SYSTEMS ANALYSIS OF NUTRIENT DISPOSAL IN
CYPRESS WETLANDS AND LAKE ECOSYSTEMS IN FLORIDA

By

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Major Department: Environmental Engineering Sciences

Models, field measurements, and computer simulations
were used to evaluate alternative systems of man's nutrient
recycling using a freshwater lake and cypress swamps in
Florida. Ecological characteristics, nutrient budgets,
organic productivity, energy relations, and interfaces with
man's economy were compared between the two ecosystems.

In Lake Alice in Gainesville, Florida, treated sewage
and thermal effluent were 82% of the inflow to the lake.
Waterhyacinths dominated the system and reduced temperature
fluctuations. Gross primary productivity measured as 15.6
to 19.4 $g\text{-}C/m^2$-day in summer. Production by phytoplankton
and submerged macrophytes in the open water ranged from 1.3
to 19.4 $g\text{-}C/m^2$-day and was damped by high flushing rates.
Nutrient levels were high in the water (0.8-2.8 mg-P/l of
phosphorus and 0.6-2.4 mg-N/l of Kjeldahl nitrogen) and in
the sediments (2.2 mg-P/g dry wt for phosphorus and 6.2
mg-N/g dry wt for nitrogen). The waterhyacinth marsh absorbed
11% of phosphorus and 49% of nitrogen inflows.

Simulated diversion of the sewage flow from Lake Alice
with a digital computer model reduced waterhyacinths by 50%
or more. Dissolved oxygen remained low. Simulated diversion
of the diluting effect of the heating plant effluent led to
complete hyacinth takeover and much greater seasonal oscilla-
tions in chemical parameters. Simulated hyacinth control
caused the greatest dissolved oxygen fluctuations when spray-
ing and periodic harvesting were tested and the least with
continuous harvesting.

Field data from a cypress dome receiving secondary sew-
age showed overflow if the water flow was greater than 2.5
cm/wk. Loading rates of up to 13.3 cm/wk were tested. Cypress
tree biomass in two experimental domes was estimated to be
13.6 and 17.5 kg/m^2. Net primary productivity was 600 g/m^2-yr
in sites in the Withlacoochee State Forest, 192 g/m^2-yr in a
wet site with diverted drainage, and 416 g/m^2-yr for a drained
site. Diurnal oxygen changes in the pond of a control cypress
dome indicated a peak of production in early spring. Light
was limited in summer by the canopy and in winter by the
shading effect of the stems. In the dome receiving sewage,
standing water was coated with a mat of duckweed stimulated
by high nutrient levels (up to 12 mg-P/l of phosphorus and
4 mg-N/l of nitrogen). After 8 months of sewage application,
phosphorus content doubled in the upper sediments, but nitro-
gen did not increase. When loading was high and water over-
flowing, 4% of the phosphorus and 76% of the nitrogen were
retained. When loading was low without much overflow, 75%

of the phosphorus and 93% of the nitrogen were absorbed.

Simulation of harvesting and drainage of a cypress dome caused excessive growth of understory and likelihood of destructive fire. Organic peat doubled in volume and tree biomass tripled over a 100-year period in a simulation featuring undisturbed conditions. Recovery time of trees after harvesting depended on the degree of harvesting and initial biomass. Simulated addition of sewage caused cypress growth only if the shading effect of the trees on the understory was significant. The angle of the sun and the deciduous nature of cypress were significant features in the simulations of annual patterns in a dome.

The two systems responded similarly to the addition of nutrients through the introduction of plants with low quality structure, intermediate in biomass between phytoplankton of the lake and trees of the dome. Relative C:N:P ratios for the systems were 38:2.7:1 for the lake and 57:12:1 for the forest. Cypress wood has an energy quality 40 times that of water-hyacinth biomass. Preliminary evaluation of cypress dome, lake, and technologically based nutrient disposal alternatives suggests that the cypress system may realize a higher work service per purchased energy invested.

INTRODUCTION

Man and nature are interconnected with many energy path-
ways that contribute to the life support of man, demonstrating
his symbiosis with nature. Domestic ecosystems such as agri-
culture and commercial forests yield food and fiber in return
for services supplied by man in fertilization, soil tilling
and pest control. Natural landscapes have ecosystems that
assimilate air and water pollution, conserve water, and con-
trol floods. Assimilation of nutrient waste is one of the
most important of the symbiotic roles of ecosystems. This
study compared two types of Florida ecosystems as they adapt
to receiving high nutrient sewage waste inputs from man. One
is a lake dominated by waterhyacinths, and the other is a
cypress wetland experimentally supplied with nutrients.
Models, measurements and computer simulations were used to
help understand the whole of man's relations to these environ-
mental systems.

The cycling of nutrients in an ecosystem is a necessary
strategy for the continual survival of that system (e.g., Odum,
1960; Pomeroy, 1970). Man, attempting to be manager and a
part of nature, is faced with a broken nutrient cycle (Figure
1) and two immediate problems. On the one hand, high inor-
ganic nutrient flows from municipal and agricultural sources

1

Figure 1. A generalized diagram showing where man has
broken the basic nutrient cycle necessary
for a viable interface of man and nature.
P represents gross primary productivity by
green plants, while R is the respiratory
processes of man and nature. Symbol
description given in Figure 22.
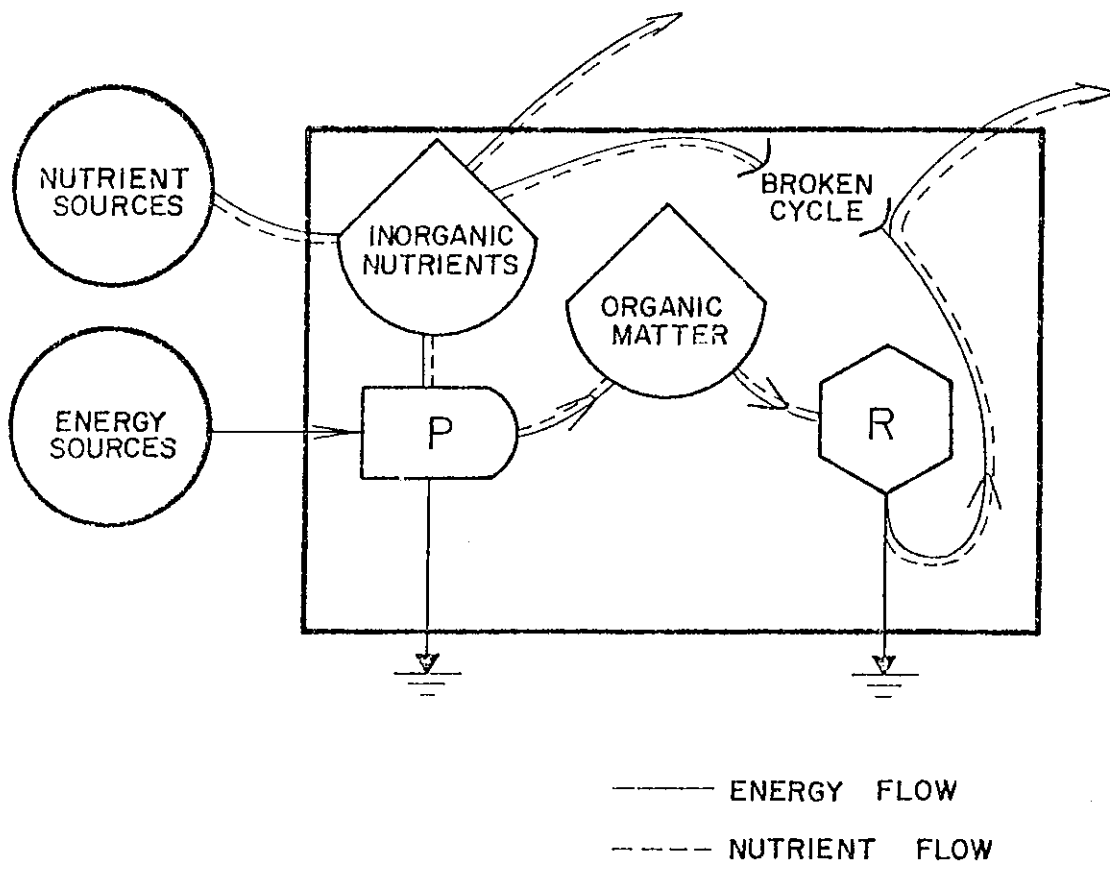
are contributing to the problems associated with eutrophica-
tion or nutrient enrichment of lakes, rivers, and estuaries.
At the same time, fertilizers for farming and forestry are
becoming increasingly expensive because of their dependence
on fossil fuel-based mining and manufacturing. These two
phenomena are shown in more detail in Figure 2, where three
alternatives for disposal of nutrient wastes are given:
eutrophication of waters, terrestrial recycling, and terti-
ary treatment by technological means. Many questions remain
unanswered about the relative costs and benefits of each
alternative.

A comparison between a lake and a cypress swamp, both
receiving secondary sewage effluent, was undertaken to draw
some general principles about high nutrient systems and to
determine relative benefits of each to man. Evaluation of
the new cypress disposal test was helped by comparison with
the conventional means of sewage disposal into an available
body of water. The comparison also allowed generalizations
of limiting nutrient concepts with systems models.

The lake site under study is Lake Alice (Figures 3 and 4),
located on the campus of the University of Florida in Gaines-
ville. It is a small lake (33 ha) with high nutrient loading
due primarily to the 2.8 million gallons per day (10.5×10^3

Figure 2. A diagram of energy flow and nutrients showing
disposal alternatives. Pathway 1 passes
nutrient wastes into bodies of water, the most
common method; pathway 2 passes nutrients to
the land; and pathway 3 uses technological
inputs for tertiary treatment with economic
and energetic costs. The wide lines indicate
major nutrient flows from the source in the
upper left, through commercial forests, agri-
culture, and man's economy to the aquatic
systems and finally to the ocean in the lower
left. Symbol description given in Figure 22.
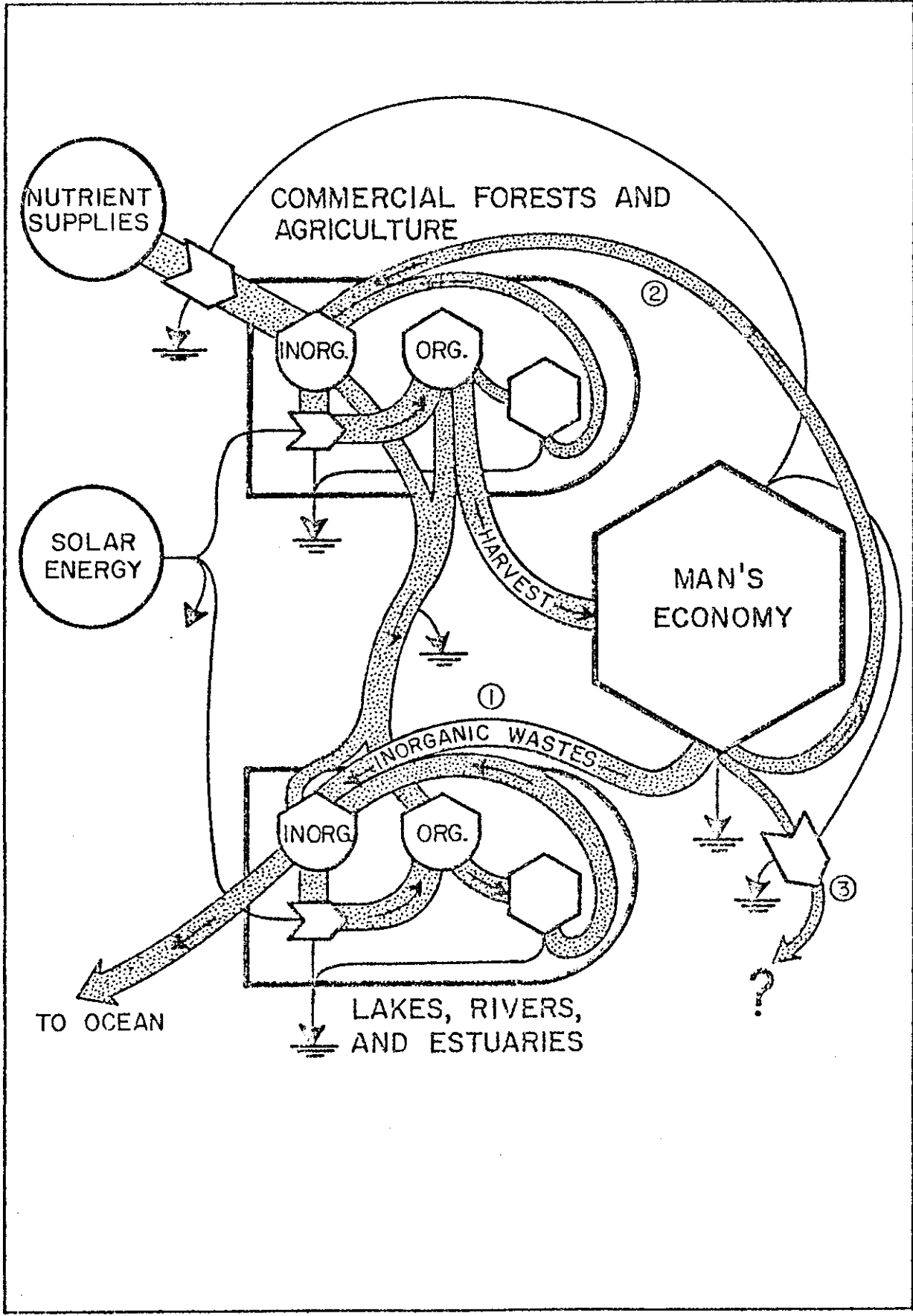
Figure 3.   General map of research areas in Alachua
             County, Florida, including Lake Alice
             research site and two cypress research
             sites.

GENERAL MAP OF RESEARCH
SITES IN ALACHUA COUNTY,
FLORIDA

N

SCALE IN MILES

Austin Cary Cypress
Research Site

State Road No. 24

Owen-Illinois Cypress
Research Site

U.S.

441

Gainesville

Corporate

Limit

Lake Alice Research Site

Newnans

University of Florida
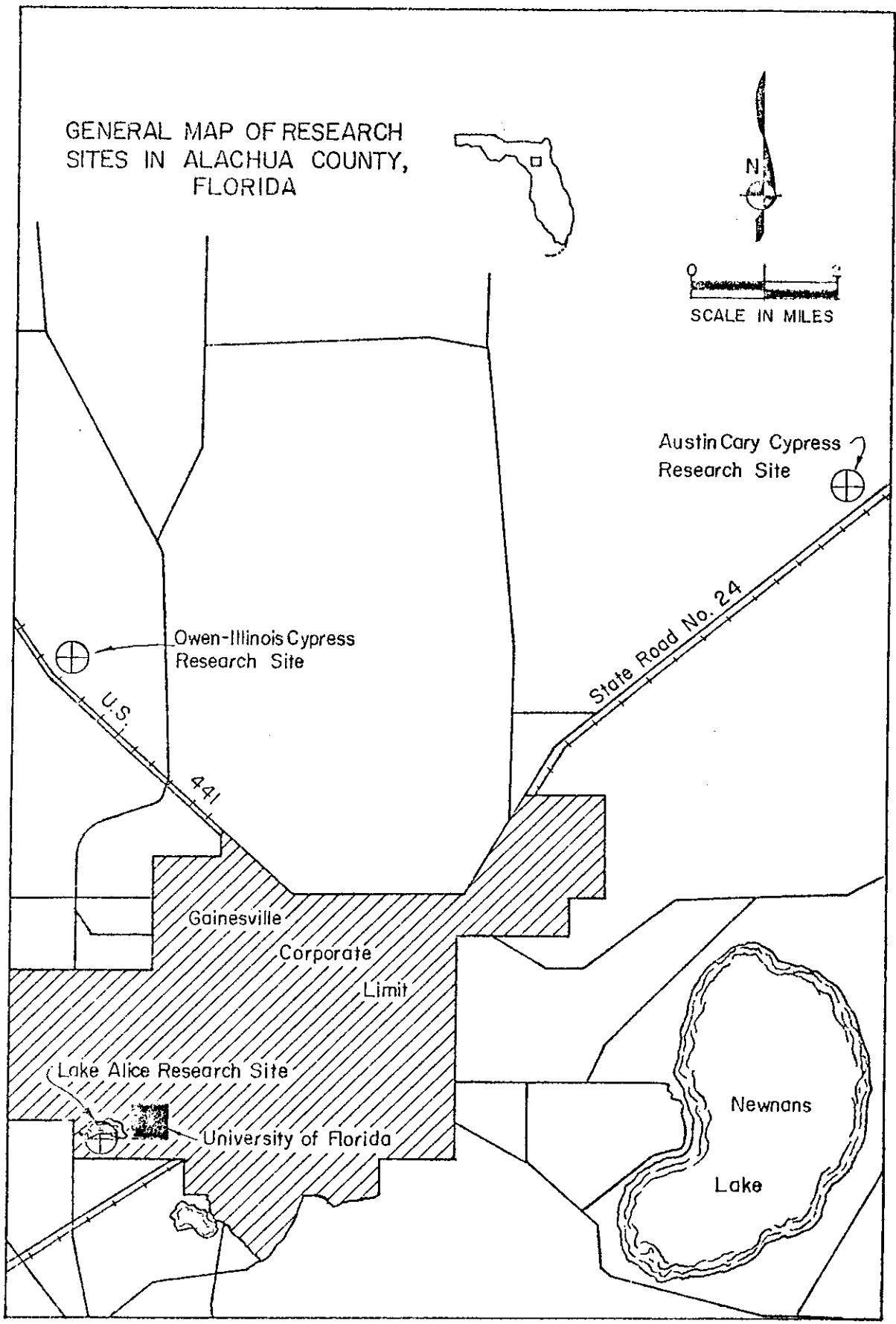
Lake

Figure 4. Contour map of Lake Alice area, Gainesville, Florida, showing approximate watershed boundary. (Obtained from USGS topographic map, 7.5 minute series, Gainesville East Quadrangle, 1966.)

LAKE ALICE WATERSHED

GAINESVILLE, FLORIDA

APPROXIMATE WATER-SHED BOUNDARY

75 — TOPOGRAPHIC CONTOURS (FT ABOVE M.S.L.)

0 KILOMETERS 1
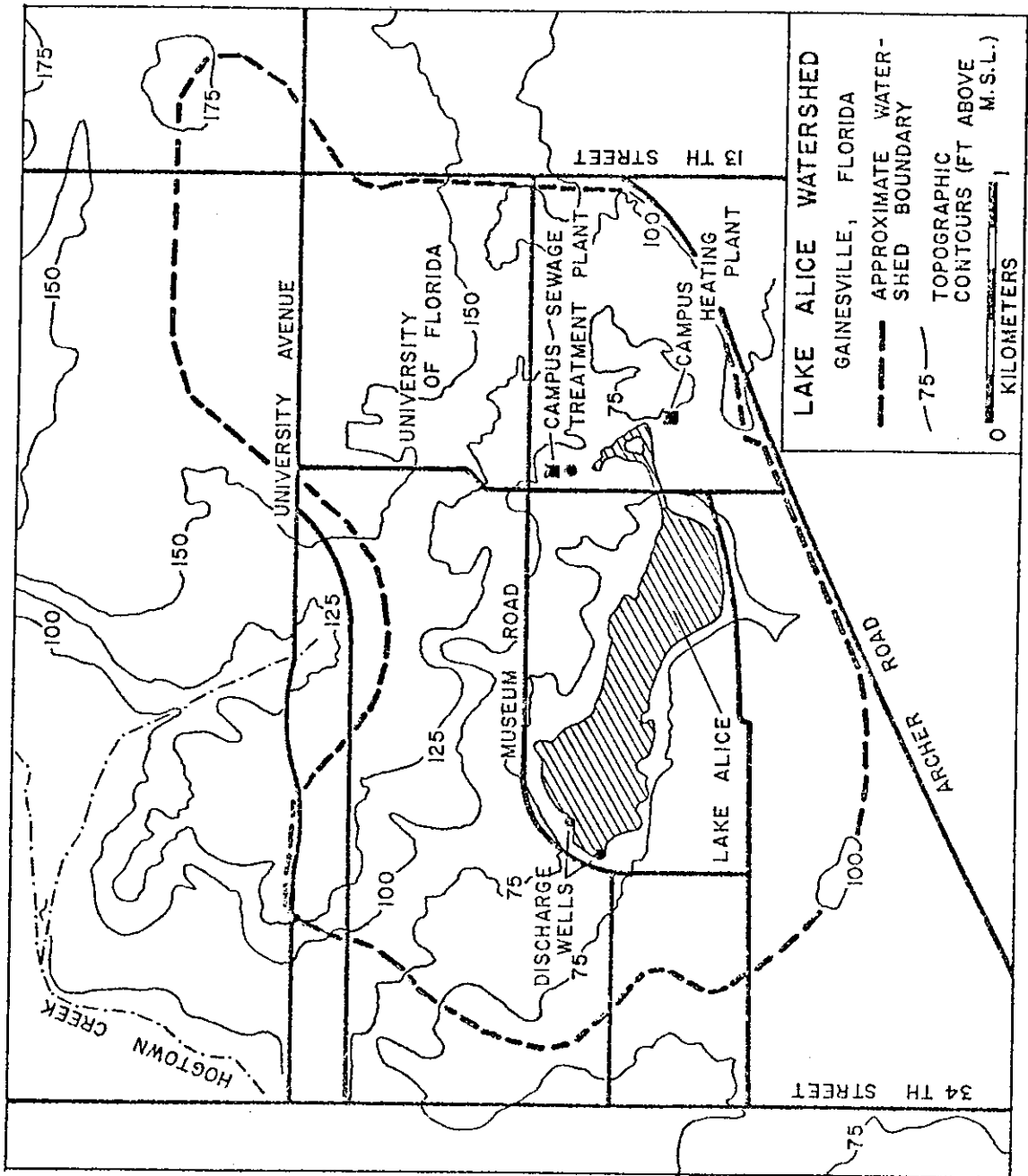
m^3/day) of secondary sewage effluent being discharged into its eastern marsh. It has been classified as highly eutrophic or even "senescent" by Brezonik and Shannon (1971); mats of waterhyacinths flourish across most of its surface. Only the western third of the lake is kept open from hyacinth cover by spraying and harvesting done for aesthetic reasons. The lake also receives heated effluent from the campus heating plant. Waters from the lake discharge to groundwater through pipes installed down to the Floridan Aquifer. Some water is pumped from the lake to irrigate surrounding agricultural fields.

The cypress wetlands used in this study (Figures 3 and 5) are the main research sites under study in a project of the Center for Wetlands, sponsored by Rockefeller Foundation and RANN division of National Science Foundation, entitled "Cypress Wetlands for Water Management, Recycling, and Conservation" (see Odum, 1972b; Odum et al., 1974). Commonly referred to as cypress domes or cypress ponds, these pockets of cypress trees are located in areas of low relief with seasonal standing water, amid drier pine flatwoods. Figure 5 shows the main experimental site north of Gainesville on land leased from Owens-Illinois, Inc. Secondary sewage and groundwater are being applied to various cypress domes at this site. In addition to sewage disposal, interactions between man and these cypress domes involve drainage, fire, harvesting of wood products, and microclimatic actions on houses.

Figure 5.   Site of experimental cypress domes northwest
            of Gainesville, Florida, on lands provided
            by Owens-Illinois, Inc.   (Contour map obtained
            from USGS topographic map, 7.5 minute series,
            Gainesville East Quadrangle, 1966.)

EXPERIMENTAL CYPRESS
WETLANDS—OWENS ILLINOIS SITE
GAINESVILLE, FLORIDA

———180——— TOPOGRAPHIC
CONTOURS
(FEET ABOVE M.S.L.)

KILOMETERS
0   1

Simplified models which display analogous features of the lake and cypress systems are given in Figure 6. These models and the more complex models in Figures 7 and 8 guided field work and were a basis for subsequent computer simulation of the lake and the cypress dome. Included are both nitrogen and phosphorus, the nutrients cited frequently as the two most important mineral elements in ecosystems. The main autotrophic components in the lake system included are waterhyacinths and an open lake phytoplankton-benthic producer community, while the cypress dome model has cypress trees and duckweed with some aquatic or semi-aquatic understory. Organic matter on the bottom is a significant storage in both systems. Dissolved oxygen is important to each ecosystem and often limiting to respiration. The hydrologic inflows are primarily rainfall, runoff, and man-introduced flows, while evaporation, transpiration, and drainage dominate the water losses. Waterhyacinth control, in the forms of mechanical harvesting and chemical spraying, and well injection are shown as the primary mechanisms of lake management in Figure 7. Manipulation of the cypress swamp by man is shown in Figure 8 to occur primarily through harvesting of trees and altering of the surrounding drainage patterns.

Eutrophication and the Waterhyacinth System

Eutrophication is the accumulation of nutrients and subsequent increase of aquatic primary productivity. Where man

Figure 6. Generalized working models for (a) lake
           system, and (b) cypress wetlands. Each
           system shares analogous state variables
           including nutrient, biomass, and sediment
           components. See Figure 22 for description
           of symbols.

(a)

(b)
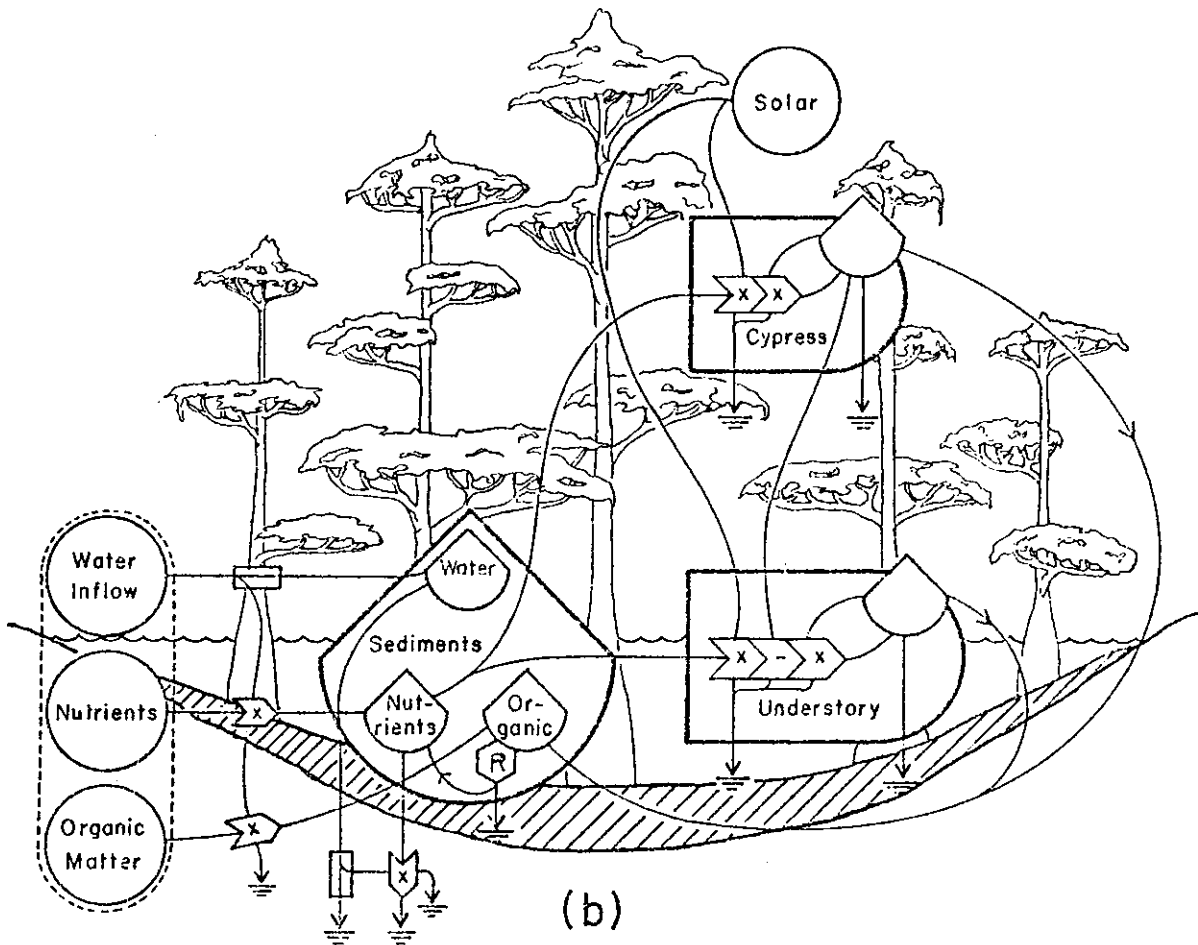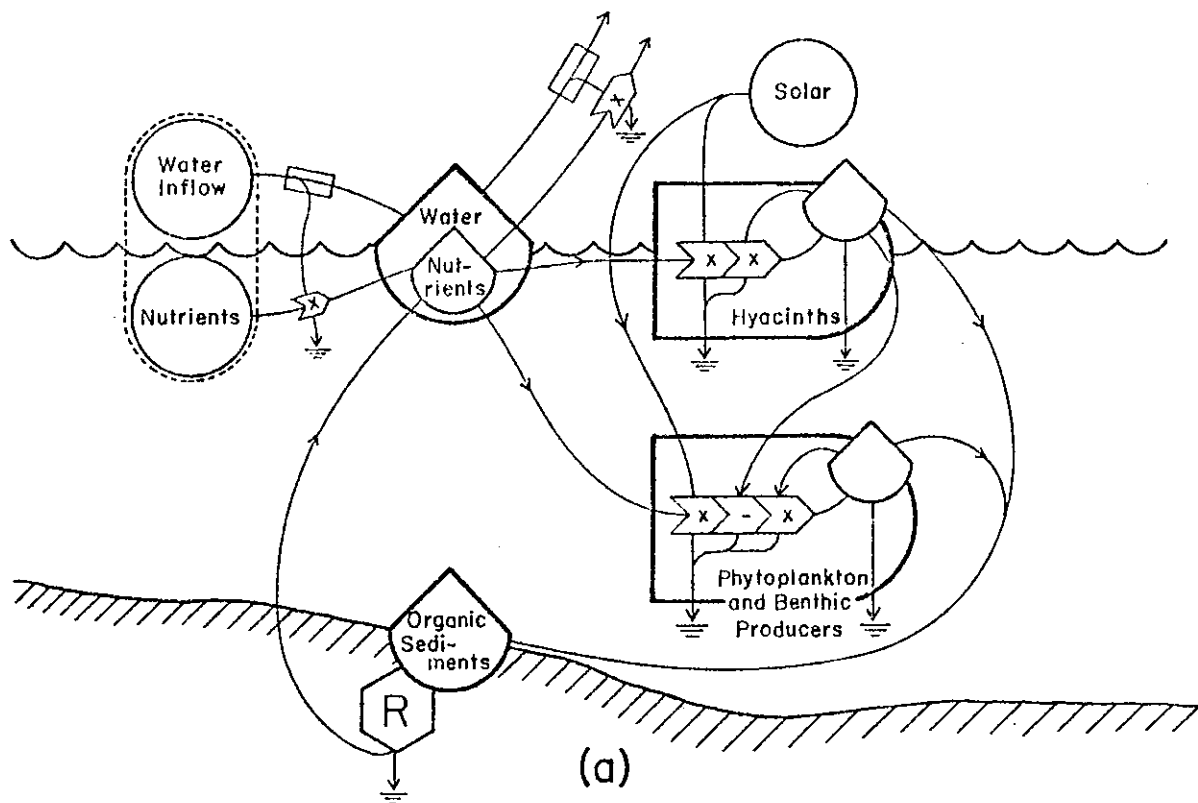
Figure 7. Systems diagram of Lake Alice. Symbol description is given in Figure 22.
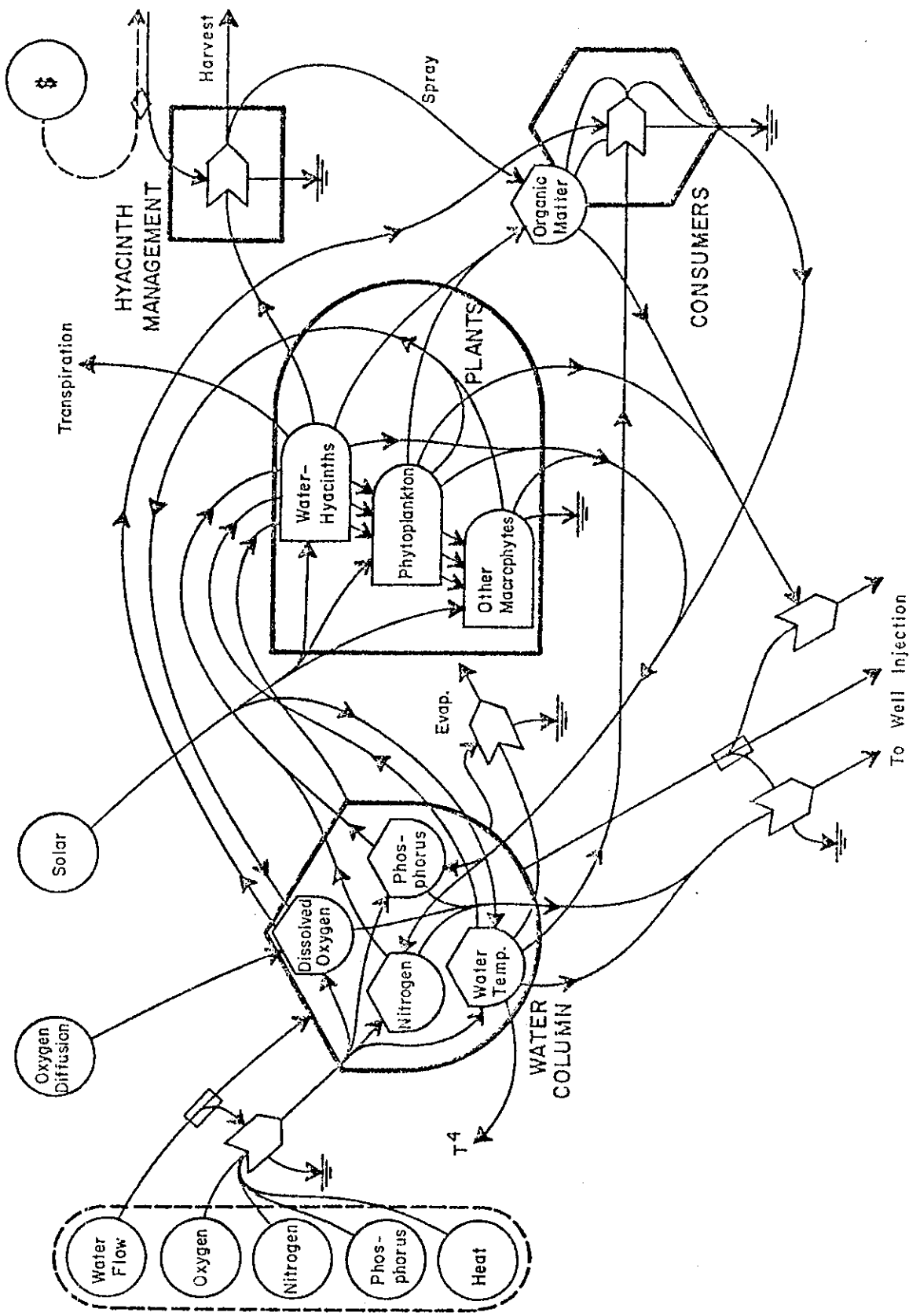
Figure 8.   Systems diagram of cypress dome.   Symbol description is given in Figure 22.
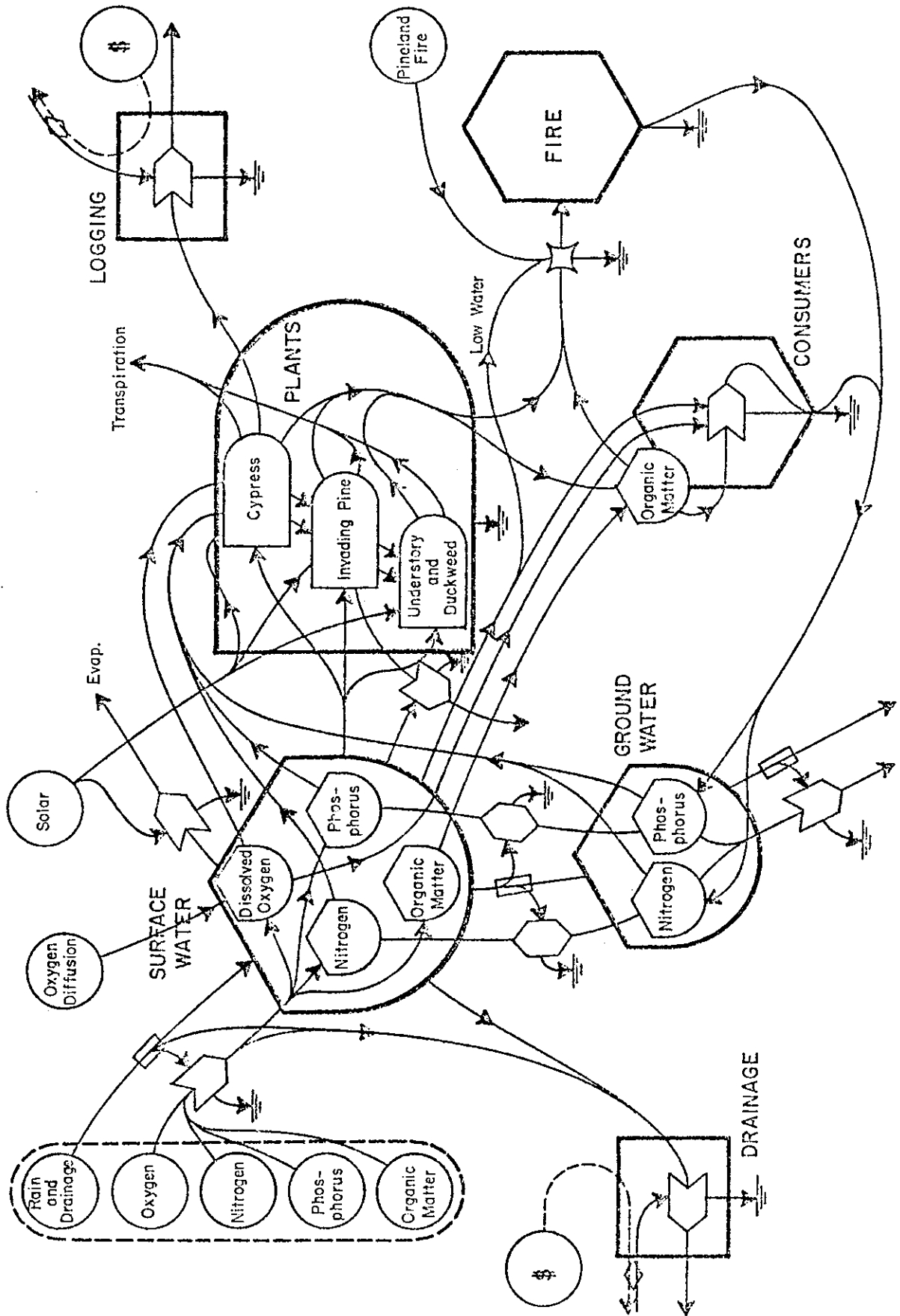
causes the nutrient additions, it is often called cultural eutrophication. Nutrients are transferred from one system (terrestrial/urban) to another (aquatic). When eutrophication is extensive, there may be associated problems for man's activities. The problems are of world-wide economic concern. Unsightly algal blooms and organic depositions may reduce recreational uses of lakes, while prolific aquatic weed growth often impedes boat traffic. Chemical, biological, and physical features change significantly, and it is often postulated that eutrophication accelerates nature's slow process of lake succession (e.g., Hasler, 1947). If nutrients originate from domestic waste, disease risks are increased. These points and others have been addressed in several edited volumes (National Academy of Sciences, 1969; Likens, 1972; Allen and Kramer, 1972; Middlebrooks et al., 1974) and individual publications (McCarty, 1966; Sawyer, 1966; Fruh et al., 1966; Fruh, 1967; Lee, 1970; and Hutchinson, 1973) and will not be discussed here further.

Florida Lakes

Florida has a wealth of freshwater lakes of varying water quality and morphometric character. They are atypical of temperate lakes as described in the classical limnology studies. Most of Florida's lakes are sinkhole lakes, a direct result of the porous karst topography of the state in which the acid conditions created by rainfall and organic accumulation tend to dissolve the underlying limestone. Because of

the mild subtropical winters, high phosphatic deposits (see Odum, 1953; Gilliland, 1973), and general shallow nature of Florida lakes, moderate eutrophic states may be usual rather than exceptional in the state. Notable exceptions are the trail ridge lakes of northcentral Florida where the lake basins are found in low nutrient, sandy deposits. The trophic states of these and other Florida lakes were examined by Brezonik and Shannon (1971) and were found to coincide well with calculated nutrient loadings.

Waterhyacinth System

One of the more common results of high nutrient and high flow conditions created by the disposal of nutrient wastes in Florida is the dominance of the waterhyacinth (*Eichhornia crassipes*). The waterhyacinth is a floating aquatic plant that has proven to be a significant economic burden to many tropical and subtropical regions of the world where open water storage is desired. It is a highly productive plant (Penfound, 1956; Westlake, 1963; Bock, 1969) when found in high nutrient waters, and populations can double their surface area coverage in two weeks (Penfound and Earle, 1948). Its floating ability and sail-like leaves give it mobility to infest new areas quickly. It generally propagates vegetatively, forming a mat of thousands of plants connected together as one by a maze of underwater stolons. The mats become impenetrable to watercraft and hamper recreational uses of lakes and rivers.

Conditions that allow invasion by waterhyacinths lead to an ecosystem very different from that which preceded it. There is a net accumulation of organic matter under the mat. Dissolved oxygen is diminished due to reduction of oxygen diffusion by the mat and to respiration of roots and decomposing hyacinths. Carbon dioxide levels increase well beyond open water values (Ultsch and Anthony, 1973). A wealth of invertebrates (O'Hara, 1967) and vertebrates (Goin, 1943) are attracted by the increased substrate and large root structure associated with the waterhyacinth. O'Hara found over 55 species among 44,000 invertebrate specimens, including a diversity of about 33 species per 1,000 individuals for insect larvae alone. Sirens, newts, and some frogs dominate the lower vertebrates. Fish life is mostly restricted to air gulpers, such as the mosquito fish (*Gambusia affinis*) and the topminnow (*Fundulus chrysotus*). Higher trophic level fishes apparently use the hyacinth coverage as feeding locales.

The hyacinth mat can be a pioneer stage for filling in a lake, followed by a succession of rooted aquatic plants and woody plants. In other cases, where sediments are continually washed away or removed, a steady state can result. Morris (1974) found that the plant seems ill-equipped to invade areas already dominated by some other aquatic plants. The mat also appears to have an effect on heat exchange between the lake and the atmosphere, stabilizing year-round water temperatures (Ultsch, 1973).

Several feedback schemes have been suggested to enable
the waterhyacinth growth to benefit man, including its use as
a protein supplement for feedlots (Boyd, 1968a,b; Taylor,
1969), as a possible pulp source for papermaking (Nolan and
Kirmse, 1974), and as a tertiary treatment of sewage wastes
(Clock, 1968; Sheffield, 1967; Boyd, 1970; Rogers and Davis,
1972; Furman et al., 1973). Apparently no extensive appli-
cations have been made to date. Control schemes have had
little success except under very intense schedules with con-
troversies raging as to the relative merits and flaws of bio-
logical, chemical, and mechanical control. Baker et al.
(1974), for example, found that white amur (*Ctenopharyngodon
idella*) at a density of 1,900 fish/ha maintained some control
of hyacinths. This was well in excess of normal fish densi-
ties for aquatic weed control.

Wetlands as Potential Nutrient Sinks

Terrestrial recycling of high nutrient wastes, one of
the pathways in Figure 2, may take on greater importance as
an alternative to eutrophication and expensive fertilizers.
A literature review of some of the many applications of waste-
water to normally dry terrestrial ecosystems is given in
Appendix A. Most of the engineering problems associated with
these projects involve the increased hydrologic loading,
which tends to transform the land system into a wet forest
little resembling its natural state. Long periods are

required for adaptation. Distribution of wastewaters to wet-
lands which are adapted to flooded conditions for at least
part of the year may be a more suitable scheme for nutrient
removal and urban runoff collection.

"Wetlands" is a very general term used for any "lowlands
covered with shallow and sometimes temporary or intermittent
waters" (Shaw and Fredine, 1956). Many different names have
evolved for these lands as a result of both cultural and eco-
logical differences. Bogs, moors, swamps, domes, marshes,
and sloughs each inspire a certain image of wetlands. Many of
these areas are being drained and altered as man continues his
urban and agronomic expansion. Niering (1968) estimates that
"as a result of drainage, dredging, filling and/or pollution
we have in the coterminous United States reduced the nation's
wetland asset to 70 million acres, slightly more than half
the original acreage (estimated 127 million acres)" (p. 177).
Florida's wetlands (Figure 9) are experiencing a similar
demise as drainage canals continue to make incisions across
the shallow landscape.

Some studies have been undertaken to evaluate potential
contributions of wetlands to nutrient uptake. Grant and
Patrick (1970) report on Tinicum marsh, an area of aquatic
perennials and annuals near Philadelphia. Significant reduc-
tions in phosphorus and nitrates were experienced. Wisconsin
marshes have been investigated by Bentley (1969) and Klopatek
(1974) for their effects on water quality and nutrient cycling.
Each investigator found seasonal fluctuations in the discharge

Figure 9. Map of Florida and Alachua County wetlands
            and urban centers (from Odum, 1972b).
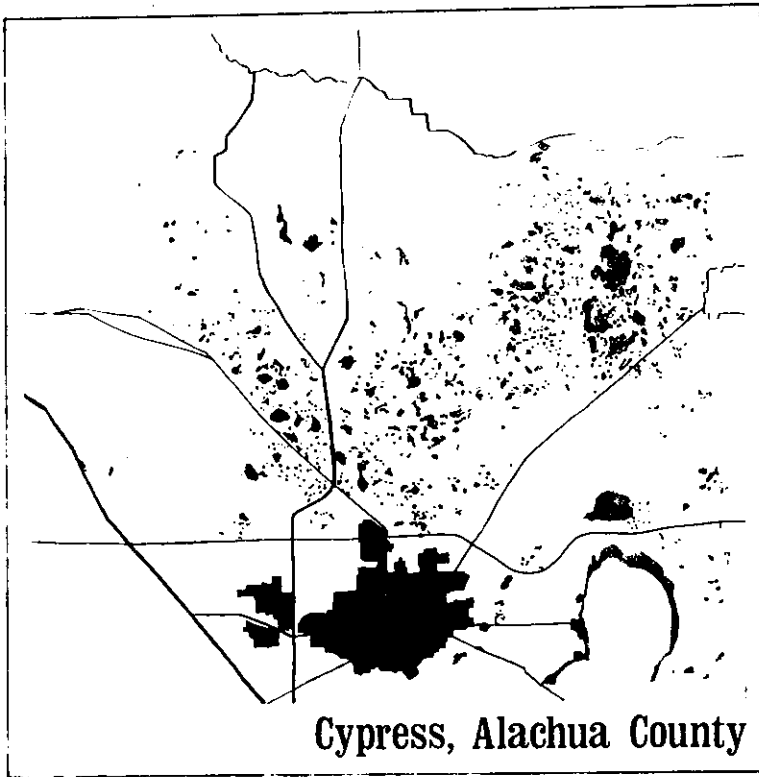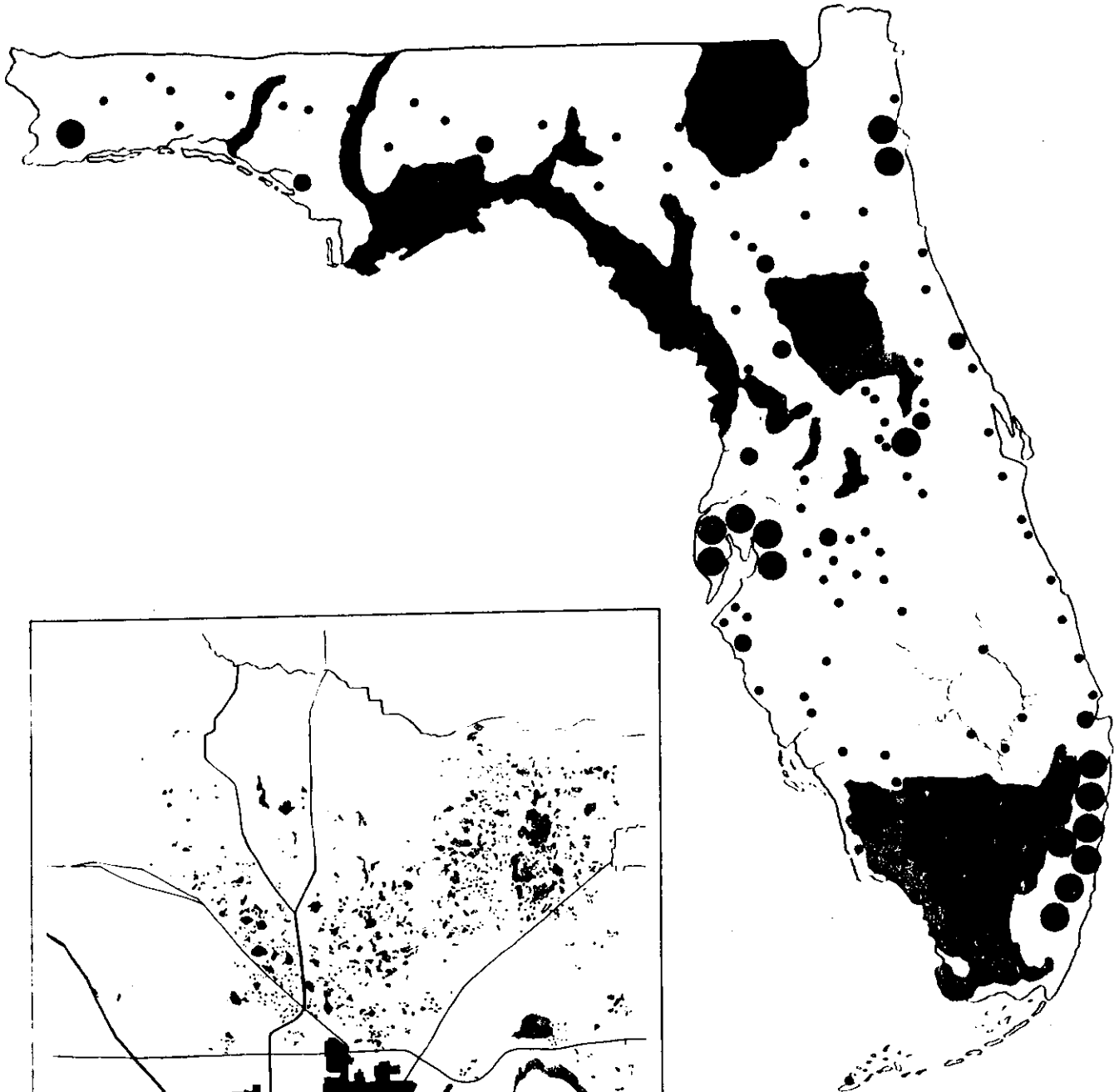
Cypress, Alachua County

POPULATION CENTERS

● 100,000-200,000

● 70,000-100,000

· 1,000-70,000

Wetlands And Urban Centers

concentrations of nutrients from the marshes, suggesting a
net uptake of the elements in the summer and a net discharge
in the nongrowing season. Kadlec, Kadlec, and Richardson
(1974) have begun a study, through field measurements and
computer techniques, on the effects of secondary sewage on a
Michigan marsh system.

Forested wetlands have only recently been researched to
any great extent for their nutrient uptake capacities. Kitch-
ens et al. (1974), in measuring the effects of South Carolina
forested wetlands on chemical, physical, and biological param-
eters, found significant reductions in phosphorus (on the
order of 50%) although reductions in nitrogen species were
not consistently observed. Brown, Bayley, and Zoltek (1974)
give preliminary evidence that a forested wetlands area in
central Florida receiving sewage for nineteen years proved
to be a nutrient sink with the added benefit of significantly
greater tree growth in the sewage-receiving area when compared
to a control area.

Cypress Domes

Cypress domes or ponds (Figure 10), dotting the land-
scape of pine flatwoods of the Atlantic and Gulf Coastal
Plains (Monk and Brown, 1965), may offer suitable sites for
the disposal of high nutrient wastes. These forested wet-
lands, generally only a couple of acres in size, are dominated
by pond cypress (*Taxodium distichum* var *nutans*), although they
often grow in association with tupelo and black gum (Penfound,

Figure 10.   Generalized profile of a cypress dome ecosystem (from Odum, 1972b).

Pineland

Cypress Dome

Treated Sewage

Hardpan

Surface
Groundwater
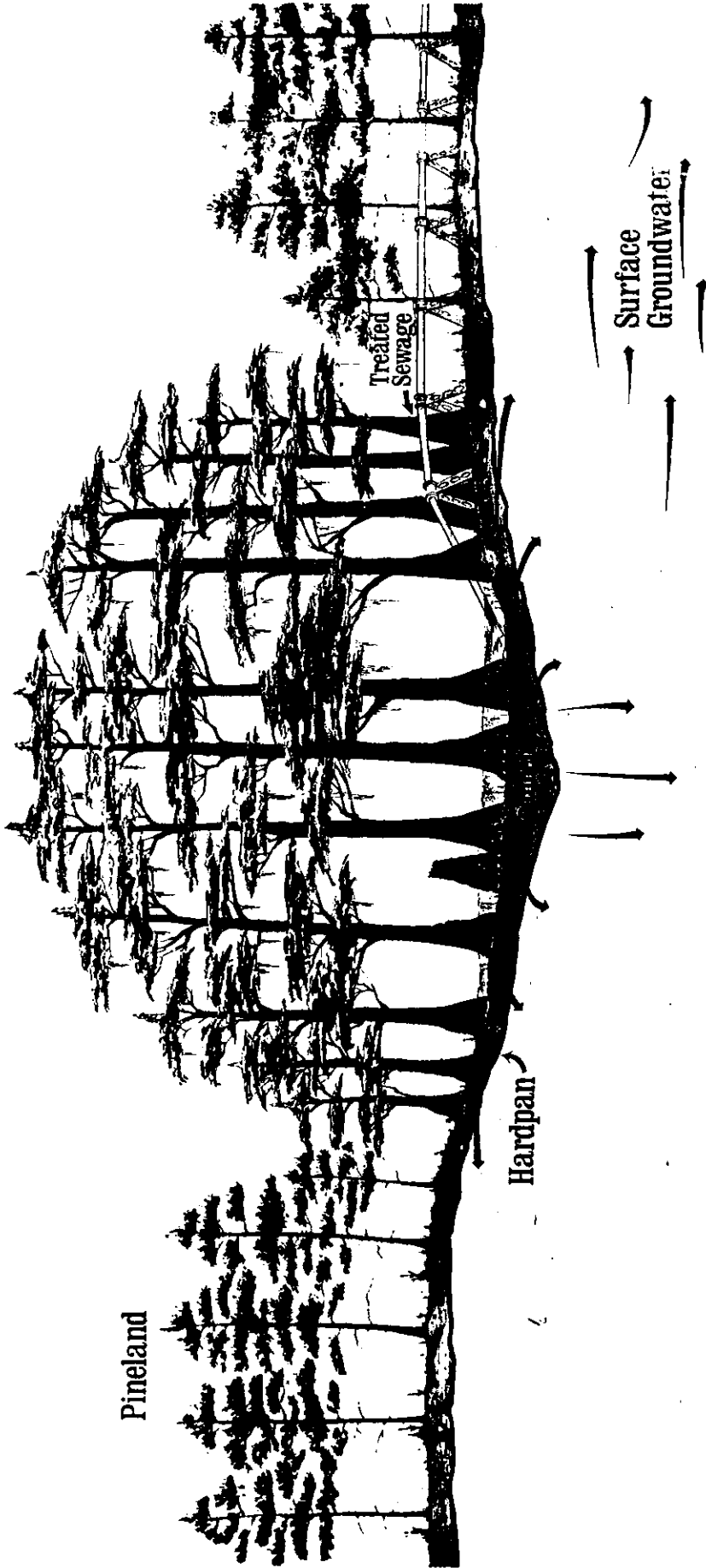
Freshwater Aquifer

Drawn by Mark T. Brown

1952). Tree species diversity has been given by Monk and McGinnis (1966) as 13 species per 1,000 individuals counted. Characteristic of these domes is a yearly period of flooding and drying, the dry period necessary for seed germination of cypress (Demaree, 1932). The dome gets its name from its profile of larger trees in the center and smaller trees near the edge. This phenomenon has been suggested to be due to soil conditions (Harper, 1927), fire (Kurz and Wagner, 1953), and a gradual increase in the water table (Vernon, 1947).

In addition to nutrient uptake, these cypress wetlands may prove to be a valuable part of the Florida landscape through their roles in timber production, storm water retention, wildlife habitats, and groundwater recharge. Cypress wood, due to its durable nature, has been especially valuable to man for many uses, from building construction to fence posts. All of these functions make the cypress dome an ideal system in which to study the fitting of man and nature together in a symbiotic partnership.

Mathematical Approaches to the Concept of Limiting Nutrients

The treatment of limiting factors in mathematical form requires unification in order to address, through mathematical modeling, problems such as eutrophication and nutrient waste recycling. Considerable speculation and some mathematical work have been applied to the effects of external factors on the process of photosynthesis in plants.

Some Early Limiting Factor Models

Early efforts on the question of limiting factors were led by Liebig (1840) in what is now commonly called Liebig's Law of the Minimum. This law states that a process is limited by the quantity of one nutrient element present in minimal quantity relative to its optimal quantity. A second principle, popular in the last half of the nineteenth century, was that of the three "cardinal points" (Sachs, 1860) whereby biological processes require a certain minimum concentration of a limiting factor to begin, attain an optimum at a certain level of the limiting factor, and diminish as maximum tolerable concentrations are exceeded. Rabinowitch (1951) suggests three general types of kinetic or limiting factor curves based on previous writers' hypotheses. These curves, plots of productivity or growth versus limiting factors, have been a popular means of displaying limiting factor relations. The first type, or Blackman type (Blackman, 1905), is shown in Figure 11a and consists of a linear ascending part terminated by a sharp break and a horizontal plateau. The interaction between sunlight or nitrogen with phosphorus is given in this example. Bose (1924) offers a slight variation (Figure 11b) in which the initial slope is dependent on the second variable, in this case, sunlight. This is referred to by Rabinowitch as a kinetic curve of the second type or Bose type. In a series of experiments Bose had verified his Law of Product, which states that "the resultant effect of the simultaneous variation of factors is not the sum, but the product of the

Figure 11.   Limiting factor curves showing possible rela-
             tionships among external factors and primary
             production: (a) first type or Blackman type
             with common initial slope and a sharp break
             in curves; (b) second type or Bose type with
             entirely different curves for different
             values of other factors; and (c) third type
             with different initial curves converging to
             a common asymptote (Rabinowitch, 1951).

(a)

(b)

(c)
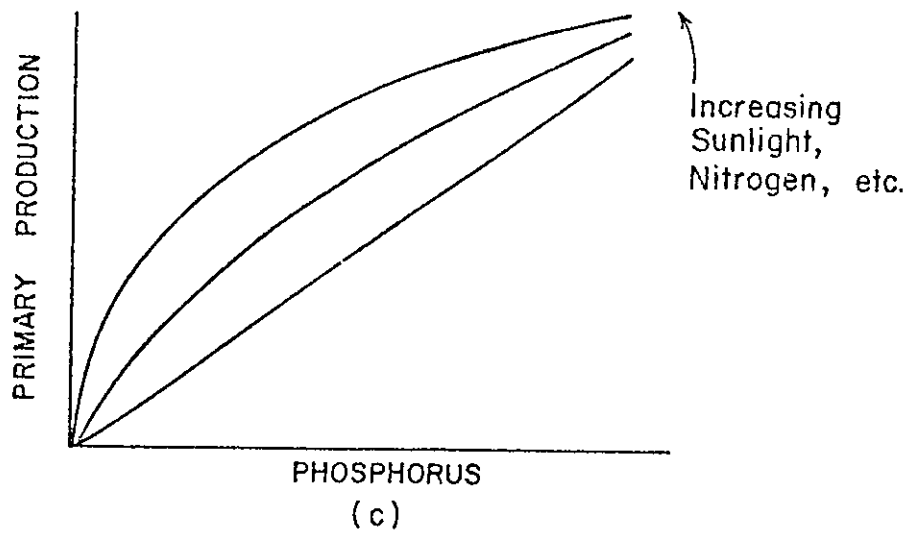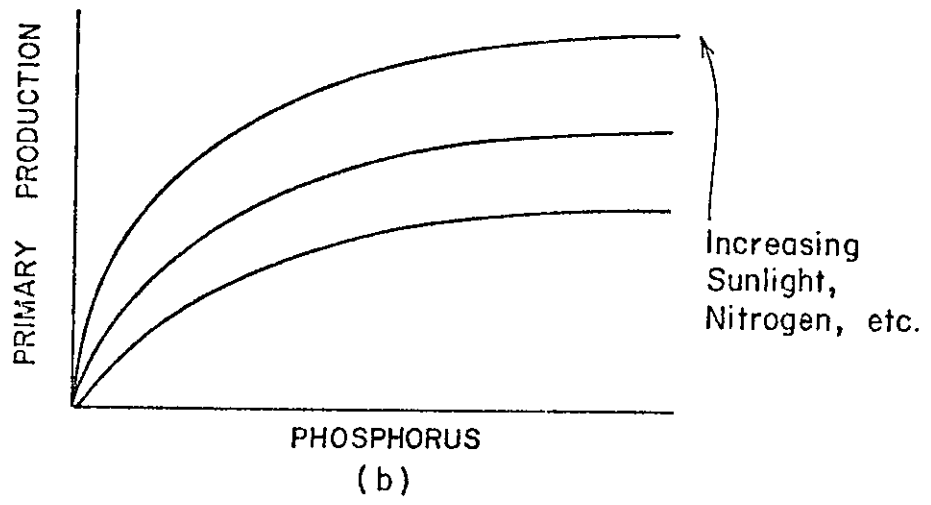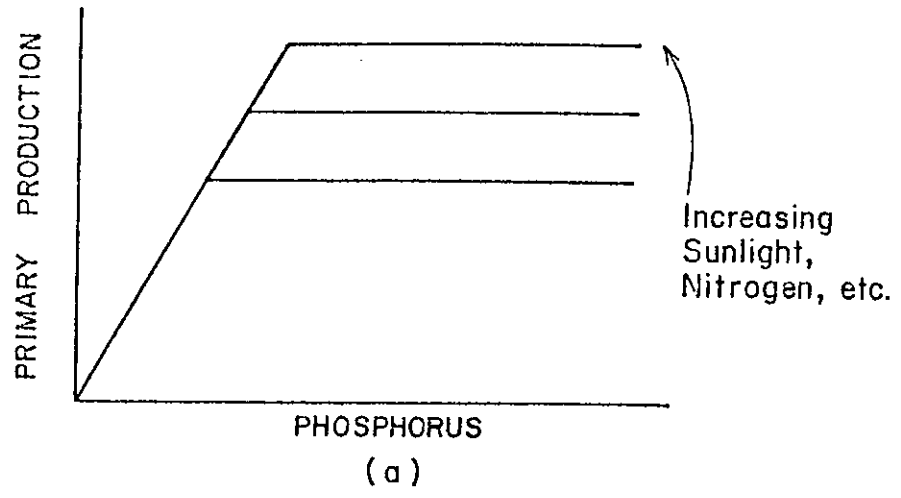
effects of the individual factors" (Bose, 1924, p. 265). A third type of curve as given in Figure 11c "is characterized by final convergence in a common saturation plateau" (Rabino-witch, 1951).

Mitscherlich (1909) presented one of the first mathematical interpretations of the limiting factor concept in the form

$$dy/dx = (A - y) k$$

or

$$\ln(A - y) = c - kx$$

where y = production

x = limiting nutrient

A = maximum productivity

k = constant.

The differential form, assuming zero initial conditions, integrates to the following:

$$y = A(1 - e^{-kx})$$

This equation is further expanded by Baule (1918) for several limiting factors into the familiar Baule-Mitscherlich equation as given by Verduin (1964):

$$P = P_{max}(1 - e^{-.7x/h})(1 - e^{-.7y/h})(1 - e^{-.7z/h})$$

where P = primary production

P_{max} = maximum primary production

$.7/h$ = a factor added to facilitate computation

x,y,z = limiting factors.

Verduin gives his modification as follows:

$$P = P_{max}(1 - 2^{-x})(1 - 2^{-y})(1 - 2^{-z}) \text{ etc.}$$

These mathematical relations produce curves similar to the Bose plot (Figure 11b) for two limiting factors, but can be expanded to any number. A general description in energy language is given in Figure 12a.

The Michaelis-Menten equation (Michaelis and Menten, 1913) is a mathematical description of the velocity of an enzymatic reaction as determined by the concentrations of the reactant or substrate. The key to the formulation is the fact that the enzyme forms an intermediate complex with the substrate. The mathematical expression, the derivation of which can be found in Brezonik (1972) and Williams and Williams (1967), is given as

$$V = \frac{V_{max} S}{K_m + S}$$

where   V = uptake velocity or reaction rate

V_{max} = maximum uptake velocity or reaction rate

S = substrate concentration

K_m = half saturation constant.

Monod (1942) offered what is now widely accepted as the analytical form for limiting nutrients:

$$\mu = \mu_o \frac{C}{C_1 + C}$$

where μ = growth rate

μ_o = maximum growth rate

Figure 12.   Various limiting factor concepts described
in energy language: (a) Baule-Mitscherlich
model for multiplication of individual
limiting factor functions; (b) Michaelis-
Menten (1913) enzyme-substrate reaction;
(c) cycling receptor model for sunlight as
given in Lumry and Rieske (1959) and
described in energy language by Odum (1971);
(d) Rashevsky (1960) respiration limiting
factor model for glucose and oxygen, as
described by Odum (1972a).   Symbols are
given in Figure 22.

$$P = P_{MAX}(1-e^X)(1-e^Y)(1-e^Z)$$

(a)

$$V = \frac{V_{MAX}\,S}{K_M + S}$$

(b)

$$V = \frac{K_1\,I}{K_2 + K_3\,I}$$

(c)

$$X = \xi y + \frac{\xi y}{1-y}$$

$$\xi = F(C_1, C_2)$$

(d)
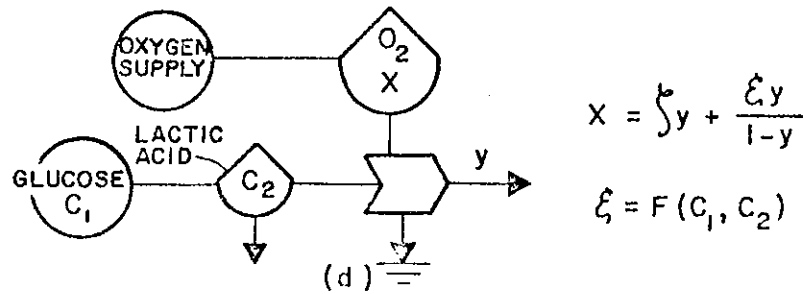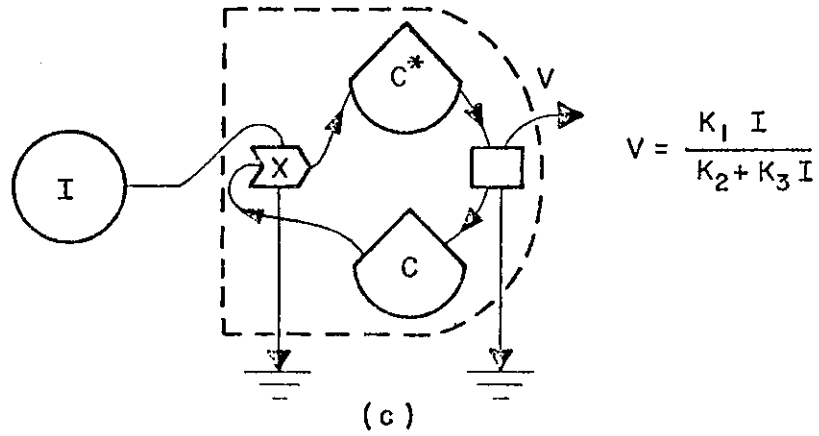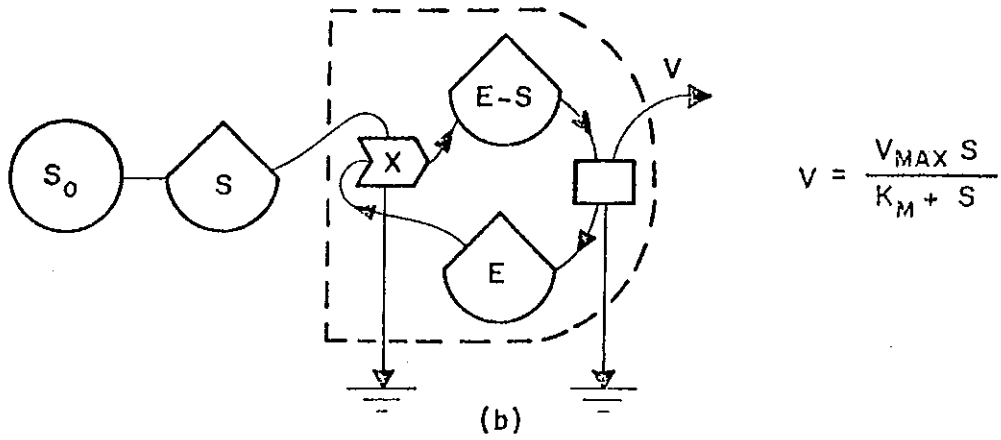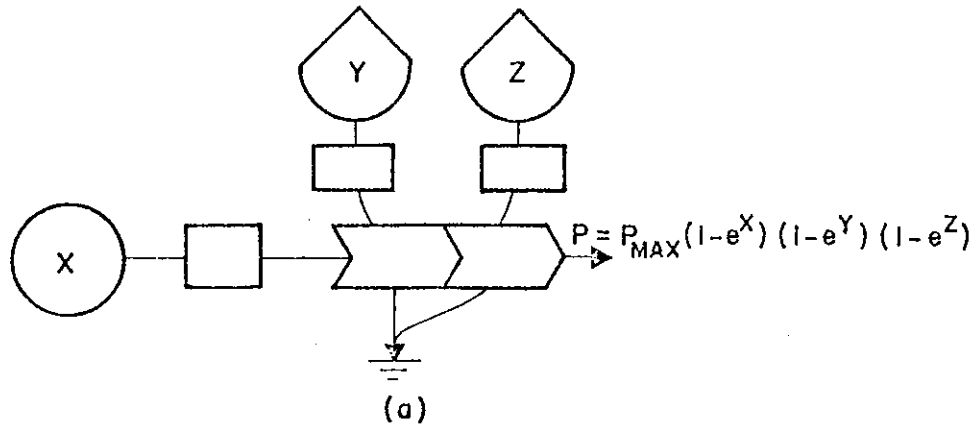
C = concentration of limiting nutrient

C_1 = concentration of nutrient for which the rate of growth is equal to half the maximum.

Monod's work has been described as being an extension of Michaelis-Menten enzyme kinetics to whole organisms, in this case bacteria (Dugdale, 1967). A translation of the Michaelis-Menten/Monod model into energy language is given in Figure 12b.

Lumry and Rieske (1959) discuss the velocity of the photochemical activity of isolated chloroplasts as being given by

$$V = \frac{p\ k_d k_1 I}{k_1 I + k_d}$$

where p = concentration factor

k_d = high light controlling factor

k_1 = low light controlling factor

I = average light.

In energy language this is simply the equation for the cycling receptor as shown in Figure 12c and already discussed by H. T. Odum (1971, 1972a).

Rashevsky (1960), in discussing cellular respiration, gives an equation for oxygen consumption as a function of the external oxygen supply and the supply of glucose:

$$x = \zeta y + \frac{\xi y}{1 - y}$$

where x = external oxygen concentration

y = relative oxygen consumption

ξ = constant

ζ = F (glucose, lactic acid).

This particular case is interpreted in energy language in Figure 12d. Rashevsky obtained several limiting factor curves from experimental data similar to those given in Figure 11b.

Ecosystem Modeling of Limiting Factors

Several authors have made attempts to apply mathematical expressions for limiting factors to specific systems models, generally phytoplankton-nutrient models. Fuhs (1969) and Fuhs et al. (1972) discuss the growth of diatoms as controlled by the excess of intracellular phosphorus over the minimum amount present during phosphorus starvation. The equation is similar to the one presented by Verduin (1964), except intracellular concentration is now important:

$$\mu = \mu_m (1 - 2^{-(a-a_0)/a_0})$$

where μ = growth rate

μ_m = maximum growth rate

a_0 = saturation level phosphorus

a = cell phosphorus.

Takahashi et al. (1973), in an estuarine model of phytoplankton growth, suggest a formula such that the slope of the production light curve at the origin is the same, irrespective of the nutrient concentration (i.e., a Blackman type curve as in Figure 11a). The mathematical formulation is given as

$$P = a\, I\, \exp[1 - aI(1+h \cdot N)/(g \cdot N)]$$

where P = photosynthesis

I = light intensity

N = nutrient concentration

a,h,g = constants.

Dugdale (1967) used the Michaelis-Menten expression as an explanation of the uptake kinetics of nitrate by phytoplankton. In a later work, MacIsaac and Dugdale (1969) caution "that a mathematical and not necessarily biochemical equivalence to Michaelis-Menten kinetics is being considered here." Half saturation constants were determined for several species of marine phytoplankton for nitrate and ammonia. Eppley et al. (1969) used similar methods but were able to generate curves showing both sunlight and nitrate as variables for several species. The Michaelis-Menten/Monod relation has since been applied to larger mathematical models by many authors, including Chen (1970), Chen and Orlob (1972), Fuhs et al. (1972), Grenney et al. (1973), O'Brien (1974), Larsen et al. (1974), Parker (1974), Bloomfield et al. (1974), and Lassiter and Kearns (1974). Chen and Orlob (1972), for example, have described a comprehensive "ecologic" model of eutrophication in which the growth rate is expressed as

$$\mu = \hat{\mu}\left(\frac{L}{k_1 + L}\right)\left(\frac{C}{k_2 + C}\right)\left(\frac{N}{k_3 + N}\right)\left(\frac{P}{k_4 + P}\right)$$

where μ = growth rate

$\hat{\mu}$ = maximum growth rate

L = light

C = CO_2 concentration

N = inorganic nitrogen

P = orthophosphate.

This formulation uses multiplication of several limiting factor terms in the Dugdale interpretation of the Michaelis-Menten/Monod relation. It produces limiting factor curves similar to the second type or Bose type as shown in Figure 11b.

Modeling of Limiting Nutrients in Energy Language

The various models for limiting interactions can be represented in energy language to gain insights about their similarities and differences. These are shown in Figure 13 with the algebraic equation for steady state conditions. In the model in Figure 13a, production is proportional to the product of two concentrations. This model alone has limited applicability, since the concentrations available to the interaction do not ordinarily hold constant.

In Figure 13b are interactions which operate through two processes that have internal limits (such as recycling limitations). Both processes are related to the Michaelis-Menten equation and when combined are empirically correct. This model has no ability to increase responses when nutrients become enriched beyond the internal limitations.

In Figure 13c a model introduced by Odum (1971, 1972a) reproduces the Michaelis-Menten equation, but has a constant external flow that causes the concentration available to the interaction to limit. This model represents the Monod usage.

In Figures 13d and 13e there are two limiting flows and two varying external concentrations. These also have typical limiting factor curves and a Michaelis-Menten relationship at

Figure 13. Limiting nutrient schemes presently used
in energy language modeling: (a) strictly
multiplicative limitation; (b) multipli-
cation of Michaelis-Menten factors;
(c) steady state limiting case as presented
by Odum (1971,1972a); and (d and e) limiting
flow concept of two flows. These last two
models are equivalent. Symbols given in
Figure 22.

(a) $P = KIN$

(b) $P = K\left(\dfrac{KI}{K+I}\right)\left(\dfrac{KN}{K+N}\right)$

(c) $P = \dfrac{KNI}{K+N}$

(d) $P = \dfrac{KJ_2N}{K+N}$

(e) $P = \dfrac{KJ_2N}{K+N}$
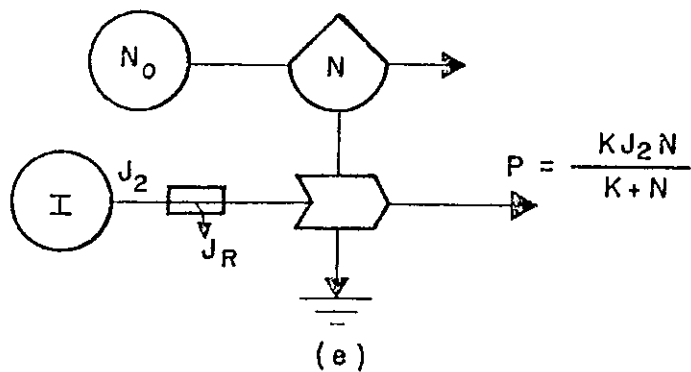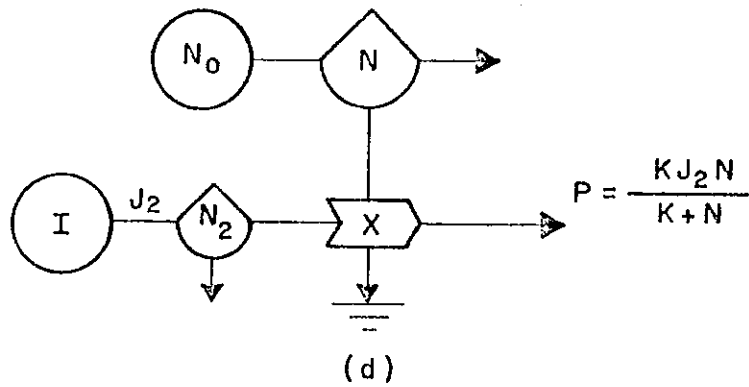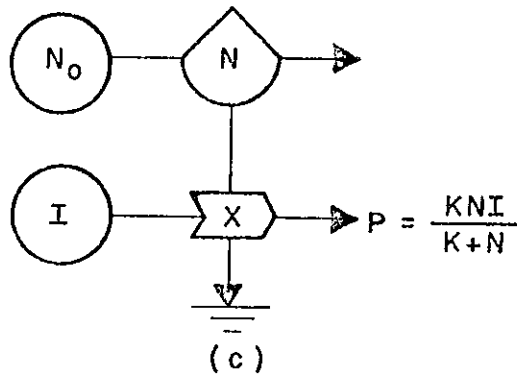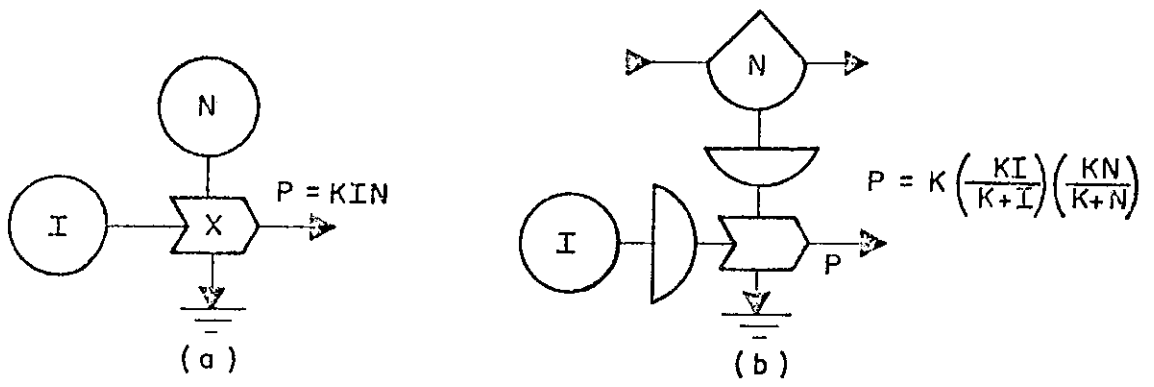
steady state. Applications of the multiplication of Michaelis-Menten model of Figure 13b and the "J_r" model of Figure 13e will be presented in this study, and their differences when applied to multiple limiting nutrient cases are given in the Discussion.

Study Areas

Northcentral Florida, in the vicinity of Gainesville, was the location of most of the data collection effort. General locations of the study areas in Alachua County are shown in Figure 3. They include the highly eutrophic Lake Alice and two sites where cypress studies have been underway. A fourth area of study, cypress wetlands in the Withlacoochee State Forest in the central part of the state, will also be discussed below.

Alachua County topography is dominated by the Ocala limestone formation (Eocene) and an overlying Hawthorne formation of phosphatic sands, clays, and limestones (Miocene). The limestone allows for a karst topography of collapse sinks formed by solution holes in the limestone and subsequent slumpage of the above sediments. Lake Alice occupies an area of multiple fractures and caverns in the Ocala limestone and has been determined to be the result of the sinkhole phenomenon (Cason, 1970). However, to the north and northeast of Gainesville, only slight slumpage is observed in the higher Hawthorne/Pleistocene-sand plateau (Pirkle and Brooks, 1959). It is in

these slight depressions that cypress domes develop and dot
the landscape of pine flatwoods. A cross-section of the
Gainesville area (Figure 14) shows the relationship of these
formations to Lake Alice and the experimental cypress area.

Lake Alice System

Lake Alice (Figure 4), located on the campus of the
University of Florida, Gainesville, was once a sinkhole fed
by a small marshy creek. Until an earthen dam was built at
the western end of Lake Alice in 1948, the extent of the lake
was about 4 ha. It has since expanded to its present size of
33 ha, due to both the dam and the addition of secondary sew-
age effluent (presently 7.3 m^3/min) and once-through condenser
water from the campus heating plant (presently 30.6 m^3/min).
The western end of the lake (Figure 15) averages less than
2 m in depth with a few small areas of about 4 m depth --
probably the original sinkholes. This half of the lake,
called the "open lake," covers about 12 ha. The eastern end
of the lake, 21 ha, is referred to as the "marsh" and is a
very shallow waterhyacinth prairie with virtually no open
water areas. The flow through the lake is generally east-
west with the inflow first going through the marsh and then
through the open lake. An arbitrary dividing line between
the two sections is a catwalk fence constructed in 1970 to
retain the hyacinth growth in the marsh. Aerial photographs
of Lake Alice are given in Figure 16.

Figure 14. A generalized cross-section of the Gainesville, Florida, vicinity showing relationship of Lake Alice and cypress domes to underlying geologic formations. Note the difference in elevation between the limestone plain to the south (90-100 ft. above MSL) and the more northern plateau (160-190 ft.) where cypress domes occur. (Adapted from diagrams by Cason, 1970; Pirkle and Brooks, 1959; and Cutright, 1974.)

