THE PHYSIOLOGICAL SIGNIFICANCE OF THE PECULIAR MORPHOLOGY OF THE PITCHER-LIKE LEAVES OF *SARRACENIA PURPUREA L.*

by

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TABLE OF CONTENTS

ABSTRACT

The physiological interaction of the pitcher-leaves of Sarracenia purpurea L. with its immediate environment is described quantitatively , in terms of radiant and detrital energy fluxes. The insectivorous nature of the plant as a functional explanation of the leaf morphology is de-emphasized. The growth of pitcher leaves under sufficient light and constant temperature is not enhanced by the presence of detritus in the pitcher-pool. The thermal buffering capacity of the water enclosed by the pitcher-leaves allows for maximum photosynthetic surface area. The pool water may also act as a reservoir for carbon dioxide for leaf photosynthesis. The water level of the pitcher in the mature leaf is probably maintained by osmotic flow through the roots from the bog medium.

ABBREVIATION AND SYMBOLS

R = radiation flux

R_n = net radiation flux

α_s = absorption coefficient of short-wave radiation

α_l = avsorption coefficient of long-wave radiation

R^i = incident radiation

R° = re-radiated radiation

α = Stephan - Boltzman constant
$= 8.130 \times 10^{-11}$ cal. cm^{-2} min^{-1} $^\circ K^{-4}$

T = temperature (Kelvin scale).

H = heat diffusion from a warm to cold body

l = latent heat of vaporization = 584 cal g^{-1}

E = rate of evaporation of water

G = heat stored in temperature changes

a = coefficient of fixation of energy
$\simeq$ 3000 cal g^{-1} for carbohydrates

D = detritus flux

α_D = absorption coefficient of detritus

S_l = storage of energy in detritus pool

b = coefficient of absorption of detritus energy
= energy content of detritus absorbed g^{-1}

B = rate of absorption of energetic compounds from detritus

M_I = metabolic dissipation of detritus by inquilines

K = coefficient of thermal conductivity

z = distance

E^l = exchange of CO_2 by plant; either uptake or loss

ΔC = difference in CO_2 concentration between sample and reference tubes in IRGA

J = flow rate of gas through assimilation chamber.

M = dry weight of leaf enclosed in assimilation chamber

C_1 = concentration of water vapor at leaf surface

C_a = concentration of water vapor in bulk air

da = thickness of unstirred layer of air above a leaf.

D = diffusion coefficient

Ψ = water potential

p = density of water (1.0 g cm^{-3})

g = acceleration due to gravity (980 cm sec^{-2})

L = height of water above reference ground level

R = gas constant (8.3143 joules $mole^{-1}$ $°K^{-1}$)

C_s = concentration of solutes

$\frac{dQ}{dt}$ = flow rate

Lp = hydraulic

A = cross-sectioned area

J^1 = flux of CO_2

x = distance

IRGA = infrared gas analyzer

L-D = light-dark

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"One cannot fix one's eyes on the commonest natural production without finding food for a rambling fancy."

Mansfield Park

A. INTRODUCTION AND DISCUSSION OF LITERATURE

Salisbury and Ross (1969) define physiological ecology: "Basically, physiological ecology attempts to gain answers to the problems of plant ecology through understanding plant functions." This study's overall purpose was to define the ecology of the pitcher-plant more precisely than before through investigation of the more subtle physiological implications of its gross morphological adaptations. As a background to the thesis, a discussion of the literature concerning pitcher-plants follows.

The waters of the pitcher-plant common to the Maritime provinces (Sarracenia purpurea L.) may be considered one of the smaller fresh-water ecosystems in existence. Paterson (1971) and Diemand (1969) have used this approach to a limited extent in studying the inquilines of Sarracenia; however, it remains novel to consider the biology of Sarracenia purpurea in the terms of limnology.

There has been considerable work done on the pitcher plant and its inquilines, but most of the study has been concerned with anatomy or biochemistry of the plant, (e.g. Lloyd), or the taxonomy and biology of the inquilines and "victims" (e.g. Judd, Swales, Paterson). The community concept of the lentic system has not been fully developed.

Superficially, the inter-relationships appear straight-forward: the pitcher-plant is a predator and insects of every known order become its prey (Judd, 1959).

However, upon examining the situation further, it appears that the pitcher-plant would be better termed a scavenger on the detritus at the bottom of its minute lake. Sarracenia must also be a primary producer in the system since its leaves are, to varying extent, photosynthetic. This function is similar to lentic system epiphytes. The relative magnitudes of the pitcher-leaf's roles have not been investigated.

Two macro-invertebrate first-order consumers and detritus feeders are of particular interest. These are Metriocnemus knabi (Chironomidae) and Wyeomyia smithii (Culcidae). Both are specific to Sarracenia purpurea L. and only the adult form leaves the pitcher-plant. There appears to be little inter-specific competition due to spatial separation of niches (Paterson, 1973). The midge larvae burrow into the layer of detritus while the mosquito larvae feed at the surface of the detritus or in the water column. Dissolved oxygen levels are high in the pitcher-plant; even in the detritus, values of five (5) milligrams per liter are not uncommon (Paterson, 1972). There is obviously no competition between the inquilines for oxygen. The source of this oxygen has not been determined; it is not known whether Sarracenia is sufficiently photosynthetic to supply the oxygen or if the level is maintained merely by diffusion from the atmosphere. Paterson (1972) postulates the latter.

What follows is a hypothetical description of the

lentic system of the pitcher-plant as a comparison of its oligotrophic state, as it opens in the summer of year one, with its relatively eutrophic state, as it begins to senesce in the fall of year two:

Post-Emergence	Senescence
1. Oligotrophic	Eutrophic[1]
2. Well oxygenated	Well oxygenated[1]
3. Medium pH	Low pH[1,5]
4. Enzymes effective	Enzymes less effective[2]
5. No symbionts	Many symbionts[2,5]
6. Small amount of detritus	Large amount of detritus[3]
7. Few bacteria	Large number of bacteria[2]
8. No mycorrhizae	No mycorrhizae[2]
9. Digestion largely via enzymes?	Digestion largely due to break-up of detritus by larvae and digestion by bacteria[4,2,1,6,7]

Many authors disagree on vital points--especially points 4, 7 and 9.

To understand the community biology of this ecosystem, however, it is necessary to be knowledgeable of the physiology of the pitcher-plant itself and how it may vary both with age and location in the bog.

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[1]Paterson, [2]Lloyd, [3]Personal Observation, [4]Plummer, [5]Swales, [6]Hepburn and St. John, [7]Mellichamp.

The purpose of the lentic system may be to replace (in function) the absent mycorrhizal complex; i.e. it may supply a site for inorganic ion uptake(Lloyd, 1942). Sarracenia purpurea flourishes in acid Sphagnum bogs where there is a low concentration of potassium ions (Plummer and Kethley 1964) and decomposition is slow; nitrogenous compounds may be supplied by decomposition within the pitcher pool.

Plummer and Kethley (1964) emphasize the pitcher-plant's amino acid requirements which they say are met by absorption through the pitcher walls. Dore Swamy (1971) has shown that growth and flowering of insectivorous plants may be inhibited without this nitrogenous supplement. Lloyd (1942) affirms that as far back as 1885, Higley showed that nitrogenous compounds are absorbed by the pitcher-leaf. At approximately the same time, Zipperer (1885) demonstrated the presence of a diastase (amylase) and a pepsin in the pool of Sarracenia. Robinson (1908) demonstrated digestion of sucrose and starch by the fluid and Hepburn et al (1927) showed that fibrin is digested in both alkaline and acid conditions although the plant protease was most effective under alkaline conditions. Wherry (1929) found a consistent difference in pH between medium (i.e. bog water) and the pitcher fluid; young pitchers exhibited alkaline pH while older pitchers were consistently acid. Mellichamp (1875) compared the rate of disintegration of venison in pitcher fluid with that in

distilled water and concluded that bacterial action was the chief mode of digestion.

Zone four of the pitcher-leaf's inner surface near the base, as described by Lloyd (1942), is devoid of cuticle except for a small space surrounding the base of each hair and is probably an absorptive zone. Zone five, at the very base of the pool, has considerably more cuticle but is still probably absorptive in nature. There are no hairs, at least in the juvenile leaf, in this zone. Fenner (1904) notes that both zones four and five become enlarged in etiolated leaves while zones one and two, which have a much thicker cuticle are smaller. No direct physiological proof exists to show that more absorption takes place in etiolated leaves but this anatomical evidence indicates that it is a possibility. This may indicate that under conditions which reduce photosynthesis, nutrient uptake is increased.

Lloyd concludes that there is "acquisition of nutrient substances containing protein, possibly vitamins and perhaps the salts of potassium and phosphorous and even others.....they (the pitcher-leaves) receive some profit, though what they receive is no sine qua non, as it is with other plants." He likens the absorption to the benefits others receive from mycorrhizal fungi.

Experiments with tracers (Plummer and Jackson, 1963) suggest that there is considerably more absorption by immature pitchers, and contradict Hepburn et al (1927) by

implying that bacteria play a major role in digestion "under certain circumstances" which Plummer and Jackson fail to define precisely. They were unable to say exactly what is absorbed by the leaves. Plummer and Kethley (1964), using tracers, were able to show absorption of zinc, iodine, cobalt, sulphur, calcium and phosphorous in solution, and absorption and translocation of radioactive sulphur and phosphorous derived from insect tissues. Absorption from solution was within a few hours while absorption from insect tissues usually took two days. Several amino acids in solution were absorbed and dipeptides were absorbed and actually hydrolyzed inside the leaf, not in the pool. Alanyl-leucine was especially absorbed and broken down in these experiments. The investigation of absorption of nutrient to this point remained qualitative.

The inorganic ions of the pitcher fluid do not necessarily have to be at a higher electrochemical state than those of the plant in order to be absorbed, if one postulates an "active" ion absorption or exclusion pump. However, one must at least determine the electrochemical gradients for the major ions in order to make conclusions about the possibility of the pitcher pool being as effective as mycorrhizae in benefiting the plant in ion absorption. Nemcĕk (1966) determined electrochemical gradients for the major inorganic ions in the pitchers of Nepenthes henryana. He postulated active pumping of Na^+ and Cl^- ions from the pitcher pool to the leaf tissue with

passive equilibrium of potassium ions. In the K^+-poor soils of the Sphagnum bogs one might expect a similar equilibrium to be set up in the Sarracenia pitcher but probably with an active pumping of potassium to the leaf, perhaps balanced by a passive leakage of Na^+ from the leaf.

As the decomposition of the detritus proceeds, the CO_2 released decreases the pH of the medium which may cause the pitcher pool proteases to be increasingly ineffective (Lloyd). In a personal communication (March 1973), C. G. Paterson stated that he believed the macroinvertebrates to be beneficial to the plant's nutrition by aiding in the breakdown of the detritus. At the least, he says that their burrowing habits cause the detritus to be rendered more digestible by bacteria which in turn would release nutrients into the water column for absorption by the leaf. This is not a new idea since Schimper stated in 1882: "Innumerable worms were present in all the leaves studied; these possibly participate in the transportation of the animal bodies into soluble compounds." Hepburn, St. John and Jones in 1927 construed this to mean that "the larvae of the insect associates possibly play a part in the digestion of the prey." They also state that "bacteria apparently live in symbiosis with the Sarracenia, drawing their nutriment from the digested insects, and aiding, to a certain extent, in the digestion of the prey." The "extent" has not been determined but Paterson (1973), has observed large amounts of bacterial activity in senescing, but still functional,

pitchers. There are a great number of species of bacteria present in the pool (Plummer and Jackson, 1963), and the determination of any dominant form is complicated by continual contamination by bacteria introduced by the prey.

Two major variables exist in the physiological and, to some extent, morphological states of Sarracenia in the field. These are age (or time after opening of pitchers) and location in the bog. The physical parameters at the periphery of the bog may vary greatly from those in the central portions.

Introductory survey courses in biology often have cause to mention insectivorous plants including Sarracenia. The carnivorous nature of the plant is stressed when comparing the characteristics of life common to both plants and animals. Assuming a voracious pitcher-plant, with a leaf morphology solely designed for insect trapping and digestion, the initial primary aims of the study were to determine the relative imputs of detrital and photosynthetic energy to the leaf and to fit this data into an overall picture of energy fluxes through the leaf.

As the study progressed, more doubt was cast on Sarracenia purpurea's epicurean intents and a secondary aim developed to discover any other possible benefits that the plant may derive from the peculiar morphology of its leaves.

"The meaning of analogy in logic is inference or procedure based on the assumption that things, whose likeness in certain respects is known, will also be found alike or should be treated as alike, in respects about which knowledge is limited to one of them. It is perhaps the basis of most human conclusions, its liability to error being compensated for by the frequency with which it is the only form of reasoning available."

Fowler

B. THE PRELIMINARY CHARACTERIZATION OF THE SYSTEM

I. BLACK-BOX CHARACTERIZATION

The ecosystem defined by the pitcher-leaf of Sarracenia may be considered in terms of black-box theory; the actual functioning parts within the boxes are not of immediate concern. The fluxes of compounds and energy from box to box are considered, remembering the interchangeability of mass and energy. The system is then characterized by influxes and effluxes in an attempt to better understand the functioning of the system as a whole. When considering energy flow in which a plant is defined as the central component, it is common to consider principally, carbon flow. This explains the dominance of the carbon cycle in Figure I which is a black-box representation of a pitcher-plant in the field. Luckily, for calculation's sake, almost all of the carbon dioxide which is present in the pitcher fluid is in the free CO_2 form because the pH of the fluid is rarely more than 5.5 (Emerson and Green, 1938). As can be seen from the composite Figure I, and its parts, Figures 1A, B, and C, there are several three-sided equilibria established of the form shown in Figure II.

The atmospheric concentration in the field may be assumed to be constant, so one need only consider changes in gaseous concentration in the other two boxes; i.e. an increase in concentration in the leaf, a decrease in

concentration in the leaf, an increase in concentration in the fluid and a decrease in concentration in the fluid. However, when dealing with the system in an assimilation chamber, complications arise because of the effects of an alteration of the atmospheric concentration; e.g., if one is to analyze CO_2 exchange as a measure of photosynthetic rate, a calculation must be made of the new equilibria set up when the carbon dioxide content of the atmosphere within the assimilation chamber is lowered. This is further discussed on Page 44 and in Experiment 3.

II. ENERGY FLUX CHARACTERIZATION

Each pitcher of a pitcher-plant cluster may be treated as a separate ecosystem with energy input from radiant energy and detritus. Energy output is in the form of radiant energy, evaporation and export of organics into the root. Some energy is stored in changing temperatures. Therefore, the sun and the environment external to the pitcher are sources and the "environment" including the atmosphere, "deep-space" and the rhizosphere are sinks. Of course, this is on a short term, small-scale basis; ultimately for us, as pointed out by Gates (1965), the sun is the source and deep-space is the sink. Although "life" or the "biosphere" appears to defy entropy, in fact, on the larger-scale, entropy is increasing and the transient state of the biosphere is "ordered" by the energy flux through it (Morowitz, 1968). One may argue that the sun too is an ordered state that is transient and negentropic; then one postulates increasingly greater energy sources or eventually a "god" which is pure negentropy. This digression serves to illustrate that in just as valid a sense, but in the opposite direction, a Sarracenia pitcher may be isolated as an ordered state produced by an energy flux from source to sink. In a growth room, the sources of energy are 1) the lights, 2) the walls which both reflect energy from the lights (analogous to skylight) and radiate energy as "black-bodies", 3) the benches which act primarily as black-bodies and 4) the "soil" which reflects and re-radiates. The

situation and calculations are simplified if the temperature and humidity are kept constant by an air conditioner. If one extrapolates to a larger natural system (consider the earth) the system does not influence significantly the external conditions around it; i.e., it does not alter the characteristics of the source or sink (the sun and deep-space). The sink is everything outside of the pitcher; i.e. the room, the rhizosphere, etc., but eventually the air conditioner which is analogous to "deep-space".

