THE BREAKDOWN OF CHINESE TALLOW TREE LEAF LITTER

AND ITS EFFECT ON THE INVERTEBRATE COMMUNITY

STRUCTURE OF EPHEMERAL PONDS

A Thesis

Presented to

the Faculty of the Department of Biology

University of Houston

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

Thomas W. La Point

August 1975

ACKNOWLEDGMENTS

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

"Hamlet: How long will a man lie i' the earth ere he rot?

Gravedigger: I' faith, if he be not rotten before he die - as we
                have many pocky corses now-a days, that will scarce hold
                the laying in - he will last you some eight year or
                nine year; a tanner will last you nine year.

Hamlet: Why he more than another?

Gravedigger: Why, sir, his hide is so tanned with his trade, that he
                will keep out water a great while; and your water is a
                sore decayer of your whoreson dead body."

                                        Shakespeare,   "Hamlet"

INTRODUCTION

This study is an attempt to explain the relationship between Chinese tallow tree (Sapium sebiferum (L) Roxb.) leaf litter and the community structure of ephemeral ponds on the University of Houston Coastal Center. Field and laboratory experiments are utilized in an effort to discern the effect of tannins on the comminution of leaf litter by reducer organisms.

A. Structure and Function of Secondary Compounds in Plants

Allelochemistry, as defined by Whittaker and Feeny (1971), involves chemicals by which organisms of one species affect the establishment, growth, health, behavior and/or population biology of organisms of another species. Most of the chemical inhibitors involved in allelochemistry are secondary compounds; their occurrence in plants are sporadic but may be specific for families, genera and species (Fraenkel, 1959). Secondary plant compounds are not necessary for the basic metabolism of plants which differentiates them from primary plant substances such as proteins, carbohydrates, nucleic acids and fats (Whittaker, 1970). Four biological functions of secondary substances which may have ecological importance can be distinguished: (1) repellents which render the plant unpalatable or toxic to animals; (2) attractants such as plant pigments and scents which attract animals to the plant; (3) phytoncides which protect the plant against pathogenic, parasitic or decay-causing bacteria and fungi; and (4), allelopathics which directly inhibit growth of other plants (Whittaker, 1970). Repellants and phytoncides may, if sufficient concentration occurs within the environment, become allelopathic (See Tannins, below).

In recent years, the importance of secondary plant compounds in plant defense and allelopathy and their concomitant influence on community

structure has become widely recognized. Whittaker and Feeny (1971)
state that there may be thousands of secondary plant compounds, but
those involved in allelopathy belong to one of five major categories:
phenylpropanes, acetogenins, terpenoids, steroids and alkaloids. Phenyl-
propane and alkaloids derive from a few amino acids (especially phenyl-
alanine, lysine, tyrosine and ornithine) while the others derive from
acetate (Fig. 1). Rice (1974) further subdivides these compounds into
fifteen chemical categories within which the chemicals are biosynthetically
related (Table 1).

Allelopathic secondary compounds must be relaesed into the surround-
ing environment to be effective. Leaching, volatilization, autointoxication
through the decomposition of litter accumulation and root exudation are
the primary mechanisms of allelopathic release. Muller (1970) notes
that plants adapt to the climate in which they live and will utilize ter-
penes as allelopathic agents in dry, hotter climates. Terpenes volatilize
well but are generally insoluable in water; a dry, hot climate would give
an advantage to terpene-containing plants (eg., Salvia and Artemisia)
whereas humid climates would not be as advantageous for these volatile
terpenes. Plants with phenolic compounds do better in humid climates
since the phenols would readily leach out. Besides leaching and volatiliz-
ing, plant metabolic substances involved in allelopathy are liberated
through the decomposition of litter (Rice, 1964). The secondary compounds
released in this manner may inhibit growth in other species directly or
indirectly, as well as self inhibition of con-specifics. Patrick (1955)
showed that soil microbes capable of utilizing amygdalin in peach litter
release hydrogen cyanide, which inhibits peach seedling growth. In

Figure 1. Metabolic relationships of the major groups of secondary compounds (large print) to primary metabolism. From Whittaker and Feeny, 1971.
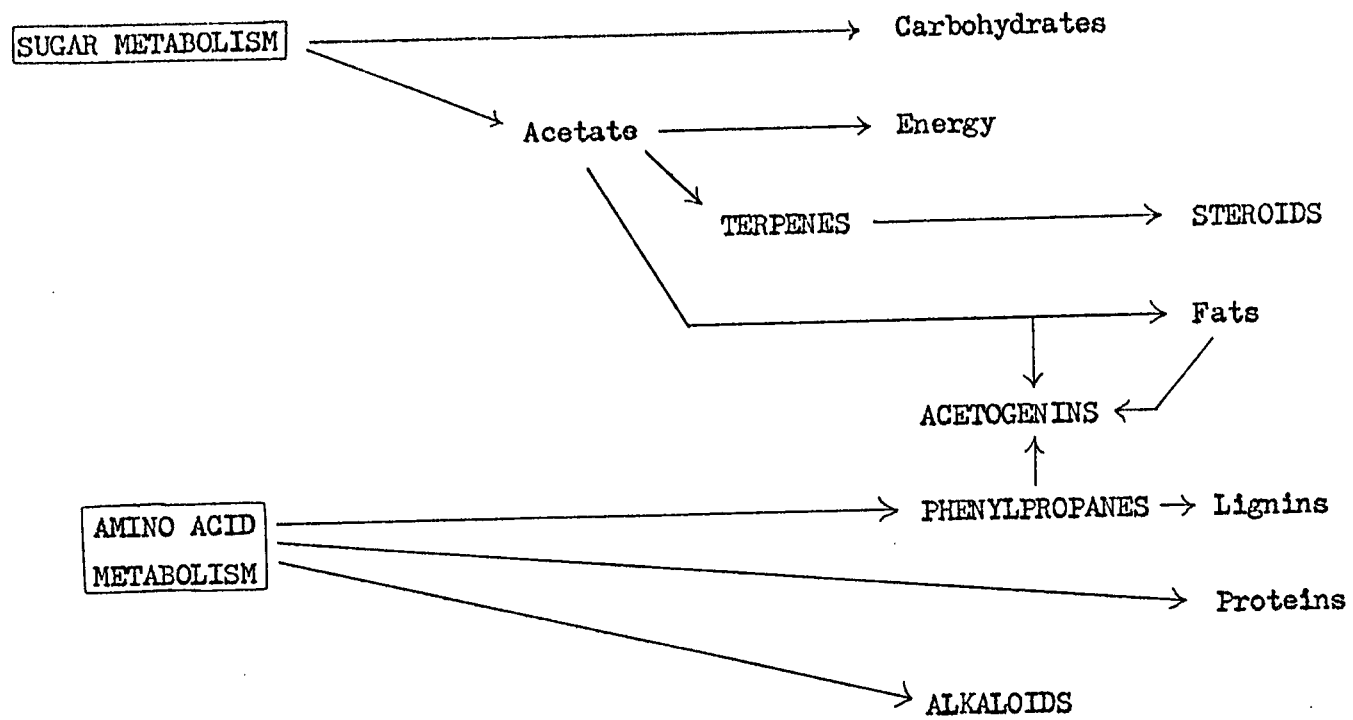
Table 1. Probable major biosynthetic pathways leading to production of

the various categories of allelopathic agents. From Rice, 1974.

HYDROLYZABLE TANNINS

Carbohydrate   DIGALLIC ACID

pyruvate

GALLIC ACID

dehydroshikimic acid

AMINO ACIDS, POLYPEPTIDES

ALKALOIDS, CYANOHYDRINS

shikimic acid

SULFIDES, MUSTARD OIL GLYCOSIDES

amino acids

PURINES, NUCLEOSIDES

acetate

SIMPLE PHENOLS

CINNAMIC ACID
DERIVATIVES

COUMARINS

mevalonic
acid

FLAVONOIDS   CONDENSED TANNINS

WATER-SOLUBLE ORGANIC ACIDS, KETONES

SIMPLE UNSATURATED LACTONES

LONG-CHAIN FATTY ACIDS

TERPENOIDS,
STEROIDS

NAPHTHOQUINONES, ANTHRAQUINONES

autoclaved soils, HCN was not released, indicating that amygdalin was
altered by microbial enzymes during decomposition. Another example of
autointoxication from the accumulation of plant parts is found in apple
trees (Boerner, 1959); roots of apple trees, upon decomposition, yield
phlorizin, a polyphenolic compound which inhibits apple seedling growth.
The last major method of allelopathic release is through root exudation.
Rice and his associates have shown that toxic metabolites are exuded from
the roots of certain plants (eg., Sorghum, Euphorbia and Helianthus)
and that these plants cause a particular species' patterning in old fields
in Oklahoma (Abdul-Wahab and Rice, 1967; Wilson and Rice, 1968).

Plants possessing defense compounds must exhibit mechanisms to
ensure that potentially autotoxic chemicals are kept from destroying or
adversely affecting the plant from which they come. Many of these chemicals
(eg., phenols, flavonoids and others) are inactivated by combining with
sugars to become glycosides; other phenols, terpenoids and resins are
polymerized into long-chain macromolecules, eg., rubber and waxes (Whittaker,
1970). Amygdalin, present in the root bark of peach, remains inactive by
keeping it separate from the enzyme which breaks it down into benzaldehyde
and hydrogen cyanide (Proebsting and Gilmore, 1941). Muller (1966)
reports that juglone, present in the black walnut, Juglans nigra, becomes
toxic upon oxidation outside the living cells. Other phenolic, terpenoid
and secondary compounds are secreted into intra- or intercellular compart-
ments or deposited in heartwood (Davies, 1971; Esau, 1967). Another
potential toxin, oxalic acid, accumulates in grasses (Gnetum and Vitis)
as oxalate crystals (Esau, 1967). The crystals can be in sufficient concen-
tration to affect their palatability to herbivores (Whittaker, 1970).

B. Structure and Function of Tannins

Flavonoid pigments are a series of related water-soluable phenolic
glycosides having in common the flavone skeleton (see IV below); flavonoids
include the anthocyanins (scarlet, purple and crimson colored), the fla-
vones (ivory or pale yellow) and smaller groups of limited occurrence
(Harborne, 1967). Flavonoids occur almost universally in higher plants;
they are not synthesized by animals, the ones occurring in butterflies
and moths arise from their diet on certain plants (eg., monarch butterflies
feeding upon milkweed) (Brower and Glazier, 1975). Vegetable tannins
are a heterogeneous group of phenolic compounds derived from flavonoids
and related to glucosides (Esau, 1967). The term tannin was introduced to
describe substances present in plants capable of converting raw animal
skins into stable (eg., decomposition-resistant) leather. Swain (1965)
defines tannins as "any naturally occurring compound of high enough molecular
weight (between 500 and 3000) containing a sufficiently large number of
phenolic hydroxyl groups to enable it to form effective cross-links between
proteins and other macromolecules". This definition is generally accepted
and will be used in this paper.