CYPRESS DOMES

SURFACE WATER TABLE

WATER TABLE AQUIFER

FLORIDAN AQUIFER

HAWTHORNE FORMATION (MIOCENE)

SUPERFICIAL SANDS (PLEISTOCENE)

LAKE ALICE

OCALA FORMATION (EOCENE)

PIEZOMETRIC SURFACE

CASING FOR LAKE ALICE INJECTION WELLS

S — N

ELEVATION, FT ABOVE MSL

200   150   100   50   0   -50   -100   -150
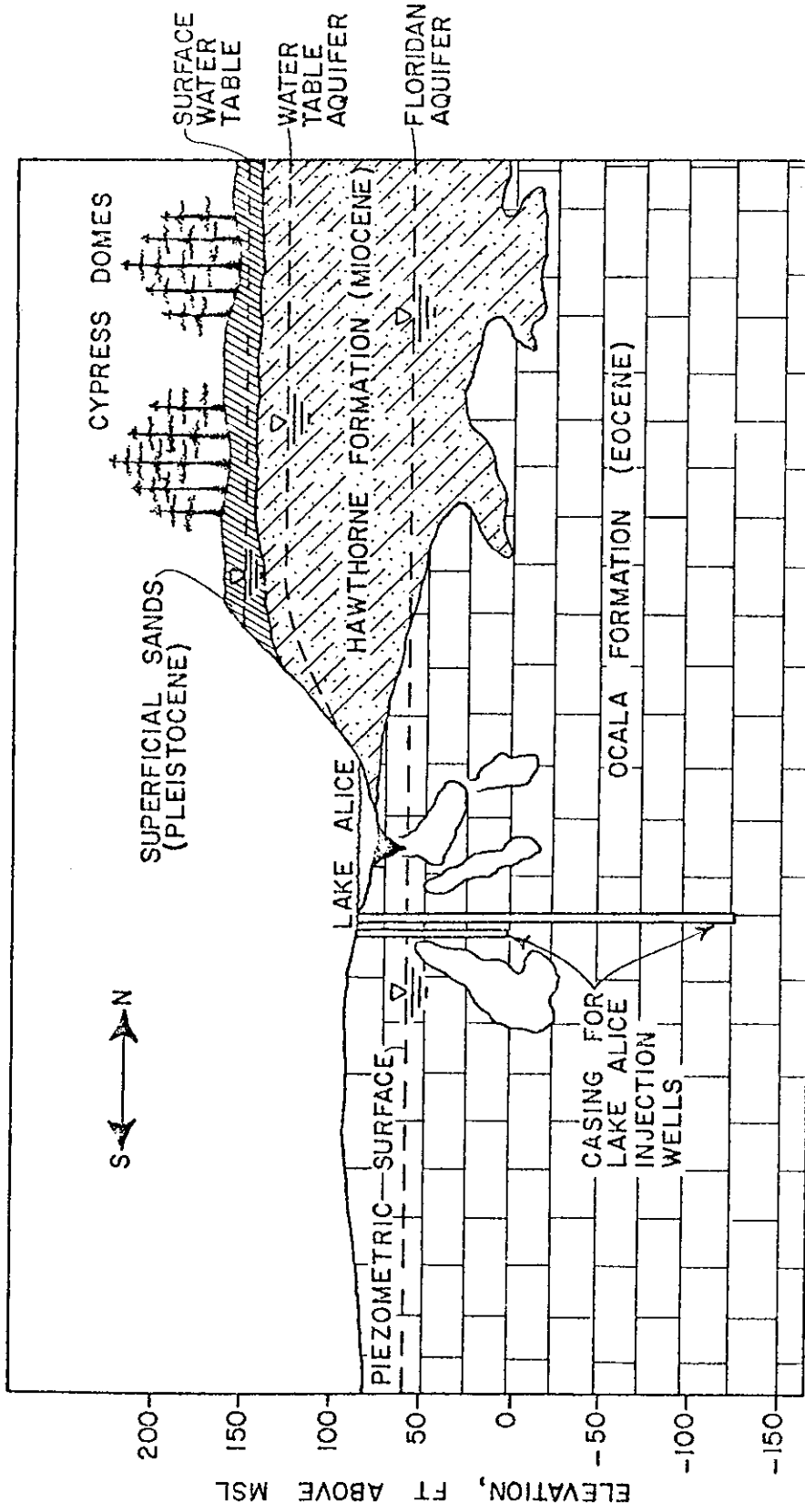
Figure 15. Bathymetric map of Lake Alice, located on the campus of the University of Florida, Gainesville, Florida. Note major inflows to the east and discharge along the western shore, creating a general flow from right to left. Circled numbers indicate sampling station numbers.
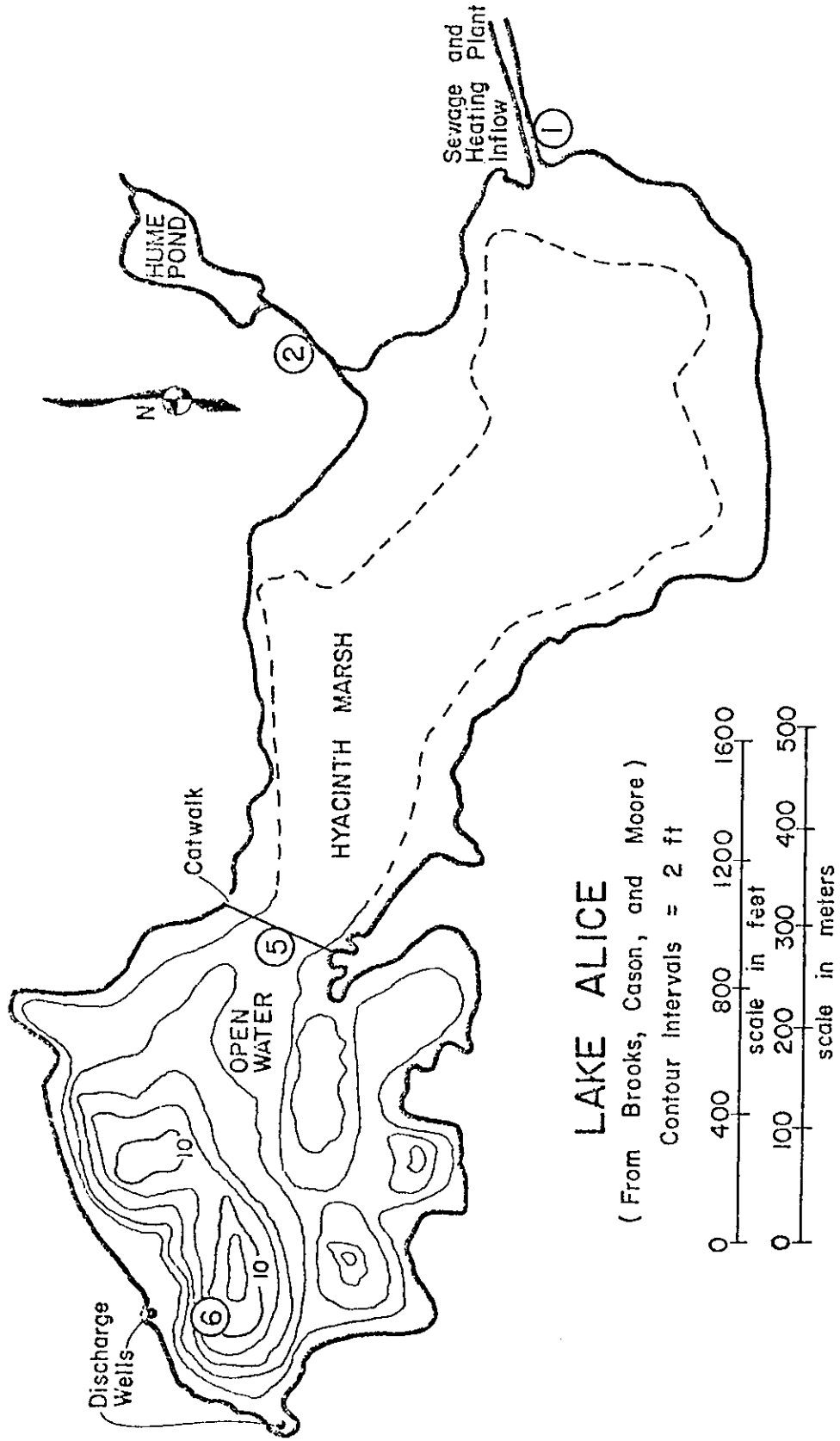
LAKE ALICE

(From Brooks, Cason, and Moore)

Contour Intervals = 2 ft

Sewage and Heating Plant Inflow

HUME POND

N

Catwalk

HYACINTH MARSH

OPEN WATER

Discharge Wells

10

10

6

scale in feet

0   400   800   1200   1600

scale in meters

0   100   200   300   400   500
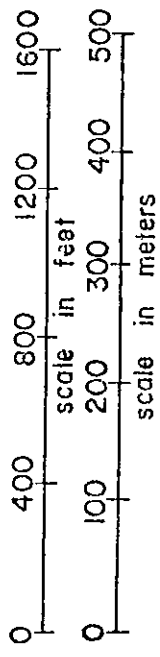
Figure 16.   Aerial photographs of Lake Alice showing
             (a) view of lake and surrounding watershed
             as seen from the west; and (b) an overhead
             view of the lake, showing the division
             between the hyacinth marsh and the open
             lake.

(a)

(b)

The lake drains into two disposal wells on the western shore which were installed in the early 1960s to provide an outflow for the man-increased hydrologic input. One well is drilled to 72 m and the other to 137 m, putting the lake effluent in contact with the upper portions of Florida's major underground water supply, the Floridan Aquifer. Lake Alice is located in an area underlain by multiple fractures and caverns, but the lake basin is generally perched above the local water table because of silty clay that has accumulated on the bottom (Cason, 1970). The lake level is usually between 68 and 70 ft above mean sea level, while the local water table is estimated to be 60 ($\pm$5) ft (Pirkle and Brooks, 1959).

The Lake Alice watershed (474 ha) is primarily urban (i.e., university campus), but a substantial area of agricultural land operated by the university drains into the lake's southern shore, and some forested areas are along parts of the northern shore. Brezonik and Shannon (1971) report 60.8% of the watershed to be urban, while fertilized crops and forests take up 27.2 and 12.0%, respectively. In addition to the major man-made flows mentioned above, Hume Pond, which collects runoff from most of the northeast part of the university campus, overflows into the northeastern corner of the marsh (about 5.1 m^2/min dry weather flow). The pond was constructed for recreational purposes and shows occasional natural level drops due to sinkhole formations in the area. There are also several smaller streams and storm water

culverts which drain into the lake, particularly along the northern shore.

Aerial photos support observers who recall Lake Alice as being waterhyacinth-free until the early 1960s (Cason, 1970). The major hyacinth problem started with the diversion of the heating plant and nutrient-laden sewage effluents into the lake in 1964. Since then, many man-hours have been spent to keep the western part of the lake open from hyacinths. A dragline is employed several times a year to keep the plants in check and chemical spraying has been used periodically over the years.

Despite its highly eutrophic condition (or possibly as a result of it), Lake Alice has an abundance of wildlife including large fish populations, an alligator population estimated at 80 individuals, turtles, and many different species of birds, including the osprey (*Pandion haliaetus*), the anhinga (*Anhinga anhinga*), and the great blue heron (*Ardea herodias*). The lake serves as an Audubon Society sanctuary, and hunting and fishing are forbidden. At one time, the area was a rookery for many varieties of herons (Jenni, 1969), but the increased water input raised the water level and killed the shoreline trees which served as nesting sites. Dead stumps of many of these trees still remain.

Lake Alice can be summarized as a shallow, highly eutrophic lake with considerable wildlife diversity. The lake in many ways resembles a slow-moving river because of its high input-volume ratio (hence, low water retention time) and its

input-output arrangement. The high nutrient levels in the lake are primarily man-made, but natural sources are also significant. The importance of the latter is suggested by high nutrient concentrations in Hume Stream, relatively high orthophosphate concentrations in natural waters around Gainesville (Kaufman, 1969), and high values of phosphorus measured at Lake Alice in the early 1950s (Odum, 1953).

Cypress Systems

Several cypress domes are being studied under varying degrees of management as part of the Rockefeller and NSF-RANN research project entitled "Cypress Wetlands for Water Management, Recycling, and Conservation" (see Odum, 1972b; Odum et al., 1974). The Owens-Illinois Research Site, located in Figure 5 and shown in more detail in Figure 17, contains the cypress domes that are under experimental manipulation. The Sewage Dome (0.53 ha) has received secondary sewage effluent from the adjacent trailer park's package treatment plant since March, 1974. At peak use, flow was approximately 94.6 m^3/day, making the application rate 12.5 cm/week. A second dome, the Groundwater Dome, has received pumped groundwater at approximately the same loading rate, also since March, 1974. A fire swept through the area on December 4, 1973, creating some damage to these domes, necessitating the addition of a new experimental dome (0.99 ha) to the project design. Sewage pumping to this dome began in December, 1974, after data for

Figure 17. General site plan of Owens-Illinois Research Site, including cypress domes, trailer park, and necessary piping (drawing by Ordway).

RESEARCH SITE PLAN
JAN. 1974

CENTER FOR WETLANDS
UNIVERSITY OF FLORIDA

LEGEND

DETAIL "A"

this study were collected, and the dome is therefore referred to as the Owens-Illinois Control Dome.

Figure 18 shows the location and access of the Austin Cary Control Dome, located at the northwest corner of the Austin Cary Memorial Forest, owned by the University of Florida. This dome is much larger (5.4 ha) and has a more mature stand of cypress growing there. It has been used in this study as the ultimate in natural conditions, complete with surrounding pine forest. It also has a distinct central pond which usually holds water throughout the year.

Figures 19 and 20 are aerial photos taken of the experimental and control areas on November 23, 1974. Figure 19a shows the Whitney Trailer Park (155 trailers) which is supplying secondary sewage to the Sewage Dome. Figure 19b shows the Sewage Dome (upper left), the Groundwater Dome (right center) and another burned dome (lower left). This last dome has also been harvested since the fire, as indicated by the sparse canopy seen in the photo. Excess groundwater has spilled over the edge of Groundwater Dome. The cleared areas shown in light color surrounding the domes give an indication of the extent of the fire. The Owens-Illinois Control Dome, prior to sewage addition, is shown in Figure 20a. The darker trees in the photo are pine which have invaded the dome and managed to survive despite the presence of standing water. An aerial view of the Austin Cary Control Dome is shown in Figure 20b.

Figure 18. Location of Austin Cary Control Dome in Austin Cary Memorial Forest, approximately 10 miles northwest of Gainesville, Florida (drawing by Ordway).

FENCE

WALDO ROAD

DIRT ACCESS ROAD

ACCESS ROAD TO CONTROL
DOME LOCATED APPROX.
1 1/2 MILES NORTH-EAST OF
ENTRANCE TO AUSTIN CARY

N

SCALE

0 — 330 ft.

CONTROL DOME

AUSTIN CARY CONTROL DOME		
CENTER FOR WETLANDS		
AUGUST 1974	SCALE: AS SHOWN	
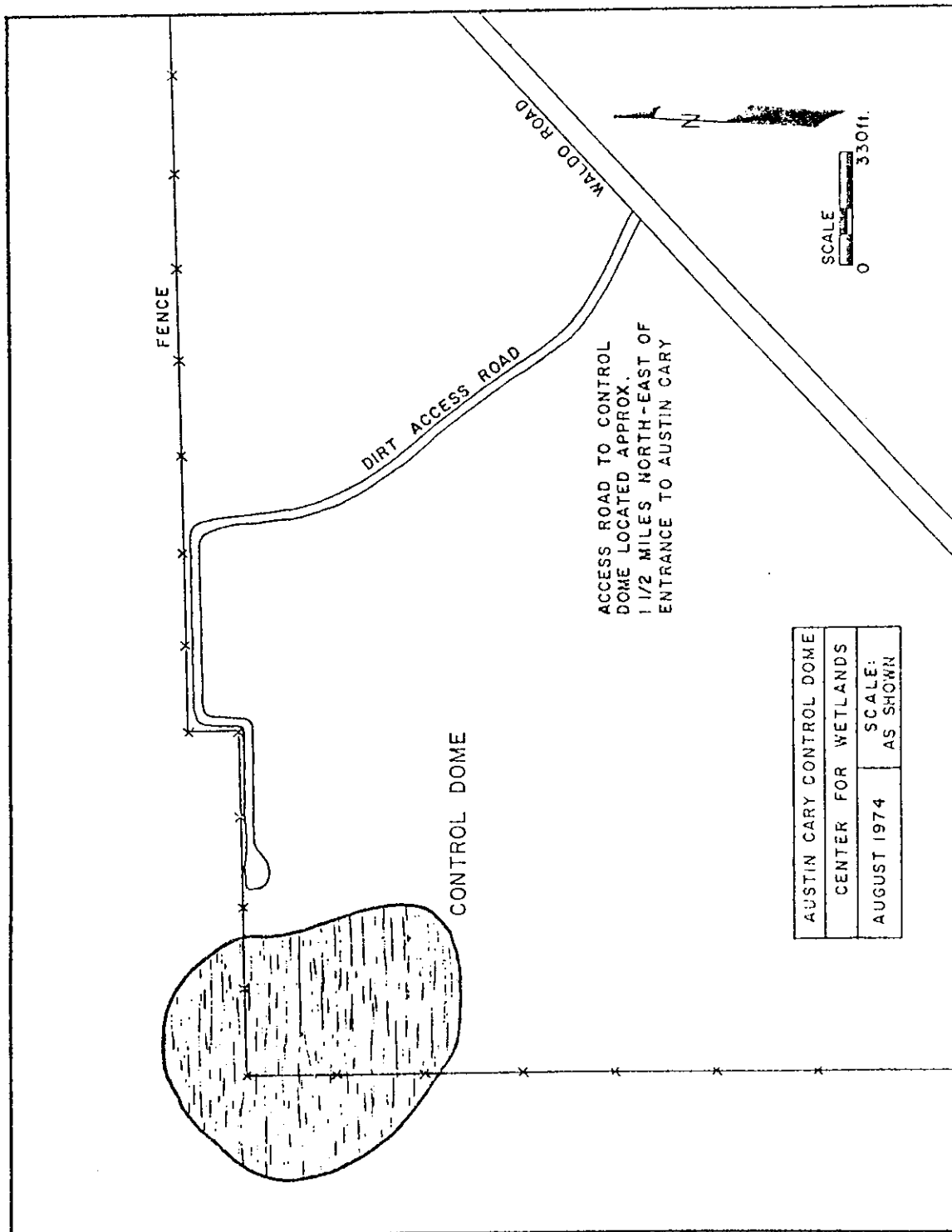
Figure 19. Aerial photographs of Owens-Illinois Research
            Site: (a) trailer park which contributes
            secondarily-treated sewage to cypress domes
            (to left of picture). The sewage treatment
            plant and its holding pond are shown in the
            upper center of the photograph. (b) Experi-
            mental cypress domes, including the Sewage
            Dome (receiving sewage effluent as of March,
            1974) -- upper left, Groundwater Dome
            (groundwater pumping as of March, 1974) --
            center right, and a third dome which has
            been stressed by drainage, fire, and harvest-
            ing -- lower left. Photos taken November
            23, 1974.
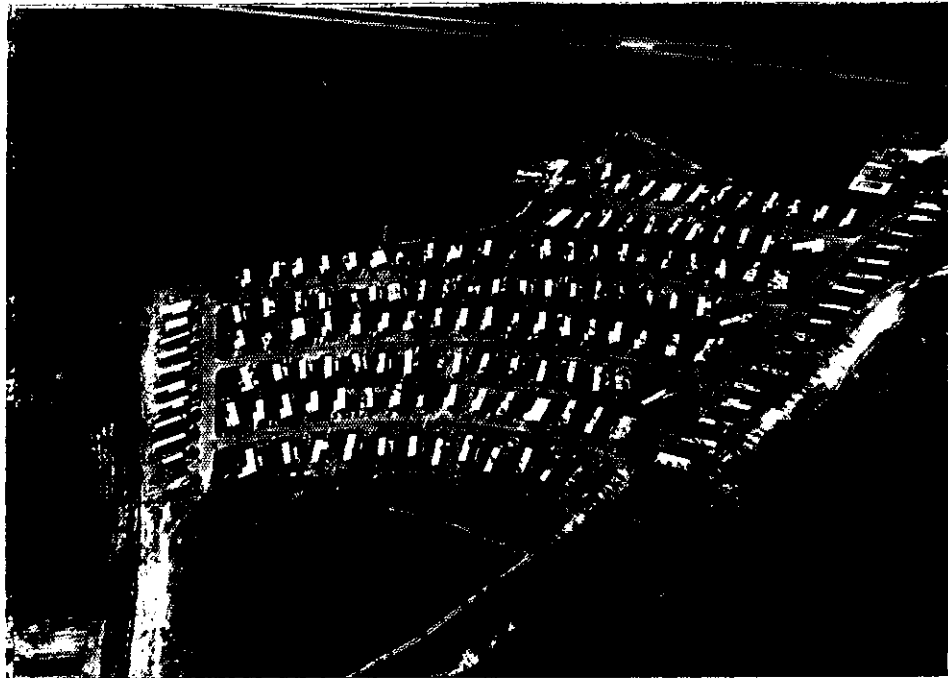
(a)
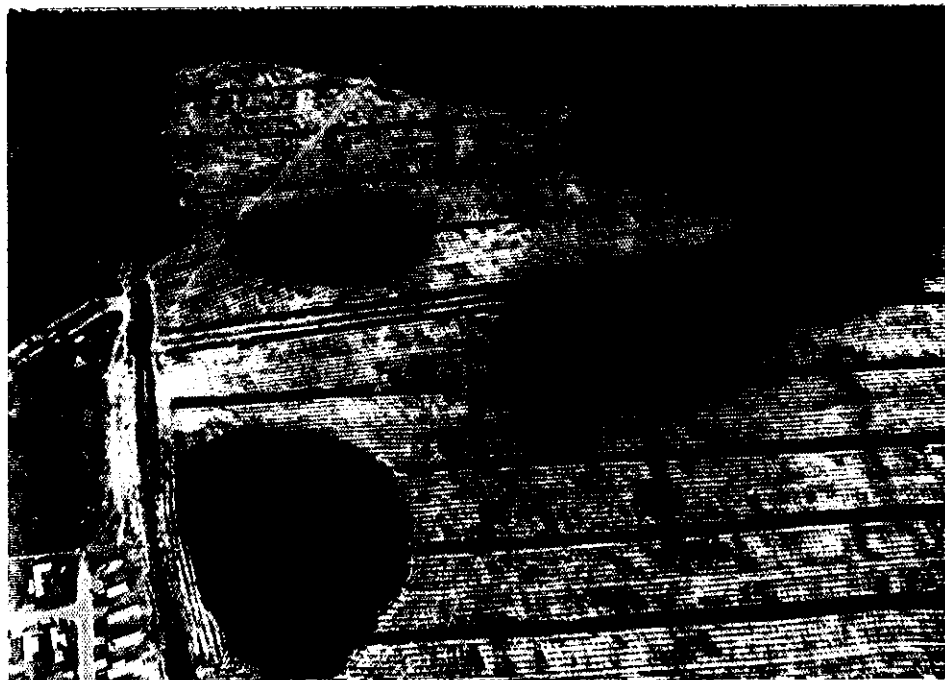
(b)

Figure 20.   Aerial photographs of (a) Owens-Illinois
Control Dome (receiving sewage effluent as
of December, 1974, hence a control in this
study), and (b) Austin Cary Control Dome
(natural conditions). Note difference in
surrounding pinelands and in canopy shades.
Photos taken November 23, 1974.

(a)

(b)

Withlacoochee State Forest

This additional site was included early in the study, due to the availability there of cypress tree growth data. The Withlacoochee State Forest is located in Pasco, Hernando, Citrus, and Sumpter Counties in central Florida, near Brooksville. Parts of the forest are located in the northwest corner of the Green Swamp, a valuable recharge area for the Floridan Aquifer, and the headwaters of the Withlacoochee River. The Richloam Tract (47,379 acres), the largest of three tracts comprising the state forest, is within the Green Swamp boundary and, because of its slow drainage to the northwest, it is dominated by cypress wetlands interspersed among the pine flatwoods. Figure 21, which outlines the Richloam unit, indicates that a considerable fraction of the area is dominated by cypress. It is from this tract that tree growth data have been made available by the Florida Division of Forestry for 204 circular plots of 0.2 acre each.

Figure 21. Map of the Richloam Tract of the Withlacoochee State Forest in central Florida. Shaded areas are locations of cypress wetlands.
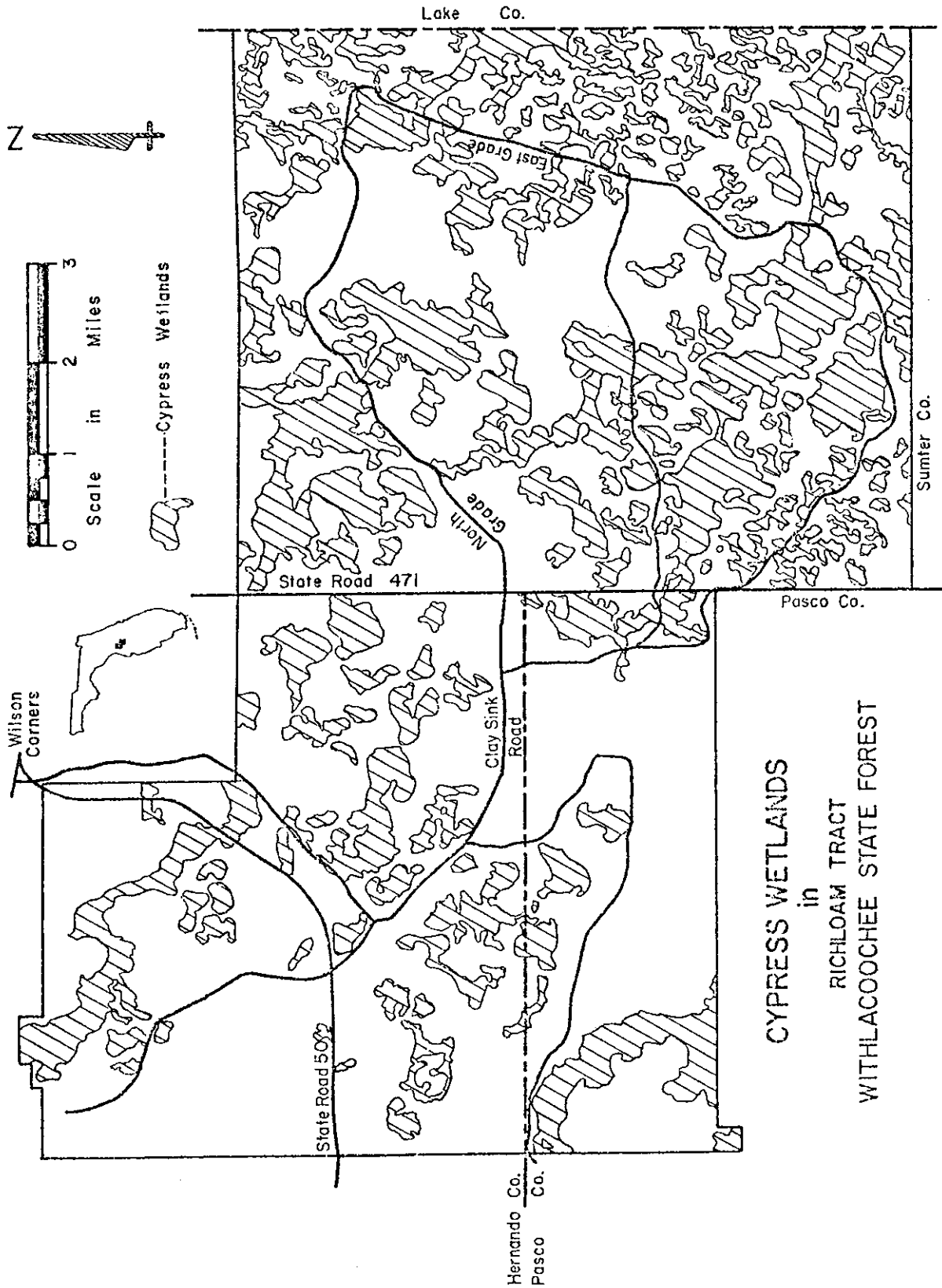
CYPRESS WETLANDS
in
RICHLOAM TRACT
WITHLACOOCHEE STATE FOREST

METHODS

Mathematical models and energy evaluations of ecosystems have data requirements that can be satisfied only through a judicious combination of field studies, literature searches, discussion with knowledgeable persons, assumptions, and estimations. This chapter presents methods used in data collection and in analyses of lake and cypress systems and then describes the modeling effort and other mathematical techniques used. Data collection involved field work and data reduction on the part of several investigators associated with two research projects (see Acknowledgments).

Data Collection for Lake Alice

Hydrologic flows were obtained through a combination of field instrumentation and data gathering from knowledgeable sources. Sewage flow and heating plant coolant flow into Lake Alice were obtained from plant operators for the two facilities. The combined flow of these two streams was measured on several occasions with Gurley and Ott current meters with good agreement between the given and measured values. The base flow from Hume Pond to Lake Alice (Figure 15) was also measured on several occasions with a current meter. Rainfall and evaporation data were obtained for the duration of the

68

study period from a meteorological station maintained by the Agronomy Department of the University of Florida 250 m south of the lake. Lake stage was monitored continuously with a Stevens water level recorder located adjacent to the board-walk dividing the marsh and open lake. Hypsographic curves, relating the stage to area and thus to volume, were calculated from existing bathymetric maps such as the one shown in Figure 15. Lake discharge was calculated from the stage data, assuming the outflow to behave as in a linear reservoir according to the equation

$$Q_o = 12.2(L - 67.00)^{1.0}$$

where Q_o = lake discharge, cfs (cubic feet per second)

   L = lake stage, ft above MSL.

Constants for the weir equation were obtained through estimation and analysis of the water level data. A general weir exponent of 1.5 was found to cause excessive outflows at high stages. Transpiration by waterhyacinths was assumed to be three times evaporation rates, based on the findings of Penfound and Earle (1948), Timmer and Weldon (1967), Knipling et al. (1970), and Rogers and Davis (1972). Runoff was then calculated through a water budget approach equating the change in storage of the lake to all the inflows and outflows as shown in the equation

$$\left(\frac{R_i + R_{i-1}}{2}\right) = \left(\frac{V(L)_i - V(L)_{i-1}}{86400}\right) - \left(\frac{Q_{I_i} + Q_{I_{i-1}}}{2}\right) + \left(\frac{Q_{o_i} + Q_{o_{i-1}}}{2}\right)$$

where R_i = runoff for day i, cfs (cubic feet per second)

   $V(L)$ = lake volume as a function of stage L, ft^3

   Q_I = net inflow, cfs

      = baseflow + direct rainfall - evapotranspiration

   Q_o = lake discharge as described above.

The water budget data and a listing of the FORTRAN program
are available under separate cover at the Center for Wetlands,
University of Florida.

Waterhyacinth measurements included aerial surveys of
the hyacinth coverage and measurements of metabolism and bio-
mass. Aerial photos obtained by J. L. Fox on three occasions
during the study aided in determining the spatial coverage of
the hyacinths, especially on the open lake. Areas were
measured with a planimeter. Waterhyacinth metabolism was
measured using an open system chamber with infrared CO_2 gas
analysis. This effort was aided by K. Dugger, T. Center, and
S. Brown. A chamber made of clear polyacetate and buoyed on
a float enclosed the plants for an area of 0.49 m^2. Air was
directed through the chamber from a blower-duct with the flow
rate determined periodically using a Hastings hot wire anemom-
eter. Slip streams of intake and exhaust gas were analyzed
with a Beckman infrared gas analyzer and CO_2 concentrations
were calculated from calibration curves. The difference in
CO_2 levels between the intake and the exhaust, when multiplied
by the flow rate, then represents the rate of carbon assimi-
lation in the chamber. A more detailed discussion of this
method is given by Carter et al. (1973). This experiment was

run for 24 hours for two different sizes of hyacinths. Integration of the resulting production curve yields both gross primary productivity and respiration, assuming day and night respiration are equal. Solar radiation was measured for this study with a 24-hour pyroheliograph (WeatherMeasure Co.) in the wavelength range 0.36-2.5 μm. Air temperature was recorded with a thermistor system (Yellow Springs Instrument Co.). The hyacinths in the chamber were harvested after the metabolism measurements, and both wet and dry weights were obtained.

Metabolism of open water was determined at several locations in the open lake, on three occasions by M. Keirn (January, March, and May), and on two occasions by the author (April and July). Metabolism was determined by measuring the diurnal change in dissolved oxygen and subsequently calculating the rate of change of oxygen. The method is outlined in more detail in Odum (1956) and Odum and Hoskin (1958). Diffusion corrections were not used in this study. Dissolved oxygen was determined at three-hour intervals on replicate samples using the Azide modification of the Winkler method (A.P.H.A., 1971).

Chemical parameters of water were determined for various sites throughout the lake during the study period of January through September, 1973, directed by P. L. Brezonik. Prior to April a spot sampling program was conducted, and after that time automatic samplers were installed at Stream 1 (Station 1), by the boardwalk separating the marsh and lake

(Station 5), and in the open lake (Station 6). Station loca-
tions are shown in Figure 15. Each sampler was set to an
eight-hour frequency, producing 21 samples per week. Mercuric
chloride was added to each bottle prior to resetting the
sampler each week. Analyses on each sample were done accord-
ing to the methods outlined in Table 1. Water temperature
was measured continuously with water temperature recorders
located at Stations 1 and 5. All data were entered on com-
puter cards and a program was written in FORTRAN to reduce
the data to monthly averages and standard deviations. In
addition, changes in water quality across the marsh were cal-
culated by the program for each parameter whenever data were
available concurrently at Stations 1 and 5. The program and
monthly output are available under separate cover at the
Center for Wetlands, University of Florida.

Sediment samples were taken in duplicate by a lake core
sampler along the boardwalk at Station 5 (see Figure 15).
Five cores (total area 114.5 cm^2) were composited in a bucket
for each replication. Lengths of the cores were estimated
with a meter stick when samples were taken. Composite samples
were allowed to settle, after which overlying water was
siphoned off. Total weight was then determined. Subsamples
were dried for approximately 24 hours at 100°C to obtain dry
weights and fired in a muffle furnace at 550°C for 24 hours
to obtain volatile solids. Total nitrogen was determined
through Kjeldahl digestion on 0.5 g (wet) of the original
composited samples. The ashed subsamples were extracted in

Table 1

SUMMARY OF ANALYTICAL PROCEDURES AND ASSOCIATED REFERENCES FOR
WATER CHEMISTRY ANALYSIS OF LAKE ALICE AND CYPRESS DOMES

Parameter	Method	Reference
pH	pH meter	A.P.H.A. (1971)
Conductivity	conductivity meter	"
Turbidity	turbidimeter	"
Color	chloroplatinate standard	"
Alkalinity	methyl-purple titration	"
Acidity	phenolphthalein titration	"
Dissolved oxygen	Winkler/Azide modification	"
Chemical oxygen demand	dichromate redox titration	"
Ortho-phosphate	molybdate blue	Murphy & Riley (1962)
Total phosphate	acid persulfate digestion	"
Total Kjeldahl nitrogen	Kjeldahl digestion	A.P.H.A. (1971)
Ammonia	alkaline phenol	E.P.A. (1971)
Nitrate	hydrazine reduction	"
Potassium	atomic absorption	"
Magnesium	"	"
Sodium	"	"
Calcium	"	"

1.0 N nitric acid for phosphorus, calcium, magnesium, potassium, and sodium determinations by the Soil Analytical Laboratory at the University of Florida.

Data Collection for Cypress Wetlands

Hydrologic measurements were based on water level records obtained from Stevens level recorders being maintained in each experimental cypress dome. Rainfall data were obtained from a rain gauge at the Owens-Illinois site. Rain records at the Beef Research Unit of the University of Florida were used for the Austin Cary Dome. Pumping schedules for the experimental domes were measured by the project engineer while outflow from the dome was estimated with a rectangular weir constructed at the discharge from the dome. Data on pan evaporation were used to estimate evapotranspiration at the Agronomy Department's meteorological station located at the University of Florida. Evapotranspiration measurements made by S. Cowles and others in October, 1974 (unpublished data), in the sewage dome matched the pan data. Runoff for the sewage dome was then calculated according to the equation

$$R_i = \frac{V_i - V_{i-1}}{t} - Q_{I_i} + Q_{o_i}$$

where R_i = net runoff into dome for day i

V_i = standing water volume for day i

Q_{I_i} = measured inflows for day i

= sewage flow + direct rainfall

$$Q_{o_i} = \text{measured outflows for day i}$$

$$= \text{weir flow} + \text{evapotranspiration}$$

$$t = \text{time interval}$$

$$= 1 \text{ day.}$$

Gross runoff was calculated by adding the net runoff to the water loss rate determined for a period of no rainfall, weir flow, or sewage pumpage. A listing of the FORTRAN program and the water budget data are available under separate cover at the Center for Wetlands, University of Florida.

Cypress tree biomass was measured at a cypress dome in the Austin Cary Forest. Diameter at breast height (DBH) was determined with a diameter tape, and total height was measured with a clinometer for 16 trees representing a wide range of DBH values. From these trees, ten were selected for harvest because they were most representative of the DBH and height values found for the trees at the experimental site. The diameter of each tree was measured with and without bark. Each tree was cut at approximately 2 ft above the ground surface with a chain saw, and the biomass was separated into leaves, small branches (less than 1 cm in diameter), large branches, and main stem. Wet weights were measured for each with a beam scale, and subsamples were taken to determine moisture content. Total height and branch length were also measured on the felled tree. The stem was then subdivided into 8-ft sections, and cross-sections of 1 to 2 in were obtained at each 8-ft interval up to 4 in in diameter. The roots of seven trees were pulled out with a tractor; dynamite

was used on one occasion to loosen the roots. Moisture content was determined for each set of roots and for stem cross-sections by drying in a kiln at 100°C for 72 hours. Seventy-five percent recovery of roots was estimated and weights were adjusted accordingly. The dry weight data for leaves, branches, stem, and stump plus roots were used as the dependent variable (y) in a regression analysis with the independent variable chosen as $x = \sqrt{DBH \times Height}$ with both DBH and height expressed in centimeters. The form of the equation used was $y = ax^b$, the form found most satisfactory for cypress by Carter et al. (1973). Leaf, branch, stem, and stump plus root biomass values were then determined for the various experimental domes using the regression relations and DBH and height data for each cypress tree in the domes. The FORTRAN program used for these calculations and results of biomass determinations are available under separate cover at the Center for Wetlands, University of Florida.

Cypress net primary production was determined from the above regressions. Measurements of cypress diameters at breast height and of height over a six-year period were made available for the Withlacoochee State Forest by the Florida Division of Forestry. These data were from 204 circular plots of 0.2 acre each, placed at fixed intervals throughout the Richloam Tract of the forest in the early 1960's as part of the Continuous Forest Inventory (CFI) data collection effort. Twenty-three CFI plots dominated by cypress were chosen from the 204 available for calculations of net

productivity. Plots were selected to include a wide range of cypress systems, the variability being determined primarily by the trees growing in association with the cypress. The DBH and merchantable height data were entered on computer cards, one card for each cypress tree. A computer program was then written in FORTRAN to determine the productivity of each cypress tree according to the following relationship:

Net Primary Productivity = change in biomass

+ litterfall + root loss.

Biomass values for each tree at the beginning and end of the measurement period were determined from regression equations discussed above which employed $\sqrt{\text{DBH x Height}}$ as the independent variable. It was first necessary to change merchantable height to total height according to relationships determined from the cypress harvest data. The average leaf biomass for each tree, determined from the above-mentioned regressions, when multiplied by six years gave an estimate of the litterfall contribution to net productivity for each tree. Root loss was estimated to be 27.7% of the total net primary production, based on data reported by Woodwell and Whittaker (1968) for a forest at Brookhaven National Laboratory. The equation for determination of net productivity on an annual basis for each site is thus given as

$$\text{NPP} = \frac{1.383}{A \cdot t} (\Delta B + t \cdot L)$$

where NPP = cypress net primary productivity in $g/m^2/yr$

A = area (809.4 m^2)

t = time (6 years)

ΔB = biomass change for all cypress trees in plot (g)

L = average leaf biomass and thus approximate litterfall for all cypress trees in plot for one year (g/yr).

The program listing and complete output for the 23 plots are available under separate cover at the Center for Wetlands, University of Florida. Total plot productivity was determined for comparative purposes from cypress productivity (NPP) by dividing the cypress productivity by the fraction of trees that are cypress.

Understory production and sunlight patterns were measured at the control cypress dome at Austin Cary Forest because of its well-developed central pond. The central pond generally has a depth of at least 0.5 m, even in the dry season. Using the same methods as in Lake Alice, measurements of underwater metabolism were made four times: November, 1973; March, May, and August, 1974. Water samples for dissolved oxygen were taken at approximately 3-hour intervals from an elevated plat-form constructed near the center of the dome. The platform was used to insure minimal disturbance of the water while sampling. Oxygen was determined on replicate samples with the Azide modification of the Winkler method (A.P.H.A.,1971). Calculations were corrected for oxygen diffusion by assuming a value of 0.034 g-O$_2$/m^2-yr at 0% saturation, a value quoted by Odum (1956) for still water. Temperature of both water and air were measured with a thermometer. Solar

radiation in the dome was measured with a 24-hour pyrohelio-
graph (Belfort Co.). Total solar radiation values were
obtained from J. Steinberg for the November, March, and May
studies with an Eppley pyranometer at a nearby research sta-
tion at Lake Mize. A WeatherMeasure pyroheliograph was used
for the August data. All solar gauges were calibrated against
each other with the Belfort instrument being used as the stan-
dard. Air temperature outside the dome was obtained from
climatological data at the nearby Beef Research Unit operated
by the University of Florida. Evaporation rates inside and
outside the dome were compared during the August experiment
with replicate atmometers. The biomass of submerged aquatic
macrophytes was determined in February with four samples,
each taken at random locations within the central pond.

Standing water chemistry samples were taken in the four
experimental cypress domes from the center to the edge on a
monthly basis from April to October, 1974 (see Brezonik et al.,
1974). The samples were collected in one-liter plastic
bottles and preserved in mercuric chloride. pH was deter-
mined within a few hours of sampling and samples were refrig-
erated for later nutrient analysis (mainly nitrogen and phos-
phorus) by the water chemistry group according to the methods
outlined in Table 1.

Sediment samples were taken in November, 1974, with a
lake sediment sampler in order to include the entire organic
layer of each dome. Five cores (total area 114.5 cm^2) were
composited for three locations in each dome (four locations

in the Sewage Dome). Total wet weight was recorded for each location. Subsamples were treated in a manner similar to the Lake Alice sediment analysis described above for dry matter, volatile solids, nitrogen, phosphorus, calcium, potassium, magnesium, and sodium.

Modeling Methods

Construction of models both for illustrative purposes and for computer simulations incorporated the energy circuit language developed by H. T. Odum (1971,1972a). A summary of the symbols used in this dissertation is given in Figure 22 along with pertinent mathematical descriptions. The various limiting factor modules already presented in Figure 13 were also used.

Computer simulation involved the use of both digital and analog facilities. The initial construction of a model and the determination of the first order, ordinary nonlinear differential equations associated with each state variable are the same in both types of simulation. An example of a differential equation is shown with Figure 22c. Constants (k) are determined by assigning the best data values to every flow (kQ) and storage (Q) and solving for the k values. From this point, the methods for digital and analog computer simulation diverge.

Figure 22. Energy language modules used for modeling and
simulation in this dissertation (Odum, 1971,
1972a):

(a) Outside source supplying energy to the
system from an unlimited storage.

(b) Heat sink, outflow of used energy with
entropy increase symbolic of the necessary
losses of energy due to the Second Law of
Thermodynamics.

(c) Storage of a quantity of energy in
the system. These are focus points for the
formulation of differential equations for
simulations and are often referred to as
state variables.

(d) Multiplicative interaction in which
the output is proportional to the product
of the forces of the two inputs.

(e) Interaction of two flows in which the
output is some unspecified function of the
two forces driving the flows. The multiplier
(d) is a special case of this more general
workgate.

(f) Composite symbol used to denote con-
sumer units such as fish or cities in which
the storage feeds back some of its energy
to enhance its uptake of even more energy.

(g) A force (x) proportional to flow J
may interact with other components in the
system.
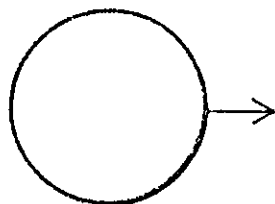
SOURCE

(a)

HEAT SINK

(b)

PASSIVE STORAGE

$$\dot{Q} = J - KQ$$

(c)

MULTIPLIER

$$J = KXY$$

(d)
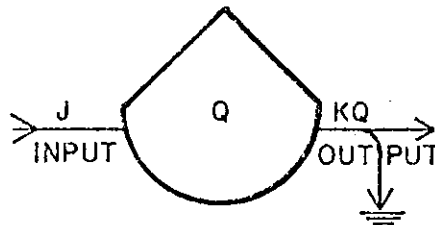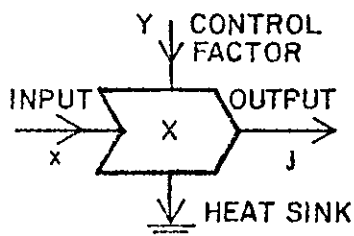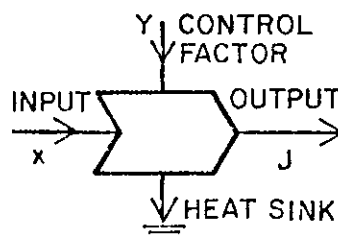
GENERALIZED WORKGATE

$$J = f(X,Y)$$

(e)
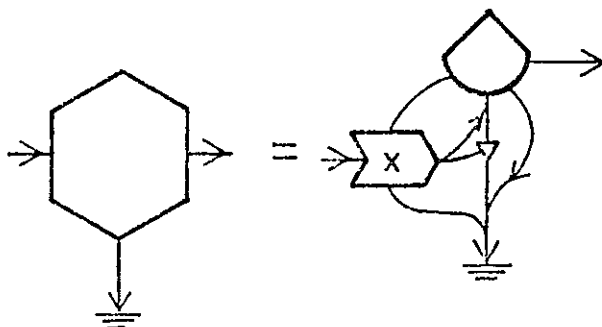
SELF MAINTAINING CONSUMER UNIT

(f)
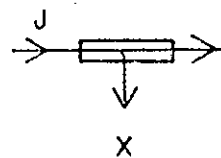
FORCE FROM A FLOW

(g)

Figure 22 - continued

     (h) Cycling receptor module of chloro-
phyll excitation in green plants. A con-
tinual flow from excited (C^*) to deactivated
stages (C) creates a downstream energy flow.
This is similar to the Lumry-Rieske model
presented in Figure 12c.

     (i) Green plant or plant community which
combines anabolism of cycling receptor (h)
with catabolism of self-maintaining consumer
unit (f).

     (j) Switch used when flows are regulated
by on-off signals such as political decisions
and sudden fires.

     (k) Constant gain amplifier used when a
very low flow (x) is being amplified by
another source but without draining the
former storage. Operation is similar to
a stereo record amplifier.

     (l) Economic transactor which shows the
general relationship between energy and
money, i.e., they flow in opposite direc-
tions. Price is often expressed as
$p = J_2/J_1$.

     (m) Two-way workgate in which flow can
go either way depending on backforces. The
negative sign indicates a linear decrease
in flow J with an increase in the driving
force.

     (n) Box often used to lump linear pro-
cesses. For example, nutrients can be
shown being recycled from a respiratory
pathway.
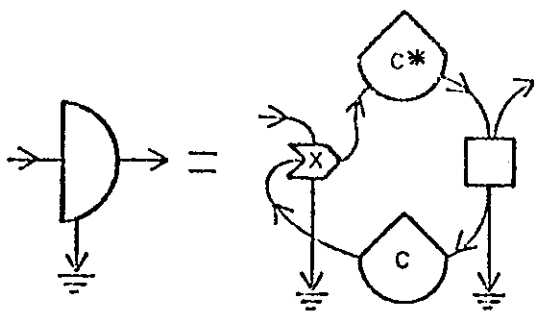
CYCLING RECEPTOR
(h)
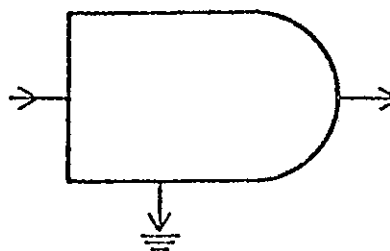
GREEN PLANT AND
OTHER PRODUCERS
(i)
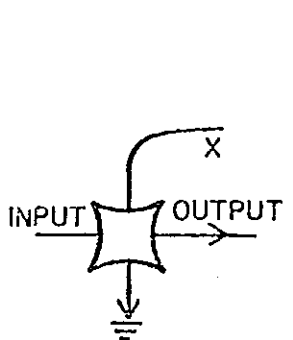
DIGITAL FUNCTIONS
(j)
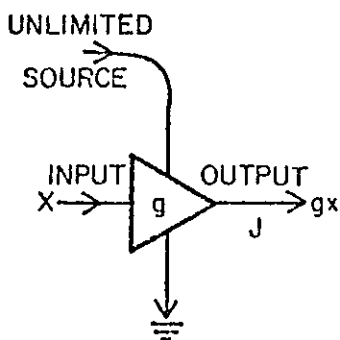
CONSTANT GAIN
AMPLIFIER
(k)
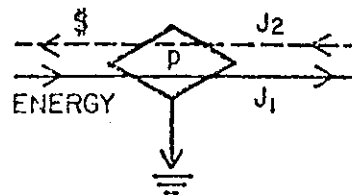
ECONOMIC TRANSACTOR
(l)
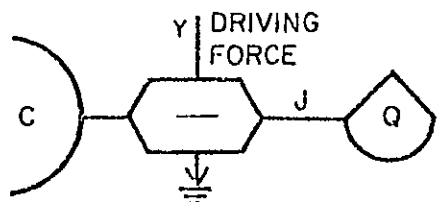
$J = K_1(1 - K_2Y)(C - Q)$

DIFFUSION MODULE WITH
NEGATIVE WORKGATE
(m)
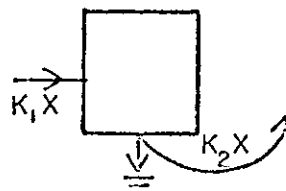
GENERAL PURPOSE BOX
(n)

Digital Simulation

A Lake Alice model was simulated in FORTRAN language with an IBM-370 time-sharing digital computer. Integration of the differential equations was done according to a finite difference approach called rectangular integration. Each equation was solved iteratively through the use of a DO loop with values being printed periodically. Initial conditions had to be specified beforehand for each state variable. For this model, a time step (Δt) of 0.1 day was used. The time step was chosen to be less than the most rapid storage turnover by at least an order of magnitude. A plotting subroutine was utilized to facilitate visual presentation of output. A program listing and sample output are available under separate cover.

Analog Simulation

Simulation by analog computer may come much closer to approximating nature than simulation by digital computer (Ricci, 1972). When integration is necessary, digital simulation requires discrete approximations such as the rectangular integration used above; the solution from analog computer is continuous. The digital computer, on the other hand, has a large storage capacity and can be used for large models that exceed the capability of an analog computer. In addition, many functions are easier to program on the digital computer; the programming effort, however, may be greater. Experimentation with a model is facilitated on the analog

computer by the easy manipulation of coefficient settings;
the digital computer requires multiple runs to attain the
same results.

In contrast with digital simulation, scaling is necessary
before simulation for analog computation. In the following
example, the equation has been scaled so that the range of
values for the state variable, Q, is 100 units. This is
called magnitude scaling. To do this, the maximum value
expected is placed in the denominator within the brackets and
in the numerator outside the brackets on the righthand side
of the equation. Denominators of Q and $\dot{Q}$ are then made the
same by dividing left and right sides of the equation by the
same denominator as Q.

$$\frac{\dot{Q}}{100} = (\frac{J}{100}) - (\frac{k \ 100}{100})[\frac{Q}{100}]$$

If the values in the parentheses are then above 10 or very
low, time scaling is necessary due to machine limitations
(Ricci, 1972). Then the time units used in the model will
no longer be equal to real machine seconds. By dividing the
righthand side of the above equation to get the values in
parentheses below 10, the division of the left side results
in a new time scale:

$$d\tau = 10dt$$

indicating a time scaling factor of 10, where τ denotes the
new time units (computer time) and t denotes the original
time (real time). In this case the computer time, indicated

by knob settings, would have to be divided by 10 to get the real time.

Once scaling is completed, analog patching diagrams are drawn and the analog computer is wired for simulation. The scaled constants are set as potentiometer values and simulations are run. The cypress dome model was run on an EAI-580 analog computer and the pond mini-model was simulated on an EAI Miniac computer. Hardware capabilities at each machine were doubled by slaving a second identical computer with the first one through trunk lines. Analog diagrams and potentiometer settings are given in Appendices C and D for the two models.

RESULTS

Results of field data and model simulations are given
for Lake Alice and the cypress wetlands. These results
include analysis of data from other investigators. Values
used in the models were based as much as possible on the
field data.

Data from Lake Alice

Data from Lake Alice include hydrologic parameters,
metabolism and biomass values of waterhyacinths, open lake
metabolism values, and water chemistry and sediment analyses.

Hydrology

Rainfall and lake level data are given in Figure 23.
The lake in general responded rapidly to rainfall and the
ensuing runoff because of the small watershed size. Several
anomalies in the water level record, however, are not explained
by rainfall. The steady increase beginning around February 21
is attributed to the elevation of the water level to facili-
tate hyacinth removal around the edges. Valves control the
discharge from the lake to the Floridan Aquifer. A similar
irregularity is noted near the end of April. Increases in
September and October occurred each weekend when the discharge

Figure 23.   Lake level and rainfall data for Lake Alice
             for the period January 18-October 14, 1973.
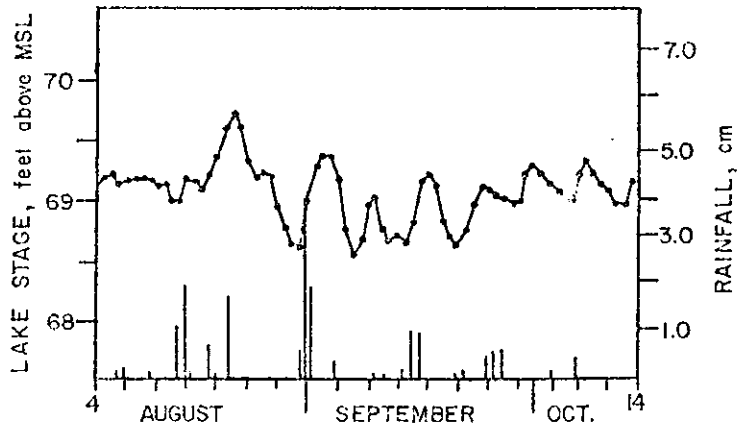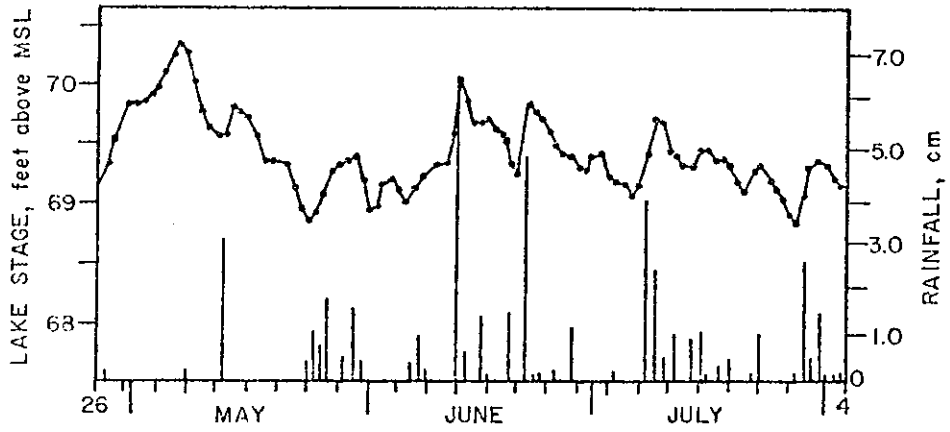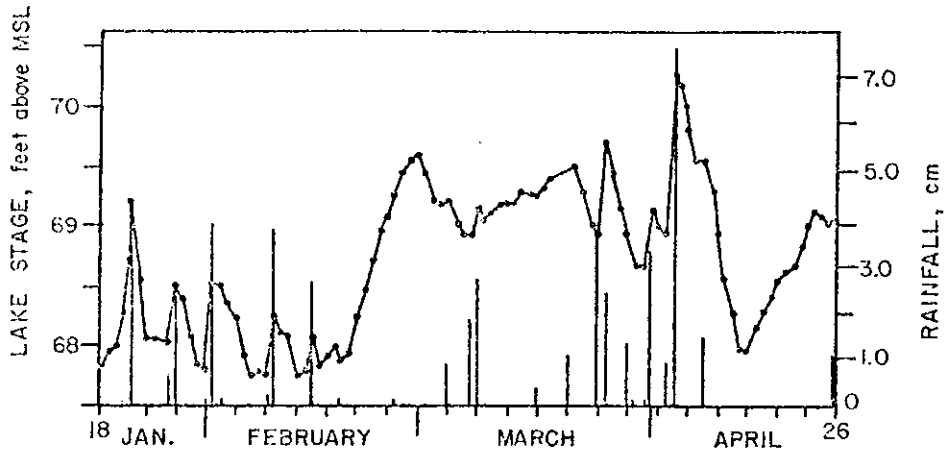
screens were not cleaned, thus allowing build-up of organic deposits and impeding flow. For most of the period of measurement a general level of 69 ft above mean sea level is assumed for a base stage.

Figure 24 gives hypsographic curves for both the hyacinth marsh and the open lake. The marsh is shown to be much shallower and to have a much flatter bottom contour than the open lake. Average depth for the marsh at a stage of 69 ft is 0.5 m while the lake has an average depth of 1.3 m. Using the relationships given in Figure 24 together with the water budget concept outlined in the Methods section, average monthly values for the various hydrologic flows associated with Lake Alice were produced (Figure 25). Flows from the heating plant, the sewage treatment plant, and Hume Pond comprise 82% of the average inflow to the lake for the period of measurements. Because of the karst formations underlying Lake Alice, the possibility exists for a bottom discharge from the lake through the solution holes seen in the bathymetric map (Figure 15), although Cason (1970) suggests that Lake Alice has long since become a perched lake with only surface outflows. It is therefore assumed that, except for evapotranspiration losses, the main lake outflow is confined to the two discharge wells located on the western shore.

Waterhyacinth Metabolism and Biomass

Results of the aerial reconnaissance of Lake Alice by J. L. Fox are shown in Figure 26, with Table 2 summarizing the

Figure 24.   Area-depth curves for Lake Alice hyacinth marsh and open lake. Volumes for a given stage can be obtained through integration of the curves.
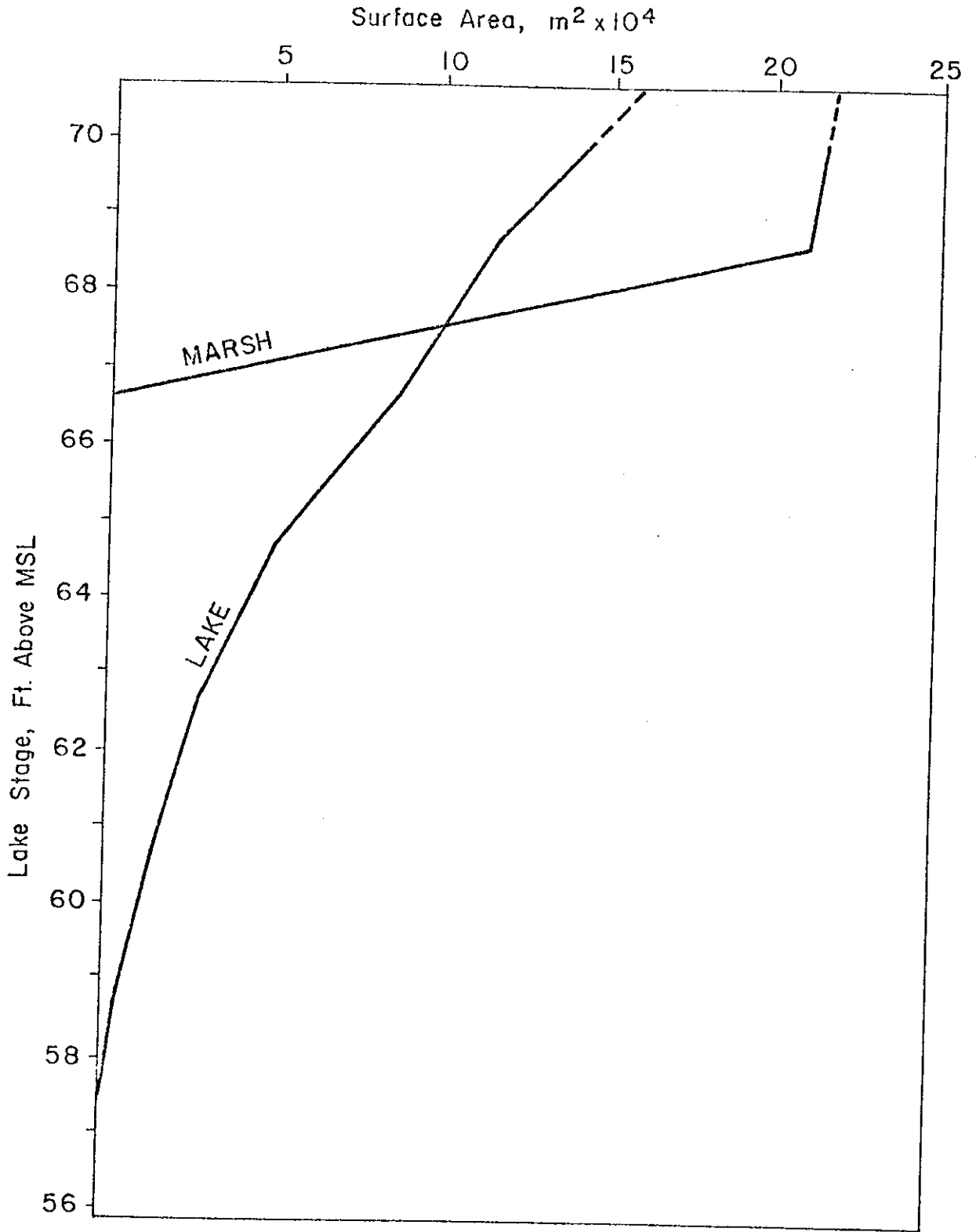
Figure 25. Hydrologic budget for Lake Alice (March-September, 1973). Flow values represent ranges of monthly averages while Lake Alice volume is for stage of 69.0 ft above MSL.

FLOW $\times 10^3$ m³/day
STORAGE $\times 10^3$ m³

Transpiration 1.8-3.1

Evaporation 0.4-0.6

Discharge 53.0-76.8

254
Lake Alice

Sewage flow 10.5

Heating plant flow 43.5

Hume stream 8.6

Direct rainfall 0.8-2.0

Runoff 6.1-21.0
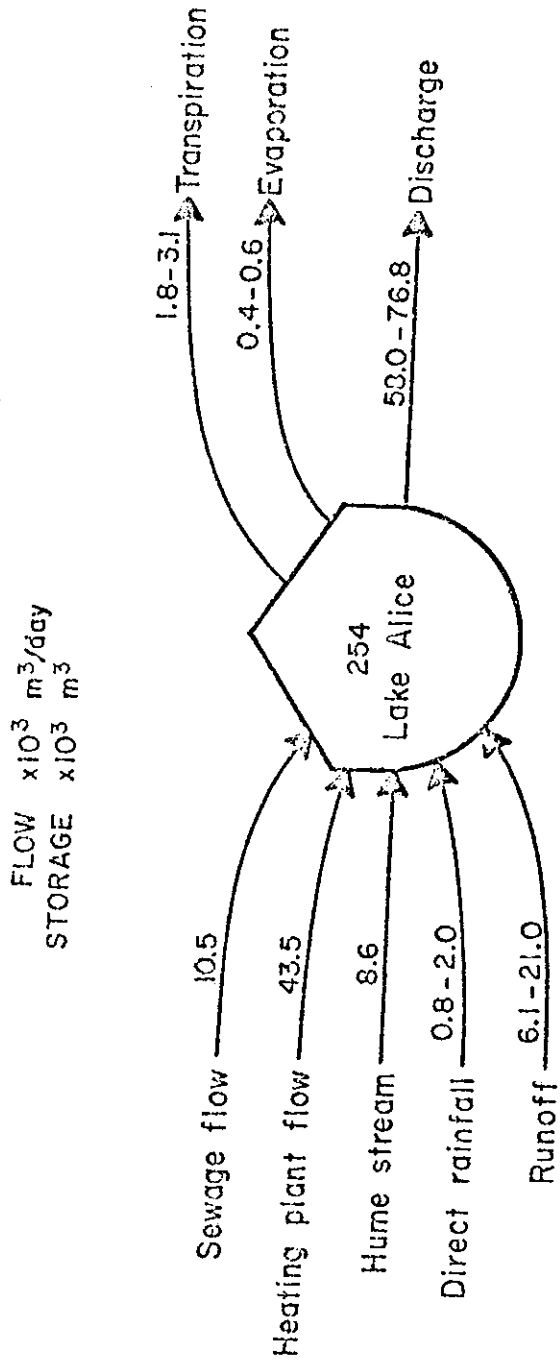
Figure 26. Lake Alice waterhyacinth coverage for
February, May, and July, 1973, based on
aerial photos obtained by J. L. Fox.

FEBRUARY

MAY

JULY

0   200   400
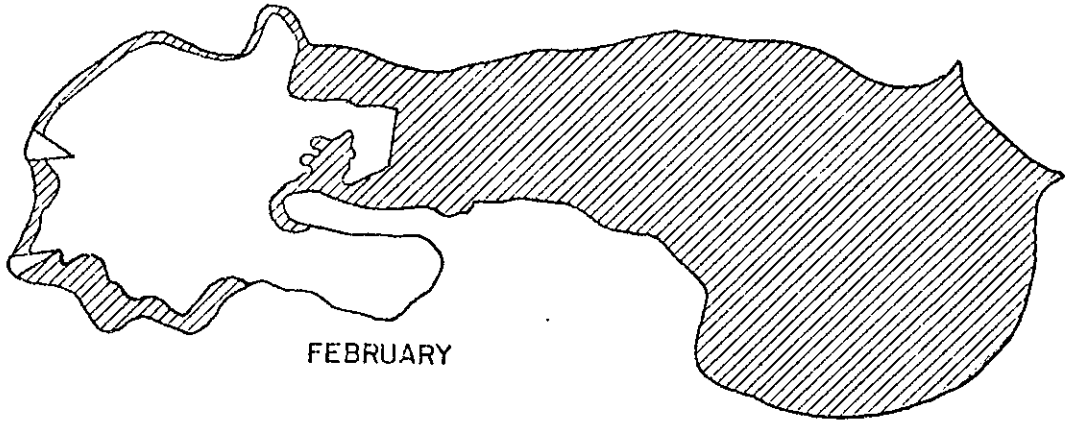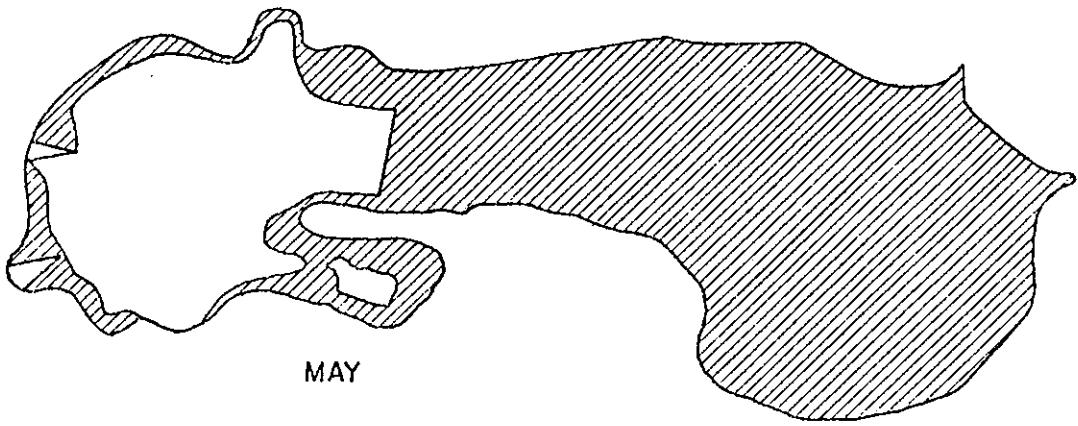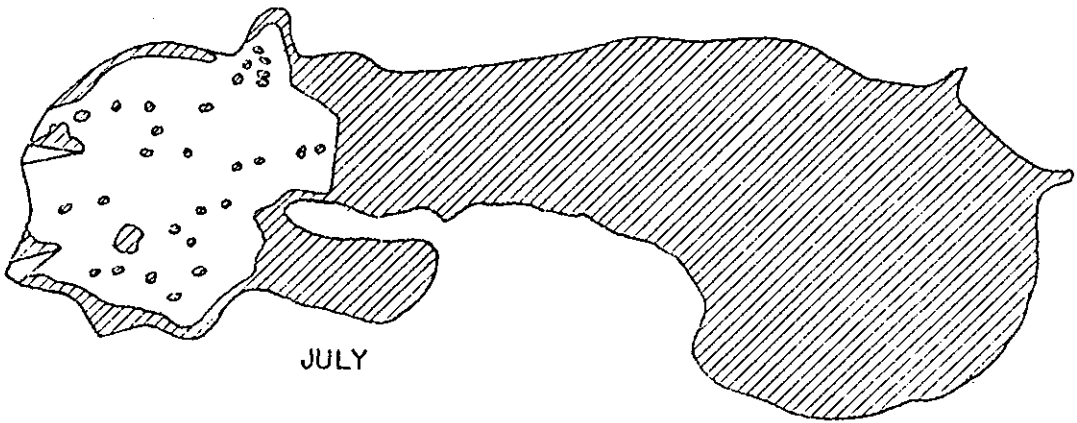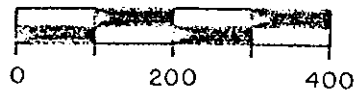
SCALE in METERS

Table 2

LAKE ALICE HYACINTH COVERAGE FOR THREE DATES IN 1973

Date	Total Lake		Open Lake Area	
	$m^2 x10^3$	%[a]	$m^2 x10^3$	%[a]
February	237	54	29	24
May	244	56	36	30
July[b]	259	59	51	42

Source: J. L. Fox aerial photographs.

[a]Total marsh area = $208 \times 10^3 m^2$

Total open lake area = $\dfrac{121 \times 10^3 m^2}{439 \times 10^3 m^2}$

[b]On the July photograph, remaining open water had spotty coverage of hyacinths.

hyacinth coverage. The marsh retained its hyacinth cover even in the winter months, and greener plants delineated the path of the warm influent during this time. Open lake coverage increased from 24% to 42% from February to July, despite substantial efforts by university personnel to keep the hyacinth population in check. The location of the hyacinth mats in the open water was generally wind-dependent, and it was once observed that a mass of hyacinths made a complete east-west return trip overnight due to shifting wind conditions.

Metabolism and biomass measurements were made on populations of two morphologically different waterhyacinths found in Lake Alice. Giant hyacinths, with an above-water height approaching 1 m, were compared with the smaller dwarf, float-bearing hyacinths. The former are representative of the marsh area where the plants are in shallower waters, are exposed to higher concentrations of nutrients, and are not disturbed by the continual control methods practiced on the open lake. The crowded conditions in this area favor the building of structure vertically rather than laterally. The dwarf hyacinths are better adapted to floating wherever the wind may take them, usually travel in small mats, and have floats on their petioles for isolated movement. They represent a less mature stage of the giant hyacinth but often retain their small stature and floats in less than optimal growing conditions (Penfound and Earle, 1948).

The diurnal curves of productivity made with infrared gas analysis of carbon dioxide and the corresponding solar

and air temperature curves are shown in Figure 27 (large hyacinths) and Figure 28 (dwarf hyacinths). Net productivity peaked for the giant hyacinths at about 1.3 g C/m^2-hr while the smaller hyacinths had a peak of only 0.65 g C/m^2-hr. Table 3 summarizes the productivity measurements. The large hyacinths displayed a very high (5.1%) efficiency in conversion of solar energy to gross production while the small plants had a 3.2% conversion. The net productivity efficiencies, however, were equal (1.6%). Comparison with published values (Table 4) shows that the net production compares well with those given by Westlake (1963), Penfound (1956), and Penfound and Earle (1948). Another value obtained for Lake Alice (Knipling, West, and Haller, 1970) appears extremely high. This value was obtained by expressing production on a leaf area basis and multiplying by the leaf area index. This calculation apparently does not give comparable results.

Biomass values, also determined for both sizes of hyacinths, are given in Table 3. The giant hyacinths were shown to have four times the biomass as the dwarf hyacinths. These values are compared with other values from the literature in Table 5 and seem to indicate that large hyacinths have been used in the past for biomass measurements. The results compare especially well with previous measurements made on Lake Alice (Knipling et al., 1970).

Figure 27.   Gross production of large waterhyacinths, solar radiation, and air temperatures. Production was determined from CO_2 infrared gas analysis.

Figure 28.   Gross production of small waterhyacinths,
             solar radiation, and air temperatures.
             Production was determined from CO_2 infrared
             gas analysis.

LARGE WATERHYACINTH
LAKE ALICE
AUGUST 11-12, 1973

AREA = 0.49 m^2

SOLAR RADIATION

AIR TEMPERATURE

GROSS PRODUCTION

RESPIRATION

SMALL WATERHYACINTH
LAKE ALICE
AUGUST 12-13, 1973

AREA = 0.49 m²
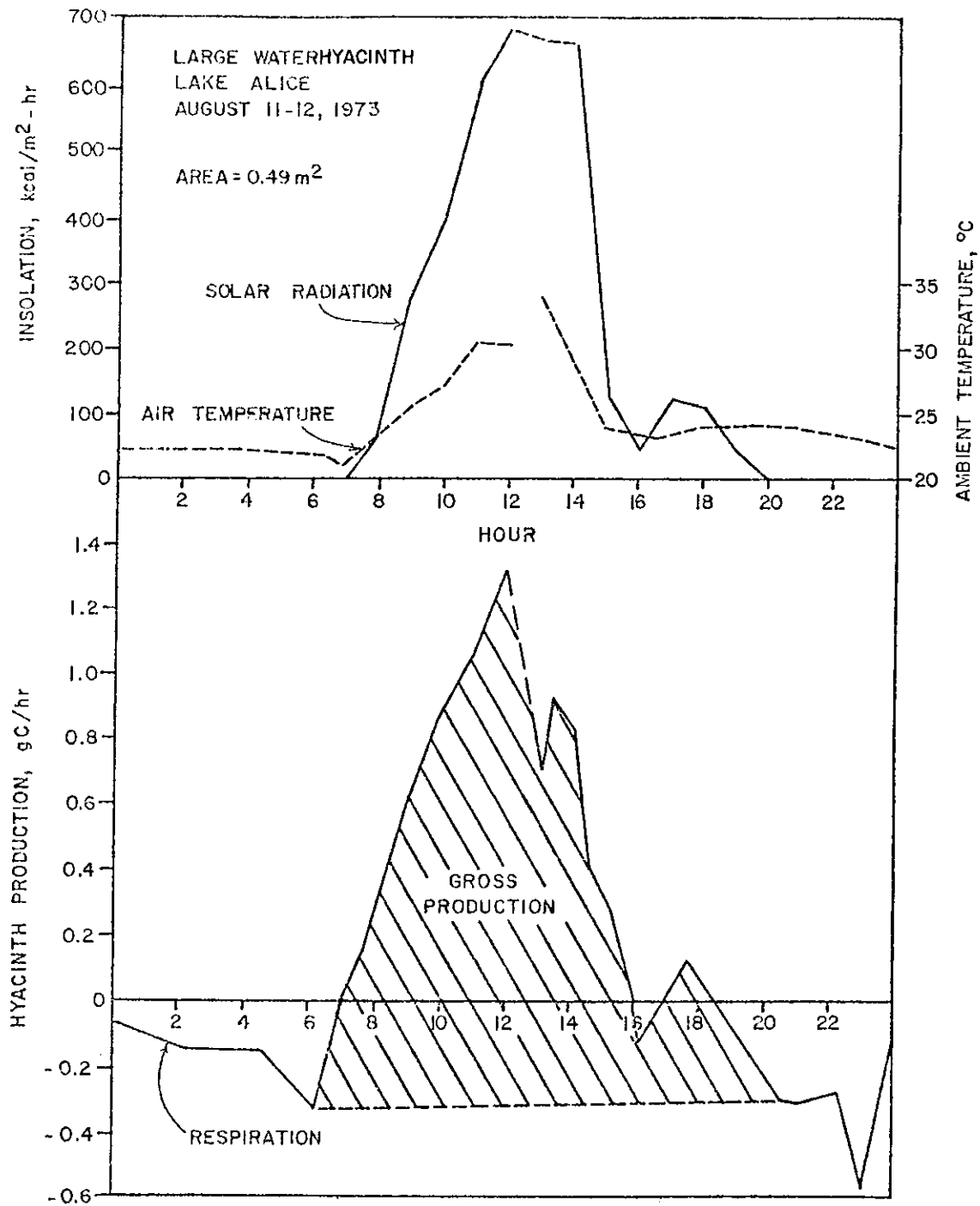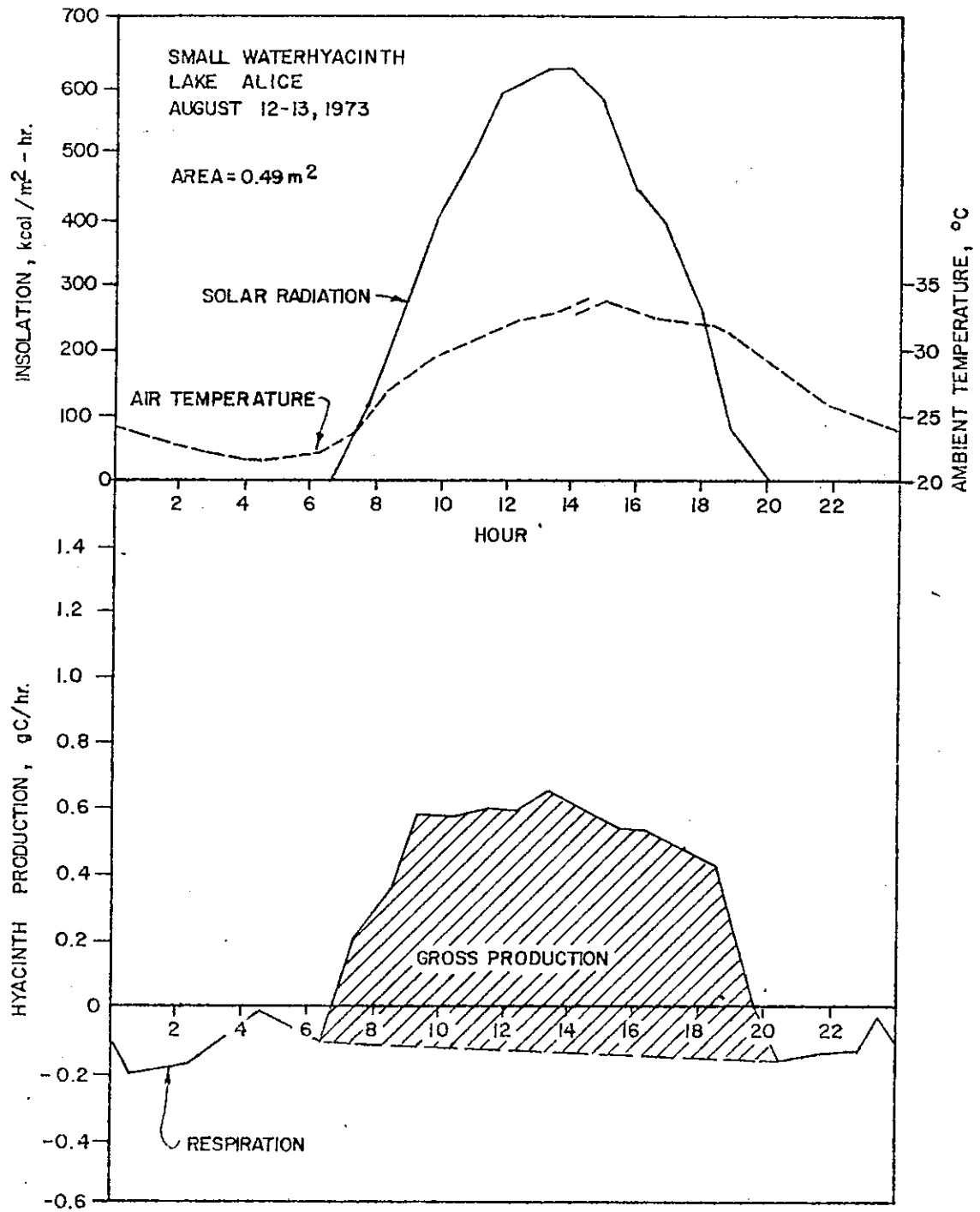
Table 3

WATERHYACINTH METABOLISM AND BIOMASS DATA
AT LAKE ALICE ON AUGUST 11-13, 1973

Parameter	Large Hyacinths	Small Hyacinths
Insolation, $kcal/m^2$-day	3750	4900
Gross production (P_g), $kcal/m^2$-day[a]	193	156
Respiration (R), $kcal/m^2$-day[a,b]	132	76
P_g/R	1.46	2.06
Net production (P_n), $kcal/m^2$-day	61	80
Efficiency, Pg/Insol., %	5.1	3.2
Efficiency, P_n/Insol., %	1.6	1.6
Biomass (dry wt), $kcal/m^2$ [c]	11272	2896
P_g/Biomass, day^{-1}	0.017	0.054

[a]Assumes 1 gC = 10 kcal.

[b]Respiration is average night respiration assumed to
be the same during the day.

[c]Assumes 1 g dry wt = 4.5 kcal (Hahn et al., 1971).
Estimated annual net productivity (no frost)--22,700 $kcal/m^2$-yr.
Estimated annual net productivity (with frost)--15,100 kcal/
m^2-yr.

Table 4

NET PRODUCTIVITY OF WATERHYACINTHS TAKEN FROM PUBLISHED MATERIAL

Source	Production	$kcal/m^2/yr$	Remarks
Penfound & Earle (1948)	5.1 g C/m^2-day	18,600	Assumes no frost
Dymond (1949)	10.8-18.0 kg/m^2-yr	48,600-81,000	
Penfound (1956)	12.7-14.6 g/m^2-day	20,900-24,000	Assumes no frost
Odum, H.T. (1957)	10-20 kcal/m^2-day	3,650-7,300	Assumes NPP is 1/2 GPP
Westlake (1963)	150 mt/ha-yr 40 mt/ha-yr	67,500 18,000	Maximum Average
Yount (1964)	21.8 kg/m^2-yr	98,000	
Knipling et al. (1970), Lake Alice	11.5 mg CO$_2$/ dm^2 leaf-hr	120,000	Assumes LAI is 7.8, I^a is 3900 kcal/m^2-day
Lugo (unpublished), Gordon's Pond	2.97 g C/m^2-day	10,800	Assumes I^a is 4320 kcal/m^2-day
Morris (1974)	2.0-20.4 g/m^2-day	3,300-33,500	Assumes no frost
This study (Table 3)	1.6% NPP eff.	22,700	Assumes I^a is 1.4 x 10^6 kcal/m^2-yr

[a] I is insolation.

Table 5

STANDING BIOMASS OF WATERHYACINTHS TAKEN FROM PUBLISHED MATERIAL

Investigator	Dry Weight	Wet Weight	kcal/m^2[a]
Penfound & Earle (1948)	7.2-16.6 tons/acre (1.6-3.7 kg/m^2)	123.1-183.0 tons/acre (27.6-41.0 kg/m^2)	7200-16,600
Dymond (1949)	1.4 kg/m^2		6300
Penfound (1956)	12.8 mt/ha		5760
Westlake (1963)	1.5 kg/m^2		6750
Knipling (1970)			
Lake Alice	2.4 kg/m^2	40.4 kg/m^2	10,800
Payne's Prairie	2.5 kg/m^2	42.4 kg/m^2	11,250
Wahlquist (1972)			
no fertilizer		17.4 kg/m^2	
phos. only		55.0 kg/m^2	
phos.+nitrogen		59.0 kg/m^2	
Fox (winter), Lake Alice		8.48-26.4 kg/m^2	
Morris (1974) Payne's Prairie Canal	0.8 kg/m^2		3600
This study (Table 3)			
large	2.50 kg/m^2	41.7 kg/m^2	11,272
small	0.64 kg/m^2	11.2 kg/m^2	2896

[a]Assumes 1 g dry wt = 4.5 kcal (Westlake, 1963; Hahn et al., 1971).

Open Lake Community Metabolism

The productivity of the open water community in Lake Alice was determined with free water changes in oxygen several times throughout the study period by the author and others to investigate both spatial and temporal variations. The results are shown in Table 6. Productivity varied from 13 to 194 $kcal/m^2$-day with both extremes occurring on the same day (May 22) in different parts of the lake. The significant spatial variation can be attributed to limitation of productivity at shallower depths, especially at Station 15. For temporal comparison, the deepest station (Station 6) provides the most data. Gross primary productivity here ranged from 24 to 117 $kcal/m^2$-day and P_g/R ratios were generally close to 1.0, with a range of 0.8 to 1.3.

Water Chemistry

The chemical characteristics of Lake Alice, summarized for three stations along the direction of flow, are given in Table 7. The values represent the range of monthly averages of daily analysis. The temporal change of the monthly averages for Station 6 (open lake) for chemical oxygen demand, conductivity, nitrogen, and phosphorus are shown in Figure 29. These values are representative of the effluent going into the Floridan Aquifer. The water can generally be summarized as hard, well buffered, and slightly alkaline, with high concentrations of allochthonous and autochthonous organic matter. The concentrations of nitrogen and phosphorus are high,

Table 6

WATER COLUMN METABOLISM FOR OPEN LAKE COMMUNITY
IN LAKE ALICE
(Values in kcal/m^2-day)

		1973				
		Jan 26[a]	Mar 21[a]	Apr 26	May 22[a]	July 31
Solar Radiation		3450	4100	2400	6130	3270
Station 5	P[b]				73	
	R[b]				64	
Station 6	P	105	62	69	117	24
	R	90	78	74	132	18
Station 10	P				194	
	R				226	
Station 11	P		34	42	122	34
	R		43	45	134	30
Station 12	P		55			
	R		49			
Station 15	P			22	13	15
	R			19	4	15
Station 16	P				112	
	R				136	

[a]January, March and May measurements were made by
M. Kiern.

[b]P = Gross Primary Production
R = Respiration

STATION LOCATIONS
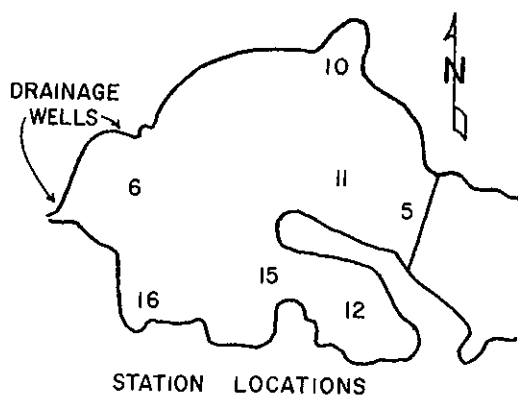
Table 7

RANGES OF WATER QUALITY PARAMETERS
(MONTHLY AVERAGES) FOR LAKE ALICE,
JANUARY-SEPTEMBER, 1973

Parameter[a]	Station 1 Influent	Station 5 Marsh Discharge	Station 6 Open Lake
pH	7.4-8.2	7.6-8.3	7.4-8.3
Water temperature (°C)	28.5-35.3	22.5-28.7	19.5-29.9
Conductivity (μmjo/cm)	429-516	379-484	405-482
Turbidity (JTU)	4.5-17.4	2.9-6.7	3.2-6.8
Alkalinity (mg $CaCO_3$/ℓ)	150-176	133-182	138-172
Dissolved oxygen[b] (mg/ℓ)	--	0.4-2.0	3.0-10.5
Chemical oxygen demand (mg/ℓ)	28.9-87.6	32.6-54.1	39.2-76.6
Total phosphorus (mg-P/ℓ)	0.79-2.45	0.86-2.10	0.93-2.84
Ortho-phosphates (mg-P/ℓ)[b]	0.28-0.90	0.73-1.00	0.28-1.00
Total Kjeldahl nitrogen (mg-N/ℓ)	1.09-2.38	0.60-1.26	0.74-1.16
NH_3 (mg-N/ℓ)	0.035-0.301	0.053-0.184	0.005-0.118
NO_3 (mg-N/ℓ)	0.61-2.00	0.008-0.938	0.001-0.635
NO_2 (mg-N/ℓ)[b]	0.05-0.08	0.01-0.03	0.02-0.04
K (mg/ℓ)[c]	1.2-8.0	0.5-6.5	0.4-5.0
Mg (mg/ℓ)[c]	9.0-17.0	5.5-16.0	5.0-16.0
Na (mg/ℓ)[c]	12-19	15-19	12-20
Ca (mg/ℓ)[c]	22-66	14-65	14-63

[a]Raw data from P. L. Brezonik.

[b]Spot samples only.

[c]Ranges of weekly composite samples.

NOTE: See Figure 15 for station locations.

Figure 29. Water quality parameters for Lake Alice open water (Station 6) based on monthly averages of daily sampling: (a) chemical oxygen demand, (b) conductivity, (c) Kjeldahl nitrogen, (d) nitrate-nitrogen, (e) ammonia-nitrogen, and (f) total phosphorus. Values are representative of quality of lake discharge to Floridan Aquifer. (Inside bars indicate standard errors and outside brackets give standard deviations.)