The simplest system to study has the fewest variables; since it is better to get results from simple systems that can be interpreted than to get results from complicated systems, that cannot. This is the rationale for the study being done in the "un-natural" environment of a growth room.

A simple system has source constant, sink constant and simple intermediary; e.g., a pitcher of Sarracenia holding an optimum amount of water--no detritus and no inquilines. This system may be compared in terms of energy flux with 1) a pitcher with measured amounts of detritus and water, 2) a pitcher with detritus and inquilines and water, and 3) an empty pitcher.

The equation with which I propose to describe the system under study is adapted from Gates (1965) and Tyree and Dainty (1972). They were primarily concerned with describing the energy relationships of large systems, in particular, the sun - biosphere - deep-space system. In most calculations, therefore, any assimilation factor or energy

dissipation in temperature changes are ignored when dealing with large systems over prolonged periods of time. These two factors, however, may become important when considering such a small system as a pitcher of Sarracenia over a time period in the order of weeks.

The influx of energy must be balanced:

$$R_n = \alpha_s (R_s^i) + \alpha_l (R_l^i) - R_l^o \quad , \qquad (1)$$

where: n = net flux

R = Radiation flux

s = short-wave radiation (0.3—3.0μm)

l = long-wave radiation (3.0—25μm)

α = absorption coefficient

α_s = 0.5—0.8; α_l = 0.97—1.0 (According to the angle of incidence); i.e. the net radiation received by a leaf equals the amount of short-wave radiation received plus the amount of long-wave radiation received minus what is re-radiated. An approximate value of the net radiation received by a leaf in sunlight is 1.0 — 1.4 cal. cm^{-2} min^{-1} (Gates 1965), as compared to the approximate value for the sun's radiation on the atmosphere at noon which is 2.0 cal. cm^{-2} min^{-1}. At 25°C (298°K) the leaf would re-radiate, according to Stephan's Law, ($\alpha T^4 = R_l^o$ where α = Stephan's constant 8.13 × 10^{-11} cal. cm^{-2} min^{-1} $^oK^4$). Therefore the leaf would absorb approximately 0.4 to 0.8 cal. cm^{-2} min^{-1} !! If this energy

were not dissipated in some way the temperature of the leaf would soon rise to lethal values of approximately 50°–60°C at which temperature αT^4 would dissipate all of the incoming radiation.

Therefore the following relation has been derived to explain the adaptation of a leaf to dissipate the absorbed energy:

$$R_n = H + lE + G + aA \ , \qquad (2)$$

where: R_n = net flux (radiant)

H = heat diffusion from a warm to cold body

l = latent heat of vaporization

E = rate of evaporation of water

G = heat stored in temperature changes

a = coefficient of fixation of energy

$\simeq 3000$ cal g^{-1} for carbohydrates

A = rate of fixation of energy

In the case of the pitcher-leaf of Sarracenia, another form of energy is also available for assimilation; i.e. the detritus pool. In order to completely describe the energy flux of the leaf this chemical energy flux must be determined.

$$\text{i.e. total energy flux} = R_n^i + D_n^i \ , \qquad (3)$$

where: R_n^i = net radiant energy influx

D_n^i = net detritus energy influx

and $$D_n^i = \alpha_D D^i , \quad (4)$$

where: α_D = absorption coefficient which depends on the size of the pitcher orifice and its attractive properties to insects

D = detritus flux which depends on the density of possible "prey"

i = inward flux to pitcher

and $$D_n^i = S + bB + M_I , \quad (5)$$

where: S = storage of energy in detritus pool

b = coefficient of absorption of energy (= energy content of detritus absorbed)

B = rate of absorption of material from detritus

M_I = metabolic dissipation of detritus by inquilines

The total influx of energy may be balanced with effluxes according to the equation:

$$R_n^i + D_n^i = H + lE + G + aA + S + bB + M_I , \quad (6)$$

"The classification of the constituents of a chaos, nothing less is here essayed."

Moby Dick

C. IN SEARCH OF A QUANTITATIVE DESCRIPTION OF THE SYSTEM

I. EXPERIMENTAL APPROACH

1. Detritus absorption

Purpose:

To determine if there is a significant measurable energetic exchange from detritus to the pitcher-leaf; i. e. to determine b and B of equation 6 (Page 15).

Methods and Materials:

On November 12th, 1973, blocks of frozen Sphagnum containing pitcher-plant clusters were dug from the large bog near Crystal Crescent Beach, Halifax County, Nova Scotia. All samples were collected within a 100 m^2 area. The frozen blocks were placed in plastic dishpans (27 cm. × 32 cm. × 14 cm.) in a growth room and "watered" with bog water collected from the stream which runs through the bog. The growth room was maintained at 21° C. ± 1° C. and 52% ± 2% relative humidity.

Most extraneous plant material, notably Ledum groendlandicum, Cladonia spp., Kalmia angustifolia, was removed from each dishpan, leaving relatively pure stands of pitcher-plants and Sphagnum spp.

The dishpans were numbered arbitrarily from one to ten and measurements of the physical conditions of the

pitcher-leaves were made. The contents of each pitcher were removed, placed in numbered capped plastic vials and frozen for future reference. The pitcher-leaves were refilled with distilled water.

Equation (1) shows that the actual amount of radiant energy absorbed by the leaf is determined by the amount of short-wave radiation absorbed plus the amount of long-wave radiation absorbed minus that which is re-radiated according to Stephan's law. The spectroradiometer measures the incident radiation in the range of 0.400 μm to 1.55 μm with reasonable accuracy. The reflectance and transmittance of plant leaves increases dramatically immediately to the long wavelength side of the red chlorophyll absorption band, resulting in the absorptance falling to a very low value. However, at wavelengths greater than 2.5 μm, plants become nearly black once again, absorbing the far infrared efficiently (Gates et al, 1965). The incident long-wavelength radiation is calculated by Stephan's law using the temperature of the soil for the radiation incident on the lower part of the pitcher and the temperature of the walls for the radiation incident on the upper part of the pitcher. The coefficient of absorption of long-wave radiation is assumed to be 1.0 (Gates 1965). Therefore the long-wave radiation is simply expressed by αT^4 where $\alpha = 8.13 \times 10^{-11}$ cal cm^{-2} min^{-1} $^{o}K^{-4}$.

The determination of the absorption coefficient for the short wavelengths was a problem. One may measure

the incident visible light and the transmitted radiation and the difference equals absorptance plus reflectance. However, one must find some method of measuring the amount of reflected light. A good approximation may be made from data provided by Gates et al (1965). The absorptance vs. wavelength relation of Sarracenia probably lies between that of regular deciduous leaves and the cacti tested since the pitcher-plant does possess a shiny cuticle and is thicker than the average deciduous leaf tested.

Besides absorbing efficiently at long wavelengths, leaves also are good emitters at the same frequency. Therefore much energy is re-radiated at wavelengths approximating 10 μm according to Stephan's relation.

In order to determine energy loss by heat diffusion (H), measurements were made of air temperature (Ta), water temperature within the pitcher (Tw) and soil (Ts). The gradients may then be noted and relation (7) applied:

$$H = k \frac{dT}{dz} , \qquad (7)$$

where: k = coefficient of thermal conductivity

z = distance

T = temperature

Evaporative flux (E) is more difficult to determine and is discussed elsewhere (Gates 1965).

G, the energy stored in temperature changes, may be

calculated from the difference in air and leaf temperatures if in fact they are sustained differences.

A, the assimilation rate of carbohydrates from radiant energy, may be calculated via gasometric techniques but was ignored in this preliminary experiment. It was hoped that the relative magnitude of this factor might "drop out" of the calculations.

S, the storage term of the detritus pool, may be determined via bomb calorimetry; i.e., the detritus pool, remaining in the pitcher after the experiment, was dried, weighed, and its energy content estimated.

M_I, the metabolic dissipation of detrital energy by the macro-inquilines, was calculated from literature values for aquatic insect larvae.

B, the rate of assimilation of energy from the detritus pool by the plant, was determined by sub tracting the sum of S and M_I from the initial energy content of the detritus pool at the beginning of the experiment. This value was then averaged over the duration of the experiment.

(a), the coefficient of fixation of radiant energy is a constant, and (b), the coefficient of fixation of detritus energy, was determined from literature values based on bomb calorimetry.

Note: Distilled water was added to the pitchers, at weekly intervals, following the measurement of pH of the pitcher fluid. The experiment was terminated after four (4) weeks, in order that the insect larvae did not have time to

mature and emerge.

Detritus and inquilines from 40 pitcher-leaves were collected in their frozen state on January 7, 1974, at the bog near Crystal Crescent Beach. On January 8, 1974, enough Wyeomyii smithii were recovered from the thawed sample to yield five (5) per pitcher in the preliminary experiment. The Metriocemus knabi were inactive and were assumed to be dead; it was later found that it simply took a longer period of above-freezing temperature to initiate activity and feeding. This may be one reason for their greater survival rate compared to W. smithii as reported by Paterson (1972). The longer requirements for breaking senescence and initiation of feeding would save them from being killed when the pitchers re-freeze after a winter thaw.

The inactive inquilines and other detritus was filtered through No. 1 Whatman qualitative filter paper and dried at 90°C for 43 hours. It was then broken up with a mortar and pestle until discrimination of tissue-type was difficult; i.e., until it was roughly homogeneous with the appearance of fine soil. The total dry weight of the detritus was 1.8635 g.; therefore, each detritus treatment was 1.8635 ÷ 40 = 0.0466 g., the average weight of the detritus per plant collected.

The experiment was initiated on January 14, 1974. The initial amount of distilled water added to all pitchers was 7 ml. The detritus (D) and inquiline (I) pitchers also received 0.0466 g. of detritus and the inquiline (I) pitchers

received five (5) mosquito larvae. The temperature and relative humidity of the room were monitored continuously throughout the experiment with a thermo- hydrograph. The accuracy of this instrument was checked every day with a sling psychrometer.

At weekly intervals, i.e., on January 21, 28, February 4 and 11, the temperature of the leaf water, the soil temperature, pH of the leaf water and the net amount of water which had left the pitcher by both evaporation and plant uptake were measured. This last parameter (water loss) was calculated after the second week by filling each pitcher to its maximum volume with distilled water and on succeeding weeks measuring the amount of water required to re-fill each. The temperatures were measured with a calibrated mercury thermometer.

The incident radiation was measured using an ISCO spectroradiometer (S.R.) with a recorder (see Figure III), using a remote probe. The probe was oriented first with its receiving face parallel to the light sources and then perpendicular to the light sources at the height of the pitcher leaves. The calibration curves of the S.R. are shown in Figures IX and X.

Figure IV shows the experimental arrangement of the clusters on February 14,1974, just prior to harvesting. Figure V shows tray No. 4 with flower stalk present. Figures VI and VII are of tray No. 7 showing the flower and leaf arrangement with white labels for identification of the

pitcher-leaves.

The pitcher-leaves were harvested on February 15, 1974; the procedure was as follows. Each pitcher-leaf was identified and severed near the crown. The contents were emptied into a beaker and any detritus which remained in the leaf was washed out with distilled water. The wet weight of the leaf was determined after blotting dry and was placed in a labelled paper bag to be dried at 80°C. The contents of the pitchers were filtered on weighed filter paper (Millipore RAWP 04700, R.A. 1.2 µm, 47 mm, white plain) and the recovered detritus and filter paper were dried at 80°C. Dry weights of the leaves and the detritus were determined after 48 hours and 72 hours of drying. If the resultant weights were not identical, the material was dried until a consistent dry weight was determined.

The percent dry weight of the leaves and the amount of detritus not recovered were determined. It was necessary to determine the amount of detritus one would expect to lose due to the technique of detritus retrieval. To do this, detritus, filter paper, and weighing pans were dried at 80°C for 72 hours. The detritus was then weighed and distributed among six pitcher-leaves in five (5) ml. of distilled water. After two hours, the leaves were removed and the detritus recovered in the same way as in the treatments above. The weight of the dried recovered detritus was compared with the initial weights.

Results and Discussion:

Approximately 42% of the pitcher leaves of any Sarracenia purpurea cluster were found to be at least 25% necrotic tissue and the leaves with the greatest amount of necrosis and those with small holes burrowed in them at the base by parasitic insects did not hold water (see Table I).

One might easily conclude that necrotic pitchers do not hold water; however, this may be placing the cart ahead of the horse. The answer may just as easily be that pitchers that cannot hold water cannot survive and become necrotic. This appears to be the case with those leaves parasitized by burrowing insects.

Table II shows the mean measured characteristics of the pitcher fluid. Each number is the mean of twelve samples. There appears to be no detectable gradient of temperature between the pitcher leaf fluid (it is assumed that this represents the leaf temperature) and the air, or the fluid and the soil. This ,perhaps, is to be expected in a controlled environment room.

The mean pH values of the three groups differ but not significantly at the 5% level due to a high variance. Paired variate analysis was used as the test statistic. The pH of the distilled water added a week prior to these measurements had a pH of 7.06. The drop in pH is expected simply due to the solution of CO_2 from the atmosphere; any difference in pH due to inquiline or bacterial activity was not detected.

There was no significant difference in the amount of water loss from the three groups of pitcher pools during the experiment. There was a mean decrease in the pool volume of 7 ml. of water. At 20°C, the evaporation of this mass of water would entail a dissipation of 4.10 Kcal of heat. There is no way of knowing from this experiment whether that was all the water which was lost from the pool volume or whether the pool is continuously replenished from root uptake of water. It has been noted that pitcher-plants growing under water stress conditions which cause even the surface of the Sphagnum to dry and turn brown, retain water in the pitcher without rain or any outside direct addition of water to the pitcher-leaf. There appear to be minimal temperature gradients sustained in the growth room environment and no external temperature fluctuation; for that reason, there would be little need for dissipation of large amounts of heat from the leaf through the pitcher pool.

Table III shows a very qualitative analysis of the texture of the recovered detritus. It was done by a visual analysis of the dried filter papers without prior knowledge of the treatment involved so that bias could be avoided. There appears to be no difference in the texture of the control samples and the detritus (D) treatment samples. Note that there was some detritus recovered from the "control" leaves. This was mostly particulate matter which was not completely washed from the leaves at the beginning of the experiment. No insect prey were recovered from any

of the control pitchers. The comparatively coarse texture of the detritus found in the (I) treatment leaves indicate that either there is an aggregation of fine particles by the inquilines or, more likely, the inquilines ingest the finer particles and reduce them to microscopical size and to perhaps a diameter of even less than 1.2 μm which would allow them to pass through the filter paper. Such fine particles could be further reduced by bacterial action (Paterson 1973).

The mean amounts recovered from the leaves are as follows:

1) Control (C) pitchers = 0.0062 g. ± 0.005 g.
2) Detritus (D) pitchers = 0.0332 g. ± 0.008 g.
3) Inquiline (I) pitchers = 0.0435 g. ± 0.007 g.

The method of retrieval of detritus was found to produce a loss of 10.8% ± 0.8% of the initial dry weight. The extra 10 mg. recovered in the inquiline pitchers is attributed to the weight of the inquilines themselves which were not separated from the detritus in the final filtration process. Recall that initially 0.0466 g. of detritus were added to each (D) and (I) pitcher. The recovery of detritus from the "control" pitchers indicates that this initial value should be increased to 0.0535 g. Thus the maximum total amount of detritus which was absorbed by each leaf in the experimental period equals the initial detritus weight minus the detritus recovered minus 10.8% of the initial

detritus weight added: (0.0553 g. - 0.0332 g. - 0.0060 g. = 0.0161 g.) assuming no dissipation of detritus energy by the inquilines. Richman and Slobodkin (1960) have emphasized the constancy of the calorific value of animal tissue. Except under starvation or storage conditions, animal tissue average about 5000 cal/g. dry wt. The calorific content of plant material is more variant with season and tissue-type but nonetheless averages between 4200 and 5000 cal/g. dry wt. Thus a value of 5000 cal/g. dry wt. may be approximated for the detritus of the pitcher pool. If the 0.0161 g. of detritus were completely absorbed by the plant this would involve an energetic uptake of only 80.5 cal over the four weeks of the experiment. The whole of the insect "prey" is not readily available for digestion and, in fact, the most energy-rich compound, chitin, is probably not digested at all in the pitcher fluid.