Tannins can be divided structurally into two distinct classes,
depending upon the type of phenolic nucleii involved. The first class is
readily hydrolyzed by acids, bases, or enzymes, to yield carbohydrates
and a number of phenolic acids; they are referred to as hydrolyzable tannins.
An example of a hydrolyzable tannin is ellagic acid. It stems from shikimic
acid (see I below) which is oxidized to become gallic acid (see II below).
Esters of gallic acid and sugars (usually glucose) will yield ellagic acid
(see III below) (Haslam, 1966; Swain, 1965). Gallic and ellagic acid inhibit

germination of various plants (Vargas and Koeves, 1959; Mitin, 1970; Chou
and Muller, 1972) and inhibit growth of nitrogen fixing bacteria (Rice, 1969).
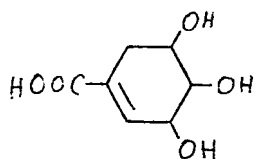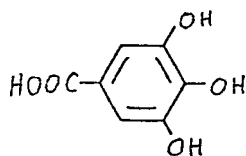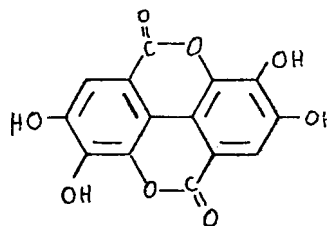
I   II   III

The second class of tannins also contain the phenolic nucleii;
however, treatment with hydrolytic reagents will not yield lower molecular
weight compounds, rather they polymerize to yield phlobaphenes (from the
Greek meaning "bark-dye"). Phlobaphenes are red-colored, acid insoluable
pigments. This second class of tannins is called non-hydrolyzable or
condensed tannins. Condensed tannins are directly related to flavonoids
and possess the basic flavone skeleton (see IV below). The A ring is of
acetate origin and the B ring of shikimic acid origin. Specifically,
condensed tannins are formed by the condensation of two or more molecules
of flavan-3-ols, such as catechin (see V below) and/or flavan-3,4-diols
such as leucocyanidin (see VI below) and smaller amounts of the other
flavonoid compounds (Swain, 1965a,b). Flavan-3-ols and flavan-3,4-diols
are related to other classes of flavonoids, all of which differ from one
another by the oxidation state of the central 3-carbon link between the A
and B rings.
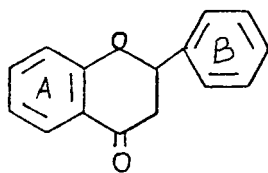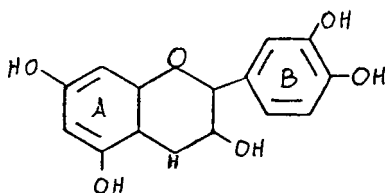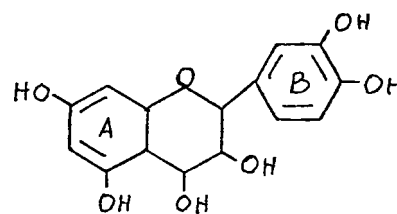
IV   V   VI

Generally, those tannins derived from flavan-3-ols and flavan-3,4-diols are specifically referred to as flavolans; the term condensed tannins used in the wider sense includes polymers of other phenols such as the hydroxystilbenes in _Picea_ and _Eucalyptus_ which polymerize to piceatannol (Swain, 1965a).

Bate-Smith has carried out extensive investigations on the occurrence of tannins in the plant kingdom (Bate-Smith, 1962; Bate-Smith and Metcalfe, 1957). He has found that hydrolyzable tannins are non-existant in the ferns, gymnosperms and monocotyledonous plants. Among the dicotyledonous plants, hydrolyzable tannins are found primarily in the Rosales and sporadically elsewhere. He found flavolans to be much more wide-spread; they are present in ferns, gymnosperms and angiosperms. Fourty-five percent of the dicots and thirty percent of the monocots surveyed possessed at least one flavolan. In general, the presence of flavolans was well correlated with woodiness; Bate-Smith (1972) suggests that the relationship between flavolans and woodiness may relate to resistance to fungal attack and lowered palatability to herbivores.

The distribution of tannins within individual plants is usually restricted to particular organs or organelles. While tannins are known from almost all types of plant tissue, they tend to be concentrated in heartwood and in leaves (Swain, 1965b). Within leaves, tannins are concentrated in the palisade cells of the parenchyma (Esau, 1967); cocoa (_Theobroma_) and banana (_Musa_) have well defined "tannin-cells" and tannin-filled vacuoles which are separated from the rest of the leaf tissue. The necessity for keeping tannins separated from the rest of the plant tissue appears to be to stop the enzymic oxidation of tannins in tissue which

would otherwise be adversely affected (Swain, 1965a).

C. Function of Tannins in Herbivory and Pathogen Resistance

The greatest concentration of tannins is in dead and dying cells (Esau, 1967). It is not known whether an increasing tannin concentration in aging cells has an effect upon normal metabolic functions; Swain (1965a) believes "they are parallel rather than sequential processes." Tannins have a protein binding capacity and Swain discusses the three types of bonds involved: (1) Hydrogen bonds form between the hydroxyl of the tannins and the free amino groups of the protein or the hydroxyl and carboxyl groups of other polymers; (2) ionic bonds between cationic groups on the tannin and anionic groups on the protein; and (3) the covalent bonding between suitable reactive groups of the tannin and protein. The dry or puckery astringent sensation arises from cross-bonding of proteins and glyco-proteins with tannins in the mouth of an herbivore (Goldstein and Swain, 1963; Bate-Smith, 1973).

Purified tannin extracts inactivate many enzyme systems; Benoit and Starkey (1968) review the enzymes which have been shown to be inactivated by high molecular weight tannins (eg., flavolans) and related phenolic compounds such as catechol, gallic acid, coumarins and flavones. Among the enzymes inactivated are: dehydrogenases, decarboxylases, amylase, invertase, cellulase, hemicellulase, pectolytic enzymes, lipase, urease, pepsin and trypsin.

The tanning of protein and the inactivation of enzymes are means by which plants possessing tannins can survive fungal and herbivore attack. As mentioned above, to keep tannins from working on the plants' own enzymes and proteins, they have to be separated. Once the plant is damaged,

the phenolic compounds oxidize and are mobilized around the necrotic region (Levin, 1971). Kiraly and Farkas (1962) show that the phenol content, expressed as chlorogenic acid, was more rapidly built up in rust-resistant wheat strains than in non rust-resistant strains. They feel that the rust infection induces biosynthesis of the phenolic compounds, hence the polyphenols become localized around the diseased area. Hillis and Inoue (1968) found that phenolic compounds (vanillin, vanillic acid, hydroquinone and an unidentified flavanol glucoside) play an important role in restricting the spread of a fungus (Amylostereum) after it is introduced into Picea trees by female European wood wasps (Sirex noctilio). Upon insertion of their ovipositors into the sapwood, the wood becomes innoculated with the fungus; soon thereafter, in trees which recover from the attack, polyphenols (particularly piceatannol) are formed in situ around the oviposition sites and appear to restrict the spread of the fungus within the tree. Piceatannol is absent in unattacked trees; hence, there is some evidence of its being formed in response to the fungal attack.

Instances have been recorded in which tannin-containing plants have effectively reduced their herbivore load. An endoparasitic nematode, Radopholus similis, which causes extensive damage to citrus trees in Florida, is inhibited by certain nematode-tolerant rootstocks (Feldman and Hanks, 1968). In the resistant strains, there is upon infection, a 27 to 300% increase in coumarins, quercitin and p-coumaric acid. In non-resistant strains, there was no increase in the bound phenolics after infection. Although the authors did not demonstrate it, they surmised that the increase in phenolic substances found in tolerant strains could be responsible for the starvation of the nematode once it had entered the tree. Feeny (1968,

1969) has shown that as little as one percent of condensed tannins in
common oak (Quercus robur L.) was enough to significantly reduce the lar-
val growth of the winter moth, Operophtera brumata. Feeny's subsequent
study of the evolutionary response of oak trees to feeding by the winter
moth showed that Q. robur increases the concentration of tannins in its
leaves seasonally as a mechanism to reduce herbivory. Todd, et al., (1971),
rearing aphids (Schizaphis graminum) on a chemically defined medium, added
commercially obtained catechol, quercetin, tannic acid, and other flavonoid
compounds to various cultures. Almost none of the aphid progeny survived
in any of the tannin cultures. Several compounds, particularly quercetin
and cinnamic acid are found in aphid resistant strains of barley. Further
studies have implicated tannins in reducing palatability of certain feeds
to rats (Glick and Joslyn, 1970a, b), chicks (Vohra, et al., 1966),
rabbits (Dollahite, et al., 1962) and cattle (Harris, et al., 1970; Cum-
mins, 1971).

D. The Effect of Tannins on Terrestrial Communities

A wide variety of organic compounds (eg., carbohydrates, phenolics,
amino acids, terpenoids and nucleotides) are excreted from plants by
leaching and/or volatilization (Muller, 1970). Tannins are readily leached
from plants and affect the structure of plant communities (Rice, 1974).
Blum and Rice (1969) found large amounts of tannic and gallic acid in the
soil beneath stands of Euphorbia supina and Rhus copalina, two annual old
field grasses in Oklahoma. These tannins effectively reduce the rate of
nitrogen accumulation in the soil and thereby influence productivity.
The decrease of nitrification lends itself to a particular succession of
plant species in which climax species are those which can use ammonium

nitrogen directly and depend less on the nitrifying bacteria (Rice and Pancholy, 1973). Tannins have been shown to inhibit seed germination in fruits (Vargas and Koeves, 1959) and sorghum (Harris and Burns, 1970). McNaughton (1968) found seed germination of _Typha latifolia_ to be completely inhibited by an aqueous extract of _Typha_ leaves but only slightly inhibited by extract treated with polyclar AT to remove the phenolics. Condensed tannins in dead leaves of beech (_Fagus silvatica_) inhibit beech seedling growth (Mitin, 1970); the non-specificity of tannins in this case leads to auto-toxicity and is another reason why the tannins are isolated in living plant tissue.

The tanning of proteins and enzyme inhibition of tannins affects the rate of decomposition of dead plant matter. Handley (1961) notes that when leaves of the birch tree, _Betula pubescens_, die at the time of leaf fall, the residual proteins of the mesophyll cells complex with the protein-precipitating substances. The complexes "cover and permeate the cellulose walls and seem to be resistant to decomposition." Although he did not identify the substances responsible, tannins were implicated through their presence in living birch leaves. Basaraba and Starkey (1966) reported that chestnut and wattle tannins (condensed tannins) form complexes with gliadin and gelatin; these complexes were resistant to aerobic decomposition by micro-organisms. Benoit and Starkey (1968a,b) reported that wattle tannin reacted with polygalacturonase, cellulase and urease. The authors noted that the reduced activity of enzymes can be an important factor in the decomposition rate of straw and other plant material. Benoit, et al., (1968) proposed that the inhibition of decomposition by tannins may be caused by one or more of the following effects:

(1) a reaction with plant proteins to produce resistant complexes; (2) the coating or incrustation of decomposable plant substances with resistant tannin complexes; (3) the complexing of plant cellulose and hemicelluloses with tannins; and (4) the reaction with microbial exo-enzymes. Coulson, et al., (1960) discuss the general role of polyphenols in the formation of mull and mor soils; they found a change in quantity of simple polyphenols grading from a maximum in fresh growing leaves, diminishing through senescent leaves to dead leaves and reaching a minimum in decayed leaves in the humus. They note that the fate of leaf nitrogen, and hence its biogeochemical mobility, is closely related to the quantity of polyphenols in leaves on the ground, since by a bridging with basic nitrogen-containing groups in the leaves the tanning agents are capable of preserving protein from rapid decay.