Chemical Oxygen Demand

(a)

Conductivity

(b)

(c)

(d)
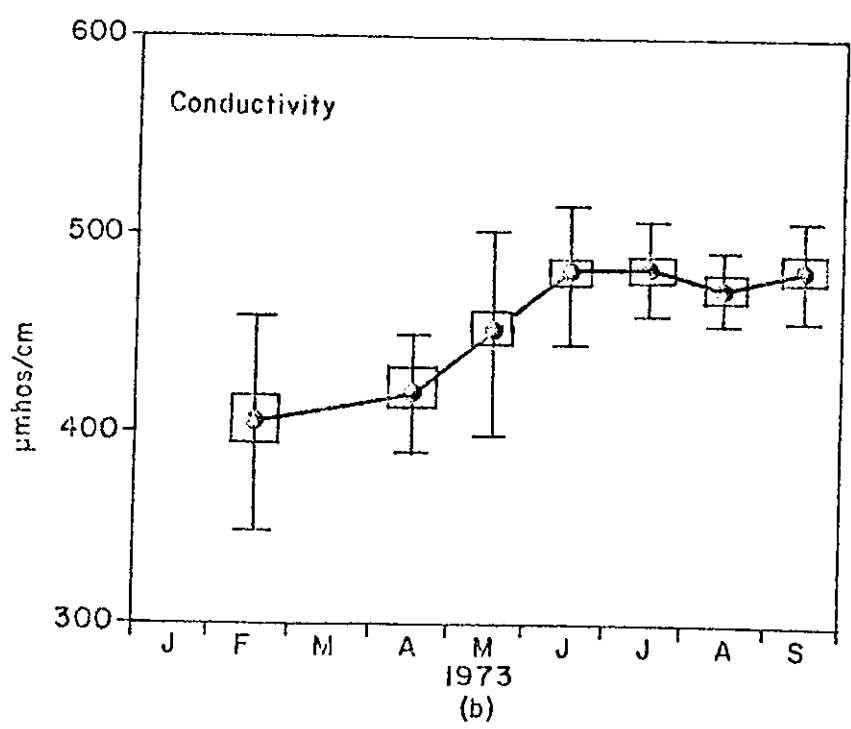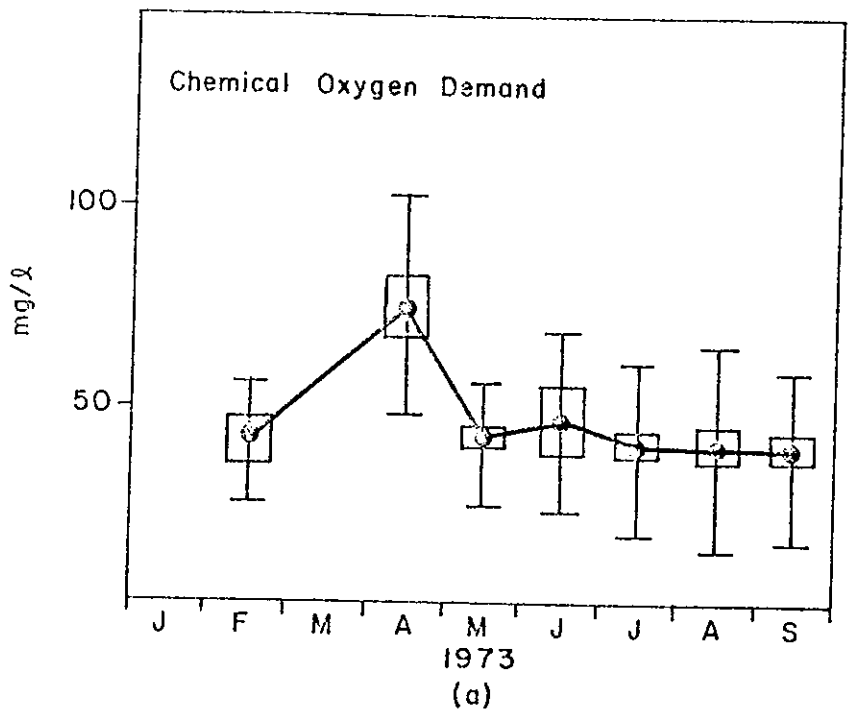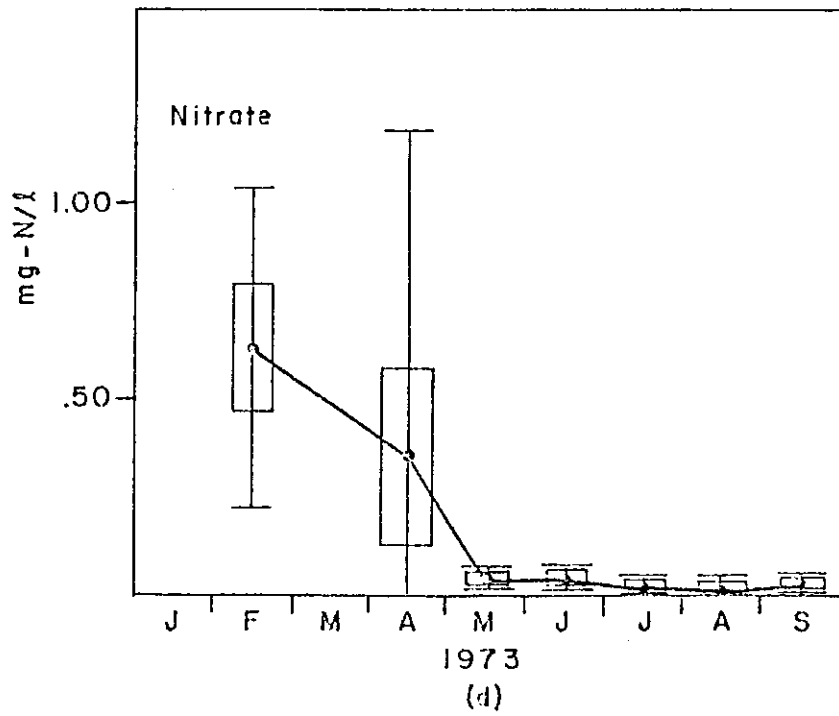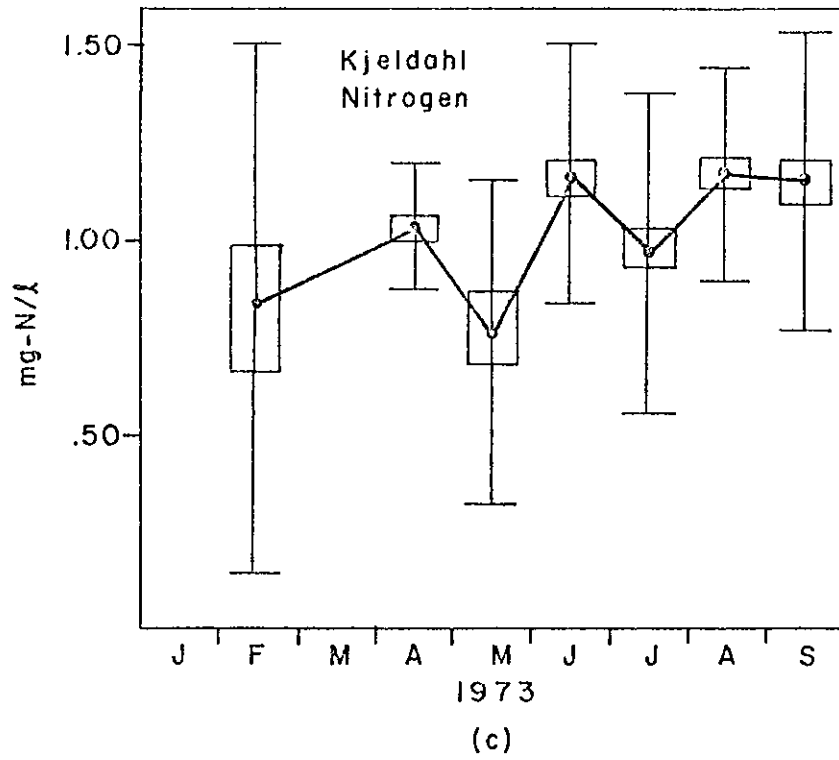
Figure 29 - continued.
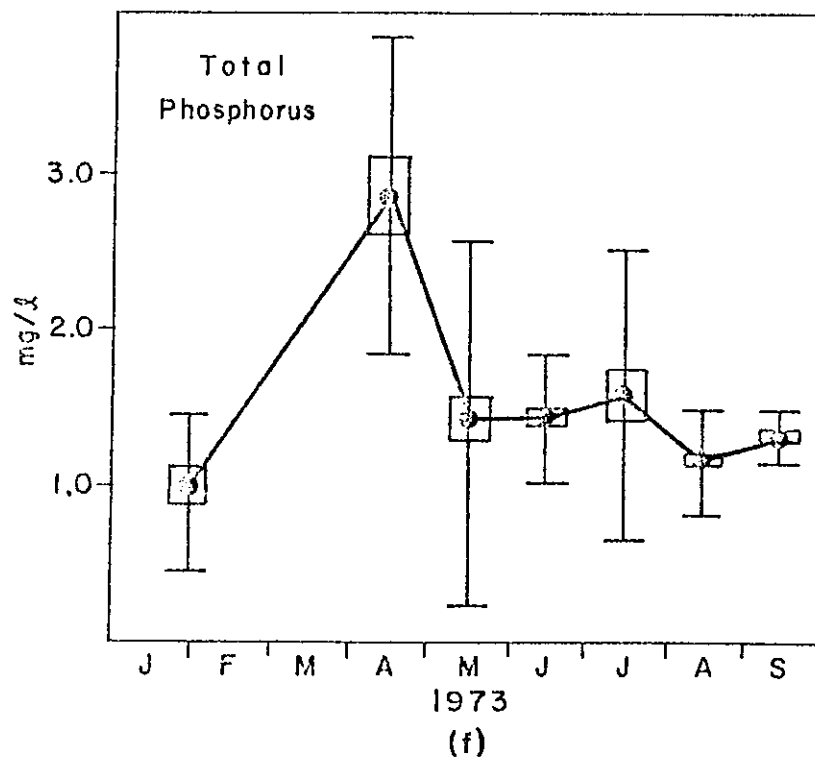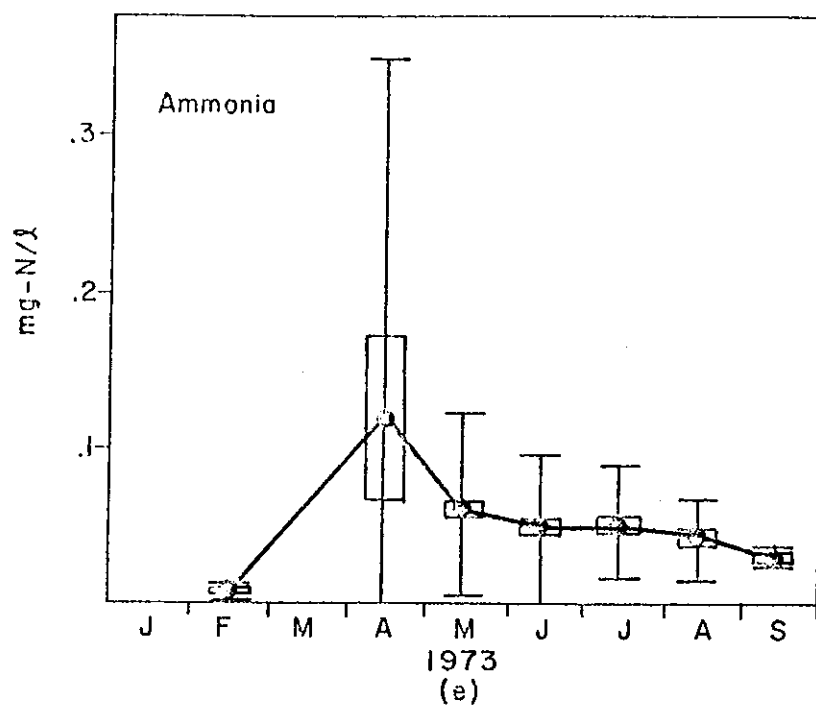
Figure 29 - continued.

primarily due to the sewage loading. Values were generally on the order of 1 to 2 mg/l in the open lake. The high fluctuations in dissolved oxygen primarily reflected diurnal changes in primary production as discussed above. Oxygen coming out of the hyacinth marsh was always found to be near zero.

In order to evaluate the effects of the hyacinth system on water quality, the differences between the influent and the effluent of the hyacinth marsh were calculated for all times in which data were available for both stations. The monthly averages of the changes across the marsh for chemical oxygen demand, conductivity, Kjeldahl nitrogen, nitrate nitrogen, ammonia nitrogen, and total phosphorus are given in Figure 30. COD and Kjeldahl nitrogen showed patterns which suggest maximum retention of organics in May and June, but net exports by the end of summer. Conductivity generally decreased 10%, possibly due to dilution from rainfall and runoff. Nitrate-nitrogen showed the most dramatic seasonal changes, going from a 0.25 mg-N/l decrease across the marsh in winter to 1.25 mg-N/l decrease by late summer. Ammonia decrease was generally 0.1 mg-N/l while phosphorus showed little if any decrease across the hyacinth marsh.

Water Temperature

Because the thermal influent to the lake undoubtedly is important to the ecosystem behavior, water temperature was monitored continuously at the inlet and outlet of the hyacinth

Figure 30. Changes in water chemistry across water-hyacinth marsh for (a) chemical oxygen demand, (b) conductivity, (c) Kjeldahl nitrogen, (d) nitrate-nitrogen, (e) ammonia-nitrogen, and (f) total phosphorus. Lines indicate averages; outside bars show standard deviations and shaded bars show standard errors; numbers in parentheses give the number of samples. These data include only those measurements when samples were concurrently available upstream and downstream.

(a)

(b)
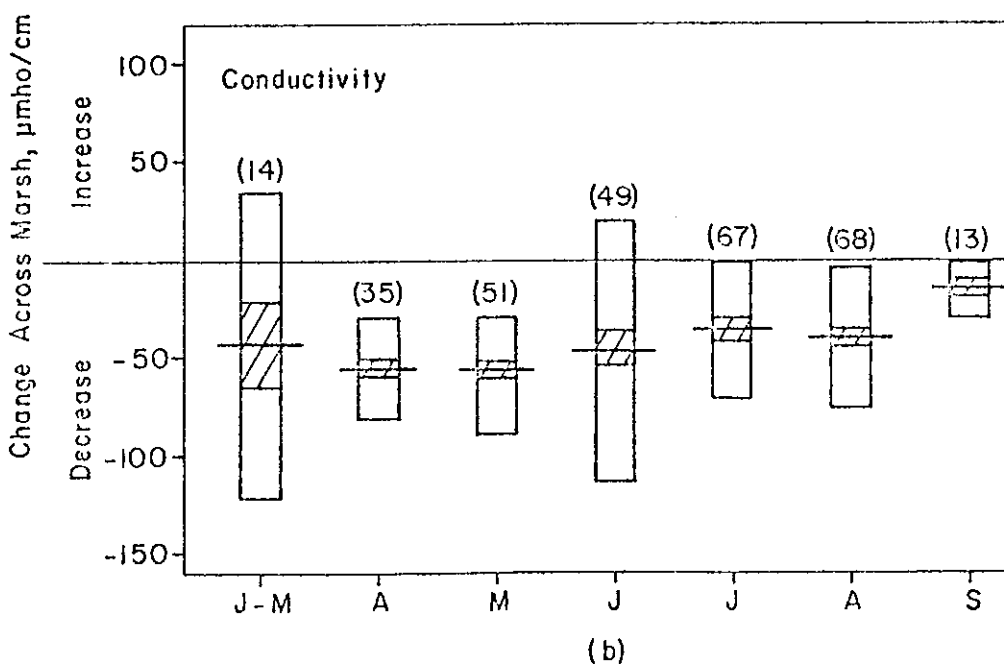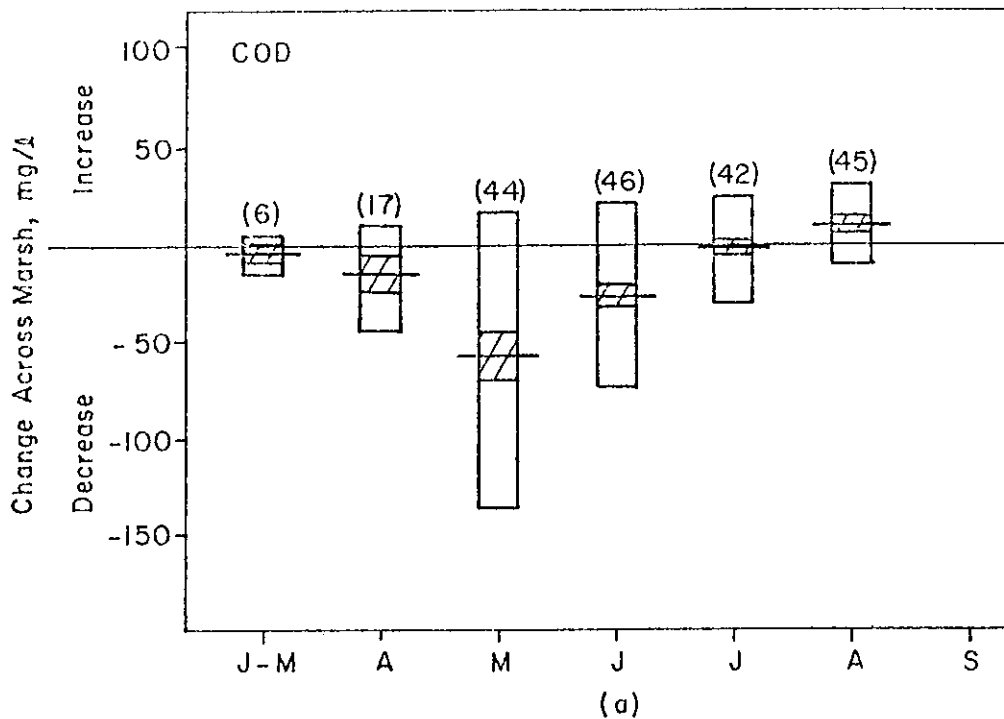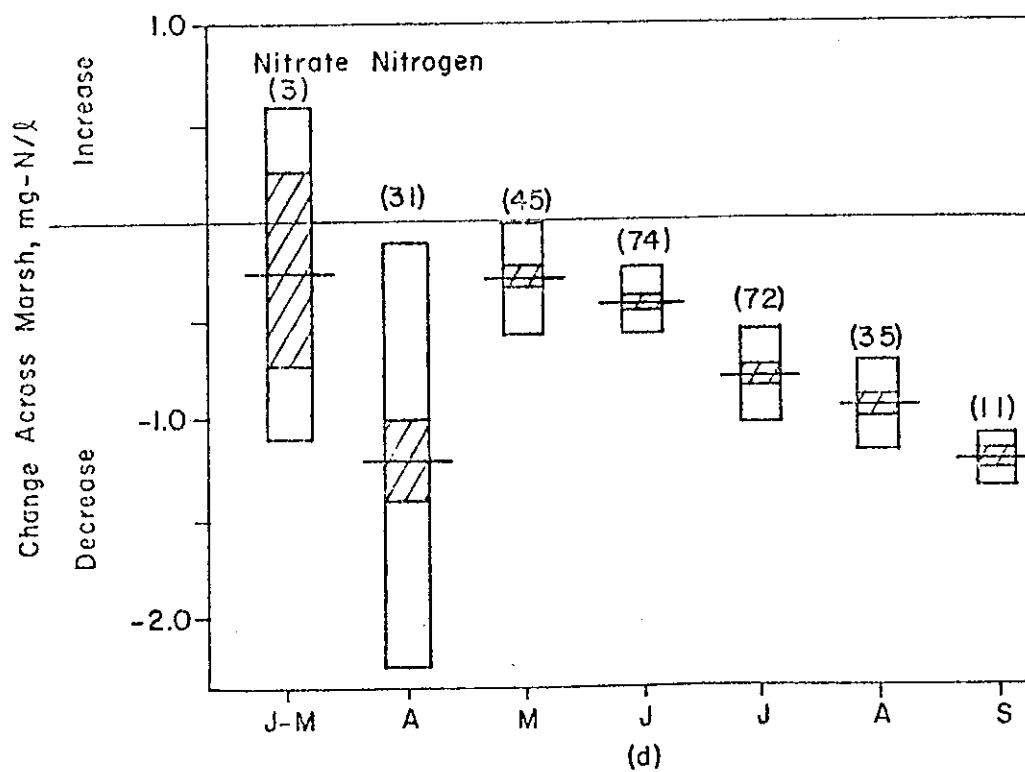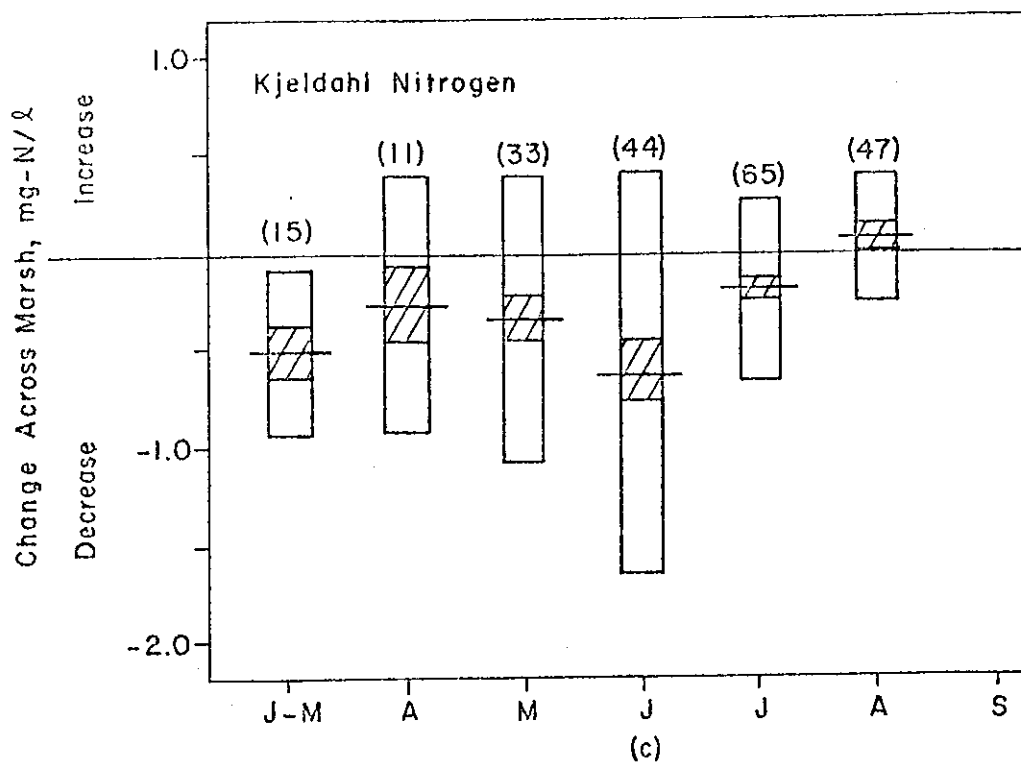
Figure 30 - continued.
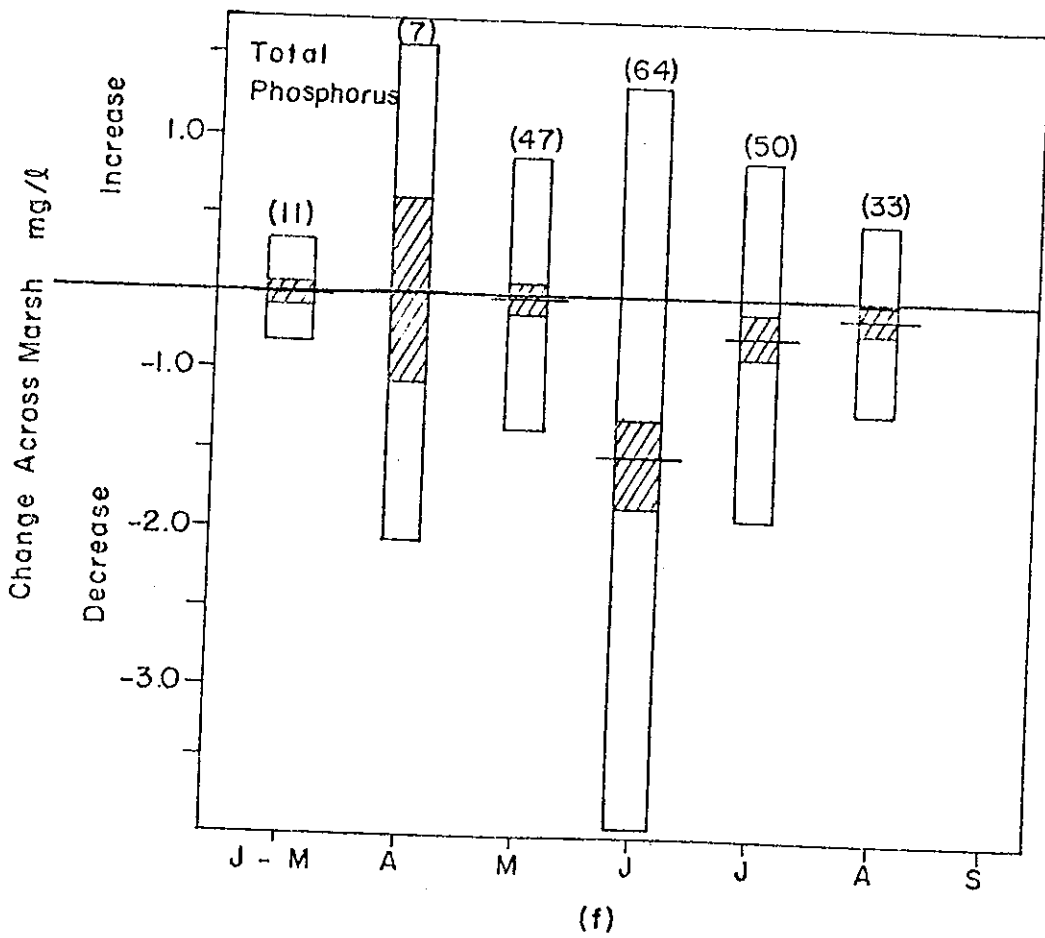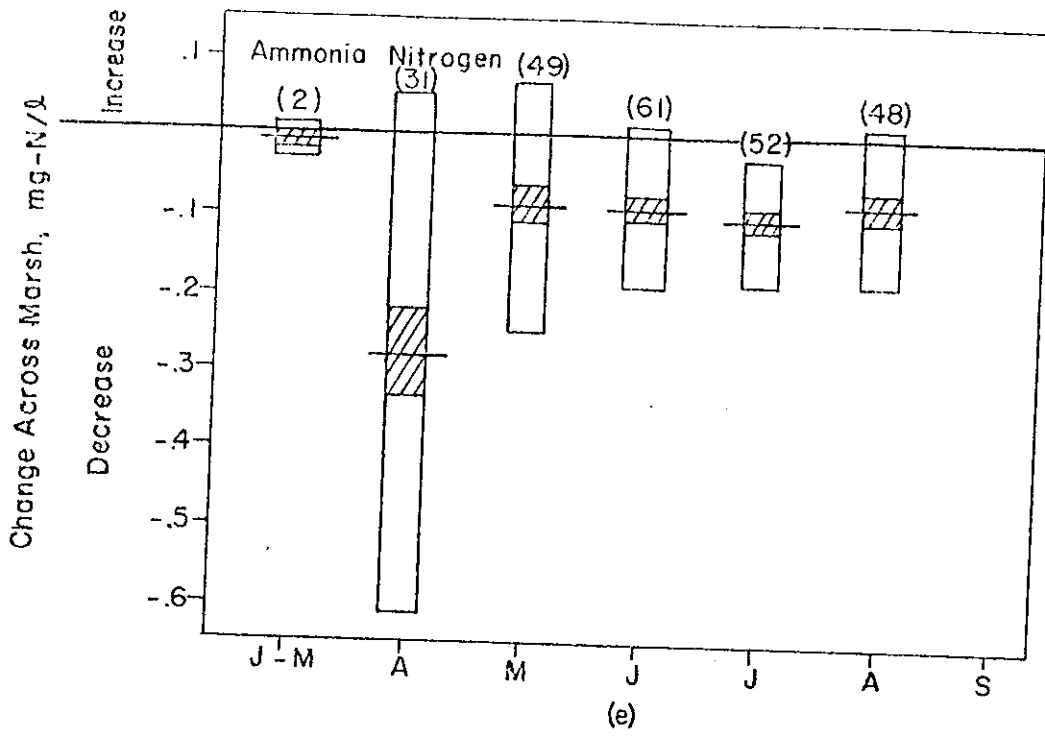
Figure 30 - continued.

marsh. Figure 31 shows the effect of the hyacinth marsh on water temperature. A significant decrease is noted across the marsh, and calculations were made to compare this decrease with what might be expected from natural cooling. Temperatures at the hyacinth marsh discharge were determined according to the method outlined by Edinger and Geyer (1965) for downstream temperatures in a flow-through cooling pond. The results concur with the findings of Ultsch (1973), who noted the effects of waterhyacinths in damping annual temperature fluctuations by maintaining lower temperatures in the summer and retaining heat in the winter.

Lake Sediments

Results of chemical analyses of bottom sediment samples from Lake Alice are given in Figure 32. Figure 32a shows the concentrations based on one gram of dry weight for nitrogen, phosphorus, and the major cations. Values were dependent on percent organics associated with each replicate. Those samples with high organics generally held higher concentrations of these elements.

Figure 32b gives the average amount of organic and inorganic sediments sampled. Average depth was approximately 10 cm. Total dry weight of the samples averaged 144.5 kg/m^2, resulting in a sample density of 280 kg/m^2. The organic fraction was 17.9 kg/m^2. If this organic accumulation is taken to be due to detrital production from waterhyacinths over the past ten years, then an accumulation rate of 0.7

Figure 31. Water temperatures for Lake Alice at influent (Station 1) and effluent (Station 5) of water-hyacinth marsh. Values are monthly averages of continuous recordings with bars indicating standard errors. The dotted line indicates a calculated water temperature for Station 5 for normal surface cooling based on the method of Edinger and Geyer (1965). These data suggest that the waterhyacinth marsh damps the annual temperature fluctuations by keeping the water warmer in winter and cooler in the summer.

Water Temperature

Marsh Influent
Station I

Marsh Effluent
Station 5

Calculated Marsh
Effluent-Station 5
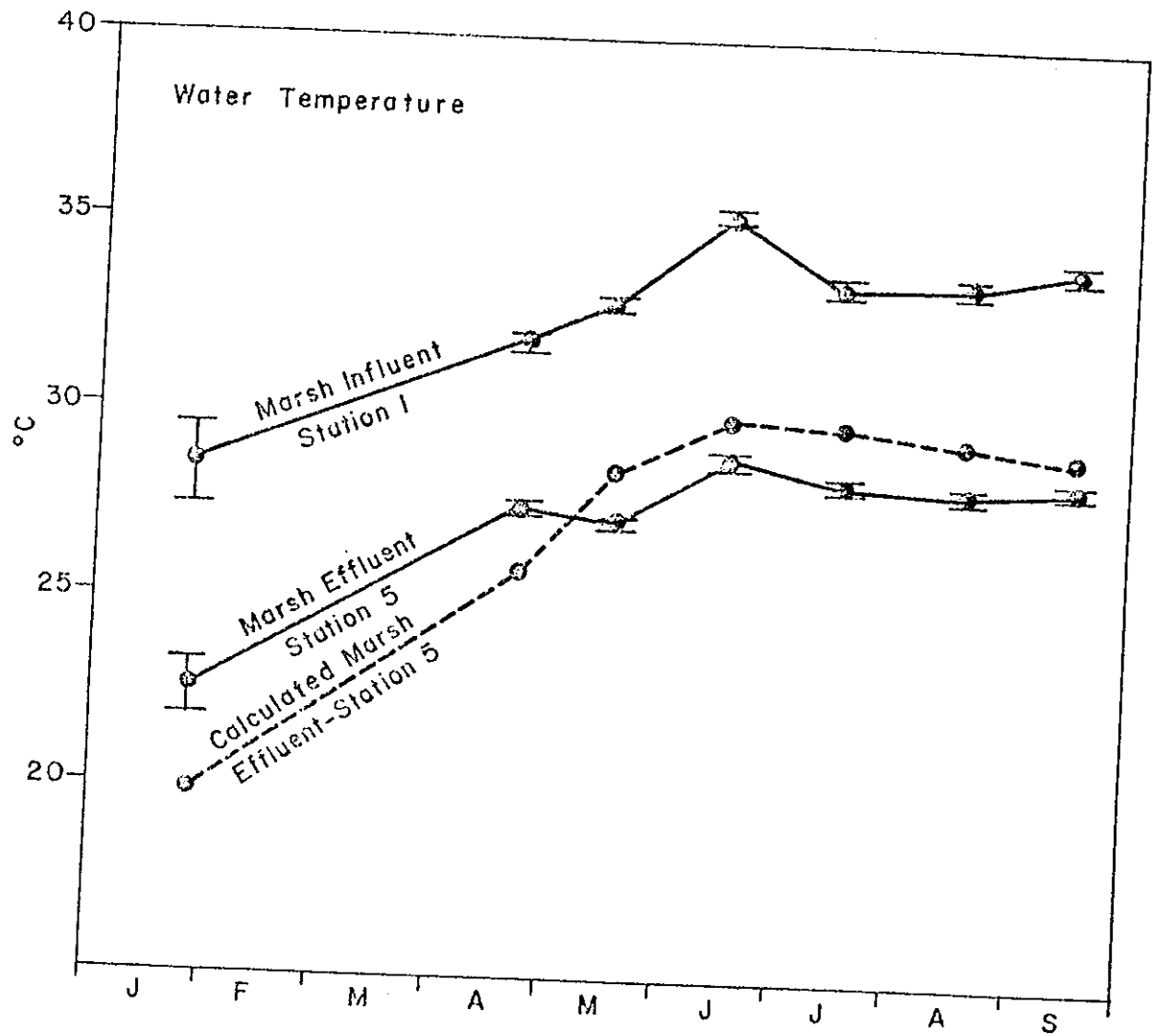
Figure 32.   Results from Lake Alice sediment analyses
including: (a) major nutrient concentra-
tions (averages, standard errors, and
standard deviations); (b) organic and
inorganic fractions of samples; and
(c) total nitrogen and phosphorus in
samples. Samples were taken to an average
depth of 10 cm.

(a)

(b)

(c)
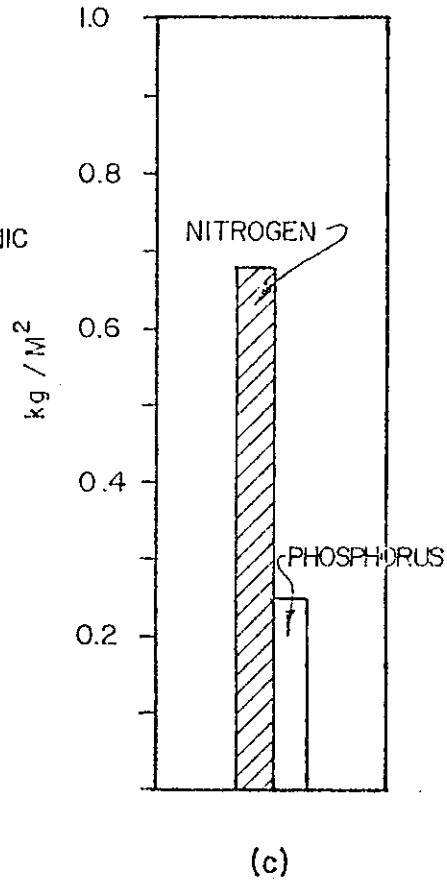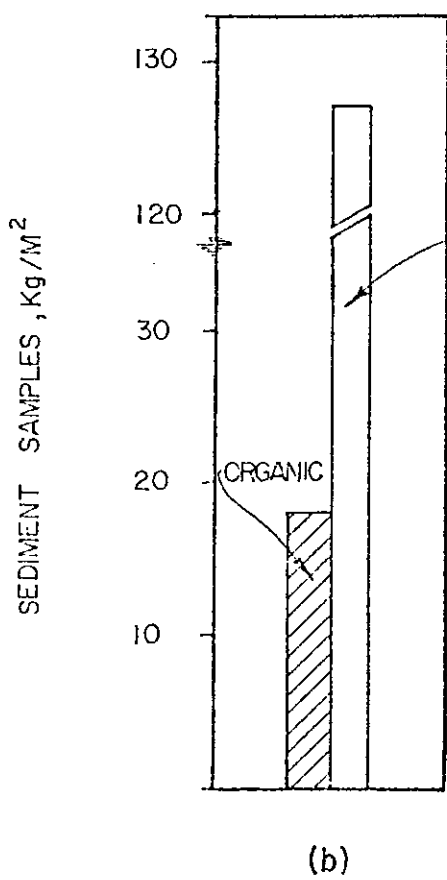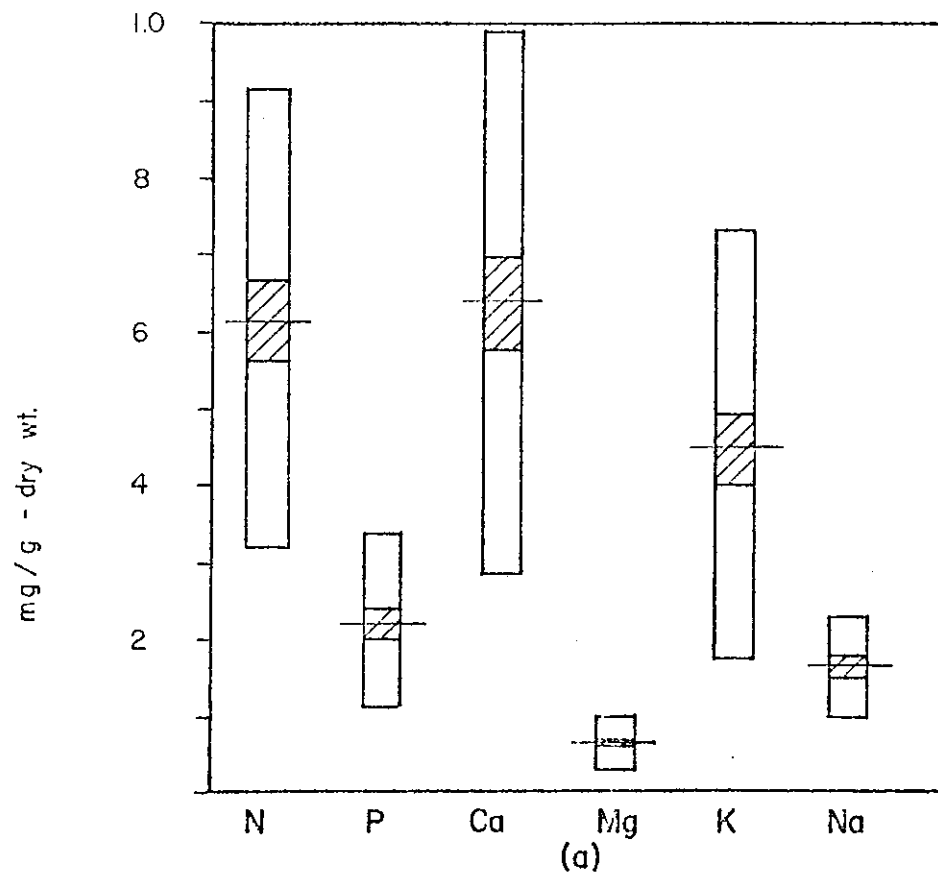
cm/yr may be approximated, assuming a bulk density of 0.25 g/cm^3 (Brady, 1974).

Figure 32c shows graphs of the total nitrogen and total phosphorus storages in the upper sediments. It is suggested that these storages are involved as both sources and sinks with the overlying waters. Nitrogen was calculated to be 675 g/m^2 while phosphorus was 250 g/m^2. This N/P ratio reflects the low ratio associated with the wastewater flowing into the lake.

Lake Alice Model

The model simulated for Lake Alice is shown in Figure 33. The two parts of the lake, the waterhyacinth marsh and the open lake, are shown separately, the marsh in Figure 33a and the open water in Figure 33b. These two sections connect in one overall model. Morphometric parameters, waterhyacinths, water chemistry, and organic sediments were considered in both sections. Benthic macrophytes and phytoplankton communities were included in the open water half as competitors with waterhyacinths. Major forcing functions were water, nutrient, and dissolved oxygen inflows, oxygen diffusion, solar radiation, and heat. Because the model was designed to run for several years, diurnal variations were neglected, and both temperature and solar radiation were described as annual sinusoidal functions. Trophic levels higher than primary producers (plants) were not considered except as generalized respiratory functions on various organic storages.

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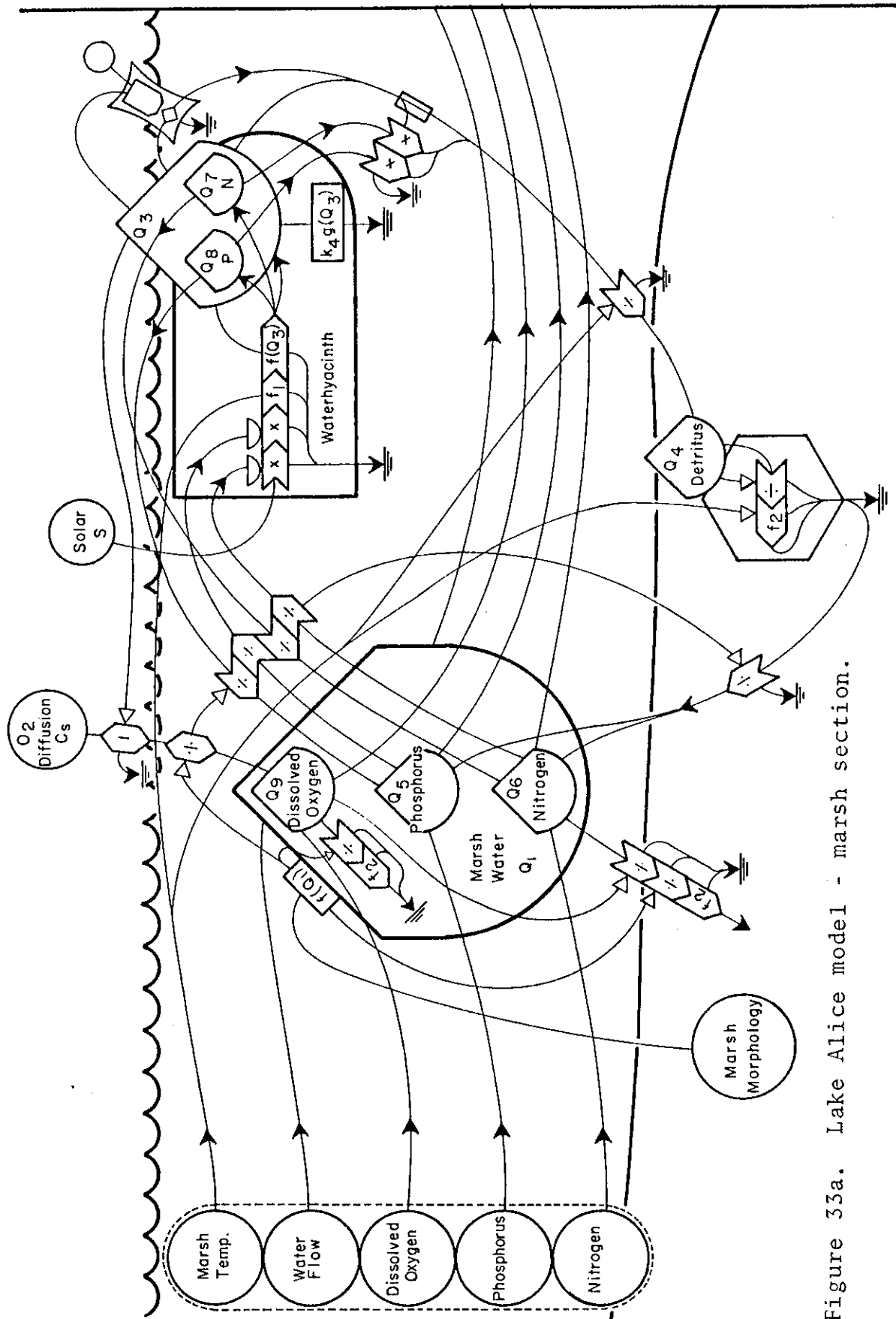
Figure 33a. Lake Alice model - marsh section.
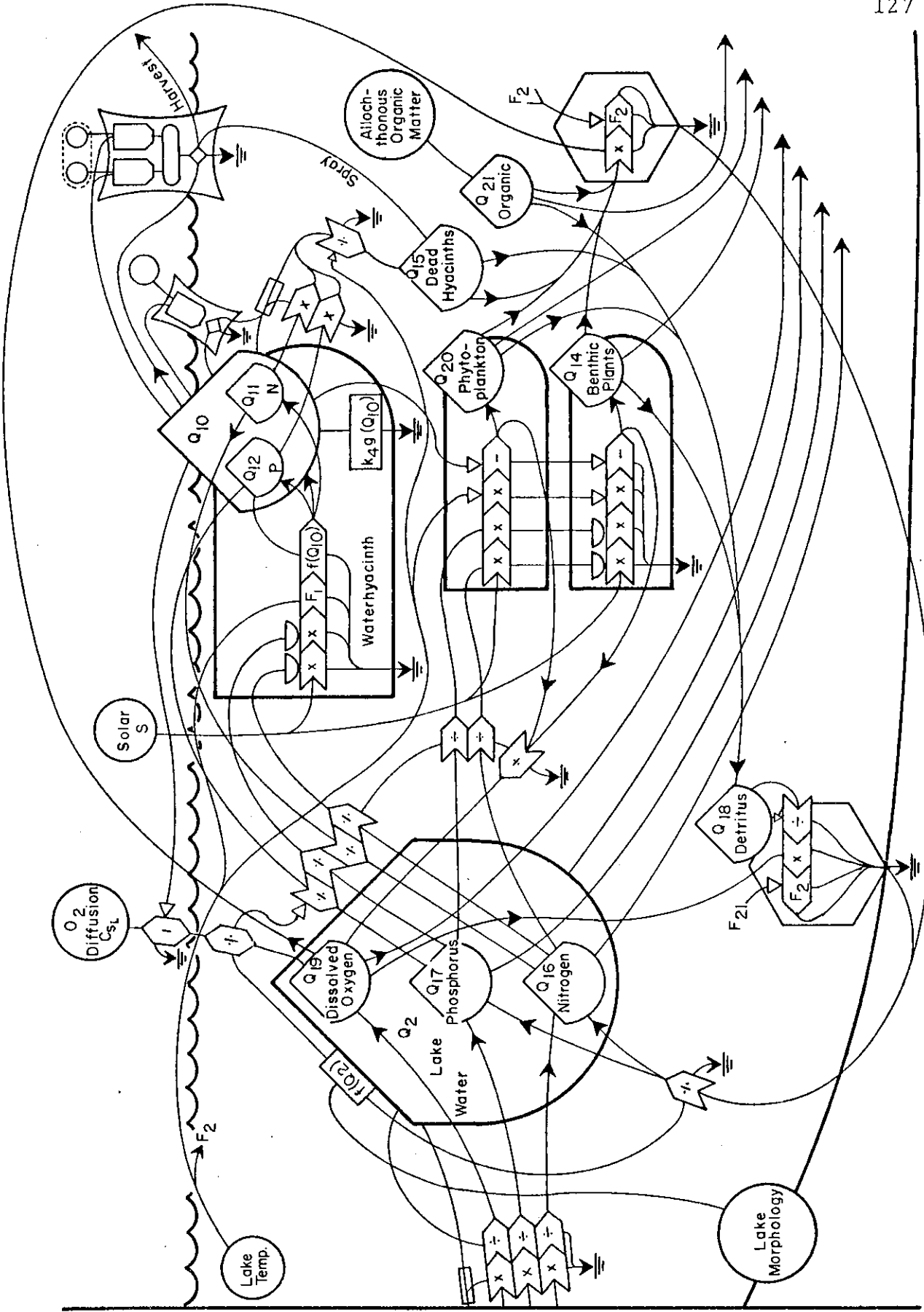
Figure 33b. Lake Alice model - lake section.

Table 8 gives the initial conditions or steady state values for the storages, sources, and pathways in the model. Figure 34 summarizes the nitrogen and phosphorus flows and storages for the two sections of the lake. (See Appendix B.)

Figure 35 gives a detailed drawing of the waterhyacinth module used for both sections of the lake. Gross production is shown to be stimulated by nitrogen, phosphorus, water temperature, and an autocatalytic function. Although nutrient regeneration is generally coupled with the respiratory pathways, the leaching of nutrients back into the water was assumed to be a linear function of their storages in the plant. Michaelis-Menten kinetics (Michaelis and Menten, 1913; Monod, 1942; Dugdale, 1967) were used to describe the nutrient-productivity relationships as shown in Figure 36. Temperature effects, respiration, and an autocatalytic function were determined through curve fitting of literature and field results as shown in Figure 37. The mathematical equivalence of the autocatalytic and respiratory functions to Michaelis-Menten is not meant to suggest a biochemical equivalence. It is also realized that the hyperbolic temperature function used (Figure 37b) makes gross production actually a pseudo-gross production, as temperature generally affects both photosynthetic and respiration pathways of a plant.

Figure 38 gives a simplified version of the water chemistry/hydrology module used in the model, while Figure 39 gives the general form of the bottom detritus decomposer module. Decomposition is shown to be stimulated by oxygen

Table 8

STORAGES AND PATHWAYS FOR LAKE ALICE MODEL SHOWN IN FIGURE 33

Parameter	Note in App. B	Description	Value	Source
Q_1		Marsh Volume	95,150 m³	Fig. 15, Fig. 24
A_1	1	Marsh Area	208,091 m²	Ibid.
D_1	1	Marsh Depth	.46 m	Ibid.
Q_2	1	Lake Volume	159,440 m³	Ibid.
A_2	1	Lake Area	121,700 m²	Ibid.
D_2	1	Lake Depth	1.31 m	Ibid.
Q_3	2	Marsh Hyacinths	11,280 kcal/m²	Table 3
Q_4	3	Marsh Detritus	80,550 kcal/m²	Fig. 32
Q_5	4	Marsh Phosphorus	1.47 g-P/m³	Table 7 (Station 1 - Station 5 average)
Q_6	5	Marsh Nitrogen	1.85 g-N/m³	Ibid.
Q_7	6	Marsh Hyacinth Nitrogen	43.9 g-N/m²	Based on hyacinth nutrient given by Knipling et al. (1970)
Q_8	6	Marsh Hyacinth Phosphorus	15.8 g-P/m²	
Q_9	7	Marsh Dissolved Oxygen	1.0 g/m³	Grab samples

Table 8 - continued

Parameter	Note in App. B	Description	Value	Source
Q_{10}	8	Lake Hyacinths	2940 $kcal/m^2$	Table 2, Table 3
Q_{11}	9	Lake Hyacinth Nitrogen	11.4 $g-N/m^2$	Same as Q_7
Q_{12}	9	Lake Hyacinth Phosphorus	4.1 $g-P/m^2$	Same as Q_8
Q_{14}	10	Lake Benthic Plants	3200 $kcal/m^2$	Based on seasonal maximum of .71 kg/m^2 for *Ceratophyllum demersum* (Westlake, 1963)
Q_{15}	--	Dead Hyacinths	--	
Q_{16}	5	Lake Nitrogen	1.10 $g-N/m^3$	Table 7
Q_{17}	4	Lake Phosphorus	1.61 $g-P/m^3$	*Ibid.*
Q_{18}	3	Lake Detritus	80,550 $kcal/m^2$	Fig. 32
Q_{19}	11	Lake Dissolved Oxygen	5.25 g/m^3	Grab samples
Q_{20}	12	Phytoplankton	36 $kcal/m^2$	Chlorophyll a measurement and estimated conversion factor
Q_{21}	13	Allochthonous Organic Matter	192 $kcal/m^2$	Based on COD values (Table 7) with phytoplankton subtracted

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Table 8 - continued

Parameter	Note in App. B	Description	Value	Source
k_1Q_1	14	Marsh Outflow	62,600 m^3/day	Balance
k_2Q_2	14	Lake Outflow	62,600 m^3/day	Balance
$k_6Q_5,\ k_6Q_5Q_1/Q_2$	23	Marsh Phosphorus Outflow	87,000 gP/day	Table 7
$k_{14}k_3f(Q_3)f(P_m)f(N_m)\cdot f_1(T_m)SUN/D_1$	24	Marsh Phosphorus Uptake by Hyacinths	70,500 gP/day	Knipling et al. (1970) (% P) and Table 3
$k_{15}Q_8/D_1$	25	Marsh Hyacinth Phosphorus Leaching	38,500 gP/day	Estimated from balance
$k_{16}Q_8(k_5Q_3/T_m)$	26	Marsh Hyacinth Detrital Loss of Phosphorus	11,400 gP/day	Knipling et al. (1970)
$k_{22}f_2(T_m)/D_1$	27	Marsh Phosphorus Mineralization	1100 gP/day	Estimated from balance
$k_7Q_6,\ k_7Q_6Q_1/Q_2$	28	Marsh Nitrogen Outflow	77,000 gN/day	Table 7
$k_{11}k_3f(Q_3)f(P_m)f(N_m)\cdot f_1(T_m)SUN/D_1$	24	Marsh Nitrogen Uptake by Hyacinths	195,800 gN/day	Knipling et al. (1970)
$k_{12}Q_7/D_1$	25	Marsh Hyacinth Nitrogen Leaching	106,800 gN/day	Estimated from balance

Table 8 - continued

Parameter	Note in App. B	Description	Value	Source
$k_{13}Q_7(k_5Q_3/T_m)$	26	Marsh Hyacinth Detrital Loss of Nitrogen	31,600 gN/day	Knipling et al. (1970)
$k_{23}f_2(T_m)/D_1$	29	Marsh Nitrogen Mineralization	3000 gN/day	Knipling et al. (1970) N/P ratio
$k_8Q_6f_2(T_m)(1-k_{24}Q_9)$	30	Denitrification	41,200 gN/day	Estimated from balance
$k_{21}Q_9$, $k_{21}Q_9Q_1/Q_2$	31	Oxygen from Marsh to Lake	63,000 g/day	Spot sampling
$k_8Q_9f_2(T_m)/D_1$	32	Marsh Oxygen Demand	595,000 g/day	Estimated from balance
$k_3f(Q_3)f(P_m)f(N_m)f_1(T_m)SUN$	33	Marsh Hyacinth Gross Production	242 kcal/m^2/day	Table 3; corrected for solar radiation of 4700 kcal/m^2/day
$k_4g(Q_3)$	34	Marsh Hyacinth Respiration	132 kcal/m^2/day	Table 3
k_5Q_3/T_m	35	Marsh Hyacinth Detrital Production	39 kcal/m^2/day	Penfound & Earle (1948)
$k_{17}k_{23}f_2(T_m)$	36	Marsh Detrital Respiration	74.5 kcal/m^2/day	Knipling et al. (1970) (% N); Westlake (1963) (4.5 kcal/g)
$k_3f(P_\ell)f(N_\ell)f(Q_{10})f(T_\ell)SUN$	37	Lake Hyacinth Gross Production	62.8 kcal/m^2/day	Tables 2 & 3

Table 8 - continued

Parameter	Note in App. B	Description	Value	Source
$k_4 g(Q_{10})$	38	Lake Hyacinth Respiration	32 kcal/m²/day	Ibid.
$k_5 Q_{10}/T_1$	39	Lake Hyacinth Detrital Production	10.8 kcal/m²/day	Same as Marsh Hyacinth
$k_{45}Q_{17}$	40	Lake Phosphorus Outflow	101,000 gP/day	Table 7 (Station 6)
$k_{14}k_3 f(P_\ell)f(N_\ell)f(Q_{10}) \cdot f(T_\ell)SUN/D_2$	41	Lake Phosphorus Uptake by Hyacinth	10,700 gP/day	Knipling (1970) (% P) and Table 3
$k_{15}Q_{12}/D_2$	42	Lake Hyacinth Phosphorus Leaching	5400 gP/day	Estimated from balance
$k_{16}Q_{12}(k_5 Q_{10}/T_\ell)$	43	Lake Hyacinth Detrital Loss of Phosphorus	1800 gP/day	Knipling et al. (1970)
$k_{49}k_{34}T_\ell Q_{16}Q_{12}SUN(1-k_{29}Q_{10})/D_2$	44	Phosphorus Uptake by Phytoplankton	5200 gP/day	Lund (1970) & Table 6
$k_{49}k_{36}Q_{20}Q_{19}f_2(T_\ell)/D_2$	45	Phosphorus Regeneration in Phytoplankton Food Chain	2600 gP/day	Lund (1970) & assuming NPP = 1/2 GPP

Table 8 - continued

Parameter	Note in App. B	Description	Value	Source
$k_{47}k_{38}T_{\ell}f(Q_{16})f(Q_{17})SUN$ $(1-k_{29}Q_{10})/D_2$	46	Phosphorus Uptake by Benthic Producers	1000 gP/day	Adams et al. (1973) & Table 6
$k_{47}k_{40}Q_{14}Q_{19}f_2(T_{\ell})/D_2$	47	Phosphorus Regeneration in Benthic Food Chain	500 gP/day	Adams et al. (1973) & assuming NPP = 1/2 GPP
$k_{14}k_{32}Q_{15}Q_{19}f(T_{\ell})/D_2$	58	Phosphorus Regeneration in Dead Hyacinths		Knipling et al. (1970)
$k_{44}Q_{16}$	48	Lake Nitrogen Outflow	68,800 gN/day	Table 7 (Station 6)
$k_{14}k_{53}f_2(T_{\ell})Q_{19}/D_2$	49	Lake Phosphorus Mineralization	5400 gP/day	Knipling et al. (1970)
$k_{11}k_3f(P_{\ell})f(N_{\ell})f(Q_{10})$ $\cdot f(T_{\ell})SUN/D_2$	41	Lake Nitrogen Uptake by Hyacinths	29,700 gN/day	Knipling et al. (1970) & Table 3
$k_{12}Q_{11}/D_2$	42	Lake Hyacinth Nitrogen Leaching	15,100 gN/day	Estimated from balance
$k_{13}Q_{11}(k_5Q_{10}/T_{\ell})$	43	Lake Hyacinth Detrital Loss of Nitrogen	5100 kgN/day	Knipling et al. (1970)

Table 8 - continued

Parameter	Note in App. B	Description	Value	Source
$k_{48}k_{34}T_\ell Q_{17}SUN(1-k_{29}Q_{10})/D_2$	44	Nitrogen Uptake by Phytoplankton	52,000 gN/day	Lund (1970) & Table 6
$k_{48}k_{36}Q_{20}Q_{19}f_2(T_1)/D_2$	45	Nitrogen Regeneration in Phytoplankton Food Chain	26,000 gN/day	Lund (1970) & assuming NPP = 1/2 GPP
$k_{46}k_{38}T_\ell f(Q_{16})f(Q_{17})SUN(1+k_{29}Q_{10})/D_2$	46	Nitrogen Uptake by Benthic Producers	47,000 gN/day	Goulder & Boatman (1971) & assuming NPP =1/2 GPP
$k_{46}k_{40}Q_{14}Q_{19}f_2(T_1)/D_2$	47	Nitrogen Regeneration in Benthic Food Chain	23,500 gN/day	Goulder & Boatman (1971) & assuming NPP = 1/2 GPP
$k_{11}k_{32}Q_{15}Q_{19}f_2(T_1)/D_2$	58	Nitrogen Regeneration of Dead Hyacinths	23,500 gN/day	Knipling et al. (1970)
$k_{11}k_{53}f_2(T_\ell)Q_{19}/D_2$	49	Lake Nitrogen Mineralization	15,100 gN/day	Knipling et al. (1970)
$k_{42}Q_{19}$	50	Dissolved Oxygen Outflow from Lake	330,000 gO$_2$/day	Spot sampling
$k_{43}k_{38}T_\ell f(Q_{16})f(Q_{17})SUN(1-k_{29}Q_{30})/D_2$	51	Dissolved Oxygen from Benthic Producers	2,010,000 gO$_2$/day	Table 6

Table 8 - continued

Parameter	Note in App. B	Description	Value	Source
$k_{43}k_{34}T_{\ell}Q_{16}Q_{17}SUN(1-k_{29}Q_{10})/D_2$	51	Dissolved Oxygen from Photoplankton	1,110,000 gO₂/day	Table 6
$k_{43}k_{36}Q_{20}Q_{19}f_2(T_1)/D_2$	52	Dissolved Oxygen Uptake by Plankton	555,000 gO₂/day	Assuming NPP = 1/2 GPP
$k_{43}k_{40}Q_{14}Q_{19}f_2(T_{\ell})/D_2$	52	Dissolved Oxygen Uptake by Benthic	1,000,000 gO₂/day	Assuming NPP = 1/2 GPP
$k_{43}k_{32}Q_{15}Q_{19}f_2(T_1)/D_2$	58	Dissolved Oxygen Uptake by Dead Hyacinths		Organic matter decay rate of $(\log_{10})K = .05$
$k_{43}k_{32}Q_{19}Q_{21}f_2(T_1)/D_2$	53	Dissolved Oxygen Uptake by Allochthonous Organic Matter	640,000 gO₂/day	Ibid.
$k_{43}k_{53}f_2(T_1)Q_{19}/D_2$	54	Dissolved Oxygen Uptake by Detritus	920,000 gO₂/day	Assumed from balance & Table 6
$k_{31}Q_{21}$	55	Outflow of Allochthonous Organic Matter	67.3 kcal/m²/day	Estimated
$k_{33}Q_{21}$	55	Allochthonous Organic Matter to Bottom	0	Estimated

Table 8 - continued

Parameter	Note in App. B	Description	Value	Source
$k_{32}Q_{19}Q_{21}f_2(T_\ell)$	53	Allochthonous Organic Matter Decay	22.1 kcal/m²/day	Organic matter decay rate, K = .05; McGauhey (1970)
$k_{32}Q_{15}Q_{19}f_2(T_\ell)$	58	Dead Hyacinth Matter Decay	--	Ibid.
$k_{52}Q_{15}$	58	Dead Hyacinth Matter to Bottom Detritus	--	Estimated turnover time of two weeks
$k_{53}f_2(T_1)Q_{19}$	54	Lake Detritus Decomposition	31.9 kcal/m²/day	
$k_{34}T_\ell Q_{16}Q_{17}SUN(1-k_{29}Q_{10})$	51	Phytoplankton Gross Production	38.4 kcal/m²/day	Table 6
$k_{36}Q_{20}Q_{19}f_2(T_\ell)$	52	Plankton Respiration	19.2 kcal/m²/day	Assumes NPP = 1/2 GPP
$k_{35}Q_{20}$	56	Plankton Outflow	18.2 kcal/m²/day	Estimated for balance
$k_{37}Q_{20}$	56	Plankton to Bottom	1.0 kcal/m²/day	Estimated for balance
$k_{38}T_\ell f(Q_{16})f(Q_{17})SUN(1-k_{29}Q_{10})$	51	Benthic Gross Production	69.6 kcal/m²/day	Table 6
$k_{40}Q_{14}Q_{19}f_2(T_\ell)$	52	Benthic Respiration	34.8 kcal/m²/day	Assumes NPP = 1/2 GPP

Table 8 - continued

Parameter	Note in App. B	Description	Value	Source
$k_{39}Q_{14}$	57	Benthic Outflow	7.0 kcal/m^2/day	Assumes 10% of GPP
$k_{41}Q_{14}$	57	Benthic to Bottom	27.8 kcal/m^2/day	Estimated from balance

Figure 34.   Summary models for nitrogen and phosphorus
             for Lake Alice in summer months. Flows
             are in kg/day, while storages represent
             average concentrations in g/m^3. Denitrifi-
             cation, mineralization, and lake runoff
             rates were determined by steady state
             assumptions and N/P ratios.

NITROGEN

PHOSPHORUS
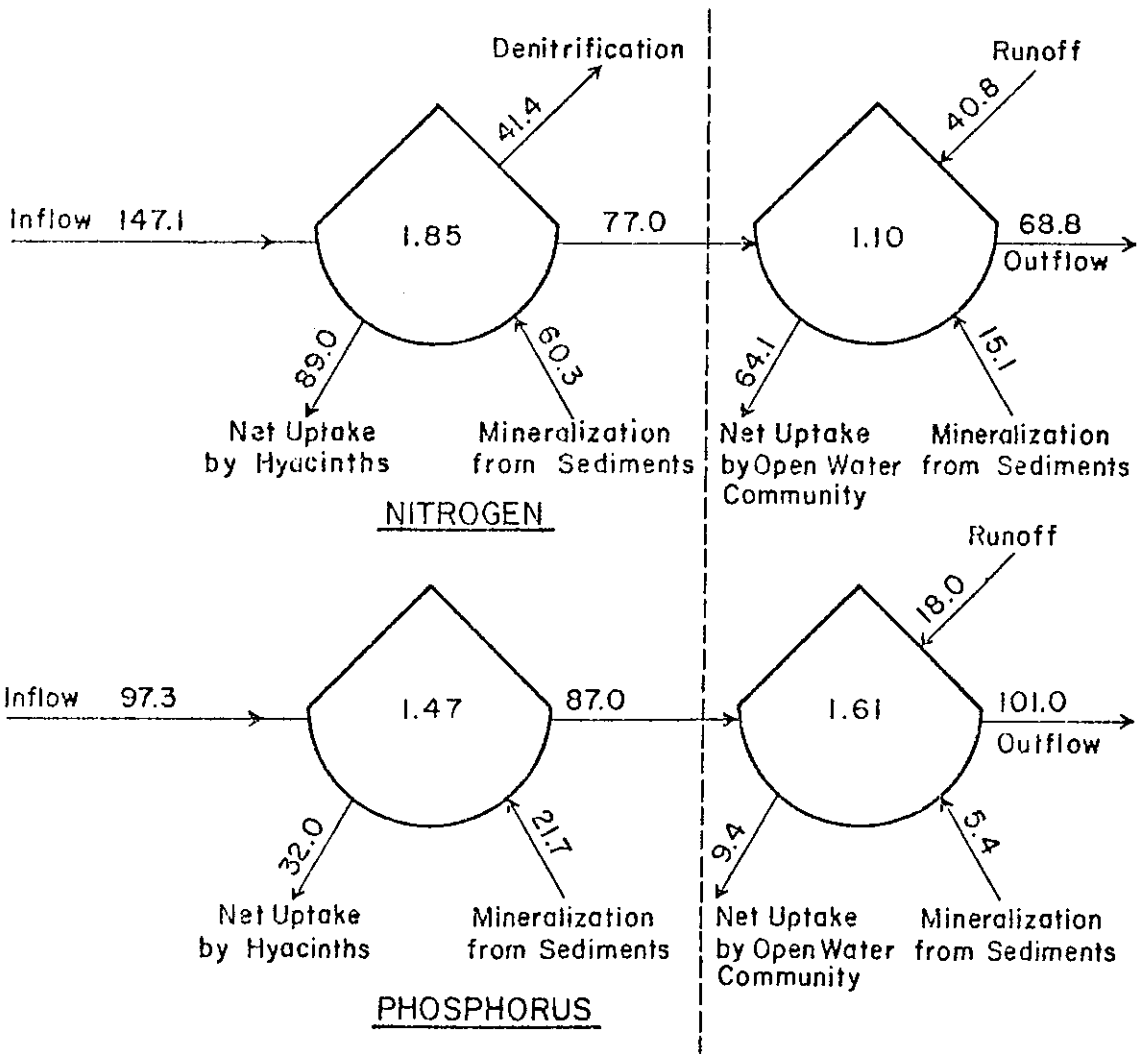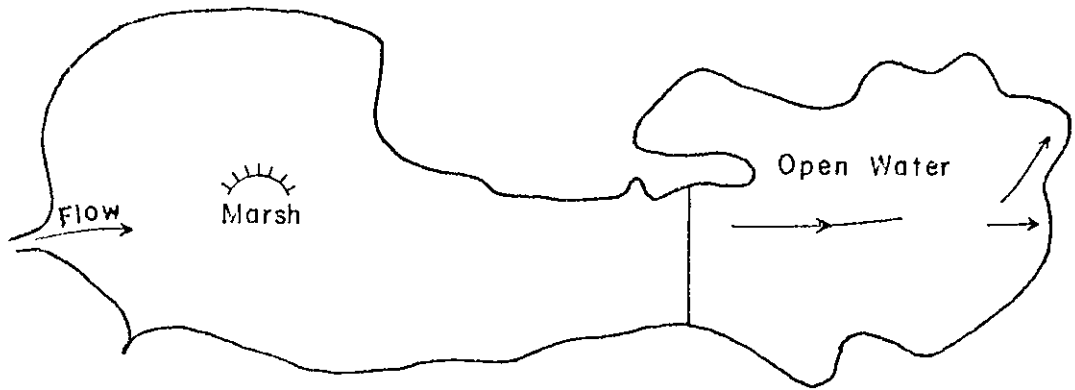
Figure 35. Waterhyacinth module used in Lake Alice model shown in Figure 33. Functions used in workgates are described in Figures 36 and 37.
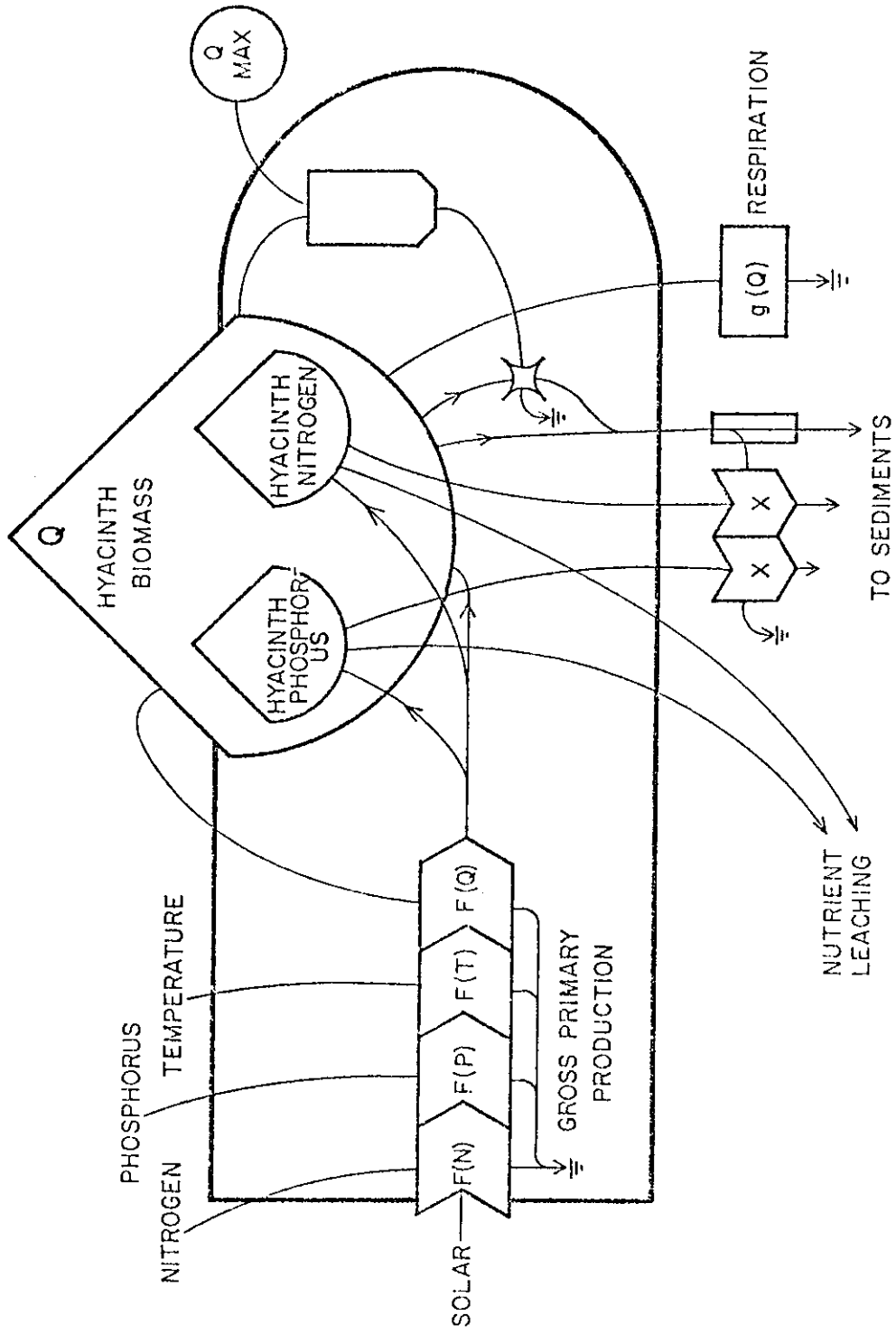
WATERHYACINTH MODULE

Figure 36.   Nutrient limiting factor curves developed
              for waterhyacinth module shown in Figure
              35:   (a) phosphorus curve determined from
              literature value of 0.1 mg-P/1 given as
              limiting value (Haller et al., 1970);
              (b) nitrogen curve determined assuming a
              suitable N/P ratio (Boyd and Vickers, 1971).
              Mathematical expressions are given in
              Table 9.

(a)

(b)
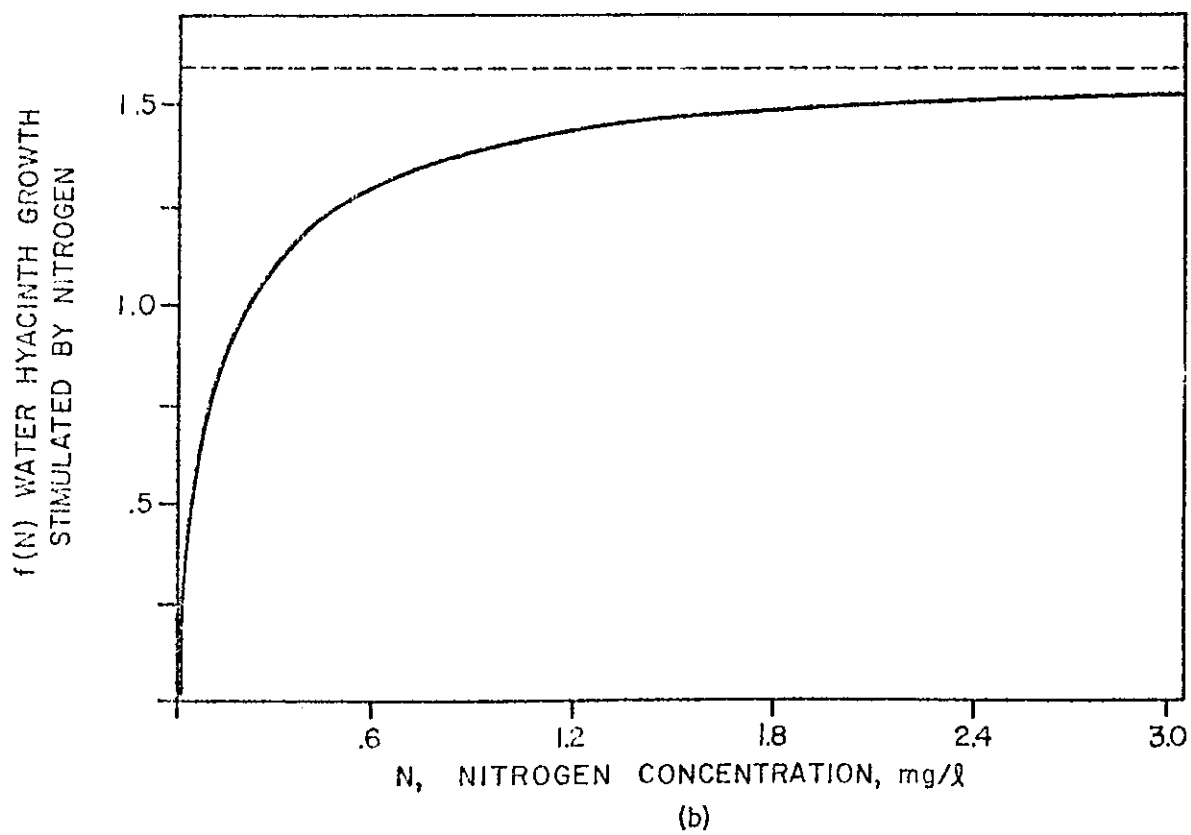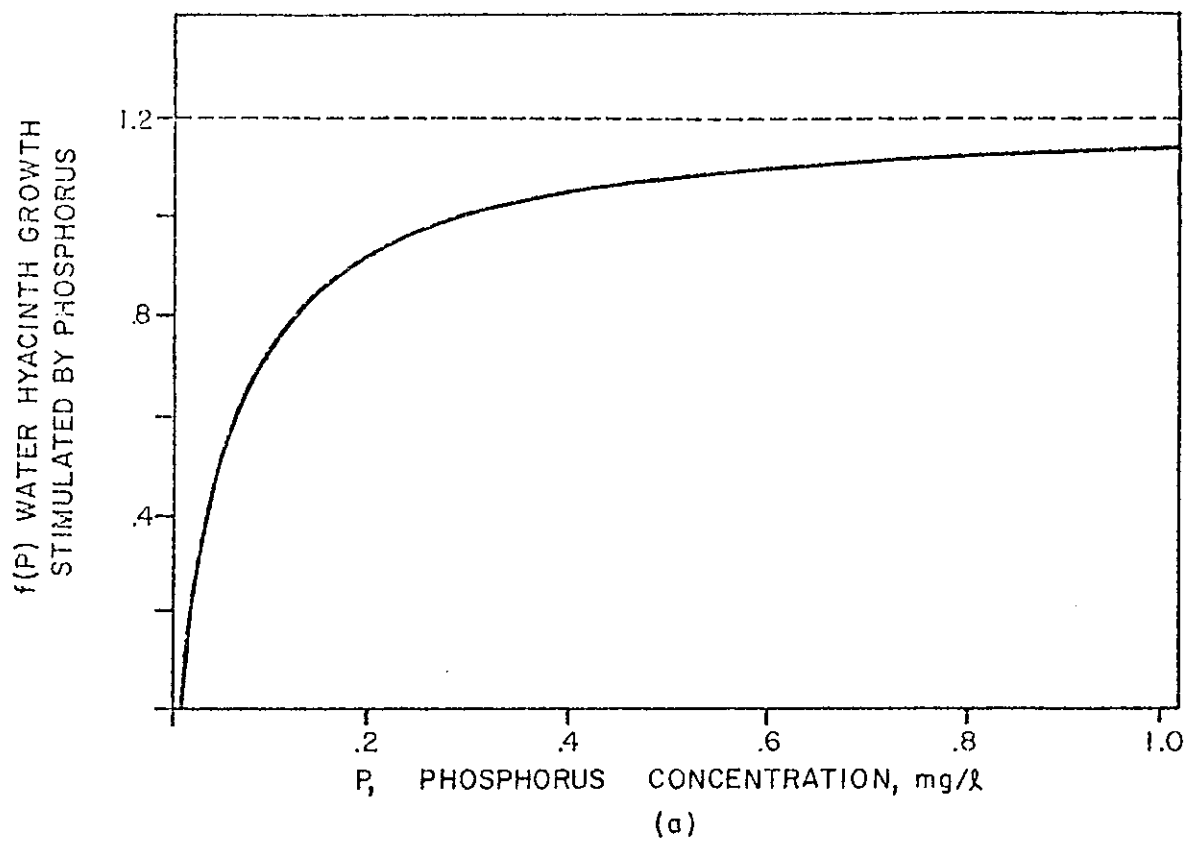
Figure 37. Empirical relationships developed for water-
            hyacinth module shown in Figure 35: (a) rela-
            tions of gross primary productivity and
            respiration to biomass as determined from
            metabolism data; (b) effect of water temper-
            ature on waterhyacinth growth as determined
            by Knipling et al. (1970). Mathematical
            expressions are given in Table 9.

(a)

(b)
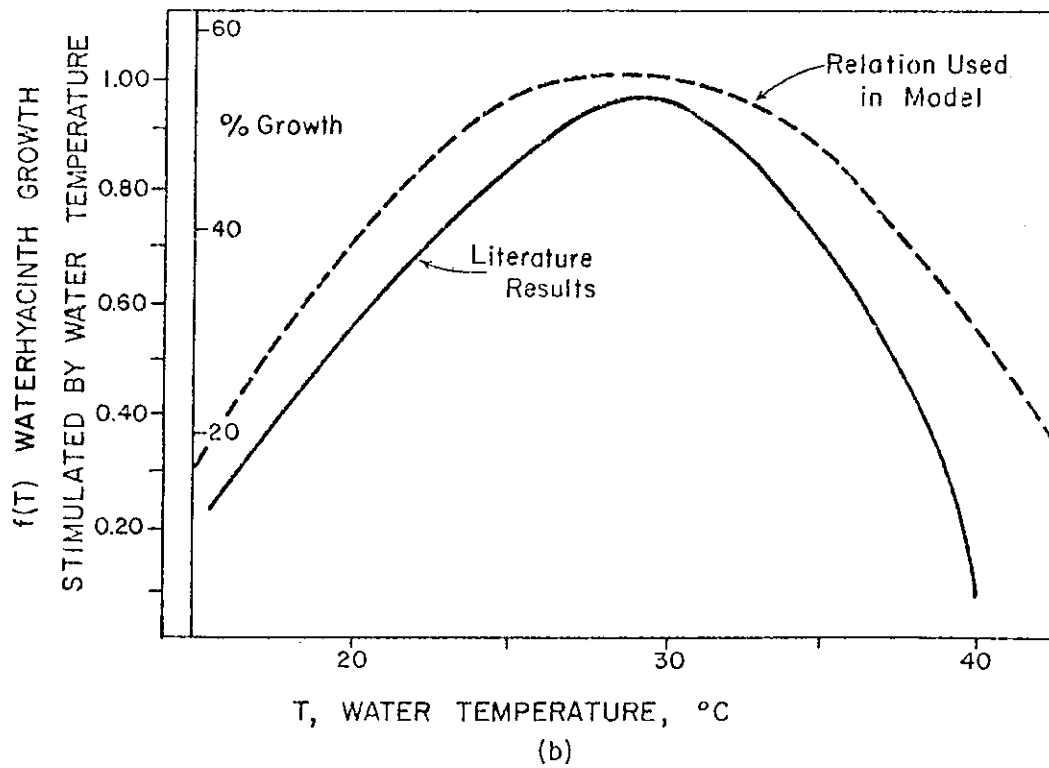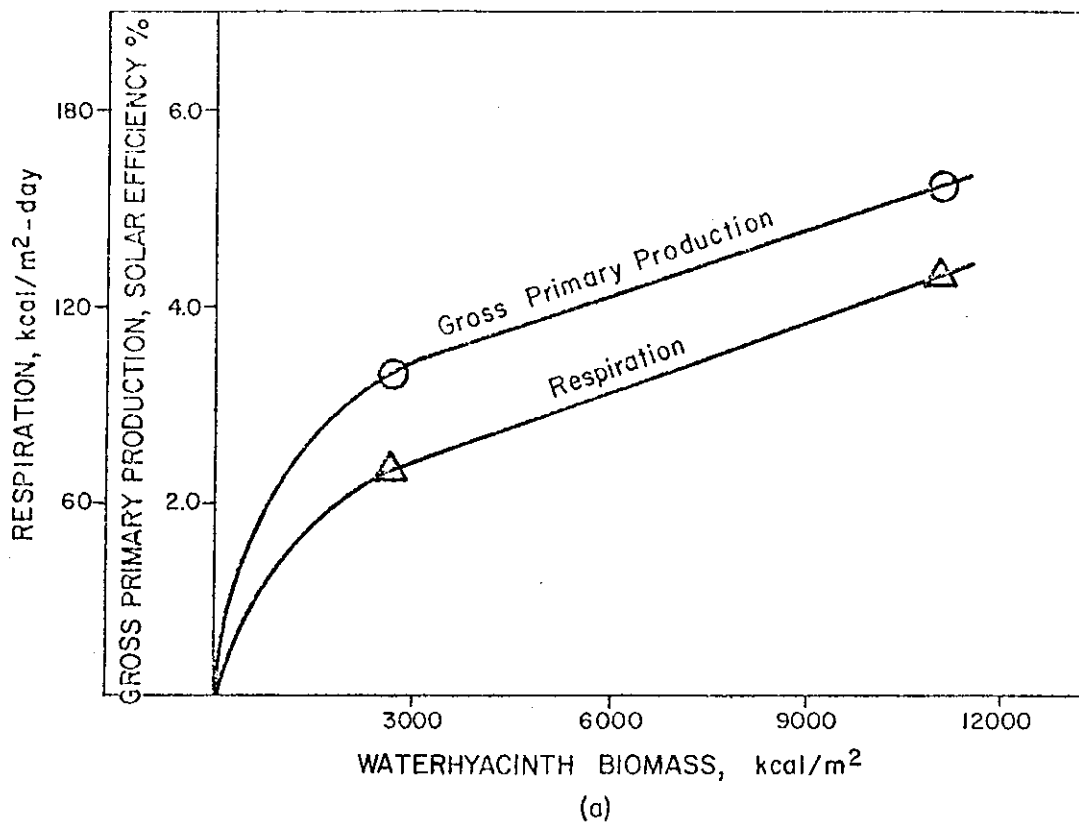
Figure 38.   Water column module used in Lake Alice model
             shown in Figure 33.   Similar modules were
             used in both the hyacinth marsh and the open
             lake.
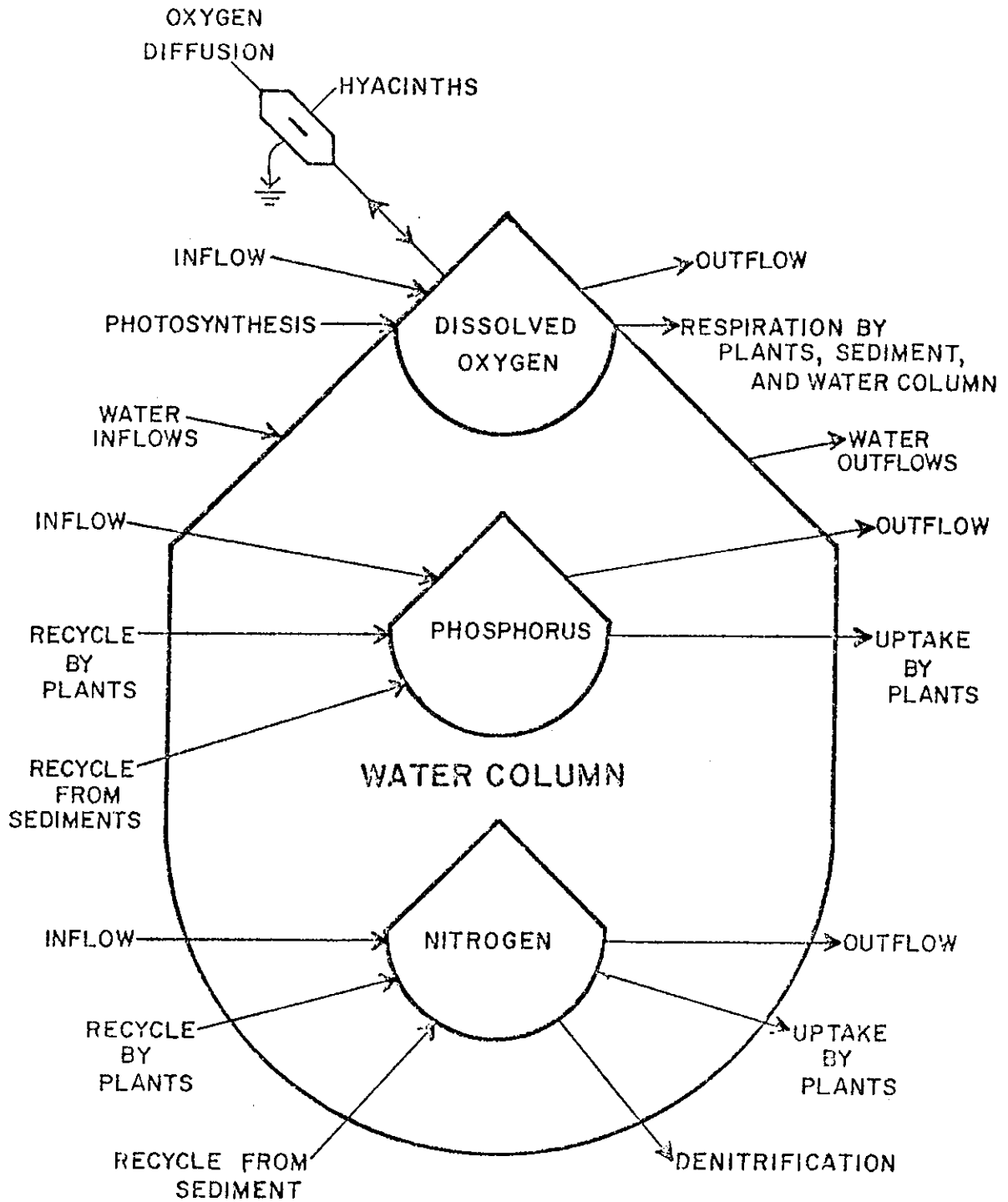
WATER COLUMN MODULE

Figure 39. Bottom detritus-decomposer module used in
            model shown in Figure 33. Similar modules
            were used in both the hyacinth marsh and
            the open lake, although anaerobic decompo-
            sition was assumed for the marsh.
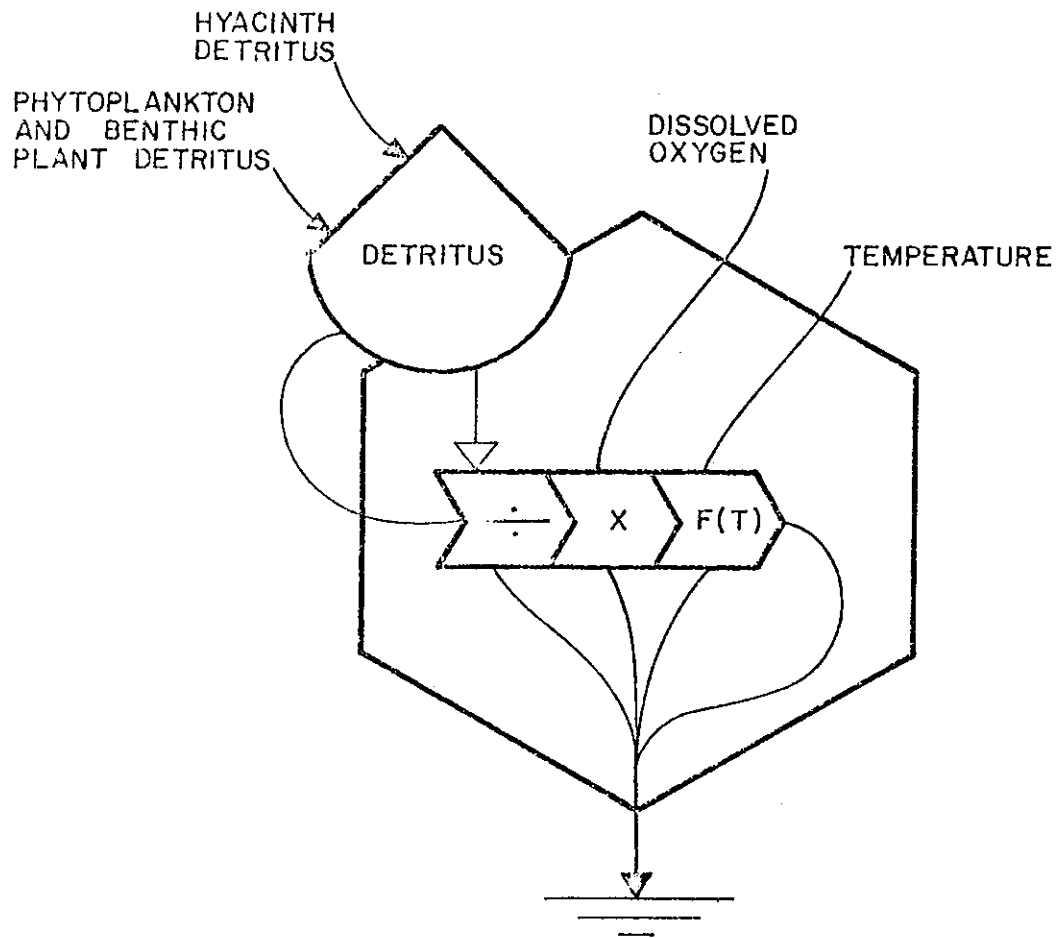
BOTTOM DETRITUS MODULE

and temperature but is not a function of its own storage,
due to a limited active depth in the sediments. The chemistry
and detritus modules were used both in the marsh and in the
open lake. Table 9 gives a listing of the 20 differential
equations used to simulate the model as shown in Figure 33.
The mathematical expressions used for various functions in
the model are also given.