One may now consider equation (5) in terms of this first experiment:

$$D_n^i = 0.0553g \times 5.00 \times 10^3 \frac{cal}{g}$$
$$= 2.76 \times 10^2 \text{ cal.}$$
$$S = 0.0332g \times 5.00 \times 10^3 \frac{cal}{g}$$
$$= 1.66 \times 10^2 \text{ cal.}$$
$$bB = 80.5 \text{ cal.}$$

Metabolic dissipation of detritus energy by inquilines may be ignored if one uses the data from the detritus treatment leaves (D).

2. Growth Under Near-optimum Conditions

Purpose:

The experiment on detritus absorption suggested that very little detritus was actually absorbed by the leaves and the treatments varied little in appearance. Therefore this experiment was designed to test the hypothesis: Growth of Sarracenia purpurea L. leaves under controlled (growth room) near-optimum conditions (i.e., constant temperature and sufficient light) is not dependent on the presence of water and/or detritus in the pitchers.

Methods and Materials:

Twenty-one Sarracenia purpurea clusters were collected from a bog at Fink's Cove (Sandy Cove) Halifax County, Nova Scotia, in Sphagnum moss and removed to the growth room in washpans. All the leaves were removed so that only new buds remained at the plants' crowns. This was done in order to produce new leaves for the growth experiment. The plants were initially watered with water collected at the bog near Crystal Crescent Beach but this was found to be impractical and after the second week of growth, tap water was used as the medium.

On July 16th, 1974, twelve plants had each regenerated one leaf, each of approximately the same size and condition. These were labelled, measured and the number of leaf primordia associated with the leaf were counted. The height was measured from the beginning of the lateral wing

since this was found to approximate the beginning of the pitcher cavity and usually the ground level. The width was the greatest width of the pitcher-leaf not including the lateral wing.

On July 18th, 1974 the experiment was initiated. The leaves were divided into three treatments:

1. Control - nothing was added to these pitchers but the orifice was gently forced open.
2. Water - these leaves were filled with de-ionized distilled water which was replenished every two days.
3. Detritus- Dried and weighed fruit fly larvae were added every Wednesday for three weeks, plus de-ionized distilled water was added and replenished every two days. De-ionized distilled water was used so that there would not be any fertilizing effect by the water (only thermal effects).

All of the leaves were originally closed and were gently forced open. At weekly intervals, the length and width of each leaf were determined, the number of leaf primordia present and the number of these which were differentiated into new pitcher-leaves were noted. On August 13th, 1974, final measurements of length and width, number of initiated shoots, total pitcher volume, and wet weights were noted for each test leaf. Before drying the leaves their light transmittance spectra were measured by placing

each in turn over the remote probe of the spectroradiometer. They were then dried at 80°C for 48 hours and their dry weights noted.

Results:

Figure XIV illustrates the growth of the pitcher-leaves of the three treatments. Because of small sample numbers, the variance is high and no significant difference between treatments is obvious. Table IV lists final values for parameters measured. No significant differences between treatments were noted for any parameter. Since only very small differences appeared in the transmittance qualities of the leaves, all the data for the three treatments was pooled and graphed in Figure XV . The ratio of the area under the curve of the transmitted light between 400 and 700 nm in wavelength to that of the area of the incident light between the same boundaries was calculated graphically and found to be ≃ 19%; i.e. 19% of the light incident on the leaves was transmitted.

Discussion:

The data supports the original hypothesis. The presence of water and/or detritus in the pitcher-leaf does not seem to give the plant any survival advantage in the growth room.

3. Gasometric Analysis

Purpose:

To determine the magnitude of the photosynthetic rate of Sarracenia purpurea leaves (factor A in equation 6) with and without the pitcher fluid present.

Methods and Materials:

Clusters of pitcher-plant leaves collected at the same time and in the same manner as those used in experiment I were tested. Several clusters were transplanted on February 14th, 1974, from the Sphagnum to vermiculite which had been previously soaked in bog water. By maintaining the plants in this way there was no possibility of interference by surrounding vegetation as there was in the Sphagnum-supported plants. The pitchers were thus easier to manipulate without fear of damage at the crown.

Analysis was done on the carbon dioxide exchange of leaves enclosed in assimilation chambers using a Beckmann IR215B Infrared Gas Analyzer (IRGA). A schematic representation of the apparatus is given in Figure VIII.

The plant chamber was made by enclosing the pitcher-leaf within a thin-walled polyethylene bag, the neck of which was sealed around the base of the stem with putty and a metal tie. An inlet tube and outlet tube were put through the bag and sealed with silicone cement. The properties and performance of the polyethylene chamber are discussed by Koller and Samish (1964); the bags certainly seemed particularly suited to study of Sarracenia leaves due to the

difficulties of fitting other types of chamber around the pitcher-shaped leaves.

Air was drawn from outside of the building by a Reciprotor A/S pump and fed to a Y-junction, one tube of which led to a bleed to provide a coarse adjustment on air flow. The other tube split again to two 2,000 ml Erlenmeyer flasks. These acted as reservoirs to counteract irregularities in the air flow caused by the pump. The reference air stream then passed through a drying column via a regulatory valve to a flow meter and then through the reference tube of the IRGA. The sample air passed from the holding flask to a copper cooling coil immersed in a salt and ice water solution. This was necessary in order to counteract the heating of the air caused by the pump. The air then passed into and through the polyethylene bag sample chamber and out to another Y-junction. One tube of the junction was immersed in water as a pressure regulator which insured that pressure did not build up in the sample chamber and cause leaks. A pressure regulator is also important since the IRGA essentially measures CO_2 density and this would be increased if pressure were increased, giving a false impression of CO_2 concentration. The usual pressure allowed was 4.4 cm of water or approximately 0.01 bar. The other branch of the Y-junction led to a flow meter and then to another bleed followed by a regulatory valve, drying tube, flow meter and the sample tube of the IRGA and the outlet.

There was a tube with needle valve regulation joining the sample and reference streams as seen in Figure VIII. This was necessary to allow outside air to bypass the sample chamber in order to zero the IRGA with ambient air passing through both the sample and reference tubes. This valve was closed when comparing sample and reference gases. The range and sensitivity of the IRGA were checked periodically by passing standard gases of known CO_2 concentration through the sample tube while ambient air passed through the reference tube. (Usual concentrations used were 290 ppm and 325 ppm).

The temperature of the air stream reaching the sample chamber was periodically checked with a telethermometer by disconnecting the tubing at the inlet of the chamber and inserting the probe into the airstream.

Experiment 3a

Purpose:

To investigate CO_2 exchange in young S. purpurea leaves in the dark and in the light, with and without water enclosed in the pitcher.

Materials:

Three young leaves (i.e. leaves which had developed from the field) were tested. Table V shows the physical parameters of these leaves.

Method:

Carbon dioxide exchange in light and dark (light intensity and quality were measured with a spectroradiometer) were measured for each leaf: (a) with and (b) without distilled water (pH - 5.7) in the pitcher. Two determinations of the CO_2-exchange rate of each leaf under both light and dark conditions were made. Sampling of CO_2 was done for thirty to forty-five minutes for each determination. Usually a steady rate of CO_2 exchange was reached within ten minutes which was sustained for the remainder of the treatment period (i.e. light or dark). All measures were made during the light cycle of the leaves' inherent light-dark cycle.

Calculations:

The uptake or evolution of CO_2 is calculated according to the following relation:

$$E' = \frac{\Delta C \times J}{M} , \qquad (8)$$

E' = exchange of CO_2; $cm^3\ sec^{-1}\ g^{-1}$ dry wt. of leaf

ΔC = difference in CO_2 concentration between sample and reference tubes; $cm^3\ cm^{-3}$

J = flow rate through the chamber; $cm^3\ sec^{-1}$

M = dry weight of leaf enclosed; g.

Results:

The results are shown in Table VI in terms of a mean value and plus or minus one standard deviation.

Discussion:

Table VI indicates that the net CO_2 exchange in the assimilation chamber was less when water was present in the pitcher than it was in its abscence. There are at least two possible explanations. Either:

1) The leaf absorbed CO_2 from the pitcher pool reservoir during photosynthetic activity when water was present and similarly released the gas predominantly into the pool during respiration. In other words, gas exchange was not through the stomata of the outer surface but through the intercellular spaces which open to the inside of the leaf adjacent to the pool. One could assume that the CO_2 exchange between the pool and the air would be much slower than the CO_2 exchange between the pool and the leaf. Thus over the short period of the monitor of gas exchange in the assimilation chamber, the apparent uptake or loss by the leaf to the atmosphere of the chamber would be minimal.

Or: 2) Perhaps the leaf directly absorbed CO_2 from

the atmosphere. This would lower the concentration of CO_2 in the immediate atmosphere about the leaf, causing the pool which was saturated with CO_2, to lose the gas into the atmosphere in an attempt to set up a new equilibrium as described on Page 44.

In either case (1) or (2), if the pitcher is filled with water, then the amount of CO_2 exchange in the assimilation chamber depends on the concentration of CO_2 in the pitcher fluid. It therefore appears that an estimate of the maximum magnitude of the photosynthetic rate of the leaves is better derived from CO_2 exchange experiments using empty pitcher-leaves.

Experiment 3b

Purpose:

To measure the inherent cycle of CO_2 exchange of the pitcher-leaf of S. purpurea.

Methods and Materials:

The leaves tested were grown in a constant temperature ($21^{\circ} \pm 1^{\circ}C$), relative humidity (53% ± 2%) and light (See Figure XI) from the crowns of Sarracenia purpurea plants which had been removed from the field and their leaves excised. The L-D cycle was 14 hr. light - 10 hr. dark. The crowns were supported by Sphagnum sp. which was kept wet and no water or insects were placed in the pitcher leaves as they developed.

Each of the two leaves tested was enclosed in a polyethylene chamber as described earlier and pictured in Figure XIV. The CO_2 sampling system was as shown in Figure VIII but the IRGA was a Beckman Model 865. CO_2 exchange of each leaf was monitored over a 24 hour period under conditions of constant temperature ($26^{\circ}C$) and continuous light.

Results:

No natural cycle of CO_2 exchange was observed. The leaf absorbed CO_2 from the airstream at a constant rate for 24 hours. This rate was the highest recorded: 9.67×10^{-5} cm^3 (CO_2) sec^{-1} g^{-1} or 6.84×10^{-1} mg. CO_2 hr^{-1} g^{-1} dry weight of leaf.

Discussion:

This experiment indicates that, given sufficient light and suitable temperature, the leaves of S. purpurea will photosynthesize at a rate not apparently influenced by any inherent metabolic cycle or rhythm . Therefore, the determination of photosynthetic rate need not be done during any particular time in the light-dark cycle of the plants. The maximum photosynthetic rate observed for S. purpurea leaves using gasometric techniques was 6.84×10^{-1} mg CO_2 hr^{-1} g^{-1} dry weight of leaf.

4. Water Uptake Into the Leaf-Pool from the Roots

Purpose:

To test the hypothesis: Young pitcher-leaves depend upon rainfall to fill them but once decomposition begins within the small lentic system, the difference in water potential between the pitcher-pool and the root medium is sufficient to draw water into the pool from the medium.

Theory:

In experiment (1) (detritus absorption), it was found that the mean loss of water added externally to each leaf, was 28 grams in four weeks. Slatyer (1967) defines the relation between evaporative flux (E) and the concentration of water at the leaf surface (C_1) and the water concentration of the bulk air (Ca) outside an unstirred layer of air (da) as:

$$E = D \frac{C_1 - C_a}{da} \qquad (9)$$

or:

$$da = D \frac{C_1 - C_a}{E} \qquad (10)$$

Equation (10) may be used to calculate the effective mean unstirred layer of air above the water surface of the leaf pool. If this value be reasonable, it would indicate that water loss from the pool may only be via evaporation from the pool surface.

Assuming a surface area of the air-water interface of the pool to be 10 cm^2;

E becomes: $1 \frac{28g}{mo.} \times \frac{1 \text{ mo.}}{2.4 \times 10^6 \text{ sec.}} \times \frac{1}{10 \text{ cm}^2}$

or: 1.17×10^{-6} g. cm^{-2} $sec.^{-1}$

Then, assuming saturation of the air adjacent to the pool and 50% R.H. of the bulk air at 20°C,

$$da = \frac{0.239 \text{ cm}^2 \text{ sec.}^{-1} \, (1.73 \times 10^{-5} \text{ g. cm}^{-3} - 9.2 \times 10^{-6} \text{g.cm}^{-3})}{1.17 \times 10^{-6} \text{ g. cm}^{-2} \text{ sec.}^{-1}}$$

$= 1.65$ cm.

This value (1.65 cm) represents the depth of the unstirred air layer in the pitcher-leaf expected if evaporation accounted in total for the loss of 28 ml. of water per leaf in experiment one. This is definitely a reasonable value. Hence, it appears that either no uptake of water from the medium to the pool occurred or that uptake into the pool was approximately equal to loss via the apoplast from the pool through the leaf. In either event, the leaves were dependent on external addition of water in order to maintain any volume. Of course, if the unstirred layer were increased to only 5 cm., each leaf would have lost as little as two ml. per week.

It was observed, in plants developing both in the growth room of experiment (1) and in the field, that small droplets of liquid formed on the inside (zones 4 and 5 as

defined by Lloyd [1942]) of newly-opened pitcher-leaves but did not appear to take up water from the soil to form a pool. However, once a pool was formed in the leaf by external water (rain; dew), it remained throughout the life of the healthy leaf even if no external water was added for long periods of time (i.e., two to three months).

If the original pitcher fluid is considered to be distilled water, as it was in experiment (1), the water potential difference between it and the medium water would tend to push water out of the leaf-pool and into the soil. Consider the water potential (ψ) of the pitcher fluid and the medium water to be described by:

$$\psi = \rho g h - RTC_s \ , \qquad (11)$$

where: C_s = concentration of solutes

R = gas constant

T = temperature (Kelvin scale)

ρ = density of water (1.0 g. cm^{-3})

g = acceleration due to gravity (980 cm $sec.^{-2}$)

h = height of water above ground level (i.e. level of medium water where $h = 0$)

Then, the water potential difference between the pitcher fluid and the medium, assuming the initial fluid to be distilled, deionized water at a level of 5 cm. above the ground level, and the concentration of the medium to be

0.01M or 10mM, is:

$$\psi_{pool} - \psi_{soil} = (4.19 \times 10^{-3} \text{ bar} - 0) - (0 - 0.24 \text{ bar})$$

$$= 0.24 \text{ bar.}$$

This positive water potential in the direction of the medium indicates the probability of a passive water flux into the soil from the leaf pool. This flux may be approximated by:

$$\frac{dQ}{dt} = L\rho \cdot \Delta\psi \cdot A \ , \qquad (12)$$

where: $\frac{dQ}{dt}$ = flow rate of water; cm^3 $sec.^{-1}$

$L\rho$ = hydraulic conductivity of passage of flow

$\Delta\psi$ = water potential difference

A = cross-sectional area of passage

If $L\rho$ is taken to be the value for self-diffusion of water at 20°C and the area of zones four and five, the inner (non-cuticular) absorptive part of the leaf, to be 2.0 cm^2, then:

$$\frac{dQ}{dt} = 10^{-5} \text{ cm}^3 \text{ cm}^{-2} \text{ sec.}^{-1} \text{ bar}^{-1} \times 0.24 \text{ bar} \times 2 \text{ cm}^2$$

$$= 5.0 \times 10^{-6} \text{ cm}^2 \text{ sec.}^{-1}$$

or 12 cm^3 during the one month period of experiment (1)

(2.4×10^6 sec.). This value would vary little with the height of the water in the pitcher-leaf.

