch, 1951), which beyond a linearly ascending portion at low light intensities, gradually ascend asymptotically, this species demonstrated an abrupt increase in slope between 3800 and 4500 foot candles (40.9 to 48.4 klux). Considering the illumination gradient within the 60 cm. tall photosynthetic chamber and the distribution of stem surface area of J. balticus, which increases from the apex downward, it is likely that linearly ascending response at low light intensity occurred asynchronously along the stem length.

Although light saturation was not totally achieved in this species at 5500 foot candles (59.2 klux), it is expected that only nominal increase in photosynthesis would be realized at higher light intensities. Graphically extrapolated (Figure 8), light compensation occurred at approximately 450 foot candles. The CO_2 compensation point (determination made at 4500 foot candles) was 80 ppm CO_2, approximately 24% less than an in situ compensation point determination (105 ppm CO_2) made one week later (30 June 1974) under conditions of full sunlight and similar temperature. The high CO_2 compensation point of J. balticus suggests its possession of the C_3 photosynthetic pathway (Goldsworthy, 1970).

Figure 8. Net photosynthesis in Juncus balticus at light intensities ranging between 0 and 5,500 foot candles (0 to 59.2 klux). Points represent net photosynthetic rates in young (●) and old (▲) stems.

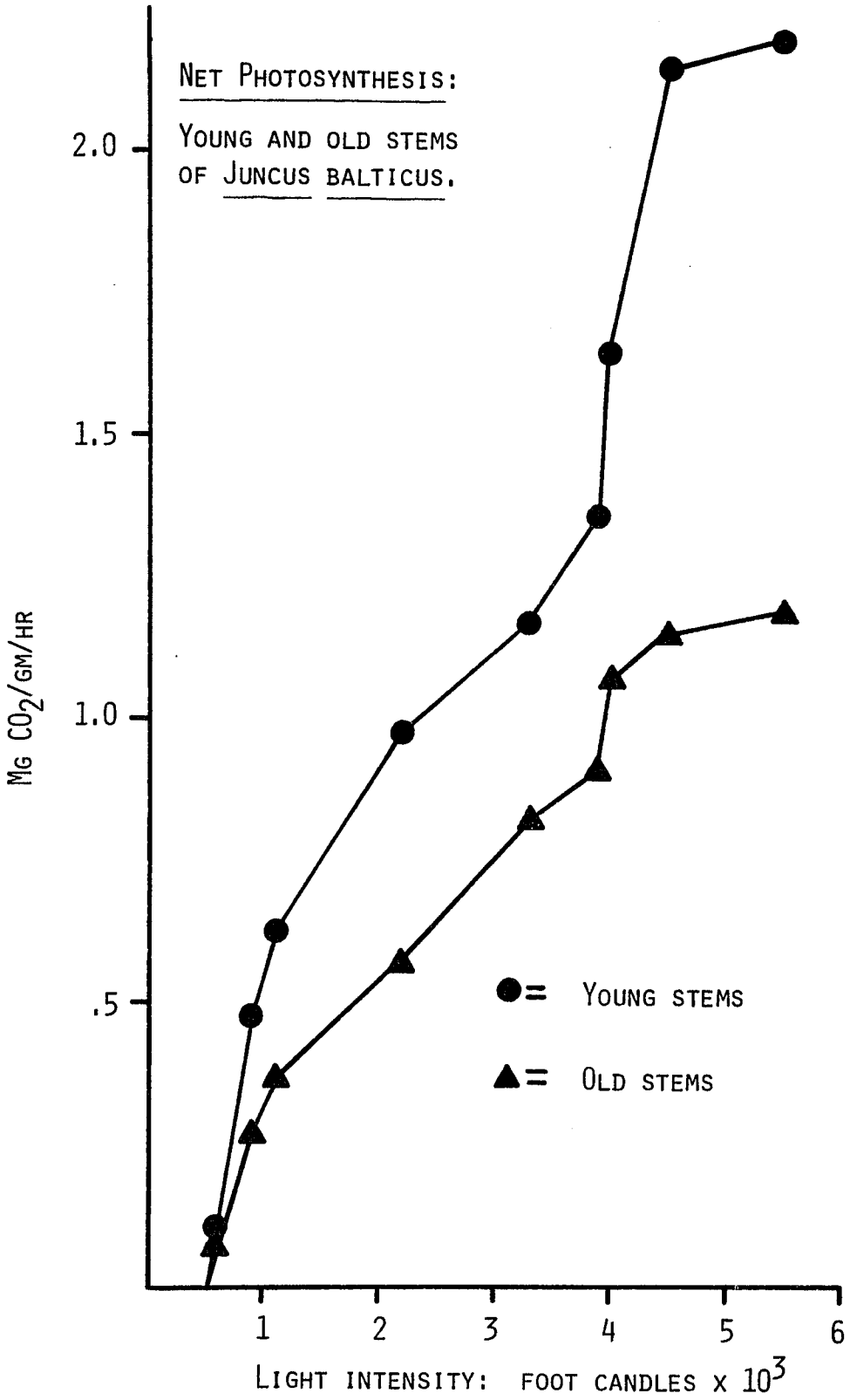
NET PHOTOSYNTHESIS:
YOUNG AND OLD STEMS
OF JUNCUS BALTICUS.
2.0
1.5
1.0
.5
MG CO_2/GM/HR
1
2
3
4
5
6
LIGHT INTENSITY: FOOT CANDLES X 10^3
●= YOUNG STEMS
▲= OLD STEMS