Simulation Results

The Lake Alice model was simulated on the IBM-370 digital
computer through rectangular integration. Values of constants
are in Appendix B. A program listing is available under
separate cover at the Center for Wetlands, University of
Florida. Table 10 gives the forcing functions used for the
first three simulations: Case I--steady state or approximate
present conditions; Case II--removal of the sewage treatment
plant inflow to the lake; and Case III--removal of the heated
effluent from the lake. The results of these simulations are
given in Figures 40, 41, and 42, respectively. The time
scale presented is two years.

Actual field data for oxygen, phosphorus, and nitrogen,
as well as the hyacinth biomass measurements, are superimposed
on the steady state solution Case I, Figure 40, suggesting
that the graphs generated were within 30% or less of plotted
data. Matching data with computer output does not, however,
lead to immediate model verification. Relationships which
are wrong can yield "verified" results if this criterion is

Table 9

DIFFERENTIAL EQUATIONS AND SPECIAL FUNCTIONS
FOR MODEL IN FIGURE 33

Equations

Marsh water

$$\dot{Q}_1 = F_1 - k_1 Q_1$$

Lake water

$$\dot{Q}_2 = k_1 Q_1 - k_2 Q_2$$

Marsh hyacinths

$$\dot{Q}_3 = k_3 f(Q_3) f(Q_5) f(Q_6) f_1(T_m) SUN - k_4 g(Q_3) - k_5 Q_3/T_m$$

Marsh detritus

$$\dot{Q}_4 = k_5 Q_3/T_m - k_{17} k_{23} f_2(T_m)$$

Marsh phosphorus

$$\dot{Q}_5 = f_2/Q_1 - k_6 Q_5 - k_{14} k_3 f(Q_3) f(Q_5) f(Q_6) f_1(T_m) SUN/D_1$$
$$+ k_{15} Q_8/D_1 + k_{22} f_2(T_m)/D_1$$

Marsh nitrogen

$$\dot{Q}_6 = f_3/Q_1 - k_7 Q_6 - k_{11} k_3 f(Q_3) f(Q_5) f(Q_6) f_1(T_m) SUN/D_1$$
$$+ k_{12} Q_7/D_1 + k_{23} f_2(T_m)/D_1 - k_8 Q_6 f_2(T_m)(1-k_{24}Q_9)/D_1$$

Marsh hyacinth nitrogen

$$\dot{Q}_7 = k_{11} k_3 f(Q_3) f(Q_5) f(Q_6) f_1(T_m) SUN - k_{12} Q_7$$
$$- k_{13} Q_7 (k_4 Q_3/T_m)$$

Marsh hyacinth phosphorus

$$\dot{Q}_8 = k_{14} k_3 f(Q_3) f(Q_5) f(Q_6) f_1(T_m) SUN - k_{15} Q_8$$
$$- k_{16} Q_8 (k_5 Q_3/T_m)$$

Marsh dissolved oxygen

$$\dot{Q}_9 = f_4/Q_1 + k_{19}(1-k_{20}Q_3)[(C_s-Q_9)/C_s]/D_1 - k_{21} Q_9$$
$$- k_{18} Q_9 f_2(T_m)/D_1$$

Lake hyacinths

$$\dot{Q}_{10} = k_3 f(Q_{10}) f(Q_{17}) f(Q_{16}) f_1(T_\ell) SUN - k_4 g(Q_{10}) - k_5 Q_{10}/T_\ell$$

Lake hyacinth nitrogen

$$\dot{Q}_{11} = k_{11} k_3 f(Q_{10}) f(Q_{17}) f(Q_{16}) f_1(T_\ell) SUN - k_{12} Q_{11}$$
$$- k_{13} Q_{11}(k_5 Q_{10}/T_\ell)$$

Lake hyacinth phosphorus

$$\dot{Q}_{12} = k_{14} k_3 f(Q_{10}) f(Q_{17}) f(Q_{16}) f_1(T_\ell) SUN - k_{15} Q_{12}$$
$$- k_{16} Q_{12}(k_5 Q_{10}/T_\ell)$$

Lake benthic plants

$$\dot{Q}_{14} = k_{38} T_\ell f(Q_{17}) f(Q_{16}) SUN(1-k_{29} Q_{10}) - k_{40} Q_{14} Q_{19} f_2(T_\ell)$$
$$- k_{39} Q_{14} - k_{41} Q_{14}$$

Lake dead hyacinths

$$\dot{Q}_{15} = k_5 Q_{10}/T_\ell - k_{32} Q_{15} Q_{19} f_2(T_\ell) - k_{52} Q_{15}$$

Lake nitrogen

$$\dot{Q}_{16} = k_7 Q_6 Q_1/Q_2 - k_{44} Q_{16} - k_{11} k_3 f(Q_{10}) f(Q_{17}) f(Q_{16})$$
$$\cdot f_1(T_\ell) SUN/D_2 + k_{12} Q_{11}/D_2 - k_{46}[k_{38} T_\ell f(Q_{17}) f(Q_{16})$$
$$\cdot SUN(1-k_{29} Q_{10}) - k_{40} Q_{14} Q_{19} f_2(T_\ell)]/D_2 - k_{48}[k_{34} T_\ell$$
$$\cdot Q_{16} Q_{17} SUN(1-k_{29} Q_{10}) - k_{36} Q_{20} Q_{19} f_2(T_\ell)]/D_2$$
$$- k_{50} k_{33} Q_{21}/D_2 + k_{11} k_{32} Q_{15} Q_{19} f_2(T_\ell)/D_2$$
$$+ k_{11} k_{53} Q_{19} f_2(T_\ell)/D_2$$

Lake phosphorus

$$\dot{Q}_{17} = k_6 Q_5 Q_1/Q_2 - k_{45} Q_{17} - k_{14} k_3 f(Q_{10}) f(Q_{17}) f(Q_{16})$$
$$\cdot f_1(T_\ell) SUN/D_2 + k_{15} Q_{12}/D_2 - k_{47}[k_{38} T_\ell f(Q_{17}) f(Q_{16})$$
$$\cdot SUN(1-k_{29} Q_{10}) - k_{40} Q_{14} Q_{19} f_2(T_\ell)]/D_2$$
$$- k_{49}[k_{34} T_\ell Q_6 Q_{17} SUN(1-k_{29} Q_{10}) - k_{36} Q_{20} Q_{19} f_2(T_\ell)]/D_2$$

Table 9 - continued

Lake phosphorus - continued

$$- k_{51}k_{33}Q_{21}/D_2 + k_{14}k_{32}Q_{15}Q_{19}f_2(T_\ell)/D_2$$
$$+ k_{14}k_{53}Q_{19}f_2(T_\ell)/D_2$$

Lake detritus

$$\dot{Q}_{18} = k_{52}Q_{15} + k_{33}Q_{21} + k_{37}Q_{20} + k_{41}Q_{14} - k_{53}Q_{19}f_2(T_\ell)$$

Lake dissolved oxygen

$$\dot{Q}_{19} = k_{21}Q_9Q_1/Q_2 - k_{42}Q_{19} + k_{19}(1-k_{20}Q_{10})[(C_{s\ell}-Q_{19})/$$
$$C_{s\ell}]/D_2 + k_{43}[k_{38}T_\ell f(Q_{17})f(Q_{16})SUN(1-k_{29}Q_{10})$$
$$- k_{40}Q_{14}Q_{19}f_2(T_\ell)]/D_2 + k_{43}[k_{34}T_\ell Q_{16}Q_{17}SUN(1-k_{29}Q_{10})$$
$$- k_{30}Q_{20}Q_{19}f_2(T_\ell)]/D_2 - k_{43}k_{32}Q_{21}Q_{19}f_2(T_\ell)/D_2$$
$$- k_{43}k_{52}Q_{15}Q_{19}f_2(T_\ell)/D_2$$

Lake phytoplankton

$$\dot{Q}_{20} = k_{34}T_\ell Q_{16}Q_{17}SUN(1-k_{29}Q_{10}) - k_{36}Q_{20}Q_{19}f_2(T_\ell)$$
$$- k_{35}Q_{20} - k_{37}Q$$

Lake allochthonous organic matter

$$\dot{Q}_{21} = k_{30}Q_1/A_2 - k_{31}Q_{21} - k_{32}Q_{21}Q_{19}f_2(T_\ell) - k_{33}Q_{21}$$

- -

Functions

$$f(Q_3) = \text{marsh hyacinth autocatalytic function} = \frac{1.25Q_3}{2500 + Q_3}$$

$$f(Q_{10}) = \text{lake hyacinth autocatalytic function} = \frac{1.25Q_{10}}{2500 + Q_{10}}$$

$$g(Q_3) = \text{marsh hyacinth respiratory function} = \frac{1.28Q_3}{2940 + Q_3}$$

Table 9 - continued

$g(Q_{10})$ = lake hyacinth respiratory function = $\dfrac{1.29Q_{10}}{2940 + Q_{10}}$

$f(Q_5)$ = hyacinth-phosphorus function for marsh = $\dfrac{1.2Q_5}{.072 + Q_5}$

$f(Q_{17})$ = hyacinth phosphorus function for Lake Alice = $\dfrac{1.2Q_{17}}{.072+Q_{17}}$

$f(Q_6)$ = hyacinth-nitrogen function for marsh = $\dfrac{1.60Q_6}{.14 + Q_6}$

$f(Q_{16})$ = hyacinth-nitrogen function for lake = $\dfrac{1.6Q_{16}}{.14 + Q_{16}}$

T_m = marsh water temperature

T_ℓ = lake water temperature

$f_1(T_m)$ = hyacinth-temperature function for marsh

$\quad = 1 - .0037(T_m-29)^2$

$f_1(T_\ell)$ = hyacinth-temperature function for lake

$\quad = 1 - .0037(T_\ell-29)^2$

$f_2(T_m)$ = respiration-temperature function for marsh

$\quad = 2(T_m-30.7)/10$

$f_2(T_\ell)$ = respiration-temperature function for lake

$\quad = 2(T_\ell-28.5)/10$

C_s = saturated dissolved oxygen for marsh = $\dfrac{475}{33.5 + T_m}$

$C_{s\ell}$ = saturated dissolved oxygen for lake = $\dfrac{475}{33.5 + T_\ell}$

Table 9 - continued

D_1 = marsh average depth

D_2 = lake average depth

A_1 = marsh surface area

A_2 = lake surface area

SUN   = solar radiation = $4000 + 2000(\cos \frac{2\pi t}{365})$

t = time in days

Table 10

FORCING FUNCTIONS FOR FIRST THREE
LAKE ALICE MODEL SIMULATIONS

Forcing Function	Case I Steady State	Case II Without Sewage Treatment Plant	Case III Without Heating Plant
F_1 Dry Weather Inflow, m^3/day	62,600	52,088	19,152
F_2 Phosphorus Inflow, g-P/day	97,300	39,900	70,495
F_3 Nitrogen Inflow, g-N/day	147,100	28,800	131,960
F_4 Dissolved Oxygen Inflow, g/day	313,000	339,000	69,480
Marsh Temperature Range, °C	26-32	26-32	17-31
Lake Temperature Range, °C	20-31	20-31	17-31

Figure 40.   Simulation results for Lake Alice model
             shown in Figure 33 for steady state condi-
             tions (Case I). Dotted lines indicate open
             lake, solid lines indicate hyacinth marsh.
             Data points (◯) show some field results
             obtained in 1973. Hyacinth data are from
             Table 3. Dissolved oxygen data are for
             individual sampling dates only on the open
             lake. Nitrogen and phosphorus data repre-
             sent average monthly values at the board-
             walk between open lake and hyacinth marsh
             (Station 5).
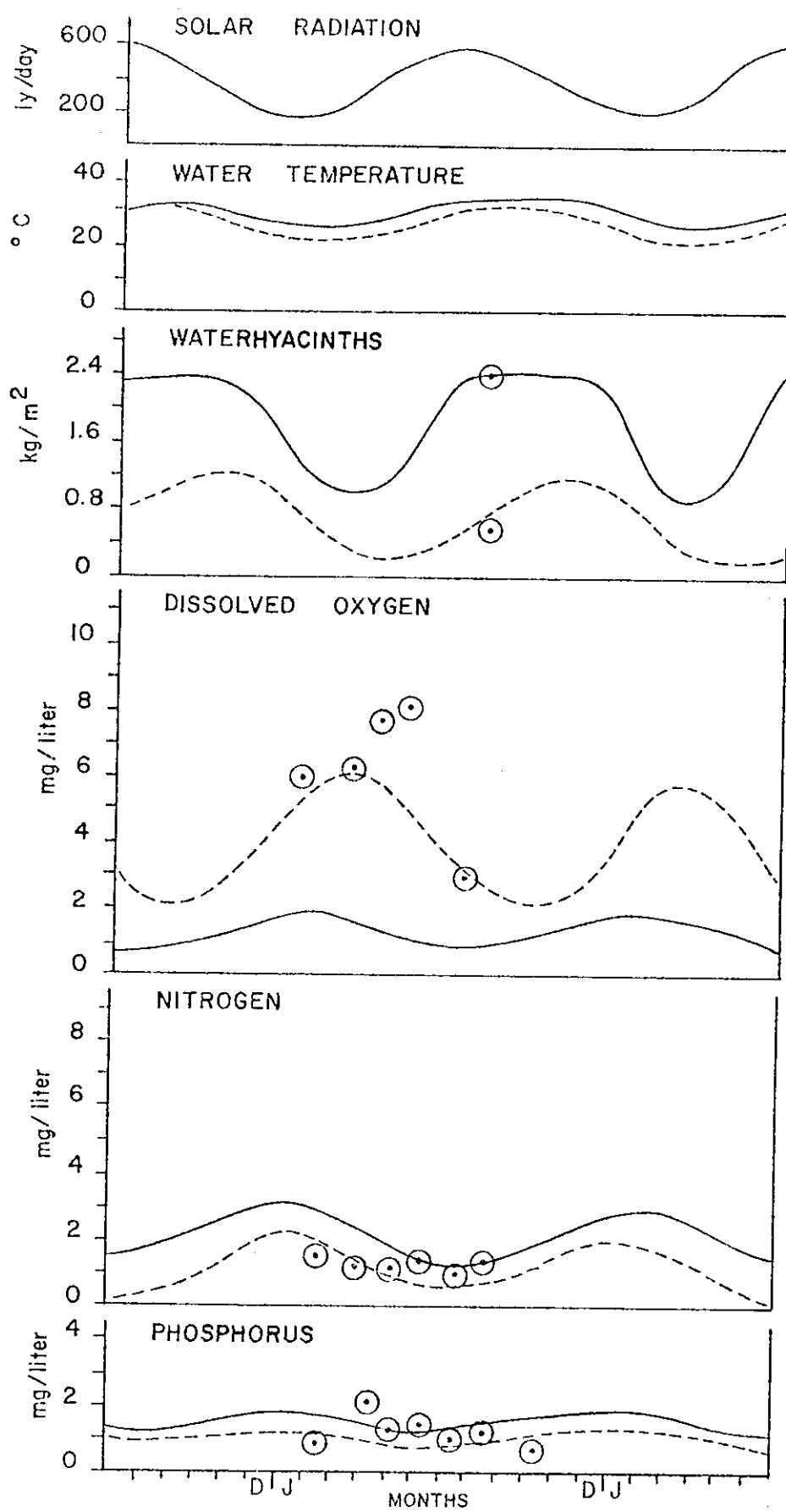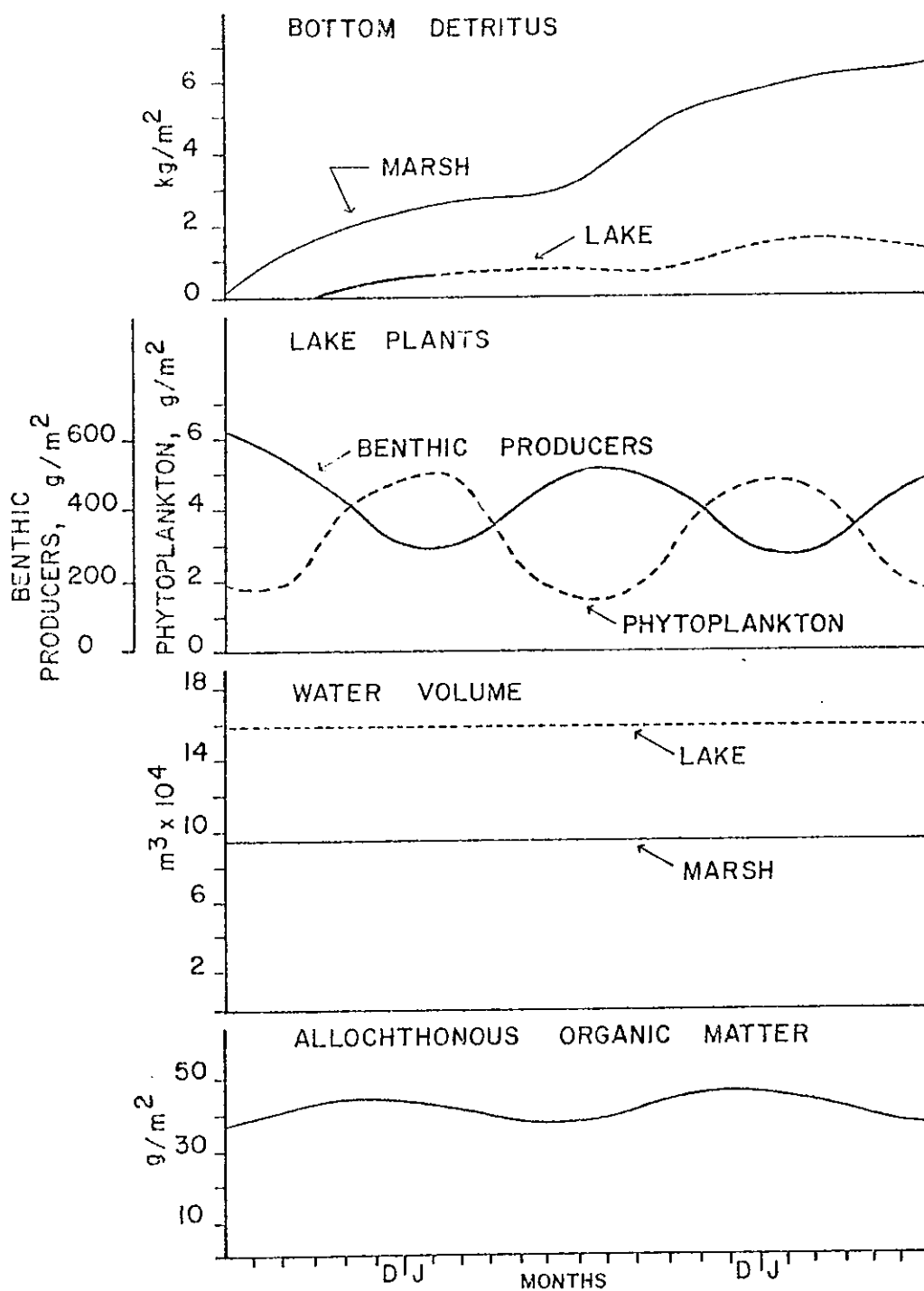
Figure 40 - continued.

used. It is probably more important to have correct variables and interactions to give the model predictive capabilities. A trade-off is obviously necessary.

In the steady state situation, waterhyacinths are shown to reach their maximum possible biomass in the marsh but to attain only half that peak in the open lake. Nitrogen fluctuates much more widely than does phosphorus. Dissolved oxygen in the marsh reaches a peak in winter while the open water oxygen attains a peak of almost 6 ppm in early spring. This is the result of an optimum mix of open water photosynthesis and minimum waterhyacinths. Marsh detritus is shown to increase by over 6 kg/m^2 in the two years, while lake detritus, because of less hyacinth production and more oxygenated waters, increased by only 1 kg/m^2.

When the sewage plant effluent is removed from the lake (Case II, Figure 41), waterhyacinths cease to be a problem in the open water after about one-half year and marsh hyacinths reach a density of less than half their original value. Urban and agricultural runoff was not included in these simulations except for the flow from Hume Pond. Thus the actual decrease of waterhyacinths to zero probably exaggerates the effects of the sewage diversion. The nutrient balance in Figure 34 shows that 35% of the nitrogen inflow and 17% of the phosphorus inflow to the open lake were not taken into account.

Dissolved oxygen in the marsh is surprisingly lower, due to the model's assumption of a constant oxygen demand for what

Figure 41. Simulation results for Lake Alice model
shown in Figure 33 assuming diversion of
sewage treatment flow (Case II). Dotted
lines indicate open lake; solid lines
indicate hyacinth marsh.
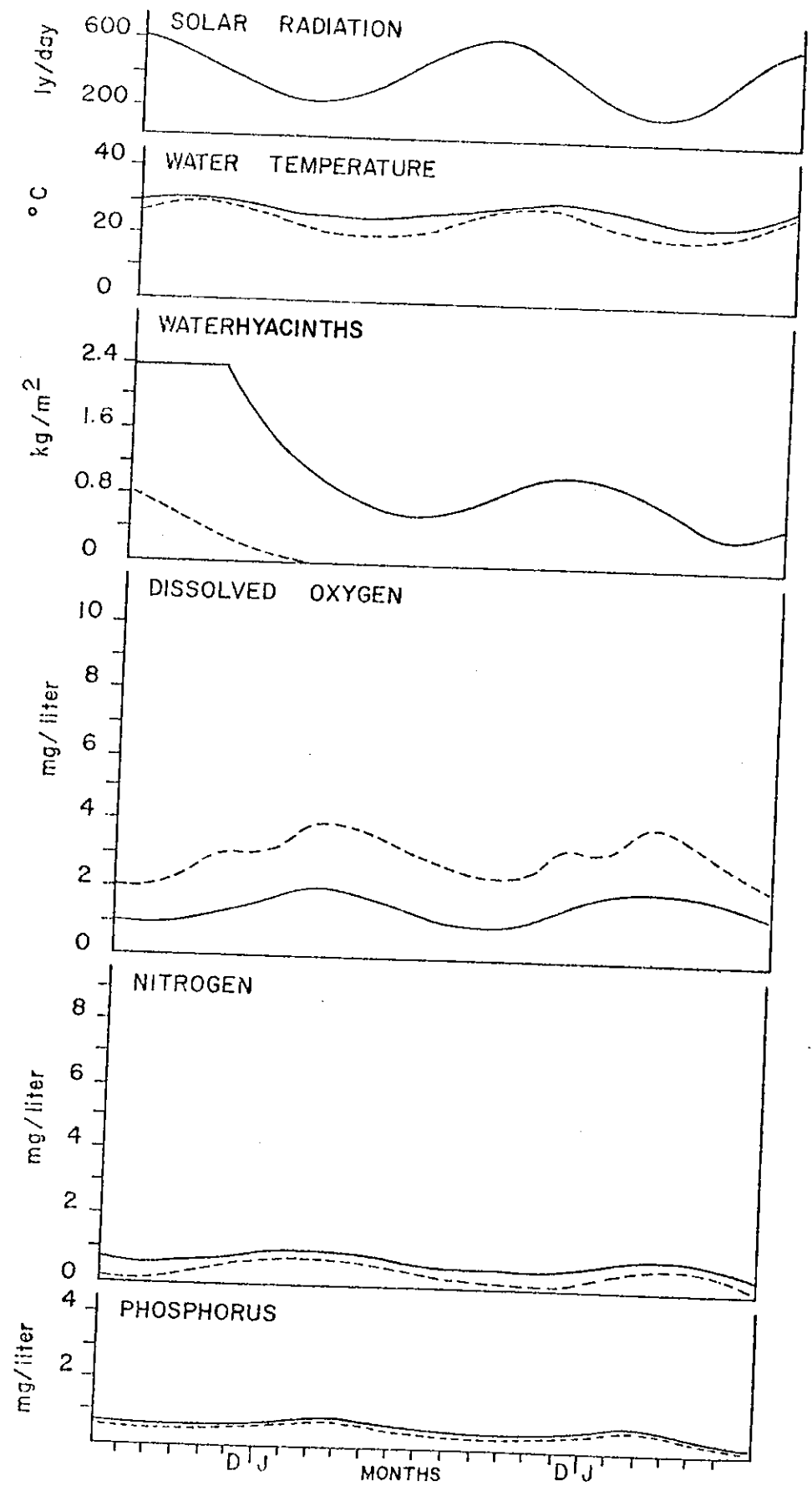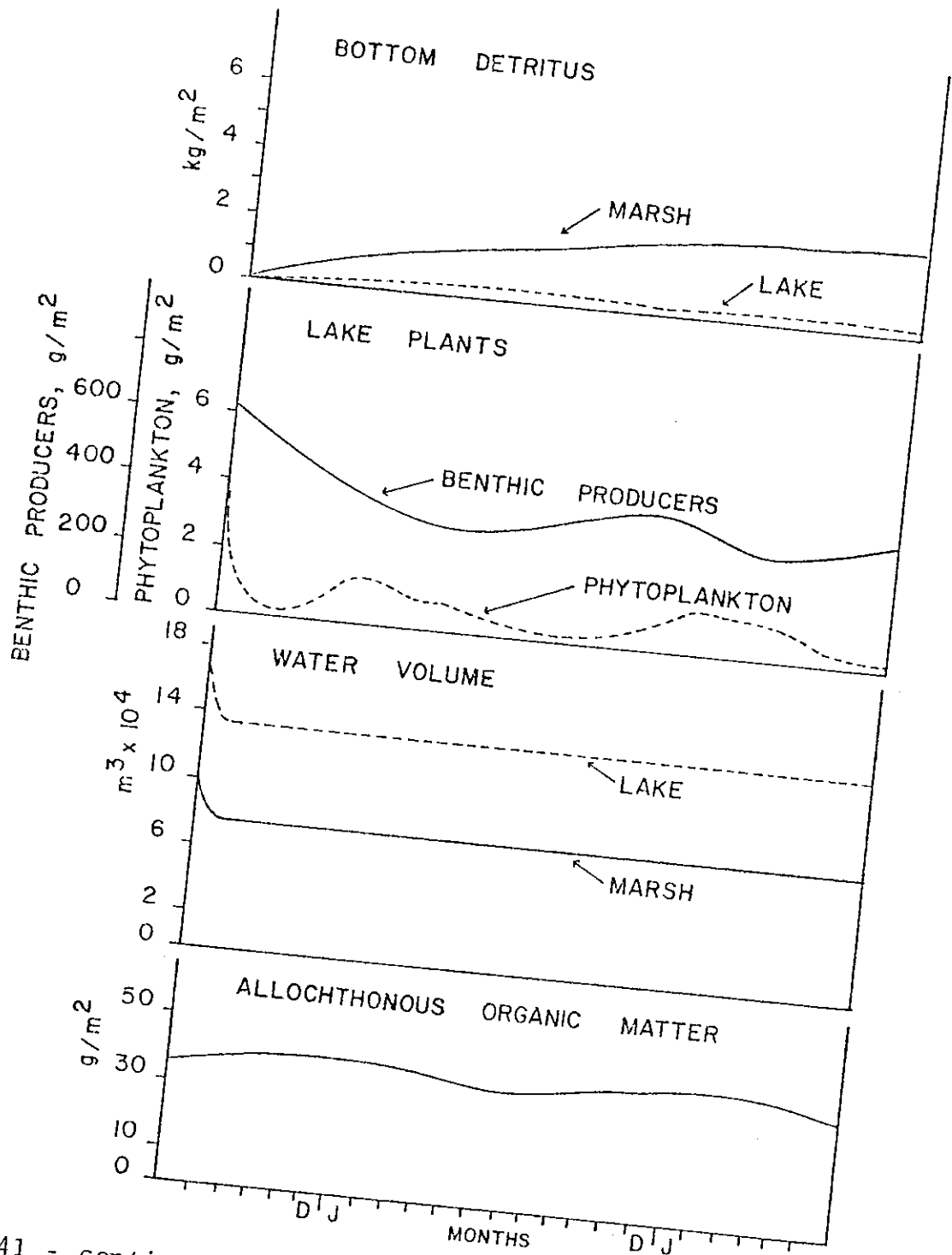
Figure 41 - continued.

is now a smaller marsh volume. Dissolved oxygen in the lake is 20% lower for the same reason, and also because there is less primary production from benthic and phytoplankton communities. Benthic plants dominate the open water after the removal of the hyacinths. This may suggest that a water-hyacinth system actually allows less diversity when productivity is low. The phytoplankton with their rapid turnover do not reach a high peak in spring. Phosphorus and nitrogen concentrations are less variable and generally less than 1.0 mg/l throughout the year. Bottom detritus is reduced to one-third of its normal accumulation.

Case III (Figure 42) depicts Lake Alice without the flow from the campus heating plant. Hyacinths are shown to take over the lake completely by the second year due to very high nitrogen (1.5 to 5.5 mg-N/l) and phosphorus (3.0 to 4.0 mg-P/l) concentrations. Marsh nitrogen reaches almost 10 mg-N/l peaks. While dissolved oxygen in the marsh remains low, the open water shows abnormally high oxygen fluctuations, due to rapid spring blooms of benthic and planktonic producers before they are shaded out by hyacinths. Higher oxygen saturation levels, due to the lower temperatures (see Table 10), also contribute to higher oxygen diffusion in the winter into both the lake and the marsh. Hyacinths are shown to have very low biomass in the winter, due to the lower winter temperatures in the water without the benefit of the heated effluent. Organic sediments increase in the marsh almost as much in this case as in steady state conditions. The lower

Figure 42. Simulation results for Lake Alice model
shown in Figure 33 assuming diversion of
heating plant effluent from lake (Case
III). Dotted lines indicate open lake;
solid lines indicate hyacinth marsh.
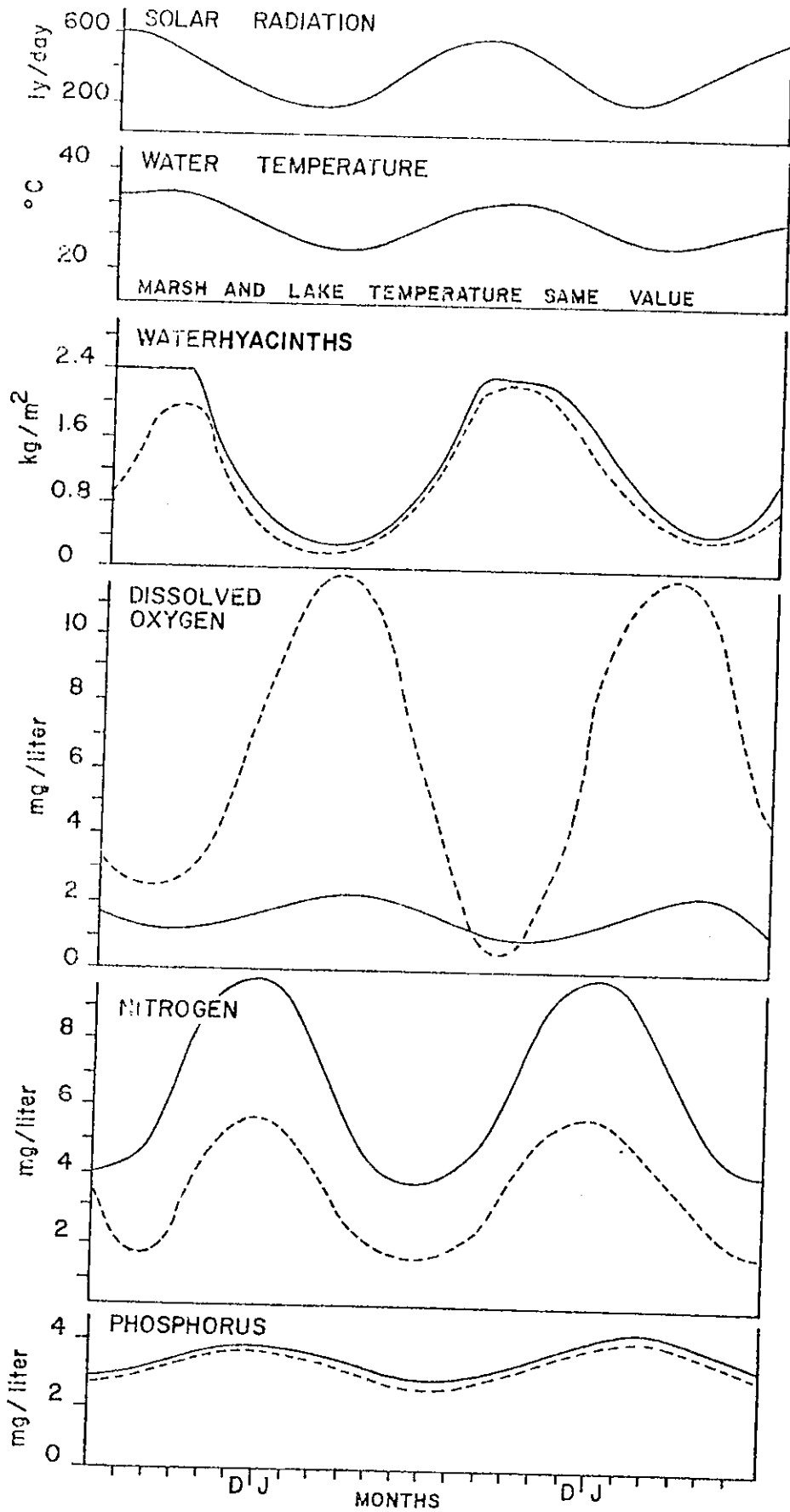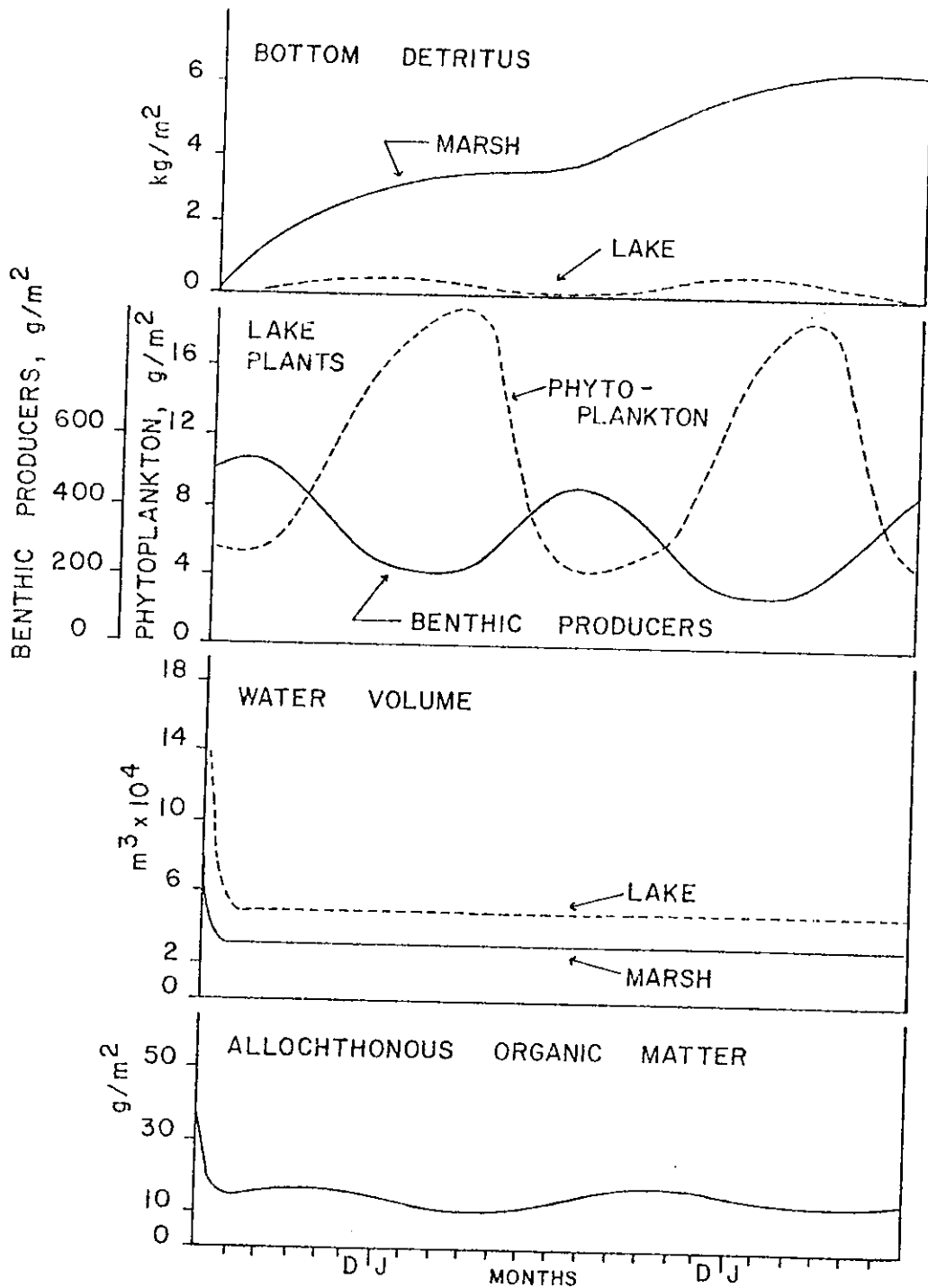
Figure 42 - continued.

temperatures permit less hyacinth productivity, which offsets lower decomposition rates. Lake sediments showed surprisingly little accumulation after two years due to the high concentrations of dissolved oxygen. In general, the higher ranges of temperatures coupled with higher primary production rates tended to create a system with a greater seasonal oscillation than is presently found in Lake Alice.

Additional simulations were done to investigate the effects of various waterhyacinth control techniques on the open lake ecosystem. Figure 43 shows simulation results of a case where hyacinths are mechanically harvested in the summer to one-tenth their original density. The harvest results in an increase of 1.5 ppm oxygen in less than one month, but there is very little change in nutrient concentrations. The benthic and planktonic producers show a marked increase due to the hyacinth removal, which undoubtedly resulted in most of the oxygen increase. The waterhyacinths do not recover to the level at the time of the harvest for two years. Bottom detritus increase is slightly less than that found in the steady state case (Figure 40).

Figure 44 gives the results of chemical spraying of waterhyacinths. The spraying causes a sharp decrease in oxygen of 2 ppm. This drop in oxygen has the immediate effect of slowing the degradation of all organic storages in the lake. Bottom detritus increases rapidly for about one month after spraying, due to the low oxygen effect and the accumulation of dead hyacinths. Again, as with the harvesting case, little

Figure 43.   Simulation results for Lake Alice model shown
             in Figure 33 assuming waterhyacinths are
             harvested mechanically.   Only simulations for
             the open lake are given.
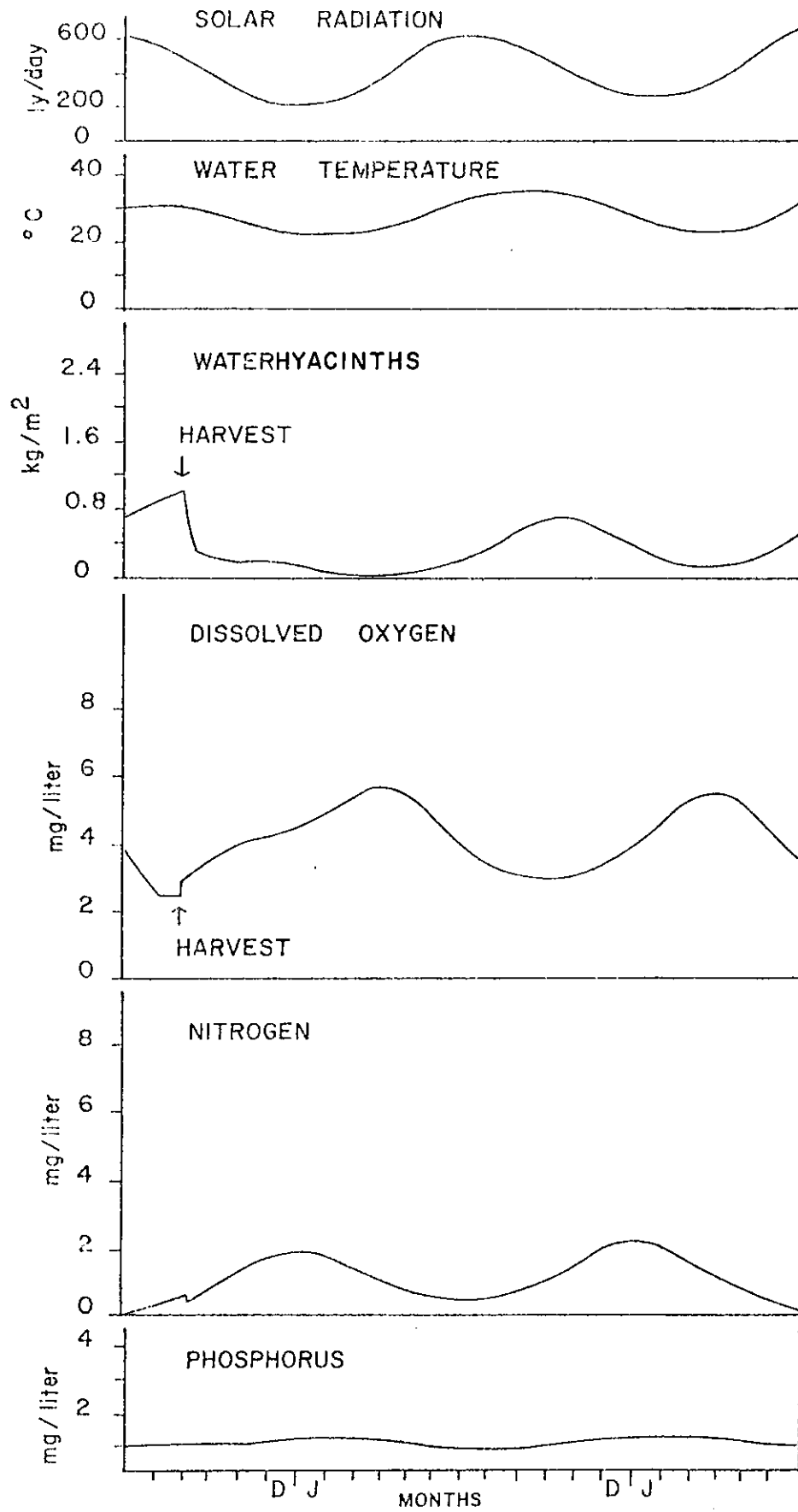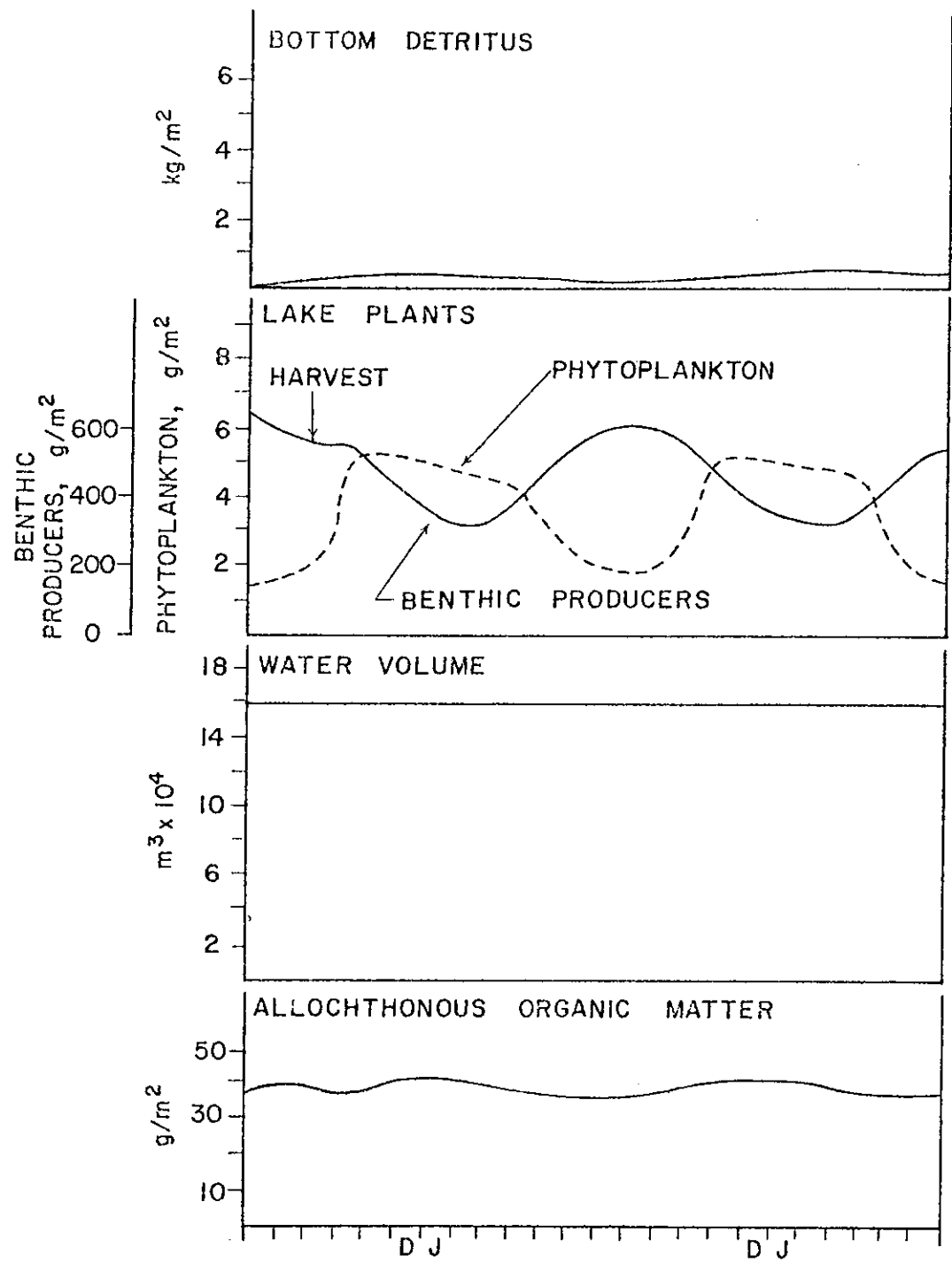
Figure 43 - continued.

Figure 44.   Simulation results for Lake Alice model shown
             in Figure 33 assuming waterhyacinths are
             sprayed with herbicides. Only simulations
             for the open lake are given.

SOLAR RADIATION
ly/day
600
200

WATER TEMPERATURE
°C
40
20

WATERHYACINTHS
kg/m²
2.4
1.6
0.8
SPRAY

DISSOLVED OXYGEN
mg/liter
8
6
4
2
SPRAY

NITROGEN
mg/liter
8
6
4
2
SPRAY

PHOSPHORUS
mg/liter
4
2

D J   D J
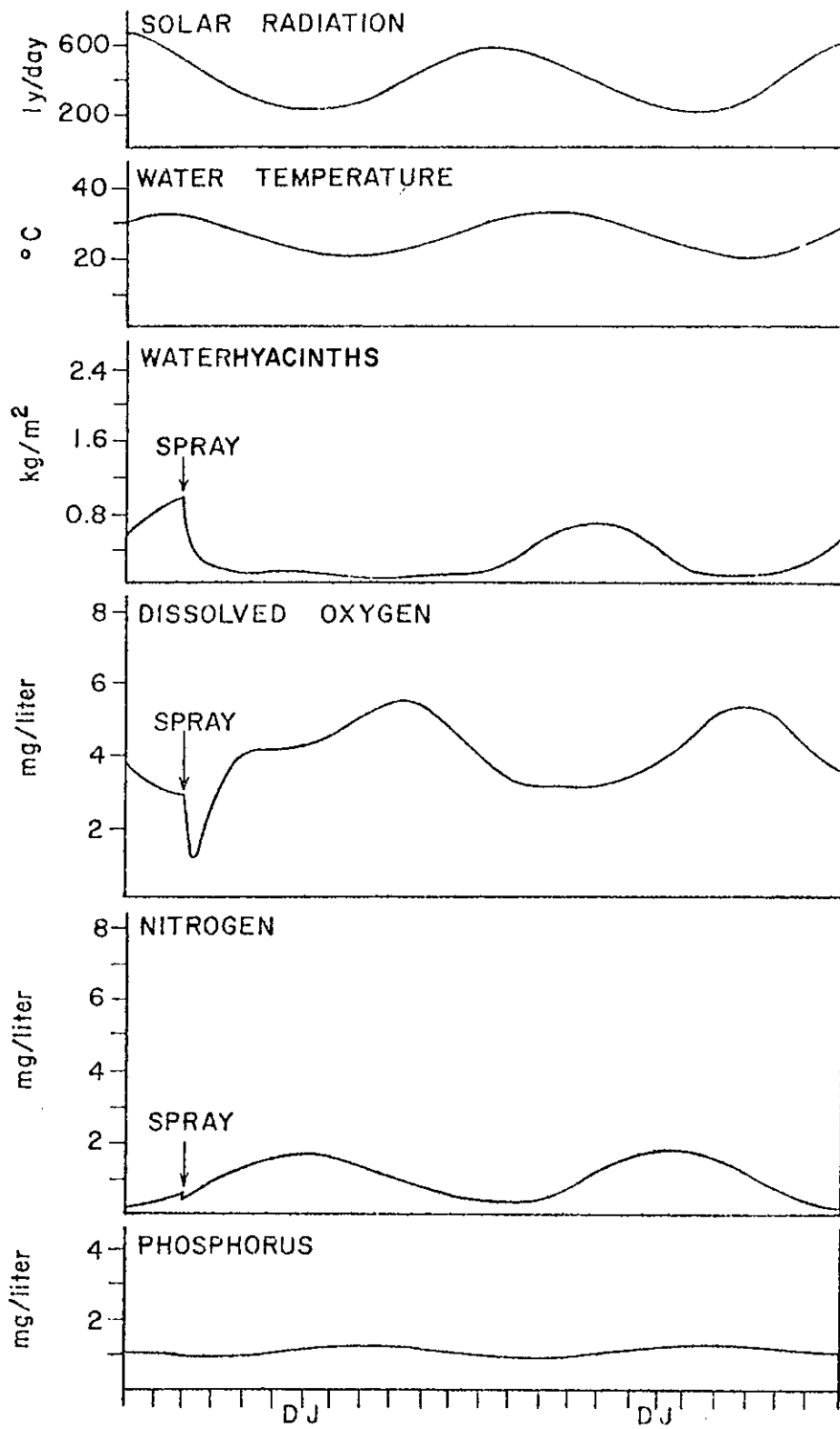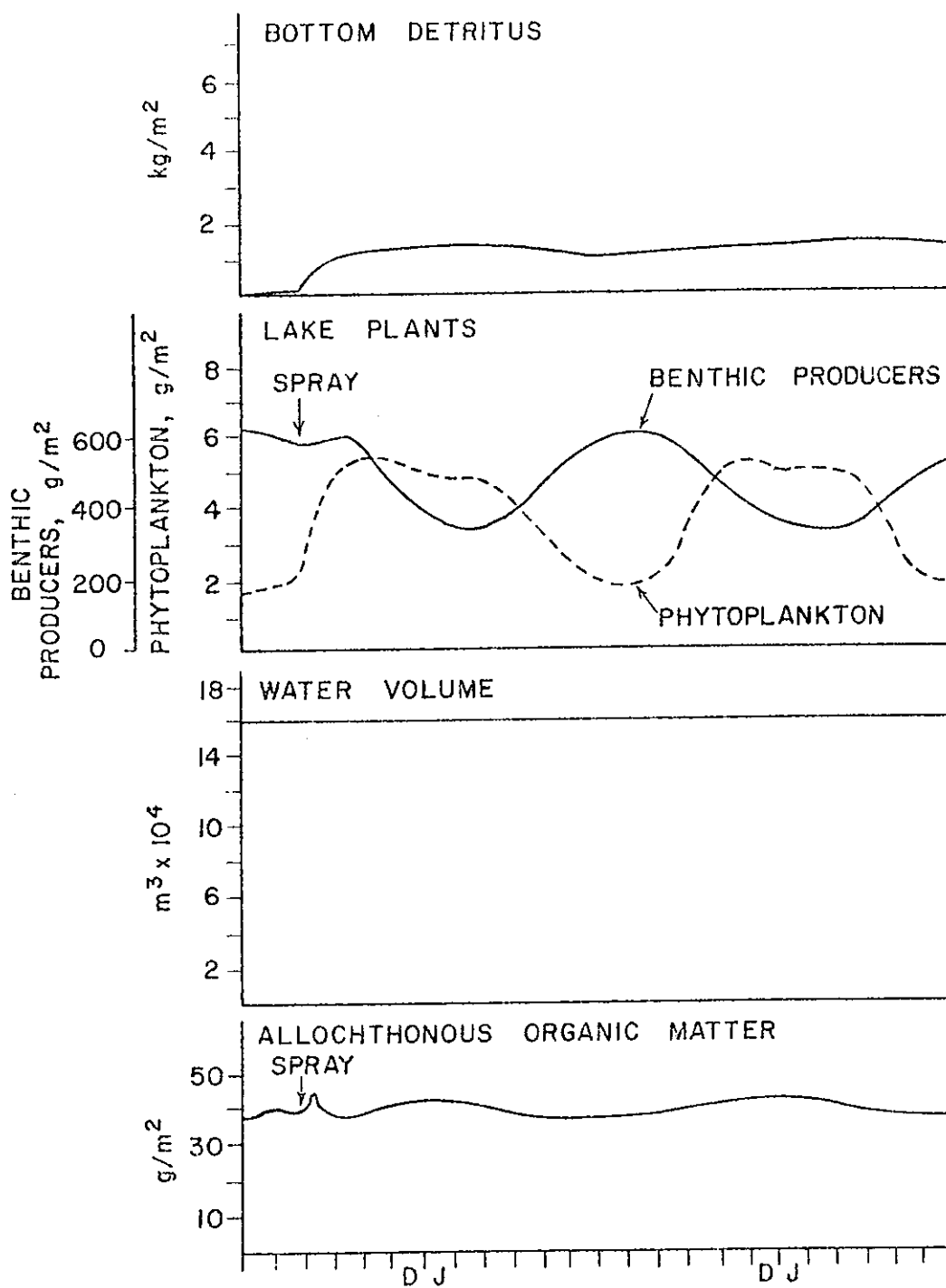
Figure 44 - continued.

change is noted in the nutrient concentrations when compared to the concentrations at steady state conditions.

Figure 45 is a summary of the effects of four different hyacinth control methods on the dissolved oxygen in the lake. The two cases just described are compared with cases in which waterhyacinths were continuously sprayed and continuously harvested. Of the four techniques, continuous harvesting allows the least oxygen fluctuation (1.6 ppm) while periodic spraying results in a range of dissolved oxygen values from 1.6 to 5.6 ppm. With continuous spraying, 2.1 ppm range is achieved, while periodic harvesting results in a 3.0 ppm range. It should be noted that these values are averages for the entire open lake and do not take into account localized effects. The general implications of the oxygen fluctuations on lake fauna, however, suggest that this comparison is a significant management consideration.

Data from Cypress Wetlands

Data gathered from the cypress wetlands include hydro-logic values, biomass and productivity of cypress trees, under-story metabolism rates, microclimatic variables, and water and sediment analyses.

Cypress Dome Hydrology

Results of cypress pond water flows and storages for March to December,1974,are shown in Tables 11 and 12 and Figures 46-48. Monthly loading rates for the two cypress

Figure 45.   Simulation results for Lake Alice model shown in Figure 33 comparing dissolved oxygen levels in the open lake for various waterhyacinth control schemes.
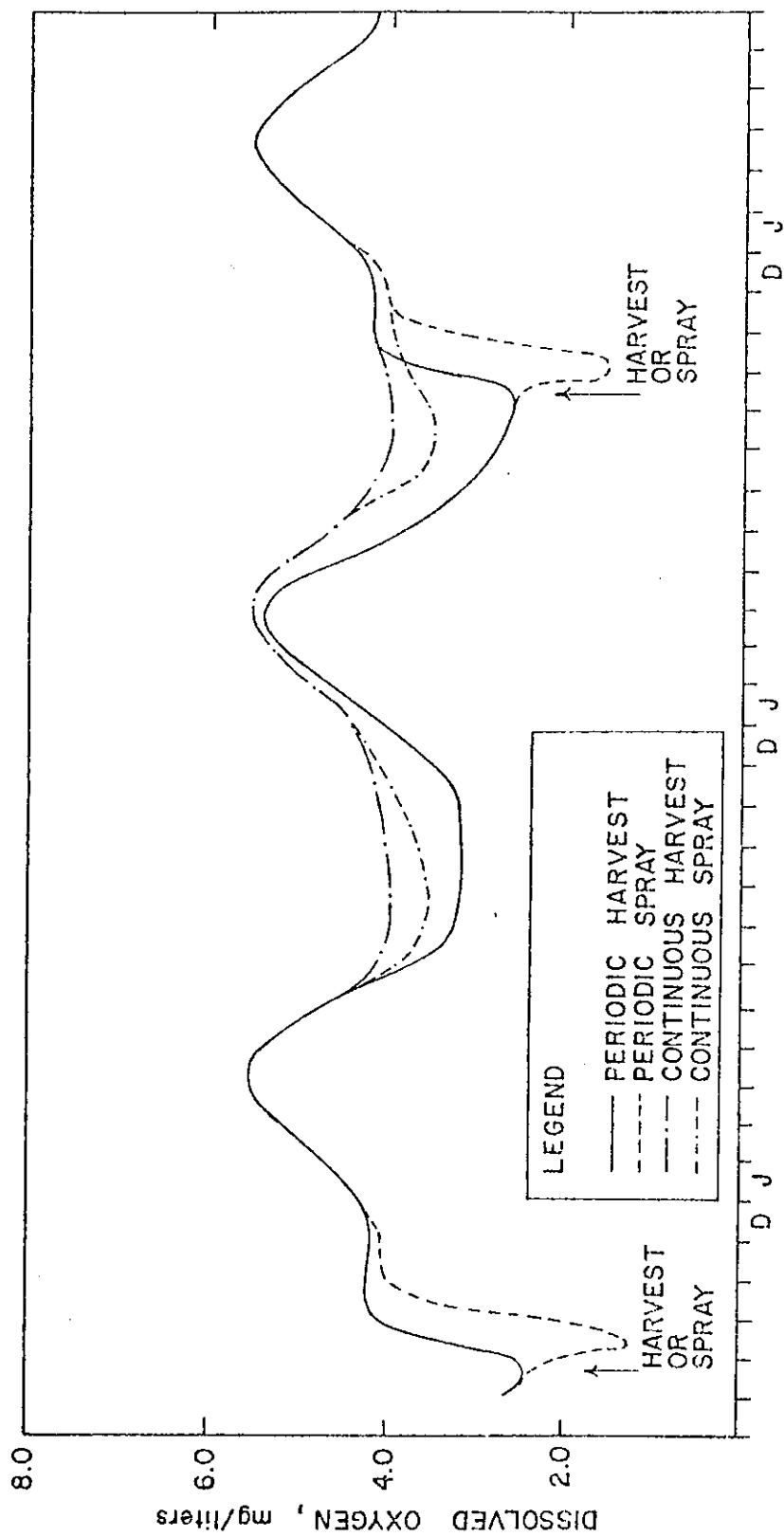
domes receiving experimental treatment are given in Table 11.
Groundwater loading was somewhat less than the sewage loading
during the peak discharge months. Standing water stage
records for the Sewage Dome, Groundwater Dome, and Owens-
Illinois Control Dome are given in Figure 46 along with corre-
sponding rainfall and loading rates. Similar data are shown
for the Austin Cary Control Dome in Figure 47. Table 12
gives the water budget determined for the last half of 1974
for the Sewage Dome while Figure 48 summarizes these monthly
flows. Groundwater discharge from the Sewage Dome was assumed
to be constant for each month, although this value was deter-
mined from only two weeks' data. This may be a simplifica-
tion for what is probably a seasonally changing flow.

Cypress Dome Biomass

The data for the ten harvested pond cypress trees are
given in Table 13. Tree dimensions ranged from 8.4 cm to
36.8 cm in DBH with height varying from 6.4 m to 22.6 m. The
ground level diameter was generally from 2 to 4 times greater
than the DBH due to the swollen buttresses that are character-
istic of cypress (Kurz and Demaree, 1934). Root depth for
those that could be pulled up generally did not go beyond 2 m.
The lateral spread of the roots seemed to be one-third of the
height in most cases. Figure 49 shows the relationship
between weight and DBH for the various plant parts. Stem,
stump, and root biomass showed a general increase with DBH
while leaf and branch weights had a more irregular pattern.

Table 11

SUMMARY OF MONTHLY LOADING RATES IN
EXPERIMENTAL CYPRESS DOMES

Month 1974	Loading Rate, m^3/day (cm/wk)	
	Sewage Dome	Groundwater Dome
March	7.7 (1.0)	14.7 (1.5)
April	13.2 (1.8)	22.7 (2.3)
May	11.0 (1.5)	17.1 (1.7)
June	--	--
July	89.1 (11.8)	70.8 (7.2)
August	100.1 (13.3)	75.7 (7.7)
September	78.5 (10.4)	75.7 (7.7)
October	83.8 (11.1)	75.7 (7.7)
November	14.1 (1.9)	68.1 (6.9)
December	29.4 (3.9)	65.9 (6.7)

Figure 46. Water level, rainfall, and pumpage records
            for the Sewage Dome, the Groundwater Con-
            trol Dome, and the Owens-Illinois Control
            Dome (natural until December, 1974).
            Records are for March-December, 1974.
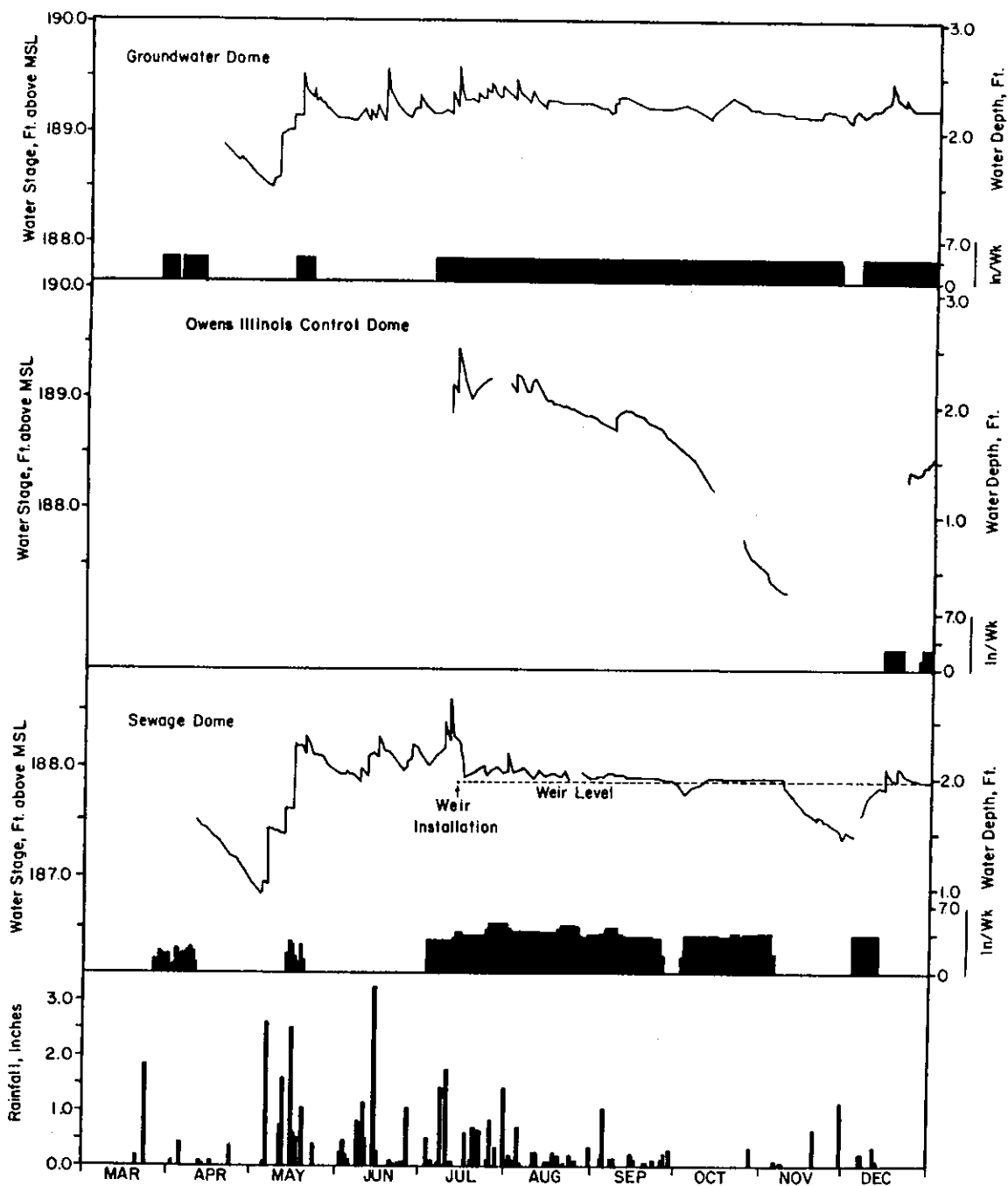
Figure 47.   Water level and rainfall records for Austin Cary Control Dome.   Records are for April-December, 1974.

AUSTIN CARY CONTROL DOME
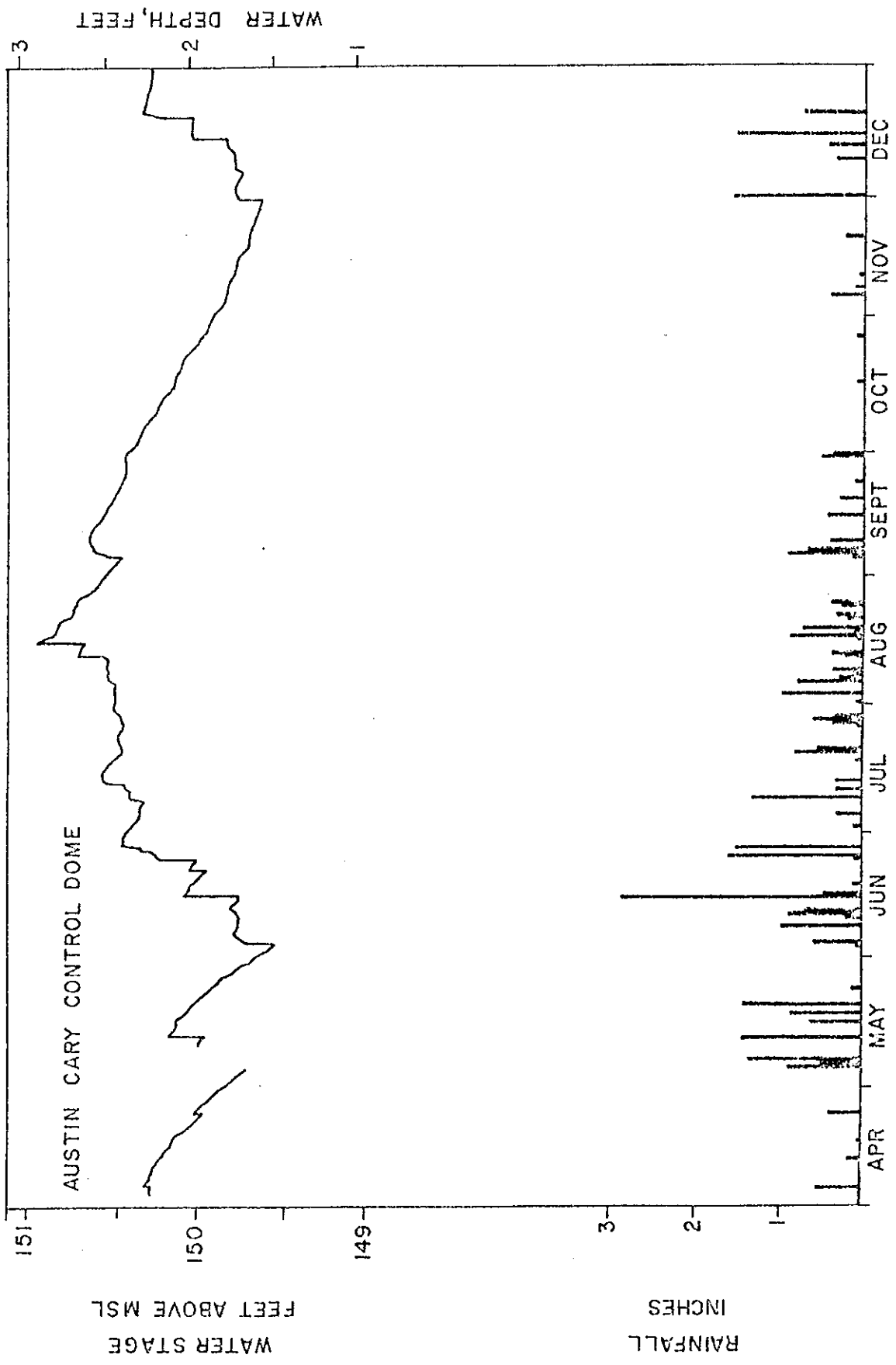
Table 12

MONTHLY AVERAGES OF HYDROLOGIC FLOWS IN SEWAGE DOME

Month, 1974	Pond Volume,[a] m³	Sewage Flow, m³/day	Rainfall, m³/day	Evapo-transporation, m³/day	Weir Flow, m³/day	Groundwater Out,[b] m³/day	Runoff, m³/day
July 23-31	2356	116.9	44.8	24.7	182.2	28.2	83.2
August	2360	100.1	14.8	24.8	194.1	28.2	129.9
September	2342	78.5	14.6	25.0	145.0	28.2	101.4
October	2287	83.8	1.4	24.3	55.5	28.2	25.3
November	1927	14.1	8.8	16.8	21.2	28.2	15.9
December	2126	29.4	15.6	12.2	17.7	28.2	38.7

[a] Pond volume includes sediments to 1.0 m, with average storage coefficient of 0.17 (Cutright, personal communication).

[b] Groundwater outflow based on November 7-19 water level decrease during period of no sewage flow, rainfall or weir flow.

Figure 48. Hydrologic budget for Sewage Cypress Dome (July-December, 1974). Flows and storage represent ranges of monthly averages.

FLOWS m³/day
STORAGE m³

Sewage Flow —— 14.1 - 116.9
Direct Rainfall —— 1.4 - 44.8
Runoff —— 15.9 - 129.9

1927 - 2360
Sewage
Cypress Dome

12.2 - 25.0 Evapotranspiration
17.7 - 194.1 Weir Discharge
23.2 Groundwater Discharge
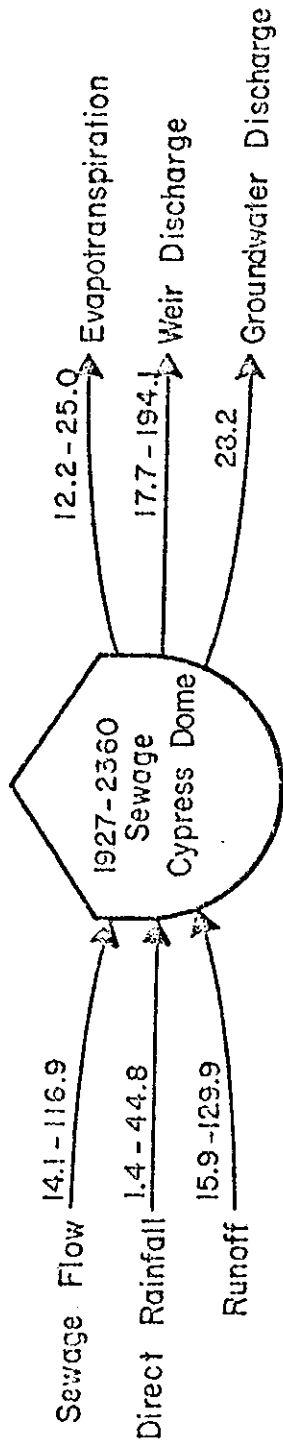
Table 13

POND CYPRESS BIOMASS DATA

	Tree Number		
	9	15	11
A. TREE DIMENSIONS			
DBH, cm	8.4	11.2	12.7
Height, m	7.8	14.0	13.3
Age, years	52	50	66
Branch length, m	17.0	12.8	26.9
Height to 4-in dia., m	.8	2.2	4.6
Root depth, m	.9	.8	.8
Root diameter, m	2.4	2.4	3.6
Ground level diameter, cm	23.6	33.8	25.6
B. DRY WEIGHTS, kg			
Leaves	.37	.80	1.7
Small branch[a]	.57	1.3	2.7
Large branch	--	--	--
Total branch	.57	1.3	2.7
Stem	7.9	21.4	31.0
Stump[b]	5.2	7.0	4.2
Roots[c]	7.0	16.3	19.8
Total	21.0	46.8	59.4
C. DRY WEIGHT DISTRIBUTION % IN:			
Leaves	1.7	1.7	2.9
Branches	2.7	2.8	4.5
Stem	37.6	45.7	52.2
Stump	24.7	15.0	7.1
Roots	33.3	34.8	33.3
D. WET-DRY RELATIONS			
Leaves dry/wet %	34.1	38.2	36.4
Branch dry/wet %	56.6	53.7	50.2
Bark dry/wet %	48.6	53.4	49.2
Wood dry/wet %	48.6	45.8	42.3
Stem dry/wet %	48.6	46.8	43.3
Root dry/wet %[d]	--	--	45.7

[a]Small branches are considered finger size (approximately 1 cm diameter) and smaller.

[b]Stump is considered to be the stem from the ground level to the level at which the tree was cut (approximately 0.6 m above the ground).

[c]Seventy-five percent recovery of roots is assumed.

[d]Root dry weight is based on one subsample.

Table 13 - extended

			Tree Number				
7	14	4	2	6	8	3	Average
15.0	19.0	22.1	25.4	29.2	32.3	36.8	21.2
16.6	17.8	16.8	18.0	20.6	20.9	24.9	17.1
66	63	119	147	123-133	162	153	101
19.6	28.0	16.5	37.1	40.9	45.5	45.5	--
6.4	11.1	12.4	14.2	16.9	17.5	18.1	--
.9	1.2	1.2	1.5	--	--	--	--
3.3	5.0	3.6	6.1	--	--	--	--
31.2	50.3	45.7	53.1	--	--	--	--
.84	1.8	1.6	3.8	4.2	2.5	5.8	--
2.3	3.5	2.9	6.8	5.4	6.3	7.8	--
--	--	8.1	9.0	23.0	12.7	12.1	--
2.3	3.5	11.0	15.8	28.4	19.0	20.9	--
47.1	77.2	116.5	161.4	218.5	258.6	399.4	--
6.7	18.8	16.1	28.2	--	--	--	--
29.7	62.1	69.1	158.8	--	--	--	--
86.6	163.4	214.3	368.0	--	--	--	--
1.0	1.1	.8	1.0				1.5
2.6	2.1	5.1	4.3				3.4
54.4	47.3	54.4	43.9				47.9
7.7	11.5	7.5	7.7				11.6
34.3	38.0	32.2	43.1				35.6
36.7	37.1	32.0	37.7	39.3	22.2	38.1	35.2
56.4	47.3	51.7	59.4	51.4	56.8	50.5	53.4
54.9	49.4	53.6	55.0	58.3	58.0	57.3	53.8
46.1	44.9	48.2	44.0	39.5	44.1	47.1	45.1
47.3	45.6	48.9	45.4	41.4	45.7	48.1	46.1
--	--	--	--	--	--	--	45.7

Figure 49. Biomass of pond cypress (*Taxodium distichum var nutans*) trees harvested in Austin Cary Forest.

LEAF BIOMASS
Kg. dry wt.

BRANCH BIOMASS
Kg. dry wt.

STEM BIOMASS
Kg. dry wt

STUMP BIOMASS
Kg dry wt.

ROOT BIOMASS
Kg. dry wt.

TOTAL BIOMASS
Kg. dry wt.

DBH, CM
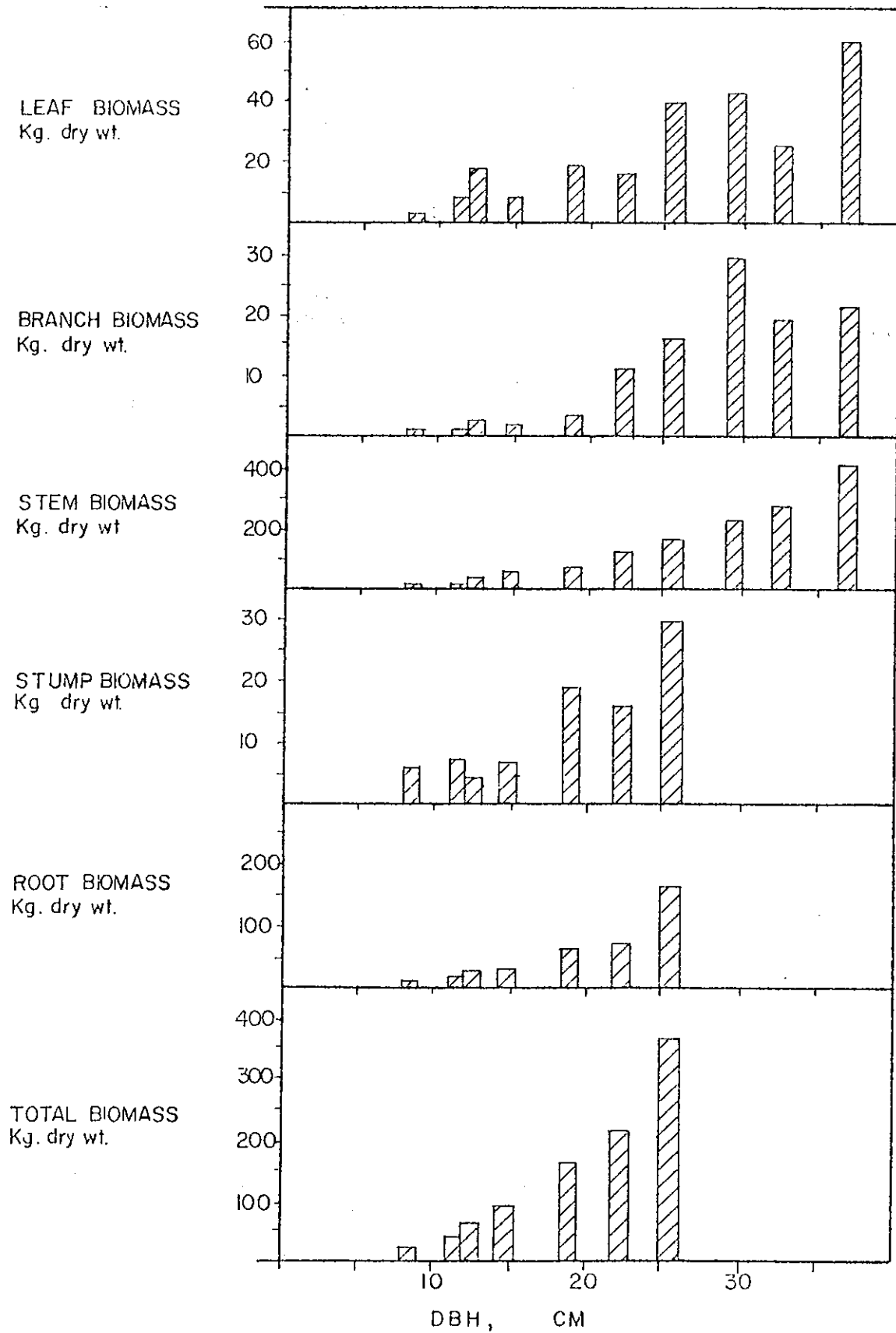
Regression analysis was carried out on the data in order to estimate values for the biomass of an entire cypress dome. Figure 50 shows the relationship between stem biomass and total biomass when analyzed according to a statistical model of the form

$$y = ax^b$$

where   y = biomass (g)

       x = $\sqrt{\text{DBH·Height}}$ (cm)

     a,b = regression coefficients.

The constants as well as the correlation coefficient (r) are given in Table 14 for leaves, branches, stem, and stump + root as dependent variables. Values for the correlation coefficient varied from 0.914 for leaves to 0.994 for the stem.

Tables 15 and 16 show the results of these regressions when applied to the DBH and height data available for the Sewage Dome and the Groundwater Dome, respectively. Dead and live trees were considered separately. Total live biomass for the cypress is 13.6-14.9 kg/m^2 dry weight; dead cypress totaled 0.3-0.6 kg/m^2, most of then killed during the fire in December, 1973. The biomass values compare well with the value of 12 kg/m^2 calculated by Spurr and Barnes (1973) for swamp and marsh systems, although significantly less than the 36.6 kg/m^2 reported by Walter (1973) for humid subtropical regions. They also compare well with data generated by Carter et al. (1973), who found a biomass of 8.9 kg/m^2 for woody plants in drained cypress stands and 17.1 kg/m^2 in undisturbed cypress stands in southwest Florida.