However, as decomposition continues within the leaf-pool, the solute concentration of the pool would necessarily increase. If this concentration exceeded the concentration of the medium, the potential for water flux into the pool from the medium would exist. Paterson's (1972) reports of thick bacterial pitcher-pools indicate that at the end of the growing season, the osmotic concentration of the pool water is relatively high.

Method and Materials:

Samples of pitcher fluid and medium were collected from Sarracenia purpurea leaves in the Sphagnum bog near Crystal Crescent Beach, Halifax County, Nova Scotia in November 1973, June 21, 1974, July 21, 1974 and August 13, 1974 and frozen until osmolalities could be determined with a Osmette freezing-point depression osmometer.

Results:

Due to a malfunction of the osmometer, it was not possible to perform the quantitative survey of comparisons of leaf-pool and medium concentrations. However, on a qualitative basis, it was found that the concentration of leaf-pools in the July samples was greater than that of the media in which they were growing.

Discussion:

It therefore appears in theory, with some experimental basis, that the young leaves depend upon rainfall to

fill them, but once decomposition releases sufficient minerals into the small lentic system, the $\Delta\psi$ is sufficient to draw water into the leaf-pool from the external medium. The pool would be most concentrated at the end of the growing season, and thus at that time of year the water enclosed would be nearly maximum. This would ensure maximum thermal buffering against autumn temperature changes.

II PITCHER WATER AND CO_2-EXCHANGE

Consider the three-cornered equilibria of carbon dioxide exchange as shown in Figure XIII when the leaf is photosynthesizing and thus exhibiting a net uptake of CO_2. There are three possible major variations of the state of the pitcher contents which may alter the CO_2 fluxes:

1) the pitcher-leaf may be empty
2) the pitcher-leaf may only contain fluid
3) the pitcher-leaf may contain fluid plus inquilines (inquilines includes all bacteria, protozoa, and macro-invertebrates)

Consider the equilibrium in case (1) when the leaf is empty. The exchange of CO_2 is only between atmosphere and pitcher-leaf. Since stomata are only present on the outside of the pitcher, CO_2 entry will occur over this area. The thick cuticle of zones 1, 2, and 3 of the inner surface as described by Lloyd (1942) would make CO_2 absorption in these zones minimal. However, the lower one-third of the inner surface (zones 4 and 5) have reduced cuticle and would allow for easy diffusion of CO_2 through their moist surfaces. (These surfaces are observed to remain moist even when soil is very dry, a condition seldom seen in the field). This increased absorptive area would enhance CO_2-uptake but would probably not be comparable to absorption at the outer surface due to the almost certain presence

of a thick layer (as much as 1 to 2 cm) of unstirred air adjacent to the inside surface.

Case (2) in which the pitcher contains only water complicates the system somewhat but may be considered quantitatively:

Assume that no exchange of CO_2 takes place between leaf and atmosphere directly; i.e. the stomata are closed tightly and the cuticle prevents direct diffusion of CO_2 through the epidermis. This would allow for CO_2 uptake into the leaf solely from the pitcher fluid. The solubility of CO_2 in water at $20^{\circ}C$ is 365×10^{-4} mole liter^{-1} (Kaye and Laby). Assume that the surface layer of water is in carbon dioxide concentration equilibrium with the air; i.e. the surface layer has a concentration of 3.65×10^{-2} mole liter^{-1} or 1.61 grams liter^{-1}. One may invoke Fick's first law to determine the possible flux of CO_2 from the atmosphere to the leaf:

$$J' = -D \frac{dC}{dx} \quad , \tag{13}$$

or

$$J' = -D \frac{\Delta C}{\Delta x} \quad , \tag{14}$$

where:

$$J' = \frac{\frac{dQ}{dt}}{A} \quad , \tag{15}$$

where: J' = flux of CO_2

$\frac{dQ}{dt}$ = flow rate of CO_2

A = area of water surface

D = diffusion coefficient

$= 2.0 \times 10^{-5}$ cm^2 sec.$^{-1}$ for CO_2 in water

ΔC = difference in concentration between surface water and absorbing surface

ΔC_{max} = concentration at water surface minus zero i.e. assume an immediate transformation of CO_2 into other compounds at the cell surface in order to generate the maximum force for diffusion

Δx = mean distance between surface and absorbing cells

$\simeq$ 5cm. in this case

Then:

$$\frac{dQ}{dt} = D \frac{\Delta C}{\Delta x} (A) \quad , \qquad (16)$$

where: $\frac{dQ}{dt} = 2.0 \times 10^{-5} \times \frac{1.61}{5} \times \frac{1}{1000} \times 15 \frac{cm^2 \times g \times litre \times cm^3}{sec \times litre \times cm \times cm^3}$

$= 9.67 \times 10^{-8}$ g sec^{-1}

$= 9.67 \times 10^{-5} \frac{mg}{sec} \times \frac{3.600 \times 10^3 \text{ sec}}{hr.}$

$= 3.48 \times 10^{-1}$ mg hr^{-1}

This value of 0.35 mg. hr^{-1} is not an inconsiderable amount but probably indicates a maximum flow rate of CO_2 in case (2).

Case (3) introduces stirring in the water column with the movements of the inquilines and this would increase

the possible flux of CO_2 to the leaf; however, if one also considers the effect of an unstirred layer of air at the air-water interface, the flux of CO_2 would be greatly reduced beyond the effects of the inquilines stirring.

The inquilines introduce CO_2 into the water column through respiration at a rate proportional to their total biomass (Hargrave 1969, Zenthen, 1953). The mean rate of respiration determined by Hargrave (1969) for insect larvae and microflora is 1.0 µl O_2 hr^{-1} mg.dry $weight^{-1}$ or an evolution of 1.86×10^{-3} mg. CO_2 hr^{-1} mg. dry $weight^{-1}$. A generous dry weight of the inquilines found in mature pitcher-plants is 10 mg. which would imply a maximum evolution of approximately 2.0×10^{-2} mg. CO_2 hr^{-1} which is an order of ten less than the maximum value for diffusion of CO_2 into the leaf from the pitcher-pool surface.

It is obvious then that at least some CO_2 supply to the leaf may be provided by the pitcher fluid. It remains to compare these possible rates with those that the leaf actually absorbs.

A maximum measured value for net CO_2 absorption in the light by a Sarracenia purpurea leaf was 9.67×10^{-5} cm^3 of CO_2 sec^{-1} g^{-1} dry weight or 6.84×10^{-1} mg CO_2 hr^{-1} g^{-1} dry weight. This is an exceptionally low value, below that of even succulent plants (Šesták et al, 1971, pg. 31). This CO_2 absorption rate probably does not indicate the true assimilation rate of the leaf since it is only a description of the net leaf-atmosphere flux. It does not detect short-

term fluxes between leaf and pitcher-pool.

The possibility for CO_2 absorption from the pool seems to be a real one. Cronquist (1961) states that "the amount of wall surface that abuts on intercellular space in the mesophyll is generally greater than the total epidermal surface presented to the air, usually on the order of 10 to 15 times as great." (pg. 582) One possible advantage to the plant of exchange of gases through the pool is the minimalization of transpiration, although this is of dubious advantage in a bog system.

III PITCHER WATER AND THERMAL RELATIONS OF SARRACENIA

Lloyd (1942) notes that "Collinson wrote to Linnaeus, 'the leaves [of the pitcher-plant] . . . are open tubes, contrived to collect rains and dews, to nourish the plant in dry weather.' This prompted Linnaeus to regard Sarracenia leaves as adapted to holding water for its needs, thus enabling it to occupy drier situations, incidentally providing water for thirsty birds." However, once the European scientists found that Sarracenia lived in "swamps", they soon discarded the theory of the water giving "refreshment" to the plant. Since that time, emphasis has been placed solely on the pool of water as an insect-trapping and digesting device. However, the pool of pitcher liquid, which is almost entirely water, yields other, perhaps even more important, benefits to the pitcher-leaf. These benefits derive directly from the physical thermal properties of water and allow the pitcher-leaf to take on its extravagent morphology with large photosynthetic surface area and a height above that of the surrounding vegetation.

The heat capacity of water is exceedingly high. Its specific heat is 1.0 cal g^{-1} $^{\circ}C^{-1}$;* the only liquid which exceeds this is ammonia with a value of 1.23.** The larger the specific heat, the smaller is the temperature rise produced by a given amount of heat. The heat of vaporization of water at 20°C is 586 cal g^{-1} and 574 cal g^{-1} at 40°C.

*(288°K) **(233°K)

This implies that the evaporation of one ml. of water is accompanied by a dissipation of 586 cal. (at 20°C) or 574 cal. (at 40°C). If one considers the mean volume of water contained by a Sarracenia leaf to be 20 ml. (a minimal value), its total evaporation would dissipate approximately 11 to 12 Kcal. of heat. As can be seen from Figure IB, heat may be conducted from the leaf to the pitcher fluid and dissipated in an evaporative flux and through conduction to the atmosphere. Thus, the leaf pool tends to stabilize the leaf temperature; less diurnal fluctuation and slower changes in leaf temperature with any change in atmospheric temperature would result. All of the reactions of the Calvin-Benson cycle are temperature dependent and a slower rate of any one would yield a slowing of the CO_2-fixation process. Lower temperatures also result in a slower rate of CO_2 diffusion in the chloroplast. Excessive temperatures also may cause stomatal closure and decreased productivity. The macroinvertebrates may even play a role in aiding conduction of heat from leaf to water and vice versa; their movements cause convective currents decreasing the size of any unstirred layers.

The large heat of fusion of water (80 cal. g^{-1}) buffers seasonal temperature changes. The pitcher-leaf survives through the winter and does not senesce until the following August or September in most cases. Paterson (1971) studied the overwintering ability of the aquatic fauna associated with Sarracenia and suggested that their survival

is facilitated by snow cover insulation. The evergreen nature of the large Sarracenia leaves is equally amazing and the snow cover is probably instrumental in this process as well. However, it has been observed that pitcher-leaves may survive winter low temperatures without snow cover at least for part of the season (personal observation at Crystal Crescent Beach Bog, Halifax County, Nova Scotia, 1973) provided they contain water. Those parts of the leaves not enclosing water and not covered by snow are observed to become necrotic within two weeks after breaking dormancy. This lends credance to the concept of the pitcher contents as a temperature buffer.

Collinson may not, in fact, have been far from the truth in his original appraisal of the function of the water in the Sarracenia leaves. Sarracenia does not occupy a dry region but the water holding capacity allows for larger leaf surface area and thus increased transpiration and gaseous exchange to facilitate photosynthesis. As early as Goebel (1881) it was noted that a "not inconsiderable amount" of water was absorbed by the leaf from the pitcher. This water is absorbed into the intercellular spaces (Lloyd, 1942; Paterson, 1973) and would become available to the transpiration stream through the apoplast.

IV THE BALANCE OF ENERGY

An attempt may now be made, using the experimental data, to quantitate and compare the terms of equation (6):

$$R_n^i + D_n^i = H + lE + G + aA + S + bB + M_I \ , \qquad (6)$$

Both H and G (respectively, heat diffusion from warm to cold body and heat storage in temperature changes) may be ignored over the period of the experiment since there were no sustained temperature gradients detected.

It becomes evident during the study that exact values for radiant energy inputs and losses could not easily be measured. Perhaps the place of greatest estimation necessary was in determining the net radiant influx of energy to the leaf. The irregular shape of the leaves caused errors in calculation of total assimilation surface and it was necessary to kill leaves and disect them to trace an accurate surface area; the orientation of the leaves made it impossible to decide on an overall coefficient of absorption since it would vary continuously with the angle of incidence and thus the curvature of the pitcher. This alone made other estimations necessary and even desirable.

The long-wave radiation output of the leaf was assumed to just cancel the long-wave input because of the dominance of black-body radiators surrounding the leaf

(walls, benches and soil) which were maintained at the same temperature as the leaf.

The measured intensity of the source at leaf level shown in Figure XI (1.02×10^{-2} cal. cm^{-2} min^{-1}) was taken as the radiation flux of short wavelength incident on the plant. The coefficient of absorption was taken to be the maximum value reported by Gates (1965), 0.8, making the net radiant influx approximately 8.0×10^{-3} cal. cm^{-2} min^{-1}. This is probably an over-estimate but one that is countered by considering the total surface area of the leaf to consist only of one side and not the internal surface, which is an under-estimation of the total assimilation surface. Therefore, the total radiant energy influx to a leaf, with an external surface area of 100 cm^2 (a mean value found by tracing several of the experimental leaves), is 100 cm^2 $\times$ 8.0×10^{-3} cal. cm^{-2} min^{-1} or 0.8 cal. min^{-1} for a total of 2.1×10^4 cal. over the total period of illumination in Experiment (1) (2.60×10^4 min.).

The net storage of energy by photosynthesis may be calculated from the data of Experiment (3). The observed maximum rate of carbon dioxide uptake was approximately 6.8×10^{-1} mg. CO_2 hr^{-1} g^{-1} dry weight of leaf. The average dry weight of the leaves tested was 0.25 g. Therefore, the carbon dioxide uptake rate may be expressed as 1.7×10^{-1} mg. CO_2 hr^{-1} $leaf^{-1}$ or 75 mg. CO_2 $leaf^{-1}$ during the 434 hours of illumination of Experiment (1). Six moles of carbon dioxide are required to produce one mole of six-

carbon sugar; therefore, the 1.7×10^{-3} moles of CO_2 taken in would produce 2.84×10^{-4} moles of carbohydrate. The average of the molecular weights of a starch unit and glucose is 171.5 g. $mole^{-1}$ and one may thus infer a production of 3.67×10^{-2}g. of carbohydrate. The coefficient of fixation of energy for carbohydrates (a) is approximately 3000 cal g^{-1} (Gates). The term (aA) then becomes $3.67 \times 10^{-2}g \times 3000$ cal. g^{-1} or 110 cal.

The terms of equation (6) and their estimated values for the growth room experiments become:

$R_n^i = 2.1 \times 10^4$ cal.

$D_n^i = 2.76 \times 10^2$ cal.

H = insignificant

lE = not determined

G = insignificant

aA = 110 cal.

S = 1.66×10^2 cal.

bB = 80.5 cal.

M_I = insignificant

However, experiment (2) showed th at approximately 20% of the net incident radiation on the leaf may be transmitted. This would reduce the value of net radiation absorbed by the leaf to 80% of 2.1×10^4 cal. or 1.68×10^4 cal. Equation (6) becomes (in cal.):

$$1.68 \times 10^4 + 2.76 \times 10^2 = 0 + lE + 0 + 64 + 166 + 80 + 0$$

or: $$lE \simeq 1.68 \times 10^4 \text{ cal.}$$

In Experiment (1), a net amount of seven (7) ml. of externally-added water was lost from the pitcher-pool per week so that approximately 28 ml. was lost during the experimental period from each leaf. This accounts for a dissipation of 586 cal. $g^{-1} \times 28g$ or 1.64×10^4 cal. It appears probable that a large amount of the radiant energy dissipated by an evaporative flux from the leaf is done so via the pitcher fluid reservoir.

V THE OMBROTROPHIC FUNCTION OF THE PITCHER-LEAF

The *Sphagnum* bog ecosystem may be described as "ombrotrophic" (e.g, Harries ,1971), literally, "food from the sky". As mentioned in the introduction, the bog water is very acid and decomposition occurs at a near-negligible rate so that the root medium of plants growing in the bog is very nutrient-poor. Almost all of the nutrients available, says Harries, are brought in via rainfall. These nutrients are soon leached out of the upper layers where root uptake of ions principally occurs. Some plants, such as the black spruce (*Picea mariana*), possess very deep root systems which allow the plant opportunity to absorb the scarce nutrients as they filter through the layers of moss. Most others, like the ubiquitous heath scrubs (*Ericaceae*), have evolved a symbiotic mycorrhizal complex which supplement the nutrient supply available.