Whether or not tannins directly inhibit the rate of litter breakdown in aquatic ecosystems (lakes, ponds and streams) has not been directly studied. Indirectly, tannins may be implicated in the rate at which leaves decompose in rivers. Mathews and Kowalczewski (1969) show that leaves of willow (Salix) and sycamore (Acer) placed in bags in the River Thames disappear before leaves of oak (Quercus). Kaushik and Hynes (1971) studied the fate of dead leaves that fall into streams; they note that amphipods, Hyallela azteca and Gammarus lacustris, and isopods, Asellus communis, fed preferentially on leaves of elm, maple and alder over oak and beech. The order of choice was the same as the order of the rates of decay for those species. The authors mention that oak and beech have more lignin than the other species; they also possess a higher tannin content and this may be a factor in the slower rate of decay (Coldwell and DeLong,

1950).

E. The Chinese Tallow Tree

1. History

The Chinese tallow tree, Sapium sebiferum (L) Roxb., was cultivated
as an ornamental plant along the Atlantic and Gulf coasts of the United
States from South Carolina to Florida and from the Texas coast northward
to Oklahoma (Russell, et al., 1969). It is native to Asia and was intro-
duced to this country as early as 1848 (Bolly and McCormack, 1950). It
has since escaped from cultivation and flourishes as a wild tree in wet
areas (Correll and Johnston, 1970). S. sebiferum belongs to the Euphorbia-
ceae (Spurge) Family; the Spurge family contains many genera which are
considered to be poisonous to vertebrates including the tung tree, Aleurites
fordii, which contains a saponin; several species of Euphorbia, which
contain gallic and tannic acids (Blum and Rice, 1969), and Ricinus communis,
which contains castor oil, a strong purgative (Kingsbury, 1964; Bradley,
1956).

Besides its use as an ornamental, S. sebiferum has been commercially
cultivated in the United States and Asia for its seeds, which contain a
high protein meal and an oil in the endosperm (called stillingia oil), and
for the vegetable tallow covering around the seed (see below; Russell, et al.,
1969). Tallow nut flour, from which the oil has been removed, is about 70
to 85% protein. However, it is low in lysine and methionine, which limits
its usefulness as a cereal grain supplement (Holland and Meinke, 1948).

The oil pressed from the tallow seed is called stillingia oil
despite the fact that the name is botanically incorrect. Stillingia is
a related genus of the same family which also posesses the oil (Huang, et al.,

1949). Formerly used as an illuminating oil in Asia (Hsu, 1928), it is used commercially as a drying oil in paints and varnishes (Huang, et al., 1949).

2. Potential Toxicity

Sapium species (including S. sebiferum) are characterized by a milky, astringent sap (Bradley, 1956). A congener of S. sebiferum, S. biloculare, possesses a latex-like sap which has an alcohol-soluable component toxic to warm-blooded vertebrates and a water-soluable saponin poisonous to fish (Bradley, 1956). The sap of S. biloculare was used by Central and Southwestern American Indians as a poison with which to tip their arrows; the corrosive action of the poison on the tissue increased the gravity of the wound. Bradley (1956) mentioned two other species of Sapium, S. indicum and S. aucuparium, which are used as fish toxins in Malay.

There have been very few investigations of specific phytoncides or repellants belonging to S. sebiferum. The work that has been done has shown that its leaves and fruits are poisonous to ruminants (Russell, et al., 1969); the fruits and leaves act as a powerful cathartic when fed to cattle and have a somewhat reduced effect when fed to sheep (Russell, et al., 1969). The toxic mechanism of S. sebiferum is not known, but the stillingia oil may be responsible, since the test subjects displayed the clinical signs of stillingia oil poisoning (eg., dehydration, weakness, and eventual death). A reference to Shimokoriyama (1949) in Harborne (1967) shows that S. sebiferum leaves contain quercitin-3-glucoside (see VII below); quercitin from adult apple trees inhibits the growth of apple seedlings (Borner, 1959; Williams, 1960).

develop a resident herbivore population. Therefore, a resident herbivore population could develop on the Chinese tallow tree in time. Alternatively, the lack of herbivory could be due to the presence of certain secondary compounds which inhibit feeding upon the plant parts.

F. Ephemeral Ponds

Ephemeral ponds are bodies of water extant for only part of the year. They may be rain-filled depressions in low lying areas of fields or they may be ponds left by intermittent streams. The periodical nature of the ponds limits the kinds of animals which can live in them. The fauna of temporary streams are comprised of five main groups (Hynes, 1970): (1) Species which survive despite the high temperatures and low oxygen content, including fish of the family Cyprinidae and some snails; (2) species which survive by burrowing into the substrate, including nematodes, oligochaetes, insects (eg., Tendipedidae and some caseless Trichoptera), crayfish and some isopods and amphipods; (3) species with eggs which survive long periods of drought, such as some stoneflies and mayflies; (4) species which re-invade once the streams become filled, including fishes, Ephemeroptera, Tendipedidae and Coleoptera; and (5) species which prefer or live only in temporary streams, including some Culicidae, Tendipedidae and Coleoptera and a few snails including _Limnaea_. The foregoing categories, except perhaps for number four, would hold for ephemeral ponds not in stream beds and hence filled only by sufficient rainfall.

Historically, ponds and lakes have been viewed as self-contained ecosystems or as independent microcosms. The importance of allochthonous (eg., externally derived) organic matter was not studied directly until

recently when limnologists realized the dependence of stream communities upon such organic input (Scott, 1958; Hynes, 1963; Darnell, 1964; Minshall, 1967,1968; Tilly, 1968; Vannote, 1970; Anderson and Grafius, 1974). Allochthonous input is important as a source of energy and nutrients in lakes also (Goldman, 1961; Szczepanski, 1965; McConnell, 1968). The importance of allochthonous organic material in woodland lakes, ponds and streams is easily seen since two-thirds or more of the annual energy requirements for primary consumer organisms is derived from leaf litter of riparian woodlands (Teal, 1957; Vannote, 1970). Thus, these are heterotrophic systems, obtaining much of their energy from the surrounding forest in the form of tree litter. Therefore, the close and important inter-relationships between terrestrial production and the structure and function of aquatic ecosystems has come under intensive study (Ross, 1963; Cummins and Wuycheck, 1971; Fisher and Likens, 1972; Cummins, et al., 1973; Cummins, 1974; Likens and Bormann, 1974).

Reducer organisms are those species which feed on whole plant litter, usually leaves, but also including seeds, stems and branches, and break it down into smaller pieces. This action increases the surface area of the litter and allows bacteria and fungi to complete the decomposition process. Since allochthonous material is a vital component of energy and nutrient turnover in woodland streams, ponds and lakes, reducer organisms play a vital role in hastening the turnover of stored energy. Several studies have shown that members of almost all the major invertebrate groups present in aquatic communities feed upon allochthonous organic matter (Jones, 1950; Hynes, 1961; Minckley, 1963; Minshall, 1967, 1968; Vannote, 1970; Anderson and Grafius, 1974).

Thus, it is of interest to determine how certain organic chemicals (eg., tannins) affect the use of this important organic input in aquatic communities. Since tannins inhibit the rate of leaf reduction and its eventual decomposition in terrestrial communities, it would seem that fewer reducer organisms would be able to utilize the tannin-containing litter; microbial decomposition would take on a greater importance in the aquatic community. However, without reducers to break up the detrital material, less surface area is exposed and the microbial release of energy and nutrients would be much slower and perhaps ultimately less than in communities unaffected by tannin-containing litter.

G. Hypotheses of the Study

The lack of herbivory suggesting that some secondary plant compound (eg., tannins) are present in the leaves of the Chinese tallow tree, leads to the hypothesis that the leaves contain tannins. If the lack of an herbivore load on S. sebiferum on the University of Houston Coastal Center is due to any secondary plant compounds contained within its leaves, it would be of interest to note the effect of Chinese tallow tree leaf fall upon the invertebrate community structure in general, and the reducers in particular, in ephemeral ponds within the forest habitat once the leaves fall and thereby enter the reducer chain of the community. I hypothesize a reduction in the number of reducer organisms in ponds affected by the Chinese tallow tree leaf fall.

METHODS

A. Habitat Description

Field studies were undertaken at the University of Houston Coastal

Center in LaMarck, Texas, to determine the effect of Chinese tallow tree

leaf litter upon the invertebrate community structure of ephemeral ponds.

The Coastal Center is within the Texas Gulf Coastal Prairie and is dominated

by nature stands of Baccharis hamilifolia (sea-myrtle) interspersed with

Andropogon glomeratus (bushy beardgrass), Spartina spartinae and S. patens

(Gulf cordgrass and salt-meadow cordgrass, respectively), Solidago sp.

(Goldenrod), Rubus trivialis (Southern dewberry) and Lonicera japonicum

(Japanese honeysuckle). The growing season is long, extending from March

through November.

The Chinese tallow tree has taken over extensive areas of the

Coastal Center since the Second World War. It forms an extremely dense

monoculture forest and is the most extensive tree species on the Coastal

Center. This tree spreads predominantly along wet areas and has followed

the network of road-side ditches, subsequently spreading out from these

areas where the surrounding soil contains abundant moisture. The most

extensive forest is in the lower, wetter areas of the Coastal Center; the

tree is found only in sparce stands in the higher areas of the Coastal

Center.

The ephemeral ponds used in this study are sections of drainage

ditches along the various roads which cross the Coastal Center. These

ponds are seasonally rain-filled, and have water in them for seven to

eight months out of the year, being filled from October through May.

Ponds were chosen because of their similarities in size and volume. The

sizes of the ponds were generally 7 to 8 m long, 2.5 to 4 m wide, and 29 to 45 cm deep. In order to test the hypotheses of this study, I monitored seven ponds on the Coastal Center; four of these ponds were in the tallow forest and the remaining three were in the grasslands. The purpose in using the grassland ponds was to have, for comparative purposes, ponds which were unaffected by any tallow tree litter input and hence, to observe differences in the biota due to the presence or absence of tannin-containing litter. The contour of the Coastal Center is such that after a flooding rain, any flow of water leads from the grassland ponds to the low-lying areas (eg., those which contain the tallow forest). This tends to hold to a minimum any "back-contamination" of Chinese tallow leaf leachate, but does allow immigration of organisms from grassland ponds to forest ponds.

The soil of the Coastal Center is characteristic of the Coastal Prairie; it is a hard clay loam (Bernard soil) with a high organic matter content. The clay soil is classified as a Vertisol by Westfall, et al., (1971). This soil retains moisture following heavy rainfall; upon drying it forms large cracks, hence it is often referred to as a cracking clay (Westfall, et al., 1971).

B. Sampling Methods

The biota in four forest and three grassland ponds was sampled monthly during the time the ponds were extant. Sampling was initiated on November 31, 1973, and continued through June 3, 1974. Replicate drag samples in each pond were taken using a rectangular net (46 cm wide by 18 cm tall) pulled along the pond bottom for a distance of 50 cm. This yielded a sample volume of 4.14×10^4 cm^3. Due to the technique (no

attempt was made to dig into the sediments) and the net's mesh size (0.74 mm), some substrate burrowers and micro-invertebrates such as the smaller nematodes, cladocerans, copepods and ostracods were not sampled. All samples were preserved with 10% formalin in the field, brought into the laboratory, sorted, counted and keyed to genus (and to species where possible).