Figure 50. Total dry weight and stem dry weight vs. $\sqrt{\text{DBH} \times \text{HT}}$ for pond cypress (*Taxodium distichum* var *nutans*). DBH is diameter at breast height in centimeters; HT is total height in centimeters.
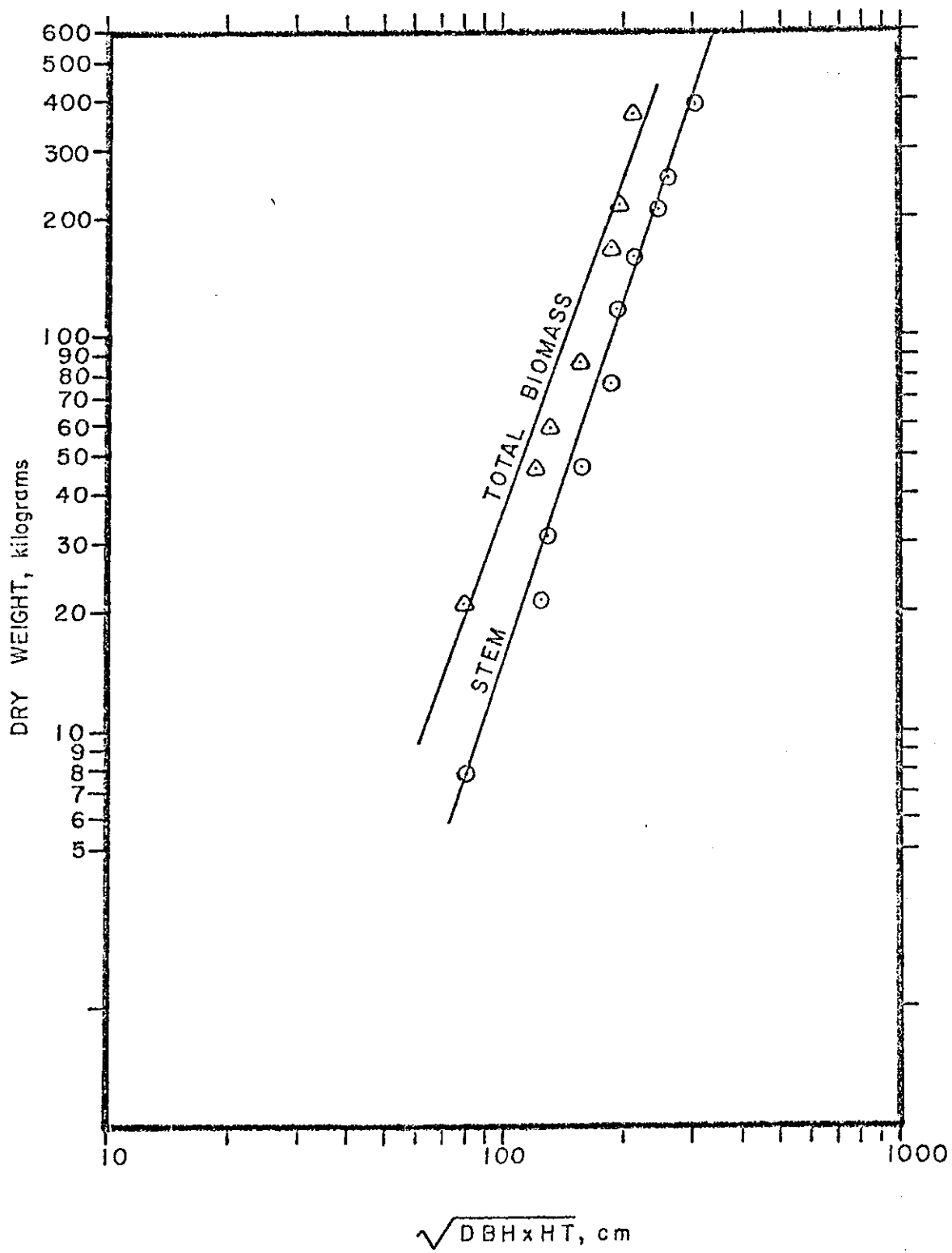
Table 14

REGRESSION ANALYSIS FOR POND CYPRESS BIOMASS

$$y = ax^b$$

y = biomass, g

x = $\sqrt{DBH \cdot Ht}$

DBH = Diameter at Breast Height, cm

Ht = Tree Height, cm

	Number of Trees n	Regression Constants		Correlation Coefficient r
		a	b	
Leaves	10	7.162×10^{-2}	1.9525	0.914
Branches	10	3.656×10^{-4}	3.1966	0.946
Stem	10	8.245×10^{-3}	3.1021	0.994
Stump + Root	7	6.550×10^{-2}	2.6840	0.946

Table 15

POND CYPRESS BIOMASS AT SEWAGE DOME

	Live	Dead
Total Biomass, g/m^2	13578	309
Leaf Biomass, g/m^2	121	--
Branch Biomass, g/m^2	529	10
Stem Biomass, g/m^2	7119	147
Root + Stump Biomass, g/m^2	5818	152
Number of Trees	269	42
Average DBH, cm	23.7	10.5
Average Height, m	17.1	9.4
Dome Area, m^2	5272	
Cypress Dead - % of Total Biomass	2.2%	
Cypress Dead - % in Numbers	13.5%	

Table 16

POND CYPRESS BIOMASS AT GROUNDWATER DOME

	Live	Dead
Total Biomass, g/m^2	17548	613
Leaf Biomass, g/m^2	160	--
Branch Biomass, g/m^2	679	21
Stem Biomass, g/m^2	9162	299
Root + Stump Biomass, g/m^2	7546	293
Number of Trees	495	87
Average DBH, cm	21.0	10.5
Average Height, m	17.4	9.7
Dome Area, m^2	6900	
Cypress Dead - % of Total Biomass	3.3%	
Cypress Dead - % in Numbers	14.9%	

Net Productivity of Cypress

Net growth or productivity was estimated with three dif-
ferent sets of data: (1) by age-biomass relationships on the
above harvested trees; (2) with cypress dimension data made
available for the Withlacoochee State Forest by the State
Division of Forestry; and (3) with cypress dimension data for
two Alachua County domes made available by Owens-Illinois Inc.

Biomass-age plots. A preliminary estimation of cypress
net productivity was obtained by plotting the total biomass
from the above tree harvest against tree age as measured by
ring counts. The relationship is shown in Figure 51a. The
slope of the line indicates a cypress net productivity of 3.1
kg/yr per tree with a correlation coefficient of .938. Shown
in Figure 51b is a plot of DBH versus age indicating an
increase of 0.16 cm/yr. Stated another way, it takes over
6 years for the cypress to increase one centimeter or 16 years
to increase by one inch. A correlation coefficient (r=.903)
was also obtained for this relationship. For comparison,
Langdon (1958) found an increase of 0.46 to 0.53 cm/yr for
baldcypress in Louisiana, three times this pond cypress value.

Withlacoochee cypress growth data. Figure 52 shows in
energy language the definition of net production which is
being determined in these calculations. The results for each
of the 23 Withlacoochee State Forest sites analyzed are given
in Table 17 and summarized in Table 18. The total number of
trees in each 0.2-acre plot varied from 6 to 115 with an
average of 58, or 290 per acre. Cypress accounted for 85%

Figure 51.   Plots of biomass and diameter as a function
             of age for pond cypress harvested in Alachua
             County: (a) the slope of the first graph
             indicates cypress growth of 3.1 kg/yr;
             (b) the second graph indicates a diameter
             increase of 0.16 cm/yr.

(a)

(b)
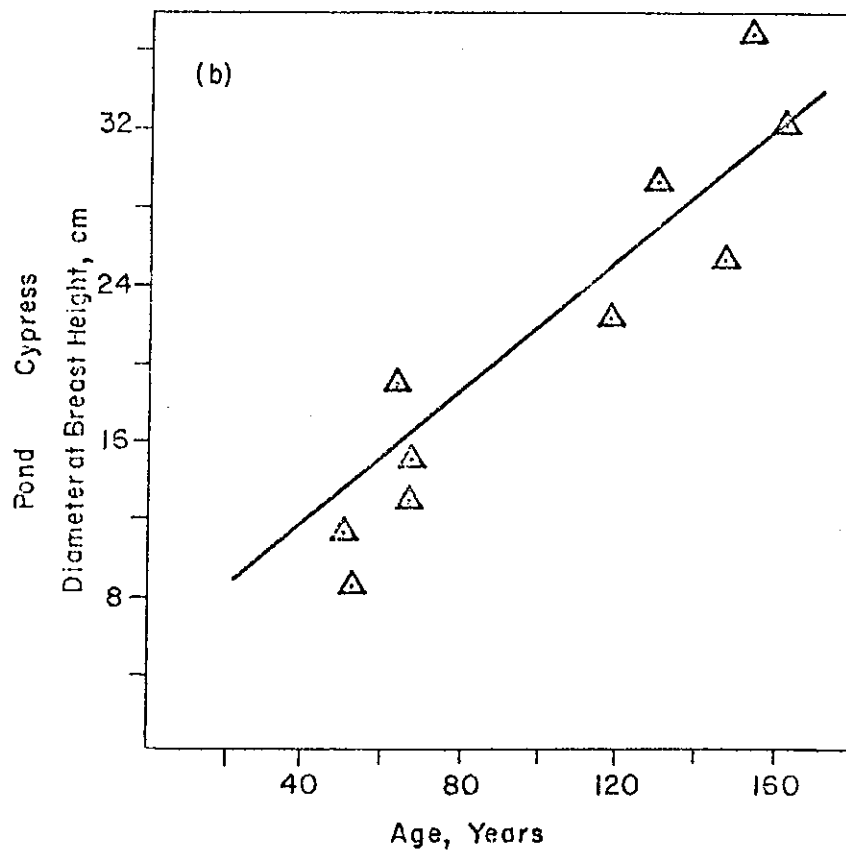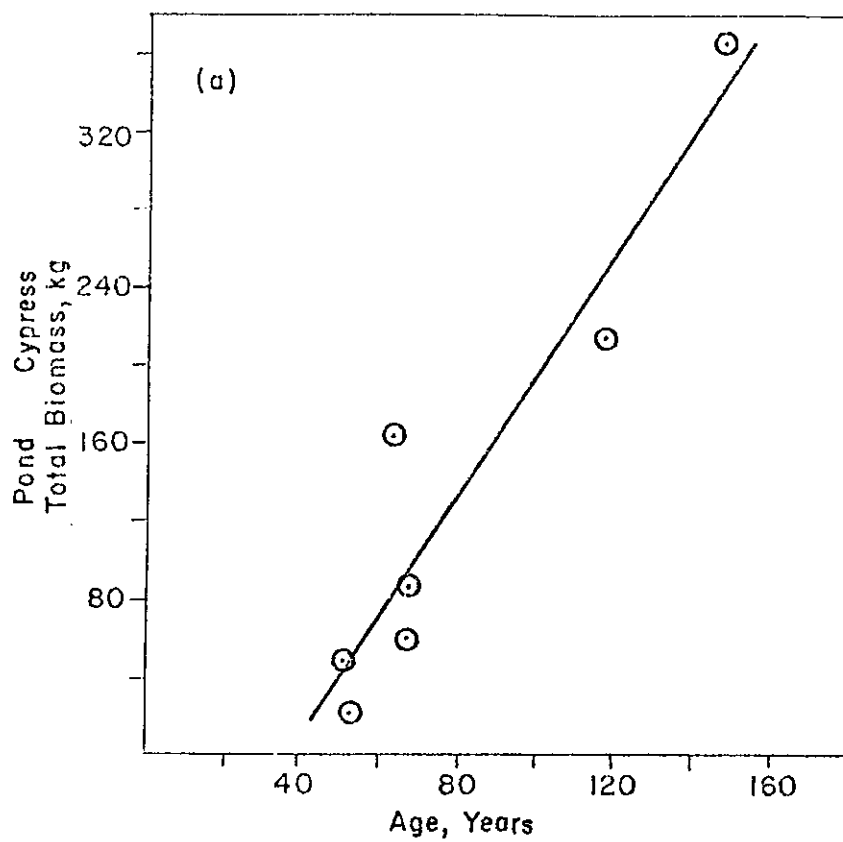
Figure 52. Energy module definition of net primary productivity ($\overline{NPP}$) used for Withlacoochee State Forest and Owens-Illinois Alachua County data. $\overline{GPP}$ indicates Gross Primary Productivity, R is respiration, $\overline{\Delta B}$ is increase in tree biomass, L is litterfall, and $\overline{RL}$ includes root loss and other miscellaneous losses.
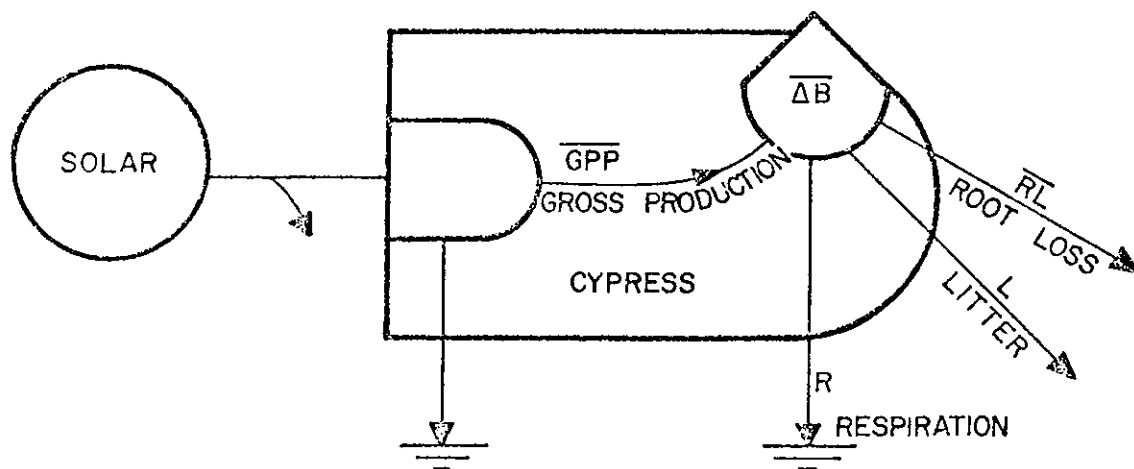
$$\frac{\overline{\Delta B}}{\Delta T} = \overline{GPP} - R - L - \overline{RL}$$

$$\overline{NPP} = \overline{GPP} - R$$

$$\overline{NPP} = \frac{\overline{\Delta B}}{\Delta T} + L + \overline{RL}$$

Table 17

RESULTS OF CYPRESS NET PRODUCTIVITY CALCULATIONS
FOR 23 PLOTS IN WITHLACOOCHEE STATE FOREST

Plot No.	No. of Trees	Density trees/m^2	Cypress		Cypress,		
			>4"DBH	<4"DBH	Avg. DBH cm	Biomass, kg/m^2	NPP g/m^2-yr
375	38	.047	17	0	26.8	7.3	191
378	56	.069	23	1	36.2	16.7	791
398	60	.074	42	1	31.6	24.6	701
415	29	.036	22	6	25.6	8.4	291
416	6	.007	4	2	34.8	2.3	215
422	97	.120	85	1	20.5	20.1	716
430	102	.126	97	2	18.5	21.0	813
431	35	.043	35	0	21.7	9.5	363
432	17	.021	17	0	19.5	3.1	160
443	65	.080	57	7	19.3	11.8	402
447	89	.110	89	0	18.0	15.7	662
461	109	.135	104	0	24.2	38.0	1143
468	58	.072	54	4	18.7	9.7	232
475	6	.007	5	0	14.8	.5	20
519	76	.094	57	0	23.4	17.8	836
528	45	.056	14	5	31.0	7.0	249
570	36	.044	22	0	16.4	3.3	91
571	71	.088	62	3	20.4	15.3	423
583	36	.044	33	0	21.0	7.8	261
623	102	.126	100	0	17.4	19.2	613
644	54	.067	40	7	18.2	7.6	296
645	37	.046	23	7	20.7	6.1	168
657	115	.142	82	7	17.7	14.5	585

Note: Cypress net productivity corrected to total plot net
production by dividing by percentage of trees considered.

Table 17 - extended

>4" DBH		% Trees Consid- ered	Corrected NPP, g/m²-yr	Other Species in Plot
NPP/tree, kg/yr	NPP/B yr⁻¹			
9.1	.026	44.7	427	Slash pine-11, tupelo gum-5, other-2
27.8	.047	41.1	1925	Ash-27, water oak-1, maple-1
13.5	.028	70.0	1001	Tupelo gum-11, maple-4, other-1
10.7	.035	75.9	383	Tupelo gum-1
43.5	.094	66.7	322	--
6.8	.036	87.6	817	Water oak-5, sweet gum, tupelo gum, maple, other-1
6.8	.039	95.1	855	Tupelo gum-2, slash pine-1
8.4	.038	100.	363	--
7.6	.052	100.	160	--
5.7	.034	87.7	458	Slash pine-1
6.0	.042	100.	662	--
8.9	.030	95.4	1198	Tupelo gum-5
3.5	.024	93.1	249	--
3.3	.039	83.3	24	Tupelo gum-1
11.9	.047	75.0	1115	Maple-8, tupelo gum-4, water oak-1, bay-1, other-5
14.4	.028	31.1	801	Maple-11, tupelo gum-9, water oak-2, slash pine, bay, ash-1
3.3	.028	61.6	148	Longleaf pine-8, slash pine-5, scrub oak-1
5.5	.028	87.3	485	Slash pine-6
6.4	.033	91.7	285	Slash pine-3
5.0	.032	98.0	626	Slash pine-2
6.0	.039	74.1	399	Tupelo gum-7
5.9	.027	62.2	270	Slash pine-7
5.8	.040	7.13	820	Tupelo gum-24, slash pine-2

Table 18

SUMMARY OF NET PRODUCTIVITY CALCULATIONS
FOR 23 CYPRESS SITES IN THE WITHLACOOCHEE
STATE FOREST AS GIVEN IN TABLE 17

Total area considered	4.6 acres
Average tree density	0.072 trees/m^2
Total number of trees	1339
Total number of cypress	1137
Cypress 4.0" DBH	
Net primary productivity (NPP)	444 g/m^2-yr
Biomass	12.5 kg/m^2
NPP/tree	7.6 kg/yr
Corrected total tree net productivity	600 g/m^2-yr

of the trees in these plots. Cypress net productivity ranged from 20 to 1143 g dry wt/m^2/yr, with an average of 444 g dry wt/m^2/yr. When corrected for other trees the average net primary productivity of the canopy is estimated to be 600 g dry wt/m^2/yr.

Alachua County cypress growth. Tree growth data were also made available by Owens-Illinois Inc. for several plots in Alachua County. Two of these plots contained a high number of cypress, and data from these plots were used to calculate cypress productivity as was done with the Withlacoochee data. In this case, however, tree data were available for four times over the period 1961-72. The results of the productivity calculations are given in Table 19 and are plotted in Figure 53. Visits to the two sites, both located near the experimental dome area, determined that one of the sites was markedly drained (No. 1027) while the other site had considerable standing water (No. 1047) and only had other species in the plot because it fell on a cypress dome-pine plantation boundary. The data indicate a much higher productivity at the drained site.

Withlacoochee Forest and Alachua County cypress productivities are compared with net primary productivity calculations for similar areas in Table 20. The comparison shows the cypress to have relatively slow growth compared to other deciduous forests. These cypress productivities and those calculated by Carter et al. (1973) for South Florida are within the same range, although the latter authors' conclusions on

Table 19

RESULTS OF CYPRESS NET PRODUCTIVITY CALCULATIONS
FOR DRY AND WET SITES IN ALACHUA COUNTY

Year	Ave. DBH, cm	Ave. Ht., m	Biomass, kg/m^2	NPP, g/m^2-yr	NPP/tree, kg/yr	% Trees Considered	Corrected NPP, g/m^2-yr [a]
			Dry Site Plot No. 1027,[b] 26 Cypress Trees				
1961	18.6	15.5	6.8				
1964	18.9	16.0	7.3	334	7.4	89.7	372
1968	19.5	16.6	8.0	363	8.1	81.3	447
1972	20.3	16.9	8.4	298	7.0	71.4	417
			Wet Site Plot No. 1047,[b] 13 Cypress Trees				
1961	22.1	17.4	5.1				
1964	22.1	17.4	5.1	88	4.0	52.0	168
1968	22.2	17.4	5.2	123	5.4	52.0	236
1972	22.3	17.4	5.3	86	3.8	52.0	166

[a]Cypress net productivity corrected to total plot net production by dividing by percentage of trees considered.

[b]Owens-Illinois, Inc., plot numbers.

Figure 53. Cypress diameter, height, biomass, and net
productivity as functions of time for two
permanent growth sites. The sites are
located in cypress domes in Alachua County
and are maintained by Owens-Illinois, Inc.
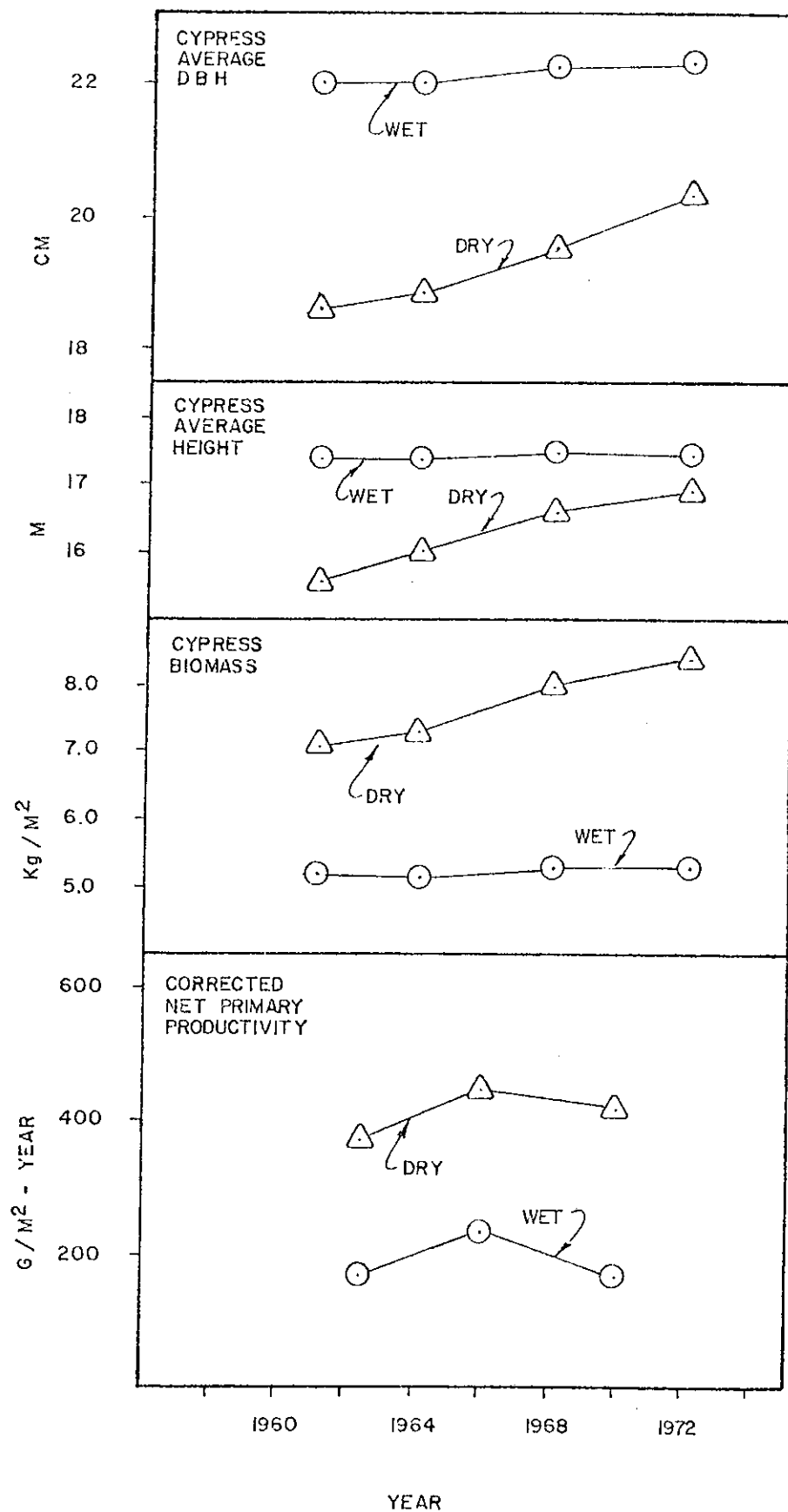
Table 20

COMPARISON OF CYPRESS NET PRODUCTION WITH
OTHER FOREST PRODUCTION VALUES

Location and System	Net Production, g/m^2-yr	Source
Oak-pine forest, Brookhaven Nat'l Lab.	1124[a]	Woodwell & Whittaker (1968)
"Temperate forest"	600-3000	Spurr & Barnes (1973)
"Swamp or marsh"	800-4000	Ibid.
South Florida drained cypress strand (Fahkahatchee Strand)	387[b]	Carter et al. (1973)
South Florida undrained cypress strand (Fahkahatchee Strand)	858[b]	Ibid.
Oklahoma oak forest	1490[c]	Johnson & Risser (1974)
Withlacoochee cypress systems, Central Florida	600[a]	This study (Table 15)
Alachua County drained cypress dome	416[a]	This study (Table 16)
Alachua County undrained cypress dome	192[a]	This study (Table 16)

[a]Total woody plant growth + litterfall + root loss.
[b]Above ground woody plant growth + litterfall.
[c]Total woody plant growth + litterfall.

drainage effects contradict the results of the Alachua County cypress domes.

Sunlight, Microclimate, and Aquatic Metabolism

Microclimate and aquatic parameters were studied over a one-year period in the Austin Cary Control Dome. Diurnal trends inside and outside of the dome for solar radiation are given in Figure 54. Figure 55 presents diurnal trends in air and water temperature, dissolved oxygen in the pond, and aquatic metabolism. Table 21 summarizes the above data while Figure 56 gives an annual summary of the results.

Air temperature in the dome appears to be somewhat higher than outside during the spring months when the canopy is open but was cooler by several degrees for the August and November readings. The minimal wind speeds experienced in the dome result in less evaporation and less heat absorption. Atmometer readings during the August experiment show 35% less evaporation in the dome than in the surrounding pine flatwoods. Water temperature varies little throughout the year with only a 9°C difference between the maximum and minimum values recorded.

The most significant trend to be noted in the solar radiation results is the spring peak of sunlight in the dome (Figure 56). Radiation in the dome goes from a high of about 50% of available radiation in early spring to below 20% in late summer. Shading continues through the fall and winter. The peak occurs prior to the development of a dense canopy

Figure 54. Diurnal variation of sunlight inside and outside of cypress dome for four times during a year: (a) November 23-24, 1973; (b) March 30, 1974; (c) May 19-20, 1974; and (d) August 10-11, 1974. Data measured at Austin Cary Control Dome. Radiation values given in Table 18.

A) Nov 23-24, 1973
Outside Dome
Inside Dome
Solar Radiation cal/cm²-min
Hour

B) Mar 30, 1974
Outside Dome
Inside Dome
Solar Radiation cal/cm²-min
Hour

C) May 19-20, 1974
Outside Dome
Inside Dome
Solar Radiation cal/cm²-min
Hour

D) Aug 10-11, 1974
Outside Dome
Inside Dome
Solar Radiation cal/cm²-min
Hour
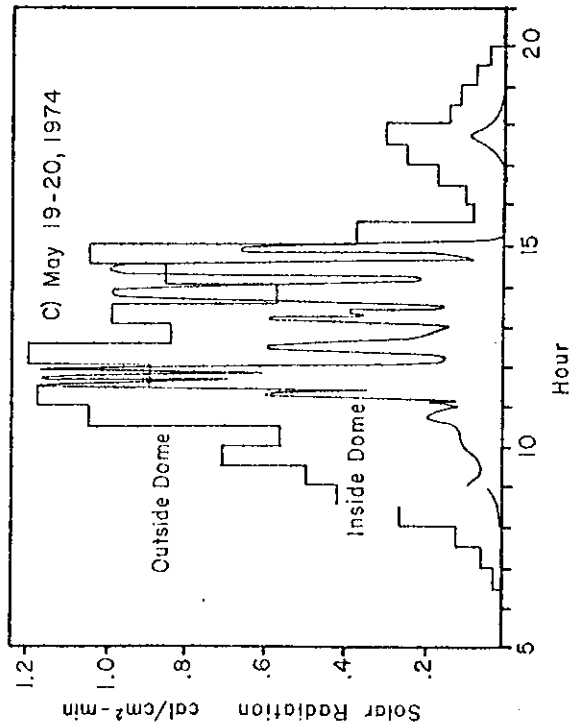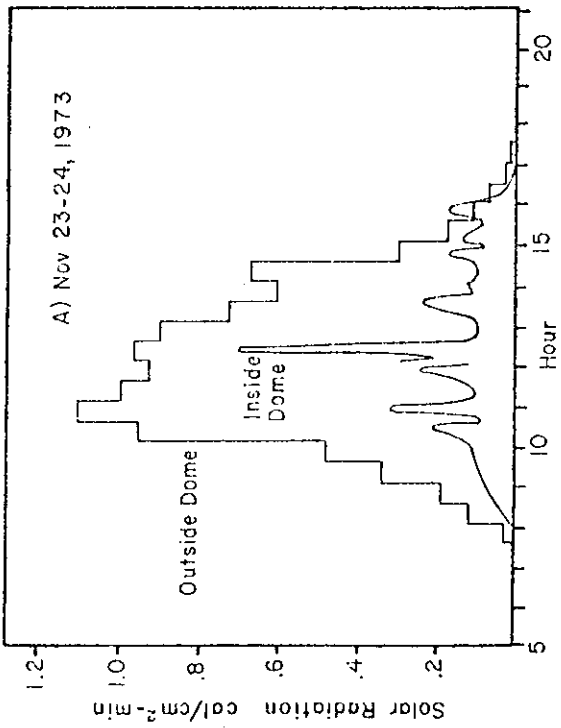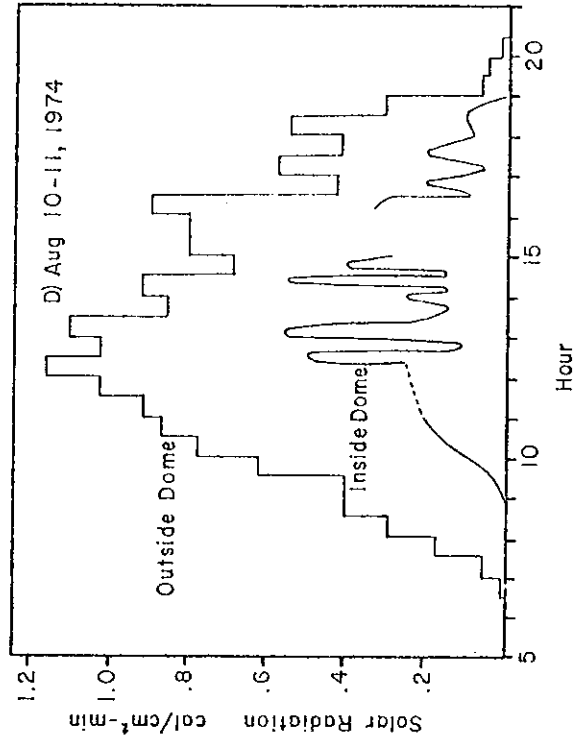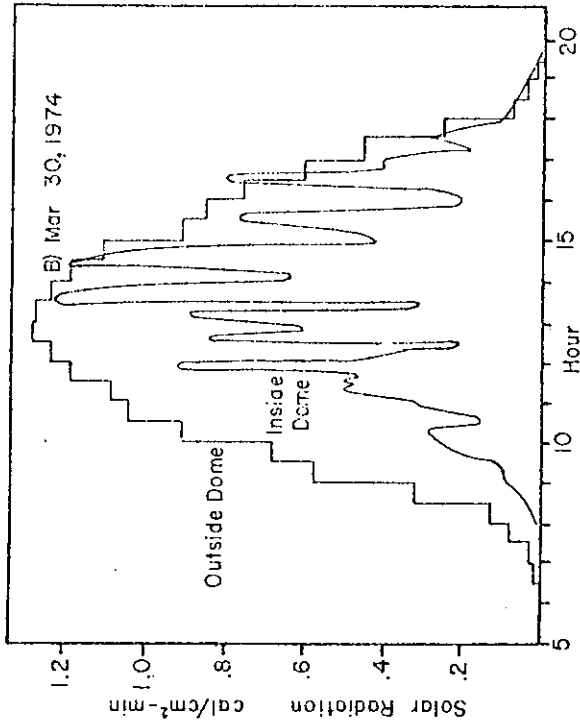
Figure 55.   Dissolved oxygen diurnal curve and corresponding rate of change curve for central pond in Austin Cary Control Cypress Dome. Solar radiation and air and water temperatures are also given. Data are for four dates throughout the year: (a) November 23-24, 1974; (b) March 29-30, 1974; (c) May 19-20, 1974; and (d) August 10-11, 1974.
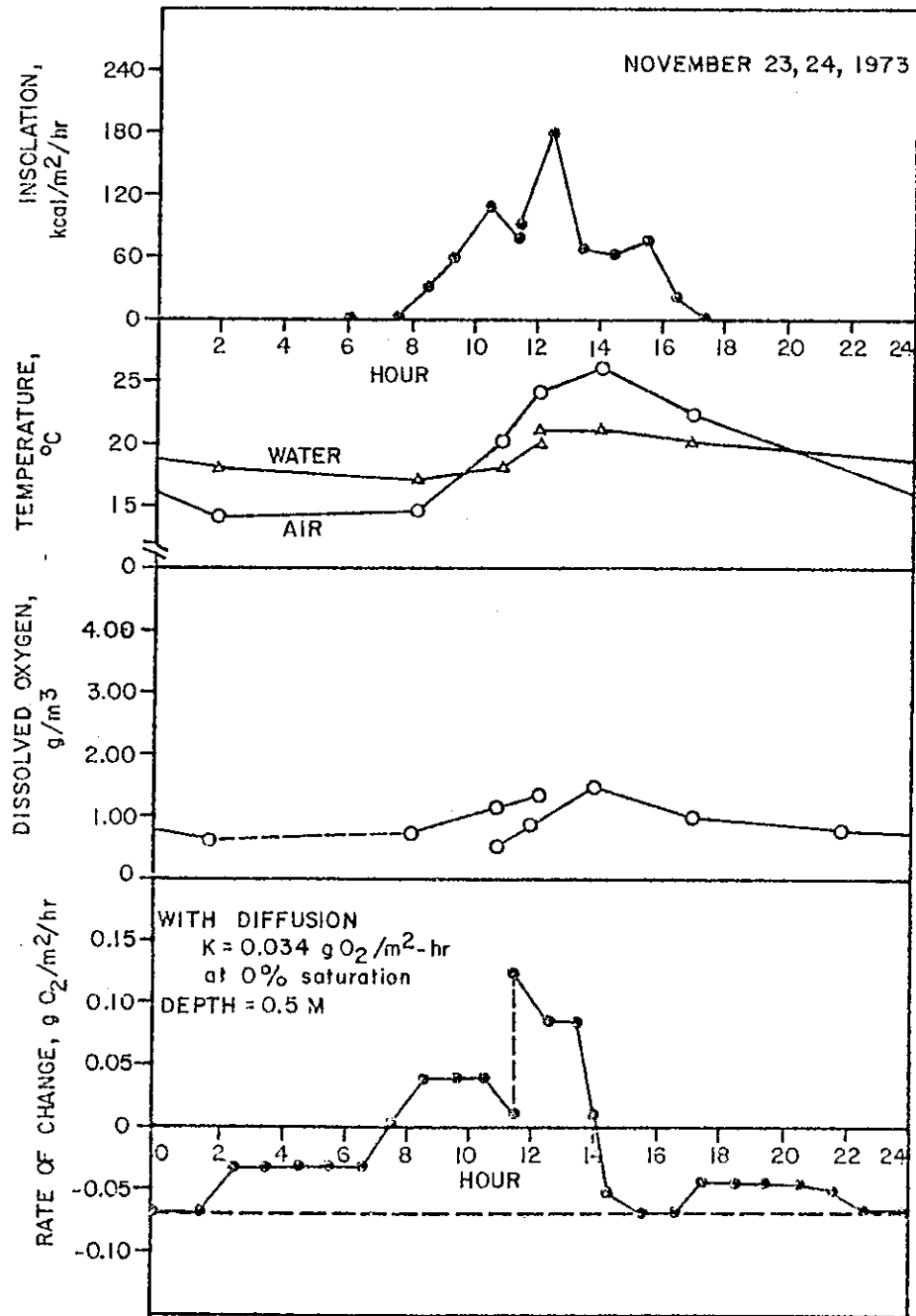
(a)
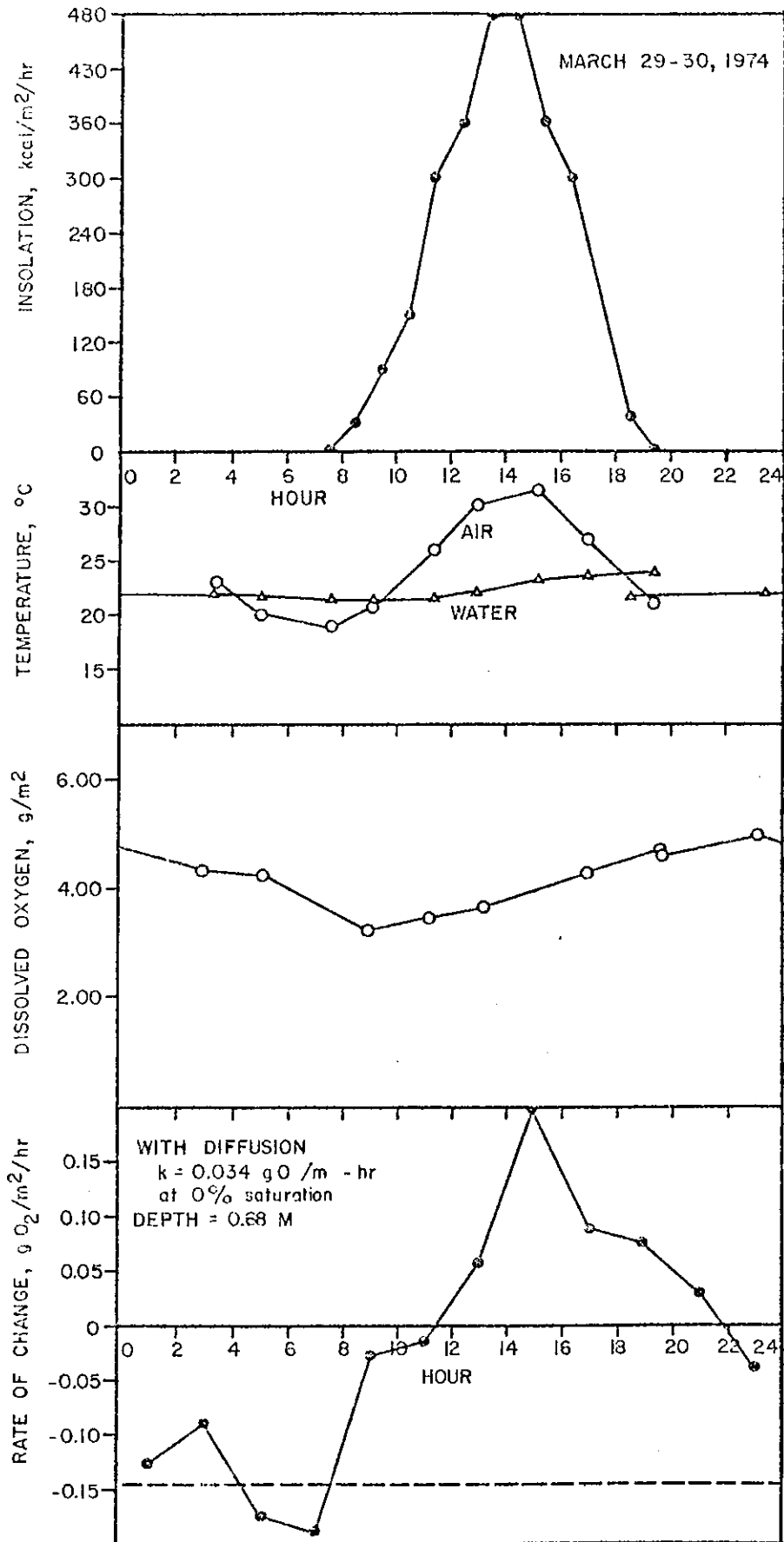
(b)

Figure 55 - continued.
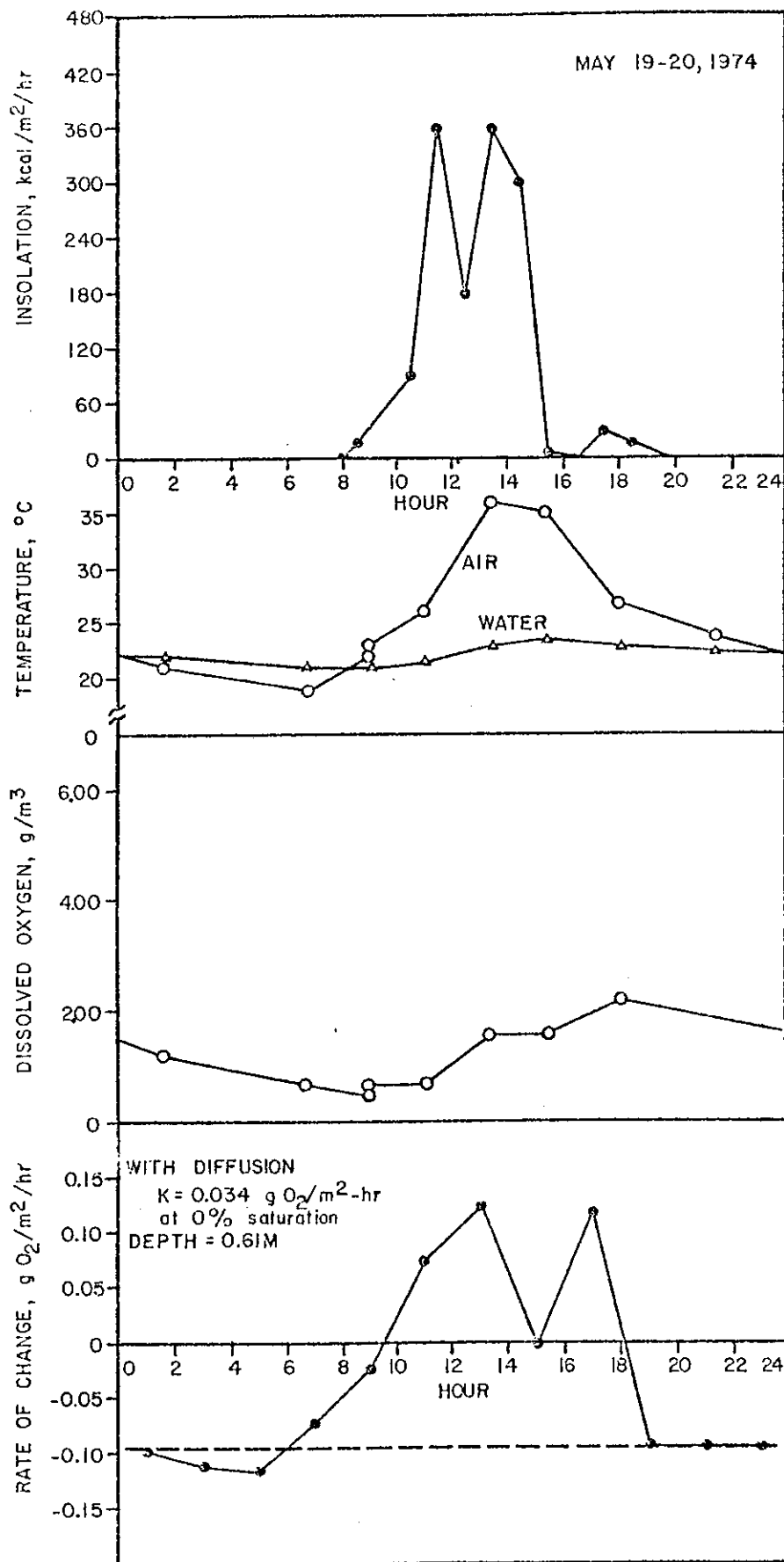
(c)

Figure 55 - continued.
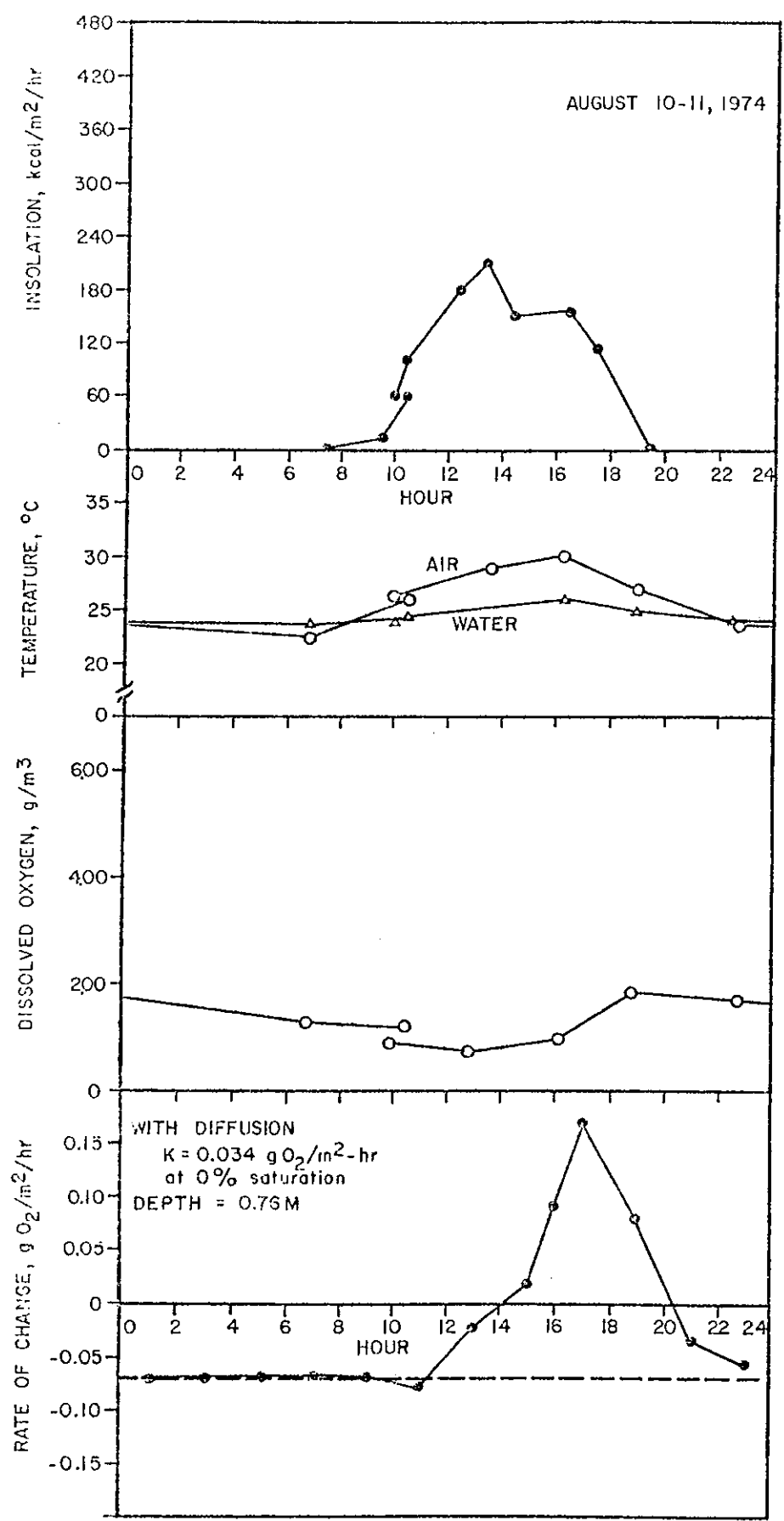
(d)

Figure 55 - continued.

Table 21

AIR AND WATER TEMPERATURE, SOLAR RADIATION
AND POND METABOLISM IN AUSTIN CARY CYPRESS DOME

	1973 November	1974 March	May	August
Air Temperature, °C				
Max. in Dome	26	31.5	36.0	30.0
Min. in Dome	14	19	19	22.5
Max. Outside Dome[a]	31.1	28.3	32.2	33.0
Min. Outside Dome[a]	17.7	18.9	17.2	22.5
Water Temperature, °C				
Maximum	21.0	23.8	23.5	26.0
Minimum	17.0	21.5	21.0	23.5
Solar Radiation				
Outside Dome, $kcal/m^2$-day[b]	2096	5200	3918	6359
Inside Dome, $kcal/m^2$-day	596	2577	1480	1150
Percent Reaching Pond	20.5%	49.6%	37.8%	18.1%
Cypress Pond Aquatic Metabolism				
Gross Production, $kcal/m^2$-day	4.0	12.8	6.9	4.7
Respiration, $kcal/m^2$-day	7.6	15.7	10.4	7.4
Gross Production/ Respiration	0.53	0.81	0.66	0.64
Gross Production/ Insolation	0.67%	0.50%	0.47%	0.41%

[a]Climatological data from Agronomy Department Beef Research Unit, University of Florida.

[b]November, March and May data from J. Steinberg.

Figure 56.   Annual patterns of solar radiation, aquatic
            metabolism, and dissolved oxygen in the
            central pond of Austin Cary Control Dome.
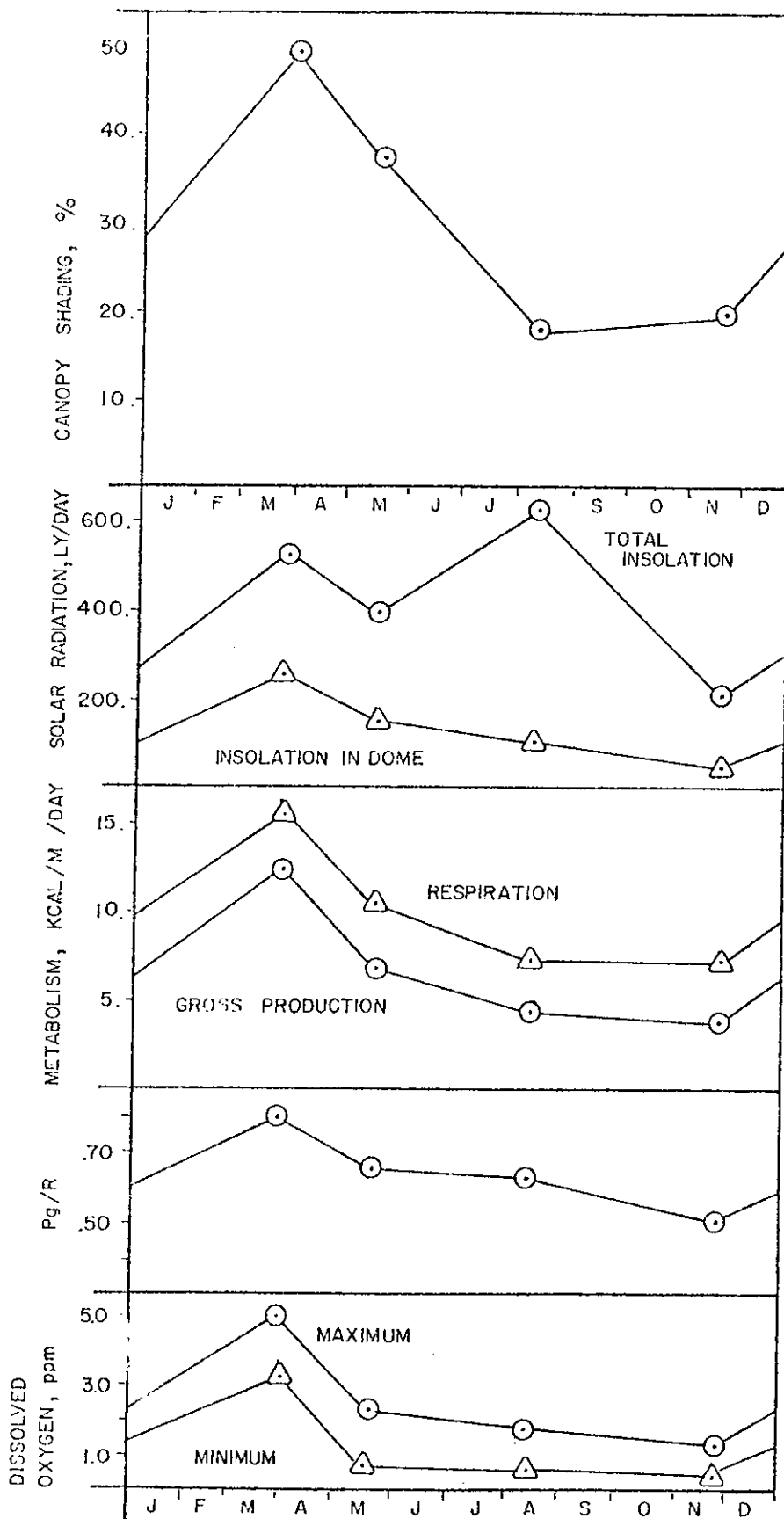
when the sun is at a critical height above the horizon. As summer progresses and the canopy continues to leaf out, a progressively lower percentage of incident radiation enters the dome. Autumn and winter bring leaf fall from the deciduous species, including the cypress, but little increase, if any, in the percent insolation reaching the central pond. Because of the sun's low position in the sky at this time of year, the blocking effect is due more to the stands of cypress trunks in the path of the sunlight. Only 20% of available sunlight was allowed in the dome in the late November measurements. Similar annual trends were noted by Hall (1972) for canopy shading of a temperate stream ecosystem.

Although the P/R ratio remained below 1.0 throughout the year (thus indicating a heterotrophic subsystem), the aquatic metabolism is likewise shown to peak in the spring. Production in the water column was dominated by the submerged mactophyte, bladderwort (*Utricularia purpurea*), although significant amounts of *Juncus repens* and small patches of *Bacopa caroliniana* were noted in semi-submerged positions. *Utricularia* biomass samples taken in February indicated a range from 2.4 to 203 g/m^2 dry weight with an average of 72 g/m^2. Planktonic producers were sparse to nonexistent although several species of diatoms were noted in water in which aquatic macrophytes had been sampled, suggesting a periphyton community associated with the bladderwort. The productivities measured, 4.0 to 12.8 $kcal/m^2$-day, are low in comparison to

those obtained for more fertile sites, yet the efficiency of solar conversion of 0.5% is not extremely low.

Understory Growth

Patterns of growth and succession of understory plants were studied in the four cypress domes. The understory plants of the cypress domes under experimental manipulation showed considerable differences in species succession and biomass from those in natural conditions. These trends and parameters are being investigated with vegetation plots maintained in each dome. Temporal variation of vegetation biomass in these plots is shown in Figure 57. A more detailed discussion is found in Ewel and Mitsch (1974).

The Sewage Dome, with its high nutrient loading, was carpeted with a bloom of filamentous algae (tentatively identified as *Oedegonium* sp.) soon after sewage was introduced in April, 1974. This was followed by a brief period of clear water until May when duckweed (*Lemna purpurea*, *Spirodella oligorhiza* and *Azolla caroliniana*) began to proliferate across the water surface. The amount of duckweed has steadily increased to values in the range of 200 g dry wt/m^2 (D. Price, personal communication). The Sewage Dome biomass as shown in Figure 57 is predominantly duckweed, although cattail (*Typha latifolia*) was beginning to appear around the dome's edge. The Groundwater Dome has a clearer water with bladderwort (*Utricularia* sp.), some duckweed, and unidentified algae dominating. Virginia chain fern (*Woodwardia virginica*) grows

Figure 57. Understory biomass as measured in permanent
vegetation plots in experimental and control
cypress domes in 1974. Measurement tech-
niques are described in more detail in Ewel
and Mitsch, 1974. Symbols used are Sewage
Dome ($\triangle$), Groundwater Dome ($\ominus$), Owens-
Illinois Control Dome ($\square$), and Austin Cary
Control Dome ($\odot$).

UNDERSTORY BIOMASS
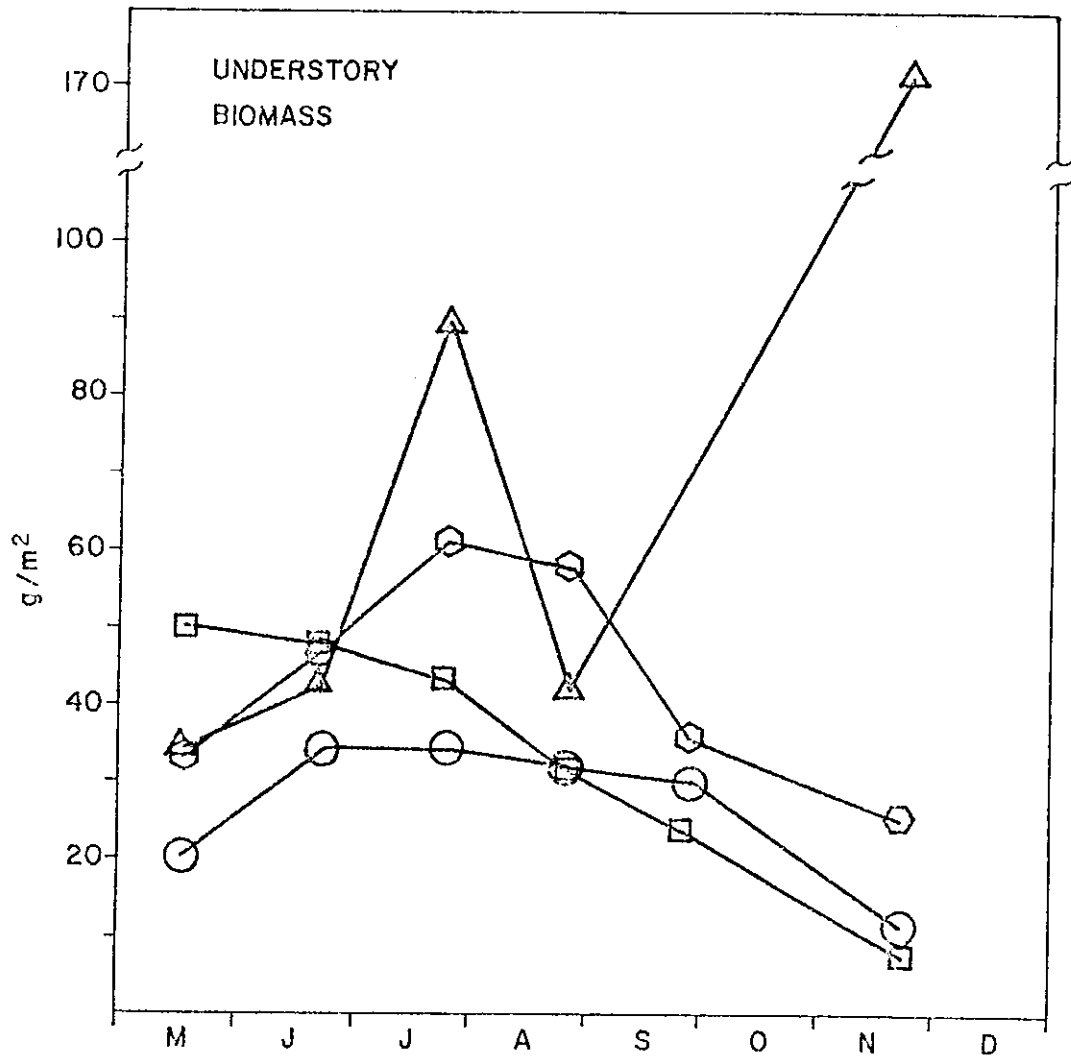
on higher ground. The Owens-Illinois Control Dome, only singed by the December fire, has *Woodwardia virginica* and *Utricularia* sp. dominating the vegetation plots although significant areas of fragrant waterlily (*Nymphea odorata*) were also noted. The Austin Cary Control Dome, with its undisturbed natural state, has a high diversity of understory vegetation. The higher areas are dominated by fetterbush (*Lyonia lucidia*) and *Woodwardia virginica*, while the central pond has profuse growths of *Utricularia purpurea*.

Water Chemistry in Experimental and Natural Cypress Domes

Water quality in general, and nutrient concentrations in particular, have shown somewhat erratic patterns in the experimental dome receiving treated sewage and the dome receiving groundwater since effluent pumping began in late March, 1974. This can be attributed to the irregular pumping schedule maintained until early July as well as to the residual effects of the previous December's fire. Some overall patterns have begun to develop since that time and comparison among the experimental and control domes offers insight into the changes to be expected in the water chemistry as brought about by sewage disposal in cypress swamps.

Table 22 gives ranges for the chemical parameters determined routinely on standing water in the four cypress domes under study. Analysis of samples taken from the center to the edge of the domes to determine spatial variation has failed to show any consistent pattern. Ammonia-nitrogen, nitrate-

Table 22

SUMMARY OF CHEMICAL CHARACTERISTICS OF DOME STANDING WATERS
(APRIL-AUGUST, 1974)

Chemical Parameter[a]	Sewage Dome	Groundwater Dome	Owens-Illinois Control Dome	Austin Cary Control Dome
pH	4.2-6.3	4.9-6.9	3.7-4.0	4.3-5.0
Conductivity, µmhos/cm	115-500	131-370	90-113	60-72
Turbidity, JTU	0.9-2.4	0.6-1.2	0.14-0.22	0.38-54.0
Color, mg-Pt/ℓ	238-884	300-1261	--	182-380
Dissolved oxygen, mg/ℓ	0.15-1.6	0.25-1.75	--	0.5-4.8
COD, mg/ℓ	--	--	274	--
T.O.C., mg-C/ℓ	29.5-82.5	29.0-54.5	110	16-32.5
Total Kjeldahl N, mg-N/ℓ	1.1-8.8	0.8-10.2	1.8-10.3	1.0-2.0
NH_3, mg-N/ℓ	0.03-6.7	0.01-3.8	0.03-4.9	0.01-0.5
NO_3, mg-N/ℓ	0.0-1.9	0-2.1	0-0.12	0.01-0.9
Ortho-P, mg-P/ℓ	0.36-4.4	0.08-0.70	0.09-0.30	0.02-1.3
Total P, mg-P/ℓ	0.52-6.8	0.10-0.70	0.15-0.42	0.03-0.57
Alkalinity, mg-$CaCo_3$/ℓ	0-174	70	0	0
Acidity, mg-$CaCO_3$/ℓ	62-80	48-54	73-105	--
Na, mg/ℓ	23.2-38.9	7.5-8.1	3.6-4.8	2.9-5.7
K, mg/ℓ	4.5-7.2	0.9-1.1	0.73	0.4-1.1
Ca, mg/ℓ	7.8-18.5	24.4-35.5	1.6-2.3	1.0-3.2

Table 22 - continued

Chemical Parameter[a]	Sewage Dome	Groundwater Dome	Owens-Illinois Control Dome	Austin Cary Control Dome
Mg, mg/ℓ	11.4-20.6	27.9-35.9	2.0	1.5-2.5
Cl, mg/ℓ	1.8-1.9	2.0-2.4	1.8	- -
F, mg/ℓ	0.15-0.22	0.32-0.37	0.12-0.14	0.07-0.11

[a]Most sample analysis and some sampling by Brezonik et al. (1974).

nitrogen, sodium, potassium, calcium, and magnesium have displayed decreases from center to edge on certain sampling dates. However, it appears that the water chemistry is relatively homogeneous except for the area immediate to the outfall.

Temporal patterns reveal useful comparisons among the four cypress domes. Figure 58a gives the results to date for standing water pH. After erratic behavior in April and May, the pH of the Sewage and Groundwater Domes has increased steadily to levels of approximately 6.0 and 7.0, respectively. The two domes remaining in their natural state display considerably lower pH values between 4.0 to 4.5. This difference in pH, with possible subsequent changes in vegetation and nutrient availability, may prove to be an important alteration of natural conditions imposed by the sewage disposal.

Nitrogen (Figure 58b,c,d) and phosphorus (Figure 58e,f) showed opposite temporal patterns in the Sewage Dome. While total Kjeldahl nitrogen and nitrates have steadily decreased (Figure 58), phosphorus has begun to accumulate (Figure 58) to the point where total phosphorus now exceeds total nitrogen. A comparison of the N/P ratios for the four domes in late August reveals a considerable range:

	N/P
Sewage Dome	0.54
Groundwater Dome	3.2
Owens-Illinois Control Dome	5.1
Austin Cary Control Dome	13.0

Figure 58. Water quality parameters for cypress dome standing water based in monthly sampling. Parameters include (a) pH, (b) Kjeldahl nitrogen, (c) nitrate-nitrogen, (d) ammonia-nitrogen, (e) total phosphorus, and (f) ortho-phosphates. Symbols used are Sewage Dome ($\triangle$), Groundwater Dome ($\odot$), Owens-Illinois Control Dome ($\square$), and Austin Cary Control Dome ($\odot$).

Figure 58 - continued.

234
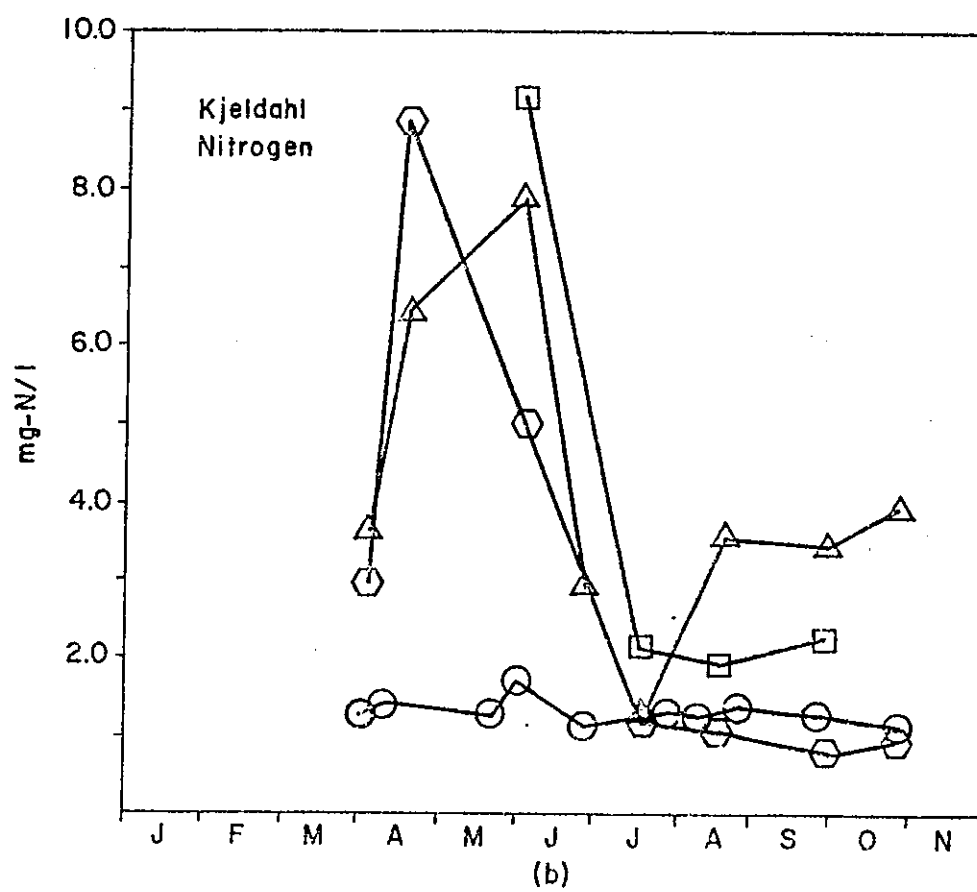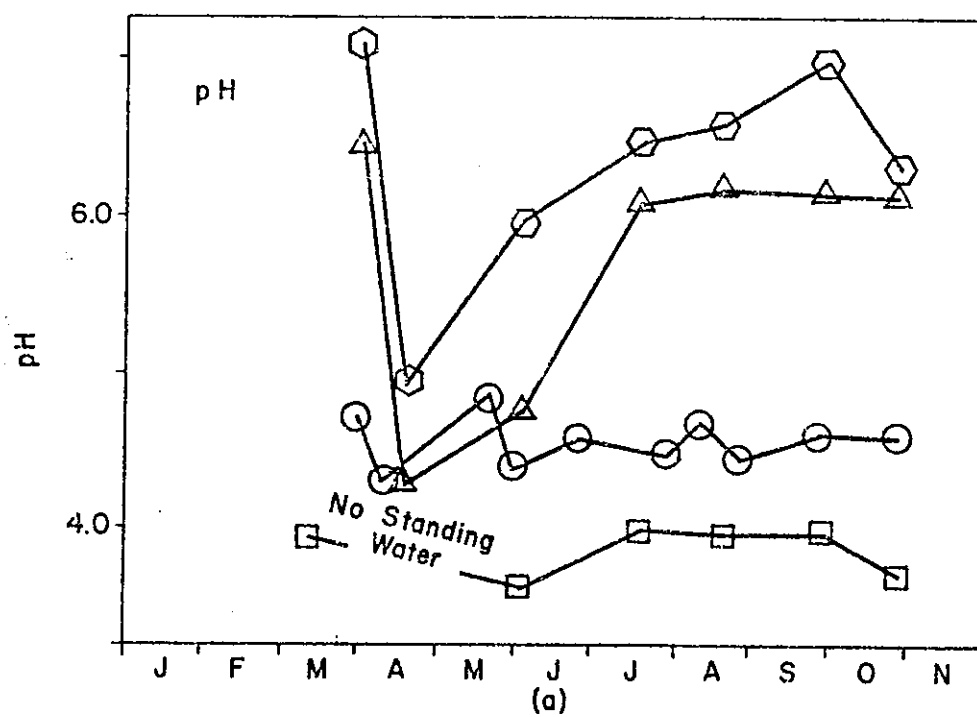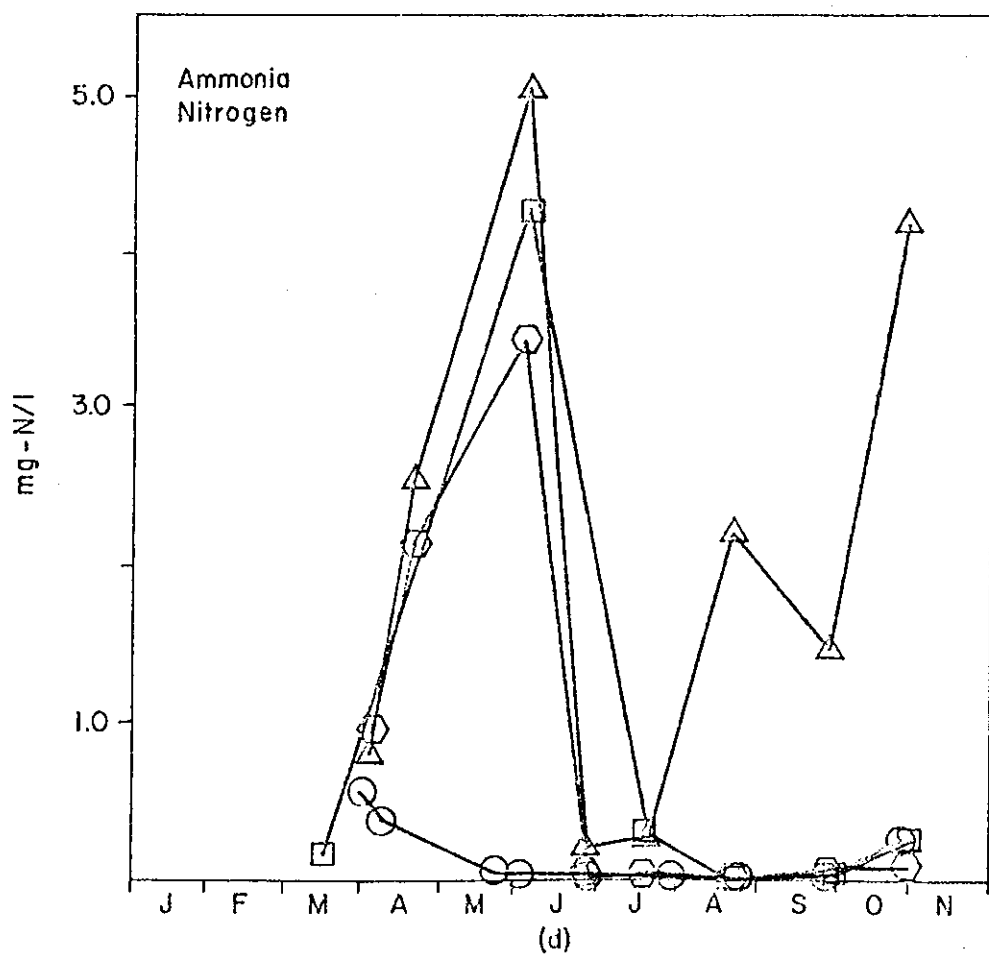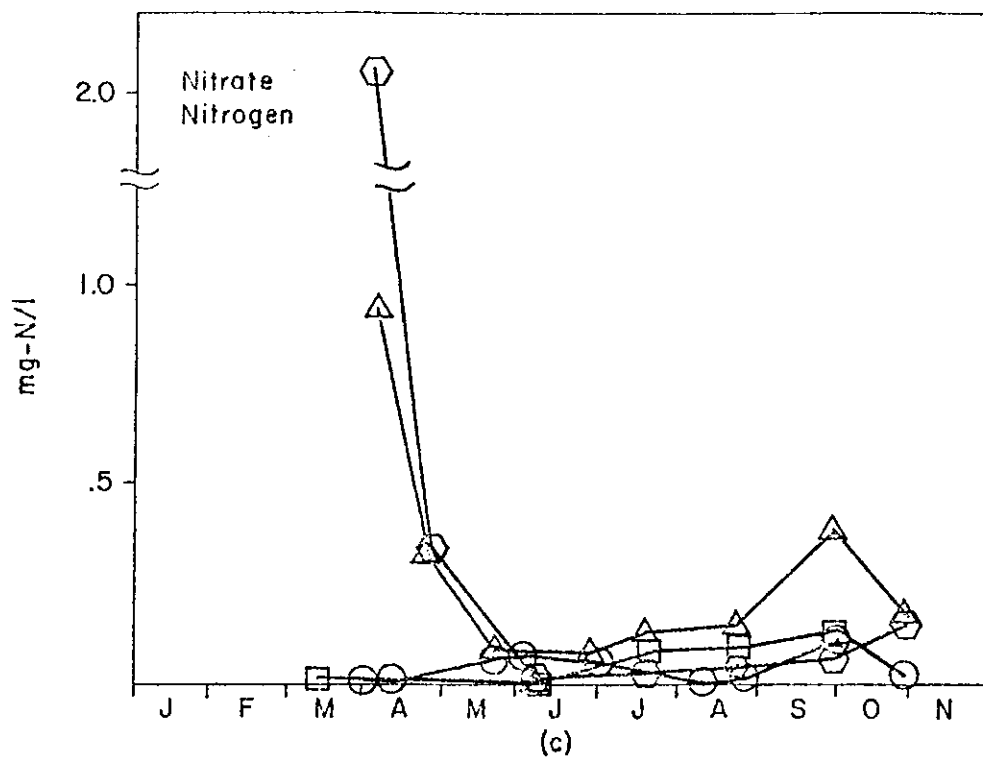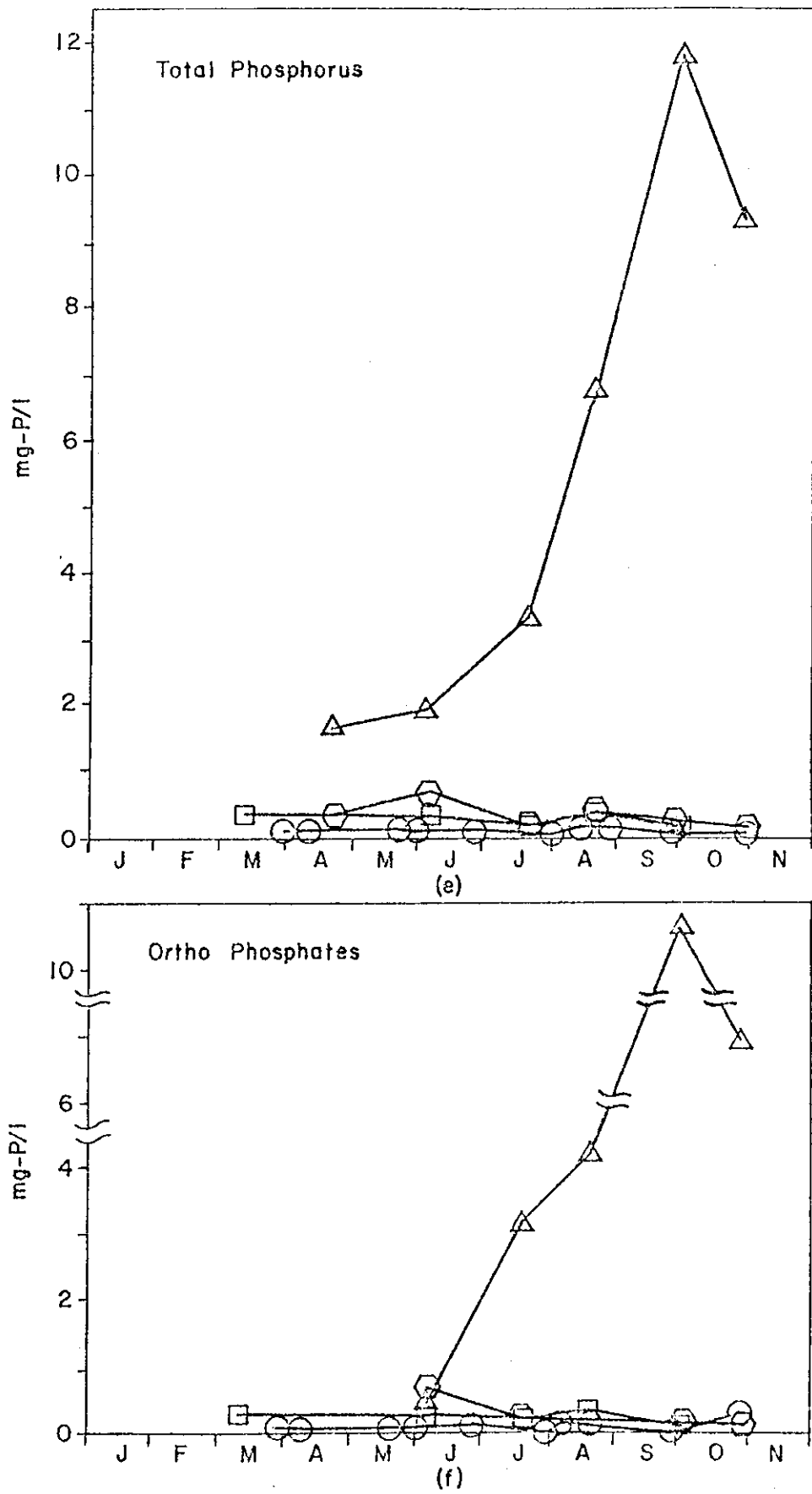
Figure 58 - continued.

The relative abundance of phosphorus in the sewage dome is a reflection of the low N/P ratio found in the sewage waste and possibly the anaerobic conditions favorable to denitrification.

Cypress Dome Sediments

Chemical analyses of cypress dome sediments obtained in November, 1974, some 8 months after pumping began, are given for the four cypress domes in Figure 59. Neither nitrogen nor phosphorus is significantly higher in the sediments of the experimental Sewage Dome although sodium and potassium are shown to have accumulated there to some degree. On the other hand, calcium and magnesium are highest in the dome receiving groundwater. Inspection of the water chemistry data in Table 22 reveals the concentrations of these four major cations in the standing water to be consistent with these results for the sediments. Percent volatile solids as a measure of the organic fraction are also given in Figure 59. The results show a considerable inorganic fraction accompanying the Sewage Dome sample while the sample from the natural dome at the Owens-Illinois site may not have included all of the organic layer.

Figure 60a gives the total amount of sediments sampled on an areal basis. Differences in sampling depths may account for the ranges in inorganic matter collected; if the thin organic layer of detritus was completely sampled, total organic matter was highest in the Groundwater Dome. Figure

Figure 59. Averages and standard deviations of nutrient
          levels and volatile solids in sediments from
          experimental and control cypress domes. Dome
          notation is as follows: S - Sewage Dome,
          G - Groundwater Dome, O-I - Owens-Illinois
          Control Dome, and AC - Austin Cary Control
          Dome. All sample analyses except nitrogen
          and percent volatile solids done by Univer-
          sity of Florida Soils Analytical Lab.
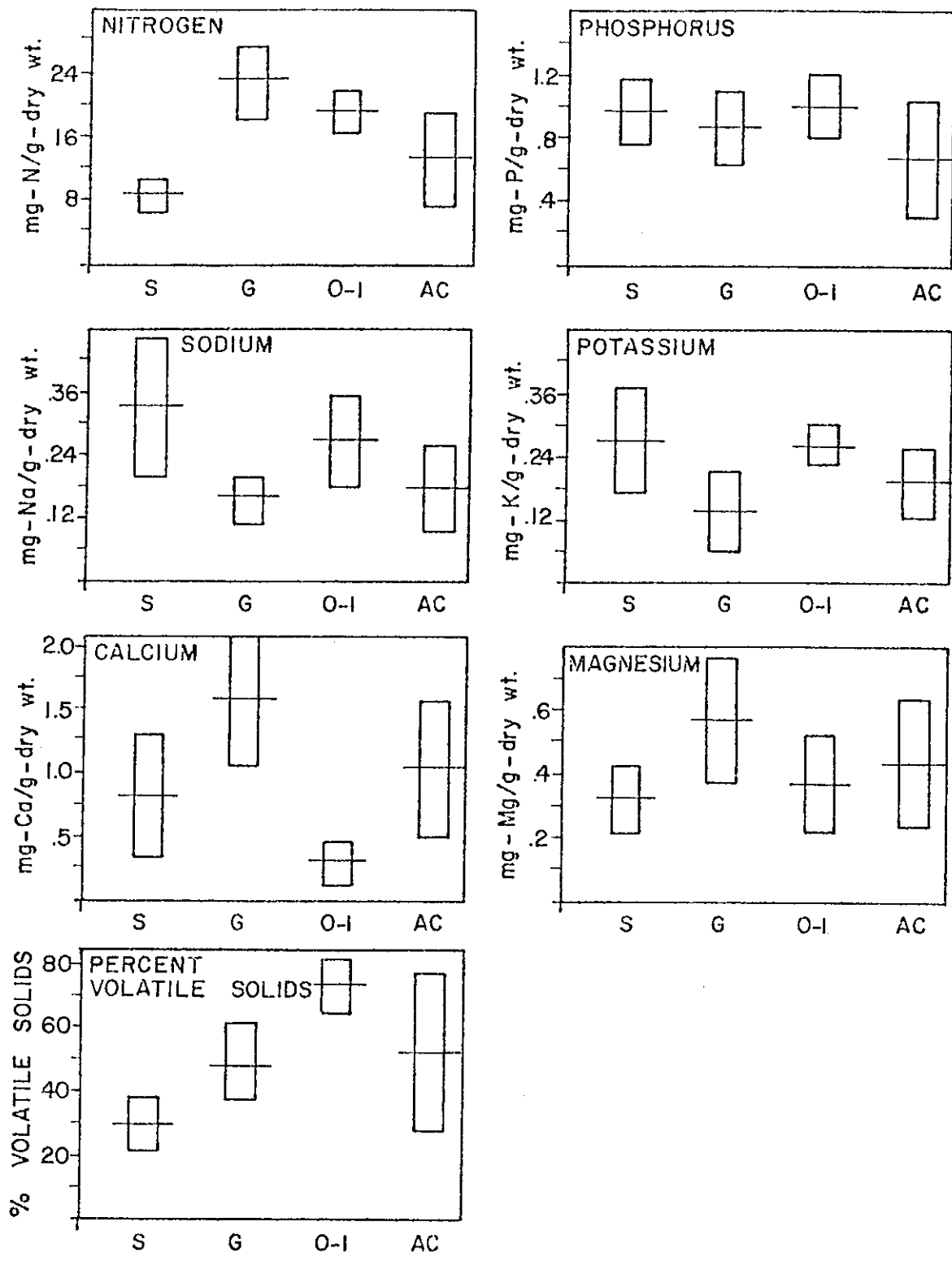
Figure 60. Sediment sample results from experimental and
control cypress domes showing (a) total amount
of organic and inorganic sediments sampled
in kg-dry wt/m^2, and (b) total nitrogen and
total phosphorus sampled in kg/m^2. Sample
depths were to the point where sediment com-
paction resisted the sampler, generally 10
to 20 cm deep. Dome notation is as in
Figure 59.