Sarracenia purpurea, however, appears to have adapted more directly to an ombrotrophic ecosystem. It catches and holds rain water so that it may absorb the nutrients directly into the leaf without an extensive and competitive root system. This pool of water also fosters bacterial decomposition of detritus, which in turn releases more nutrient material which is at least available to the leaf via apoplastic pathways.

The pitcher-plant is therefore uniquely adapted

to survival in the bog; although its spatial niche is similar to that of the Ericaceae, its functional niche is quite different.

Every theory of events in nature is necessarily based on some process of simplification and is to some extent, therefore, a fairy tale.

Sir Napier Shaw

D. CONCLUSIONS

The purpose of the study was to define a specific system (the pitcher-leaf system) and examine its energy relations in an attempt to better understand its organization. Theoretically, it was influenced by Morowitz (1968) and his general thesis that flow of energy through a system acts to organize the system ; Gates (1965) provided the mechanistic influence.

The essential question in the investigation became : " Why has Sarracenia purpurea L. evolved the leaf morphology it possesses?" ; i.e., what adaptive or competitive advantage does the pitcher-like morphology of the leaves afford the plant?

It appears,from consideration of the radiant energy fluxes, that the original selective advantage of a leaf form which will catch and hold water would not be one of nutrition but rather one of thermal buffering and heat dissipation. This allows for a greater leaf surface area and increased total photosynthetic production. With the pitcher-leaf full of water, the plant exhibits a similar functional morphology, in terms of temperature regulation, to that of a succulent plant. This near-xerophytic adaptationdoes not seem odd if it is compared with the morphology of the surrounding flora; e.g., Ledum groendlandicum which has small, almost needle-like, leaves with hairy undersurfaces which obviously cut down on transpiration losses.

The water level within the pitcher-pool is initiated by rain or dew but is probably maintained by osmotic flow through the roots from the bog medium.

It has been shown that the three-cornered flux equilibrium of CO_2 (Figure XIII) between leaf, atmosphere, and leaf-pool water allows for a carbon dioxide reserve which is available to the leaf without the necessity of open stomata. The leaf-pool is then a probable source of inorganic carbon.

The rainwater retention may give S. purpurea a competitive advantage over the surrounding flora in terms of nutrient absorption. If the experiments of Plummer and Kethley (1964) do indicate foliar absorption and not merely ion exchange with the apoplast, the pitcher-leaf allows a different functional niche and a unique adaptation to growth in an ombrotrophic environment.

With the introduction of water to the leaf-pool in the field must come allochthonous detritus. This combination of medium and varied food supply provides varied niches for aquatic ecosystem development, in particular, decomposer activity on the detritus. The dominant assumption in much of the literature and undergraduate teaching that Sarracenia purpurea actually absorbs relatively large amounts of insect tissue is ill-founded. The actual quantity of chemical energetic uptake by the leaf from the pool is small. However, the minerals that are usually released by decomposer activity in the soil but are present in only small quantities in the surface layers of the Sphagnum, become relatively

abundant within the pitcher-pool due to bacterial action (Paterson,1973;Plummer and Kethley,1964). In this way,the pitcher-pool and the detritus reservoir act more as an enclosed"soil" rather than an external "stomache". Certain amino acids are also released by the decomposer action within the pool (Plummer and Kethley,1964). Absorption of these nutrients could originally occur through breaks in the cuticle or through degeneration of cuticle which is evident in the lower internal surface of the pitcher-leaf (Lloyd's zones 4 and 5). This may allow for uptake via the apoplast to the symplast. However, the experimental data concerning detritus absorption by the plant from the enclosed pitcher-pool does not support the concept of the pitcher-leaf as a structure solely designed to capture and digest insects. In fact, the growth of pitcher-leaves under sufficient light and constant temperature is not enhanced by the presence of detritus in the pitcher-pool at all (Figure XIV).

In short, the peculiar morphology of the pitcher-like leaves of Sarracenia purpurea L.allows it both environmental and competitive advantages. The water within the leaf-pool functions to dissipate heat, and affords a buffering capacity against leaf temperature fluctuations, thus stabilizing temperature-dependent metabolism.The pool water may act as a reservoir for carbon dioxide in solution for photosynthesis. The literature suggests that the freshwater ecosystem releases minerals and amino acids which

are available for absorption by the leaf ; however, evidence was found which tends to de-emphasize this as a functional explanation of the leaf morphology.

It is concluded that the leaves of Sarracenia purpurea L. are not principally adapted as insect-catching devices although they do definitely perform that function. The morphology is rather an adaptation to a number of environmental requirements ; i.e., a mechanism for maximum photosynthetic area, and optimum balance between water and carbon dioxide exchange and, probably, nutrient uptake.

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APPENDIX

TABLE I: NECROSIS IN PITCHER-LEAF CLUSTERS

CLUSTER #	TOTAL NO. OF LEAVES	NO. OF LEAVES >25% NECROTIC	NO. OF NECTROTIC LEAVES WITHOUT FLUID
I/1	4	0	0
I/2	1	0	0
I/3&4	11	6	5
II	15	7	5
III/1	5	2	2
III/2	7	4	2
IV	24	14	9
V	7	4	4
Sub-total	74	37	27**
VI	11	4	no
VII	21	7	data
VIII	18	7	available
IX	3	0	
X	6	1	
TOTAL	133	56*	

* % of leaves necrotic = $\frac{56}{133}$ = 42%

** % of necrotic leaves without fluid = $\frac{27}{37}$ = 73%

% of non-necrotic Leaves without fluid = 0%.

TABLE II: MEAN CHARACTERISTICS OF PITCHER FLUID

TREATMENT**	TEMPERATURE* (^{o}C)	pH*	WATER LOSS*** (ml wk^{-1} $pitcher^{-1}$)
CONTROL	21.3	4.97	7.3
DETRITUS	21.2	5.33	6.5
INQUILINE	21.1	5.44	6.2

* Jan. 21/1974 before addition of distilled water to pitcher-leaf,

T_{air} = 21.3, $T_{soil\ (1\ cm)}$ = 21.1, $T_{soil\ (5\ cm)}$ = 21.5^{o}C

** No significant difference between treatments (12 samples per treatment) for any of the parameters.

*** In the period Jan. 21 - 28, 1974.

T_{air} = 21.3^{o}C ± 1^{o}C

Relative humity = 55% ± 4%

TABLE III: QUALITATIVE ANALYSIS OF TEXTURE OF RECOVERED DETRITUS

TEXTURE*	NO. OF CONTROL SAMPLES	NO. OF DETRITUS SAMPLES	NO. OF INQUILINE SAMPLES
3	7	8	1
2	2	0	2
1	3	3	7

* KEY: 3 = fine particles dominant

2 = medium particles dominant

1 = coarse particles dominant

TABLE IV: GROWTH PARAMETERS OF *S. PURPUREA* GROWN UNDER NEAR-OPTIMUM CONDITIONS

	TOTAL SHOOTS	TOTAL VOLUME	WET WEIGHT	DRY WEIGHT
CONTROL	2.5 ± 1.3	16.1 ± 3.5	1.786 ± 0.32	0.2902 ± 0.0667
WATER	1.5 ± 1.0	14.6 ± 6.2	1.887 ± 0.38	0.2986 ± 0.0560
DETRITUS	1.25 ±0.5	11.4 ± 7.6	1.416 ± 0.57	0.2309 ± 0.0947

TABLE V: PHYSICAL PARAMETERS OF LEAVES TESTED IN EXPT. (3)

PARAMETER	LEAF* 1	2	3	4	5
Volume (max) (ml)	31	14.5	10.5	-	15
Length (cm)	7.5	4.5	4.5	8.6	5.6
Diam. of pitcher orifice (cm)	2.8	2.5	2.0	2.3	2.7
Width of lateral wing (cm)	6.8	4.5	4.5	7.1	5.6
Height of lateral wing (cm)	1.6	1.4	2.3	1.3	1.5
Width of top wing (cm)	5.9	5.2	4.2	4.8	5.6
Height of top wing (cm)	3.8	2.6	2.1	3.5	3.1
Wet weight (g)	2.623	1.416	1.169	2.870	1.943
Dry Weight (g)	0.425	0.270	0.178	0.663	0.344
Medium of growth	Sphagnum	Vermiculite	vermic.	vermic.	Sphagnum
Airstream temp.	20°C	22°C	22°C	22°C	22°C
Airstream relative Humidity	≈50%	≈50%	≈50%	≈50%	≈50%

* Leaves 1, 2 and 3 were used in Expt. (3(a))
Leaf 4 was used in Expt. (3(b))
Leaf 5 was used in Expt. (3(c))

TABLE VI: CO_2 EXCHANGE IN YOUNG LEAVES

	CO_2 evolution in dark	CO_2 Uptake in light
	($\times 10^{-6}$ cm^3 sec^{-1} g^{-1} Leaf dry wt.)	
Water in Pitcher	15.0 ± 10.0	10.0 ± 9.2
No Water in Pitcher	28.5 ± 5.7	30.0 ± 6.1

FIGURES

Figure I - Black-box representation of a pitcher-plant in the field.

Figure IA - Black-box representation of carbon fluxes when there is a net uptake of CO_2 by the leaf and a net production of CO_2 by the pitcher contents when inquilines are present.

Figure IB - Black-box representation of radiant energy fluxes when the leaf temperature is greater than the temperature of its environment.

Figure IC - Black-box representation of "lesser" fluxes.

Figure II I - Picture of spectro-radiometer and spectro-radiometer recorder.

Figure IV - Picture of S. Purpurea clusters in experiment (1), Febuary 14, 1974.

Figure V - Tray no. 4, Expt. (1), showing flower.

Figure VI and VII - Tray no. 7, Expt. (1), showing flower and leaf arrangements.

Figure VIII - Diagram of CO_2 analysis system.

P = pump	DT = drying tube
C = hose clamp	V = needle valve
F = 2000 ml. flask	RT = reference tube
cc = cooling coil	ST = sample tube
sc = sample chamber	IRGA = infrared gas analyzer
pr = pressure regulator	R = recorder
fm = flow meter	

Figure IX - Calibration curve for remote prove of spectroroadiometer. (Visible range) Note: Correction Factor = Actual Spectral Intensity of Standard measurer S. I. on meter. Distance from source = 10 cm. (Four determinations of each point)

Figure X - Calibration curve for remote probe of spectroradiometer (Infrared range). (One determination of each point).

Figure XI - Spectral distribution and intensity of artificial lighting in growth room during experiment (1). Note: Data collected with ISCO spectro-radiometer and attached recorder. Remote probe used at leaf-level directed at light sources. Area under curve between 400 and 700 m. is 57 cm^2 where 1 cm^2 = 12.5 uW cm^{-2}. Total incident radiation (400-700 m) = 1.02×10^{-2} cal. cm^{-2} min^{-1}.

Figure XII - Spectral distribution and intensity of wall-reflected light. Note: Remote probe at leaf-level directed at wall.

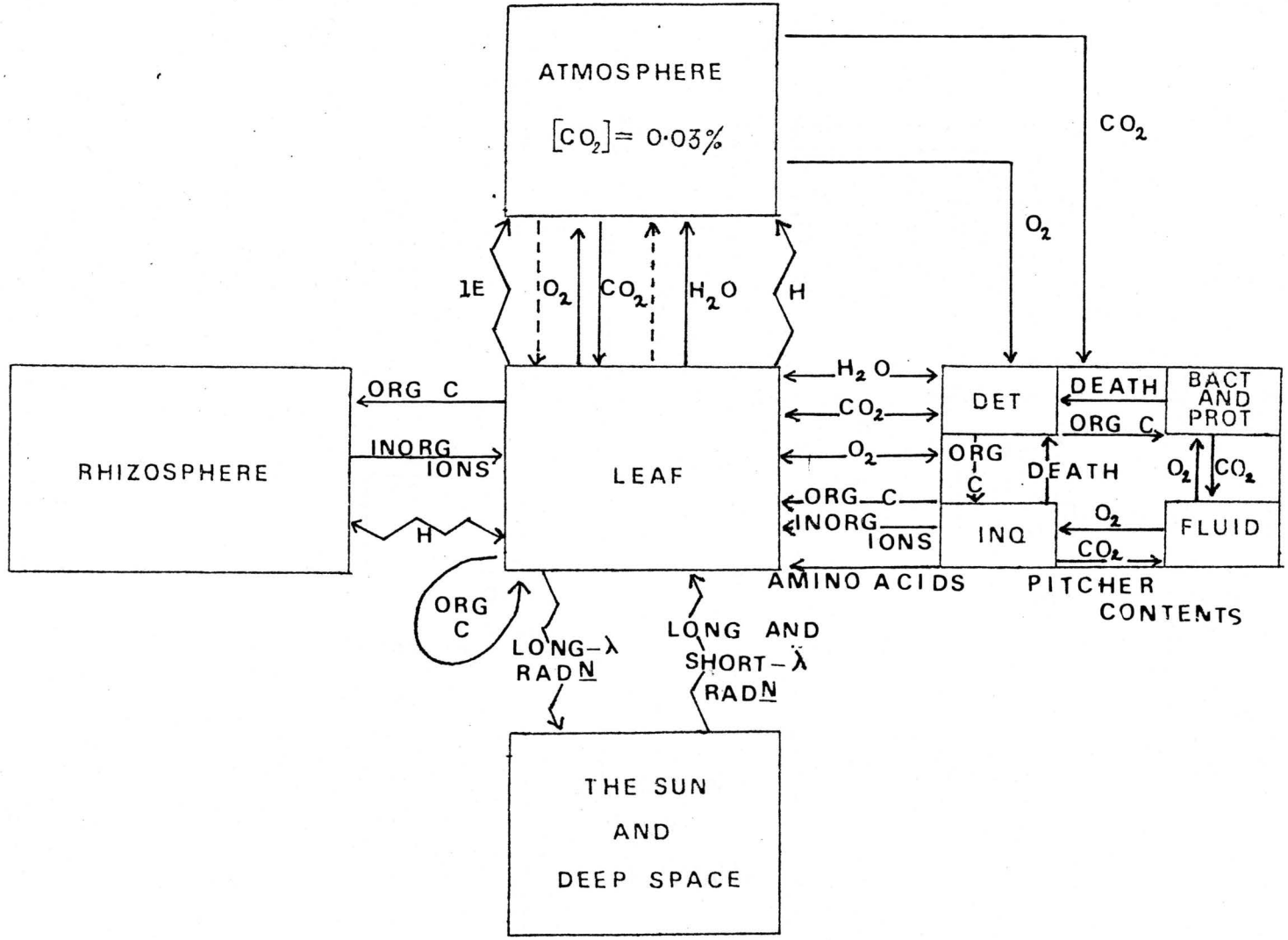
Figure XIII - Dirgram of CO_2 flux when the leaf is photosynthesizing.

Figure XIV - Growth of leaves with time in experiment. (2).
Note: Each point is the average of four plants.
W = water
C = control
D = detritus

Figure XV - Distribution and intensity of incident and tranmitted light in experiment (2) showing one standard deviation for transmitted spectrum (12 plants tested).

Figure XVI - Picture of leaf enclosed in polyethylene bag assimilation chamber for CO_2 - flux experiments.