Certain physical and chemical factors were also measured on the same dates the ponds were sampled to determine any differences between forest and grassland ponds. These measures included dissolved oxygen (Winkler method, see Welch, 1948), water pH and water temperature. The measures were taken at established points within each pond and close to the bottom. Care was taken to ensure that no more than 20 minutes passed between the time of sampling and the pH determination in the Coastal Center laboratory. Water temperature was measured with a Yellow Springs Instruments telethermometer.

Although the ponds to be compared were initially chosen for uniformity in size, differences in their exposures could result in their volumes changing at different rates, which in turn may affect species composition and numbers within the ponds. Pond volumes were calculated for each sampling date to establish rates of filling and evaporation using measures of length, width and depth taken at 50 cm intervals along the long axis of each pond. The ponds are only filled by seasonal rain. Rainfall is monitored continuously at the Coastal Center weather station, allowing daily, weekly and/or monthly totals to be used for lag-period determinations. Incident radiation (in foot-candles) at the surface of each pond was measured with a light meter; as a measure of exposure, this might correlate

with the ponds' evaporation rates.

Tannin concentration in intact tallow tree leaves and fruit (husk and seed, separately) was monitored seasonally using the acidified vanillin test (Burns, 1963, 1971). This test is specific for astringent plant compounds eg., flavan-3-ols, the flavan-3,4-diols (= leucoanthocyanidins), and their oligomers and polymers (= flavolans) (Goldstein and Swain, 1963; Haslam, 1966). The acidified vanillin method was developed to estimate the tannin content of grain sorghum (Sorghum bicolor) and other forage crops; Cummins (1971) found that a positive reaction (showing tannin content) in grain sorghum was negatively correlated with invitro dry matter digestibility for ruminants.

Relative tannin content was determined by placing one gram dry weight ground leaf in a 125 ml flask and adding 50 ml methanol. The flask was swirled occasionally to mix the contents and left to stand at room temperature for 24 hours. One ml of the resultant supernatant was added to each of six test tubes, followed by the addition of 5 ml vanillin-HCl reagent (prepared just before use by combining equal volumes of 8% conc. HCl in methanol and 4% vanillin in methanol). The samples were read on a Beckman spectrophotometer at 500 mμ; the vanillin-HCl solution is used as a blank.

The transmittance obtained with the sample was compared to a standard curve (Fig. 2) prepared with commercially obtained catechin (Sigma Chem. Co.) to determine tannin content. Values for the standard curve were obtained by adding 100 mg catechin to 50 ml methanol; dilutions from full strength to 1:9 were prepared. One ml of each dilution was pipetted into each of four test tubes. After the 10 dilutions (40 tubes)

Figure 2. Standard curve for tannin concentration, expressed
as catechin equivalents, using commercial D-catechin
(Sigma Chem. Co.). Points plotted are five separate
determinations and the line is hand-fitted through
the means.
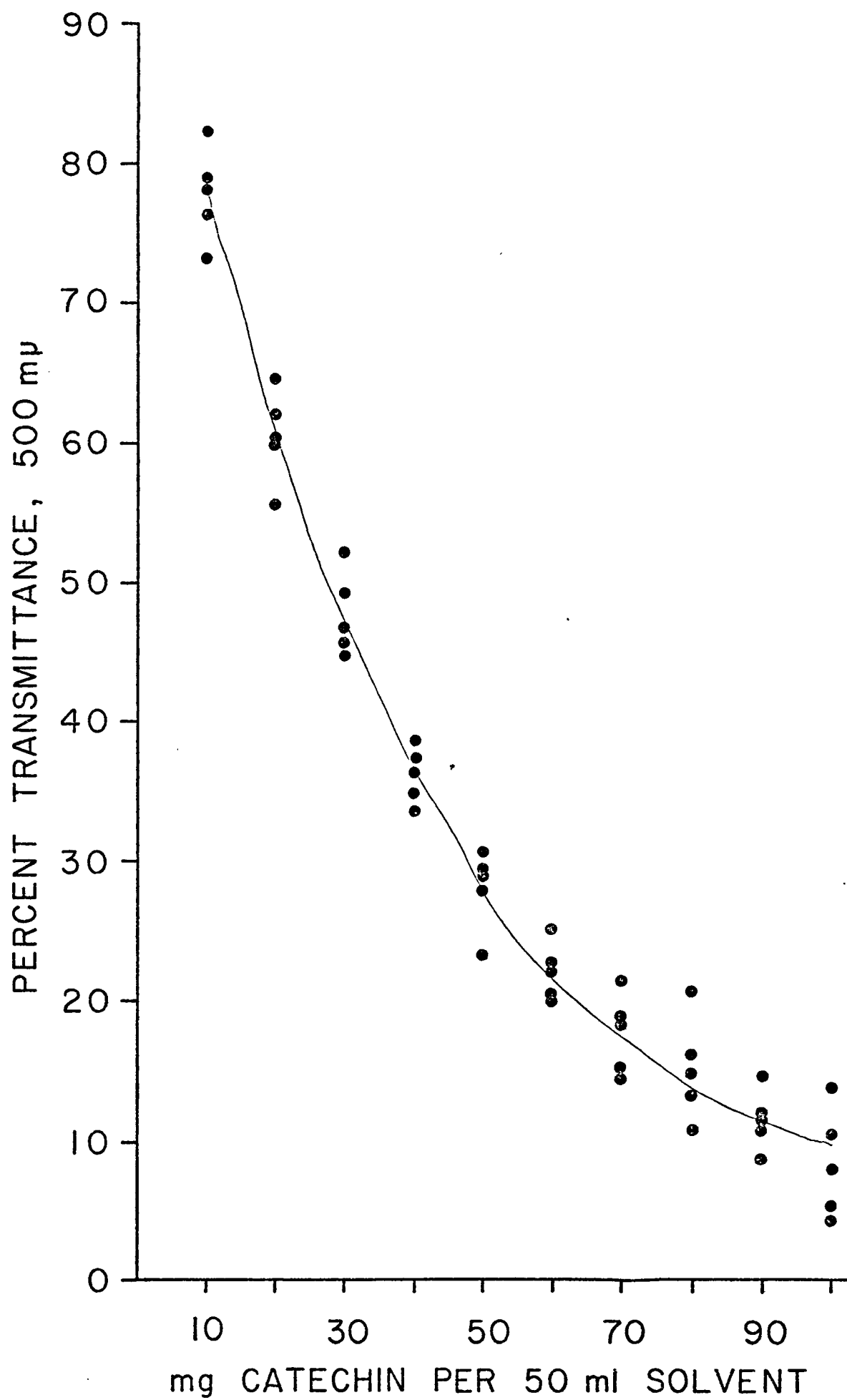
were prepared, 5 ml of the vanillin HCl reagent was added to each. The standard curve was constructed by plotting percent transmittance versus the catechin concentration.

The leaves used for the tannin analysis were picked off of Chinese tallow trees in March, June and November, 1974. Leaves were picked from the sunny side of the trees (south-facing) and were the largest leaves on the tree. This procedure minimized differences between leaves due to exposure and maturity. Leaves of at least 15 different trees were collected and "lumped" into a sack; from this collection, leaves were randomly drawn for the tannin determination.

One field experiment was designed to observe possible changes in the biota of two of the forest ponds into which leaves had been excluded. These two ponds were covered with a nylon mesh (0.158 cm mesh size) during the fall of 1973-74 to eliminate litter input from the tallow forest during the autumn leaf fall over the ponds. Leaves which fell onto the screen were pulled off weekly to minimize leaf-leaching into the ponds. These leaves were piled in an area where they could not leach back into the ponds, and after an interval of six weeks the leached leaves were added once again to the covered ponds to restore the original leaf substrate and minimize alterations in the biota by artificially removing bottom structure. After a few months of sampling it became qualitatively apparent that there were no differences between the two covered and two uncovered forest ponds. Subsequent quantitative analysis showed this observation to be correct. This will be further discussed below (see Results).

A field experiment was initiated during December, 1974, in which tallow leaf leachate was added to one of the grassland ponds to determine

whether differences in the invertebrate structure between the forest and the grassland ponds stem from some toxic substance in the Chinese tallow tree leaf leachate. Particular emphasis was placed on determining the effect of this leachate solution on the reducer organisms. A 100 gallon Nalgene container was filled with Chinese tallow tree leaves and 55 gallons of well water added; the leaves leached for two weeks. After the leaves were leached, they were taken out of the water and the leachate solution was added to the grassland pond. A similar quantity of well water was added to the second grassland pond as a control; the third grassland pond, to which nothing was added, was monitored concurrently to note seasonal changes in the biota. The quantity of leachate added to the ponds amounted to 5% of the pond volumes. The leachate concentration in the pond was monitored colorimetrically as a relative index of leaf leachate concentration. Physical factors as well as the biota were monitored over the next two month period, weekly during December, then at two week intervals in January, following procedures outlined above.

Another field experiment was initiated during December, 1974, to monitor the rate at which reducer organisms feed upon Chinese tallow leaves, and to monitor the rate at which tannins leach out of leaves falling into forest ponds, since differences in the biota between forest and the grassland ponds may be caused by an inability of reducer organisms to utilize Chinese tallow tree leaf litter as an energy source. Twelve large-pore bags of nylon mesh (mesh size = 0.7 cm) were filled with a measured weight of Chinese tallow leaves which had been collected by shaking various tallow trees and collecting the leaves which fell. Small pore Nitex nylon bags (mesh size = 64 μ) were similarly filled; all bags

were 10 cm by 10 cm in size. Collecting leaves by shaking the trees rather than picking leaves off of the trees ensured that I was collecting leaves that were ready to fall and become part of the litter layer. The pore size of the large-pore bags allowed all but the largest mesofauna into the bag; mesofauna includes insect larvae, aquatic isopods, amphipods and immature crayfish, smaller molluscs, nematodes and aquatic Acari (Wallwork, 1970). Small-pore bags keep out all but the smaller nematodes, Acari and Protozoa. The bags were placed on an aluminum grid to facilitate recovery from the forest pond bottom; two replicate small-pore and two replicate large-pore bags were randomly removed from the grid weekly through December and then bi-weekly in January. The leaf packs were removed to the laboratory, rinsed, air dried to constant weight, weighed, and the tannin content determined.

In January and March, 1975, laboratory survival experiments were undertaken using the isopod, Asellus militaris and the amphipod, Crangonyx shoemackerii, to determine the toxicity of Chinese tallow leaf leachate on these organisms. Four concentrations of tallow leaf leachate were made from an original concentration of 178.5 gm dry leaf weight in five liters of distilled water. The original concentration was arbitrarily set at 100% and the four concentrations used were 50%, 33%, 16% and 0% (a control of distilled water). For each of these species, four replicate 400 ml bottles with 10 adult individuals each were set up for each of the four concentrations. The experiment was run for seven days at room temperature during which time the bottles were continuously aerated; the animals were not fed during the run, since the intent was to observe if any direct toxic effects could be noted due to the leachate solution.

The number of individuals surviving were counted daily.