(a)

(b)
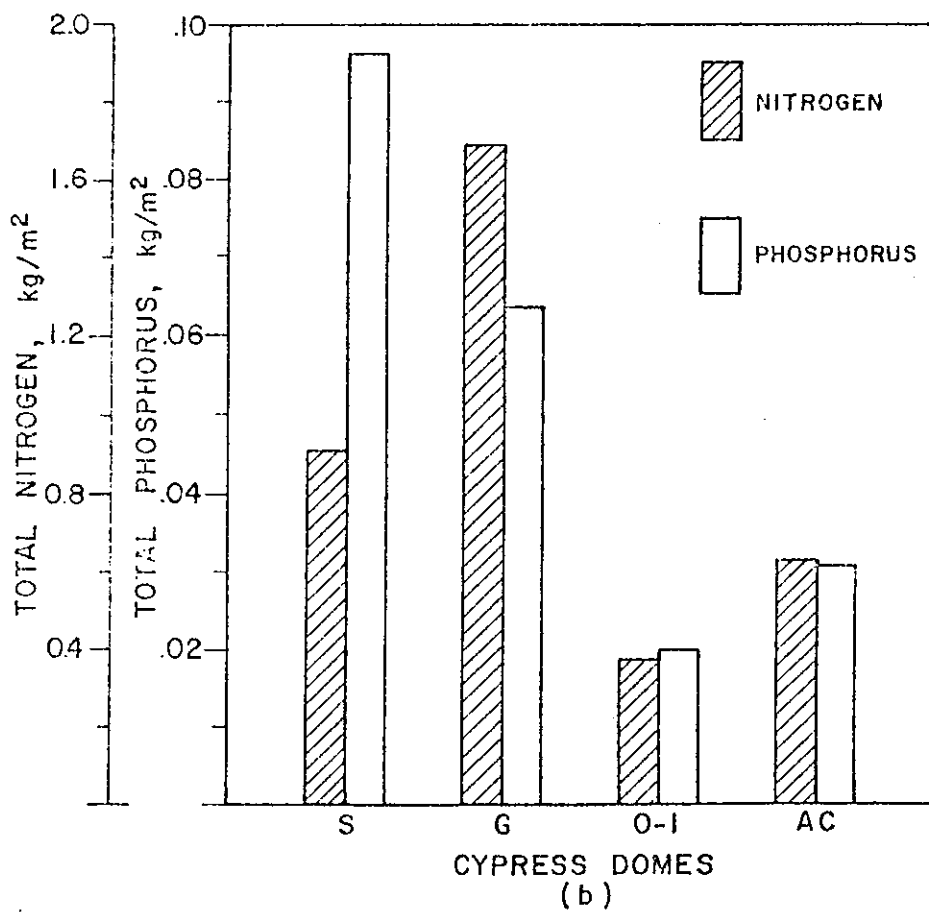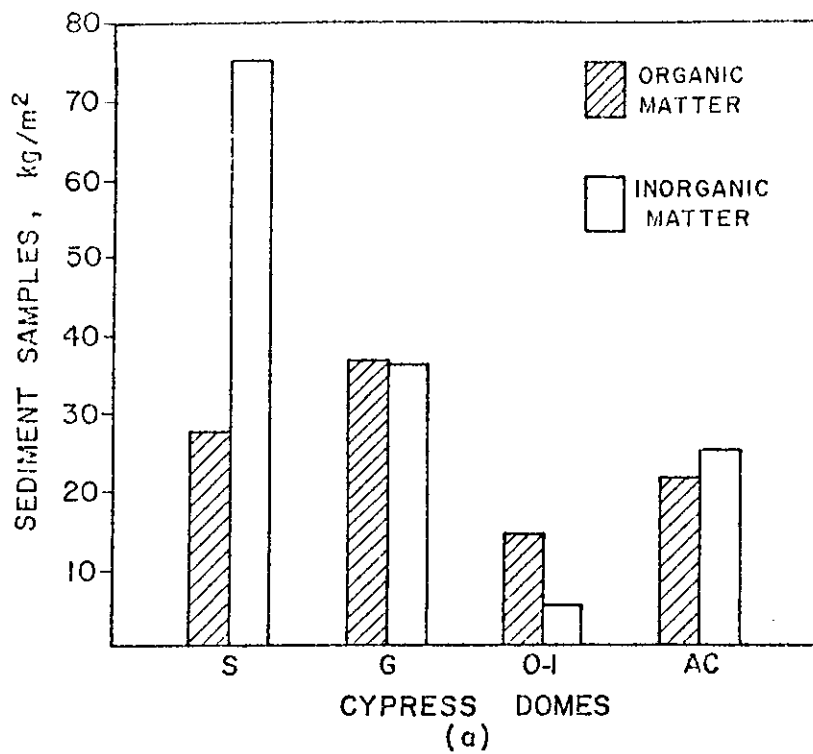
60b gives the total nitrogen and phosphorus on an areal basis (concentrations given in Figure 59 are multiplied by the sample size in Figure 60a). If similar sampling depths were used, the data indicate considerable accumulation of both nitrogen and phosphorus in the sediments of the Sewage Dome and the Groundwater Dome. There is a question, however, of whether the large sample sizes in the Sewage and Groundwater Domes reflect higher depositions or just a greater sampling depth. The latter situation was difficult to control due to the standing water and the nebulous sediment-water interface.

Figure 61 presents nutrient profiles found in the sewage dome sediments by Coultas prior to the effluent pumping. Note the high clay layer near 90 cm depth which impedes ground-water percolation. The nutrient levels of the top two samples, roughly analogous to the sampling depth of the previously pre-sented results, average 0.45 mg-P/g-dry wt and 11.2 mg-N/g-dry wt. When compared with the concentrations given in Figure 59 after 8 months of sewage application, a slight decrease of 20% in nitrogen is noted while phosphorus has increased 109%. It should be kept in mind, however, that different laboratory and field methods were used to generate these two sets of numbers. The graphs in Figure 61 give average concentrations of 0.26 mg-P/g-dry wt and 3.17 mg-N/g-dry wt for the top 100 cm, assumed here as the predominant root zone in the dome.

Figure 61.   Nitrogen and phosphorus soil profiles for
              the Sewage Dome prior to effluent applica-
              tion (data from Coultas, 1974).
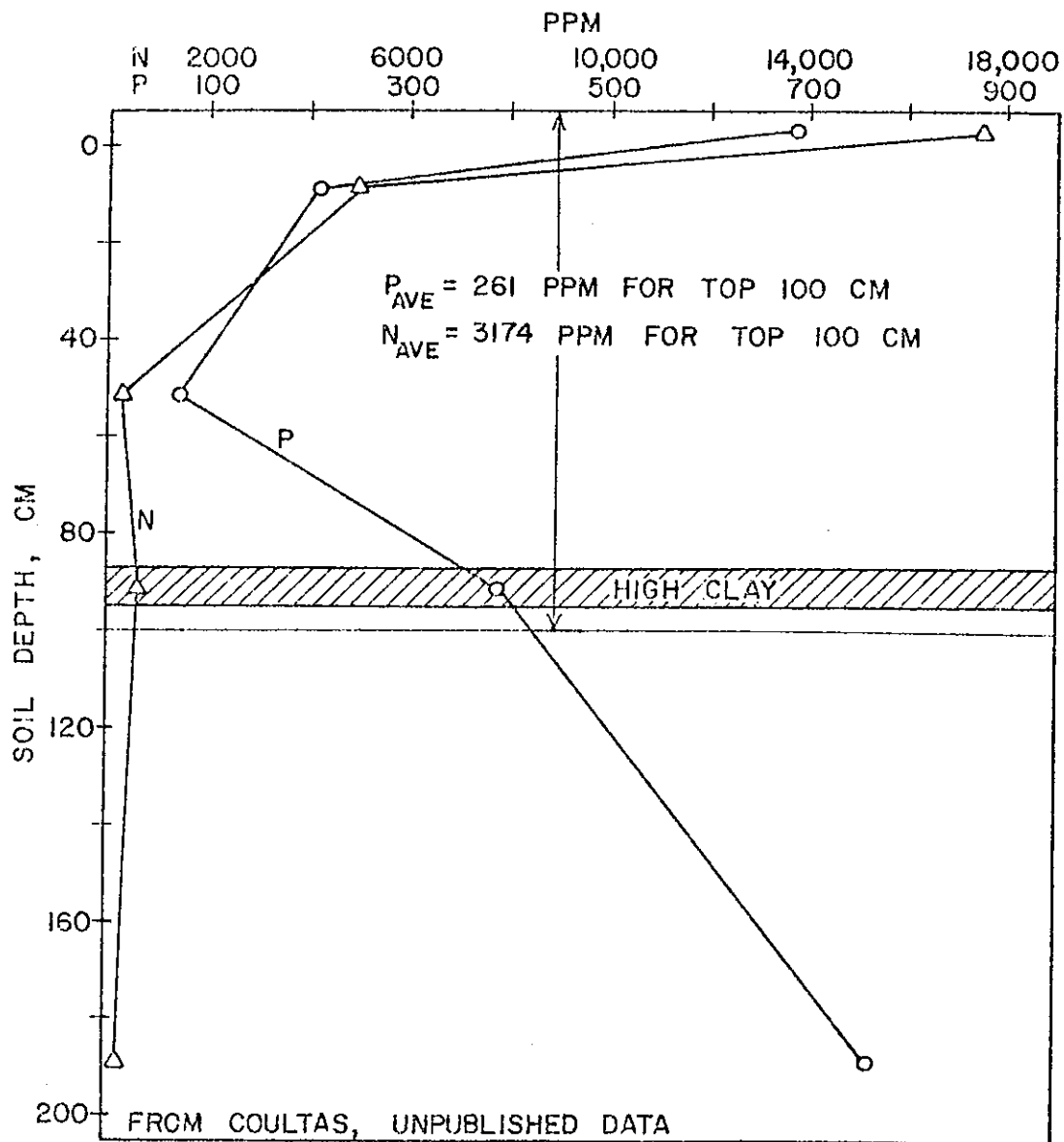
PPM

| N | 2000 | 6000 | 10,000 | 14,000 | 18,000 |
| P | 100 | 300 | 500 | 700 | 900 |

$P_{AVE} = 261$ PPM FOR TOP 100 CM

$N_{AVE} = 3174$ PPM FOR TOP 100 CM

P

N

HIGH CLAY

SOIL DEPTH, CM

FROM COULTAS, UNPUBLISHED DATA

Systems Analysis of Nutrient Disposal in Cypress Wetlands and Lake Ecosystems in Florida.
Volume 2
CFW 75-15

by
William J. Mitsch

Cypress Dome Model

The model simulated for the cypress dome system is shown in Figure 62. As with the lake model, it is a more detailed conception of the preliminary model shown in Figure 6, although it has less detail than the complex model shown in Figure 8. It was designed to deal with several management questions involving cypress domes, including the optimum rate of harvesting, possible effects of fire, and the disposal of secondary sewage.

The model was divided into two autotrophic components, the cypress trees and the understory plants. The sediment storage in Figure 62 is shown to consist of nitrogen, phosphorus, organic peat, and water. The model was designed to run for 10 to 100 years, so annual variations in solar radiation were ignored. Likewise, such flows as litterfall and gross primary production were determined from yearly averages. Two pathways for decomposition were designed into the model, their operation dependent on the water level.

Fire was simulated as a pulse of varying frequency from outside the system and was designed to have an effect on the dome only if the water level was low compared with the organic deposits. Should both low water and a fire pulse occur, the dome would burn with an intensity related to the understory and peat build-up and inversely to the water level. It is this intensity, in turn, which burns the cypress trees. When the intensity exceeds a certain threshold, cypress trees will be killed.

Figure 62.   Model of cypress dome used in simulation.
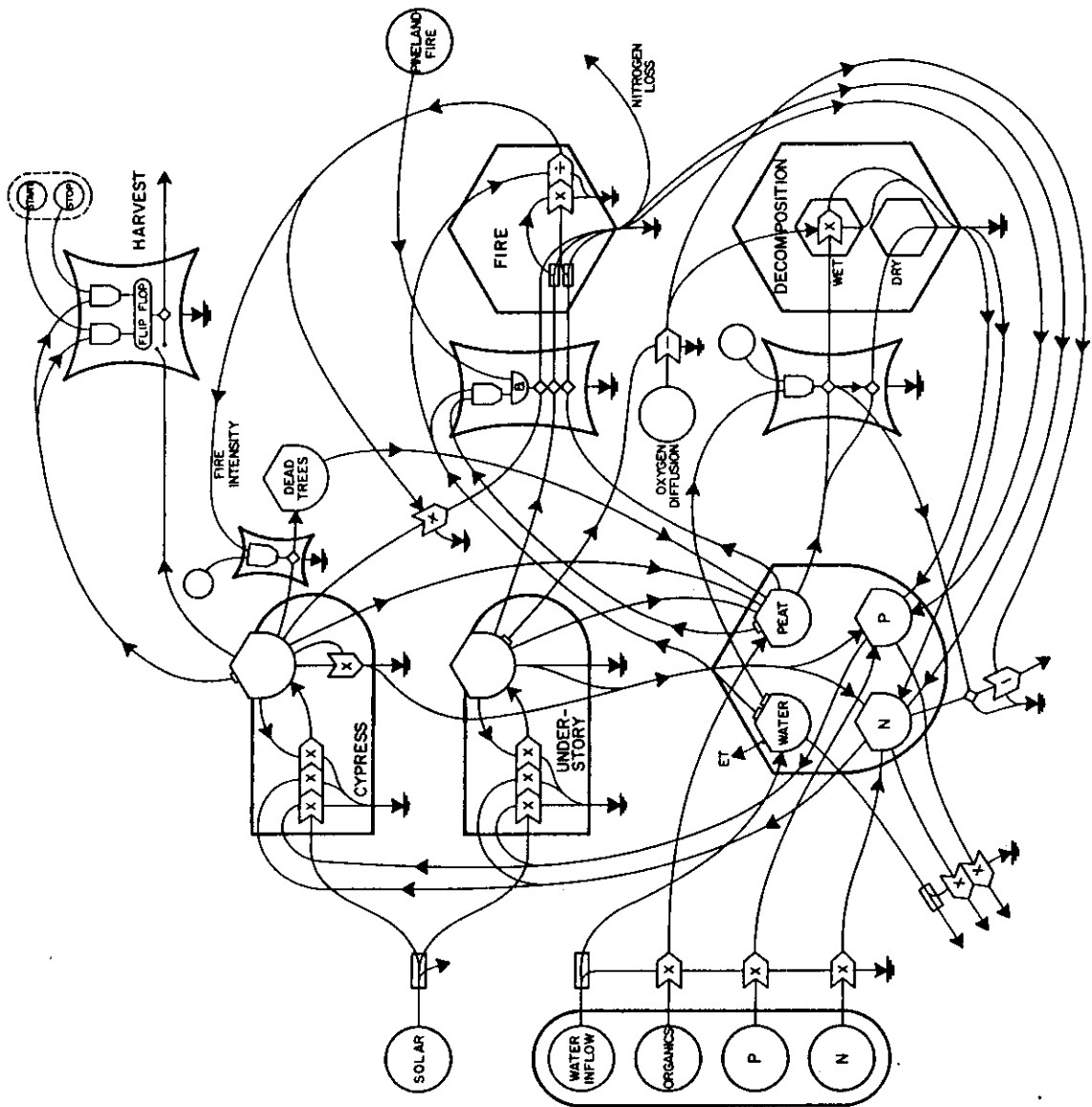
Harvesting of cypress wood was modeled such that the biomass at which harvesting begins and a lower value at which it stops can be programmed as external variables. The difference between the two thresholds is the harvest yield.

Primary productivity in this model was limited by the "J_r" limiting factor concept as presented in Figure 13e. Two versions were used in the simulations and are presented in Figure 63. The first, or nonstratified approach (Figure 63a), assumes equal competition for sunlight between the two autotrophic compartments in the model. A second scheme, shown in Figure 63b, assumes stratification of sunlight with the cypress canopy having a competitive advantage. Each plant compartment can utilize 5% of the flow that is available to it.

Table 23 gives the initial conditions or steady state values for the storages and flows in Figure 62. Figure 64 summarizes the nitrogen and phosphorus flows for a cypress dome under natural conditions. Table 24 gives the differential equations used for the model. (See Appendix C.)

Simulation was accomplished on two EAI-580 analog computers slaved together. Magnitude scaling was accomplished according to the methods outlined in the previous chapter. The necessary analog patching diagram as well as the coefficient values and scaled pot values are given in Appendix C.

Simulation Results

Simulation results for the model shown in Figure 62 are given in Figures 65 through 75. Figure 65 shows an

Figure 63.   Sunlight limitation models used in simula-
             tion of cypress dome model of Figure 62:
             (a) nonstratified case in which neither
             autotroph has competitive advantage;
             (b) stratified approach in which cypress
             has shading advantage over understory.
             Numbers in parentheses are relative amounts
             of sunlight used as initial conditions for
             each case.
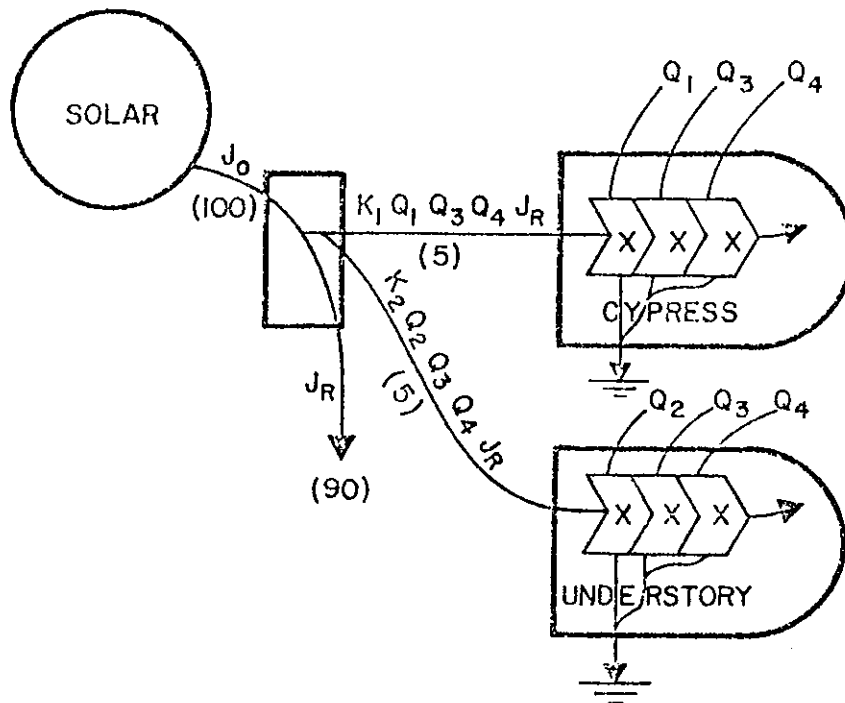
(a)
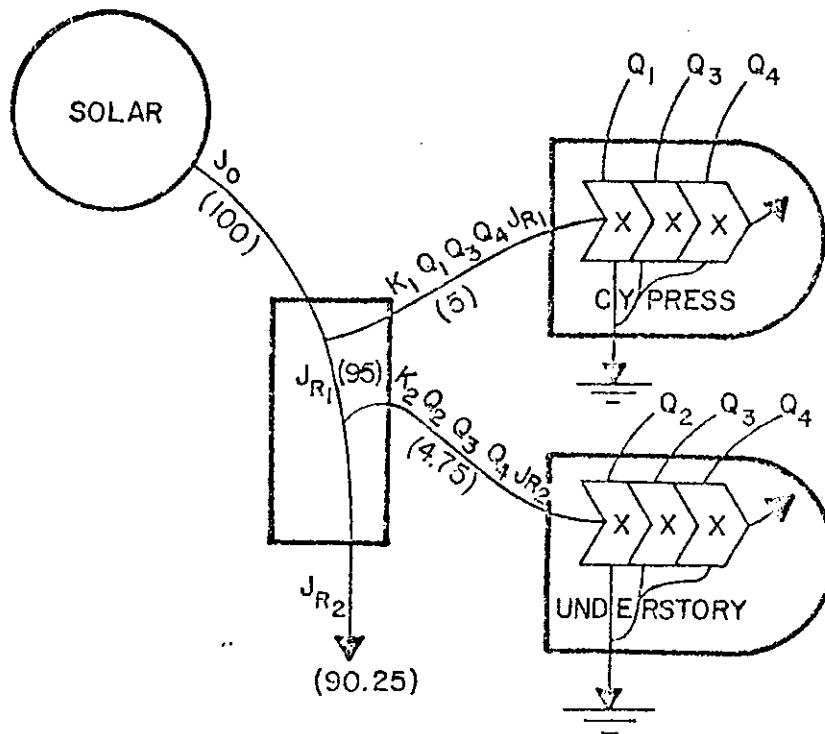
(b)

Table 23

STORAGES AND PATHWAYS FOR CYPRESS DOME MODEL SHOWN IN FIGURE 62

Parameter	Note in App. C	Description	Value	Source
Q_1	1	Cypress Biomass	68,000 kcal/m^2	Table 15
Q_2	2	Understory Biomass	400 kcal/m^2	Fig. 57, Ewel & Mitsch (1974)
Q_3	3	Nitrogen Storage	4160 g/m^2	Fig. 61, Coultas (1974)
Q_4	4	Phosphorus Storage	340 g/m^2	Ibid.
Q_6	5	Water Storage	0.32 m^3/m^2	Cutright (1974), Ordway
Q_7	6	Organic Storage	78,000 kcal/m^2	Coultas (1974), Brady (1974), Fig. 60
Q_8	7	Dead Cypress	0.0	Assumption
$k_3 Q_1 Q_3 Q_4 J_r$	8	Cypress Gross Primary Production	3277 kcal/m^2-yr	Cowles (1974), Table 15
$k_5 Q_1^2$	9	Cypress Respiration	1721 kcal/m^2-yr	Table 18, Table 15; assumes R=GPP-NPP
$k_7 Q_1$	10	Cypress Litterfall	1214 kcal/m^2-yr	Table 15
$k_8 Q_1 Q_2 Q_7 / Q_6$	11	Cypress Biomass Lost to Fire	1/k = 10 days	Estimated turnover time
$k_9 Q_1$	11	Cypress Harvest	$t_{1/2}$ = 4 days	Estimated half life

Table 23 - continued

Parameter	Note in App. C	Description	Value	Source
$k_4Q_2Q_3Q_4J_r$	12	Understory Gross Primary Production	2591 kcal/m^2-yr	Table 21
$k_{10}Q_2$	13	Understory Respiration	1295 kcal/m^2-yr	Assumed equal to 1/2 GPP
$k_{11}Q_2$	13	Understory to Organic Storage	1295 kcal/m^2-yr	Assumed equal to 1/2 GPP
$k_{13}Q_2$	11	Understory Biomass Lost to Fire	$1/k = 1$ day	Estimated turnover time
J_6	14	Organic Inflow	0-1700 kcal/m^2-yr	Brezonik et al. (1974)
$k_{57}Q_8$	15	Dead Cypress to Organic Storage	$1/k = 20$ yrs.	Estimated turnover time
$k_{15}Q_7J_7$	16	Underwater Site Decomposition	2464 kcal/m^2-yr	Table 21; total respiration minus understory respiration
$k_{16}Q_7$	16	Dry Site Decomposition	536 kcal/m^2-yr	Assumed dry to wet decomposition from field data
$k_{17}Q_7$	11	Organic Storage Lost to Fire	$1/k = 1$ day	Estimated turnover time
J_3	17	Water Inflow	7.9 m/yr	Table 12; value normalized for average rainfall year

Table 23 - continued

Parameter	Note in App. C	Description	Value	Source
$k_{18}Q_6$	18	Water Outflow	6.4 m/yr	Table 12
$k_{19}Q_6$	18	Evapotranspiration	1.5 m/yr	Table 12
J_7	19	Dissolved Oxygen	1.1 g/m^2	Table 21
J_4	20	Phosphorus Inflow	1.26 g-P/m^2-yr	Brezonik et al. (1974)
$k_{21}Q_4Q_6$	21	Phosphorus Outflow	0.0	Assume retention of nutrients in dome
$k_{22}k_3Q_1Q_3Q_4J_r$	22	Phosphorus Uptake by Cypress	0.36 g-P/m^2-yr	Phosphorus content of cypress
$k_{23}k_5Q_1$	23	Phosphorus Leaching by Cypress	0.19 g-P/m^2-yr	Ibid.
$k_{26}k_8Q_1Q_2Q_7/Q_6$	24	Phosphorus from Cypress Fire	--	Ibid.
$k_{24}k_4Q_2Q_3Q_4J_r$	25	Phosphorus Uptake by Understory	0.46 g-P/m^2-yr	Phosphorus content of understory plants
$k_{25}k_{10}Q_2$	26	Phosphorus Leaching by Understory	0.23 g-P/m^2-yr	Ibid.
$k_{27}k_{13}Q_2$	27	Phosphorus from Understory Fire	--	Ibid.
$k_{41}k_{15}Q_7J_7$	28	Phosphorus Recycle-- Wet Decomposition	0.34 g-P/m^2-yr	Phosphorus content of organic layer, Coultas (1974)

Table 23 - continued

Parameter	Note in App. C	Description	Value	Source
$k_{42}k_{16}Q_7$	28	Phosphorus Recycle--Dry Decomposition	0.07 g-P/m^2-yr	Ibid.
$k_{28}k_{17}Q_7$	29	Phosphorus from Organic Storage Fire	--	Ibid.
J_5	20	Nitrogen Inflow	10.3 g-N/m^2-yr	Brezonik et al. (1974)
$k_{29}Q_3Q_6$	21	Nitrogen Outflow	0.0	Assume retention of nutrients in dome
$k_{30}k_3Q_1Q_3Q_4J_r$	22	Nitrogen Uptake by Cypress	5.6 g-N/m^2-yr	Nitrogen content of cypress
$k_{31}k_5Q_1$	23	Nitrogen Leaching by Cypress	2.9 g-N/m^2-yr	Ibid.
$k_{36}k_8Q_1Q_2Q_7/Q_6$	30	Nitrogen from Cypress Fire	--	Assumes 60% loss of nitrogen
$k_{34}k_4Q_2Q_3Q_4$	25	Nitrogen Uptake by Understory	6.9 g-N/m^2-yr	Nitrogen content of understory plants
$k_{35}k_{10}Q_2$	26	Nitrogen Leaching by Understory	3.4 g-N/m^2-yr	Ibid.
$k_{37}k_{13}Q_2$	30	Nitrogen from Understory Fire	--	Assumes 60% loss of nitrogen, Lewis (1974)
$k_{39}k_{15}Q_7J_7$	28	Nitrogen Recycle--Wet Decomposition	12.3 g-N/m^2-yr	Nitrogen content of organic layer, Coultas (1974)

Table 23 - continued

Parameter	Note in App. C	Description	Value	Source
$k_{40}k_{16}Q_7$	28	Nitrogen Recycle--Dry Decomposition	2.6 g-N/m^2-yr	Ibid.
$k_{38}k_{17}Q_7$	30	Nitrogen from Organic Storage Fire	--	Assumes 60% loss of nitrogen, Lewis (1974)
$k_{32}Q_3Q_2$	31	Denitrification	8.1 g-N/m^2-yr @ $Q_2 = 4000$	Estimation from sewage dome nutrient balance

Figure 64.   Summary models for (a) nitrogen and (b)
             phosphorus flows in an undisturbed cypress
             dome.   Table 23 gives references and cal-
             culations.

Flows   g/m²-yr
Storages   g/m²

Nitrogen
(a)

Phosphorus
(b)
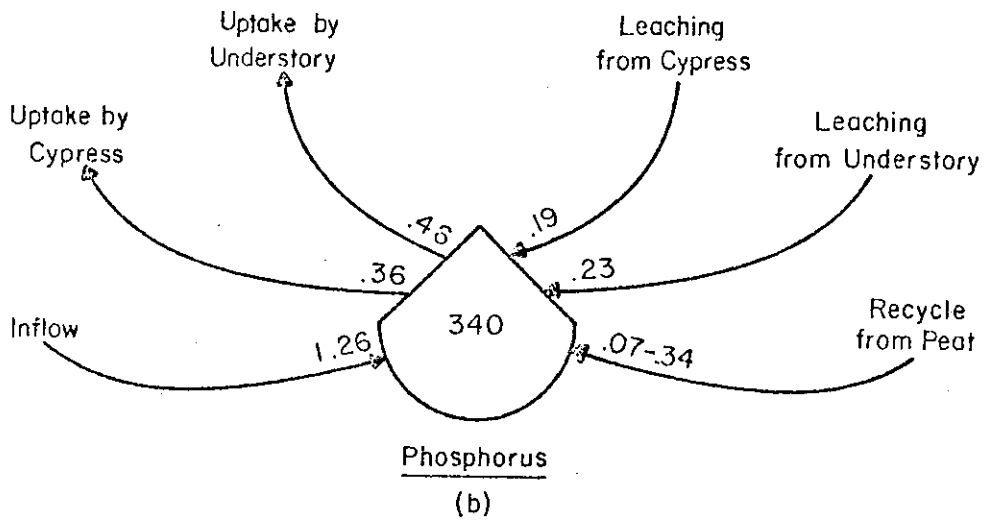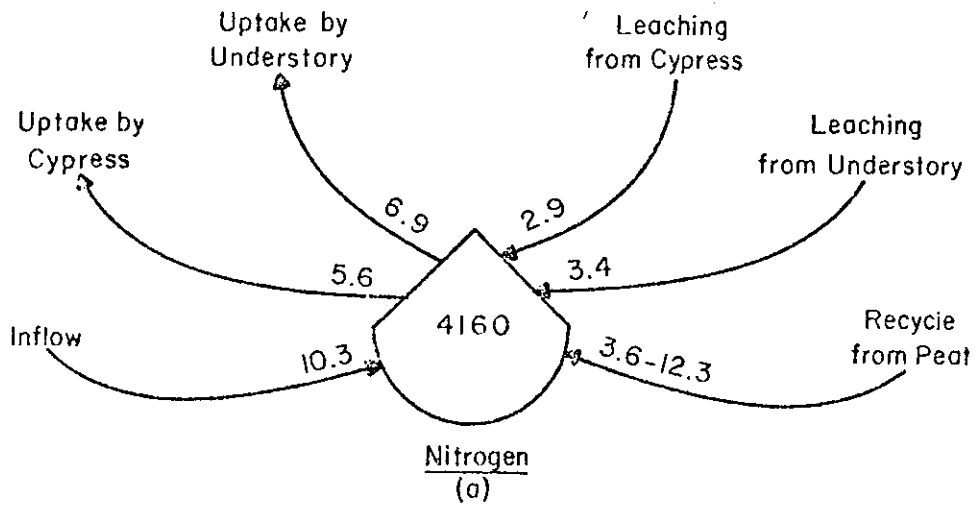
Table 24

DIFFERENTIAL EQUATIONS FOR CYPRESS DOME
MODEL IN FIGURE 62

Cypress

$$\dot{Q}_1 = k_3 Q_1 Q_3 Q_4 J_r - k_5 Q_1^2 - k_7 Q_1 - k_8 Q_1 \left(\frac{Q_2 Q_7}{Q_6}\right) - k_9 Q_1 - k_{56} Q_1$$

Understory

$$\dot{Q}_2 = k_4 Q_2 Q_3 Q_4 J_r - k_{10} Q_2 - k_{11} Q_2 - k_{13} Q_2$$

Nitrogen

$$\dot{Q}_3 = J_5 - k_{29} Q_3 Q_6 - k_{30} k_3 Q_1 Q_3 Q_4 J_r - k_{34} k_4 Q_2 Q_3 Q_4 J_r$$

$$+ k_{31} k_5 Q_1^2 + k_{35} k_{10} Q_2 + k_{39} k_{15} Q_7 J_7 + k_{40} k_{16} Q_7$$

$$- k_{32} Q_2 Q_3 + k_{36} k_8 Q_1 \left(\frac{Q_2 Q_7}{Q_6}\right) + k_{37} k_{13} Q_2 + k_{38} k_{17} Q_7$$

Phosphorus

$$\dot{Q}_4 = J_4 - k_{21} Q_4 Q_6 - k_{22} k_3 Q_1 Q_3 Q_4 J_r - k_{24} Q_2 Q_3 Q_4 J_r$$

$$+ k_{23} k_5 Q_1^2 + k_{25} k_{10} Q_2 + k_{41} k_{15} Q_7 J_7 + k_{42} k_{16} Q_7$$

$$+ k_{26} k_8 Q_1 \left(\frac{Q_2 Q_7}{Q_6}\right) + k_{27} k_{13} Q_2 + k_{28} k_{17} Q_7$$

Water

$$\dot{Q}_6 = J_3 - k_{18} Q_6 - k_{19} Q_6$$

Organic Peat

$$\dot{Q}_7 = J_6 + k_7 Q_1 + k_{11} Q_2 - k_{15} Q_7 J_7 - k_{16} Q_7 - k_{17} Q_7 + k_{57} Q_8$$

Dead Cypress

$$\dot{Q}_8 = k_{56} Q_1 - k_{57} Q_8$$

Table 24 - continued

Sunlight

$$J_o = J_r + k_1 Q_1 Q_3 Q_4 J_r + k_2 Q_2 Q_3 Q_4 J_r \quad \text{(nonstratified)}$$

or

$$J_o = J_{r2} + k_1 Q_1 Q_3 Q_3 J_{r1} + k_2 Q_2 Q_3 Q_4 J_{r2} \quad \text{(stratified)}$$

Figure 65.   Simulation results for cypress dome model
             shown in Figure 62 for undisturbed con-
             ditions.
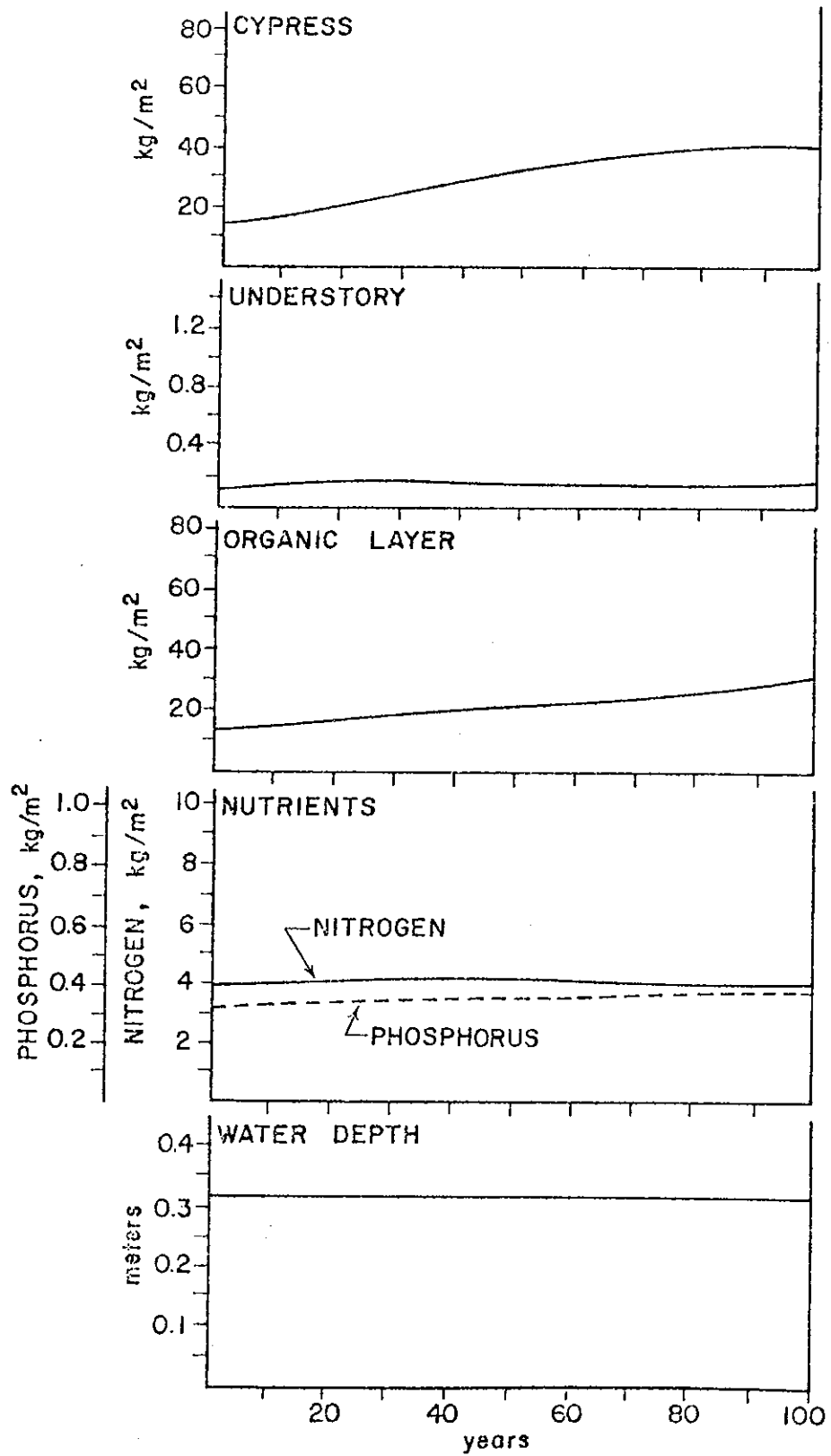
approximation to normal undisturbed growth of a cypress dome over a 100-year period. Cypress appears to be leveling off at around 40 kg/m^2, approximately three times its initial biomass (the biomass of the Sewage Dome). Understory biomass remained low, a situation that has been noted in undisturbed cypress domes in the Withlacoochee State Forest and often in South Florida (J. Browder, personal communication). Organic peat doubled in the 100 years to around 30 kg/m^2. Nutrients remained substantially unchanged, with a slight increase noted for phosphorus. Because of the generalized hydrologic parameters used in this model and because of a relatively rapid turnover, the water storage soon achieves steady state in this and all ensuing simulations.

Figures 66 and 67 give the results of simulated logging in the cypress dome. The first simulation is for harvesting of a young cypress dome for a yield of 10 kg/m^2. Harvesting occurs when the biomass reaches 15 kg/m^2 and stops when 5 kg/m^2 is remaining in this case. For an older cypress dome (Figure 67), the same yield is simulated for harvest thresholds of 40 kg/m^2 to 30 kg/m^2. Forty-five years is required for both of these domes to recover to the point where they can be harvested again. Note the rapid increase in understory biomass each time cypress is harvested.

By varying the lower threshold for stopping the harvesting, a family of curves was obtained showing a range of yields possible under the different regimes for both the large biomass and the small biomass domes. Simulations are not shown

Figure 66. Simulation results for cypress dome model
shown in Figure 62 for harvesting in a
young dome. Cypress is harvested when
biomass reaches 15 kg/m^2 and stops when
5 kg/m^2 is attained, giving a yield of
10 kg/m^2.
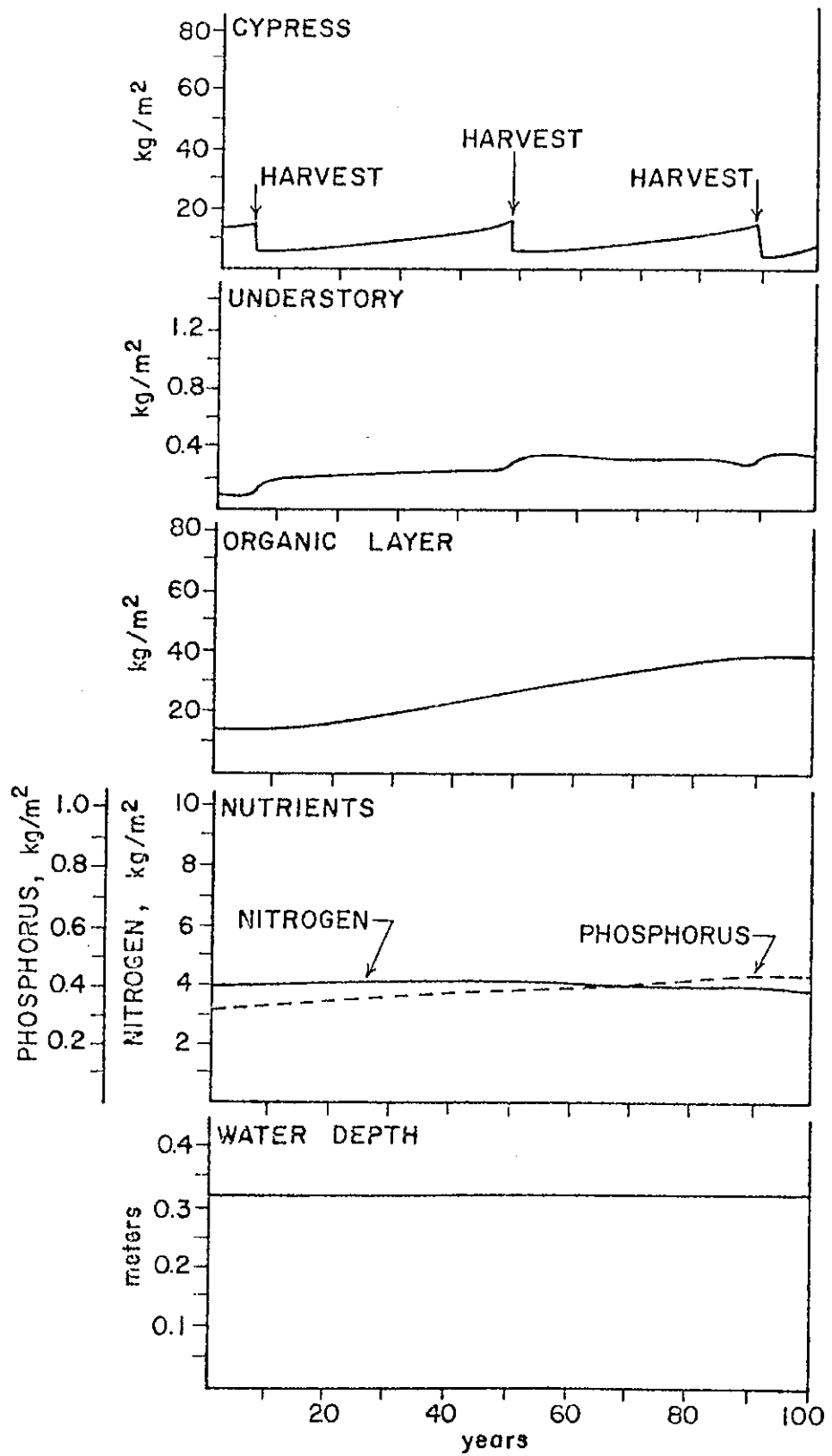
Figure 67.   Simulation results for cypress dome model
             shown in Figure 62 for harvesting of an
             older or more mature dome. Cypress is
             harvested when biomass reaches 40 kg/m^2
             and stops when 30 kg/m^2 is attained,
             giving a yield of 10 kg/m^2.
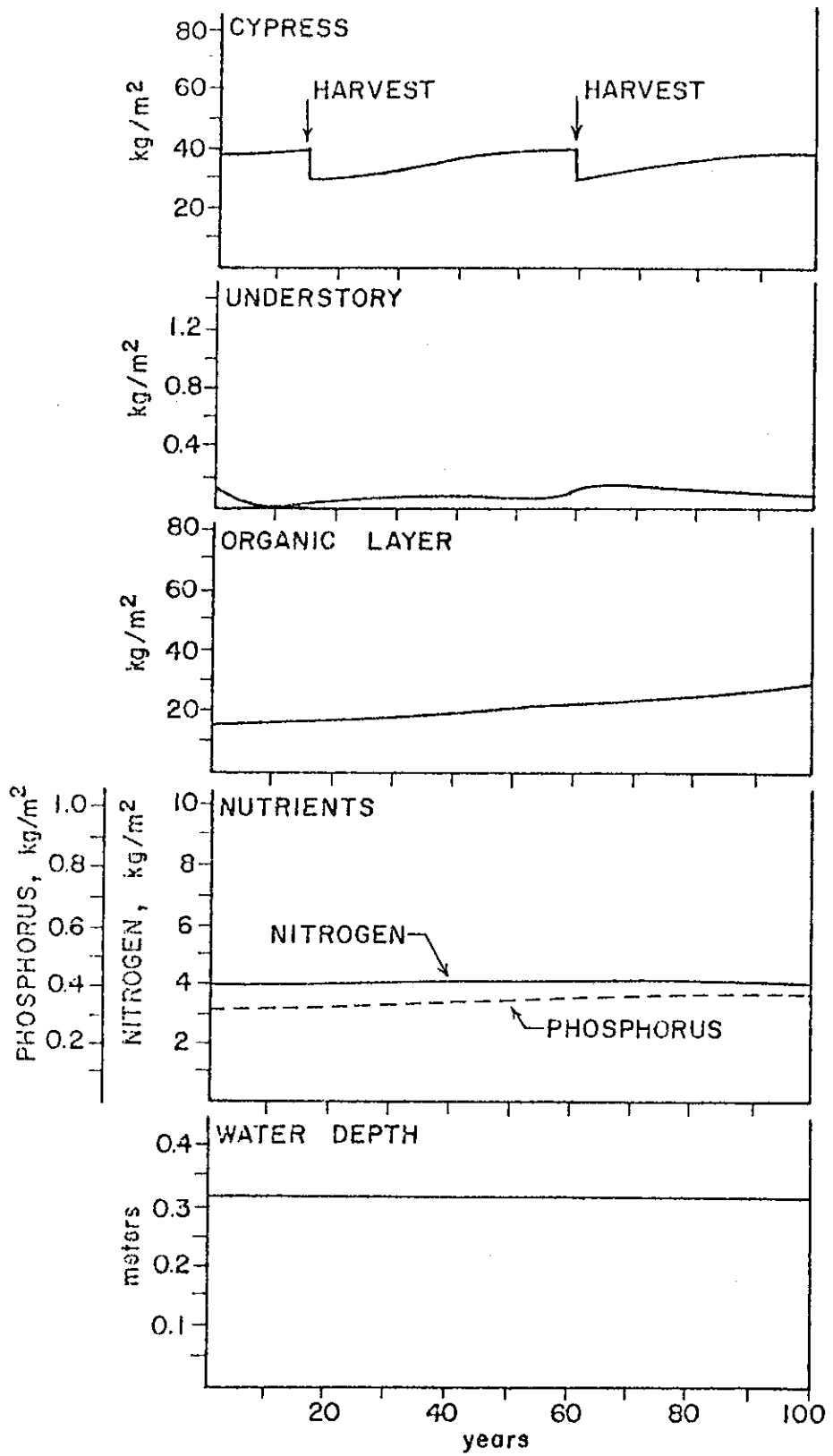
for these additional cases, but Figure 68 summarizes the relationships between yield, or biomass harvested, and the time which is required for the dome to recover to its harvestable threshold again. Note the decrease in recovery time of the young dome as larger yields are taken. The old dome, on the other hand, takes longer to recover from small yields but provides a much more dependable wood supply as yields over 9-10 kg/m^2 are harvested.

Figures 69 through 72 give simulations showing the effects of fire in a cypress dome. To simulate the proper conditions, water inflow was cut to one-third of its original value. Figure 69 shows the results of a fire occurring every 10 years, while Figure 70 gives a case where fire occurs only every 100 years. Fire had no significant adverse effect on cypress in either case. The recycling of nutrients and reduction in competition from the understory caused by fire every 10 years actually stimulated some additional cypress growth. This suggests a role of fire similar to that found in the more frequently burned pine flatwoods.

Figures 71 and 72 give results of simulations where fire is combined with cypress harvesting. In these cases, the fire intensity reaches a great enough threshold to kill many of the cypress trees. The harvesting allowed the understory to accumulate enough fuel to achieve such a hot fire. Dead cypress trees are shown to appear for the first time in these simulations and the understory reaches maximum values about ten times the initial conditions. This might suggest the

Figure 68.   Relationships between harvesting yield of
             cypress domes and time necessary for the
             dome to recover.   Points were obtained
             from simulations similar to those shown
             in Figures 66 and 67.
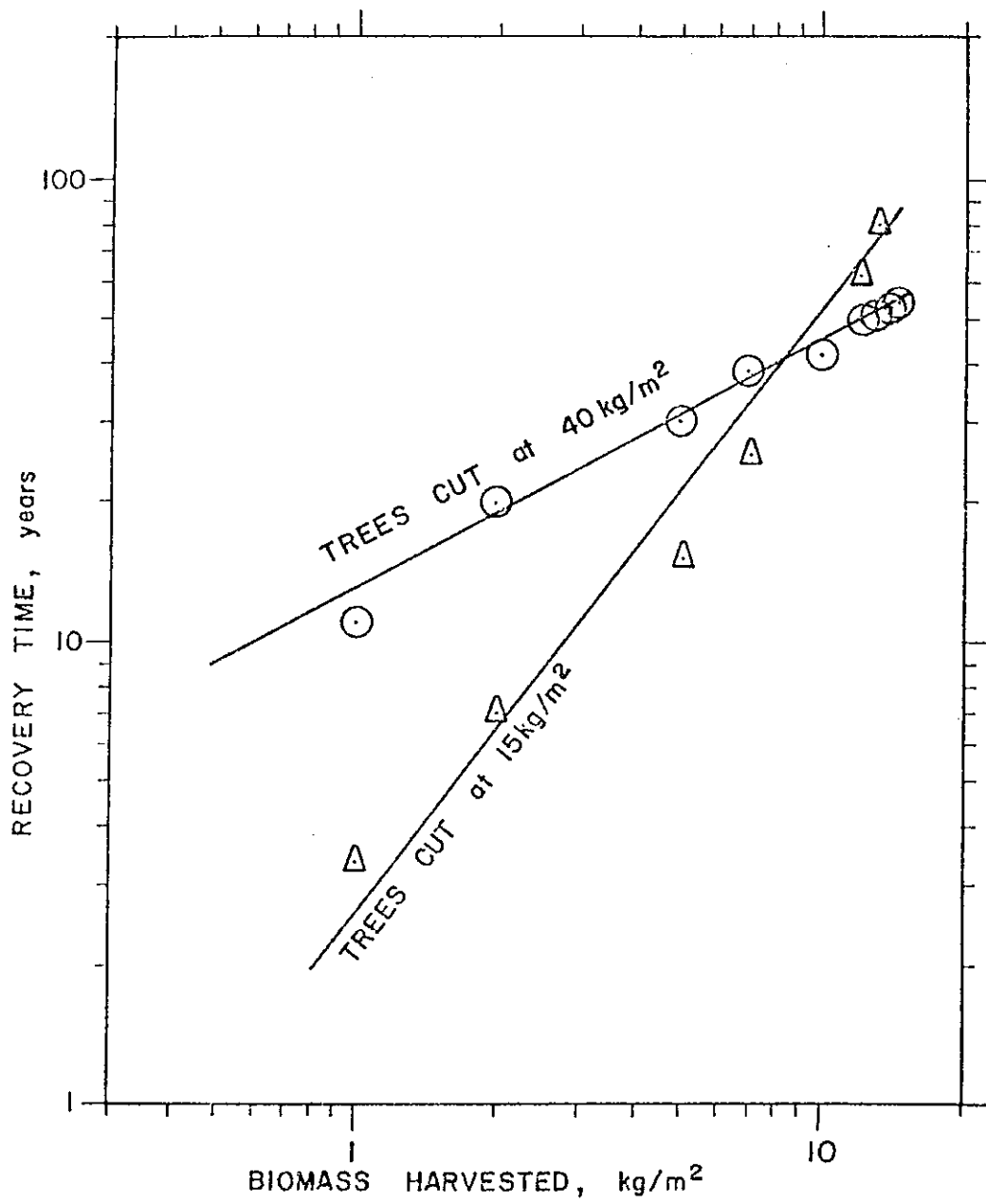
Figure 69.   Simulation results for cypress dome model
             shown in Figure 62 assuming fire occurs
             every 10 years.
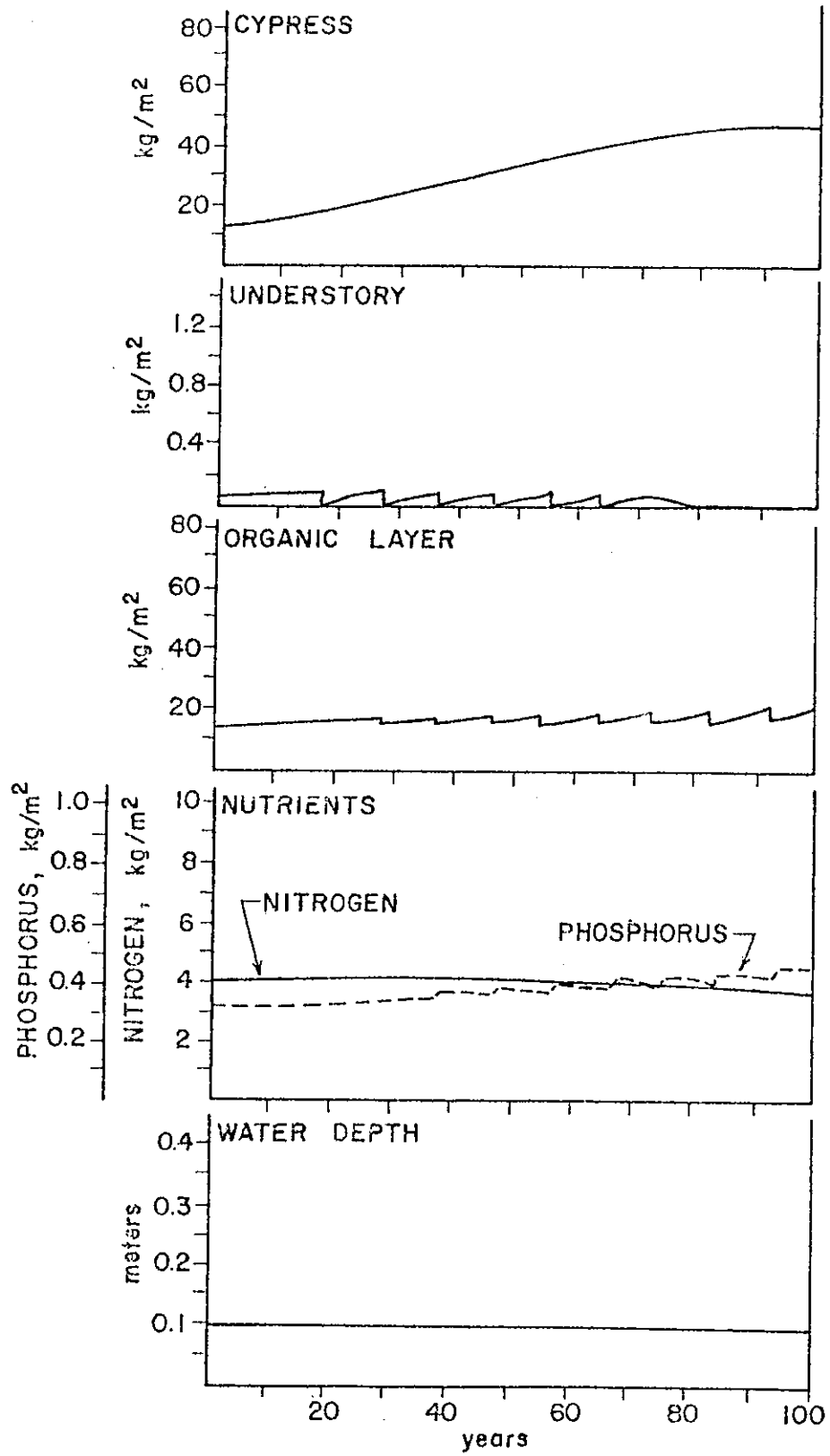
Figure 70.   Simulation results for cypress dome model
             given in Figure 62 assuming that fire occurs
             every 100 years.
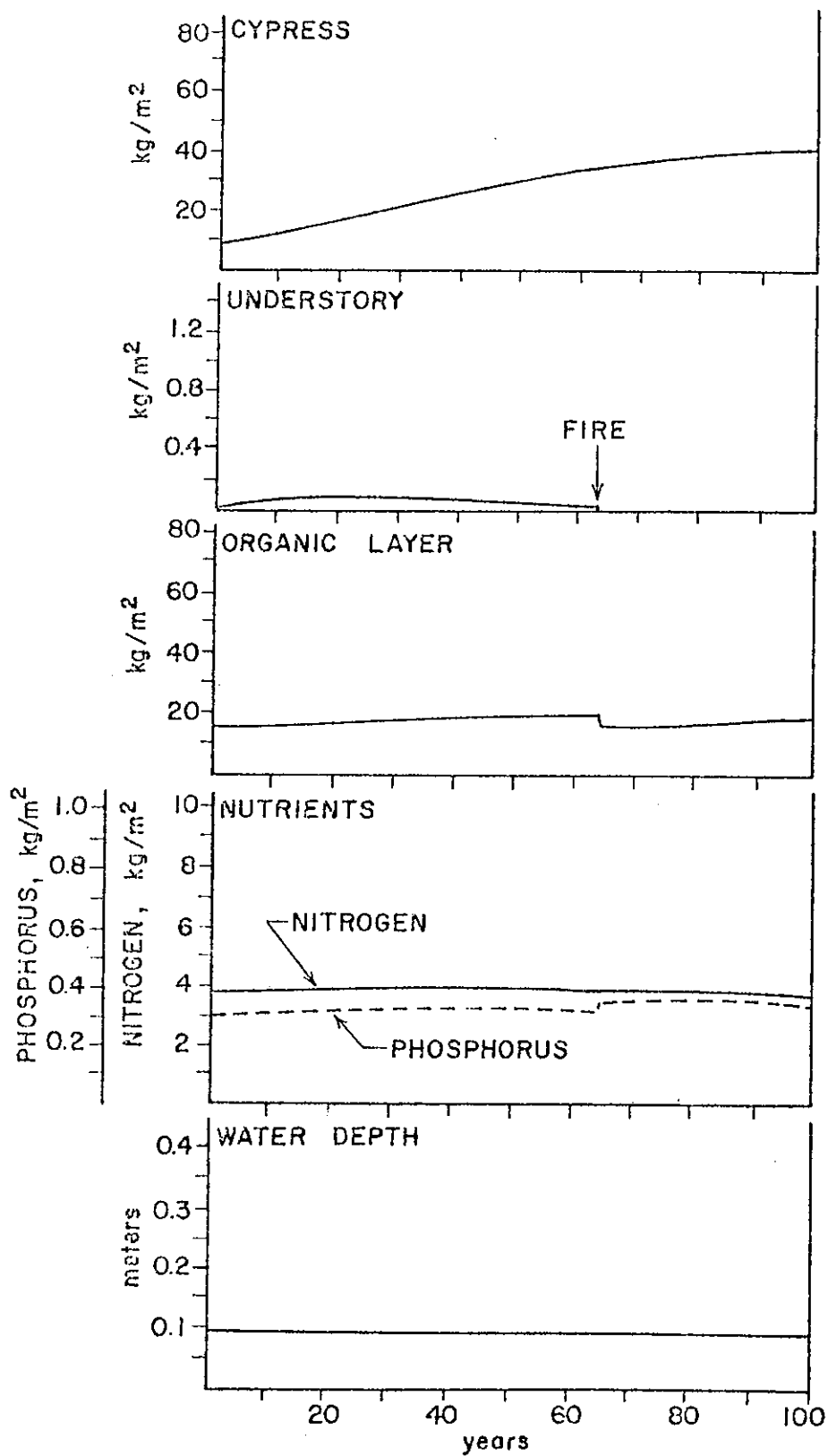
Figure 71.   Simulation results for cypress dome model
given in Figure 62 assuming a fire every
10 years combined with cypress harvesting
when a certain threshold of biomass is
achieved.
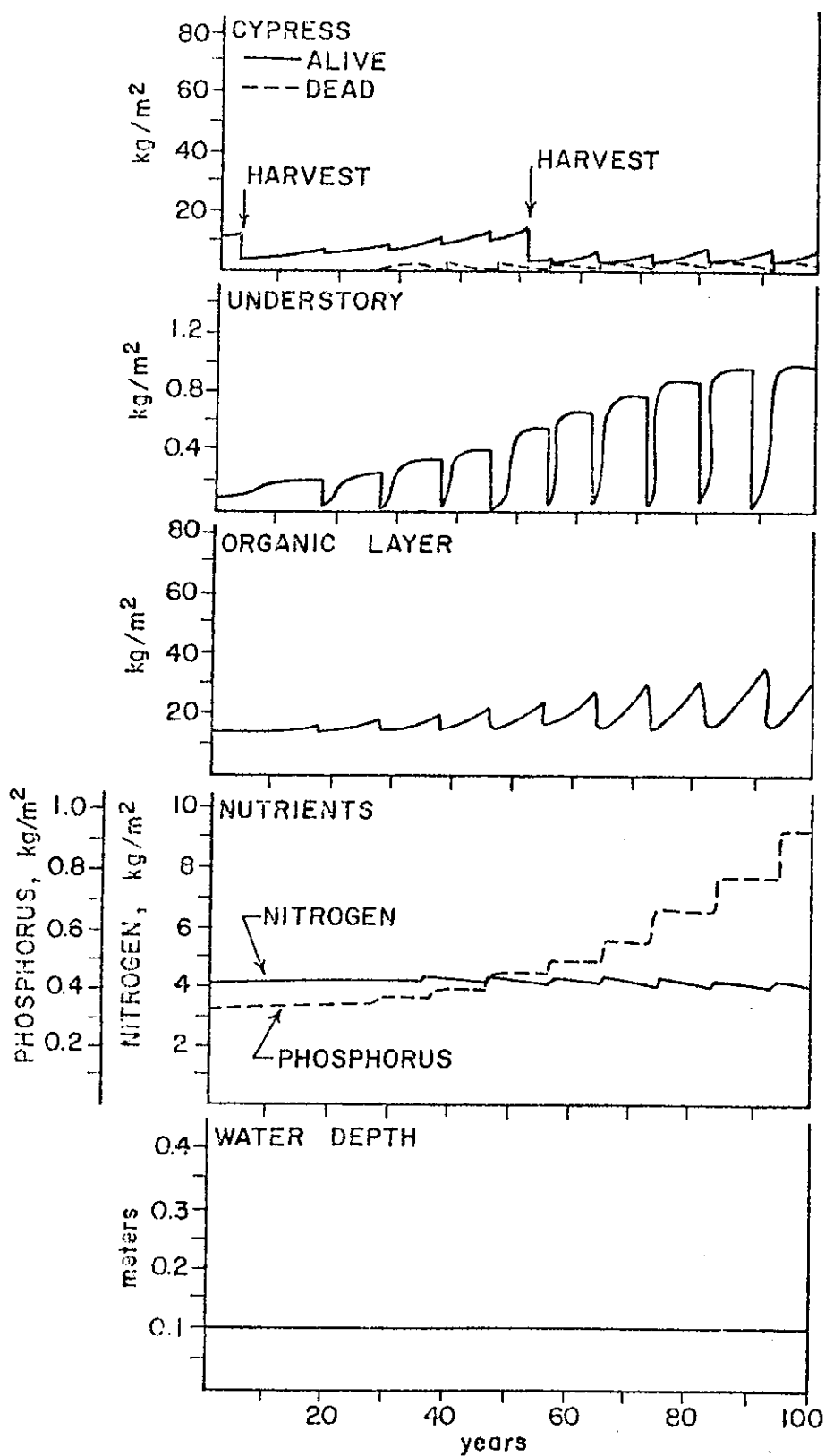
Figure 72. Simulation results for cypress dome model
            given in Figure 62 assuming a fire every
            100 years combined with cypress harvesting
            when a certain threshold of biomass is
            achieved.
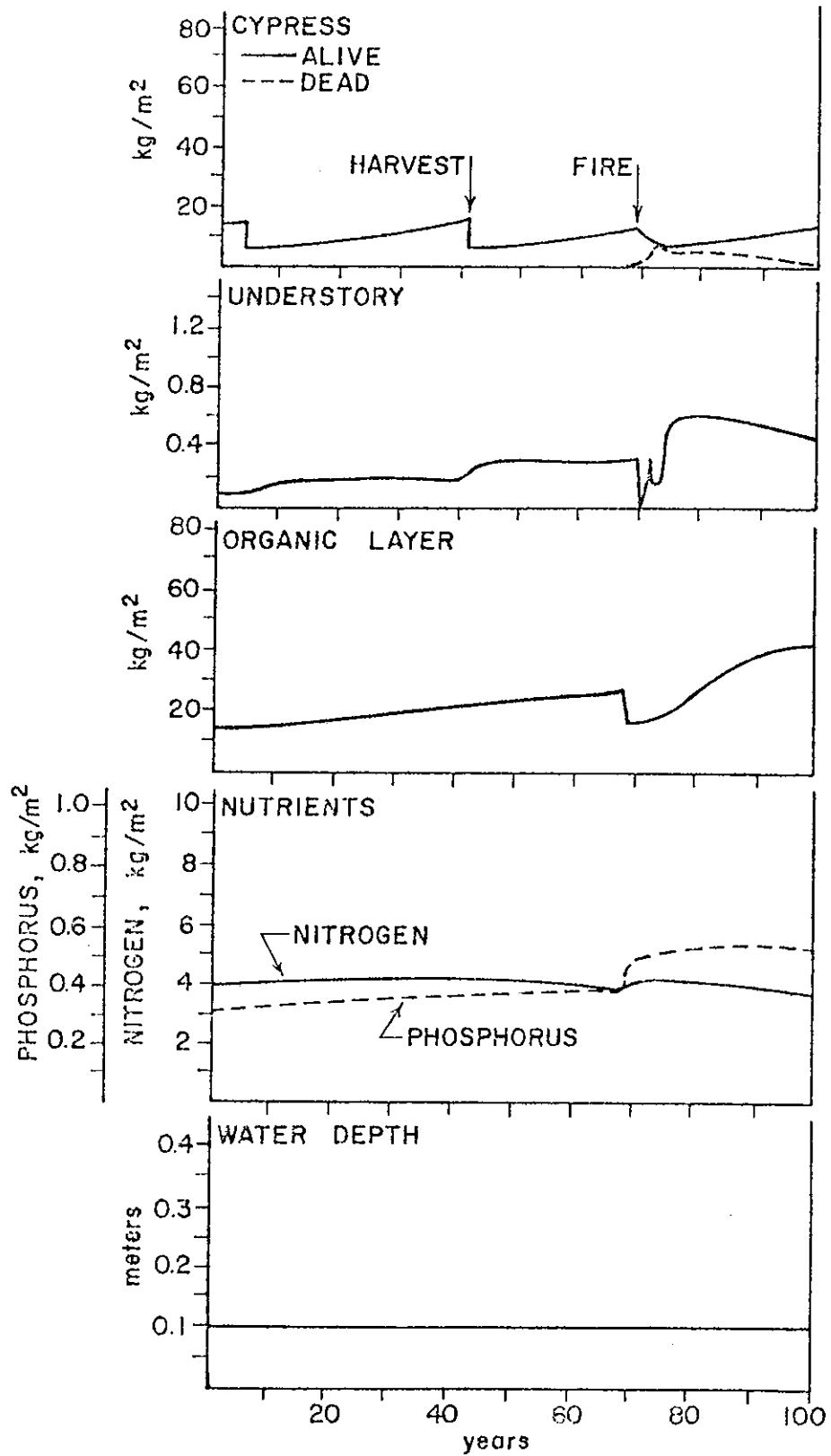
replacement of the cypress dome by a less structured marsh. Indeed, Wells (1928) suggests that fire will often change a cypress swamp into a "shrub-choked open swamp."

Addition of secondary sewage to the cypress dome was simulated for a 30-year period at application rates of 0, 1, and 2 in/wk. Nutrient concentrations of the additions were based on preliminary data by Overman. The results of the 0 and 2 in/wk applications for different sunlight conditions are given in Figures 73 and 74. One-inch applications achieved intermediate results in all cases and are not shown. The simulation was done twice to compare the effects of the two theories about sunlight limitation presented earlier. This turned out to be critical to the results of the simulations. Diagrams of the energy language interpretation of each limitation case are given in Figure 63. The difference, simply stated, is that in Figure 73 the cypress and understory have equal opportunities for capturing sunlight, while in Figure 74 the cypress intercepts most of the sunlight, filtering what is left to the understory.

The sunlight difference led to drastically different results. In the case where sunlight was equally available (Figure 73), the understory increased to five times its undisturbed value with little change noted in cypress production. Because of the increased productivity of the understory, the organic layer increased threefold over normal conditions. Phosphorus doubled in storage over the 30-year simulation period, while nitrogen actually showed a slight decrease.

Figure 73.   Simulation results for cypress dome model
             given in Figure 62 assuming both the addi-
             tion of secondary sewage at a rate of 2
             in/wk and no addition of sewage. Note the
             rescaling of cypress and time scales.
             This simulation assumes that cypress and
             understory vegetation do not compete for
             light as in the model of Figure 63a.
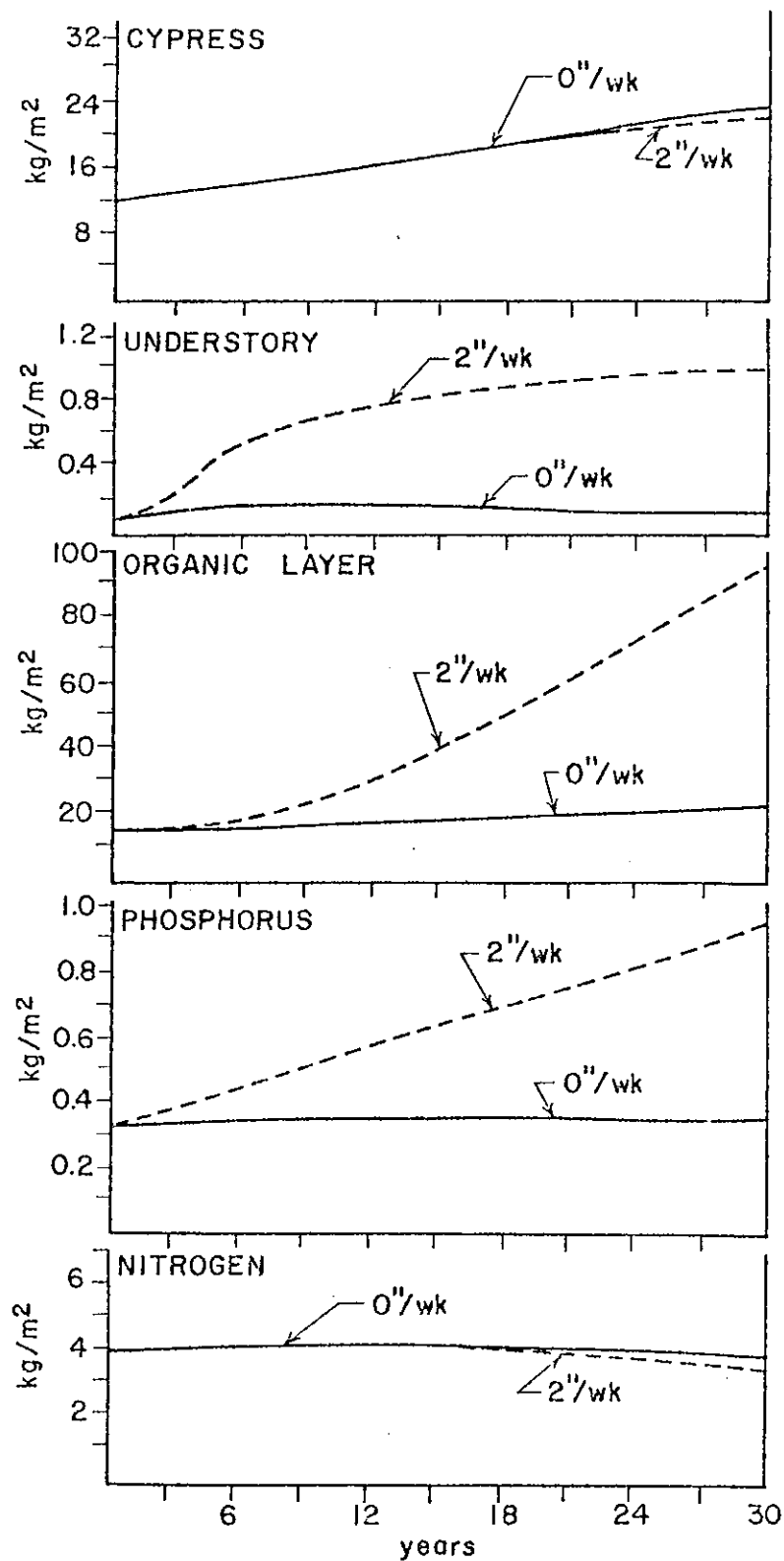
Figure 74. Simulation results for cypress dome model
given in Figure 62 assuming both the addi-
tion of secondary sewage at a rate of
2 in/wk and no addition of sewage. Note
rescaling of cypress and time scales.
This simulation assumes that cypress inter-
cepts sunlight first, filtering what is
left to the understory vegetation. This
competition is shown in energy language
in Figure 63b.
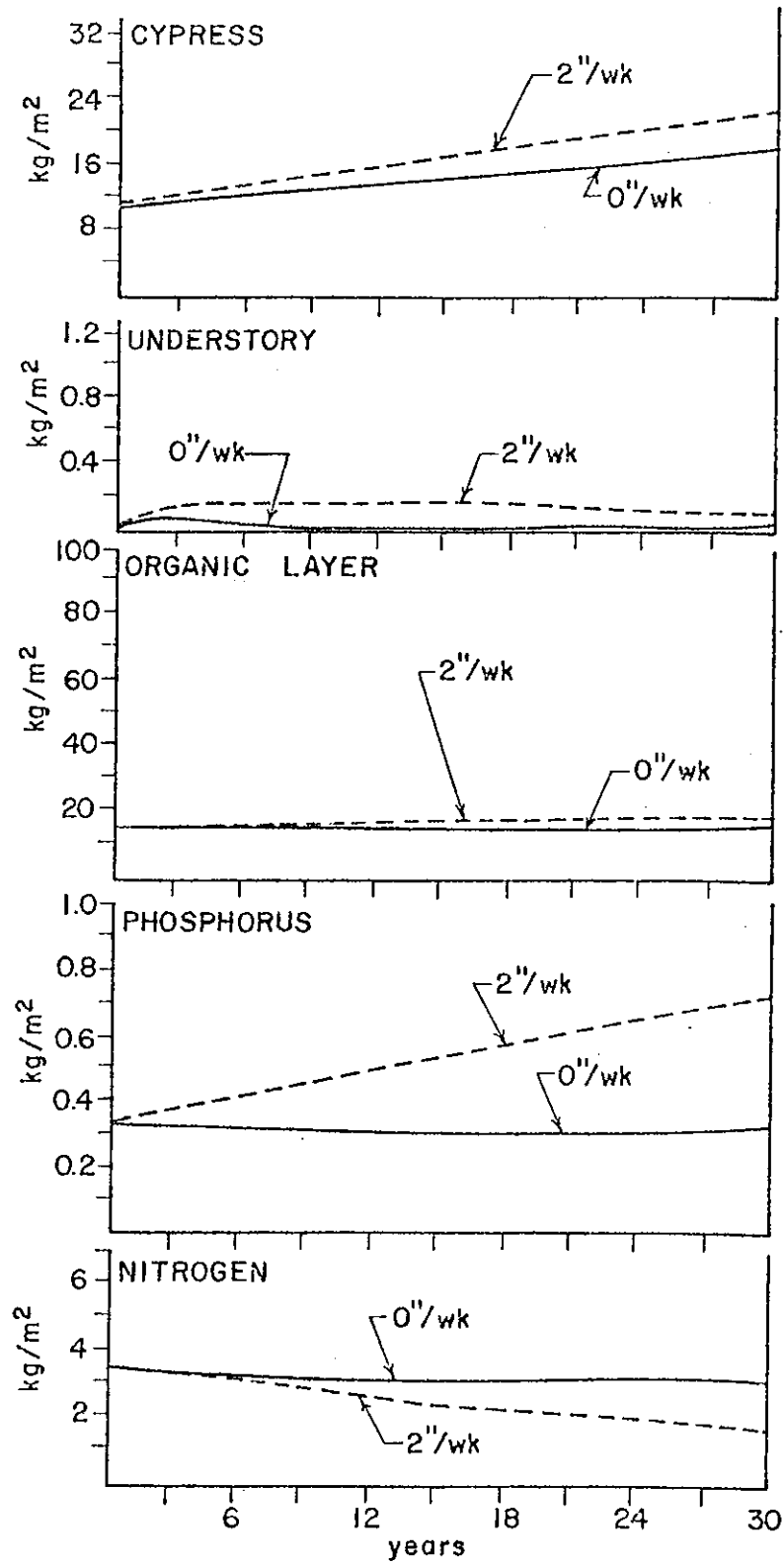
The effect of high phosphorus additions to an ecosystem in actually decreasing the nitrogen storage had been shown previously in models by Gilliland (1973).

The second simulation shown in Figure 74 gives significantly different results. In this simulation cypress production of wood increased by 25% for 1 in/wk and by 50% for 2 in/wk. The understory, while increasing some in this simulation, does not attain values similar to those of the previous case. Organic storage showed only a slight increase and phosphorus accumulated to 125% of the undisturbed value in 30 years. Nitrogen showed a greater decrease than in the previous case.

The differences between these two simulations are summarized in Figure 75. When the release of the sunlight limitation gives understory and cypress equal chances for the available nutrients (Figure 73), the understory species capable of fast turnover set up a rapidly spinning loop of biomass and peat build-up as shown in Figure 74. The cypress is outcompeted. However, when the cypress is given the advantage of shading as shown in the model of Figure 63b, the cypress is able to out-compete the understory and nutrients are stored in the cypress biomass, with little additional recycling through litterfall. Each case has its own merits and faults, and our real-life experiment will probably prove to be a compromise between these two models, should it be continued for this long a period.

Figure 75.   Major phosphorus flows and percent changes
             in storages resulting from the addition of
             2 in/wk secondary sewage as shown in the
             simulations in Figures 73 and 74:
             (a) summary of results obtained from the
             simulation assuming equal competition
             between cypress and understory; (b) summary
             of results obtained from the simulation
             assuming stratified shading by cypress.
             Percent changes are for the 30-year simu-
             lation period when results are compared
             with undisturbed conditions, and the wide
             arrows denote major pathways in each case.

(a)

(b)
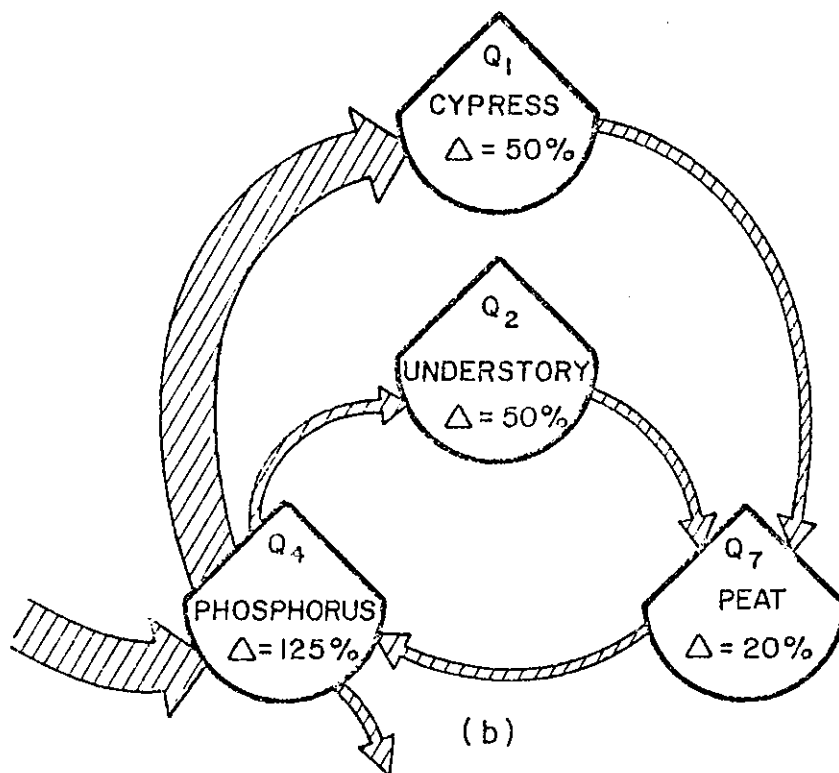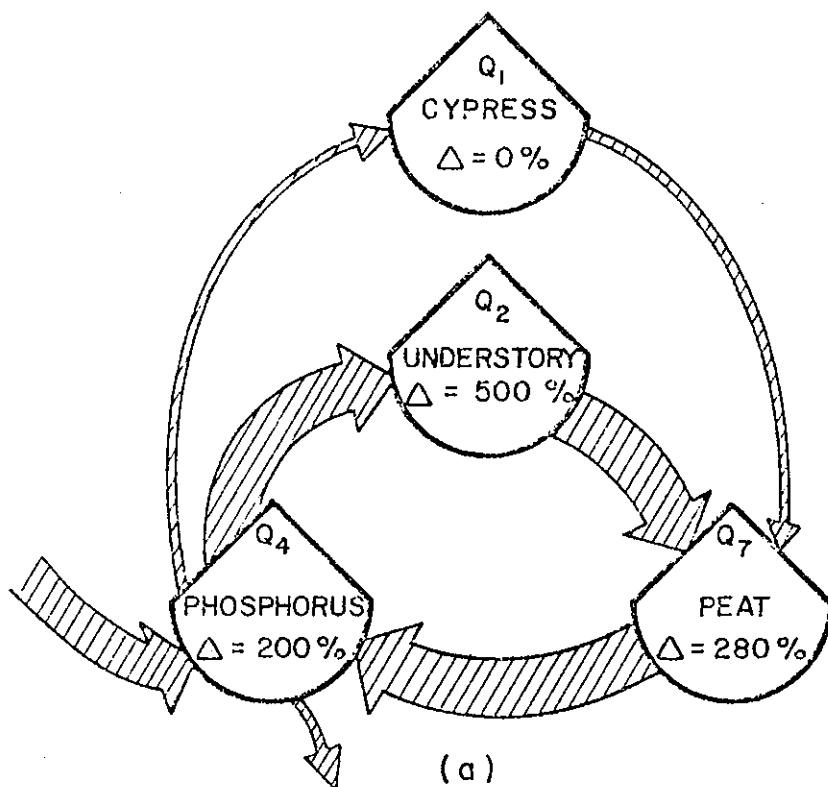
Cypress Pond Mini-Model

A mini-model, shown in Figure 76, concentrated on meta-
bolic pathways in the understory of a cypress dome and is
based, for the most part, on the measurements obtained in the
Austin Cary Control Dome (see Figures 54, 55 and 56). The
purposes of the model were: (1) to obtain an accurate, yet
simple representation of the annual interactions between the
solar radiation input and the organic compartments inside the
dome, including aquatic components; and (2) to show possible
effects of management schemes on the ecosystem through simu-
lation of the model. The model was designed to investigate
annual cycles and had the advantage of field data acquisition
for model verification.

Table 25 gives the values of the storages and pathways
for the model shown in Figure 76. Differential equations
used are given in the legend of Figure 76. The coefficient
values, the analog patching diagram, and pot settings are
given in Appendix D.

In the model, primary production in the understory is
attenuated both by the trunk biomass of the surrounding
cypress trees when the solar angle is low (winter) and by the
overhead canopy formed by cypress leaves when leaf biomass
is full (summer). Thus, the solar altitude, or earth angle,
is the primary source for annual solar radiation patterns.
Primary production in the pond increases the amount of dis-
solved oxygen in the pond, while the respiratory demands of

Figure 76. Mini-model of seasonal change in cypress pond showing pathways, storages, and mathematical terms used in simulation. The equations used to simulate the model on analog computer are:

$$Q_1 = \text{constant}$$

$$\dot{Q}_2 = k_{13}A - k_{14}Q_2 - k_{10}Q_2$$

$$\dot{Q}_3 = k_4A(1-k_3Q_1)(1-A)(L-k_5Q_2) - k_7Q_3(Q_4/L)) - k_{17}Q_3$$

$$\dot{Q}_4 = k_6A(1-k_3Q_1)(1-A)(1-k_5Q_2) - k_8(Q_4/L)Q_3) - k_{15}(Q_4/L)$$

$$\dot{Q}_5 = k_{17}Q_3 + k_{10}Q_2 - k_9(Q_4/L)$$
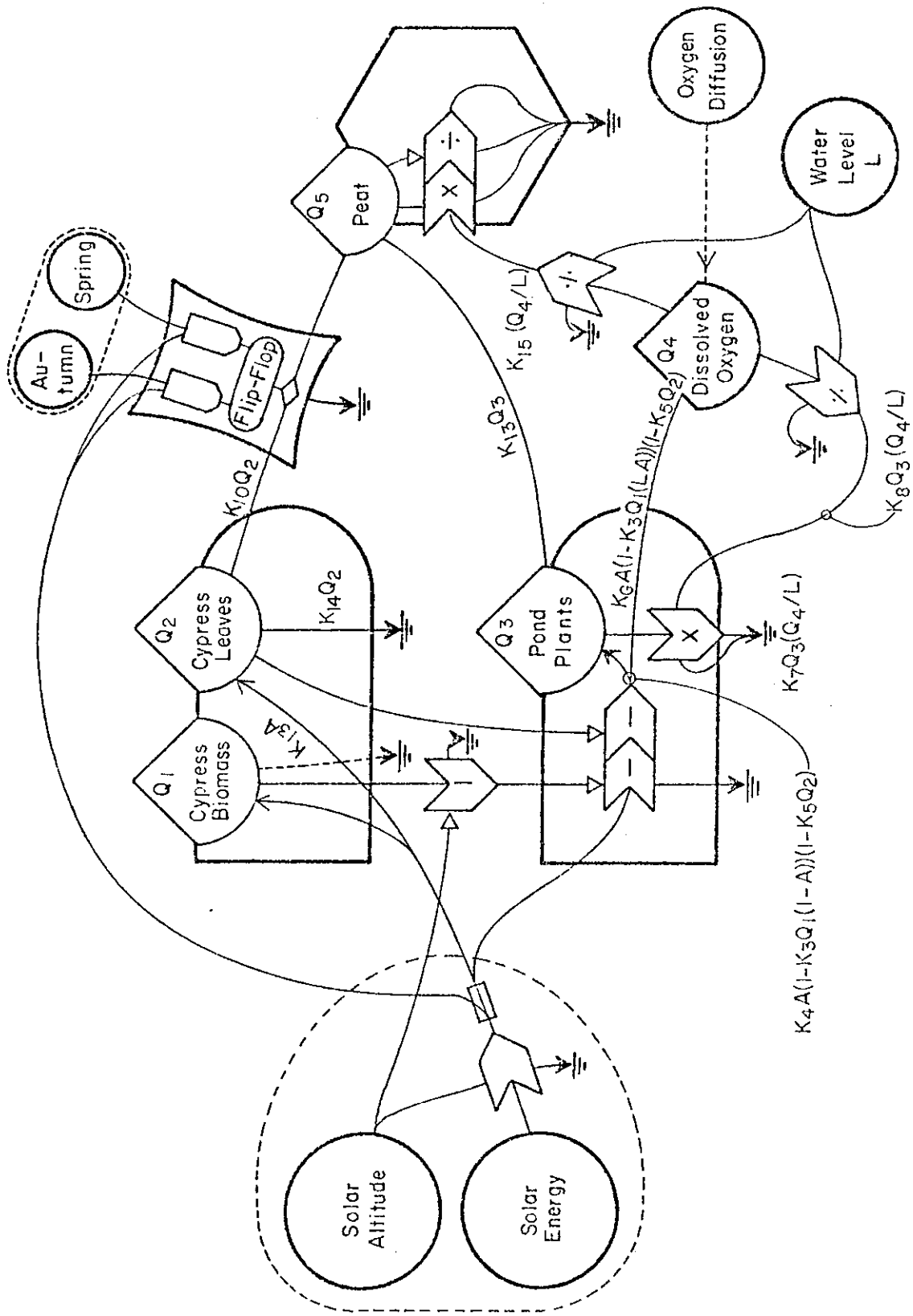
Table 25

STORAGES AND PATHWAYS FOR CYPRESS POND MINI-MODEL SHOWN IN FIGURE 76

Parameter	Note	Description	Value	Source
Q_1	1	Cypress biomass	180,000 kcal/m^2	Table 15
Q_2	2	Leaf biomass	2700 kcal/m^2 (max)	Table 15
Q_3	3	Pond plants	360 kcal/m^2	Figure 57
Q_4	4	Dissolved oxygen	1.0 g/m^2	Figure 56
Q_5	5	Bottom organic storage	48,800 kcal/m^2	Brady (1974)
A	6	Solar altitude	37°-83°	Eagleson (1970)
$k_{13}A$	7	Cypress leaf gross production	3300 kcal/m^2-yr (ave)	Carter et al. (1973)
$k_{14}Q_2$	8	Leaf respiration	3940 kcal/m^2-yr (max)	Ibid.
$k_{10}Q_2$	9	Litterfall	$k_{1/2}$ = 7 days	Assumed half life
$k_4A(1-k_3Q_1(1-A))$ $(1-k_5Q_2)$	10	Pond plant gross production	2590 kcal/m^2-yr	Figure 56
$k_7Q_3(Q_4/L)$	11	Pond plant respiration	1095 kcal/m^2-yr	Estimated
$k_{17}Q_3$	11	Pond plant detrital production	1095 kcal/m^2-yr	Estimated

Table 25 - continued

Parameter	Note	Description	Value	Source
$k_9(Q_4/L)$	12	Aerobic consumer respiration	$1680 \ kcal/m^2$-yr	Figure 56, Table 21
$k_6A(1-k_3Q_1(1-A))$ $(1-k_5Q_2)$	13	Oxygen gross production	$575 \ gO_2/m^2$-yr	Proportional to energy flows
$k_8Q_3(Q_4/L)$	13	Plant oxygen respiration	$243 \ gO_2/m^2$-yr	Ibid.
$k_{15}(Q_4/L)$	13	Consumer oxygen demand	$373 \ gO_2/m^2$-yr	Ibid.
L	--	Water level	0.5 m	Estimated

both the pond producers and the decomposers in the bottom organic matter decrease it. Water level is shown to have an inverse effect on the oxygen uptake of these organisms, because while oxygen production in the pond is measured in terms of unit area, the respiratory demands are a function of dissolved oxygen concentrations, i.e., in terms of a unit volume. Thus, a value of 2 $g-O_2/m^2$ in the dissolved oxygen compartment is equivalent to 4 $g-O_2/m^3$ in a pond 0.5 m deep. Organic matter accumulation is based both on litterfall from the above canopy and on death of pond producers. Decomposition is shown not to be a function of the amount of organic matter present, since it is assumed that decomposition occurs only at the surface. Cypress metabolism is shown in dotted lines because the turnover time is much too slow for this model and so is treated as a constant. Oxygen diffusion likewise is assumed to be an order of magnitude less than the dominant flows and is ignored.