Figure XVII - Picture of CO_2 - analysis system.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[CO2] = 0·03%
CO2
O2
1E
O2
CO2
H2O
H
RHIZOSPHERE
ORG C
INORG IONS
H
LEAF
H2O
CO2
O2
ORG C
INORG IONS
DET
DEATH
ORG C
BACT AND PROT
ORG C
DEATH
O2
CO2
INQ
O2
CO2
FLUID
AMINO ACIDS
PITCHER CONTENTS
ORG C
LONG-λ RADN
LONG AND SHORT-λ RADN
THE SUN AND DEEP SPACE

FIGURE I

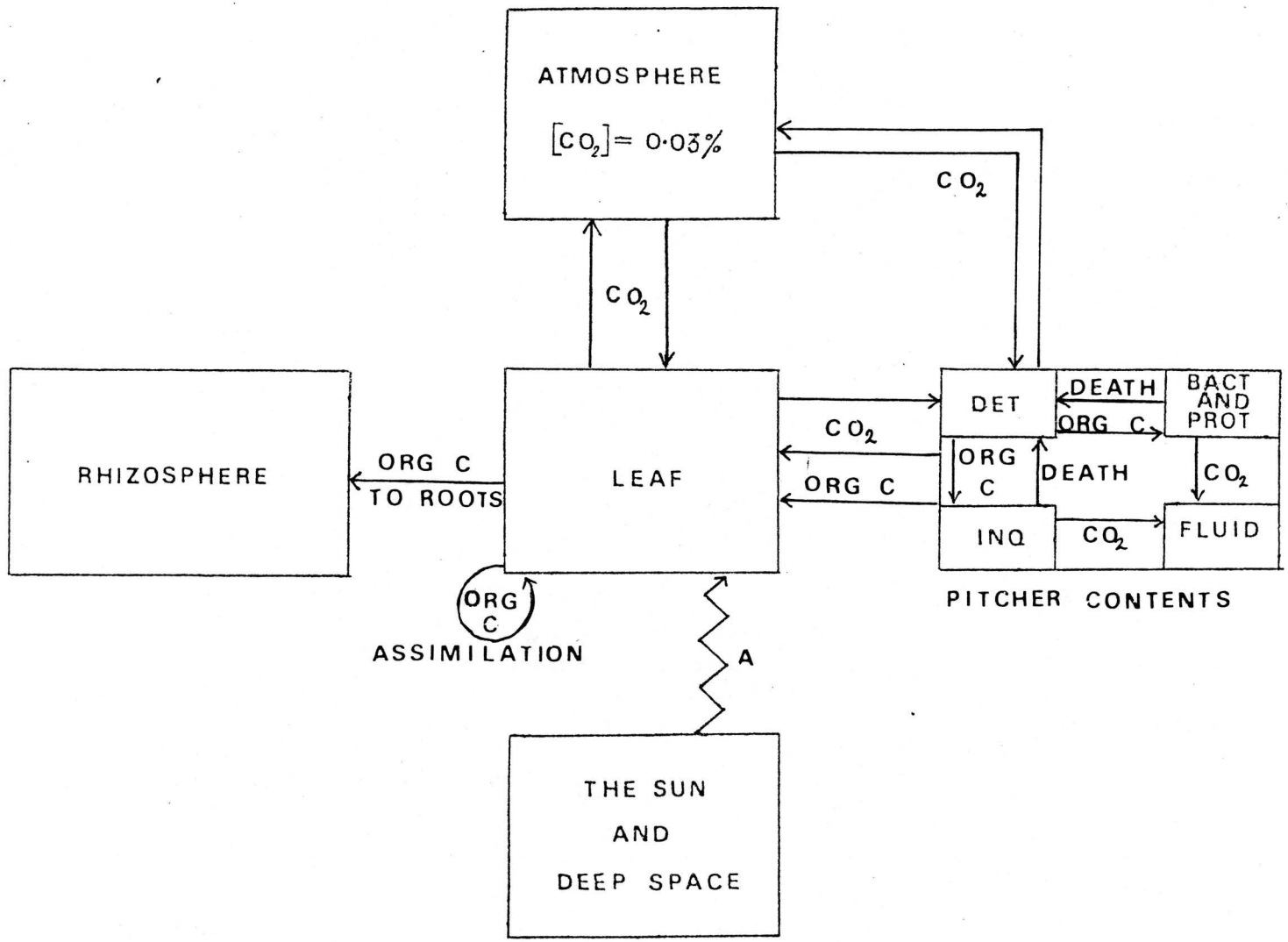

ATMOSPHERE
[CO2] = 0·03%
CO2
CO2
CO2
RHIZOSPHERE
ORG C
TO ROOTS
LEAF
DET
DEATH
BACT
AND
PROT
ORG C
CO2
ORG
C
DEATH
CO2
ORG C
INQ
CO2
FLUID
PITCHER CONTENTS
ORG
C
ASSIMILATION
A
THE SUN
AND
DEEP SPACE

FIGURE IA

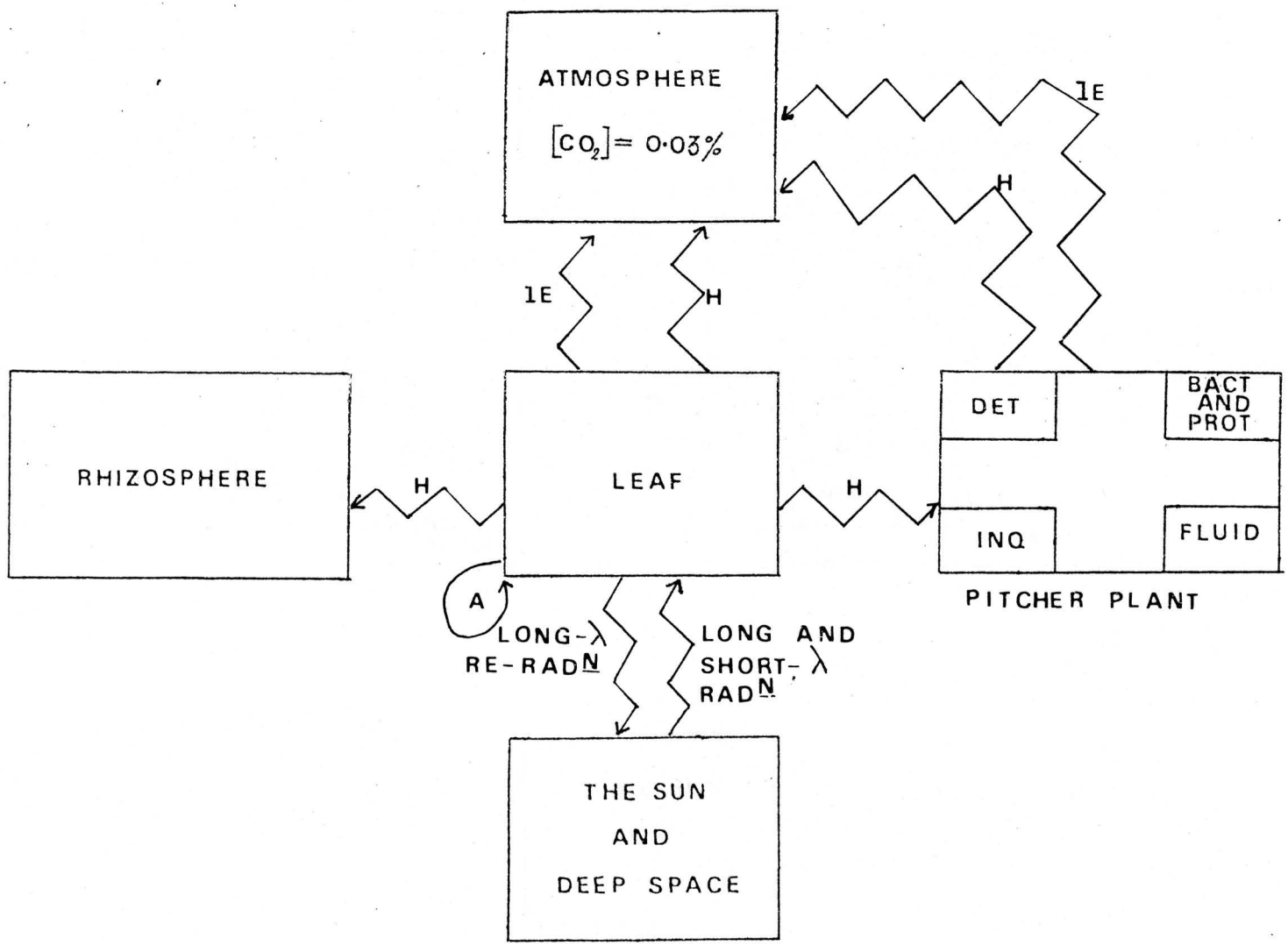
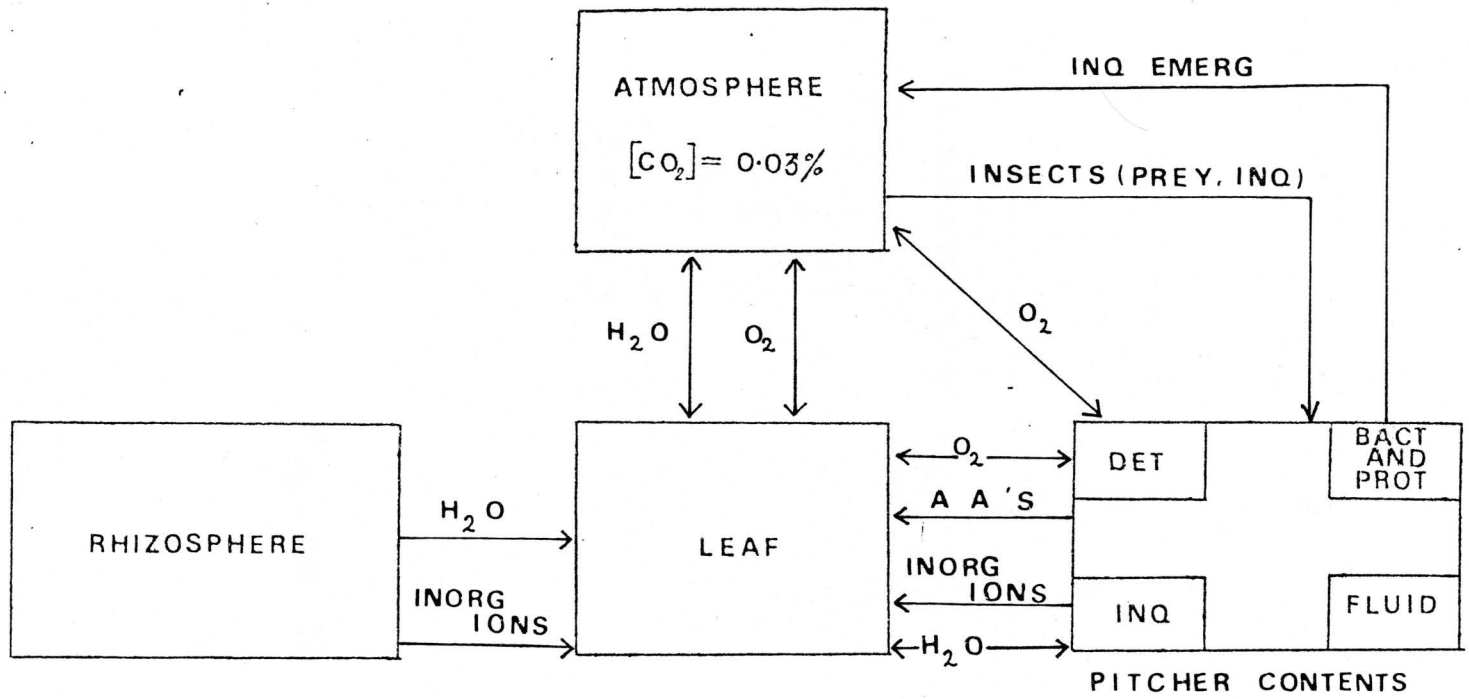

ATMOSPHERE
[CO2] = 0·03%
1E
H
1E
H
RHIZOSPHERE
H
LEAF
H
DET
BACT AND PROT
INQ
FLUID
PITCHER PLANT
A
LONG-λ RE-RADN
LONG AND SHORT-λ RADN
THE SUN AND DEEP SPACE

FIGURE 1B



THE SUN
AND
DEEP SPACE

FIGURE 1C

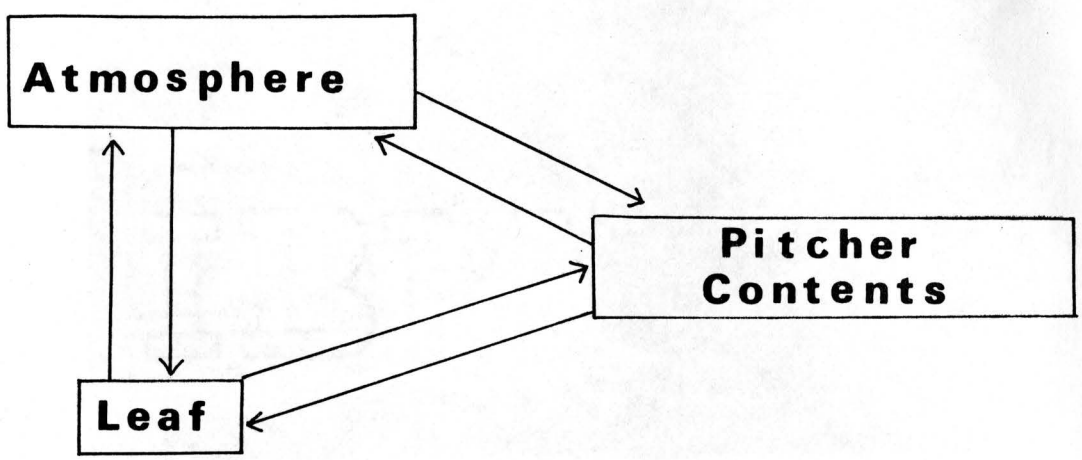
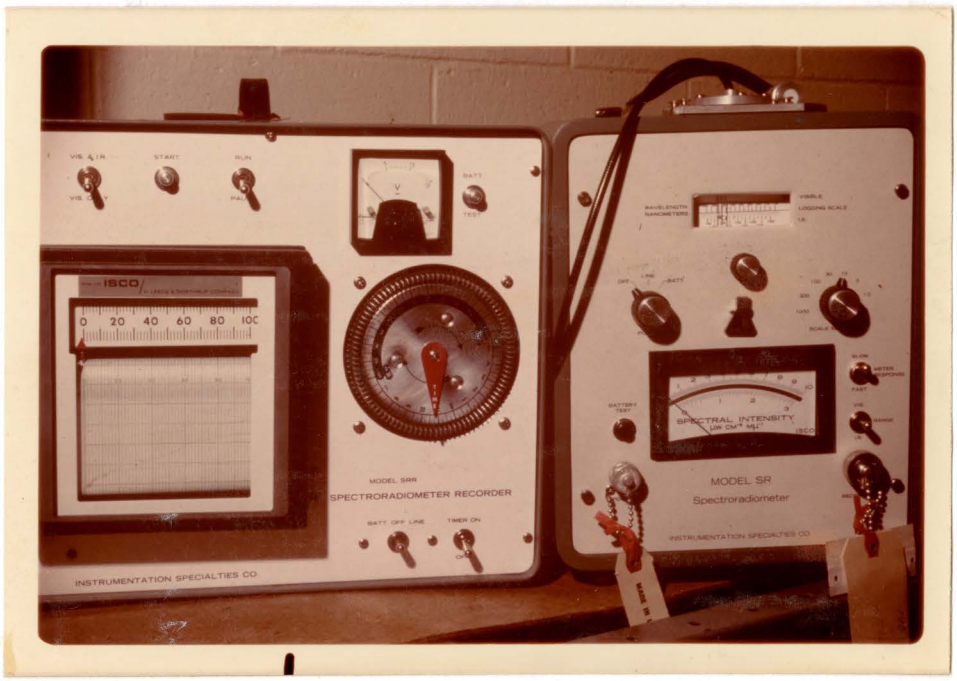


Figure II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MODEL SRR
SPECTRORADIOMETER RECORDER
INSTRUMENTATION SPECIALTIES CO.
SPECTRAL INTENSITY
MODEL SR
Spectroradiometer
INSTRUMENTATION SPECIALTIES CO.