A similar laboratory experiment was initiated in March, 1975, to determine if tannins in solution inhibit feeding on grassland litter by the same organisms: A. militaris and C. shoemackerii. Commercially obtained d-catechin (Sigma Chem. Co.), a known tannin, was used in the same experimental design previously described: four replicate bottles of catechin solution at concentrations which incorporate ranges maximally found in forest ponds. The concentrations used were 10% (weight/volume), 6%, and 3% of d-catechin in distilled water, with a control of distilled water. As in the leaf leachate experiment, ten adults of each species were placed in 400 ml bottles and four replicate bottles were used for each concentration. To avoid death by starvation, the isopods and amphipods were fed grass litter which had been obtained at the same time they were captured from the field. One-half gram dry weight of grass litter was added to each jar. The bottles were continuously aerated and kept at room temperature; this experiment also ran for seven days and the number of individuals surviving was counted daily.

RESULTS

A. Taxonomic Representation

All taxa encountered during the seven month sampling period are
listed in Table 2. The total period was divided into three "seasons"
based largely upon pond temperature and pond volumes; the months lumped
were December, January and February (winter), March and April (spring),
and May and June (early summer). All orders except for Trichoptera (In-
secta), Acari and Hydracarina (Arachnida) had representative species in
both the forest and grassland habitats. There were 54 species in both
the forest and grassland habitats of which 33 species were shared by the
forest and grassland habitats. The forest ponds had 6 unique species;
the grassland ponds, 15. The fauna of both habitats was similar with
the majority of species sommon to both habitats. Many of the unique species
in both habitats are predacious or herbivorous; however, most were of a
"transient" nature, being caught only a few times or a few caught only
once. The large standard errors of the mean numbers caught per sample for
these species indicate the few caught within any seasonal sample. Certain
Oligochaeta (Dero sp.) and Diptera (the Tendipedidae) were numerically
predominant in both habitats. Generally, population densities tended to
be larger within the grassland ponds.

There were the same number of predators in both habitats (Table 3).
There were fewer herbivores in the forest ponds and approximately the same
number of reducer species. The reducer species can be further categorized
into functional groups based upon particle size and character of food;
such categorization has been used in previous studies (Nelson and Scott,
1962; Vannote, 1970; Cummins, 1973, 1974; Anderson and Grafius, 1974).

Table 2. The mean number of individuals within the species captured seasonally. The number tabled is the mean per drag (2 drags per pond) plus the standard error. Data for each season were averaged for four forest ponds and two grassland ponds; December, January and February are the winter months, March and April are the spring months, and May and June the early summer months. Trophic designations, derived from the literature, are listed in the first column as R (= reducer), P (= predator) and H (= herbivore).

| | | FOREST | | | GRASSLAND | | |
		Winter	Spring	Summer	Winter	Spring	Summer
CLASS OLIGOCHAETE							
PLESIOPORA							
Naididae							
Aulophorus furcatus Mueller	R	0.73± 0.36	0.06± 0.06	0.00	0.00	0.37± 0.37	0.37± 0.37
Dero Oken	R	27.05± 5.65	28.56± 7.15	63.62± 25.93	11.80± 8.83	10.50± 3.64	10.62± 5.39
Chaetogaster Von Baer	P	0.00	0.50± 0.22	0.06± 0.06	1.00± 1.00	0.71± 0.67	0.50± 0.27
Allonais Sperber	R	0.31± 0.32	0.00	0.37± 0.26	0.76± 0.52	0.25± 0.25	2.75± 1.82
CLASS HIRUDINEA							
PHARYNGOBDELLIDA							
Erpobdellidae 1	P	0.05± 0.05	0.06± 0.06	0.50± 0.50	0.30± 0.30	0.75± 0.53	0.00
CLASS CRUSTACEA							
ISOPODA							
Asellidae							
Asellus militaris Hay	R	1.63± 0.61	2.25± 1.20	0.00	10.20± 2.58	2.55± 0.79	0.88± 0.64
AMPHIPODA							
Gammaridae							
Crangonyx shoemackeri Hubricht and Mackin	R	0.36± 0.19	0.18± 0.14	0.06± 0.06	2.60± 1.10	1.25± 0.66	0.25± 0.25

Table 2, Continued.

		FOREST			GRASSLAND		
		Winter	Spring	Summer	Winter	Spring	Summer
DECAPODA							
Astacidae							
Procambarus simulans Faxon	R	0.31± 0.17	1.50± 0.38	0.50± 0.16	3.50± 1.33	5.00± 2.48	0.62± 0.50
Palaemonidae							
Palaemonetes kadiakensis Rathbun	R				0.20± 0.20	0.37± 0.26	0.87± 0.44
CLASS INSECTA							
EPHEMEROPTERA							
Siphlonuridae							
Siphlonuris Eaton	H	1.36± 0.34	0.06± 0.06	0.00	4.00± 1.30	2.00± 0.87	0.62± 0.32
Caenis Stephens	H				0.20± 0.20	0.00	1.62± 0.87
ODONATA							
Coenagrionidae							
Lestes Leach	P	0.21± 0.12	0.00	0.00			
Enallagma Charpentier	P				0.10± 0.10	0.12± 0.12	0.00
Ischnura Charpentier	P				0.10± 0.10	0.25± 0.16	0.25± 0.25
Libellulidae							
Ladona Needham	P				0.20± 0.20	0.00	0.00
HEMIPTERA							
Corixidae							
Trichocorixa Kirkaldy	H	0.00	0.18± 0.14	0.25± 0.19	0.00	0.12± 0.12	6.00± 4.77
Veliidae							
Microvelia Weston	P	0.05± 0.05	0.06± 0.06	0.00	0.10± 0.10	0.00	0.00
Notonectidae							
Buenoa Kirkaldy	P	0.00	0.31± 0.15	1.18± 0.64	0.10± 0.10	0.75± 0.53	3.12± 1.23
Gerridae							
Tachygerris Drake	P	0.00	0.00	0.06± 0.06			

Table 2, continued.

		FOREST			GRASSLAND		
		Winter	Spring	Summer	Winter	Spring	Summer
COLEOPTERA							
Hydrophilidae							
Berosus Leach	H-R				0.10± 0.10	0.00	0.25± 0.16
Derallus Sharp	H-R				0.00	0.00	0.37± 0.37
Tropisternus Solier	H-R	0.15± 0.11	0.00	0.00	1.30± 0.67	0.25± 0.25	0.12± 0.12
Dytiscidae							
Thermonectus Dejean	P	0.57± 0.27	0.06± 0.06	0.00	0.30± 0.30	0.00	0.00
Laccophilus Leach	P	0.00	0.06± 0.06	0.06± 0.06	0.00	0.12± 0.12	0.00
Dryopidae							
Helichus Erichson	H				0.00	0.12± 0.12	0.00
Gyrinidae							
Dineutus MacLeay	P				0.00	0.00	0.12± 0.12
TRICHOPTERA							
Psychomyiidae							
Polycentropus Curtis	H				0.00	0.00	0.12± 0.12
Hydroptilidae							
Oxyethira Eaton	H				0.00	0.12± 0.12	0.00
DIPTERA							
Tendipedidae							
Tendipes Meigen	H-R	14.10± 3.03	94.56± 35.78	45.43± 12.07	1.50± 0.62	0.25± 0.25	6.00± 2.74
Pentaneura Phillippi	H-R	0.15± 0.16	0.81± 0.42	17.37± 6.26	1.20± 0.80	0.75± 0.31	19.00± 3.74
Pelopia Meigen	H-R	0.36± 0.27	0.00	0.00	0.10± 0.10	0.00	0.00
Calopsectra sens. lat.	H-R	0.00	0.00	0.81± 0.52	0.00	33.00± 25.15	114.00± 36.53
Tendipedini	H-R	1.47± 0.47	4.50± 1.40	9.31± 2.64	5.20± 1.48	35.25± 20.99	142.00± 42.11

Table 2, continued.

		FOREST			GRASSLAND		
		Winter	Spring	Summer	Winter	Spring	Summer
DIPTERA, cont.							
Ceratopogonidae							
Alluaudomyia Keiffer	?	0.05± 0.05	0.00	0.00	0.00	0.62± 0.62	0.00
Leptoconops Skuse	?	0.31± 0.32	0.18± 0.10	1.06± 0.35	0.20± 0.20	6.62± 2.34	2.50± 0.96
Stilobezzia Coq.	?				0.00	0.00	0.25± 0.25
Forcipomyia Meigen	?	0.00	0.00	0.06± 0.06	0.00	0.00	0.75± 0.41
Culicidae							
Chaoborus Lichtenstein	P	1.47± 0.50	1.50± 0.60	8.87± 3.64	0.00	0.25± 0.25	0.87± 0.52
Anopheles Meigen	R	0.15± 0.16	0.18± 0.19	0.00	0.00	0.75± 0.75	0.00
Tipulidae							
Tipula Linnaeus	R	0.05± 0.05	0.00	0.00			
Limonia Meigen (?)	R	0.00	0.06± 0.06	0.00	0.40± 0.40	0.00	0.00
Phalacrocera Schiner	R	0.00	0.12± 0.12	0.00	0.00	0.12± 0.12	0.00
Tabanidae							
Chrysops Meigen	R				0.00	0.12± 0.12	0.00
COLLEMBOLA							
Sminthuridae							
Sminthurides (Bour.)	R	0.10± 0.07	0.00	0.00			
Entomobryidae							
Isotomurus Mueller	R	0.94± 0.49	0.87± 0.66	0.00	0.30± 0.21	0.37± 0.26	0.00
CLASS ARACHNIDA							
ACARI							
PROSTIGMATA 1	P	0.05± 0.05	0.00	0.00			
HYDRACARINA 1	P	0.05± 0.05	0.00	0.06± 0.06			

Table 2, continued.

| | | FOREST | | | GRASSLAND | | |
		Winter	Spring	Summer	Winter	Spring	Summer
CLASS GASTROPODA							
BASOMMATOPHORA							
Physidae							
Physa Draparnaud	H-R	1.89± 0.50	0.25± 0.19	0.75± 0.40	0.10± 0.10	0.00	0.62± 0.62
Planorbidae							
Promenetus Baker	H	1.15± 0.34	1.31± 0.37	1.93± 0.62	11.10± 11.00	0.25± 0.25	0.00
Ancylidae							
Gundlachia Pfeiffer	H				0.30± 0.21	0.12± 0.12	0.00
Lymnaeidae							
Lymnaea Lamarck	H-R	0.31± 0.19	0.00	0.06± 0.06	0.10± 0.10	0.00	0.00
CLASS PISCES							
Gambusia affinis	P	0.00	2.62± 1.13	0.62± 0.24	0.80± 0.61	6.62± 3.90	2.75± 1.00

Table 3. Numbers* of species within trophic levels in ephemeral ponds
on the Coastal Center.

	Forest	Grassland
Predators	12	12
Herbivores	12	19
Reducers	20	22

*These totals will not coincide with species totals because some species
are considered in more than one category.