FIGURE 8

DISCUSSION

Algal Productivity

The seasonal distribution of algal productivity observed in this study suggests a pattern of exchange between planktonic and epipelic algal populations similar to that reported by Brown and Austin (1973). The taxonomic similarity between these two components of the autotrophic community has already been noted and the possibility of biologically or physiochemically induced habit transformations should not be dismissed. The phytoplankton productivity curve, being bimodal (late summer peak of considerably less importance than that of early summer) may indicate colonization of the open water by algal organisms generally restricted to the substrate.

The seasonal distributions of both phytoplankton and periphyton productivity might be explained by changes in the status of available nutrients within the pond. Although direct determinations of the nutrient status of the pond were not made, it is felt that autotrophic activity is limited by a general paucicity of nutrients. Notably, the soil of the Lake Michigan sand dunes is impoverished in this regard (Olson, 1958). Algal growth in the pond, subsequent to the early summer flush of phytoplankton growth, is largely limited to the benthic substrate where microbially mediated nutrient release from the sediments may be stimulated by rising

temperature (Hutchinson, 1957). During late summer, microbial activity possibly provides a nutrient supply in excess of epipelic algal requirements, thus enabling the reestablishment of the phytoplankton. Nutrient (silica) release from living macrophytes has been cited (Jørgensen, 1957) in the rapid growth of diatomaceous epiphytes following their coincidentally occurring exclusion from the plankton due to silica depletion.

Surface inhibition of planktonic algal photosynthesis by light of high intensity has been widely observed (Talling, 1957; Jonasson and Mathiesen, 1959; Goldman et al., 1963; among others). Likely unimportant in deep lakes, this inhibition may be significant in shallow basins (Wetzel, 1964). The observed pattern of photosynthesis with respect to depth in the dune pond, counters this common phenomena however, and is difficult to resolve. The greater photosynthetic activity near the surface, observed during the growing season, would seem to be partially explained by increased turbidity within the lower stratum resulting from the unavoidable agitation of the flocculent substrate while positioning the sampling bottles for in situ incubation. However, the converse (greater photosynthesis near the substrate) evidenced during the dormant season, occurred under similarly disturbed conditions. The artifactual state of increased turbidity was normally dissipated within 0.5 hour after placement of the sampling bottles, and it is felt that this problem had a lesser effect on the vertical distribution of phytoplankton productivity than the presence of dissolved and particulate humic

substances, which appeared to be most concentrated in the pond water during the growing season.