Simulation Results

The results of the simulations are given in Figures 77 through 81. Case 1, shown in Figure 77, represents an approximation of the current steady state conditions believed to exist at the Austin Cary Control Dome. Data obtained from field measurements are superimposed on the graphs. While agreement of field data with model output does not necessarily verify a model's basic assumptions, the simplicity of this model allows one to be satisfied intuitively about the model's

Figure 77. Simulation results for cypress pond mini-
model shown in Figure 76 for present steady
state conditions (Case 1). Data points
indicate field data for 1973-74 as given
in Table 21 and Figure 56 for the Austin
Cary Control Dome. Solar altitude, shown
by the dotted line, was calculated accord-
ing to Note 6 in Appendix D.
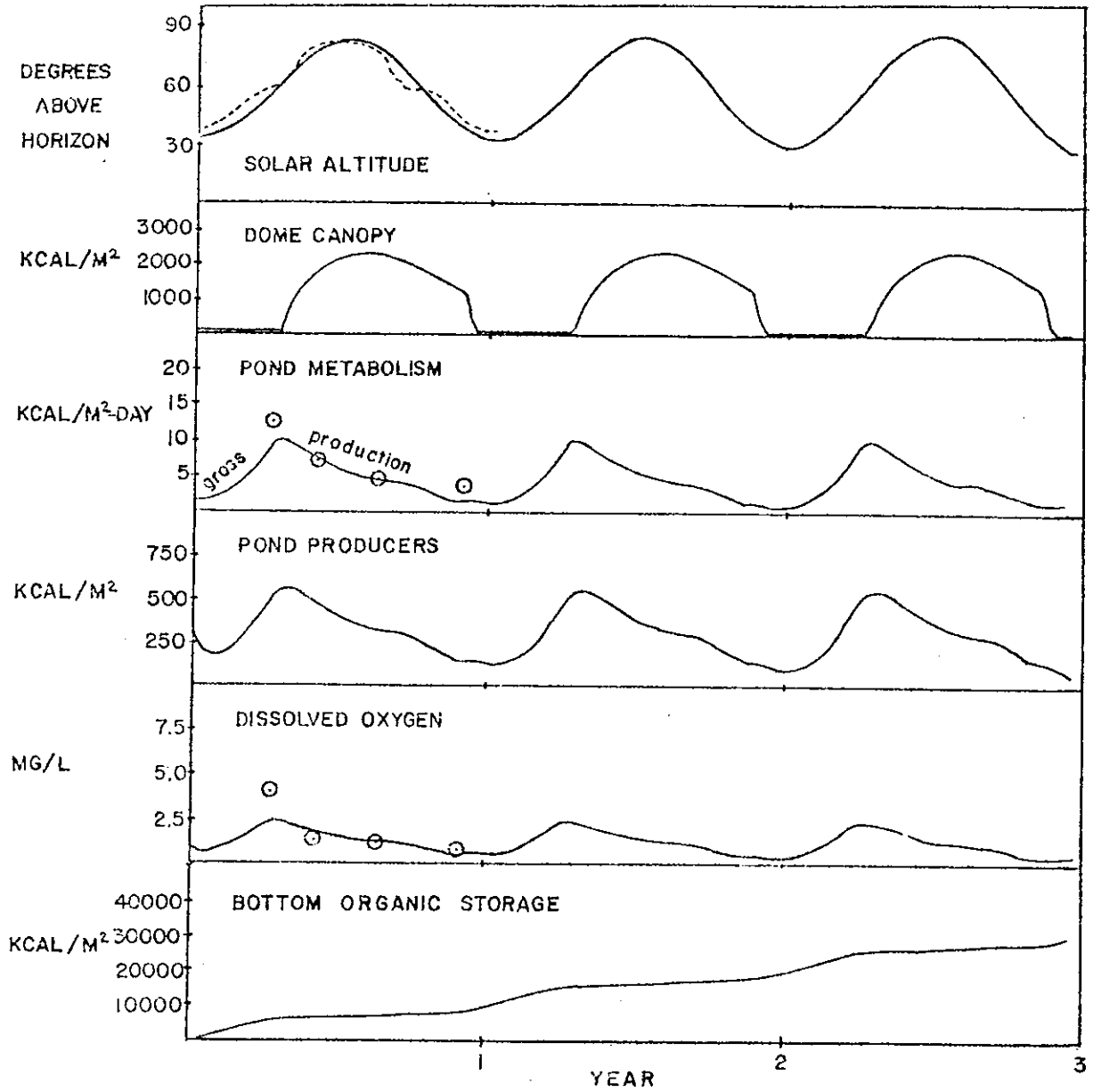
postulates. The simulation shown for Case 2 (Figure 78) represents the effect on the metabolic pathways in a cypress dome of either a harvesting schedule or a fire which might remove half of the trees. Partial destruction of the trees allows both productivity and the amount of dissolved oxygen to increase; the annual fluctuations in these compartments are damped as well. The simulation for Case 3 (Figure 79) shows the extreme situation, in which all the trees are removed. The levels of the producer population and of dissolved oxygen increase considerably, as before.

The most significant pattern seen by the comparison of Cases 1, 2, and 3 (Figures 77, 78, and 79) is the tendency of the understory to go from a system that follows annual sunlight patterns (as in Figure 79) when no cypress canopy exists to one in which a definite springtime peak is observed (Figure 77) in a well-developed dome. In the intermediate situation, the spring peak (Figure 78) is not pronounced, and production in the pond is 33 to 50% less than that which would occur with no canopy. Table 26 gives a comparison of the range of values obtained from the three cases above plus one additional case in which sunlight is assumed to be unaffected by stem blockage (Case 4, Figure 80). Pond metabolism and thus biomass and oxygen levels are much higher in the winter for Case 4 than were noted in the steady state simulation, although summer values are only slightly higher. The stem blockage is therefore shown to have a considerable effect, by itself, on the amount of primary production in the cypress

Figure 78.   Simulation results for cypress pond mini-
model shown in Figure 76 assuming removal
of half the tree biomass by fire or
harvesting (Case 2).
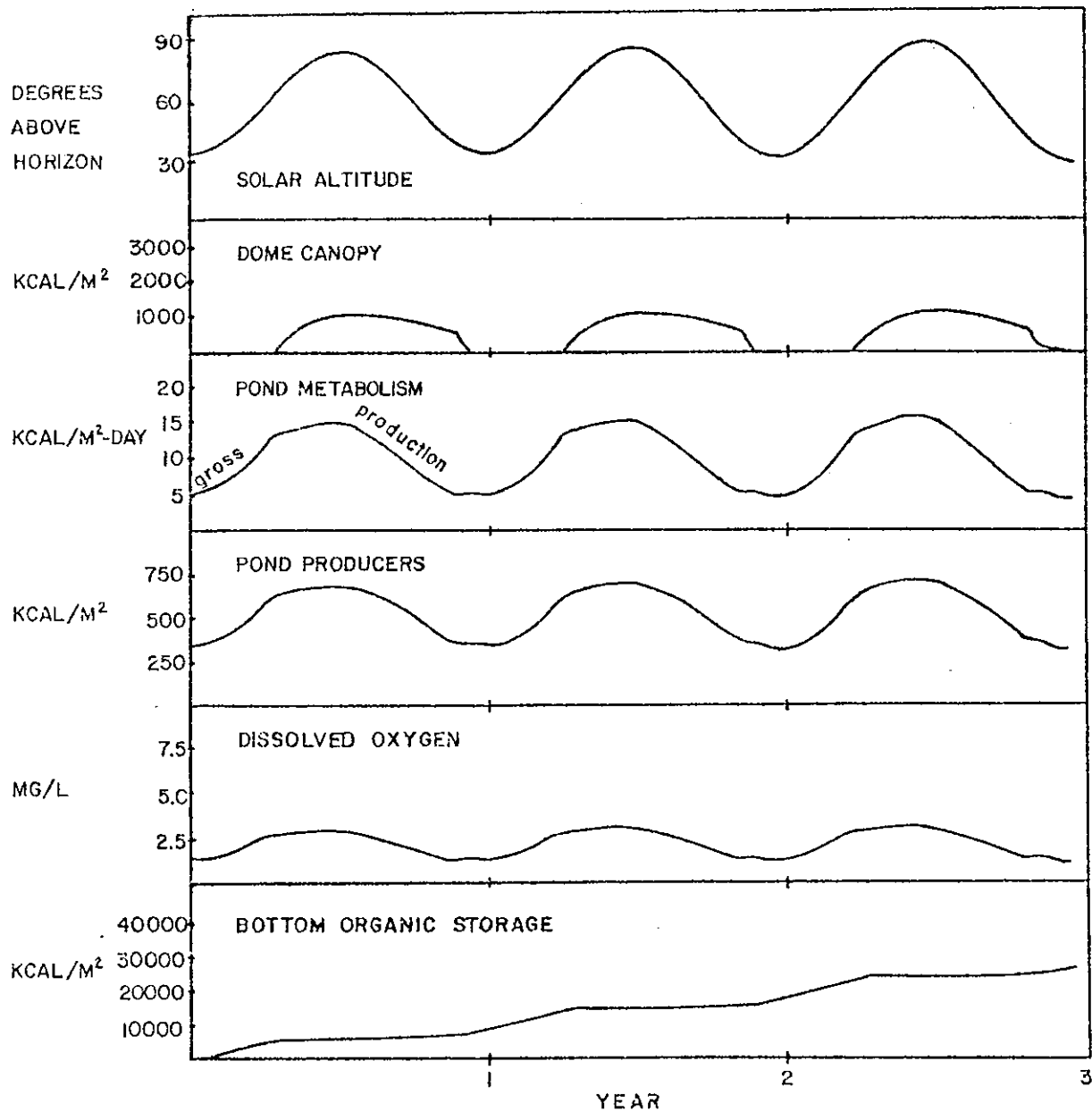
Figure 79. Simulation results for cypress pond mini-
model shown in Figure 76 assuming removal
of all the tree biomass by fire or
harvesting (Case 3).
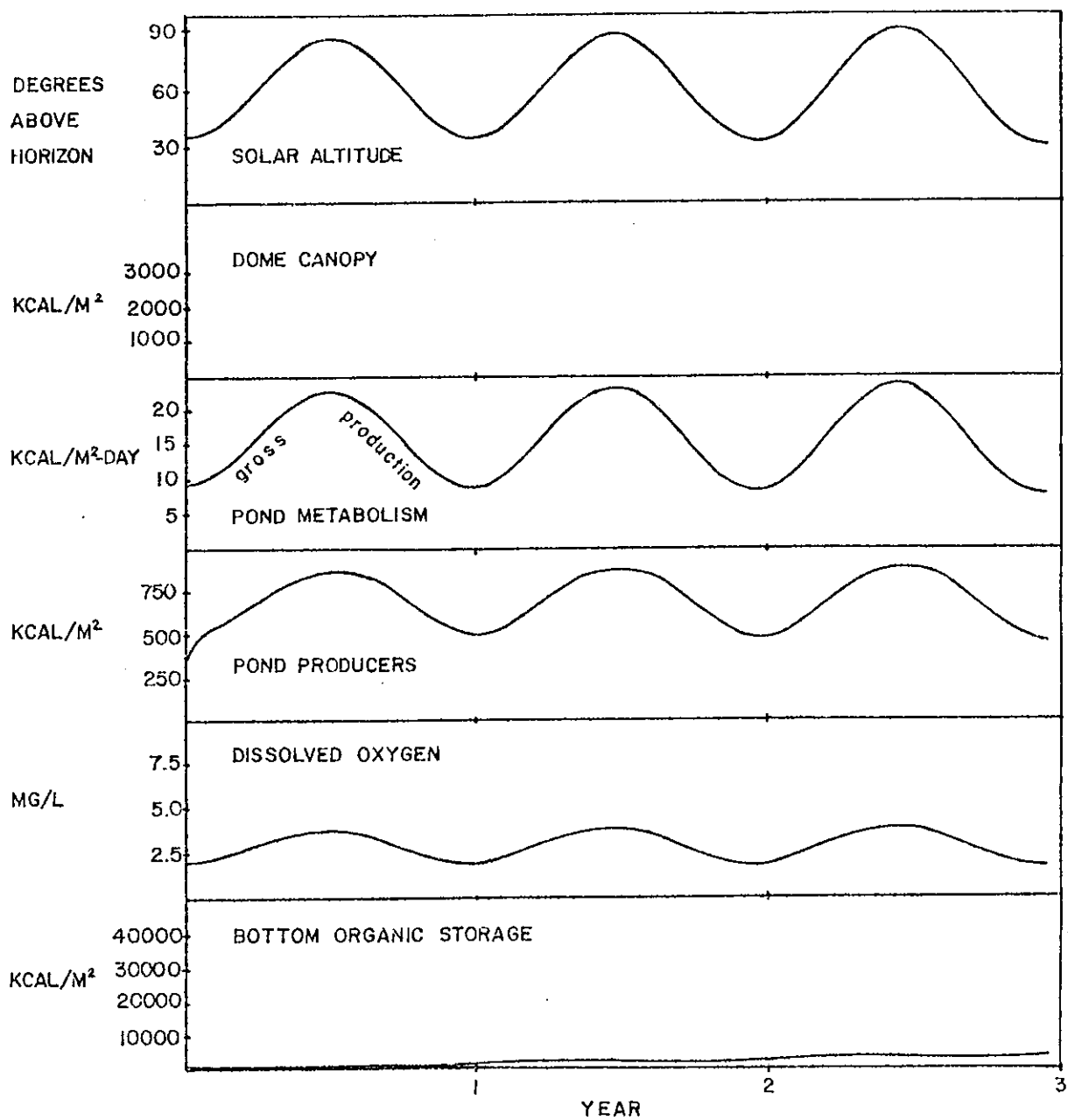
Figure 80.   Simulation results for cypress pond mini-
model shown in Figure 76 for sunlight
assumed to be unaffected by stem blockage
(Case 4).
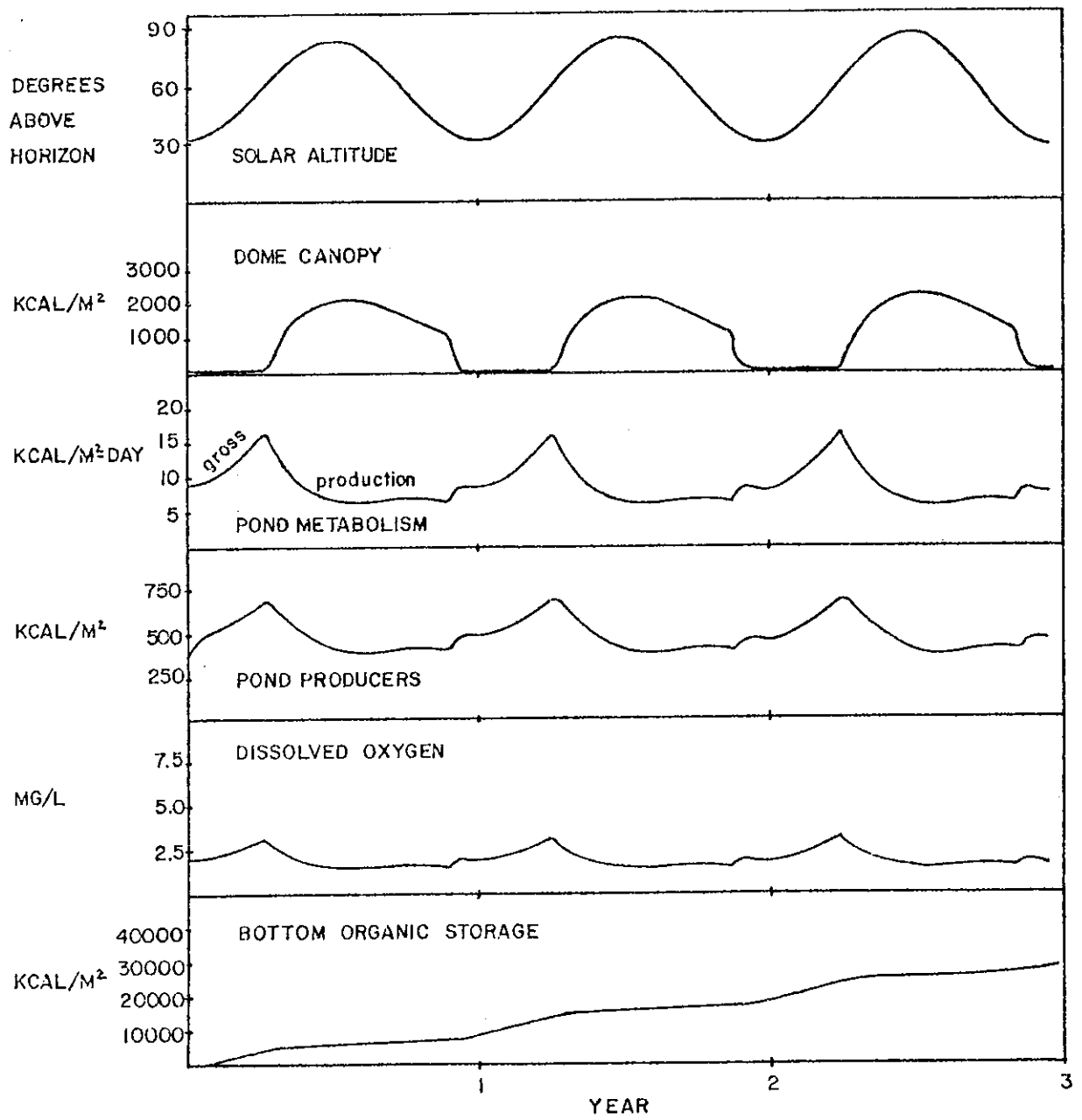
Table 26

COMPARISON OF CYPRESS POND MINI-MODEL SIMULATIONS
(CASES 1, 2, 3, AND 4) FOR MODEL IN FIGURE 76

Case	Pond Gross Production kcal/m2-day	Pond Biomass kcal/m2	Dissolved Oxygen mg/1	Peat Storage[a] cm/yr
1. Full cypress	1-10	100-550	0.5-2.5	1.6
2. Half cypress	5-15	300-700	1.0-3.0	1.3
3. No cypress	9-24	500-850	2.0-4.0	0.2
4. No stem blockage	6-16	400-700	1.5-3.0	1.6

[a]Increase in organic storage based on estimated organic density of 8 lb/ft^3 (Brady, 1974).

dome. Organic storage in all four cases was shown to rely mainly on litterfall, as expected.

Case 5 (Figure 81) was simulated for the hypothetical situation of a continuous (evergreen) canopy. Pond metabolism in this case did not respond with a spring peak as observed in Case 1. While maxima and minima were similar to Case 1, the notable peak in spring was absent. This might suggest that the deciduous nature of cypress enhances its seedling survival by allowing maximum infiltration of light at a time corresponding with the dry conditions necessary for seed germination. The deciduous strategy also allows annuals and understory in general to build organic structure early in the year before the canopy has fully developed.

Figure 81.   Simulation results for cypress pond mini-
             model shown in Figure 76 for case of
             hypothetical evergreen canopy (Case 5).
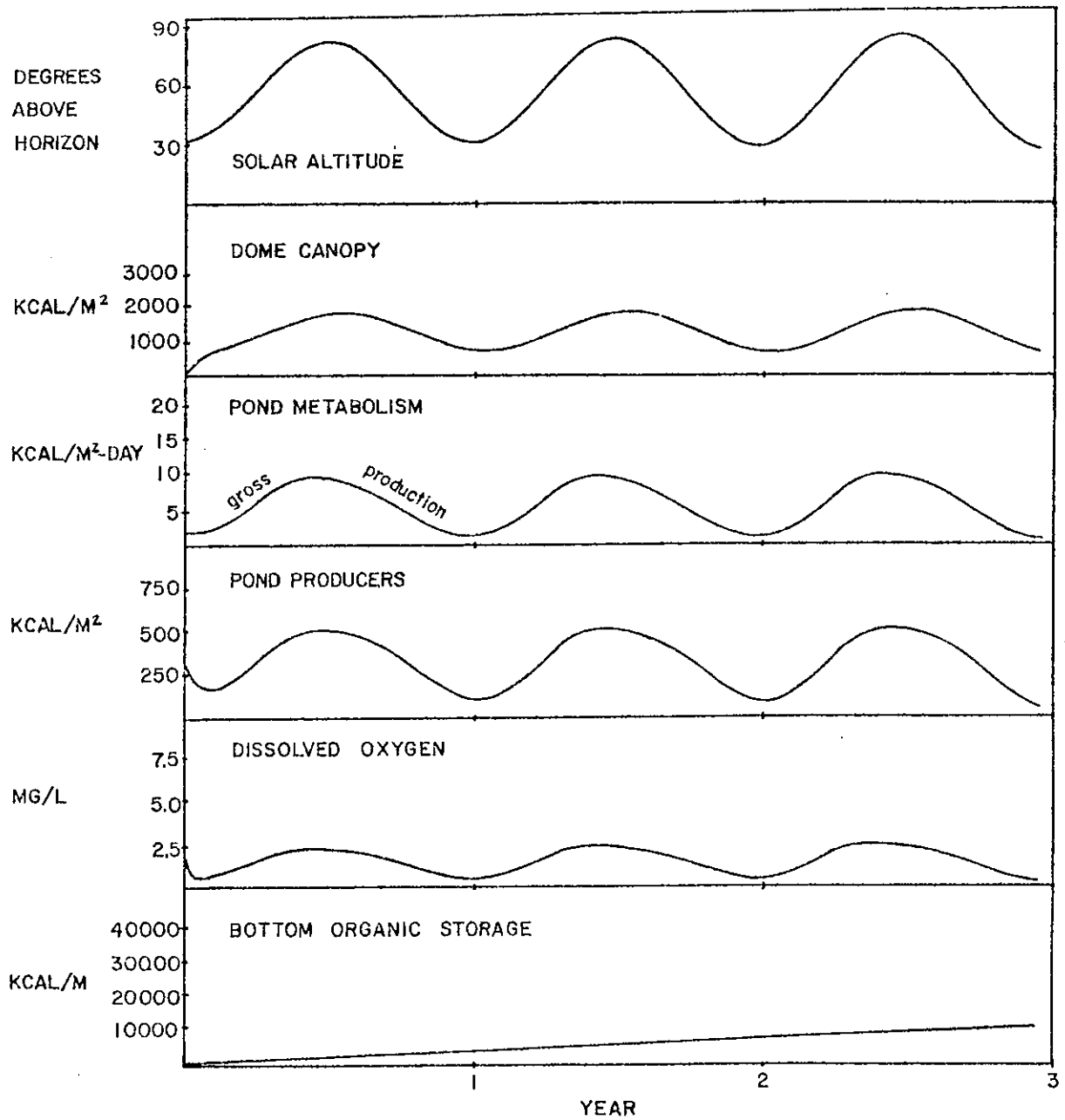
DISCUSSION

The models, measurements, and simulations that have been
presented show similarities and differences that develop when
high-nutrient wastewater is introduced into lakes and cypress
swamps. Other management practices and their implications
became apparent in the investigation and were also investi-
gated by the same methods. Comparisons involving energy
evaluations should therefore lead to a synthesis of concepts
concerning such alterations of natural ecosystems, and recom-
mendations may follow from such a synthesis.

Comparison of Eutrophic Cypress Dome and Eutrophic Lake

Before the addition of nutrients, there was little simi-
larity between the two systems. The autotrophs that dominated
in natural conditions were cypress trees in the dome and
phytoplankton in the lake. In both cases, however, the addi-
tion of nutrients caused rapidly growing species to develop
(see Figure 82). The quickly developing mat of waterhyacinths
replaced the phytoplankton community in the lake and, in the
cypress swamp, duckweed productivity became predominant under
the sparse cypress canopy. Simulations of models suggest
that in an unburned cypress dome surrounded by forested areas

303

Figure 82. Comparison of autotrophic pathways in low
            and high nutrient conditions for (a) Lake
            Alice and (b) sewage cypress dome. The
            dotted lines indicate pathways stimulated
            by the eutrophic conditions. The water-
            hyacinths have a shading advantage over
            the phytoplankton but the reverse is true
            for the duckweed invading the cypress dome.

WATERHYACINTHS

2.5

0.01

PHYTOPLANKTON

SOLAR

NUTRIENTS

X

0.3 gP/m²-day

17.9

ENRICHED LAKE

(a)

NOTES:
— — — High Nutrient Conditions
——— Low Nutrient Conditions
All Storages in kg/m²

CYPRESS

13.6

0.2

DUCKWEED

SOLAR

NUTRIENTS

X

0.02-0.2 gP/m²-day

26.6

CYPRESS DOME

(b)
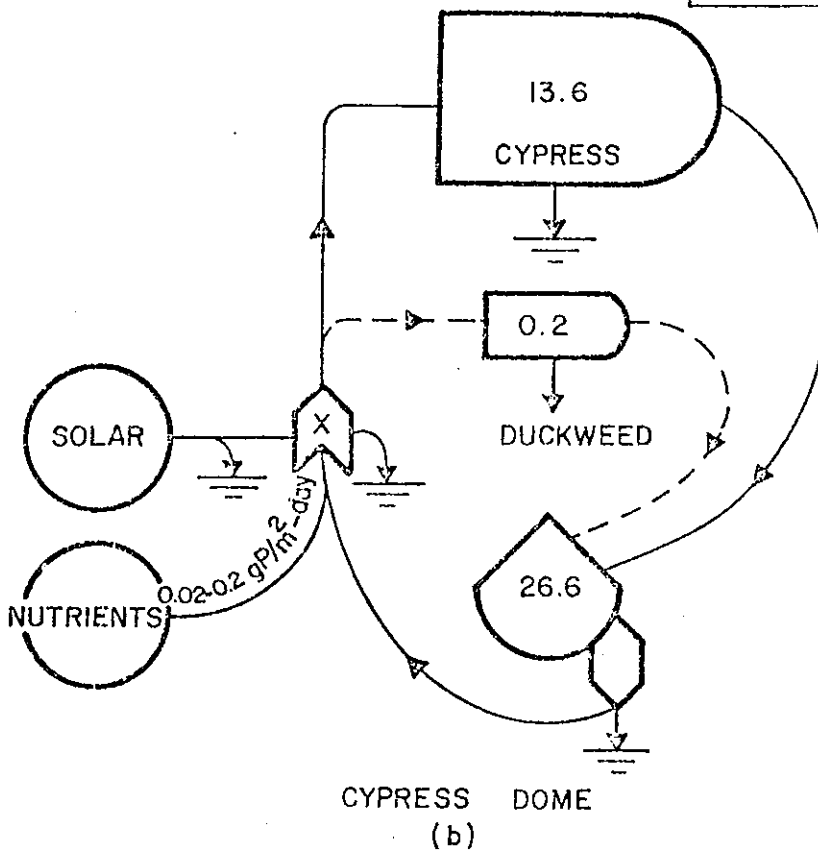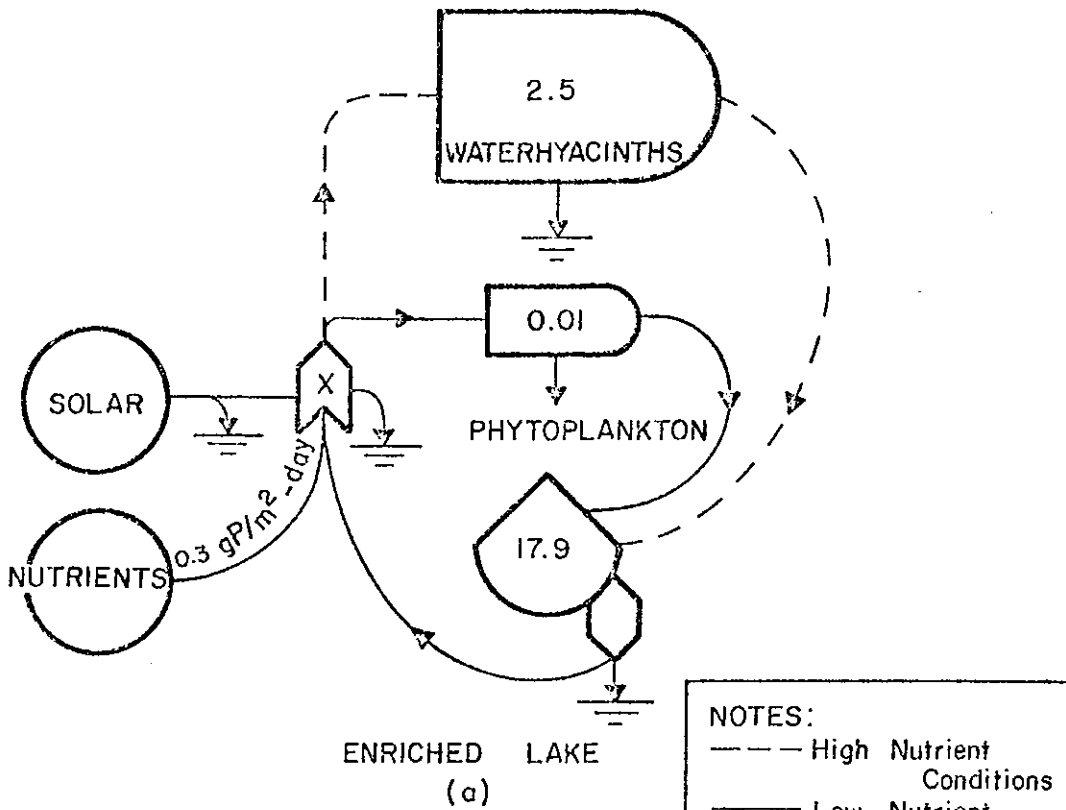
to keep out side light, the growth may not have been so pro-
nounced. As the burned trees renew their canopy, the duck-
weed may yet be shaded by the persistent cypress and neighbor-
ing pines.

Another possibility is that the understory will eventu-
ally dominate. If it does gain a competitive advantage over
the cypress, it may not be obvious for many years. The trees
would probably die for lack of root oxygen or fail to propa-
gate due to seedling failure. There is no sign of the former
occurring but artificial planting or drawdown may be required
to keep the latter from happening.

It is possible that the addition of nutrients has made
the two systems more similar. The introduced plants have low
quality structure in both cases and are intermediate between
the phytoplankton of a lake and the trees of a dome. Anaero-
bic environments were created and organic matter began to
accumulate. But because of the differences in turnover times
between phytoplankton and cypress trees, the results of eutro-
phication of a forested swamp will not be completely told for
many years.

Figure 83 gives the relative importance of plants, sedi-
ments, and water for organic, nitrogen and phosphorus storages
in each system. Waterhyacinths, while representing only 18%
of the cypress dry weight, have the capability of holding
more phosphorus and 37% as much nitrogen as the cypress,
based on average nutrient contents. One of the important
differences between the systems, however, is the amount of

Figure 83.   Diagrams showing the percent storages of
             organics, nitrogen, and phosphorus in plant
             biomass, available sediments, and standing
             water for Lake Alice and in the sewage
             cypress dome. The values for nitrogen and
             phosphorus in the dome sediments and trees
             represent values prior to sewage applica-
             tion. Assuming organic matter to be half
             carbon, the following C:N:P ratios by
             weight are obtained:

                 Lake - 38:2.7:1
                 Dome - 57:12:1

PLANTS 2.5   WATER 0.1

SEDIMENTS
17.9

LAKE
TOTAL 20.5

PLANTS
13.8

SEDIMENTS
26.6

WATER
0.1

CYPRESS DOME
TOTAL 40.5

ORGANIC STORAGES, kg/m^2

PLANTS 43.9   WATER 3.7

SEDIMENTS
675

LAKE
TOTAL 722.6

PLANTS 117   WATER 1.8

SEDIMENTS
4160

CYPRESS DOME
TOTAL 4278.8

NITROGEN STORAGES, g/m^2

PLANTS 15.9   WATER 2.9

SEDIMENTS
250

LAKE
TOTAL **268.8**

PLANTS 7.5   WATER 5.0

SEDIMENTS
340

CYPRESS DOME
TOTAL 352.5

PHOSPHORUS STORAGES, g/m^2

nutrients continually available to the plants. In the lake both the phytoplankton and the waterhyacinths draw nutrition from the water column, the nutrients in the sediments being limited by mineralization and reentrainment restraints. In the cypress dome the nutrients which accumulate in the sediments are still available to the cypress for the production of useful work, e.g., making wood. In fact, the duckweed may be thought of as a transport mechanism for nutrients from the standing water to the root zone. The analogous organic matter lost to the bottom of a lake or hyacinth marsh may be kept out of circulation for a long time.

Comparison of Nutrient Uptake

Both the waterhyacinth marsh of Lake Alice and the experimental cypress dome receiving sewage have both been shown to be potential sinks for nutrients under certain management conditions. The waterhyacinth system is well known for its dominance in response to a rich flow of nutrients; what the system will ultimately be in the cypress dome is not certain yet. In many areas of high nutrients, duckweed and cypress have been observed growing together. Both systems studied here represent experiments in ecological engineering where man, either intentionally or inadvertently, has attempted to utilize the natural system for the absorption of wastes without greatly jeopardizing the integrity of that system.

Tables 27 and 28 give monthly removal percentages of both nitrogen and phosphorus for each system. For the sampling period, during which there was constant loading, the Lake Alice marsh averaged 11% uptake of phosphorus and 49% uptake of nitrogen. Under varied loading rates, the cypress dome experienced a weighted average uptake of 4% phosphorus and 76% nitrogen. The nutrients lost from the dome were calculated as those flowing out the overflow weir and do not represent the potential uptake of the dome under proper loading conditions. The December 1974 loading rate of 3.9 cm/wk, for example, resulted in 75% removal of the phosphorus and 93% nitrogen removal. These percentages for the dome do not take groundwater loss into account. Using the calculated groundwater recharge rate for the dome and the increase in nutrients from upstream to downstream wells, 70 g P/day is estimated to be leaving the dome as groundwater. This amounts to 12% of the phosphorus applied. Well data for nitrogen were erratic with no consistent patterns available for a similar comparison.

Waterhyacinth Marsh

Nitrogen-phosphorus ratios of the inflow to Lake Alice were generally on the order of 1:1 to 3:1 by weight. By comparison, waterhyacinth biomass contains about 0.4% P and 2.6% N (Boyd, 1970) or an N/P ratio of 6:1. There seems to be some nitrogen limitation in the hyacinth marsh, and the results of chemical analyses and computer modeling would seem

Table 27

NITROGEN AND PHOSPHORUS REMOVAL EFFICIENCIES
OF LAKE ALICE WATERHYACINTH MARSH

Date 1973	Marsh Influent[a]		Marsh Effluent[a]		Percent Removal	
	g-P/m^3	g-N/m^3	g-P/m^3	g-N/m^3	P	N
January-March[b]	0.79	3.09	0.86	1.44	-9[c]	53
April	2.02	3.69	2.10	1.22	-4[c]	67
May	1.32	1.88	1.29	1.18	2	37
June	2.45	2.69	1.45	1.44	41	46
July	1.34	2.08	1.06	1.04	21	50
August	1.24	2.31	1.05	1.29	15	44
Average					11	49

[a] Water flow in and out of marsh assumed to be equal.
[b] January through March data based on spot samples.
[c] Minus sign indicates net export.

Table 28

NITROGEN AND PHOSPHORUS REMOVAL EFFICIENCIES
BY CYPRESS DOME RECEIVING SEWAGE (SURFACE WATER ONLY)

Date 1974	Sewage Inflow[a]			Weir Outflow[b]			Percent Removal	
	m³/day	g-P/m³	g-N/m³	m³/day	g-P/m³	g-N/m³	P	N
July	116.9	8.2	15.5	182.2	5.02	1.56	5	84
August	100.1	"	"	194.1	5.95	3.16	-41[c]	60
September	78.5	"	"	145.0	3.35	2.60	24	69
October	83.8	"	"	55.5	10.95	3.64	12	84
November	14.1	"	"	21.2	--	--	--	--
December	29.4	"	"	17.7	3.40	1.85	75	93
					Weighted Average		4	76

[a]Sewage inflow concentrations based on composite sample for week of June 7-14 (Brezonik).

[b]Weir outflow concentrations based on spot sampling (Brezonik).

[c]Minus sign indicates net export.

to bear this out. Very little change in total phosphorus is noted for the test period except for June when a wide variance is also experienced (see Figure 30f). Almost every species of nitrogen, however, decreases significantly every month (see Figure 30c,d,e). The tendency of nitrogen to have more notable annual patterns was also seen in the Lake Alice model simulations. Nitrogen had very significant sinusoidal patterns with winter peaks and summer minima (see Figure 40). These annual oscillations were damped with the removal of the sewage treatment plant effluent in one simulation (Figure 41) and exacerbated when the heated effluent was diverted (Figure 42) in another simulation. Phosphorus was shown in the simulations to be little affected either by hyacinth uptake or any other annual cycle.

Another possible nitrogen sink, denitrification, may also be significant in the marsh. Sheffield (1967) noted in nutrient uptake tests with a hyacinth pond that nitrogen decreased significantly when anaerobic conditions stabilized. The near anaerobic conditions under the Lake Alice hyacinth marsh coupled with the high temperatures make good conditions for denitrification to occur. Nitrate values approached zero at the marsh outflow for the late spring and summer months (Figure 29d). The nutrient summary model in Figure 34 suggests that 28% of the inflowing nitrogen is lost in the marsh through denitrification in the summer.

The waterhyacinth marsh can be regarded as a nitrogen sink due to the fact that denitrification is accelerated by

the high temperature on a year-round basis. A seasonal pulse
of both nitrogen and phosphorus removal is superimposed during
the growing season. Because of the low N/P ratios associated
with the influent, the percent removal and annual patterns are
much more noticeable for nitrogen than phosphorus. The high
flow rates, which insure that a significant percent of the
nutrients will not be taken up by the system, are necessary,
however, for vigorous growth of the waterhyacinths.

Cypress Dome

The cypress dome loading rate was particularly important
in determining the effectiveness of the swamp in nutrient
removal. High loading rates (10 cm/wk and more) were main-
tained for much of the experiment (see Figure 46) and were
responsible for high volumes of essentially untreated surface
flow going out of the dome. Loading rates of 2.5 to 5.0
cm/wk probably represent the maximum applications possible on
a yearly average to avoid excessive overflow. If wastewater
inflows are kept within these limits, removal percentages
close to 100% may be possible for nutrients. This, of course,
ignores the nutrients which may be transported out with the
groundwater flow, estimated to be about 3.7 cm/wk.

Many physical, chemical, and biological processes
affected the concentrations of nutrients in the standing
waters and thus in the overflow water. Low redox conditions
may have increased the solubility of phosphorus in the stand-
ing water. Precipitation and organic settling would tend to

reduce the concentrations in the overlying waters. As the water passes through the soil, in addition to the obvious filtering of colloidal and suspended particles, chemical filtration in the forms of ion exchange, adsorption and precipitation may have been significant (Ellis, 1973). However, plant uptake and denitrification seemed to dominate this system as they do in Lake Alice. Denitrification is suggested by the significant values of nitrates in the effluent (1.1 to 4.4 mg-N/1), the low values in the standing water (Figure 58c), the anaerobic conditions under the duckweed, and the low concentrations of nitrogen found in the sediments (Figure 59). High concentrations of nutrients found in the duckweed suggest that this floating plant stores and transports nutrients to the bottom. The uptake by the cypress trees is more difficult to determine and will require several years of further study of cypress response. The point remains, however, that if the cypress sediments are used to "filter" the slowly percolating wastewater and catch the detrital inputs, those nutrients which are captured may be available to the roots of the cypress. The large storages and slow growth rates dictate a study over many years to investigate these responses of the swamp.

Energy Quality of Waterhyacinths and Cypress Wood

The true value of an energy source or storage is not always its caloric value. When energy is upgraded, such as from coal to electricity, many new uses and a greater

versatility make the upgraded energy of higher quality. This concept, called energy quality (Odum, 1974), may be inversely related to the thermodynamic principle of entropy, a relative measure of the unavailability of energy to do useful work. Energy quality factors have been calculated for one form of energy relative to another by assuming that those processes of man and nature which are presently converting energy from one form to another are at an optimum as witnessed by their survival in selection processes. Lem (1973) and Zucchetto (1975), for example, show that the energy quality factor of electricity relative to coal is 3.7. The same type of analysis can be used to determine the energy quality of waterhyacinth biomass and cypress wood relative to sunlight.

For the waterhyacinth, Figure 84a summarizes data on primary production as gathered from Lake Alice (Table 3) and gives an energy quality factor of hyacinth stored quality relative to sunlight of 62.

Cypress wood, on the other hand, is a slow growing, durable wood of much greater quality as suggested from Figure 84b which gives cypress wood an energy quality factor relative to sunlight of 2350.

Thus cypress wood is shown to be almost 40 times the quality of waterhyacinth biomass. This is not surprising when one considers that cypress has long been referred to as "the wood eternal" (U.S. Dept. of Commerce, 1932; Neubrech, 1939). It has a wide diversity of uses and vast quantities of the wood were shipped to Europe and other points soon

Figure 84.   Determination of energy quality factors
             of (a) waterhyacinths and (b) cypress
             wood.

Energy   Quality   Factor

$$\frac{4000}{64} = 62 \frac{Kcal\ sunlight}{Kcal\ organic\ matter}$$

WATERHYACINTHS

(a)

Energy   Quality   Factor

$$\frac{4000}{1.7} = 2350 \frac{Kcal\ sunlight}{Kcal\ wood}$$
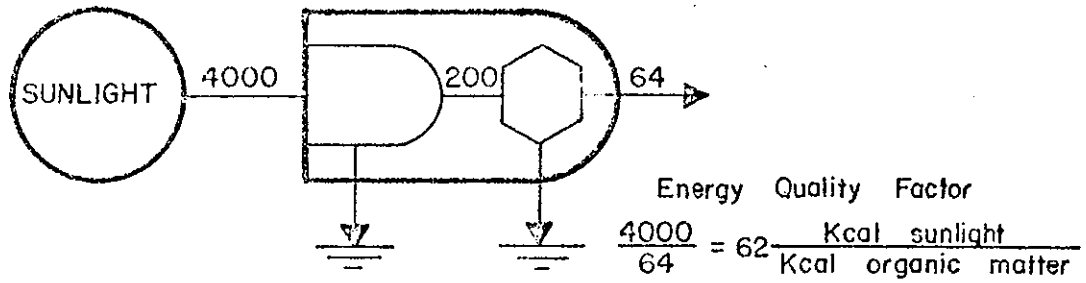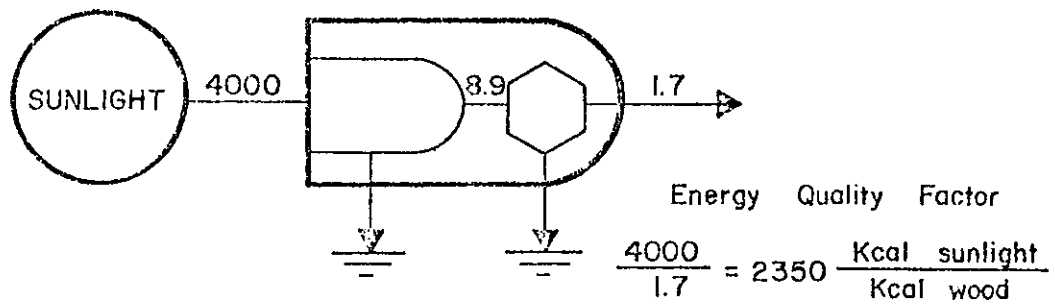
CYPRESS

(b)

after the New World was discovered. On the other hand, despite at least one professional society and millions of dollars of research, no widespread uses have been found for the waterhyacinth.

Preliminary Evaluation of
Nutrient Disposal Alternatives

Some important energy and economic flows associated with the alternatives to nutrient disposal presented by Lake Alice and the cypress dome are shown in Figure 85. Also shown are theoretical models based on the general principles of disposal of secondarily-treated wastewater (Figure 85a) and on tertiary treatment as a technological choice (Figure 85d). Evaluations of the change in energy and money flows of man's economy as each system treats the high nutrient wastewater allows preliminary comparison. The comparisons here were based on a wastewater flow of 2.8 million gallons per day (mgd), the flow of sewage into Lake Alice.

By putting all the energy flows on a common energy quality basis, the relative energy contributions of the alternatives can be ascertained. Energy conversion factors, such as the ones calculated in the previous section, were used to put energy flows on an energy quality basis. By using these conversion factors, the work potential rather than the kilocalorie value becomes the standard of analysis. Table 29 presents some of the conversion factors used by Odum, Brown et al. (1975) to convert energy flows to their fossil fuel

Figure 85.   Energy diagrams showing various alternatives
              for the disposal of 2.8 million gallons per
              day of secondary high-nutrient sewage:
              (a) theoretical case whereby an increase in
              sunlight-based energy leads to an attraction
              of 2.5 times its value. Based on the pres-
              ent energy intensiveness of the nation, this
              is the ideal nature-fossil fuel balance for
              a region; (b) disposal into Lake Alice with
              resulting increased lake productivity and
              economic flows; (c) disposal into 289 hec-
              tares (2.5 cm/wk) of cypress swamps where
              benefit of additional wood production may
              be realized; (d) technologically based
              tertiary treatment where no natural system
              is utilized.
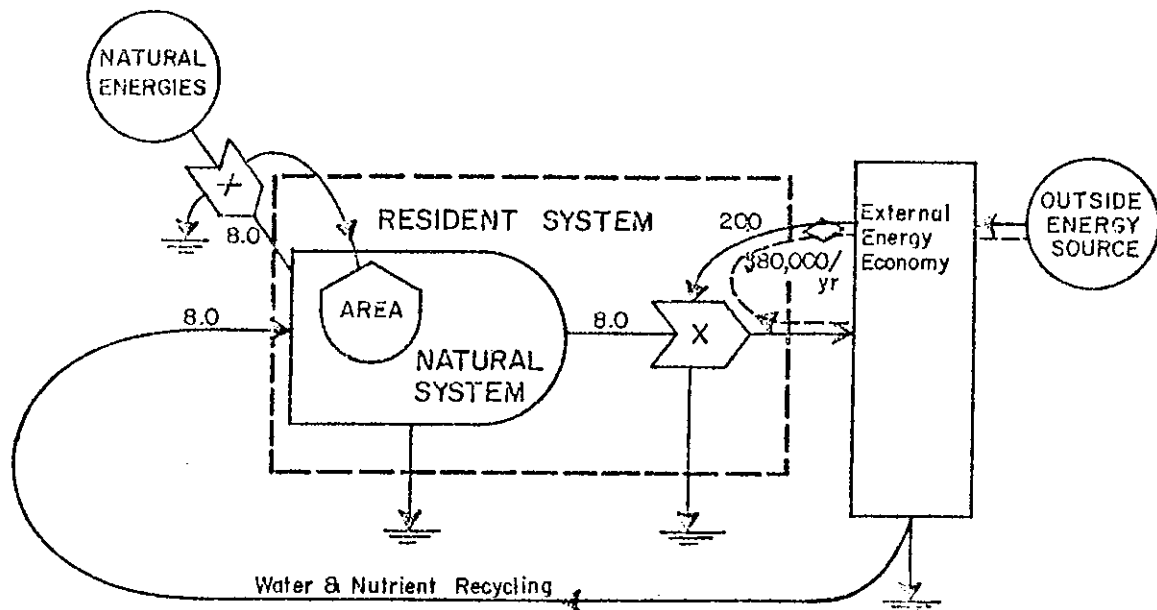
(a)
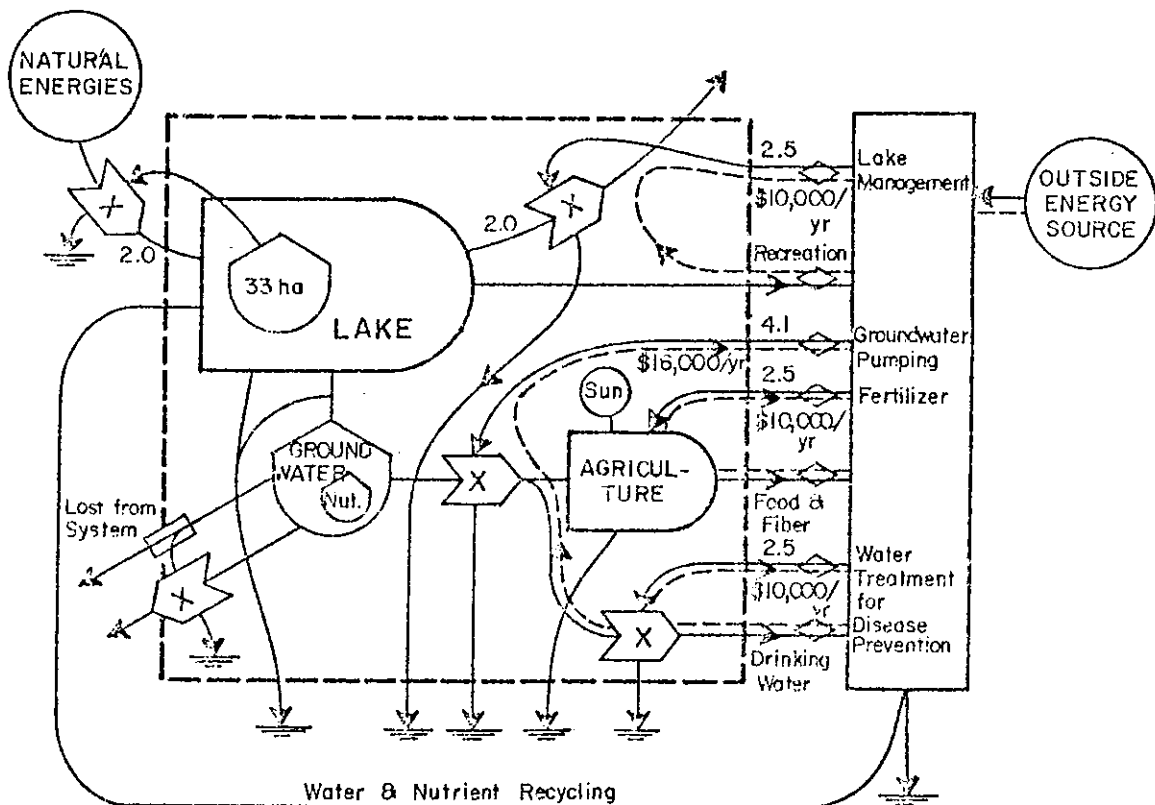
(b)
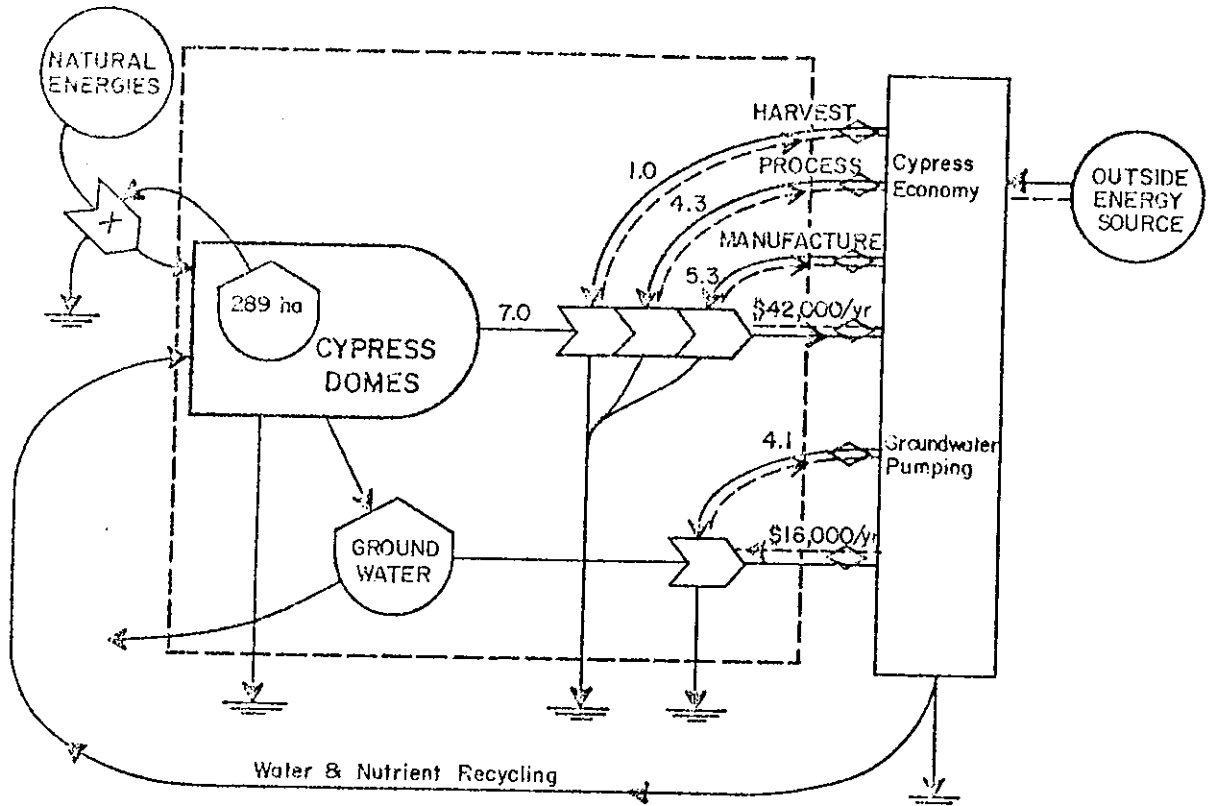
(c)
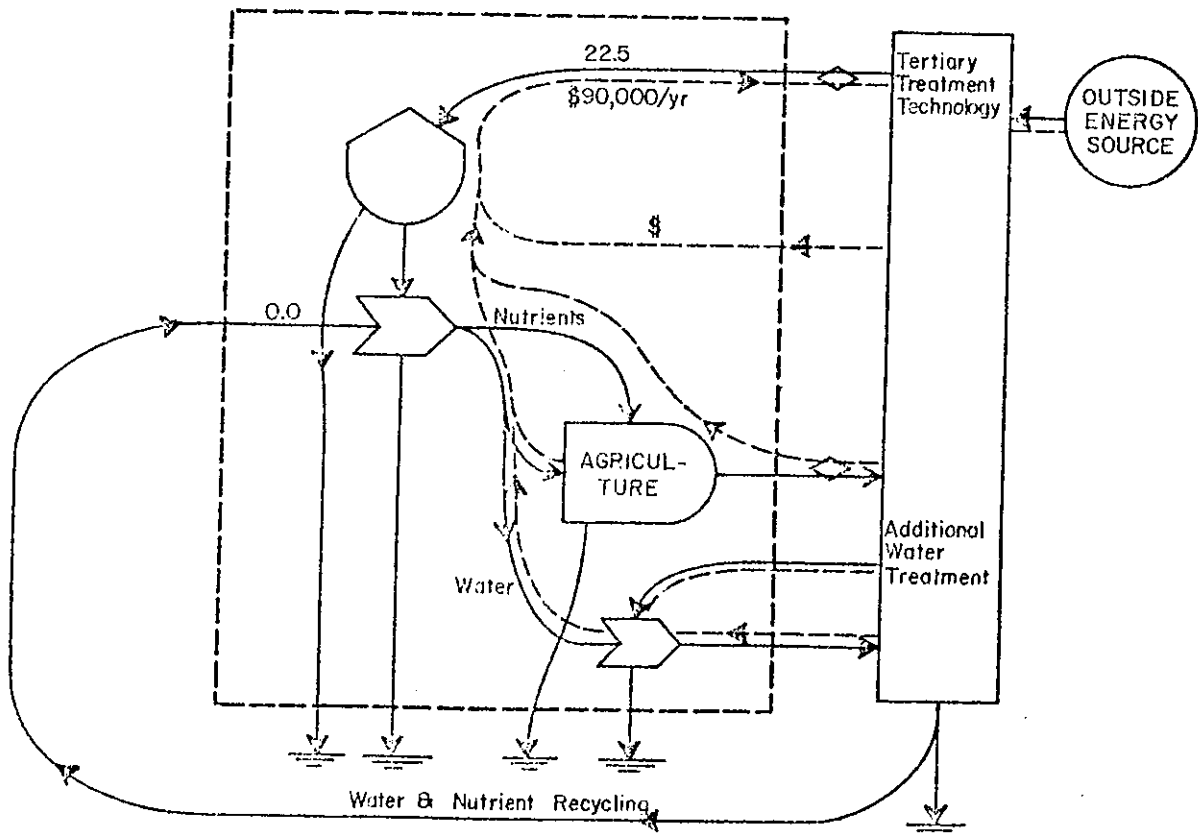
(d)

Figure 85 - continued.

Table 29

QUALITY FACTORS RELATING
DIFFERENT TYPES OF ENERGY FLOW

Energy Conversion Process	Energy Quality Factor[a]
Sunlight to Gross Production	100
Gross Production to Wood	10
Gross Production to Fossil Fuel	20
Wood to Fossil Fuels	2
Wood to Electricity	8
Gross Production to Fossil Fuels	20
Sunlight to Fossil Fuels	2,000
Sunlight to Cypress Wood	2,350[b]
Hydrostatic Head to Fossil Fuel	0.63[c]
Electricity to Fossil Fuels	0.27[d]
Total Work Exchanged for U.S. Dollars	25,000 kcal/dollar

[a]See Odum (1974), Odum, Brown et al. (1974) and Zucchetto (1975).

[b]From this study.

[c]Boynton, personal communication.

[d]Zucchetto (1975).

equivalents (FFE). For example, gross primary production of
natural systems may be put in fossil fuel equivalents by
dividing its role of flow by 20. When only money flow was
known, energy flow for each dollar was estimated as 25,000
kcal as an average ratio for the United States (Odum, 1975a).

Odum, Brown et al. (1975) have suggested that if high
quality energy such as fossil fuel is available from outside,
that resident system will win out which can use some of its
low quality sunlight-based energy to attract and interact with
the high quality energy to generate exports in exchange.
Based on the nation's economy as a whole, 1 kcal FFE of sun-
light on the average has been attracting 2.5 kcal FFE of
fossil fuels to the resident economy. The ratio will change
as the nation's energy intensiveness changes. Figure 85a
shows a general diagram for the disposal of 2.8 mgd of nutri-
ent wastewater. The high energy quality of the nutrients
gives that flow a value of 8.0×10^8 kcal FFE/yr (see Note a
on Table 30) if it is matched by enough sunlight (intensity
x area) to get a net increase in 8.0×10^8 kcal FFE/yr from
the natural system. This increase in resident natural energy
flow can therefore theoretically attract 20.0×10^8 kcal
FFE/yr from external sources. The model shows that the dis-
posal of the 2.8 mgd of secondary sewage into a natural system
has the capability of increasing the money flow in the local
economy by $80,000/yr or approximately $0.08/1000 gallons of
secondary sewage. This assumes no limitations of sunlight to
the natural area.

The summary model for Lake Alice (Figure 85b) shows changes in both the natural energy and purchased energy with that disposal method. The small size of the lake relative to the high nutrient loading causes the increase in productivity to be only one-fourth of what is possible. This is a sunlight-limited system. Maintenance of the lake, presently at $10,000 per year, is required to keep the lake's recreational function within the community. The piping of the effluent from the lake directly to the Floridan Aquifer, however, is the largest cost. To bring that water back to ground level for man's agricultural and domestic needs requires additional costs. Moreover, some of the nutrients transported from the lake are lost to dilution by the groundwater and their possible fertilization benefits must be replaced with purchased fertilizers. In addition, the model shows that disease may travel through the porous limestone to drinking water supplies, entailing the additional cost of water treatment.

In a cypress system (Figure 85c), a loading rate of 2.5 cm/wk allows the water to percolate slowly through the soil to the aquifer, leaving nutrients behind. Some of the water goes into transpiration and evaporation, necessary processes in a normally functioning ecosystem. The nutrients increase metabolism as in the lake but over a much greater area. The economic flow is amplified with the production of high quality cypress wood. The inputs to this system include the work of harvesting, the work of finishing the wood, and possibly even

the work of building a cypress wood house or some other manu-
factured goods.

Tertiary treatment (Figure 85d) is maintained on pur-
chased energy and does not interact with other natural energy
to help generate the values to attain economic investment;
high quality energy is used in large amounts without amplifi-
cation of natural energy. Fossil fuels are used to split the
wastewater into two flows, nutrients and clean water. Both
may have valuable uses for agriculture and domestic use
although the latter requires additional treatment. Tertiary
treatment methods such as ammonia stripping may lose nitrogen
to the atmosphere.

A summary of these alternatives in fossil fuel equiva-
lents for 2.8 mgd of secondary sewage is shown in Table 30.
By dividing fossil fuel costs by sewage flow money values per
volumes of water were found: Lake Alice, 4.5¢/1000 gal,
cypress system, 5.7¢/1000 gal. The lake model shows a much
greater expenditure of fossil fuels for the amount of natural
energy being released. This system may be a poor alternative.
The cypress disposal method has a ratio of fossil fuel to
sunlight of 2.1, close to the 2.5 theoretical ratio. This
system may be the one selected for as natural energies are
recognized for their importance to the local economy. Ter-
tiary treatment has large requirements of purchased energies
not matched with resident energies, according to the model.
The cost of this system, including the additional water treat-
ment for disease control, is 9.9¢/1000 gal. The ratio of

Table 30

CHANGES IN ENERGY FLOWS CAUSED BY THE DISPOSAL OF 2.8 MILLION GALLONS PER DAY SECONDARY SEWAGE UNDER DIFFERENT ALTERNATIVES. ENERGY FLOWS IN KCAL FOSSIL FUEL EQUIVALENTS (FFE) x 108/YR

Energy Flow	Theoretical Economic Attraction Model (Fig. 85a)	Lake Alice Disposal (Fig. 85b)	Cypress Dome Disposal (Fig. 85c)	Tertiary Treatment (Fig. 85d)
Change in sunlight-based energy flow	8.0[a]	2.0[c]	7.0[h]	--
Change in fossil fuel work	20.0[b]	11.6	14.7	25.0
Management		2.5[d]		
Groundwater pump		4.1[e]	4.1[e]	
Nutrient recovery		2.5[f]		
Water treatment		2.5[g]		2.5[g]
Lumber harvest			1.0[i]	
Lumber process			4.3[i]	
Lumber manufacture			5.3[i]	
Technological P removal				13.8[j]
Technological N removal				8.7[k]
Fossil fuel/sunlight	2.5	5.8	2.1	--

Footnotes to Table 30

^{a}Energy quality of nutrient flow of 2.8×10^6 mgd (10.5×10^4 m^3/day) @ 10 ppm P. One mole of PO$_4$ yields 13,000 kcal gross photosynthesis (Odum, 1960).

$$\left(\frac{13,000 \text{ kcal sugar}}{1 \text{ mole P} \times 31 \text{ g-P/mole}}\right)\left(0.05 \frac{\text{kcal FFE}}{\text{kcal sugar}}\right) = 21 \text{ kcal FFE/g-P}$$

$(10.5 \times 10^3 \text{ m}^3/\text{day})(10 \text{ g-P/m}^3)(21 \text{ kcal FFE/g-P})(365) = 8.0 \times 10^8 \text{ kcal FFE/yr}$

^{b}The increase in attracted fossil fuels due to an increase in 8.0×10^8 kcal FFE/yr in the natural sector is

$(8.0 \times 10^8 \text{ kcal FFE/yr})(2.5) = 20.0 \times 10^8 \text{ kcal FFE/yr}$

^{c}Change in Lake Alice metabolism due to nutrient additions, assume one-half of metabolism due to wastewater inflows:

Hyacinths (Table 3)--$(22,700 \text{ kcal/m}^2\text{-yr})(21 \times 10^4 \text{ m}^2)(1/20) = 2.4 \times 10^8 \text{ kcal FFE/yr}$

Open lake (Table 6)--$(75 \text{ kcal/m}^2\text{-day})(365 \text{ days/yr})(12 \times 10^4 \text{ m}^2)(1/20) = 1.6 \times 10^8 \text{ kcal FFE/yr}$

Total $= 4.0 \times 10^8$ kcal FFWE/yr

Change $(1/2)(4.0 \times 10^8 \text{ kcal FFWE/yr}) = 2.0 \times 10^8 \text{ kcal FFWE/yr}$

^{d}Lake Alice Management Costs:

$(\$10,000/\text{yr})(\text{N. Lake, pers. comm.})(25,000) = 2.5 \times 10^8 \text{ kcal FFE/yr}$

^{e}Water recovery costs - pumping costs to bring water back to ground level

flow $= 1944$ gpm; pump efficiency $= 50\%$; electrical efficiency $= 50\%$

Footnotes to Table 30 - continued

^eWater recovery costs (cont.)

$$Bhp = \frac{(1944)(10 \text{ ft})}{(3960)(.5)} = (9.8 \text{ hp})(5.62 \times 10^6 \text{ kcal/yr/hp}) = 0.55 \times 10^8 \text{ kcal/yr}$$

$$[(0.55 \times 10^8 \text{ kcal/yr})/(0.5)][3.7 \text{ kcal FFE/kcal elect}] = 4.1 \times 10^8 \text{ kcal FFE/yr}$$

^fNutrient recovery costs - cost to replace lost nutrients.

fertilizer cost $7.95 per 100 lb of 10-10-10 (E. DeBellevue, pers. comm.)

lost nutrients (P)--$(10.5 \times 10^3 \text{ m}^3/\text{day})(1.5 \text{ g-P/m}^3)(365) = 5.75 \times 10^6 \text{ g-P/yr}$

$$\frac{(\$0.795/\text{lb P})}{(454 \text{ g/lb})} (5.75 \times 10^6 \text{ g-P/yr}) = (\$10,067/\text{yr})(25,000) = 2.5 \times 10^8 \text{ kcal FFE/yr}$$

^gAdditional water treatment for disease prevention: chlorination of water supply cost - $.01/1000 gal (cost from water treatment plant, Gainesville, Fla.)

$$(\$.01/1000 \text{ gal})(2.8 \times 10^6 \text{ gal/day})(365) = (\$10,220/\text{yr})(25,000)$$
$$= 2.5 \times 10^8 \text{ kcal FFE/yr}$$

^hIncrease in cypress growth: assume net production increases by 33% due to nutrients (Brown, Bayley and Zoltek, 1974) - cypress wood production = 1.7 kcal/ m2-day. Assume 2.5 cm/wk application rate which would then require 289 ha of cypress. Assume cypress wood energy quality of 2350 kcal sunlight/kcal wood (Figure 84),

$$(0.33)(1.7 \text{ kcal/m}^2\text{-day})(2350/2000)(365 \text{ days/yr})(2.89 \times 10^6 \text{ m}^2)$$
$$= 7.0 \times 10^8 \text{ kcal FFE/yr}$$

ⁱFossil fuel work stimulated by cypress production: harvest costs - $66/1000 bd-ft for rough-cut lumber (State Div. of Forestry, pers. comm.). Total harvest value of 289 ha of cypress domes

$$(\$66/1000 \text{ bd-ft})(24 \text{ bd-ft/tree})(0.05 \text{ tree/m}^2)(2.89 \times 10^6 \text{ m}^2) = \$229,000$$

Footnotes to Table 30 - continued

Assume 33% increase in wood due to sewage in 19 years (Brown et al., 1974),

$$\frac{(\$229,000)(0.33)}{19\ \text{years}} = (\$3975/\text{yr})(25,000) = 1.0\text{x}10^8\ \text{kcal FFE/yr}$$

Finished wood cost = \$350/1000 bd-ft (M. Brown, pers. comm.), therefore

process cost = \$350-66 = \$284/1000 bd-ft

$(284/66)(1.0\text{x}10^8) = 4.3\text{x}10^8$ kcal FFE/yr

Assume manufactured product cost is twice the materials cost as with a house (M. Brown, pers. comm.),

$(350/66)(1.0\text{x}10^8) = 5.3\text{x}10^8$ kcal FFE/yr

^{j}Tertiary treatment cost for phosphorus removal: for 2.8 mgd sewage treatment plant (chemical precipitation), capital cost = \$0.13x10^8, operating cost = \$0.04/1000 gal (Smith, 1968). Assume 25-year depreciation and 10% annual interest rate,

$(\$0.13\text{x}10^6)(0.11017)$ = \$14,322/yr

$(\$0.04/1000\ \text{gal})(2.8\text{x}10^6\ \text{gal})(365)$ = $\underline{40,880/\text{yr}}$

$\$55,202/\text{yr} \times 25,000 = 13.8\text{x}10^8$ kcal FFE/yr

^{k}Tertiary treatment cost for nitrogen removal: for 2.8 mgd sewage treatment plant (ammonia stripping), capital cost = \$0.13x10^6, operating cost = \$0.02/1000 gal. Assume 25-year depreciation and 10% annual interest rate,

$(\$0.13\text{x}10^6)(0.11017)$ = \$14,322/yr

$(\$0.02/1000\ \text{gal})(2.8\text{x}10^6\ \text{gal})(365)$ = $\underline{20,440/\text{yr}}$

$\$34,762/\text{yr} \times 25,000 = 8.7\text{x}10^8$ kcal FFE/yr

yield to high quality energy is small. The high fossil fuel cost to divide nutrients from water only to combine them again in agricultural practices raises questions about the overall merits of the process. These models suggest that the cypress may yield a higher realized work service per purchased energy invested. The calculations are very tentative, since the cypress experiments are in early stages and the response of the trees to nutrients is still under study. All economic interactions have obviously not been considered, including the value of the natural systems for wildlife and relative distribution costs of the alternatives.

Succession in Lake Alice

The marsh half of the lake is well entrenched with waterhyacinths although it has been observed that rooted aquatics are making inroads around the edges as the organic deposits continue to build up. The open lake, however, is continually experiencing man's manipulation through hyacinth harvesting and spraying. It may be in a quasi-steady state. The question still remains as to whether the waterhyacinth would necessarily dominate the deeper open lake should control methods be curtailed. It was covered completely before control measures started.

In Table 6 it was shown that the community metabolism of the water column was not necessarily a function of solar radiation alone despite the abundance of nutrients. These great

variations in solar efficiency may be partially explained by the flushing of the lake during periods of high runoff. Figure 86 shows a plot of photosynthetic efficiencies at Stations 6 and 11 as a function of lake level, which is a measure of the amount of water discharging from the lake. A good correlation was found for Station 11 (r=.95) with less significance found for Station 6 (r=.68). (The causal relationship may not be linear.) The Lake Alice open water community thus maintains a rate of production which is hydrologically dependent. Similar cases are discussed by Brook and Woodward (1956) for some small Scottish lakes and by Dickman (1969) for a small lake in British Columbia. Both studies found low rates of phytoplankton productivity associated with high rates of flushing.

The open water production in Lake Alice was not dominated by phytoplankton. Simultaneous light-dark bottle measurements during three of the community metabolism tests indicate 17-46% of the community production is due to plankton (M. Kiern, personal communication). Most of the production is probably associated with several fine-branching hydrophytes found in great abundance in the lake, especially *Ceratophyllum demersum*, *Najas guadalupensis*, and a filamentous green algae similar to *Spirogyra* sp. These plants break off into semi-submerged masses and are very susceptible to the prevailing lake currents. Increased lake flow may have a flushing effect on these macrophytes as well as on the plankton. Campus workers clean the screens protecting the discharge daily because of

Figure 86.   Open lake phytoplankton-submerged macrophyte production efficiencies as a function of lake stage for two stations in Lake Alice, where lake stage is a measure of discharge from the lake.
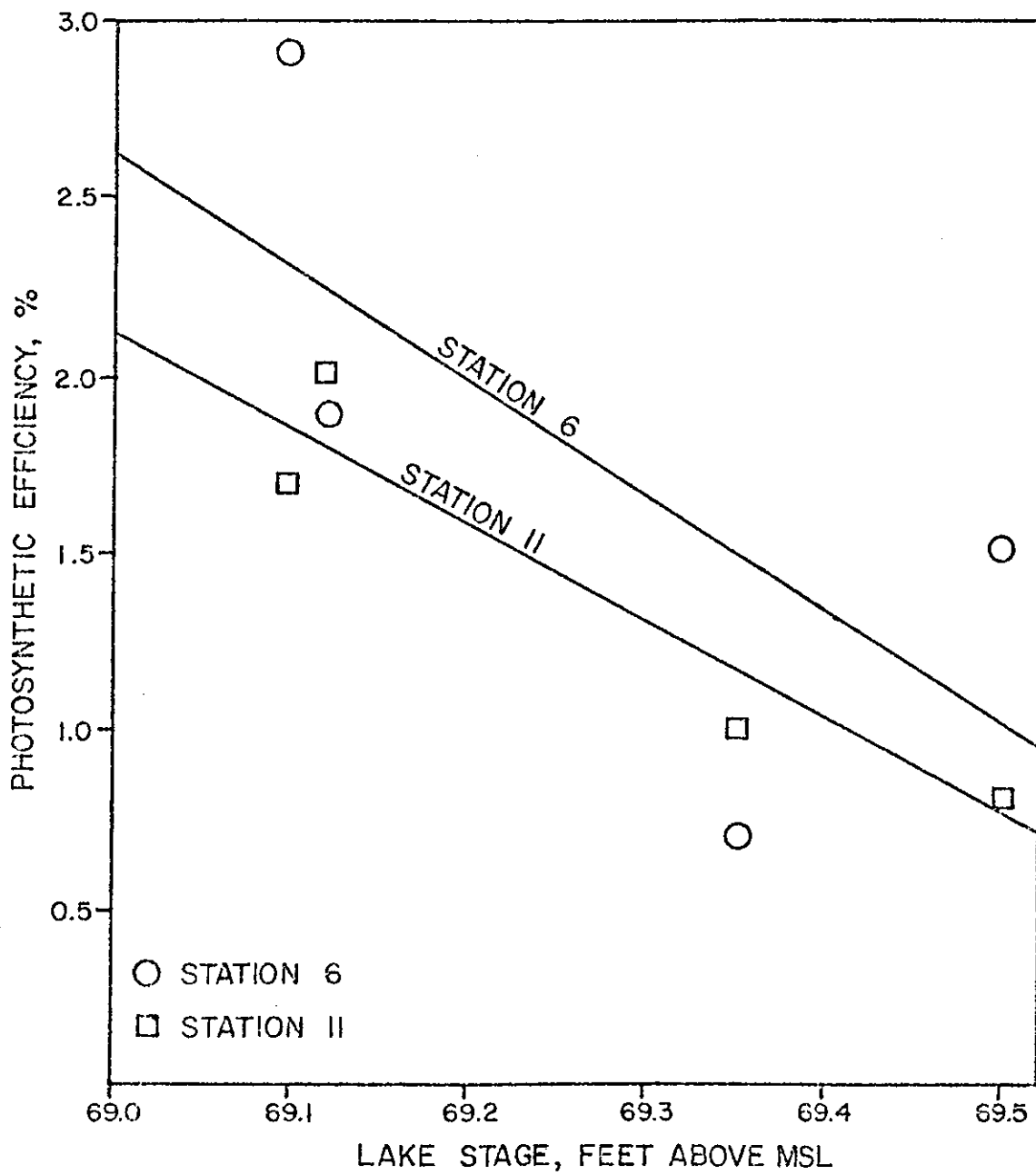
the buildup of sloughed-off organic matter from the lake. The submerged aquatic macrophytes and phytoplankton may trade off in dominance throughout the year similarly to the yearly succession described by Goulder (1969) for an English pond. Simulation results for the Lake Alice model also suggest that winter blooms of phytoplankton are followed by spring peaks of the submerged aquatics with their slower turnover (see Figure 40).

The waterhyacinth, when introduced to the above system of high nutrients and flows, has several distinct advantages over the plankton system in its ability to maximize productively. Carbon dioxide metabolism studies indicated that the small waterhyacinth was well adapted to covering large areas quickly due to its high P/R ratio. Only after it has covered an area by spreading laterally (due mainly to vegetative reproduction) and crowding occurs does the plant begin to put more of its captured solar energy into the maintenance of large structures, expanding vertically. The higher productivity of hyacinths was enhanced by the flowing water which continually replenished the nutrient supplies to its roots. The high net productivity of hyacinths contributed a substantial amount of detrital matter that was continually deposited on the bottom, making conditions less than optimal for benthic production. Continuous mats of large hyacinths, with each plant connected to its neighbors through a network of stolons, are very resistant to movement even in moderate currents. The smaller mats move more easily but are adapted to move in

the direction of the wind rather than in the direction of the
flow unless the current is especially high. Thus the factor
which keeps phytoplankton and submerged aquatics from com-
pletely dominating this highly eutrophic lake serves as an
additional energy source to the waterhyacinth and does not
help to keep the hyacinth population in check. Lake Alice
is thus a system well designed for waterhyacinth domination
and control efforts can at best delay the inertia of this
natural succession.

Cypress Tree Production

The growth of cypress trees depends on factors other
than available nutrients. Drainage patterns, water levels
and fluctuations, interspecific competition, pH, and sediment
depth may all influence the primary production of the cypress.
Indeed, a controversy still remains as to whether the differ-
ence between the fast-growing bald cypress of riverine and
lake shore systems and the slow-growing pond cypress of domes
and sloughs are due to environmental factors, to a difference
in species, or a difference in density. The availability of
cypress growth data over several years from the Withlacoochee
State Forest and from Alachua County allowed some calculations
to be made evaluating the importance of various factors on
cypress growth.

Withlacoochee State Forest

The plots analyzed for cypress net productivity in the Withlacoochee State Forest were classified according to the associations in which the cypress were growing. The three general classifications used were (1) cypress-pine association, (2) cypress-tupelo gum association, and (3) cypress-mixed hardwood association. Only those plots which contained species in addition to cypress could be used in this analysis. Productivities were calculated and plotted against tree density for these plots in Figure 87. Productivity was correlated with density for the cypress-pine (r=.955) and the cypress-tupelo (r=.932) associations. No correlation was found for the hardwood sites. The cypress-tupelo system shows a greater net productivity than the cypress-pine association, a finding that may verify the results of Carter et al. (1973) concerning drainage effects on cypress. The appearance of pine, generally slash pine, in the cypress plots often indicates well-drained conditions due to the low tolerance of that species for saturated soil. Cypress in association with tupelo, on the other hand, indicates poorly drained conditions, with standing water for at least most of the year. The slopes of the lines in Figure 87 give an indication of the net production per tree and are calculated as

cypress-pine association   5.0 kg/tree-yr

cypress-tupelo gum association   6.9 kg/tree-yr

While the cypress-hardwood values do not form a significant relationship in Figure 87, it must be noted that most of

Figure 87. Relationship between tree density and system net primary productivity for three cypress associations: cypress-pine, cypress-tupelo, and cypress-mixed hardwoods. Net production includes wood, litter and root loss calculated on an annual basis.
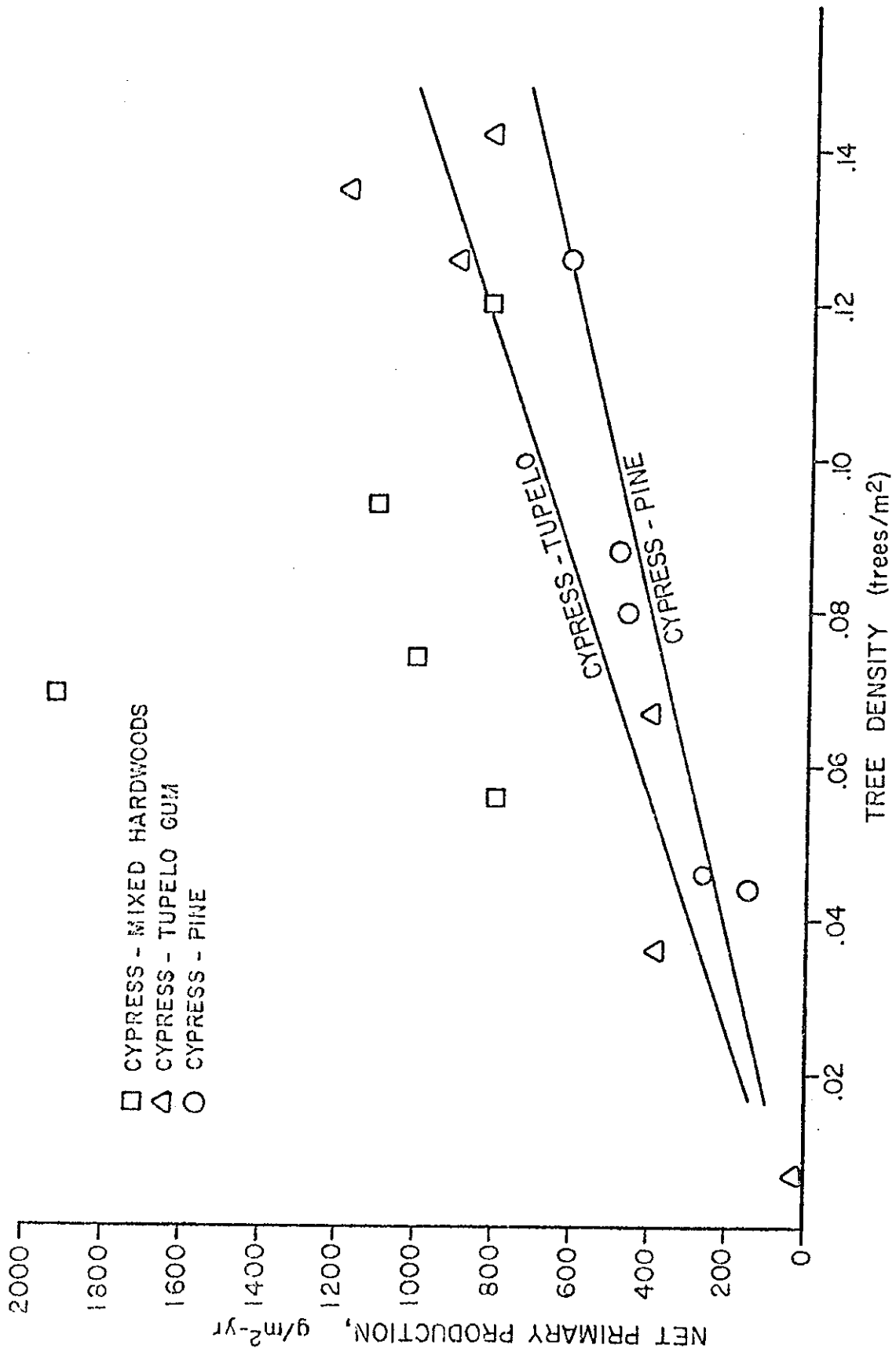
these plots display a much greater net productivity than either the pine or tupelo sites. Plot 378 contains, in addition to 24 cypress, 27 ash, one water oak, and one maple and is the only plot positively identified as being in a riverine system, being located on the Little Withlacoochee River. This plot had an excessively high productivity of 1925 g/m^2-yr.

Alachua County Cypress Domes

Results of the calculations from tree growth data from two Alachua County cypress domes indicate that cypress in a drained site were growing at a significantly greater rate than were those at an undrained site. The drained site was being invaded by pine as witnessed by the decreased dominance of the cypress (89.7% to 71.4% in 11 years) while the species composition at the wet site, which fell on the boundary of a dome, was constant over the same period. The average production values calculated for the two sites were:

cypress dry site - 7.5 kg-tree-yr

cypress wet site - 4.4 kg/tree-yr

These results seem to contradict those of the Withlacoochee analysis until one considers some additional variables. The wet Alachua County site was semi-surrounded by an earthen berm which, in this case, was preventing water from draining out of the dome, thereby increasing the time that the cypress were flooded. In addition, the dry site data show that the most recent cypress growth was less than either of the previous two rates, indicating that the pine may in fact be

beginning to slow the cypress growth through competitive mechanisms. The Withlacoochee results can therefore be used more to suggest the relative interspecific competition of cypress with either pine or tupelo rather than strictly drainage conditions.

A summary of the factors influencing cypress tree growth as determined from the results of both of these sites is thus:

(1) Cypress trees grow better in drained conditions than in undrained conditions. Growth is slowest when the natural hydroperiod is damped by continual flooding.

(2) As pine trees invade an undrained cypress site, the cypress will be out-competed by the fast-growing, evergreen pine. Thus the increased cypress productivities due to more oxygen in the root zone will be quickly offset by the tree's poor ability at interspecific competition.

(3) A cypress-tupelo association indicates a drainage condition favoring continued cypress dome survival and high levels of tree productivity.

(4) Cypress-riverine and mixed hardwood systems have been shown to have net productivities of up to three times that of the more stagnant cypress domes, thereby indicating the importance of the moving water energies on ecosystem function.

Cypress Domes and Fire

The fire that swept the experimental cypress dome area on December 4, 1973, prior to sewage pumpage provided some information as to the role of fire in cypress domes. Subsequently, fire was also included as part of the cypress model simulations.

Table 31 gives the effects of the fire on the sewage and groundwater domes at the experimental sites. In both domes the fire had a "cleansing action" on the invading species in the dome and proved to be a significant selection pressure for monospecific cypress system survival. Over 90% of the pine, both in terms of numbers and biomass, were eliminated from each dome. The fire also killed 13 to 15% of the cypress trees but this amounted to only 2 to 3% of the cypress biomass. This suggests, as expected, a decreased susceptibility of cypress to fire with age and lends credence to the theory put forth by Kurz and Wagner (1953) that the cypress dome shape is due to the more significant effect of fire nearer the edges where the smaller cypress trees are. While half of the total number of trees were eliminated, only one-fourth to one-fifth of the biomass was killed.