These functional groups are important to an understanding of detritus utilization in aquatic systems. Taxa found in the Coastal Center ponds with representative species included in a given functional category are shown in Table 4. Examples of shredders are the isopods and amphipods; these animals feed on coarse particulate organic matter usually greater than one mm in diameter and consisting of leaves, sticks, fruits and flowers. Sediment-deposit feeders, which include the Tendipedidae and Oligochaeta, feed upon fine particulate organic matter on and beneath the sediment surface at the bottom of the ponds. Cummins (1974) notes that their importance in nutrient cycling is in aggregating small particles into feces which are re-ingested by other fine particle feeders. The food value and nutrient worth of these feces often increases through re-ingestion. Scrapers are often difficult to trophically define; they are equipped to remove attached algae (both alive and dead) and fungi from exposed surfaces, hence serve as both reducers and herbivores. In the Coastal Center ponds, scrapers are represented by the snails (Gastropoda) and by the Hydrophilidae. I suspect the reason for finding more scraper organisms in the grassland ponds is the lush growth of epiphytic algae. The last category of reducer organisms is the filter feeders. These organisms, represented by the Culicidae and Tabanidae, filter fine particulate organic matter out of the water column; they serve to concentrate this matter as feces which can be re-ingested as mentioned above.

Among the species found in the ephemeral ponds on the Coastal Center, There were similar numbers of crayfish (Procambarus simulans Faxon) ($x^2_{r, k=3, N=7} = 4.79$, p<.085), amphipods (Crangonyx shoemackerii Hubricht and Mackin) ($x^2_{r, k=3, N=7} = 5.36$, p < .085), and significantly greater numbers of isopods

Table 4. Functional categorization of pond reducer organisms according to particle size and character of food. From Cummins, 1974.

Shredders	Sediment-Deposit Feeders	Scrapers	Filter Feeders
Tipulidae (Both - Rare)	Tendipedidae (Both)	Hydrophilidae (Grassland)	Tabanidae (Grassland - Rare)
Amphipods (Grassland)	Oligochaeta (Forest)	Lymnaeidae (Forest - Rare)	Culicidae (Forest)
Isopods (Grassland)	Collembola (Forest)		
Astacidae (Grassland)			
Paleomonidae (Grassland)			

The habitat in which they predominate is listed in parentheses behind each listing.

(Asellus militaris Hay) ($X^2_{r,\ k=3,\ N=7}$ = 7.79, p < .016) in the grassland
ponds than in either the covered or uncovered ponds (Friedman's two-way
analysis of variance by ranks) (Siegel, 1956). These species represent
the primary "shredder" reducer organisms present in the grassland ponds
(Figs. 3 - 5).

The Shannon-Weaver diversity index, which stems from mathematical
information theory and which estimates the diversity (or "information")
per individual in a many species population (Pielou, 1969), expresses the
uncertainty of predicting from which species an individual chosen at
random in a community will come (Pielou, 1969). The Shannon-Weaver
diversity index is given by: $H' = -\Sigma\ p_i \log p_i$, where $p_i = n_i/N$, N =
total number of individuals, and n_i = the number of individuals in each
of i species, where i = 1,2,3..., s, the total number of species. As
long as the base of the logarithm is kept consistent throughout all
calculations, any base can be used; in this study logarithm to the base 10
is used.

There are three assumptions involved in the use of H': (1) the
collection is a random sample from some larger, conceptually infinite
population; (2) the member species are randomly distributed and (3) all
the species of a given community are represented in the collection (Pielou,
1969; Poole, 1974). In practice, these assumptions are often violated
but the error is assumed to be small if the sample size is large (Poole,
1974).

Given that all the species in a community are sampled (assumption
#3, above), it is then possible to calculate the evenness component of the
diversity measure. The evenness measure is given by: $J' = H'/H'_{max}$ =

Figure 3. The mean number of _Procambarus simulans_ Faxon captured

per sample. Grassland ponds = open circles; uncovered

forest ponds = closed circles; covered forest ponds
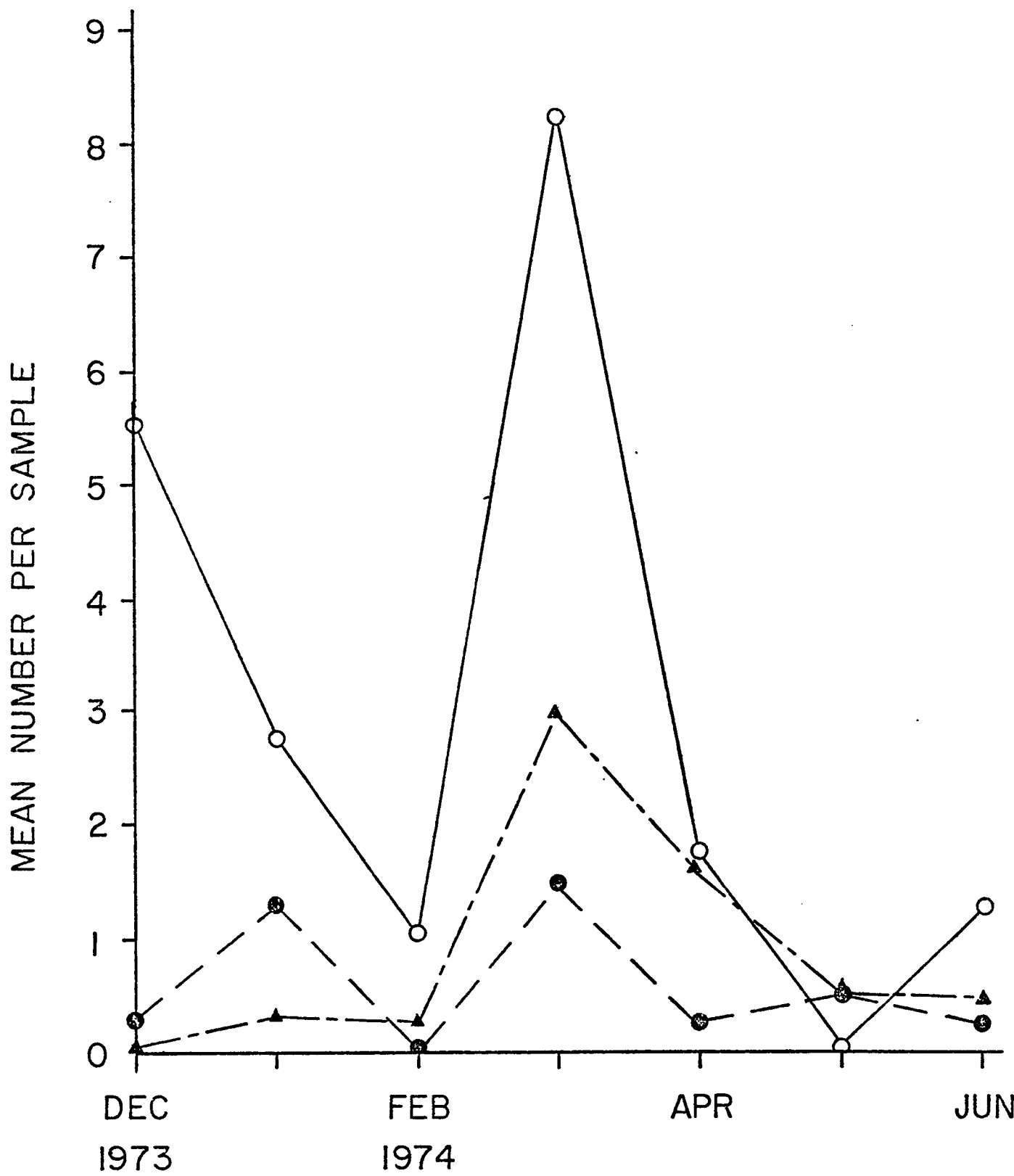
= closed triangles.

Figure 4. The mean number of *Crangonyx shoemackerii* Hubricht
and Mackin captured per sample. Grassland ponds =
open circles; uncovered forest ponds = closed circles;
covered forest ponds = closed triangles.
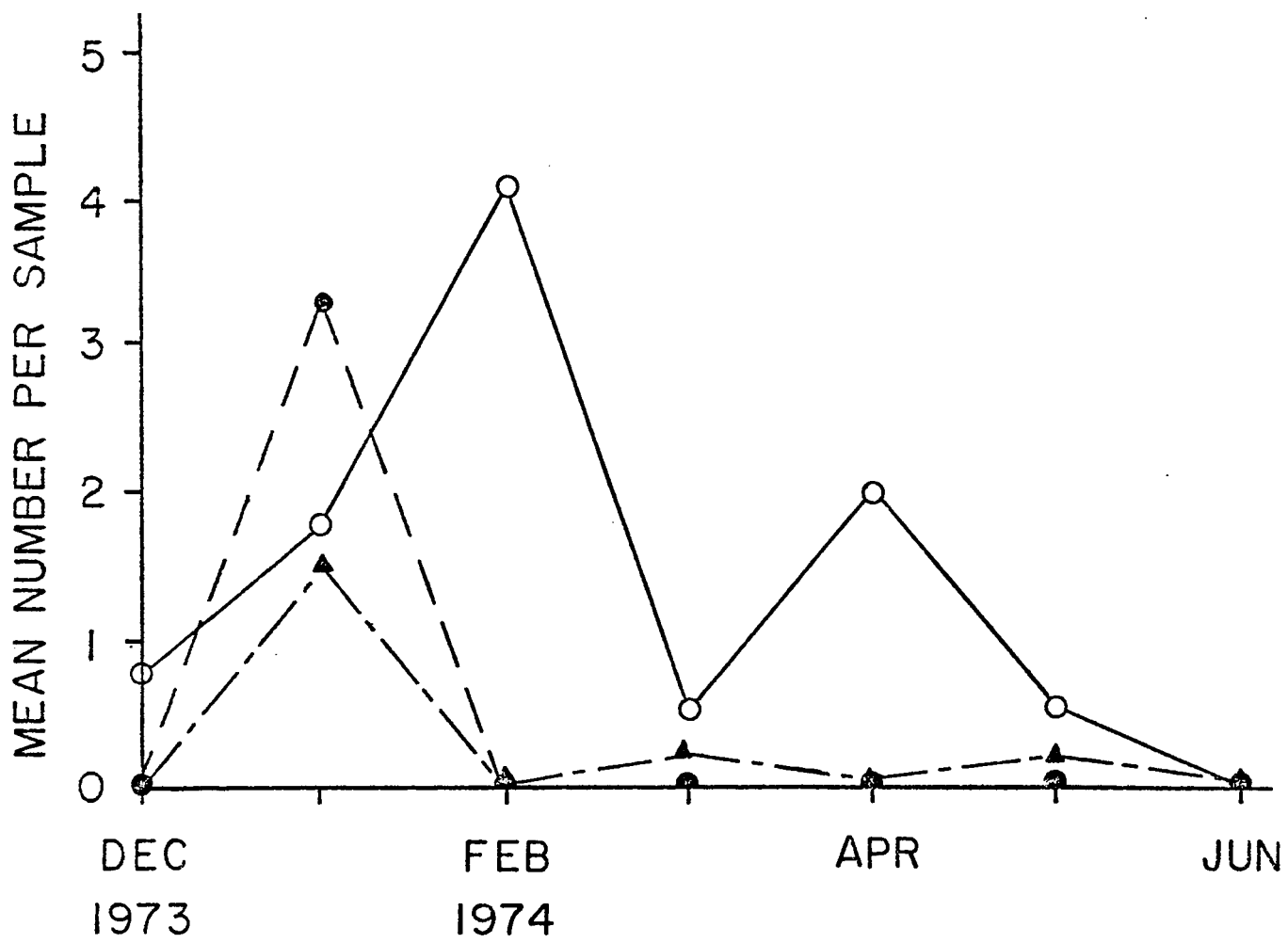
Figure 5. The mean number of <u>Asellus</u> <u>militaris</u> Hay captured