Placement of bottles on the pond bottom for in situ incubation of epipelic periphyton samples resulted in the same conditions of temporary turbidity as discussed in regard to the positioning of phytoplankton bottles. During the study, great care was taken to reduce the extent and duration of such conditions however, thereby minimizing the potential for underestimation of photosynthesis due to unnatural light attenuation. In regard to estimated rates of algal photosynthesis (planktonic and benthic), the effect of these conditions on photosynthesis measurements is felt to be small.

Particularly relevant to this study, a potentially serious source of error in estimating the productivity of epipelic periphyton arises from the expansion of small experimentally measured surfaces to larger areas. Productivity estimates based on small samples, may not be entirely representative of the whole, the potential for error increasing with substrate heterogeneity. The epipelic periphyton in this study appeared quite homogeneously distributed however, and it is felt that error involved in expansion from sample area to a square meter basis was relatively small.

Self absorption of beta particles, caused by layering of epipelic algal material on the membrane filters, may have affected the counting during the late summer period of maximum periphyton biomass. During the remainder of the year however, layering of the sample material was not appreciable. This problem may result in underestimated rates of photosynthesis and can be circumvented by

combustion of the organic material for radioassay in gas phase (Wetzel, 1964), but this approach is tedious and maximum sample size is limited. Because of this and other technical difficulties involved in benthic applications of the ^{14}C technique, many investigators have used the oxygen method (Pomeroy, 1959; Pamatmat, 1968; Hargrave, 1969; among others). In a recent paper (Hunding and Hargrave, 1973) on the primary productivity of benthic algae, the two methods (^{14}C and oxygen) were shown to give similar results and it was pointed out that neither of the two was free from experimental artifacts and assumptions. The ^{14}C method however has the advantage that it does not necessitate the determination of a photosynthetic quotient (usually assumed), and furthermore it may be the only suitable method where low production would be expected.

Macrophyte Biomass and Productivity

Considering the dynamics of growth and seasonal productivity of the macrophytes of the dune pond, it is important to reiterate that *Juncus balticus* composed greater than 90% of the autotrophic biomass. It is felt, in fact, that subsequent discussion concerning the macrophytes is essentially a treatment of the dynamics of growth and productivity of *J. balticus*.

Laboratory investigations on *Juncus balticus* indicated a decline in net photosynthetic potential with leaf age. This decline has been described in a variety of terrestrial species (Wilson and Cooper, 1969; Osman and Milthorpe, 1971) and also in an aquatic emergent, *Typha latifolia* (McNaughton, 1973). These observations

may be attributed to either increased respiratory demands or to decreased carboxylation activity in the older stems. Both of these factors were likely important in rapidly curtailing macrophyte net production by mid summer as determined using the harvest method. Since both young and old shoots of J. balticus demonstrated identical CO_2 compensation points (80 ppm) in laboratory investigations, seasonally decreased net photosynthetic potential in the older shoots was unlikely related to increased respiratory demands within the shoots themselves. It is important to point out however that this conclusion is not applicable to whole plants, since the "roots" were not included in the laboratory measurements. "Root" respiration very likely increased as the photosynthetic capacity of the macrophytes affected by shoot senescence became reduced.

The importance of the rhizomal and rooted portions of the macrophytes cannot be overemphasized in this study. Below ground portions annually represented > 90% of the total macrophyte biomass. Similarly high values have been cited for Scirpus lacustris and for Phragmites communis, but the majority of values given for other "perennial reedswamp plants" are somewhat less (Westlake, 1965, 1968). Boyd (1971) estimated the contribution by "roots" to the total biomass of Juncus effusus at about 10%. This value is probably too low however, since root removal in the J. effusus study was not systematically accomplished. To my knowledge, no data exist on the biomass of any other species of Juncus.

Shoot to "root" translocation, occurring during the early summer, undoubtedly represents the movement of carbohydrates

produced in excess of the capacity of the leaves to utilize or store them. Increased below ground storage in Typha spp., evidenced at the onset of fall dormancy, has been similarly interpreted by Jervis (1969), who suggests that decreased respiratory activity in the fall allows greater net production at that time. Although some downward translocation was evidenced during the fall in the dune pond study, below ground biomass accrual was balanced by above ground biomass loss, and I have not considered this accumulation to be net production.