FIGURE III

FIGURE IV

FIGURE V

FIGURE VI

FIGURE VII

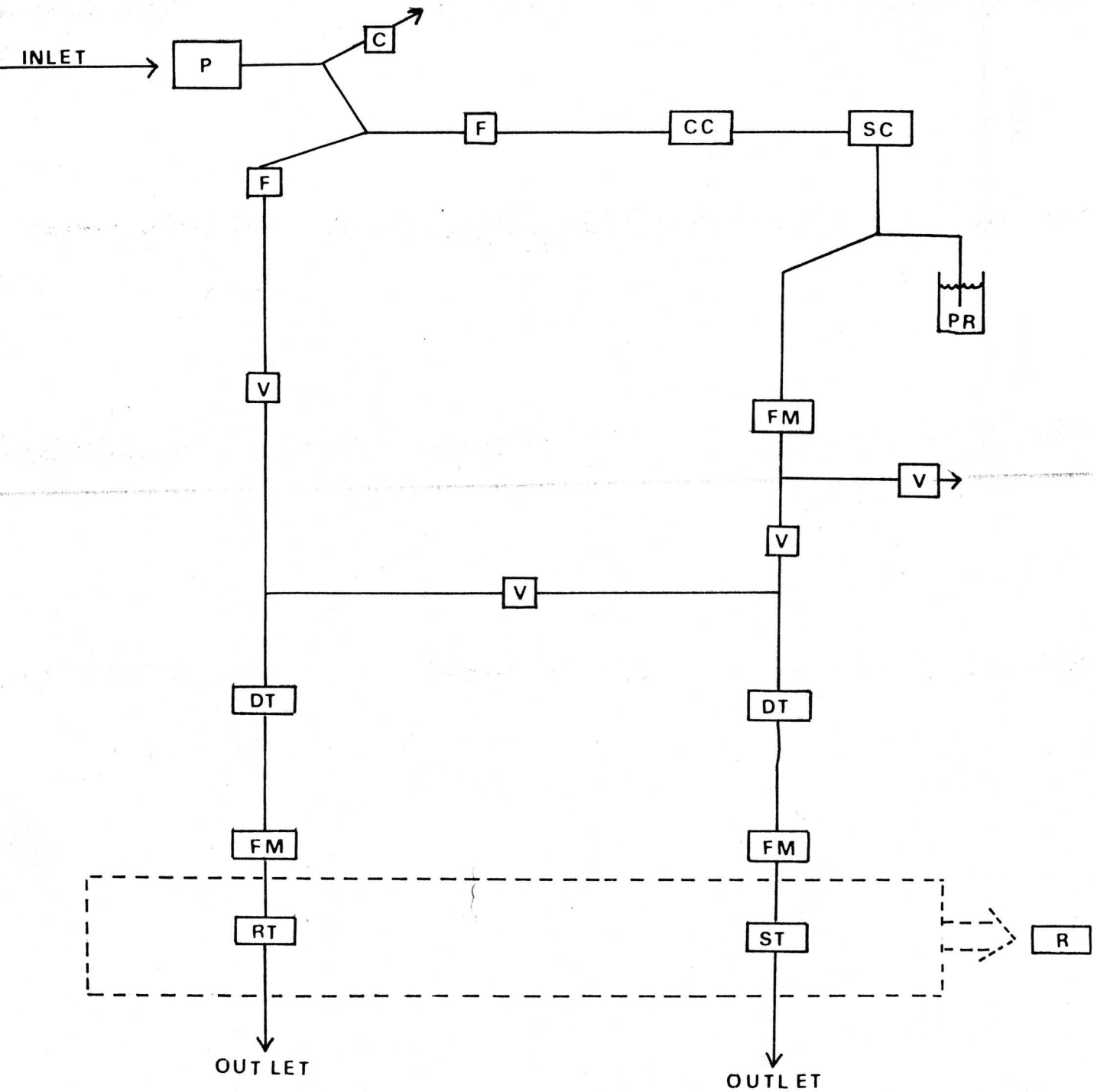


FIGURE VIII

FIGURE IX

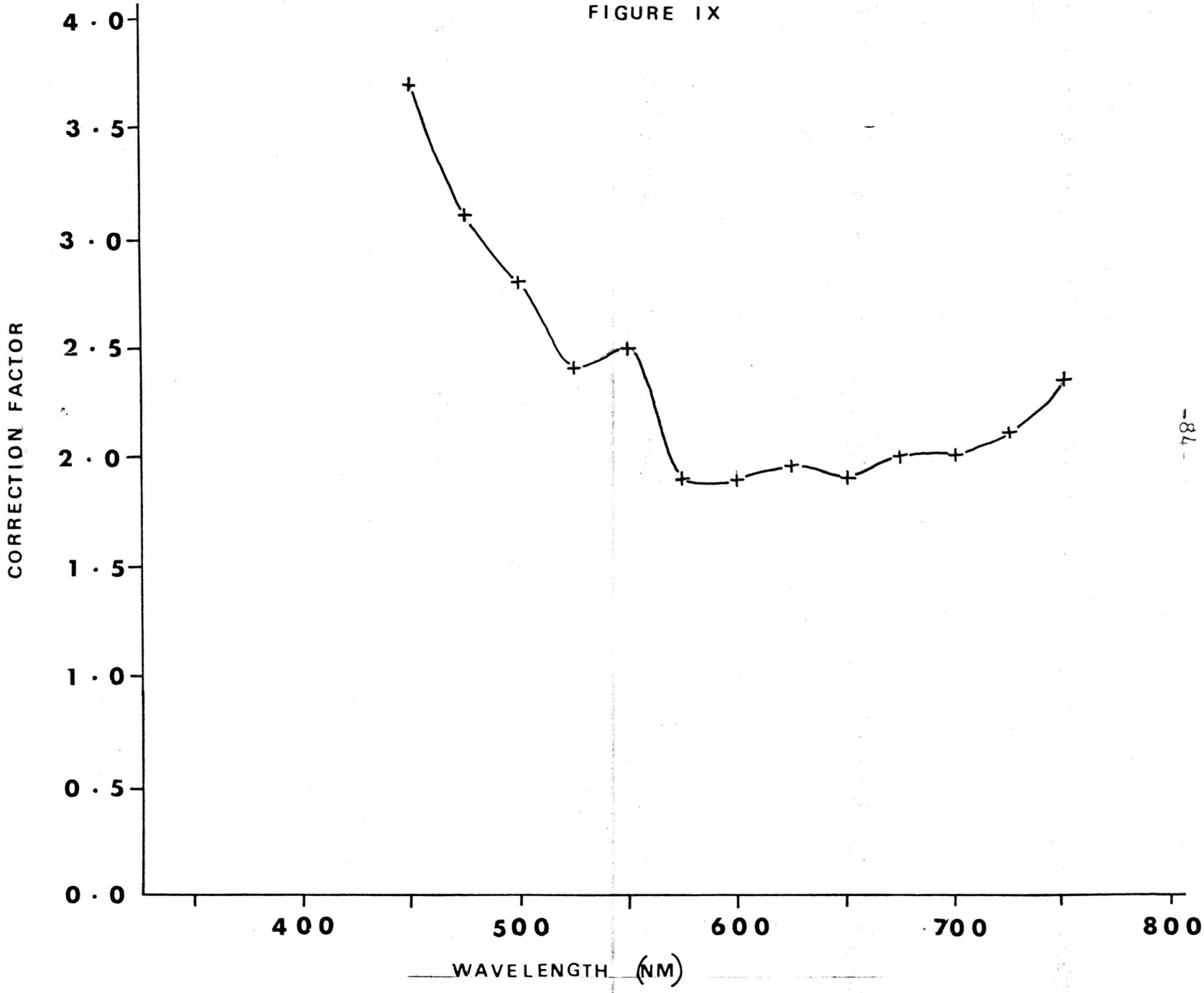
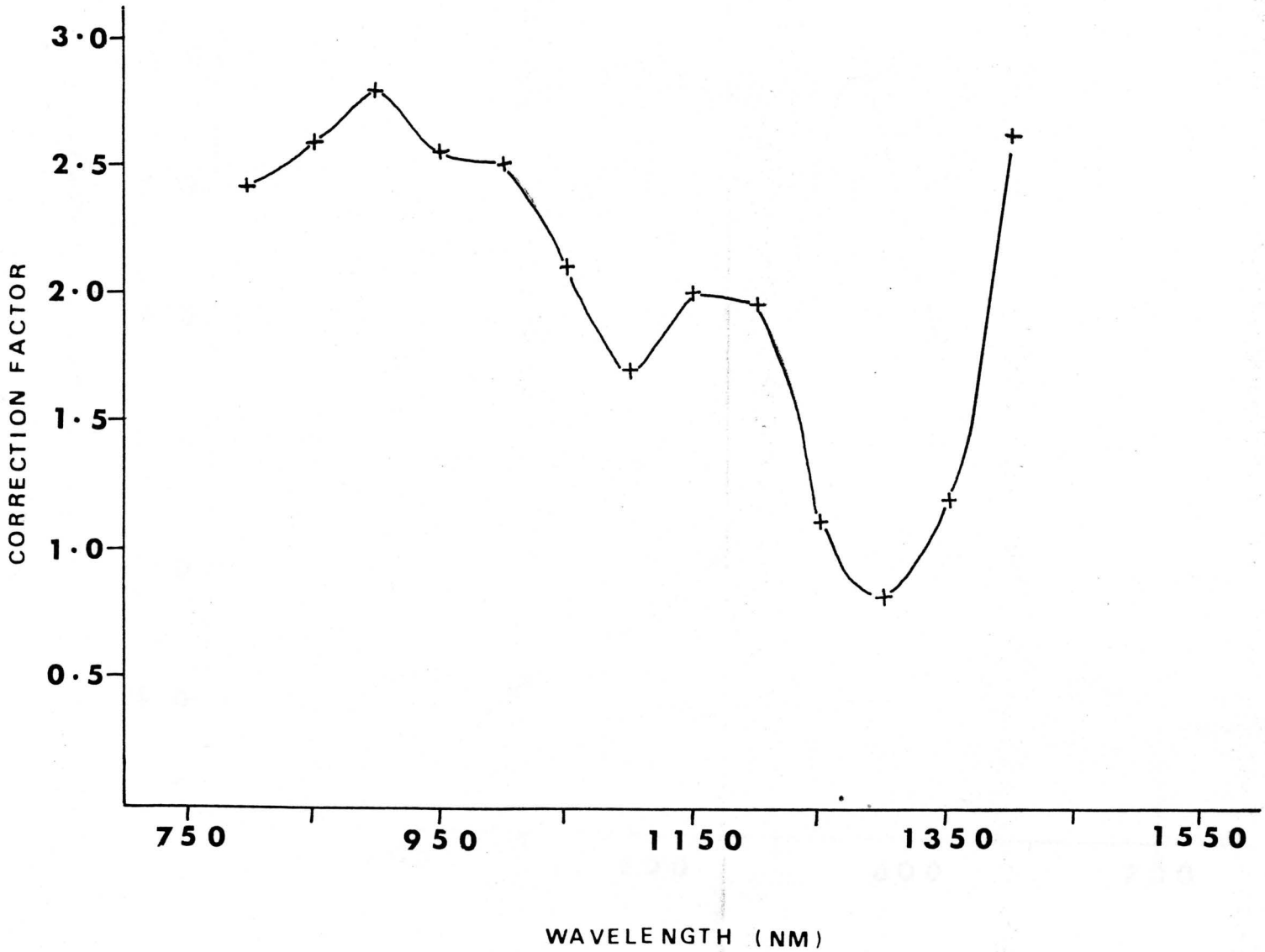

4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
CORRECTION FACTOR
400
500
600
700
800
WAVELENGTH (NM)

FIGURE X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2·5
2·0
1·5
1·0
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CORRECTION FACTOR
750
950
1150
1350
1550
WAVELENGTH (NM)

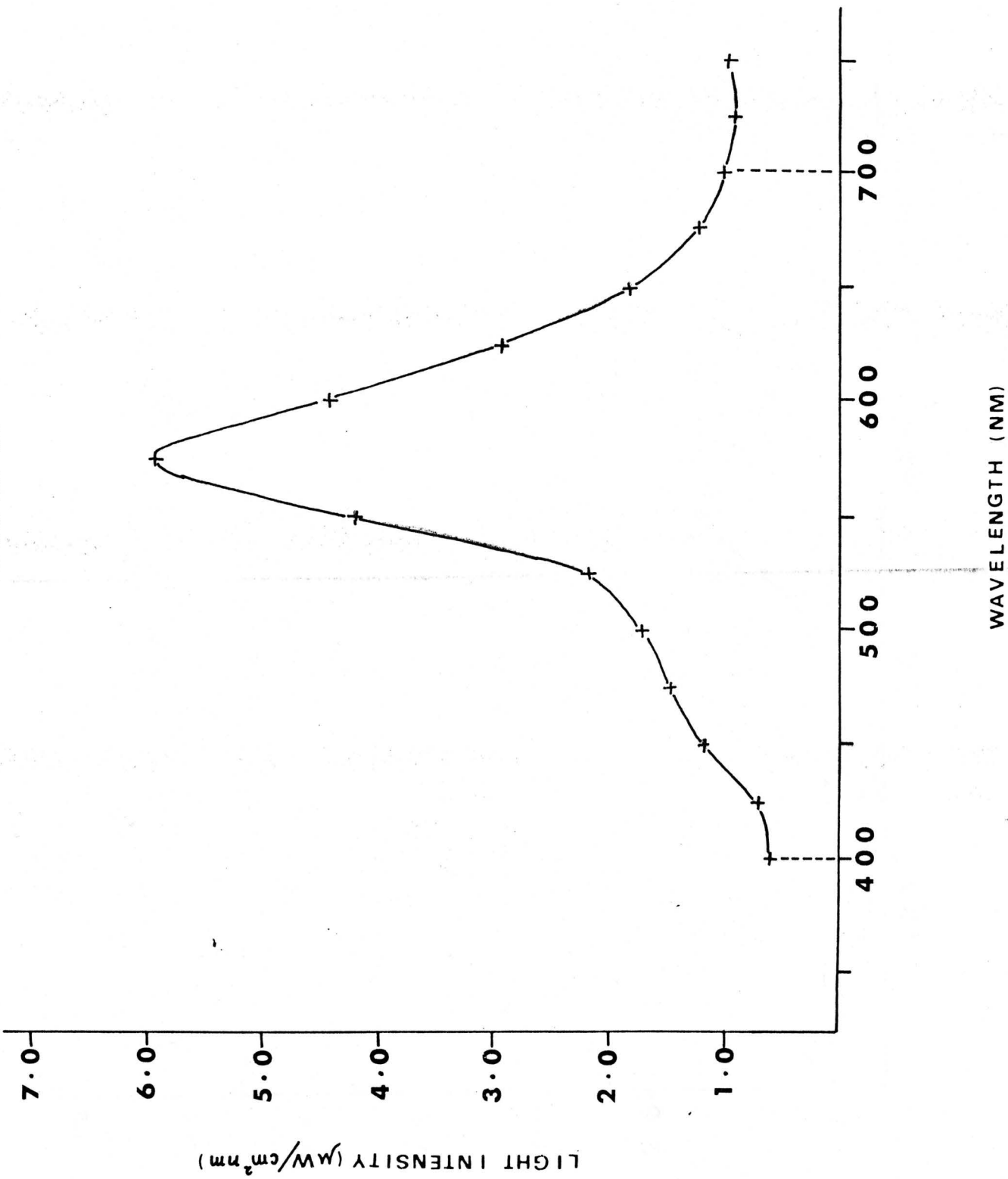
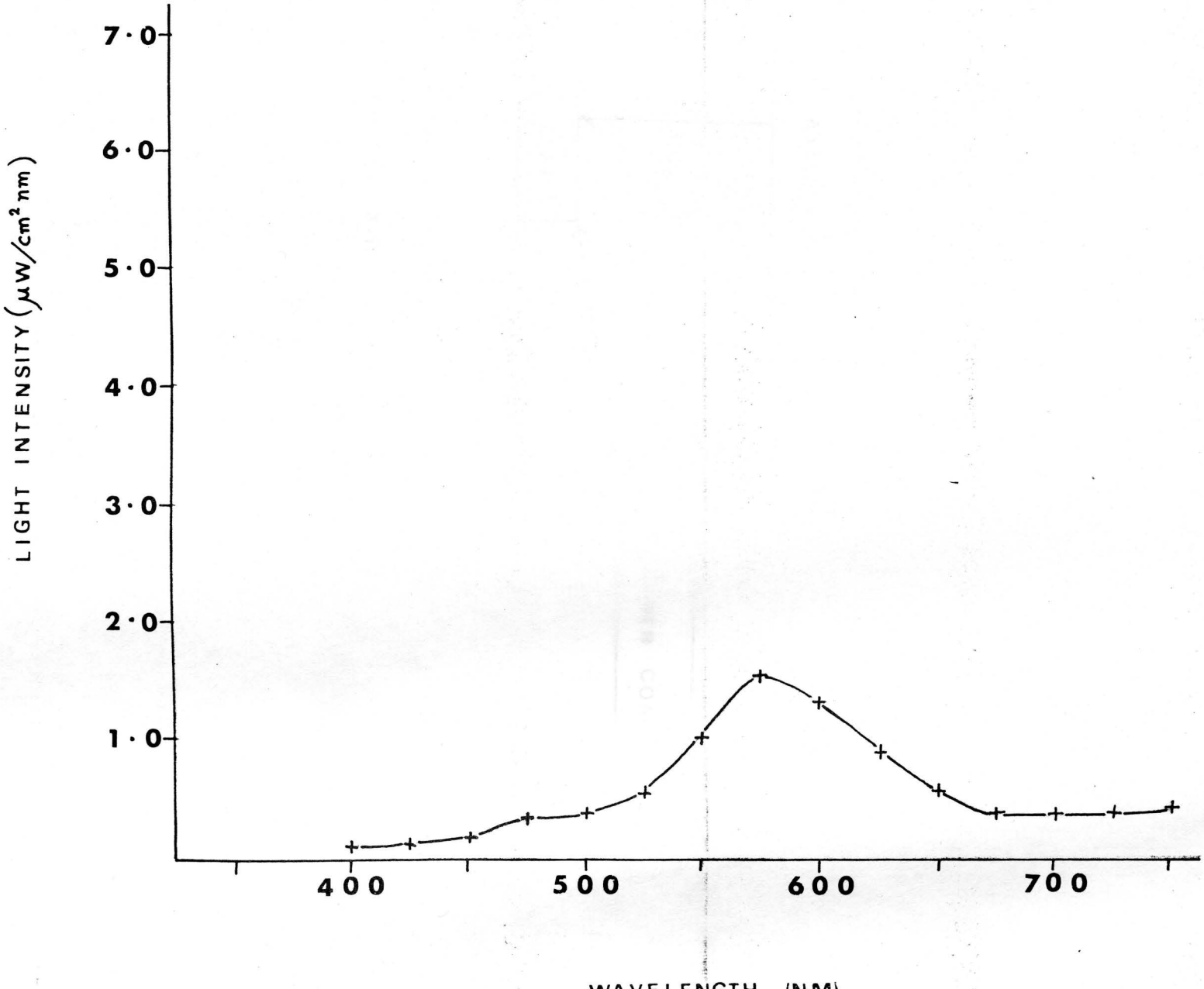