per sample. Grassland ponds = open circles; un-

covered forest ponds = closed circles; covered forest

ponds = closed triangles.
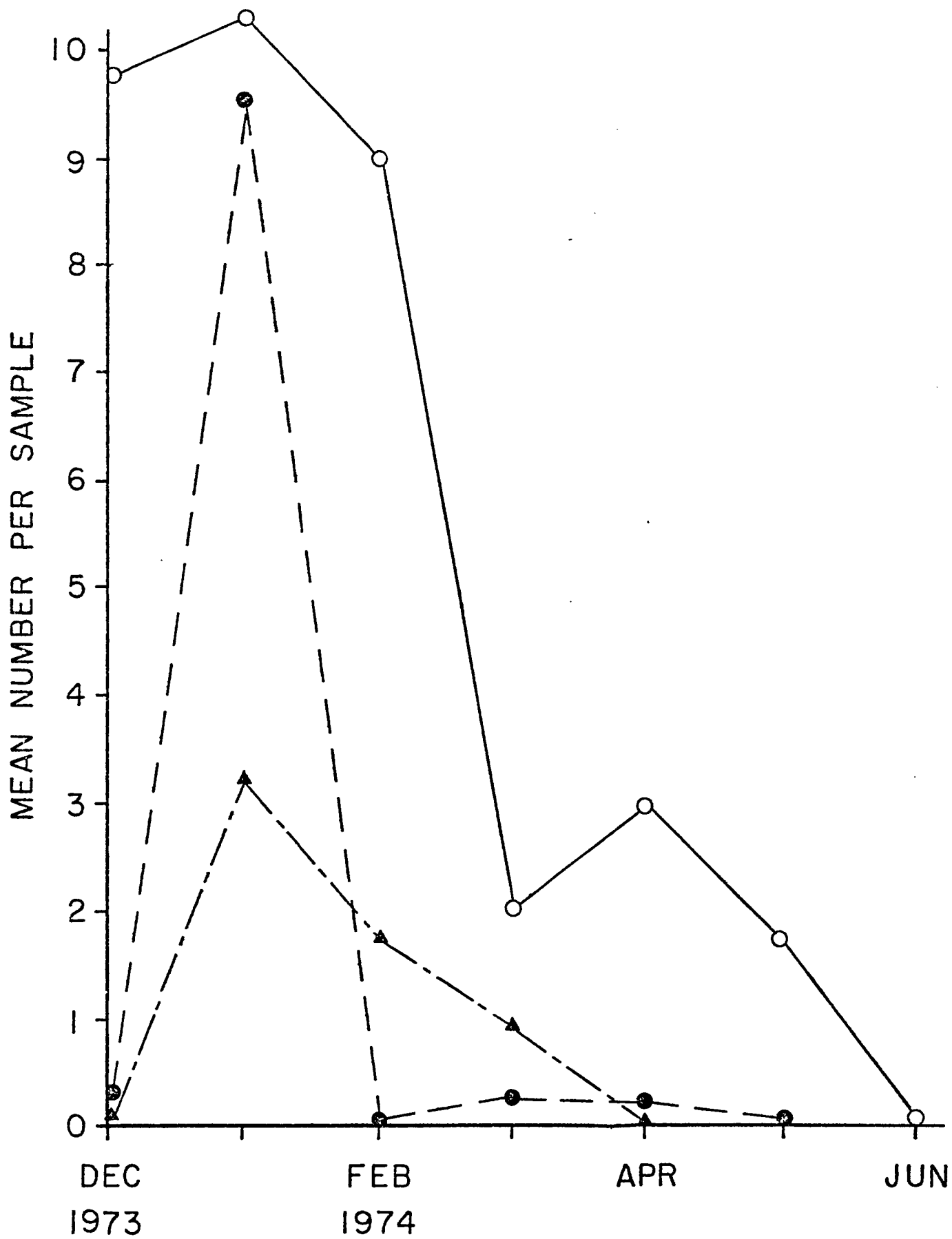
H'/log s, where s is the total number of species in the community. An s-species population has a maximum diversity only if all the species are present in the same proportion, 1/s, and therefore: H'_{max} = $-\Sigma$ 1/s log 1/s = log s (Pielou, 1969).

In the grassland ponds, the Shannon-Weaver index of diversity (H') decreases linearly (significant regression at p = 0.001) over months (Table 5 and Fig. 6); the diversity uniformly decreases through the year as does the evenness (J') (Fig. 7). The decrease in H' and J' reflect large numerical increases in a few species (notably in the Tendipedidae) (Table 2). The increase in the number of species in the grassland ponds is significant ($F_{6, 21}$ = 2.20, 0.1 > p > 0.05) (Table 5 and Fig. 8), and is probably a result of transient species sampled during the spring months.

The variation in H' of the forest ponds deviates significantly (Table 6 and Fig. 6) as does the number of species captured ($F_{5,21}$ = 2.65, 0.1 > p > 0.05; and $F_{5,21}$ = 3.73, p = 0.05, respectively), from a linear regression either because of sampling error or the pulses of precipitation (see below) which may introduce new species to the forest ponds. There is a seasonal decrease in the number of species throughout the year.

There are significant differences ($F_{2,54}$ = 7.84, p = 0.01) in H' between the covered and uncovered forest ponds and between these and the grassland ponds (Table 7). An SNK test (Sokal and Rohlf, 1969) confirmed that the uncovered and uncovered forest ponds have a lower H' than the grassland ponds. There are significant differences ($F_{5,54}$ = 3.92, p = 0.05) in H' between the months with H' decreasing seasonally. The number of species captured differ between the forest and grassland ponds (Table 7);

Table 5. Grassland linear regression ANOVA on H' and the number of
species.

H' (log)

Source	df	MS	F
Months	6	.0397	2.0119^{ns}
Linear	1	.1803	15.6153^{***}
Deviation	5	.0115	0.5856
Error	21	.0197	

The regression equation is Y = .82975 + .04012X

species

Source	df	MS	F
Months	6	21.2381	$2.1970^{(0.1 > p > 0.05)}$
Linear	1	85.7500	10.2871^{***}
Deviation	5	8.3357	0.8623
Error	21	9.6667	