Late season below ground biomass accumulation may represent a strategy for survival whereby current above ground structure is resolubilized, transported, and stored in below ground organs for metabolic use during the winter or for the reformation of photosynthetic organs at the beginning of the next year's growing season. Such a strategy would likely be of great value particularly following periods of significant loss (35%) of macrophyte biomass as evidenced between 1973 and 1974.

"Root" to shoot translocation, continued production of new shoots, "root" respiration, and mortality were all likely responsible for the mid through late summer depletion of below ground biomass stores. Discussion of translocation processes in aquatic plants with reference to the role of roots and other submerged organs (Sculthorpe, 1967; Bristow and Whitcombe, 1971; among others) has been largely limited to the absorption and utilization of inorganic nutrients. In a similar context, the translocation of carbohydrates has been discussed for terrestrial grasses (for example, Smith and Leinweber,

1971; Singh and Coleman, 1974) and crop plants (Milthorpe and Moorby, 1974). Although the macrophyte community became increasingly dominated by older shoots as the growing season progressed, new shoots were continually produced, replacing losses of the older due to damage and mortality. As demonstrated by the harvested plot gas exchange experiments, the dominant respiratory component of the pond, during the growing season, was the below ground macrophyte biomass. High levels of respiratory activity were likely attributable to energetic demands imposed on the rooted organs in maintaining meristematic, translocation, and absorption processes.

Ash content estimates, compared to published values tabulated by Westlake (1965), are similar to those presented for sedges and grasses, but are somewhat lower than the content listed for other aquatic plants. Ash content of the living shoots, ranging between 2 and 4% of the dry weight, compared most closely with that of Juncus effusus (Boyd, 1971) which contains between 3 and 5% ash on a dry weight basis. Westlake's contention (op. cit.) concerning the lack of seasonal variations in the ash content of freshwater plants, apparently applicable to the above ground biomass, was not justified in this study with respect to below ground material. Seasonal variations in the ash content of the below ground biomass (7% change in 1973 and 6% change in 1974) may be related to patterns of translocation and mineral availability, although no data are available to examine these possibilities.

The calculation of macrophyte productivity, based on changes in below ground biomass (see results) seems to be unique to this

study. Moreover the observed pattern of significant below ground biomass accrual during the early summer, counters that observed in the few wetland studies in which below ground biomass estimates have been made (for example, see Westlake, 1966; Jervis, 1969; Bernard, 1974a, 1974b). In the studies cited here, below ground biomass peaks were reported in the fall, minima occurring during the early summer following a period of rapid spring depletion. It is not known whether the reverse of this pattern (as reported for Juncus balticus) represents a species characteristic, or an adaptation for existence in dune pond habitats. Perhaps an annual study of the dynamics of "root" growth of this species in a different habitat would resolve this question.

In spite of various confounding factors and technical difficulties involved, the harvest (biomass) approach used to estimate the productivity of macrophytes in this study remains the most commonly used, and perhaps the most accurate (Wetzel and Hough, 1973). Most suitable in estimating the productivity of plant populations demonstrating negligible losses between sampling periods (Westlake, 1963, 1965), the harvest technique has also been adapted to populations subject to high mortality (Mathews and Westlake, 1969). As will be subsequently discussed, a major drawback of this technique is its limitation to the measurement of large particulate matter, turnover estimates being empirically based on the accumulation of nondecomposed litter.

Alternate methods for determining productivity of aquatic macrophytes are few and these have been infrequently employed.

Moreover, it appears that our knowledge concerning the physiology of submerged macrophytes, particularly in regard to internal gas exchange (cf. Hartman and Brown, 1967; Hough, 1974), has lagged methodological advances in productivity analyses based on *in situ* metabolic techniques. Recently Wetzel and Hough (1973) have emphasized that estimates based on oxygen change and radio-carbon methods may be of questionable value or totally erroneous.