Models were simulated to examine the effects of various management activities on the influence of fire in cypress domes. Because fire intensity is directly related to understory biomass and accumulated organic matter and inversely related to water level, any human activity which tends to

Table 31

EFFECTS OF FIRE ON BIOMASS AND NUMBERS OF TREES IN CYPRESS DOMES

Species	Live		Dead		% Decrease	
	Number	Biomass, kg/m^2	Number	Biomass, kg/m^2	Number	Biomass
			Sewage Dome			
Cypress	269	13.59	42	0.31	13.5	2.2
Pine	11	0.29	152	3.55	92.8	92.4
Hardwoods	3	0.04	122	0.66	97.6	94.3
Total	283	13.92	316	4.52	52.7	24.5
Total before fire[b]	599	18.50	--	--	--	--
			Groundwater Dome			
Cypress	495	17.55	87	0.61	14.9	3.3
Pine	9	0.09	180	3.39	95.2	97.4
Hardwoods	116	0.52	447	0.99	79.4	65.5
Total	620	18.16	714	4.99	53.5	21.5
Total before fire[b]	1334	23.19	--	--	--	--

[a]Does not include leaves.
[b]Includes additional biomass of leaves.

increase the former or decrease the latter would increase the probability of a serious fire. Simulations of low water alone (Figures 69 and 70), while allowing fire into the system, did not result in severe stress on the cypress trees. The understory and peat layer were not able to reach high enough values to feed a large fire, thus showing fire to have the same clearing and recycling role that it has in the surrounding pine flatwoods. But when harvesting of cypress is combined with low water conditions, disastrous fires resulted. With the removal of cypress, the understory is given a chance to accumulate significant amounts of organic matter, both in the standing biomass of the understory and in the duff layer. When drainage takes place, these organic storages are excellent fuel for a large fire such as the one experienced at our experimental cypress domes. Simulations accordingly resulted in the killing of some cypress (Figures 71 and 72).

Analysis of the Limiting Nutrient Concept

Several concepts were used in this dissertation to represent mathematically the concept of limiting nutrients. In the Lake Alice model, limiting factor terms of the Michaelis-Menten type were multiplied together. This model is shown in energy language and mathematical form with resulting limiting factor curves in Figure 88a. As one factor is increased, output curves level to plateaus due to that factor's limitations. As with limiting factor experiments, the height of the plateau

Figure 88. Comparison of energy language, mathematics, and limiting factor curves for three methods of modeling limiting factors: (a) multiple Michaelis-Menten factors; (b) sunlight limitation model; and (c) model with self-limitation imposed with limiting factor concentrations.

ENERGY LANGUAGE

MATHEMATICS

LIMITING CURVES

a)
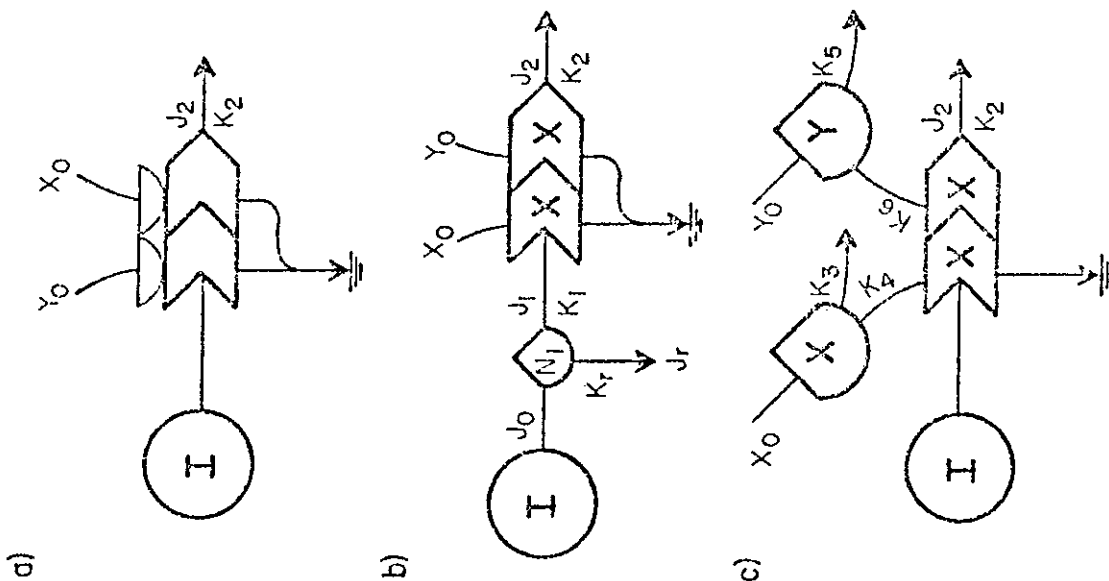
$$J_2 = K_2 I \left(\frac{K_3 Y_0}{K_4 + Y_0} \right) \left(\frac{K_5 X_0}{K_6 + X_0} \right)$$

INCREASING Y_0

X_0

J_2

b)

$$J_2 = \frac{K_2 X_0 Y_0 J_0}{K_r + K_1 X_0 Y_0}$$

INCREASING Y_0

X_0

$\dfrac{K_2 J_0}{K_1}$

J_2

c)

$$J_2 = K_2 I \left(\frac{X_0}{K_3 + K_4 Y I} \right) \left(\frac{Y_0}{K_5 + K_6 X I} \right)$$

INCREASING Y_0

X_0

$\dfrac{K_2 I Y_0}{K_6}$

J_2
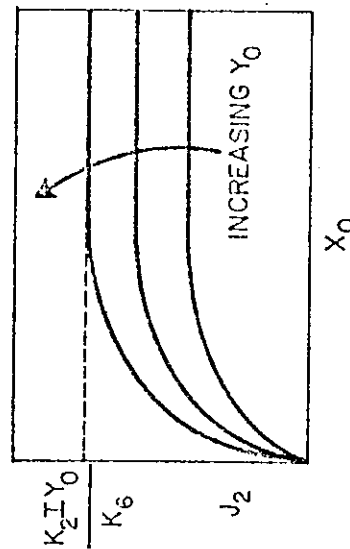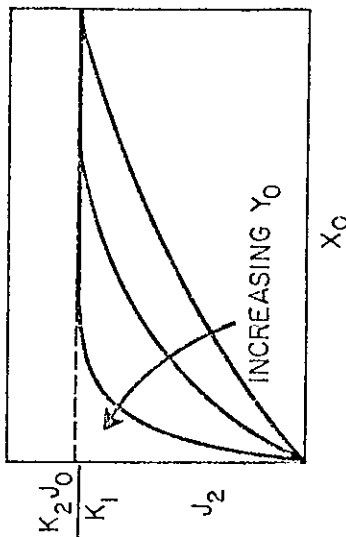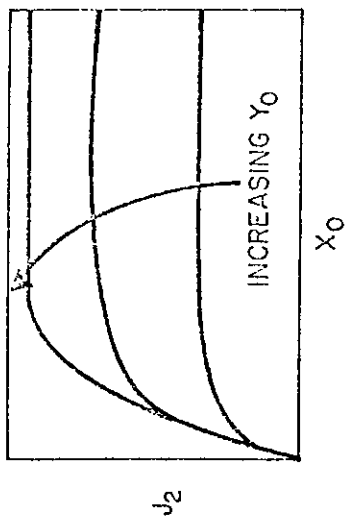
is dependent on the concentrations of the second limiting factor.

In Figure 88b, concentrations are controlled at the point of inflow and simpler expressions result. When two nutrients are interrelated in this manner and their concentrations are held constant, the mathematical equation resembles a Michaelis-Menten-type expression. This does not reduce, however, to the equation of Figure 88a. If nutrient levels are low, productivity is proportional to the product of sunlight and the two nutrients. As levels increase, productivity reaches a maximum level which is only a function of sunlight. Thus the curves converge.

In Figure 88c, rates of inflows are controlled, the local concentrations vary, and the expression is more complex, as developed by Rashevsky (1960) and reviewed by Odum (1972a). The resulting limiting factor curves are similar to those in Figure 88a, but the mathematical equations are not the same. Limitation in this model is caused by the depletion of one storage when the second has high inflows. This may explain the behavior of the nitrogen in Figures 73 and 74 when excessive phosphorus was simulated in the cypress dome model. Gilliland (1973), in a model similar to the one in Figure 88c, found that one limiting factor (nitrogen) was pulled almost to zero by the additions of large amounts of a second limiting factor (phosphorus).

The use of the Michaelis-Menten equation in a multiplicative form for several limiting factors as in Figure 88a was

the subject of discussion at a recent eutrophication modeling conference (Middlebrooks et al., 1974). Cordeiro et al. (1974) stated that "the Monod expression does not represent the dynamics of microbial cell growth and the multiplication of factors does not give the growth rate for multiple limiting nutrients." Bloomfield et al. (1974) and Parker (1974) also question the multiplication of Monod-type expressions while Lassiter and Kearns (1974) summarize several objections to this type of model:

> It has been criticized as resulting in values which are too small when more than one factor is sub-optimal. . . . Second, it may be interpreted to mean that the rate of growth of phytoplankton is a function of the external concentration of each nutrient independent of all others. . . . Third, although the equation deals with multiple nutrients, it affords no capability for uptake or growth as a function of nutrients internal to the cells (p.134).

These objections, while well founded, are generally aimed at a modeling problem that has been restricted to the growth of pure algae cultures in laboratory conditions. In these experimental conditions, as shown by Mitscherlich (1909) and Bose (1924), the mathematical models predict the actual system accurately. Systems modeling, however, must transcend isolated monoculture approaches in order to deal with real systems that, through succession and natural selection, tend towards maximization of energy flows (Lotka, 1922) with continual redesign of ecosystems. Odum (1967,1975b) also gives reasons for multiplicative relationships being preferable over chains of Michaelis-Menten terms.

The second model, presented in Figure 88b, predicts the same productivity for various combinations of nutrients. This suggests the interesting concept that ecosystems, through tight cycling, species substitution, and other mineral cycling strategies, can utilize different ratios of limiting factors to achieve the same power flows. This model, however, assumes that nutrient supplies are large and sunlight is limiting.

The third model, shown in Figure 88c, may be a more typical way to represent limiting factors when depletion of storages is a common occurrence, i.e., when the uptake through photosynthesis has a dramatic effect on the concentrations. The possibility of excesses on one nutrient causing a shortage of a second, as discussed by Gilliland (1973), presents an interesting observation from this model. This model may better represent the actual workings of nutrient limiting cases than the previous two, especially for low nutrient conditions. The second model (Figure 88b) is more applicable, however, when only sunlight is limiting.

Recommendations for Management

The interfacing of man and nature through ecological engineering finds particular applications when the disposal of high nutrient wastewater is considered. The importance of water and nutrients as amplifiers for energy flows in both domestic and natural ecosystems suggests that these waste-waters be treated not as burdens to be discarded but as

misplaced resources. Some general recommendations for management can be suggested from this comparative study of two disposal methods.

1. A pattern of localized disposal sites for small communities and subdivisions whereby secondary sewage wastes are recycled to nature without overloading may be preferable to the concentration of high flows in a centralized system. Cypress domes, because of their ability to absorb large quantities of nutrients under flooded conditions, offer suitable disposal sites for such a scheme in Florida.

2. Loading rates for cypress domes should not exceed 2 to 5 cm/wk, especially in the wet season. The management of cypress domes under artificial loading may also require recognition of nature's limitations with periodic drawdowns.

3. If tree harvesting is to be a part of man's symbiotic relation with cypress swamps, what better way is there to prevent damaging fires than to maintain standing water with wastewater application. Models showed that dry cypress domes are more susceptible to serious burning when harvesting is part of the management.

4. Waterhyacinth mats cannot be expected to take up high percentages of nutrients, because their requirements for high flow rates make high losses inevitable. However, the use of a hyacinth pond to treat water prior to disposal in a cypress dome would have the advantage of maximum uptake in the summer months when the cypress disposal method is hydrologically taxed. In the winter, when hyacinth growth is not

so vigorous, the dome percolation would be greatest.

5. Groundwater injection of high nutrient water may be wasting resources that require replacement with pumped groundwater and purchased fertilizers. The application of these waters to the land may offer what have previously been hidden savings in time of excess energy.

6. If control efforts are necessary in a eutrophic body of water, continual management patterns rather than periodic ones are preferable. A steady state ecosystem can develop around man's activities when sharp perturbations are not caused.

7. The expenditure of large amounts of fossil fuel technology on tertiary treatment for nutrient removal may prove to be an unwise investment when natural systems can be found to do the job at a smaller cost or possibly with a net benefit. Water and nutrients separated at the sewage plant only to be united again in a downstream agricultural system may suggest a poor vision of the whole system.

8. High temperature effluents, such as the one maintained in Lake Alice, may best serve a function when mixed with high nutrient flows in prolonging the growing season for plant nutrient uptake. Simulations suggest that diversion of the heated waters from a eutrophic body of water may create a highly oscillating system.

APPENDIX A

A REVIEW OF THE LITERATURE
ON LAND DISPOSAL OF NUTRIENT WASTES

Because of the extensive problems associated with eutrophication of bodies of water, investigators and planners have begun to look at other schemes for the disposal of nutrient wastes. Land disposal of wastewaters, once a fairly common practice for man, has made a reappearance as an alternative solution to this problem. As fossil fuel supplies to man begin to level off or decline, energy-expensive tertiary treatment processes for nutrient diversion will appear less attractive and land disposal may become a more suitable alternative. Also of overriding significance will be the importance of nutrient recycling from urban centers in lieu of a fossil fuel-based fertilizer industry for the production of food and fiber.

A wealth of data from previous land disposal studies is available to augment several recently initiated investigations. Application of wastewater to land, primarily from municipal and industrial sources, has been a fairly common practice of disposal in the last half of this century, especially in those arid regions where groundwater recharge and supplemental irrigation needs make water a limiting factor in itself. Sullivan (1974) verifies a total of 347 land application sites in the United States, most of which are located in the Southwest. A brief review of some important land disposal projects follows. Discussion of these applications is accommodated by dividing the systems into three groups: agronomic-grass systems, soil filter systems, and forested systems. Each of

these classifications has certain turnover times and loading capabilities that make them distinct.

Agronomic and Grass Systems

Many of the land disposal locations described in the literature involve wastewater application to agronomic and grass systems. A summary of some of the important research sites is given in Table A-1. Merz (1956) and Crites (1974) document the long-time use of raw and primary sewage effluent for cropland irrigation at Bakersfield, California. The wastewater was first applied in 1912, and crop yields are reported to vary from slightly below to well above the county-wide average. However, nitrate values in the unconfined aquifer were found to range as high as 60 mg/1, indicating a possible groundwater contamination over the many years of operation. Day et al. (1962,1963) report on an investigation in Tucson, Arizona, where secondary sewage was used for irrigation of barley fields. They document greater grain yields on sewage plots than on those plots receiving well water with nitrogen, phosphorus, and potassium in amounts equivalent to the sewage. However, lower barley and malt quality was noted. Dairy waste land disposal for irrigation is discussed by Breska and Erickson (1956) and McKee (1957), while using cannery wastes for spray irrigation is the subject of papers by Sanborn (1953), Monson (1960), and Bendixen et al. (1969). The last authors report 93% reduction for nitrogen and 84%

Table A-1

EXAMPLES OF AGRONOMIC AND GRASS SYSTEMS USED
AS LAND DISPOSAL SITES FOR WASTEWATER

Location	Dates	System Receiving Waste	Type of Application	Application Rate, cm/wk	Type of Waste	References
Bakersfield, Calif.	1912-present	agronomic	irrigation ditches	3.4	primary sewage effluent	Merz (1956) Crites (1974)
Kraft Food Co.		agronomic	spray	17.5	dairy wastes	McKee (1957)
Several eastern U.S. canneries	1947-53	pastures, alfalfa fields, etc.	spray	7.5-10	cannery & dairy wastes	Sanborn (1953)
International Paper Co., Bodcau Bayou, La.	1952-64	agronomic	application as needed		paper mill effluent	McCormick (1959) Vercher et al. (1965)
Arizona Ag. Exp Sta., Tucson, Ariz.	1957-58	barley fields	flood	2.6	secondary sewage effluent	Day et al. (1962) Day et al. (1963)
Northwest Ohio processing plant	1961-65	perennial grass system, reed canarygrass	spray-overland flow	12.9	cannery waste	Bendixen et al. (1969)
Penn State U. State College, Pa.	1963-present	agronomic plots	spray	2.5-5	secondary sewage effluent	Kardos (1967)

Table A-1 - continued

Location	Dates	System Receiving Waste	Type of Application	Application Rate, cm/wk	Type of Waste	References
Penn State U.	1965-69	perennial grass system, reed canarygrass	spray	5	secondary sewage effluent	Sopper (1973)
Penn State U.	1972-73	grass	overland flow	7.3-29.3	secondary sewage effluent	Butler et al. (1974)
FWQA Ada, Oklahoma	1967-68	hydroponic grass system	flooding	52.5-105	secondary sewage effluent	Law (1969)
U. of Arizona Tucson, Ariz.	1971-72	turfgrass-soil system	percolation in 20 liter pots as needed	--	secondary sewage effluent	Sidle & Johnson (1971)
Muskegon Co., Michigan	1974	cleared land	spray irrigation	4.4	secondary sewage effluent	Bauer & Matsche (1973) Bastian (1973)

for phosphates. Chapman (1962) gives some results of pasture development when sewage effluent is applied. McCormick (1959) and Vercher et al. (1965) report on a series of experiments by International Paper Company and Louisiana State University along Bodcau Bayou from 1952 to 1964, brought about because of farmers' claims that paper mill effluents were adversely affecting cattle, crops, and soil in the area. The results showed no detrimental effect of crop irrigation with the wastewater but little increase in growth over ordinary irrigation. Kardos (1967, 1970) reports on one of many land disposal projects at the Pennsylvania State University, State College, Pa., where, since 1963, agronomic plots of corn, wheat, red clover, and alfalfa have received seasonal spraying irrigation of secondary sewage effluent. Alfalfa yields increased 139%, corn silage 39%, corn grain 78%, and oats grain 70%, with essentially all the nitrogen and phosphorus removed by the plant soil system. The author estimates that 129 acres is necessary to dispose of 1 million gallons of wastewater per day, equivalent to an application rate of 5 cm/wk. He cautions, however, that, "Since any disposal system must operate on a year-round basis, in northern climates, when higher plant forms become dormant in the winter period, the living filter system must rely more on the adsorptive capacity of the soil and less on the reduced activity of the microbes and the roots of perennial plants" (Kardos, 1970, p. 27).

Grass systems are similar to other agronomic systems for land disposal in the equivalent turnover times of the plants.

Law (1969) found in a one-year study in Oklahoma that hydro-
ponic grass systems, held in 5.6 m^2 tanks and subjected to
7.5 to 15 cm/day of secondary sewage, removed only 4-8% nitro-
gen, 2-5% phosphorus, and 6-22% potassium. Sidle and Johnson
(1971) applied secondarily-treated sewage to common bermuda
grass (*Cynodon doctylon*) and annual rye grass (*Lolium molti-
florum*) and found nitrogen removal greater than 40%. Sopper
(1973) cites perennial grasses as most suitable for wastewater
sites because of their fibrous root systems, sod-forming
capabilities, wide environmental tolerance, long period of
growth, and high nutrient uptake. At Penn State, studies
revealed a renovation efficiency (harvested/applied) of 97.3%
for nitrogen and 35% for phosphorus for a reed canarygrass
system (Sopper, 1973). A diagram of the nutrient flows in
that system is given in Figure A-1. Examination of the dia-
gram reveals the sewage effluent to have a low N/P ratio, and
the percolating groundwater to have an excessively high N/P
ratio, leaving an obvious build-up in phosphorus in the soil
over time. It was found that despite the high renovation
efficiency for nitrogen, the "average concentration of
nitrate-N in the percolate at the four-foot soil depth during
the six-year period was 3.5 mg/l in the effluent irrigated
areas and 0.2 mg/l in the control areas." This additional
nitrogen was suggested to originate in the native soil nitro-
gen. Butler et al. (1974), in another Penn State study, how-
ever, found that "no significant reduction in phosphate or
nitrate concentrations was observed in secondary treated
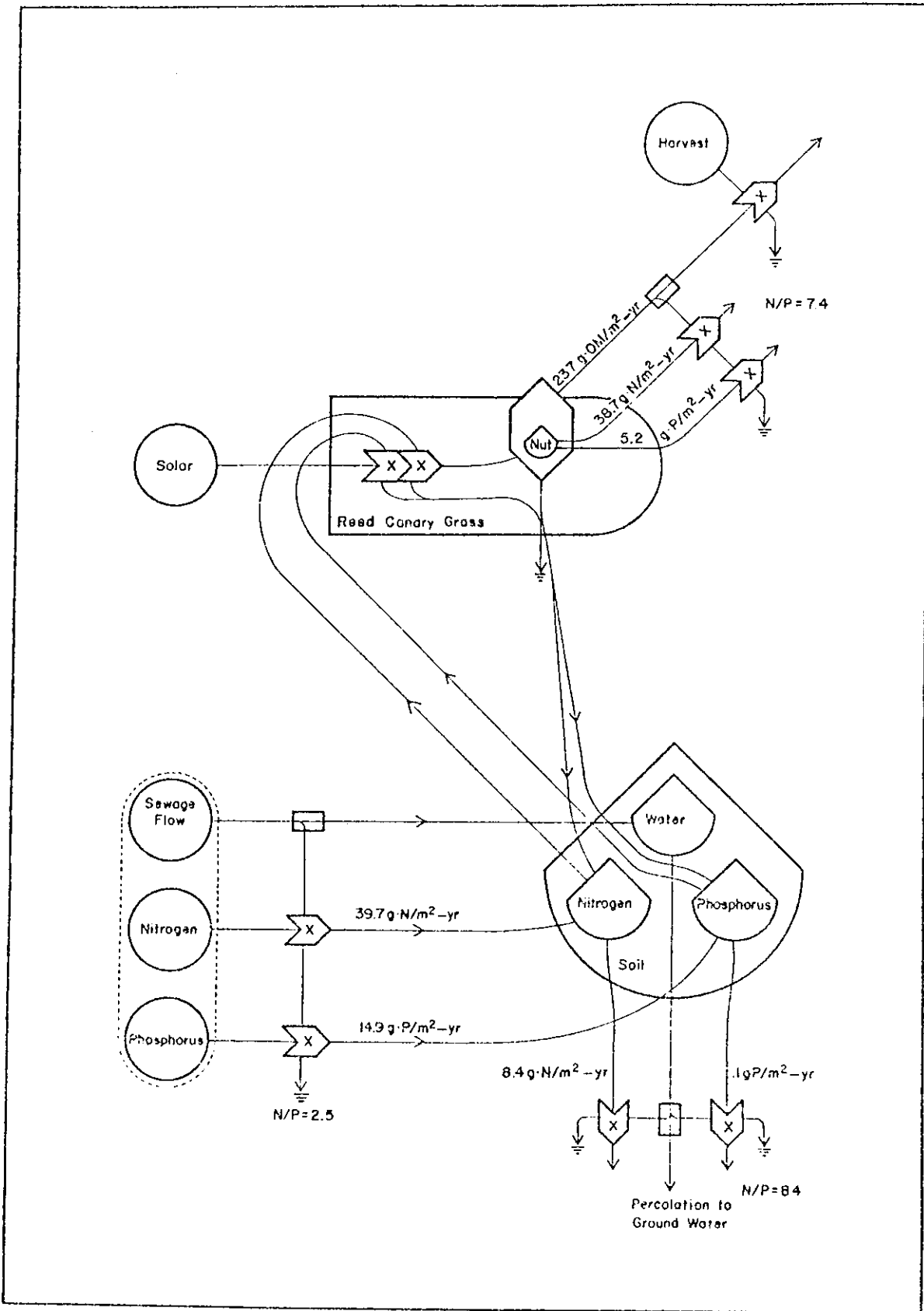
Figure A-1. Nutrient balance in energy language of secondary sewage being applied to reed canarygrass system (from Sopper, 1973).

municipal sewage effluent after grass filtration" for reed canarygrass when the system was designed on sloping sites for overland flow.

Soil Filter Systems

Many wastewater disposal projects (Table A-2) have been designed primarily for artificial recharge of groundwater to augment potable water supplies. In this type of system, maximum infiltration rates are designed into the project, thus requiring soils which are generally very sandy with high vertical permeabilities. Vegetative growth is either not present or actively discouraged. Artificial recharge has been widely practiced in Europe for many years (McMichael and McKee, 1966). For example, a system in the Netherlands, using the sand dunes on the North Sea, has been in operation since 1940 (Baars, 1957). Israel has carried out a pilot plant operation at Ashqelon in anticipation of extensive use of wastewater disposal in sand dune areas (Amramy, 1968). Because of clogging of the soil, an operating cycle of 2 to 3 days' wetting with 7 to 8 days' drying was adopted. Potable water standards, however, were not attained at a depth of 20 m due to higher than recommended values of dissolved iron and man-ganese. Nitrate values were also excessive with an average of 16.2 mg/1 at 80 m in depth. The Southwest has been in-volved in many water reclamation projects with the most not-able being Flushing Meadows near Phoenix (Bouwer, 1968,1973).

Table A-2

EXAMPLES OF SOIL FILTER SYSTEMS USED AS LAND DISPOSAL SITES FOR WASTEWATER

Location	Dates	System Receiving Waste	Type of Application	Application Rate, cm/wk	Type of Waste	References
Leiden Waterworks Leiden, the Netherlands	1940-present	sand dunes	surface spreading	210-280	Rhine River water	Baars (1957)
Flushing Meadows Phoenix, Arix.	1957-present	sand recharge basins	surface spreading	234	secondary sewage effluent	Bouwer (1968, 1973)
Whittier Narrows L.A., Calif.	1962-65	sand recharge basins	surface spreading	77.7	secondary sewage effluent	McMichael & McKee (1966)
Santee, Calif.	1959-72	dry river bed	intermittent spray irrigation	--	secondary sewage effluent	Merrell et al. (1967) Merrell & Ward (1968)
Dan Region Project Ashuelon, Israel	1960-65	sand dunes	surface spreading 2-3 days wetting, 7-8 days drying	100-160	sewage lagoon discharge	Amramy (1968)

Whittier Narrows near Los Angeles (McMichael and McKee, 1966), and the Santee California Reclamation Project (Merrell et al., 1967; Merrell and Ward, 1968). Both Flushing Meadows and Whittier Narrows projects experienced problems, however, with high nitrate values. The percolate at Whittier Narrows "exceeded the recommended limit of the U.S.P.H.S. drinking water standards of 1962 by a factor of two or three" (McMichael and McKee, 1966, p. ix) while the Flushing Meadow project experienced nitrate concentrations of 25 to 35 mg-N/l for dry schedules and 1 to 10 mg-N/l for a wetter inundation schedule.

Forested Systems

Attention has shifted more recently to using forested systems (Table A-3) as a means of tertiary treatment of sewage waste in addition to groundwater recharge. The potential for combining large storages of nutrients in both tree biomass and the soil offers, at least in theory, a significant sink for nutrients now accelerating eutrophication in bodies of water. In discussing the use of forests and trees to renovate wastewater, Sopper (1971b) suggests that "the utilization of the higher plants as an integral part of the system to complement the microbiological and physiochemical systems in the soil is an essential component of the living-filter concept and provides maximum renovation capacity and durability to the system."

Table A-3

EXAMPLES OF FORESTED SYSTEMS USED AS LAND DISPOSAL SITES OF WASTEWATER

Location	Dates	System Receiving Waste	Type of Application	Application Rate, cm/wk	Type of Waste	Reference
Gerber Products Fremont, Mich.	1953-60	hardwood seedling plantation black willow (*Salix nigra* Marsh) box elder (*Acer negundo* L.) cottonwood (*Populus deltoides*, Bartr.) balsam popular (*populus balsamifera*)	spray	5	cannery waste	Rudolph & Dils (1955) Rudolph (1957) Dietz & Frodey (1960)
Seabrook Farm Co., Seabrook, N.J.	1950-57	oak-hickory association, black oak (*Quercus velutina* L.) white oak (*Quercus alba* L.)	spray	29-44	food processing wastewater	Mather (1953) Little et al. (1959)
Detroit Lakes Minn.	1955-59	wooded knoll	spray	117	secondary sewage effluent	Larson (1960)
Louisiana State U.		slash pine (*Pinus elliottii*)	irrigation	1.5-3.0	paper mill effluent	Jorgensen (1965)

Table A-3 - continued

Location	Dates	System Receiving Waste	Type of Application	Application Rate, cm/wk	Type of Waste	Reference
Penn State U., State College, Pa.	1963-present	mixed hardwood forest (*Quercus alba* L.,*Quercus velutina* L., *Quercus rubra* L., *Quercus coccinea* Moench)	spray	2.5-5	secondary sewage effluent	Sopper & Sagmuller (1966) Pennypacker et al. (1967) Sopper (1968a, 1971a,1971b, 1973)
Penn State U.	1963-69	red pine (*Pinus resinosa* Ait.) plantation	spray	2.5-5	secondary sewage effluent	Ibid.
Penn State U.	1963-present	old field planted with white spruce (*Picea glauca* Moench voss.)	spray	5	secondary sewage effluent	Ibid.
Huron-Manistee Nat'l Forest Cadillac, Mich.	1970-present	jack pine (*Pinus banksiana* Lamb.) plantation	spray	3.1	secondary sewage effluent	Urie (1973)
Michigan State U. Middleville, Mich.	1972-present	red pine (*Pinus resinosa* Ait.) plantation	spray	2.5-8.8	secondary sewage effluent	Urie (1971) Sutherland et al. (1974)
Maloney Canyon San Bernardino Nat'l Forest, Calif.	1971-present	chaparral	spray	2.5-8.9	secondary sewage effluent	Younger et al. (1973)

Table A-3 - continued

Location	Dates	System Receiving Waste	Type of Application	Application Rate, cm/wk	Type of Waste	Reference
Mt. Sunapee State Park, N.H.	1971-present	mixed hardwood forest on mountain slope	spray	5 summer only	secondary sewage effluent	Frost et al. (1973)
Michigan State U. East Lansing, Mich.	1973-present	mixed hardwood system combined with lake-marsh system	spray	--	secondary sewage effluent	Bahr et al. (1974)
Brookhaven Nat'l Lab, Long Island, N.Y.	1973-present	pitch pine forest (*Pinus rigida* Mill) & oak-pine stand (*Quercus alba* L., *Q. coccinea* Moench, *P. rigida*)	spray	5	primary & secondary sewage effluent	Woodwell et al. (1974)

One of the first projects involving large applications
of wastewater to terrestrial systems was located at Seabrook,
New Jersey, where wastes from a food processing plant were
applied to an oak-hickory forest (Mather, 1953; Little et al.,
1959). A rotating spray nozzle system of application was
used, resulting in marked changes in the vegetation. Within
a radius of 11 m of each spray nozzle, 59% of the trees 1 in
in diameter and greater died in the seven years of operation.
In one plot, all trees within a 30 m radius were killed.
Spraying also virtually eliminated tree reproduction, all
native shrubs, and most of the native herbs. In addition,
soil analysis showed increases in pH, nitrogen, phosphorus,
calcium, magnesium, and potassium. In general the hydraulic
loading as well as the means of waste disposal created a sys-
tem of water tolerant shrubs and herbs significantly differ-
ent than the initial oak-hickory forest. A hardwood seedling
plantation in Fremont, Michigan (Rudolph and Dils, 1955;
Rudolph, 1957; Dietz and Frodey, 1960), was subjected to
spray application of cannery wastes. While initial tree sur-
vival and growth were reported to exceed control plots after
3 years, it was reported some 15 years after the operation
began that all of the trees were eliminated due to icing
(Urie, 1971). Larson (1960) reports on one of the few early
applications of sewage effluent to woodlands. This project,
located at Detroit Lakes, Minnesota, showed considerable
recharge of the groundwater supply but at the price of dras-
tic increases in chlorides (9 to 130 ppm) and nitrate

nitrogen (1 to 31 ppm) in the percolate. Jorgensen (1965) attempted to increase the growth of a slash pine (*Pinus elliotti*) plantation through application of paper mill effluents in Louisiana, but no significant increase in growth was reported.

Probably the most ambitious look at wastewater application to forested ecosystems has taken place at the Pennsylvania State University where three forests, one natural and two managed, have been sprayed with secondary sewage effluent since 1963. The design of the disposal system and subsequent results have been described extensively in the literature (Kardos et al., 1968; Kardos, 1970; Parizek et al., 1967; Pennypacker et al., 1967; Sagmuller and Sopper, 1967; Sopper and Sagmuller, 1966; Sopper, 1968a,1968b,1971a,1971b,1973). The natural system, a 60-year-old mixed oak stand, was able to adsorb essentially all of the phosphorus in the wastewater and 70 to 80% of the nitrates, both measured at 120 cm soil depth. Average annual growth of the oak was not significantly greater than the control with the 2.5 cm/wk application rate, but response was favorable to 5 and 10 cm/wk rates. A red pine (*Pinus resinosa* Ait.) plantation, however, did not fare as well, with nitrate removals of 0 to 70.6% removal reported. Pine growth was reported to vary from slightly above to well below the control group and after 6 years of receiving wastes, every tree from one plot was felled by high winds following a wet snowfall (Sopper, 1971a), again illustrating the effects of excessive hydrologic loads on formerly dry terrestrial

systems. The vegetation of the third forested system was an old field community planted with white spruce (*Pinus glauca* Moench Voes.) seedlings. Growth in height of the saplings increased from 62 to 200% over the control. After seven years of application, the average height of the control plot was 2 m, while the irrigated plot showed an increase to 6 m. Ground vegetation was shown to increase 126% over the control.

Since 1970, many new projects utilizing irrigation of forested areas have started. In Michigan alone, sewage effluents are being applied to a jack pine (*Pinus banksiana* Lamb.) plantation (Urie, 1973), a red pine (*Pinus resinosa* Ait.) plantation (Sutherland et al., 1974), and a mixed hardwood system (Bahr et al., 1974). Other new projects include sewage waste being applied to a chaparral system in California (Younger et al., 1973) and a New Hampshire mixed hardwood forest (Frost et al., 1973). Woodwell et al. (1974) discuss a new experiment to explore the relative uses of aquatic and terrestrial systems for the recovery of nutrients from secondary sewage.

The return of wastewater to terrestrial systems, as outlined above, is not without significant shortcomings. Some of the more frequently occurring problems seen in these and other studies are summarized as follows:

1. Excessive nitrate concentrations are often encountered in the groundwater because this anion is not readily retained by soil colloids (Alexander, 1971). High nitrate concentrations in drinking water are reported to cause

serious and occasionally fatal poisonings of infants (Public Health Service, 1962). Aeration of soils between applications has caused increased nitrification. Increases in chlorides, manganese, and iron, causing primarily aesthetic and taste problems in drinking water, have also been encountered.

2. When spray nozzles are used, considerable tree damage, seedling mortality, and often tree death result within an effective radius. This is compounded in northern climates by icing problems.

3. Many heavy metals and other inorganics may tend to build up in the upper soil horizon due to adsorption and precipitation, possibly to toxic levels.

4. Organic matter, transported with the wastewater, tends to accumulate and clog soil pores, causing problems associated with anaerobic conditions and reduced vertical permeability.

5. Hydraulic loading rates saturate the soil, often create ponding, and in general, diminish oxygen diffusion into the root zone, thereby creating conditions not conducive to terrestrial vegetation survival.

6. As forested projects continue for several years, the system will self-design to the new chemical and hydraulic regimes, and its ability to ward off natural catastrophe is weakened. Thus the red pine plantation at Penn State, responding to saturated soil conditions with a shallow root system, was eliminated by an ice storm.

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APPENDIX B

SUPPLEMENTAL MATERIAL FOR LAKE ALICE MODEL
AS GIVEN IN FIGURE 33 AND TABLE 8

Table B-1

CALCULATED COEFFICIENT VALUES FOR
LAKE ALICE MODEL IN FIGURE 33

Parameter	Calculated Value	Parameter	Calculated Value
k_1	0.6579	k_{32}	0.022
k_2	0.3926	k_{33}	0.0
k_3	0.027	k_{34}	1.62×10^{-4}
k_4	132.0	k_{35}	0.51
k_5	0.10	k_{36}	10.16×10^{-2}
k_6	0.621	k_{37}	3.3×10^{-2}
k_7	0.437	k_{38}	3.2×10^{-4}
k_8	0.134	k_{39}	2.19×10^{-3}
k_{11}	3.89×10^{-3}	k_{40}	2.07×10^{-3}
k_{12}	1.81×10^{-2}	k_{41}	9.13×10^{-3}
k_{13}	8.86×10^{-5}	k_{42}	0.3926
k_{14}	1.4×10^{-3}	k_{43}	0.237
k_{15}	1.81×10^{-2}	k_{44}	0.3926
k_{16}	8.86×10^{-5}	k_{45}	0.3926
k_{17}	257.1	k_{46}	5.55×10^{-3}
k_{18}	2.86	k_{47}	1.11×10^{-4}
k_{19}	4.80	k_{48}	1.11×10^{-2}
k_{20}	5.0×10^{-5}	k_{49}	1.11×10^{-3}
k_{21}	0.6579	k_{50}	5.8×10^{-3}
k_{22}	5.3×10^{-3}	k_{51}	4.0×10^{-3}
k_{23}	1.44×10^{-2}	k_{52}	0.0715
k_{24}	0.20	k_{53}	6.4
k_{29}	0.835×10^{-4}		
k_{30}	114.6		
k_{31}	0.377		

Notes for Table 8

1. Lake and marsh morphology parameters determined from
    area-depth curve in Figure 24; for stage of 69.0 ft:

	Marsh	Lake
area, m^2	208,091	121,700
volume, m^3	95,150	159,440

    Average marsh depth = (95,150)/(208,091) = 0.46 m

    Average lake depth = (159,440)/(121,700) = 1.31 m

2. Marsh hyacinth assumed to be biomass of large water-
    hyacinths in Table 3.

    Q_3 = 11,280 kcal/m^2

3. Marsh and lake detritus assumed to be value measured at
    Station 5 and given in Figure 32.

    (17,900 g/m^2)(4.5 kcal/g) = 80,550 kcal/m^2

4. Average values of marsh and lake phosphorus determined
    from water chemistry data for April-Sept., 1973 (Table 7):

    | | Phosphorus, mg-P/ℓ |||
	Station 1 Marsh Inflow	Station 5 Marsh Outflow	Station 6 Open Lake
April	2.02	2.10	2.84
May	1.32	1.29	1.39
June	2.45	1.45	1.44
July	1.23	1.06	1.58
August	1.24	1.05	1.13
September	1.00	--	1.29
Average	1.56	1.39	1.61

8. Hyacinth biomass for July estimated to be 7000 $kcal/m^2$ for areas covered by open lake; average coverage for open lake for July is 42% (Table 2):

$$(0.42)(7000) = 2940 \ kcal/m^2$$

9. As in Note 6 for waterhyacinth nutrients:

Nitrogen   1.75% of dry wt

Phosphorus   0.63% of dry wt

$$(.0175)(2940)/(4.5) = 11.4 \ g\text{-}N/m^2$$
$$(.0063)(2940)/(4.5) = \ \ 4.1 \ g\text{-}P/m^2$$

10. Lake benthic plants dominated by *Ceratophyllum demersum*; Westlake (1963) found .71 kg/m^2 as seasonal maximum for this species:

$$(710 \ g/m^2)(4.5 \ kcal/g) = 3200 \ kcal/m^2$$

11. Average oxygen for April and May, 1973, diurnals at Station 6 in open lake were 5.0 and 5.5, respectively:

$$(5.0 + 5.5)/2 = 5.25 \ g/m^3$$

12. Phytoplankton biomass--unpublished data by M. Kiern show Lake Alice chlorophyll $\underline{a}$ to be around 40 mg/m^3. Strickland and Parsons (1972) give conversion factor of chlorophyll $\underline{a}$ to plant carbon of 25 to 100.

$$(40 \times 10^{-3} \ g\text{-}chl\text{-}\underline{a}/m^3)(70 \ g\text{-}C/g\text{-}chl\text{-}\underline{a})$$
$$\cdot (10 \ kcal/g\text{-}C)(1.31 \ m) = 36 \ kcal/m^2$$

13. Allochthonous organic matter determined from COD measurements of water and then subtracting phytoplankton biomass:

Average COD $(mg\text{-}O_2/\ell)$ May-Sept., 1973 = 41.4

$$(41.4 \ g\text{-}O_2/m^3)(.9375 \ g/g\text{-}O_2)(4.5 \ kcal/g)$$
$$\cdot (1.31 \ m) - 36 \ kcal/m^2 = 192 \ kcal/m^2$$

14. Water flow (dry weather only) from Figure 25:

Heating plant flow	$43.5 \times 10^3 m^3/day$
Sewage plant flow	$10.5 \times 10^3 m^3/day$
Hume stream	$\underline{8.6 \times 10^3 m^3/day}$
	$62.6 \times 10^3 m^3/day$

15. Phosphorus concentration from Station 1 (Note 4) = 1.56 $g\text{-}P/m^3$; phosphorus concentration average for Hume stream = 1.52 $g\text{-}P/m^3$

$$(1.56 \ g\text{-}P/m^3)(54 \times 10^3 m^3/day) = 84.2 \times 10^3 \ g\text{-}P/day$$
$$(1.52)(8.6 \times 10^3) \qquad = \underline{13.1 \times 10^3 \ g\text{-}P/day}$$
$$97.3 \times 10^3 \ g\text{-}P/day$$

16. Nitrogen concentration for Station 1 (Note 5) = 2.47 $g\text{-}N/m^3$; nitrogen concentration for Hume Stream = 1.58 $g\text{-}N/m^3$

$$(2.47 \ g\text{-}N/m^3)(54 \times 10^3 m^3/day) = 133.4 \times 10^3 \ g\text{-}N/day$$
$$(1.58 \ g\text{-}N/m^3)(8.6 \times 10^3 m^3/day) = \underline{13.7 \times 10^3 \ g\text{-}N/day}$$
$$147.1 \times 10^3 \ g\text{-}N/day$$

17. Unpublished data by Padgett found dissolved oxygen of 5 ppm on inflow stream; assuming the same for Hume Stream:

$$(5 \ g/m^3)(62.6 \times 10^3 m^3/day) = 313 \times 10^3 \ g\text{-}O_2/day$$

18. Because most calculations are based on April-Sept., 1973, measurements, solar radiation values were obtained for same period from E. Farber:

Month	Solar Radiation, $(kcal/m^2-day)$
April	5090
May	5090
June	4950
July	4700
August	4420
September	3940
Average	4700

19. Oxygen diffusion in marsh assumed to be low due to hyacinth coverage. From Odum (1956) $K = .08$ $g-O_2/m^2-hr$ @ 100% deficit:

    Average marsh temperature (Note 21) = 30.7°C

    Saturated O_2 = 7.4 ppm

    Deficit = $(7.4 - 1.0)/7.4$ = .865

    Diffusion = $(.08$ $g-O_2/m^2-hr)(24$ $hr/day)(.865)$
    $\cdot (20,809/m^2)$ = 345×10^3 $g-O_2/day$

20. From Ultsch (1973):

	Under Hyacinths	Open Water
Ave. temp., °C	12.7	13.0
Ave. D.O., ppm	4.0	7.7
Saturation D.O., ppm	10.3	10.2

Diffusion under hyacinths = K_H $(10.3-4.0)/10.3$

$= K_H$ (0.612)

Diffusion open water $= K_O$ $(10.2-7.7)/10.2$

$= K_O$ $(.245)$

If oxygen consumption is the same,

$$K_O \ (.245) = K_H \ (.612)$$

$$K_O = 2.5 \ K_H$$

$\therefore$ diffusion is cut down by waterhyacinths by

2.5 x open water diffusion coefficient

$$= (2.5)(.08) = 0.20 \ g\text{-}O_2/m^2\text{-}hr$$

Oxygen saturation for lake (average temperature

= 28.5°C, Note 21) = 7.66 ppm

$$(0.20)(24)(7.66 - 5.25/7.66)(121,700) = 183 \times 10^3$$

$$g\text{-}O_2/day$$

21. Average temperatures for April-Sept., 1973 (Figure 31), for both marsh and lake:

Month	Marsh Temperature, °C	Lake Temperature, °C
April	29.5	24.1
May	30.0	26.9
June	32.2	29.4
July	31.0	30.8
August	30.7	30.8
September	31.0	29.2
Average	30.7	28.5

22. Organic flow from marsh to lake:

Month	COD, mg-O_2/ℓ Station 5
May	34.5
June	50.8
July	41.6
August	37.9
September	--
Average	41.2 g-O_2/m^3

$$(41.2 \text{ g-O}_2/\text{m}^3)(.9375 \text{ g/g-O}_2)(62.6 \times 10^3 \text{m}^3/\text{day})$$

$$\cdot (4.5 \text{ kcal/g})/(121,700 \text{ m}^2) = 89.4 \text{ kcal/m}^2\text{-day}$$

$$(\text{for lake area})$$

23. From Note 4, marsh phosphorus outflow concentration is 1.39 mg/

$$(1.39 \text{ g/m}^3)(62.6 \times 10^3 \text{m}^3/\text{day}) = 87,000 \text{ g-P/day}$$

24. Nutrient uptake by hyacinths based on hyacinth gross production (242 kcal/m^2-day, Note 33) and nutrient content (0.63% P, 1.75% N, Note 6).

$$(.0063 \text{ g-P/g})(242 \text{ kcal/m}^2\text{-day})(208,091 \text{ m}^2)/4.5 \text{ kcal/g}$$

$$= 70,500 \text{ g-P/day}$$

$$(.0175)(242)(208,091)/4.5 = 195,800 \text{ g-N/day}$$

25. Nutrient leaching by hyacinths based on hyacinth respiration (Note 34) and nutrient content (0.63% P, 1.75% N, Note 6).

$$(.0063)(132)(208,091)/4.5 = 38,500 \text{ g-P/day}$$

$$(.0175)(132)(208,091)/4.5 = 106,800 \text{ g-N/day}$$

26. Nutrient loss to bottom with hyacinth detritus production based on detrital production (Note 35) and nutrient content (0.63% P, 1.75% N, Note 6).

$$(.0063)(39)(208,091)/4.5 = 1,100 \text{ g-P/day}$$

$$(.0175)(39)(208,091)/4.5 = 31,600 \text{ g-N/day}$$

27. Mineralization of phosphorus from bottom assumed to balance inflow (Note 15), outflow (Note 23) and net hyacinth uptake (Notes 24 and 25):

$$\text{Mineralization} = 87,000 + 70,500 - 38,500 - 97,300$$

$$= 21,700 \text{ g-P/day}$$

28. From Note 5, marsh nitrogen outflow concentration is 1.23 mg/ℓ.

$$(1.23)(62.6 \times 10^3) = 77,000 \text{ g-N/day}$$

29. Mineralization of nitrogen based on N/P ratio (Note 6) and phosphorus mineralization (Note 27).

$$(21,700)(.0175/.0063) = 60,300 \text{ g-N/day}$$

30. Denitrification determined by balance of inflow (Note 16), outflow (Note 28), net hyacinth uptake (Notes 24 and 25) and mineralization (Note 29):

$$\text{Denitrification} = 147,100 + 60,300 + 106,800$$
$$- 195,800 - 77,000$$
$$= 41,400 \text{ g-N/day}$$

31. Oxygen concentration from marsh to lake (Note 7), and flow (Note 14):

$$(1.0 \text{ g/m}^3)(62.6 \times 10^3 \text{m}^3/\text{day}) = 63,000 \text{ g-O}_2/\text{day}$$

32. Marsh oxygen demand determined with balance of inflow (Note 17), diffusion (Note 19) and outflow (Note 31):

$$\text{Marsh oxygen demand} = 313,000 + 345,000 - 63,000$$
$$= 595,000 \text{ g-O}_2/\text{day}$$

33. Marsh waterhyacinth gross production:

From Table 3, gross production of large water-hyacinths is 193 kcal/m^2-day for 3750 kcal/m^2-day solar radiation. From Note 18, solar radiation for measurement period is 4700 kcal/m^2-day.

$$(193)(4700/3750) = 242 \text{ kcal/m}^2\text{-day}$$

34. Marsh hyacinth respiration from Table 3: 132 kcal/m^2-day.

35. Marsh detrital production:

Penfound and Earle (1948) found 35% of hyacinth mat as detritus; .˙. detrital production is assumed to be 35% of net production:

$$0.35 \ (242 - 132) = 39 \ kcal/m^2\text{-}day$$

36. Detrital respiration in marsh:

Take nitrogen mineralization (Note 29) and nitrogen content of organic matter (Note 6):

$$(60,300 \ g\text{-}N/day)(4.5 \ kcal/g)/$$
$$(.0175 \ g\text{-}N/g)(208,091 \ m^2)$$
$$= 74.5 \ kcal/m^2\text{-}day$$

37. Lake hyacinth gross production:

Assume small hyacinth production from Table 3, solar radiation from Note 18, and hyacinth coverage from Table 2:

$$(156 \ kcal/m^2\text{-}day)(4700/4900)(0.42)$$
$$= 62.8 \ kcal/m^2\text{-}day$$

38. Lake hyacinth respiration:

Respiration from Table 3 and percent coverage from Table 2:

$$(76 \ kcal/m^2\text{-}day)(0.42) = 32 \ kcal/m^2\text{-}day$$

39. As in Note 35:

$$0.35 \ (62.8 - 32.0) = 10.8 \ kcal/m^2\text{-}day$$

40. Phosphorus near outflow in open lake (Note 4) and flow (Note 14):

$$(1.61 \ g\text{-}P/m^3)(62.6 \times 10^3 m^3/day) = 101,000 \ g\text{-}P/day$$

41. Nutrient uptake by lake hyacinths based on hyacinth gross production (Note 37) and nutrient concentration (Note 6):

$$(.0063 \text{ g-P/g})(62.8 \text{ kcal/m}^2\text{-day})(121,700 \text{ m}^2)/$$
$$4.5 \text{ kcal/g} = 10,700 \text{ g-P/day}$$
$$(.0175)(62.8)(121,700)/4.5 = 29,700 \text{ g-N/day}$$

42. Nutrient leaching by lake hyacinths based on hyacinth respiration (Note 38) and nutrient concentration (Note 6):

$$(.0063)(32)(121,700)/4.5 = 5,400 \text{ g-P/day}$$
$$(.0175)(32)(121,700)/4.5 = 15,100 \text{ g-N/day}$$

43. Nutrient loss of hyacinth production as in Note 26 with lake detritus production (Note 39) and nutrient contents (0.63% P, 1.75% N, Note 6):

$$(.0063)(10.8)(121,700)/4.5 = 1800 \text{ g-P/day}$$
$$(.0175)(10.8)(121,700)/4.5 = 5100 \text{ g-N/day}$$

44. Nutrient uptake by phytoplankton with phytoplankton gross production of 38.4 kcal/m^2-day (Note 51) and average nutrient concentration for phytoplankton of 5% N and 0.5% P (Lund, 1970):

$$(.005 \text{ g-P/g})(38.4 \text{ kcal/m}^2\text{-day})(121,700 \text{ m}^2)/$$
$$4.5 \text{ kcal/g} = 5200 \text{ g-P/day}$$
$$(.05)(38.4)(121,700)/4.5 = 52,000 \text{ g-N/day}$$

45. Nutrient regeneration by phytoplankton is assumed to parallel phytoplankton respiration (Note 51):

$$(.005)(19.2)(121,700)/4.5 = 2600 \text{ g-P/day}$$
$$(.05)(19.2)(121,700)/4.5 = 26,000 \text{ g-N/day}$$

46. Nutrient uptake by benthic plants with plant production of 69.6 kcal/m^2-day (Note 51): average nitrogen content of 2.5% N (Goulder and Boatman, 1971) and .05% P (Adams et al., 1973):

$$(.0005 \text{ g-P/g})(69.6 \text{ kcal/m}^2\text{-day})(121,700 \text{ m}^2)/$$
$$4.5 \text{ kcal/g} = 1000 \text{ g-P/day}$$
$$(.025)(69.6)(121,700)/4.5 = 47,000 \text{ g-N/day}$$

47. Nutrient regeneration by benthic plants is assumed to parallel respiration (Note 52) and nutrient concentrations as in Note 46:

$$(.0005)(34.8)(121,700)/4.5 = 500 \text{ g-P/day}$$
$$(.025)(34.8)(121,700)/4.5 = 23,500 \text{ g-N/day}$$

48. Nitrogen near outflow in open lake (Note 5) and flow (Note 14):

$$(1.10 \text{ g-N/m}^3)(62.6 \times 10^3\text{m}^3/\text{day}) = 68,800 \text{ g-N/day}$$

49. Lake nitrogen mineralization from bottom; assume N and P concentrations of bottom to be similar to hyacinth biomass (0.63% P, 1.75% N, Note 6) and bottom detritus decomposition as in Note 54.

$$(.0063 \text{ g-P/g})(31.9 \text{ kcal/m}^2\text{-day})(121,700 \text{ m}^2)/$$
$$4.5 \text{ kcal/g} = 5400 \text{ g-P/day}$$
$$(.0175)(31.9)(121,700)/4.5 = 15,100 \text{ g-N/day}$$

50. Dissolved oxygen near outflow (Note 11) and flow (Note 14):

$$(5.25 \text{ g/m}^3)(62.6 \times 10^3\text{m}^3/\text{day}) = 328,000 \text{ g-O}_2/\text{day}$$

51. Benthic plant and phytoplankton gross production from Table 6:

Month	Solar Efficiency, %
January	3.0
March	1.5
April	2.9
May	1.9
Average	2.3

Total: $(4700 \text{ kcal/m}^2\text{-day})(.023) = 108 \text{ kcal/m}^2\text{-day}$

Oxygen production: $(108 \text{ kcal/m}^2\text{-day})(121,700 \text{ m}^2)/$

$(.9375 \text{ g/g-O}_2)(4.5 \text{ kcal/g}) = 3.12 \times 10^6 \text{ g-O}_2/\text{day}$

Approximately 35.5% of production due to phytoplankton (M. Kiern, personal communication).

Phytoplankton $(.355)(108) = 38.4 \text{ kcal/m}^2\text{-day}$

$(.355)(3.12\times10^6) = 1.11 \times 10^6 \text{ g-O}_2/\text{day}$

Benthic plants $(.645)(108) = 69.6 \text{ kcal/m}^2\text{-day}$

$(.645)(3.12\times10^6) = 2.01 \times 10^6 \text{ g-O}_2/\text{day}$

52. Respiration of lake plants; assume respiration = one-half gross production (Note 51):

Phytoplankton $(38.4 \text{ kcal/m}^2\text{-day})(0.5) = 19.2$

$\text{kcal/m}^2\text{-day}$

$(1.11 \times 10^6 \text{ g-O}_2/\text{day})(0.5) = 0.555$

$\times 10^6 \text{ g-O}_2/\text{day}$

Benthic plants $(69.6)(0.5) = 34.8 \text{ kcal/m}^2\text{-day}$

$(2.01 \times 10^6)(0.5) = 1.00 \times 10^6 \text{ g-O}_2/\text{day}$

53. Allochthonous organic matter decomposition; assume
$K_{\log 10}$ = .05/day:

  Allochthonous organic matter = 192 kcal/m^2 (Note 13)

   (192)(.05)(2.303) = 22.1 kcal/m^2-day

 Oxygen consumption

  (22.1 kcal/m^2-day)(121,700 m^2)(.9375 g/g-O$_2$)

   ·(4.5 kcal/g) = 0.64 x 10^6 g-O$_2$/day

54. Detritus decomposition; assume P/R for lake = 1.0.

  P = 108 kcal/m^2-day (Note 51)

  R = 108 kcal/m^2-day

  Bottom respiration = remaining respiration after

   plants (Note 52) and allochthonous demands

   (Note 53):

  R = 108 - 19.2 - 34.8 - 22.1 = 31.9 kcal/m^2/day

 Oxygen consumption

  (31.9)(121,700)/(.9375)(4.5) = 0.92 x 10^6

  g-O$_2$/day

55. Allochthonous organic matter from lake:

  Assumes inflow - decomposition = outflow.

  Therefore, allochthonous organic matter to bottom

  detritus assumed to be zero and

  Outflow = 89.4 - 22.1 = 67.3 kcal/m^2-day

56. Phytoplankton flushing and bottom deposition combined
are equal to the gross production (Note 51) minus
respiration (Note 52), assuming steady state:

  38.4 kcal/m^2-day - 19.2 kcal/m^2-day

   = 19.2 kcal/m^2-day

Because phytoplankton is susceptible to flushing, assume

$$\text{bottom deposition} = 1.0 \text{ kcal/m}^2\text{-day}$$

$$\underline{\text{plankton outflow} = 18.2 \text{ kcal/m}^2\text{-day}}$$

$$19.2 \text{ kcal/m}^2\text{-day}$$

57. Benthic plant flushing and bottom deposition combined are equal to the gross production (Note 51) minus respiration (Note 52), assuming steady state:

$$69.6 - 34.8 - 34.8 \text{ kcal/m}^2\text{-day}$$

Estimate 10% of gross production flushes from the lake:

$$\text{bottom deposition} = 7.0 \text{ kcal/m}^2\text{-day}$$

$$\underline{\text{benthic outflow} = 27.8 \text{ kcal/m}^2\text{-day}}$$

$$34.8 \text{ kcal/m}^2\text{-day}$$

58. Dead hyacinths are assumed to decay at $K_{\log 10} = 0.05$ (McGauhey, 1970); actual decay rate, converted to natural logs is $(.05)(2.303) = .11515$; nutrient regeneration assumes hyacinth nutrient concentration of 0.63% P and 1.75% N (Note 6); turnover time of dead hyacinths estimated at two weeks from field observations.

APPENDIX C

SUPPLEMENTAL MATERIAL FOR CYPRESS DOME MODEL
AS GIVEN IN FIGURE 62 AND TABLE 23

Table C-1

CALCULATED COEFFICIENT VALUES FOR
CYPRESS DOME MODEL IN FIGURE 62

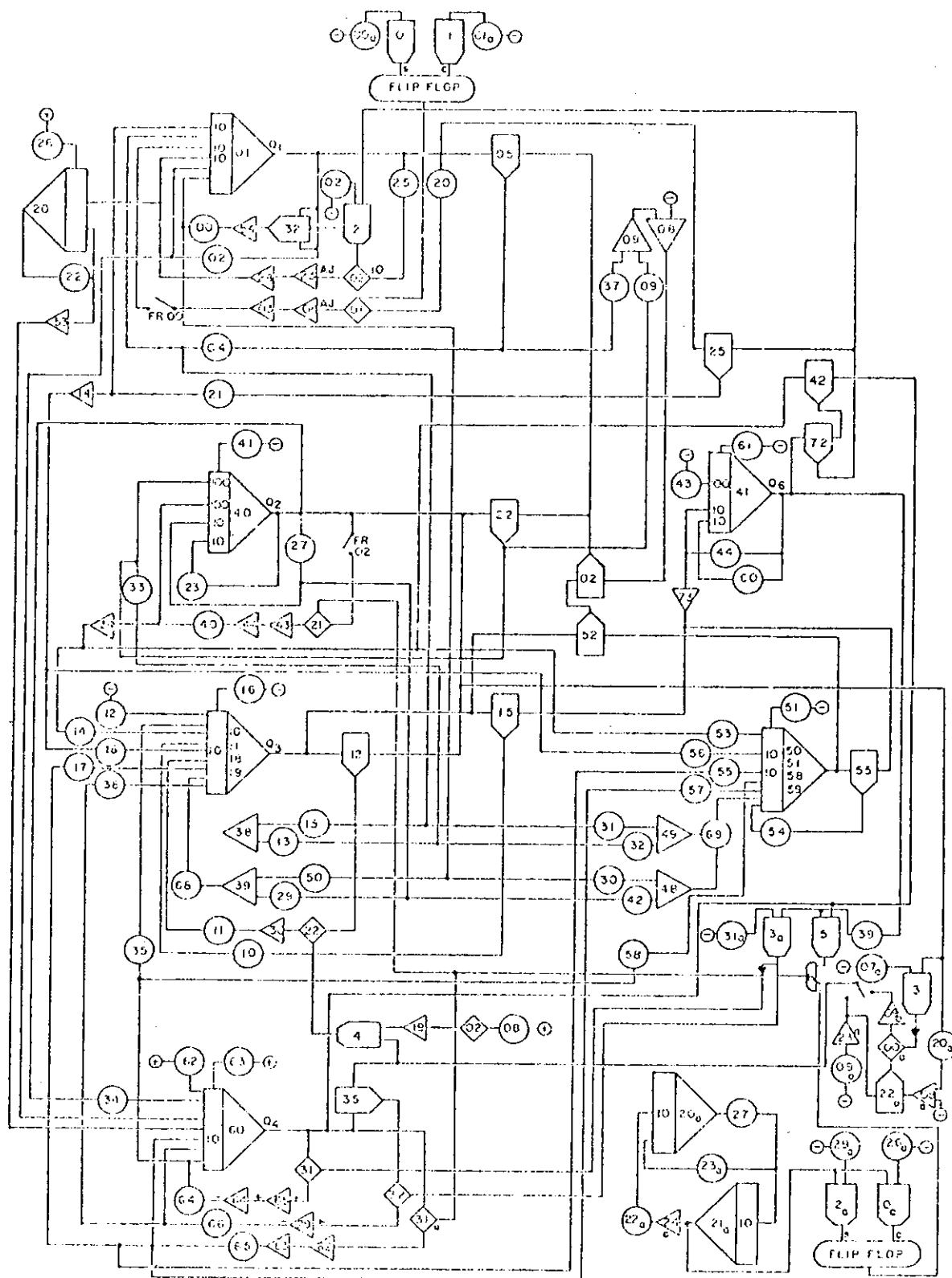| Parameter	Calculated Value	Parameter	Calculated Value
k_1	0.577×10^{-12}	k_{28}	1.3×10^{-4}
k_2	0.982×10^{-12}	k_{41}	1.3×10^{-4}
k_3	2.51×10^{-14}	k_{42}	1.3×10^{-4}
k_4	3.48×10^{-12}	k_{29}	0.0
k_5	3.72×10^{-7}	k_{30}	1.7×10^{-3}
k_7	1.78×10^{-2}	k_{31}	1.7×10^{-3}
k_8	3.74×10^{-7}	k_{32}	4.87×10^{-7}
k_9	63.2	k_{34}	2.7×10^{-3}
k_{10}	3.24	k_{35}	2.7×10^{-3}
k_{11}	3.24	k_{36}	6.8×10^{-4}
k_{13}	365	k_{37}	1.1×10^{-3}
k_{15}	2.92×10^{-2}	k_{38}	2.0×10^{-3}
k_{16}	6.87×10^{-3}	k_{39}	5.0×10^{-3}
k_{17}	365	k_{40}	5.0×10^{-3}
k_{18}	20.1	k_{56}	$1,500$
k_{19}	4.56	k_{57}	0.05
k_{21}	0.0	k_{33}	2.0
k_{22}	1.1×10^{-4}		
k_{23}	1.1×10^{-4}		
k_{24}	1.8×10^{-4}		
k_{25}	1.8×10^{-4}		
k_{26}	1.1×10^{-4}		
k_{27}	1.8×10^{-4}		

Figure C-1.   Analog diagram of cypress dome model.

Table C-2

POT SETTINGS FOR ANALOG DIAGRAM IN FIGURE C-1

Pot #	Parameter	Setting	Pot #	Parameter	Setting
00	k_5	0.0237	39	k_{53}	0.800
02	k_7	0.0178	40	k_{13}	0.999 (x100)
04	k_3	0.366	41	Q_2	0.04
09	k_2	0.982 (x10)	42	k_{25}	0.180
10		0.00	43	J_3	0.158 (x100)
11	k_{32}	0.0049	44	k_{18}	0.201 (x100)
12	J_5	0.0010	50	k_{31}	0.850
13	k_{34}	0.270	51	Q_4	0.340
14	k_{37}	0.110	52	J_4	0.0013
15	k_{30}	0.850	53	k_{27}	0.180
16	Q_3	0.416	54	k_{21}	0.00
17	k_{38}	1.00	55	k_{28}	0.65
18	k_{36}	0.34	56	k_{26}	0.55
20	k_9	0.999 (x10)	57	k_{41}	0.065
21	k_8	0.999 (x10)	58	k_{42}	0.065
22	k_{57}	0.05	60	k_{19}	0.456 (x10)
23	k_{11}	0.324 (x10)	61	Q_6	0.64
24	Q_1	0.136	62	J_6	0.00
25	k_{56}	0.999 (x10)	63	Q_7	0.156
26	Q_8	0.00	64	k_{16}	0.007
27	k_{10}	0.324 (x10)	65	k_{17}	0.999 (x10)
29	k_{35}	0.270	66	k_{15}	0.292
30	k_{23}	0.550	68		0.10
31	k_{22}	0.550	69		0.10
32	k_{24}	0.180			
33	k_4	0.508 (x100)	00a	k_{51}	0.40
34	k_{11}'	0.0648	01a	k_{52}	0.10
35	k_{40}	0.025	02a	k_{55}	0.046
37	k_1	0.2885 (x10)	07a	k_{50}	0.40
38	k_{39}	0.025	08a	k_{54}	0.100

Table C-2 - continued

Pot #	Parameter	Setting	Pot #	Parameter	Setting
09a	J_7	0.108			
20a	k_{33}	0.2 (x10)			
22a	k_{61}	0.0628			
23a	k_{62}	0.00			
26a	k_{65}	0.850			
27a	k_{60}	0.0628			
29a	k_{64}	0.900			
31a	k_{58}	0.34			

Notes for Table 23

1. From Table 15, cypress biomass = 13.6 kg/m^2

   (13,600 g/m^2)(5 kcal/g) = 68,000 kcal/m^2

2. Average understory biomass for undisturbed conditions, May-August, 1974 (Ewel and Mitsch, 1974):

Owens-Illinois Control Dome	90 g/m^2
Austin Cary Control Dome	70 g/m^2
Average	80 g/m^2

   (80 g/m^2)(5 kcal/g) = 400 kcal/m^2

3. Nitrogen for 100 cm depth 3174 ppm, Figure 61 (Coultas, 1974)

   Average bulk density = 1.31 g/cm^3 (Coultas, 1974)

   (3.174 mg-N/g)(1.31 g/cm^3)(100 cm)(10) = 4160 kg/m^2

4. Phosphorus for 100 cm depth 261 ppm, Figure 61 (Coultas, 1974)

   Average bulk density = 1.31 g/cm^3 (Coultas, 1974)

   (.261 mg/g)(1.31 g/cm^3)(100 cm)(10) = 340 g/m^2

5. Surface water for sewage dome assuming half maximum storage = 787 m^3 (Ordway). Groundwater for sewage dome assuming 100 cm depth, .17 storage coefficient (Cutright) and 5272 m^2 area:

   1 m x 5272 m^2 x .17 = 896 m^3

   (787 m^3 + 896 m^3)/5272 m^2 = .32 m

6. From sewage dome before application, Coultas (1974) found organic layer = 6.25 cm.

   Bulk density $\cong$ 0.25 g/cm^3 for organic soils (Brady, 1974)

$$(6.25 \text{ cm})(0.25 \text{ g/cm}^3)(5 \text{ kcal/g})(10,000) = 78,000$$
$$\text{kcal/m}^2$$

7. Assume no initial fire.

8. Cowles (1974) found GPP = 14.06 gC/kg dry wt @ solar 4876 kcal/m^2-day; GPP = 12.91 gC/kg dry wt @ solar 4847 kcal/m^2-day; cypress leaf biomass = 121.4 g/m^2 (Table 15)

$$\frac{(14.06 \text{ gC/kg dry wt})(10 \text{ kcal/gC})(.1214 \text{ kcal/m}^2)(100)}{(4876 \text{ kcal/m}^2\text{-day})}$$

$$= 0.35\%$$

$$\frac{(12.91)(10)(.1214)(100)}{4847} = 0.32\%$$

Average efficiency = 0.335%

Assuming 8-month production:

$$(1.46 \times 10^6 \text{ kcal/m}^2\text{-yr})(8/12)(.00335) = 3277$$
$$\text{kcal/m}^2\text{-yr}$$

9. Cypress respiration:

Cypress net productivity, Owens-Illinois data
= 6.1 kg/tree-yr (Table 19)

Cypress tree density for sewage dome = .051
tree/m^2 (Table 15)

NPP = (6100 g/tree-yr)(.051 tree/m^2)(5 kcal/g)
= 1556 kcal/m^2-yr

Respiration = GPP - NPP
= 3277 - 1556 = 1721 kcal/m^2-yr

10. Assume twice leaf biomass for sewage dome (Table 15)
to be total litter fall:

$$(121.4 \text{ g/m}^2)(2)(5 \text{ kcal/g})/(1 \text{ yr}) = 1214 \text{ kcal/m}^2\text{-yr}$$

11. Assumptions for fire and harvesting are for constants of fast turnover relative to tree time scale of the model.

12. Average of 4 pond metabolism measurements (Table 21) is 7.1 kcal/m^2-day

    (7.1 kcal/m^2-day)(365 days/yr) = 2591 kcal/m^2-day

13. Respiration and detritus production each assumed to be one-half of gross primary production.

    Respiration = 12.95 kcal/m^2-yr

    Organic accumulation = 1295 kcal/m^2-yr

14. Model assumes no input of peat-building organic matter; actual total dissolved carbon input estimated for TOC measurements of 26 gC/m^3 (Brezonik et al., 1974) and estimated runoff of 6.6 m/yr (see Note 17).

    (26 gC/m^3)(6.6 m/yr)(10 kcal/gC) = 1700 kcal/m^2-yr

15. Estimated 20-year turnover time for dead trees to bottom organics.

16. Decomposition rates of wet and dry:

    Austin Cary Control Dome total respiration = 10.3 kcal/m^2-day (Table 21)

Wet decomposition:

    Total respiration - plant respiration = bottom respiration

    (10.3 kcal/m^2-day)(365 days/yr) - 1295 kcal/m^2-day
    = 2464 kcal/m^2-yr

Mitsch, Ewel and Abood (1974) found that decomposition of cypress needles under wet conditions is 4.6 times faster than dry conditions:

Dry decomposition:

$$2464/4.6 = 536 \text{ kcal/m}^2\text{-yr}$$

17. Total water inflow

Total rainfall is 52 in/yr or 1.3 m/yr

July-December, 1974, data (Table 12) gave 4.4 m/yr

average runoff; normalizing for average rainfall:

$$(4.4)(.1425 \text{ in/day}/.0945 \text{ in/day}) = 6.6 \text{ m/yr}$$

total runoff = 1.3 + 6.6 = 7.9 m/yr

18. Evapotranspiration (Table 12):

$$(0.40 \text{ cm/day})(365 \text{ days/yr})/100 = 1.5 \text{ m/yr}$$

Outflow assumes balance:

$$7.9 - 1.5 = 6.4 \text{ m/yr}$$

19. From Table 21, average dissolved oxygen = 1.8 g/m^3.
Average depth = 0.6 m.

$$(1.8 \text{ g/m}^3)(0.6 \text{ m}) = 1.1 \text{ g/m}^2$$

20. June-September, 1974, average of well #22 (Brezonik
et al., 1974):

Total Kjeldahl nitrogen	1.30 $g\text{-}N/m^3$
Total phosphorus	0.16 $g\text{-}P/m^3$

P inflow $(0.16 \text{ g/m}^3)(7.9 \text{ m}^3/\text{yr}) = 1.26 \text{ g-P/yr}$

N inflow $(1.30 \text{ g/m}^3)(7.9 \text{ m}^3/\text{yr}) = 10.3 \text{ g-N/yr}$

21. Nutrient outflow assumed minimal compared to inflow.

22. Nutrient uptake by cypress:

Analysis of cypress biomass:

P	545×10^{-6}	g-P/g dry wt
N	85×10^{-4}	g-N/g dry wt

$$(3277 \text{ kcal/m}^2\text{-yr})(545 \times 10^{-6} \text{ g-P/g dry wt})/5 \text{ kcal/g}$$

$$= 0.36 \text{ g-P/m}^2\text{-yr}$$

$$(3277)(85 \times 10^{-4})/5 = 5.6 \text{ n-N/m}^2\text{-yr}$$

23. Nutrient leaching from cypress. Cypress concentration as in Note 22; assume respiration parallels nutrient return:

$$(1721 \text{ kcal/m}^2\text{-yr})(545 \times 10^{-6} \text{ g-P/g})/5 \text{ kcal/g}$$

$$= 0.19 \text{ g-P/m}^2\text{-yr}$$

$$(1721)(85 \times 10^{-4})/5 = 2.9 \text{ g-N/m}^2\text{-yr}$$

24. Assumes same phosphorus concentrations as in Note 22.

25. Nutrient uptake by understory:

Average of 11 understory plant samples:

P 897×10^{-6} g-P/g dry wt

N 133×10^{-4} g-N/g dry wt

$$(2591 \text{ kcal/m}^2\text{-yr})(897 \times 10^{-6} \text{ g-P/g})/5 \text{ kcal/g}$$

$$= 0.46 \text{ g-P/m}^2\text{-yr}$$

$$(2591)(133 \times 10^{-4})/5 = 6.9 \text{ g-N/m}^2\text{-yr}$$

26. Nutrient leaching from understory. Understory concentrations as in Note 25; assume respiration parallels nutrient return:

$$(1295 \text{ kcal/m}^2\text{-yr})(897 \times 10^{-6} \text{ g-P/g})/5 \text{ kcal/g}$$

$$= 0.23 \text{ g-P/m}^2\text{-yr}$$

$$(1295)(133 \times 10^{-4})/5 = 3.4 \text{ g-P/m}^2\text{-yr}$$

27. Assume same phosphorus concentration as in Note 25.

28. Recycle of nutrients with decomposition:

Composition of organic matter (Coultas, 1974):

P 689×10^{-6} g-P/g dry wt

$$N \quad 250 \times 10^{-4} \text{ g-N/g dry wt}$$

Decomposition rates as in Note 16.

Wet recycle: P

$$(2464 \text{ kcal/m}^2/\text{yr})(689 \times 10^{-6} \text{ g-P/g})/5 \text{ kcal/g}$$
$$= 0.34 \text{ g-P/m}^2\text{-yr}$$

Wet recycle: N

$$(2464)(250 \times 10^{-4})/5 = 12.3 \text{ g-N/m}^2\text{-yr}$$

Dry recycle: P

$$(536)(689 \times 10^{-6})/5 = 0.07 \text{ g-P/m}^2\text{-yr}$$

Dry recycle: N

$$(536)(250 \times 10^{-4})/5 = 2.6 \text{ g-N/m}^2\text{-yr}$$

29. Assume same phosphorus concentrations as in Note 28.

30. Recycle of nitrogen by fire: 60% of available N is lost (Lewis, 1974);

∴ effective recycle N percentages in fire:

    Cypress $(.0085)(.4) = 34 \times 10^{-4}$ g-N/g dry wt

    Understory $(.0133)(.4) = 53.2 \times 10^{-4}$ g-N/g dry wt

    Organic peat $(.025)(.4) = 100 \times 10^{-4}$ g-N/g dry wt

31. Denitrification for natural conditions based on extrapolation from sewage dome conditions; at 0.0 dissolved oxygen, denitrification may be as high as 70% of inflow. Inflow (Note 20) = 10.3 g-N/m^2-yr.

    @ 0.0 ppm O_2 denitrification $= (0.7)(10.3 \text{ g-N/m}^2\text{-yr})$
$$= 7.2 \text{ g-N/m}^2\text{-yr}$$

    @ 1.1 ppm O_2 denitrification = 0.0

APPENDIX D

SUPPLEMENTAL MATERIAL FOR CYPRESS POND MINI-MODEL
AS GIVEN IN FIGURE 76 AND TABLE 25

Table D-1

CALCULATED COEFFICIENT VALUES FOR
CYPRESS POND MINI-MODEL IN FIGURE 76

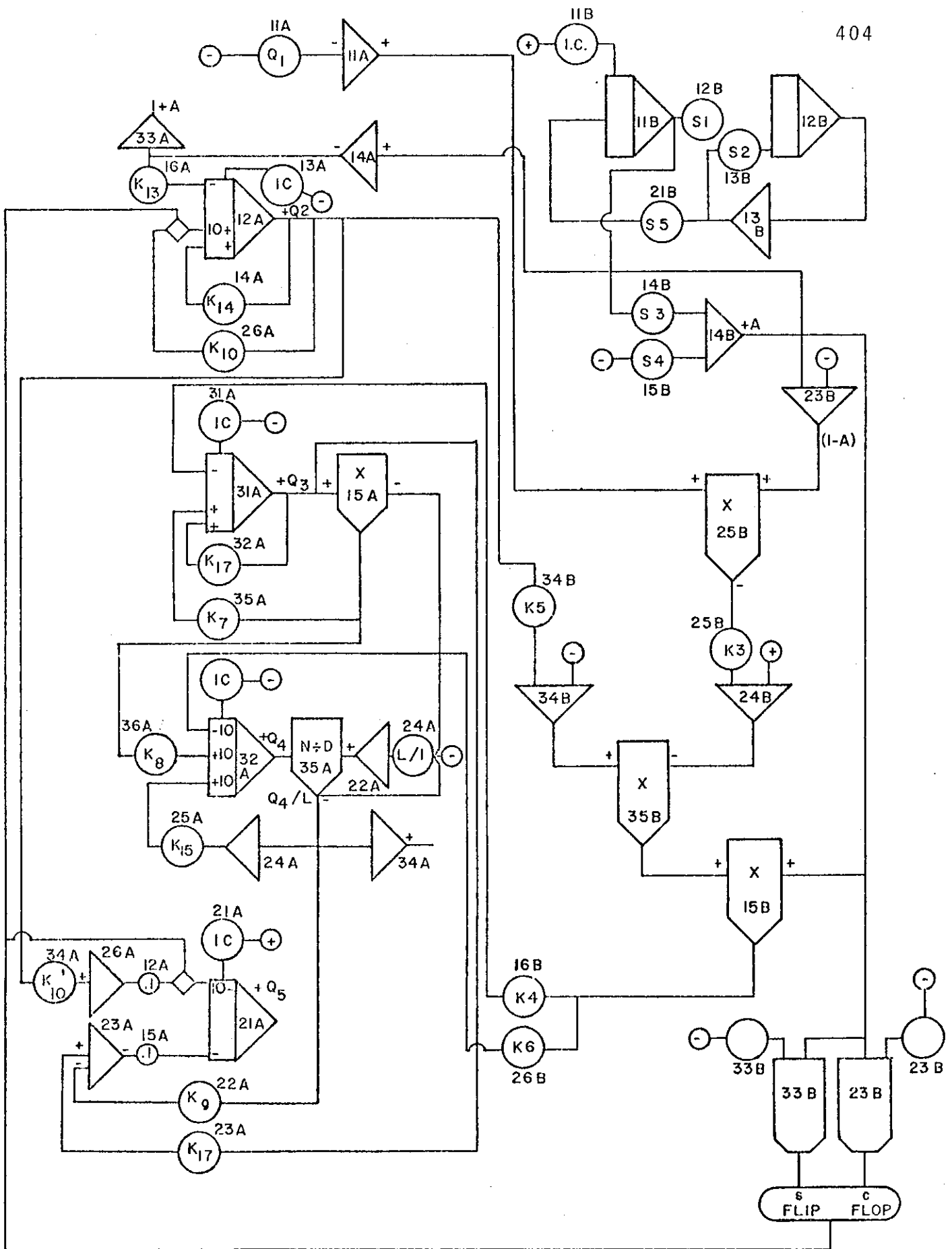| Constant	Original Value
k_{13}	3,267
k_{14}	1.458
k_{10}	36.1
k_4	8,965
k_7	1.521
k_{17}	3.042
k_6	1,992
k_8	0.338
k_{15}	186.6
k_{17}	3.042
k_{10}	36.1
k_9	839.5

Figure D-1. ANALOG DIAGRAM FOR CYPRESS POND MODEL

Table D-2

POT SETTINGS FOR ANALOG DIAGRAM IN FIGURE D-1

	Board No. A			Board No. B	
Pot #	Parameter	Setting	Pot #	Parameter	Setting
11A	$[Q_1/300000]$	.618	11B	I.C. Sine wave	1.000
12A		.100	12B	J_1 Frequency	.005
13A	I.C. $[Q_2/5000]$	.000	13B	S_2 Feedback	.000
14A	k_{14}	.015	14B	S_3 S.A. ampli-tude	.300
15A		.100	15B	S_4 S.A. mean	.700
16A	k_{13}	.007	16B	k_4	.090
21A	I.C. $[Q_5/50000]$	.000	21B	S_5 Frequency	.007
22A	k_9	.017 (x.1)	23B	Comparator for Litterfall	.750
23A	k_{17}	.006 (x.1)			
24A		.500	25B	k_3	.216 (x10)
25A	k_{15}	.187 (x10)	26B	k_6	.199 (x10)
26A	k_{10}	.036 (x10)	33B	Comparator for Litterfall	.420
31A	I.C. $[Q_3/1000]$	.360			
32A	k_{17}	.030	34B	k_5	.152 (x10)
33A	I.C. $[Q_4/10]$	.100			
34A	k_{10}	.036			
35A	k_7	.152			
36A	k_8	.338 (x10)			

Notes to Table 25

1. Austin Cary biomass estimated at 40 kg/m^2

    $$(40,000 \text{ g/m}^2)(4.5 \text{ kcal/g}) = 180,000 \text{ kcal/m}^2.$$

2. Cypress leaf biomass for mature dome such as the Austin Cary Control Dome estimated to be five times value on Table 15 for Sewage Dome:

    $$(120 \text{ g/m}^2)(4.5 \text{ kcal/g})(5) = 2700 \text{ kcal/m}^2.$$

3. Field data gave average biomass of *Utricularia* sp. of 72 g/m^2:

    $$(72 \text{ g/m}^2)(5 \text{ kcal/g}) = 360 \text{ kcal/m}^2.$$

4. Dissolved oxygen yearly average at Austin Cary pond is approximately 2 ppm (Figure 55) and average depth of 0.5 m

    $$(2 \text{ g/m}^3)(0.5 \text{ m}) = 1.0 \text{ g/m}^2$$

5. Bottom organic storage based on 0.25 ft active layer and 8 lb/ft^3 density of organic soil (Brady, 1974):

    $$(0.25 \text{ ft})(8 \text{ lb/ft}^3)(454 \text{ g/lb})(10.76 \text{ ft}^2/\text{m}^2)(5 \text{ kcal/g})$$
    $$= 48,800 \text{ kcal/m}^2$$

6. Solar angle determined from the following equation given by Eagleson (1970):

    $$\sin\alpha = \sin\delta \, \sin\Phi + \cos\delta \, \cos\Phi \, \cos\tau$$

    where α = solar altitude

    δ = earth declination

    Φ = latitude = 30°

    τ = time angle = 0° for noon

A sample calculation for a monthly average:

for January $\delta = -23°4'$

$\sin\alpha = \sin(-23°4')\sin(30°) + \cos(-23.4°)\cos(30°)\cos(0°)$

$= (-0.392)(0.50) + (0.920)(0.866)(1.0)$

$= 0.601$

$\alpha = 36°57'$

Month	Solar Altitude, Degrees	Scaled,[a] 0.0-1.0
January	37	0.41
February	43	0.48
March	52	0.58
April	58	0.64
May	75	0.83
June	82	0.91
July	83	0.92
August	78	0.87
September	61	0.68
October	57	0.63
November	46	0.51
December	38	0.42

[a]Assumes 90° is scaled to 1.0.

7. Carter gives 385 g/m^2-yr production; assume GPP/NPP = 5.1 (Bayley, personal communication) and 1/3 production goes into leaf production:

Total productivity = (385 g/m^2-yr)(5.1)(5 kcal/g)

$= 9800$ kcal/m^2-yr

Leaf productivity = (9800)/3 = 3300 kcal/m^2-yr.

8. Leaf respiration:

$$\text{Total gross production (Note 7)} = 9800 \text{ kcal/m}^2\text{-yr}$$

$$\text{Net production (385 g/m}^2\text{-yr x 5)} = \underline{1925 \text{ kcal/m}^2\text{-yr}}$$

$$\text{Respiration} = 7875 \text{ kcal/m}^2\text{-yr}$$

Estimate average leaf respiration to be 1/4 of total:

$$(7875)/4 = 1970 \text{ kcal/m}^2\text{-yr}$$

Peak respiration for calculation of coefficients is assumed to be double:

$$(1970)(2) = 3940 \text{ kcal/m}^2\text{-yr}$$

9. Assume that half litterfall occurs in 7 days.

10. Average of 4 field measurements of aquatic production from Table 21:

November 4.0 kcal/m^2-day

March 12.8 " "

May 6.9 " "

August $\underline{4.7}$ " "

7.1 kcal/m^2-day (365 days/yr) = 2590 kcal/m^2-yr

11. Plant respiration and detrital production estimated to be 3.0 kcal/m^2-day each:

$$(3.0)(365) = 1095 \text{ kcal/m}^2\text{-yr}$$

12. Total respiration for low oxygen (2 ppm, Note 4) is estimated to be November reading (Table 21) of 7.6 kcal/m^2-day:

$$\text{Benthic R} = \text{total R} - \text{plant R}$$

$$= 7.6 - 3.0$$

$$= 4.6 \text{ kcal/m}^2\text{-day (365 days/yr)} - 1680 \text{ kcal/m}^2\text{-yr}$$

13. Oxygen values assume a conversion of 4.5 kcal/g-O_2 based on 4.5 kcal/g organic matter (Westlake, 1963) and 1 g-O_2/g organic matter estimated from photosynthetic equation:

Production (2590 kcal/m^2-yr)/4.5 kcal/g-O_2

    = 575 g-O_2/m^2-yr

Plant respiration (1095)/(4.5 = 243 g-O_2/m^2-yr

Consumer respiration (1680)/(4.5) = 373 g-O_2/m^2-yr

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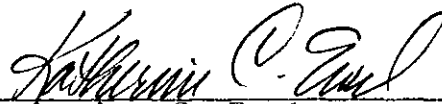
BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.
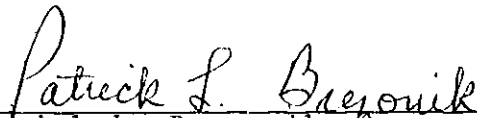
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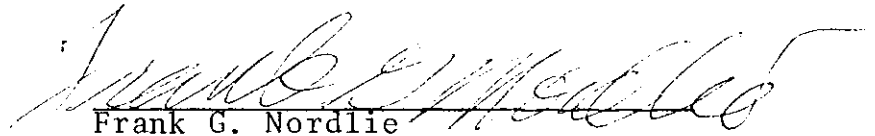
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This dissertation was submitted to the Graduate Faculty of
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