LIGHT INTENSITY (μW/cm²nm)
7.0
6.0
5.0
4.0
3.0
2.0
1.0
400
500
600
700
WAVELENGTH (NM)

FIGURE XI

FIGURE XII


7·0
6·0
5·0
4·0
3·0
2·0
1·0
LIGHT INTENSITY (μW/cm² nm)
400
500
600
700
WAVELENGTH (NM)

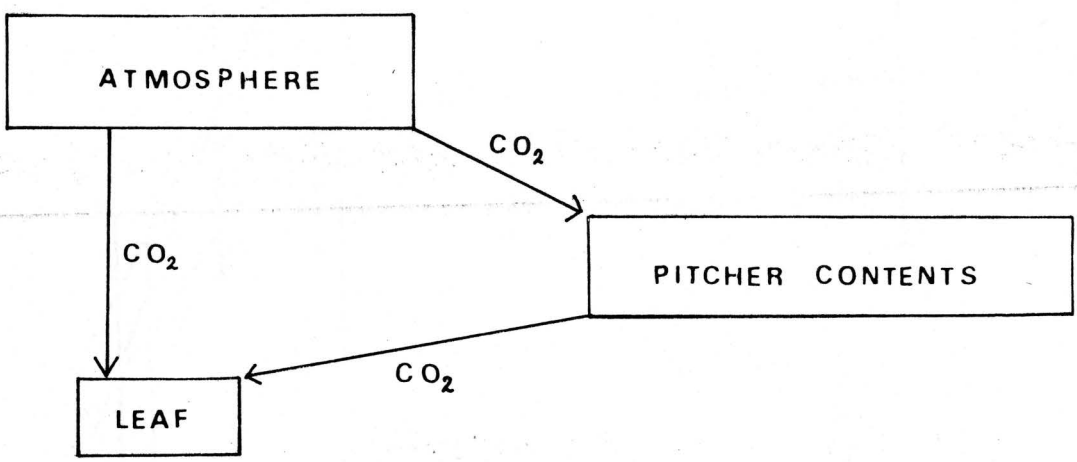


FIGURE XIII

FIGURE XIV

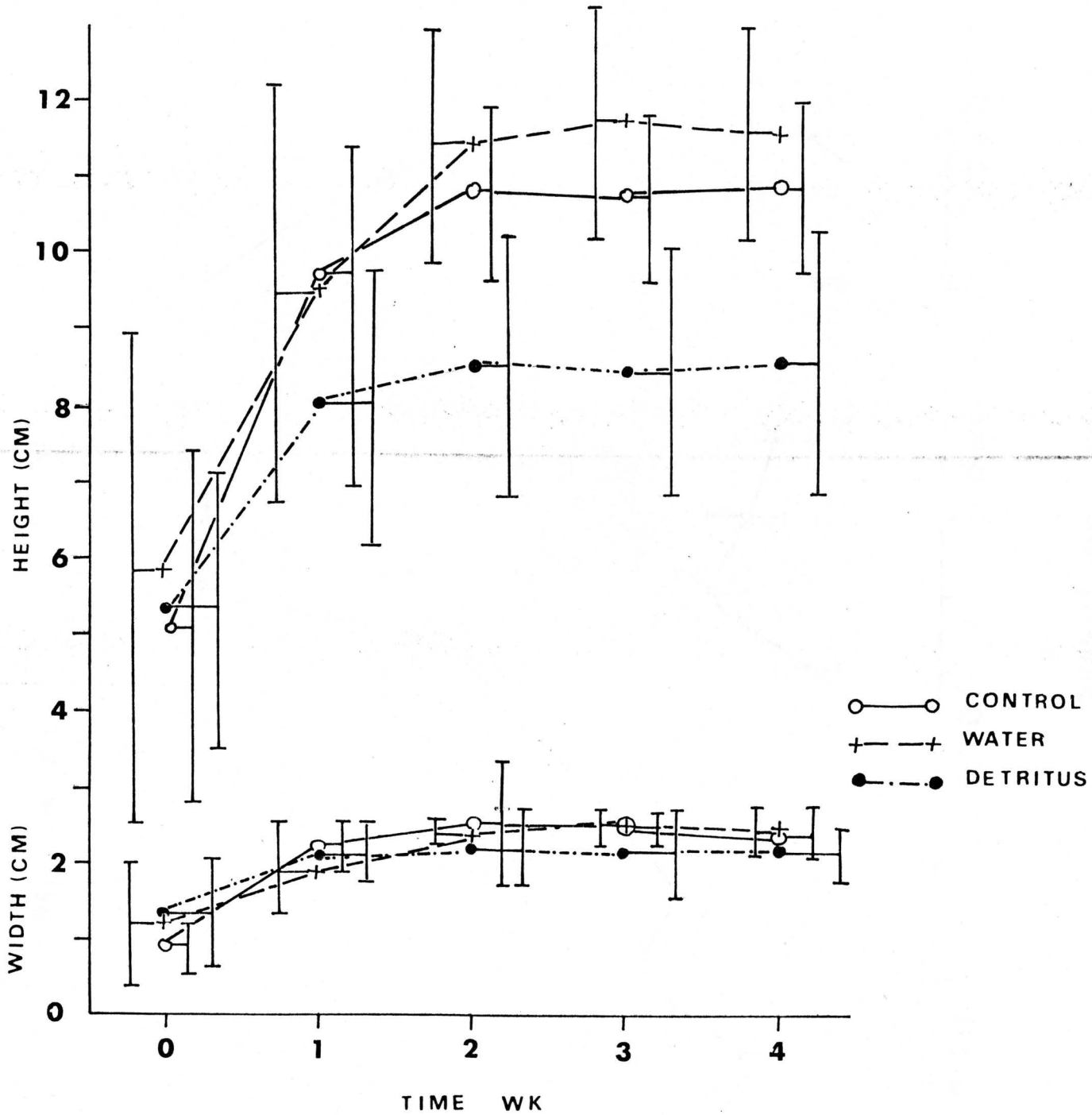
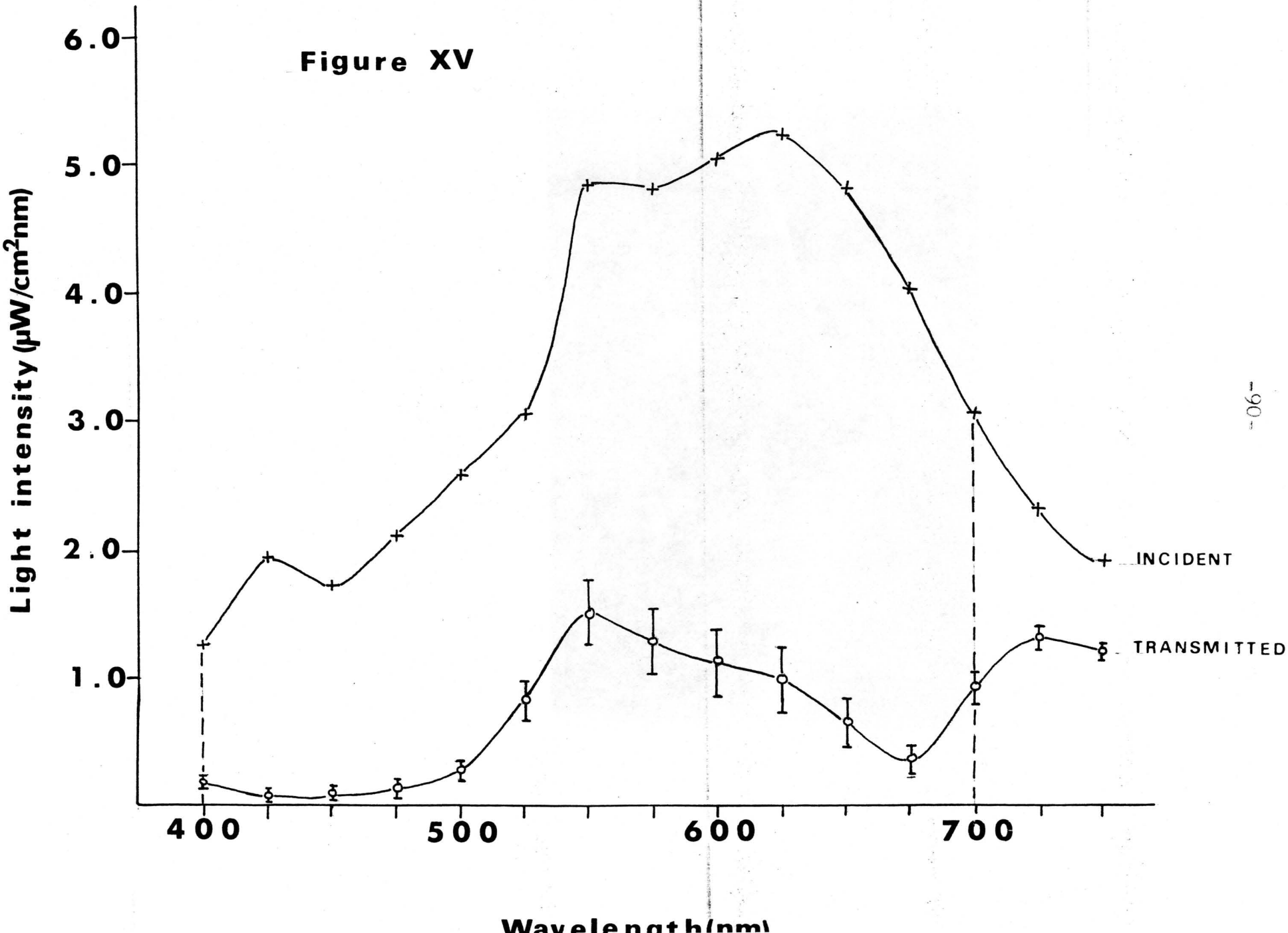

12
10
8
6
4
2
0
HEIGHT (CM)
WIDTH (CM)
0
1
2
3
4
TIME WK
CONTROL
WATER
DETRITUS

Figure XV


6.0
5.0
4.0
3.0
2.0
1.0
Light intensity (μW/cm²nm)
400
500
600
700
Wavelength(nm)
INCIDENT
TRANSMITTED

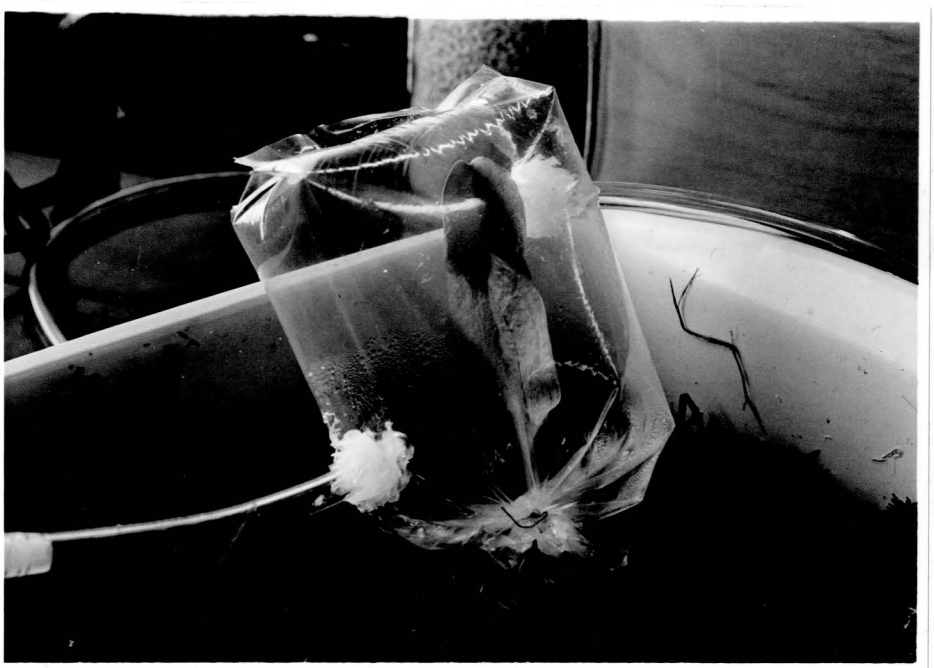


FIGURE XVI

FIGURE XVII