Ecosystem Metabolism

During the annual period of October 1973 through October 1974, a P/R ratio of 1.45 was estimated, reflecting the annual net ecosystem production of approximately 61.8 gmC/m^2 (Table 17). If based only on the macrophyte biomass and litter, considered collectively, this amount of production would represent an annual increase in macrophyte material of approximately 10% over estimates made in October 1973. However, when based on total ecosystem organic mass, including the biomass of other living components (algae and animals) as well as dissolved and particulate detrital mass in addition to macrophyte litter, 61.8 gmC/m^2 accumulation undoubtedly represents considerably less than 10% annual accrual.

Considering the quantitative importance and rapid turnover characteristics of dissolved organic matter (D.O.M.) in aquatic systems (Wetzel et al., 1972), an attempt to balance the carbon budget (i.e., explain deviation from P/R = 1.0) based on particulate mass would be relatively meaningless. Indeed net ecosystem production in this study cannot be accounted for on the basis of increased

Table 17. Annual Carbon Budget[1] For The Dune Pond.

	$gmC/m^2/year$
Gross Photosynthesis	199.5
Autotrophic Respiration	72.7
Net Photosynthesis:	
Macrophyte	77.4
Epipelic Periphyton	32.4
Phytoplankton	17.0
Total	126.8
Heterotrophic Respiration	65.0
Net Ecosystem Production	61.8

[1] It is assumed that allochthonous inputs are negligible.

macrophyte biomass or litter. Assuming that particulate losses (i.e., herbivory and other sources of export) were small, D.O.M. loss (not measured) may account for the 61.8 $gmC/m^2/yr$. not respired autochthonously. Changes in the water table in response to flucuations in the water level of Lake Michigan (see results) may have been important in seasonally flushing the pond.

Net ecosystem production represented a significant portion (49%) of annual net primary production (Table 17). Changes in the capacity of the pond to either respire (51%) or export (49%) net primary production, presumably in a detrital form, would be reflected in changes in both net ecosystem productivity and the P/R ratio. Non respiratory loss of perennially maintained biomass would not affect these characteristics however, both of which are calculated on the basis of production and not biomass. With this point in mind,

the significant reduction (35%) in macrophyte biomass (below ground), which occurred during the summer of 1973, may have had no effect on the P/R ratio (undetermined) at that time.

Tilly (1968) cites estimates of assimilation efficiency from a number of aquatic studies. These range from 0.2% for Root Spring (Teal, 1957) to 8.0% for Silver Springs, Florida (Odum, 1957). The annual assimilation efficiency calculated for the dune pond (GPP/L = 0.42%, where L = one-half solar incidence at the pond surface) falls within this range but is somewhat lower than most cited. Efficiencies greater than 10%, observed under manipulated conditions (Thomas, 1955; McIntire and Phinney, 1965), are uncommon and generally can be explained by the very low light intensities used. Low efficiencies are expected under natural conditions since light saturation usually excludes a significant amount of incident light from usage. Aside from physiological considerations, assimilation efficiency, when measured on an areal basis under natural conditions, is dependent upon the total surface available for photosynthesis. This surface can loosely be considered a function of standing crop per unit area. The relatively low standing crop in the dune pond is thought to be an important factor in limiting assimilation efficiency.

The phenomenon of photorespiration, well known in terrestrial plants (Hatch et al., 1971; Zelitch, 1971) has recently been examined in submerged aquatic plants (Hough and Wetzel, 1972; Hough, 1974). Gas exchange methods for estimating photosynthesis generally do not distinguish between mitochondrial (dark) respiration

and photorespiration. By failing to compensate for the photorespiratory effect on the CO_2 concentration of the light chamber, gross photosynthesis, corrected only for dark respiratory activity, was potentially underestimated in this study. The extent of such underestimation is unknown and could only have been resolved by simultaneously measuring rates of photosynthesis and photorespiration.

Afternoon depressions in gross photosynthesis observed in this study are consistent with similar patterns of net photosynthetic depression demonstrated in submerged angiosperms (Hartman and Brown, 1967; Hough, 1974; and others) and in phytoplankton populations (Doty and Oguri, 1957; and others). Hough and Wetzel (1972) speculated that "afternoon depressions" in net photosynthesis in aquatic plants are associated with increases in photorespiration. If photorespiratory activity is important in determining diurnal patterns of net photosynthesis, patterns of gross photosynthesis (uncorrected for photorespiration) would be expected to mimic those of net. Observed diurnal variations in gross photosynthesis (dune pond study) closely approximate variations in net photosynthesis, schematically depicted by Hough (1974).

Direct measurement of the aqueous CO_2 flux within the metabolic chambers, was not made during this study, as it was assumed that the aqueous flux (corrected for temperature variation) could be estimated from CO_2 partial pressure changes in the overlying atmospheric volume of the chambers (see equation 2 in methods). This calculation can be criticized because it ignores the inhibitory effect of diffusive resistance to CO_2 exchange across the air-water

interface. Theoretical aspects of CO_2 diffusion are complex, but have been applied to natural systems (Emerson, et al., 1973). Respiratory rate determinations would have been potentially underestimated in this study during periods of incubation when the evolution of CO_2 within the aqueous volume of the dark chamber exceeded CO_2 evasion into the gaseous volume. It is felt however that CO_2 exchange in the pond was in most cases sufficiently rapid to minimize this potential source of error and it is assumed that the error involved on an annual basis was small. High rates of CO_2 exchange across the air-water interface have been reported in a eutrophic lake, of the Canadian Shield (Schindler et al., 1972) where CO_2 invasion was found to equal algal net production (Schindler and Fee, 1973) and in an oligotrophic artic pond (Coyne and Kelley, 1974) where CO_2 evasion rates were estimated. Importantly, gross assimilation estimates in the dune pond study would not have been affected by this potential problem, since respiratory underestimates (dark chamber) would have been balanced by assimilation overestimates (light chamber), there being no net effect on the calculation of gross photosynthesis (dark chamber CO_2 flux - light chamber CO_2 flux).

Metabolic Implications Regarding Macrophyte Productivity

As previously demonstrated, the rapid accumulation of below ground biomass temporally corresponded to peak assimilatory activity (metabolic measurements) by the macrophytes, both occurring during the early summer. Net below ground biomass production during this

period however, is quantitatively difficult to interpret on the basis of observed gross assimilatory activity (gas exchange data). Calculations show that the magnitude of net production (including algal) could be explained on the basis of measured gross assimilation only if the ratio of net production to gross assimilation approximated 1.0 during the early summer. Although macrophyte respiration rates likely were relatively low at that time, they certainly could not have been zero, thus alternate explanations were sought for this phenomenon.

Evidence exists for CO_2 absorption by the "roots" of submerged freshwater plants (Brown, 1913; Bristow, 1969; Wium-Anderson, 1971), yet quantification of this process or the elucidation of its importance in photosynthesis, has yet to be resolved. The absorption, translocation, and photosynthetic fixation of CO_2 withdrawn from the substrate, quite obviously confounding gas exchange measurements, would result in underestimated photosynthesis determinations. CO_2 uptake by the "roots" of submerged plants may represent an adaptive advantage in aquatic environments where free CO_2 is limiting (i.e., hard water lakes). Such a mechanism would also be valuable to emergent plants, which might become limited by the atmospheric CO_2 supply during periods of calm air and active photosynthesis. It is of course also possible that inadequacies of the gas exchange method itself were responsible for the disparity between gas exchange and harvested estimates of production noted during the early summer.

As the magnitude of autotrophic respiration becomes large relative to that of heterotrophic respiration, net primary

productivity (always greater than or equal to net ecosystem productivity) can be approximated by metabolic estimates of net ecosystem productivity irrespective of export losses. Assuming that these two productivity values approach equivalence in this study during mid to late summer (the period of maximum autotrophic respiration), total net primary productivity at that time can be roughly estimated on the basis of the integrated difference between assimilation and respiration curves (Figure 4). Algal net primary production (^{14}C estimate) during this period explains only about 60% of total net primary production, calculated on the basis of the above argument, thus underestimated (harvest estimate) late season net production by the macrophytes is indicated.

Autolytic release of dissolved organic matter (D.O.M.) by Scirpus subterminalis has been shown to represent a very significant portion of the net production (Otsuki and Wetzel, 1974). In that study, estimates were made under both aerobic and anaerobic conditions, and 30 to 40% losses were reported to have occurred within 5 days after tissue death. Since the biomass (harvest) technique is limited to the measurement of large particulate matter (living biomass and nondecomposed litter), the release and turnover of D.O.M., originating from newly formed macrophyte litter via autolytic and (or) microbial processes, may have resulted in an underestimate of macrophyte net production.

The excretion of D.O.M. by living submersed macrophytes has also been shown to be quantitatively important to the measurement of photosynthetic rates (Wetzel, 1969; Wetzel and Manny, 1971).

I feel that excretory losses of D.O.M. from the living shoots were probably unimportant in the dune pond however, since nearly 70% of the shoot biomass was normally located above the air-water interface. Speculation on below ground D.O.M. loss lacks substantiation, since data on this possibility is nonexistant. Organic leakage from this very important fraction of the macrophyte biomass, might afford a collateral explanation, in addition to those already proposed for the mid through late summer depletion of below ground storage, as well as resulting in a potentially underestimated determination of macrophyte productivity.

Comparisons With Other Studies

Total net primary production estimates, based on detailed analysis of the productivity of component autotrophic populations, are relatively few. Total annual production (126.8 gmC/m^2) for the dune pond is approximately 2.5 times less than that estimated for eutrophic Borax Lake (Wetzel, 1964), but is comparable to oligotrophic Lawrence Lake, the total annual production of which was estimated at 171.2 gmC/m^2 (Wetzel et al., 1972). Compared on the same basis, it appears that production within arctic ponds (Stanley, 1974), similar in size and depth to the dune pond, is approximately 5 times less than the dune pond estimate. The production hierarchy of autotrophic components within the dune pond (macrophytes > periphyton > phytoplankton) is also characteristic of arctic ponds, and this pattern likely applies to the majority of shallow systems, in which macrophyte establishment is not impeded.

Expressed on the basis of dry weight using appropriate conversion factors, total net primary production in the dune pond can be approximated at 300 gm/m^2 annually. This value is comparable to values suggested by Whittaker (1970) for temperate grassland and continental shelf ecosystems.

A review of plant productivity by Westlake (1963), summarizes some of the data available on phytoplankton production. Annual production of phytoplankton in the dune pond (17.0 gmC/m^2) is approximately 25% of suggested values for ocean and lake phytoplankton, and only 15% of the value suggested for coastal phytoplankton. Comparisons on an areal basis can be misleading however, particularly in shallow lakes and ponds since the volume of water overlying a given unit of area is often much less than the euphotic equivalent in deeper basins. Expressed on a volumetric basis, annual phytoplankton production in the pond can be approximated at 41.5 gmC/m^3, which probably exceeds production of phytoplankton in many lakes and in the open ocean.

The importance of littoral producers (i.e., macrophytes and periphyton) in basins having a morphometry such that the ratio of colonizable littoral zone to pelagic zone of production is large, must be reemphasized. Contributions by the macrophytes and periphyton collectively accounted for approximately 87% of the total annual production of the dune pond. The importance of littoral producers has been similarly demonstrated in other basins. Treated collectively, production by the macrophytes and periphyton accounted for greater than 70% of total annual production in Borax Lake (Wetzel, 1964),

Marion Lake (Hargrave, 1969), Lawrence Lake (Wetzel et al., 1972), Char Lake (Welch and Kalff, 1974) and an arctic pond (Stanley, 1974). Since the majority of the lakes of the world are small and have large littoral surfaces available for colonization, the importance of macrophyte vegetation and littoral microflora cannot be ignored in studies concerning lake ecosystem structure and function.

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