The regression equation is Y = 6.85714 + .87500X

Figure 6. The mean diversity (H') per sample calculated for
the combined covered and uncovered forest ponds
(closed circles) and the grassland ponds (open
circles). Original values are given in Appendix i.
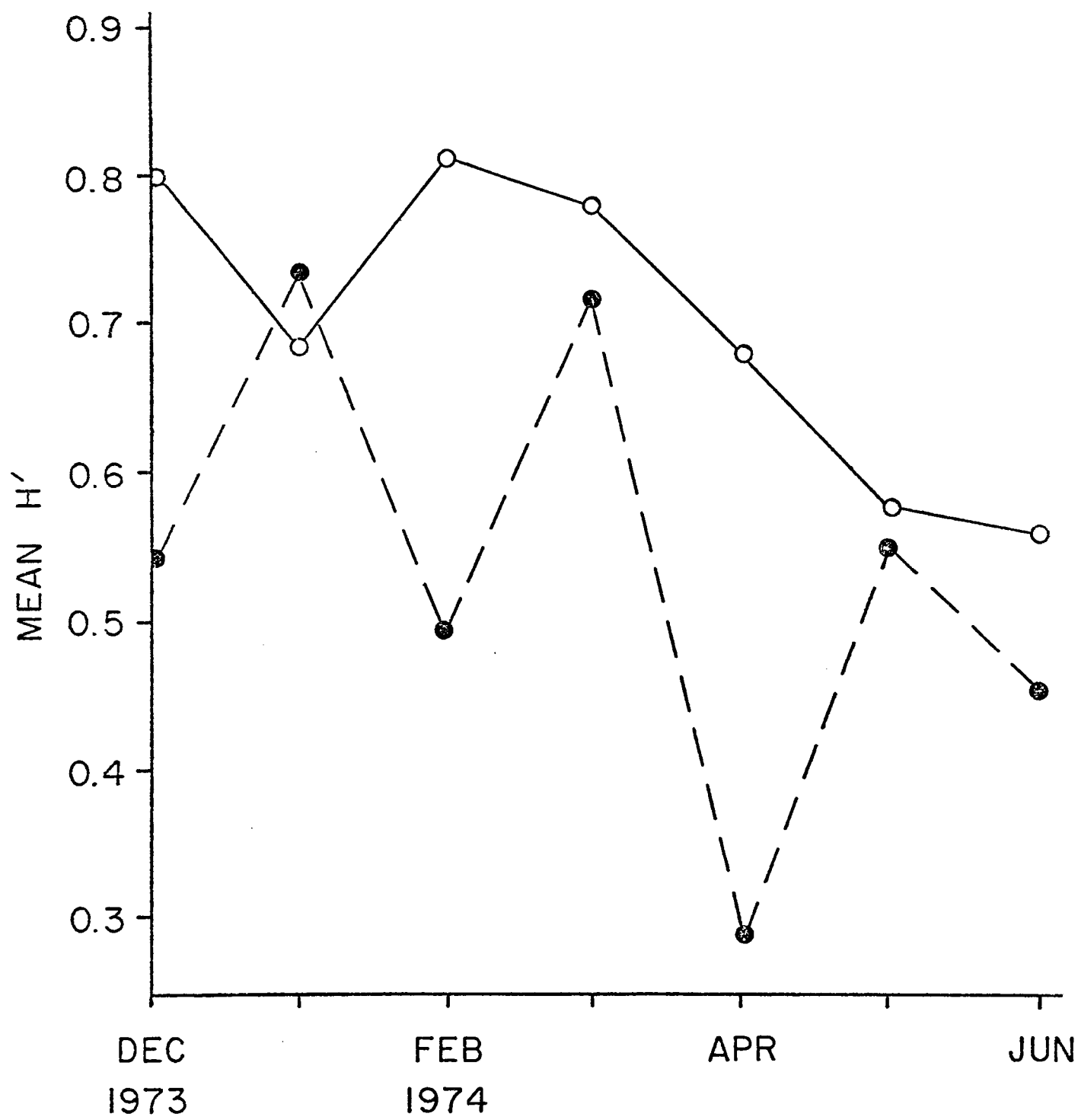
Figure 7. The mean evenness (J') per sample calculated
for the combined covered and uncovered forest
ponds (closed circles) and the grassland ponds
(open circles). Original values are given in
Appendix i.
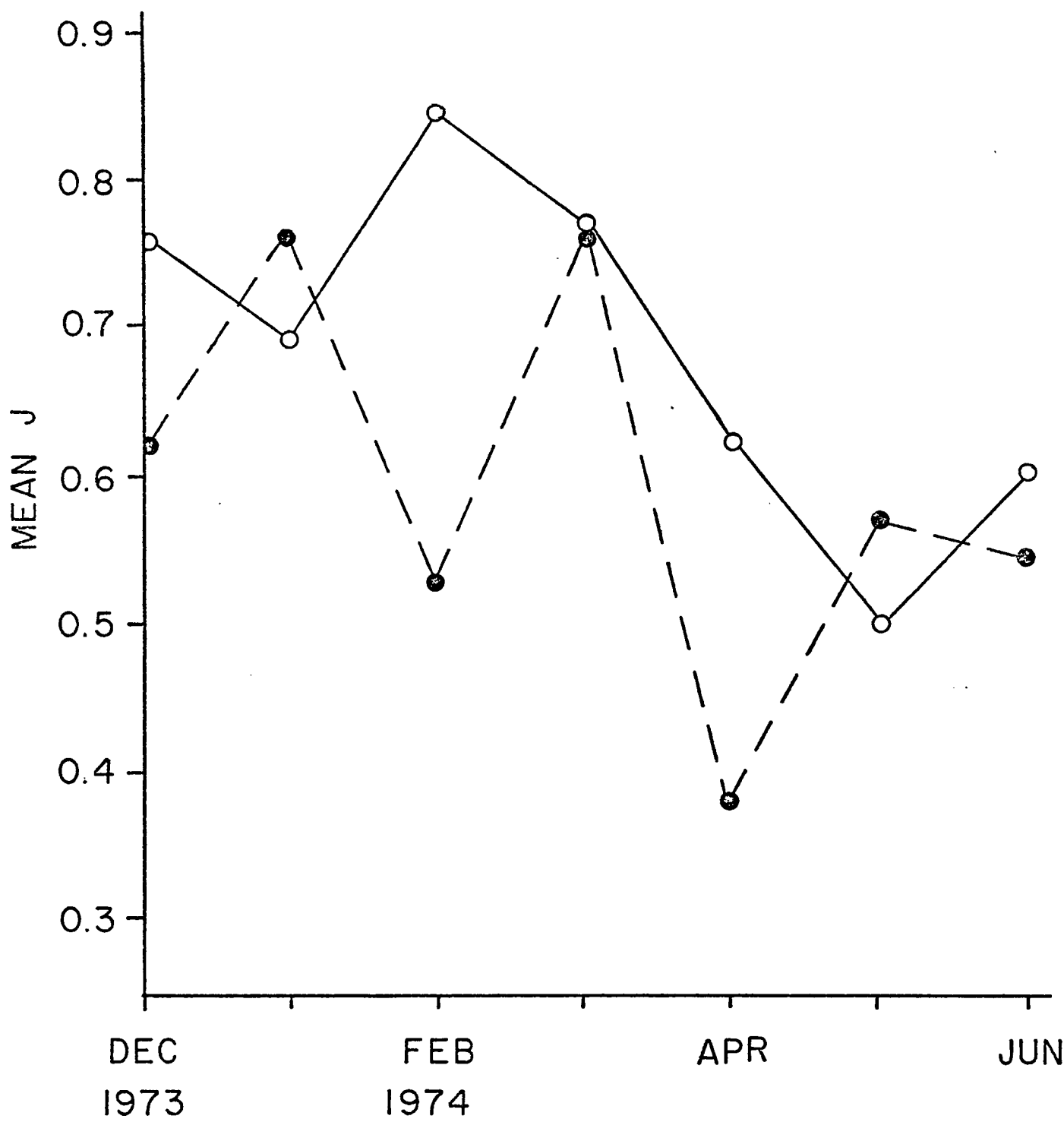
Figure 8. The mean number of species captured per sample
for the combined covered and uncovered forest
ponds (closed circles) and the grassland ponds
(open circles). Original values are given in
Appendix i.
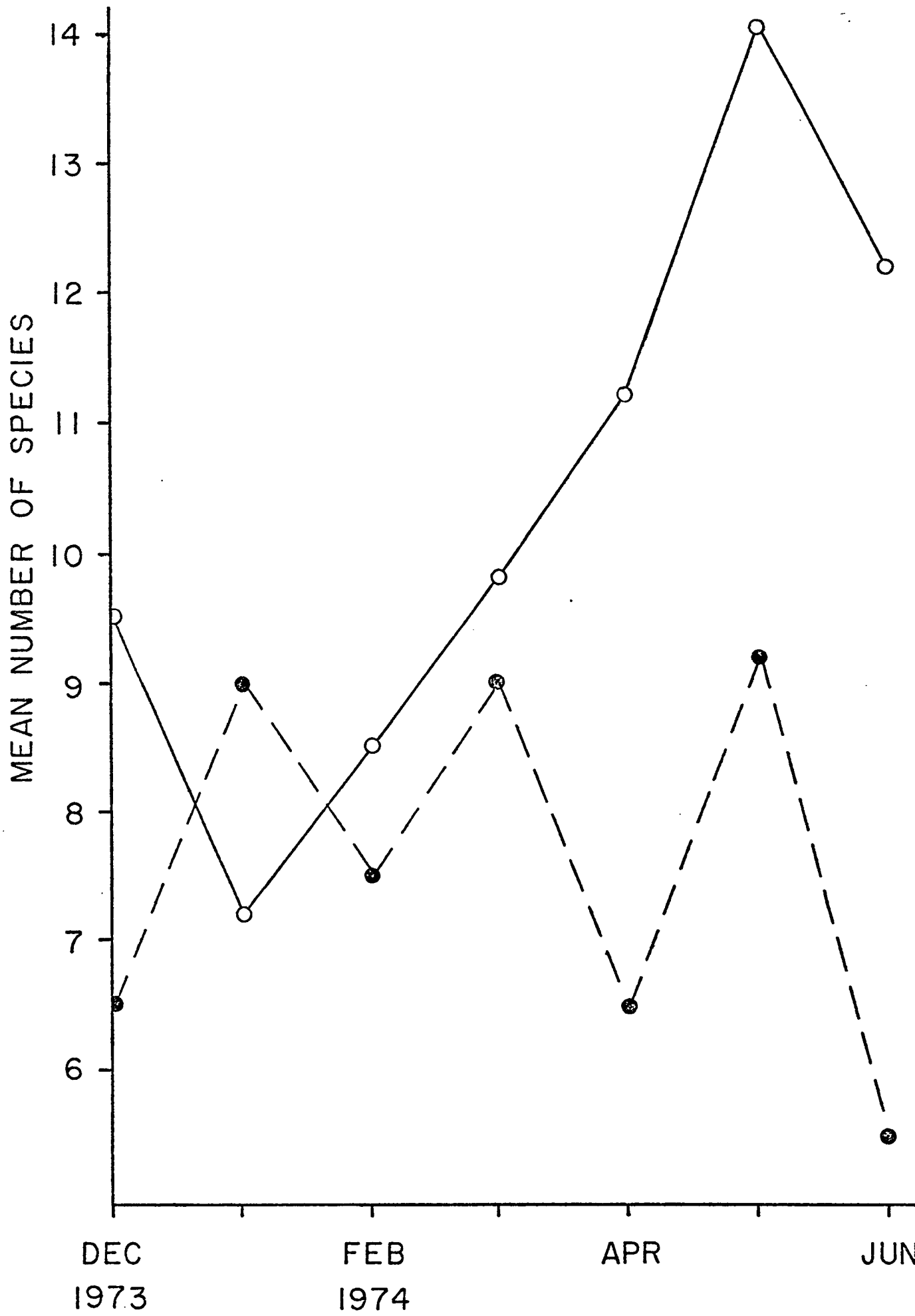
Table 6. Forest linear regression ANOVA on H' and the number of species.

H' (log)

Source	df	MS	F
Months	6	.0426	$2.4330^{(0.1 \; p \; 0.05)}$
Linear	1	.0237	0.5119^{ns}
Deviation	5	.0464	$2.6484^{(0.1 \; p \; 0.05)}$
Error	21	.0175	

The regression equation is Y = .91854 - .01456X

species

Source	df	MS	F
Months	6	8.9881	3.2128^{*}
Linear	1	1.7500	0.1677^{ns}
Deviation	5	10.4357	3.7302^{*}
Error	21	2.7976	

The regression equation is Y = 8.10714 - .12500X

* = 0.05

Table 7. Two-way ANOVA between ephemeral ponds over months on the Coastal Center.

H' (log)

Source	df	MS	F
Months	5	.1084	3.9162^{*}
Ponds	2	.2169	7.8359^{**}
Months X Ponds	10	.0479	1.7305^{ns}
Error	54	.0277	

species

Source	df	MS	F
Months	5	10.7556	1.7082^{ns}
Ponds	2	78.5139	12.4698^{***}
Months X Ponds	10	13.3806	2.1252^{*}
Error	54	6.2963	

$* = 0.05$; $** = 0.01$; $*** = 0.001$

there were no significant differences in the number of species captured among the months. The difference in the number of species between ponds increased as the season progressed, the effect becoming evident especially in the late spring months of April and May. As noted above, the difference between the two habitats in the number of species may not be biologically significant because many of the species caught in the grassland habitat during the spring and early summer were rare species; these species were caught only once or were represented by only a few individuals. Hence, the ponds are probably closer in species composition than the test indicates.

As mentioned in Methods, there were no significant differences between the covered and uncovered forest ponds in the number of species present or the kinds of species. While leaves were kept from falling directly into the covered ponds, no attempt had been made to eliminate drainage from the surrounding forest. Any of the rains could have leached the leaves from surrounding trees and this would have contributed to run-off into the covered as well as the uncovered ponds. Another factor which would ameliorate any differences that might occur by excluding leaf fall is that when it rained more than 1 to 1.5 inches in one 24 hour period, the ponds flooded, allowing tallow leaf leachate and some leaves to enter the covered ponds. During the seven month period the ponds were extant, this occurred ten times (Table 8). Leachate might not affect the grassland ponds because of the infrequent, sparse stands of Chinese tallow trees in the grassland habitat and the ponds' position on higher ground on the Coastal Center. The result of this experiment stresses the importance to the organisms in the ponds of leachate from leaves which do not fall directly into the ponds and runoff into the ponds from the surrounding woodlands.

Table 8. Total monthly rainfall and the number of days of heavy rain.

1973 DEC	1974 JAN	FEB	MAR	APR	MAY	JUN
2.867	10.415	1.61	4.015	3.245	11.455	1.245
(1)	(3)		(2)	(1)	(3)	

The number of days of greater than 1.5 inches of rain in one 24 hour period are listed in parentheses.

B. Physical Factors

Among the physical factors measured, temperature (Table 9 and
Fig. 9) stayed consistantly and significantly ($F_{2,231}$ = 334.99, p = 0.001)
cooler throughout the sampling period in the forest ponds. Water temp-
erature tended to be higher within both the forest and grassland habitats
than the mean monthly air temperature; however, their variances cannot
easily be compared because the water temperatures were consistently re-
corded between the hours of 1100 and 1300 hours D.S.T., while the air
temperature represents 24 hour averages. However, the seasonal trend is
borne out; the pond temperatures reflect the warming trend from winter
to summer. The forest ponds remain cooler, probably because of the
shade afforded them by the trees.

Rainfall (Fig. 10) reflects two large pulses of precipitation:
one in the winter and the second in the early summer. These two large
peaks in January and May result from two days in each month of greater
than 3.0 inches of rainfall each.

Pond volumes in the grassland and forest (Fig. 11 and Table 9)
decrease seasonally, reflecting the seasonal decrease in precipitation
and an increase in evapotranspiration of the trees. Stanhill (1970)
calculated that a short grass meadow in Oak Ridge, Tenn. evapotranspired
only one-fourth as much as a nearby mixed oak forest; while he believes
the value to be high, he refers to a study by Douglass (1967) in comparable
geographic areas which shows that the annual water loss from forests
should be 15% greater than that for meadows. The decreasing volume of
the Coastal Center forest ponds may result from the loss of water to the
trees. The last point on the graph reflects a large rainfall of more

Table 9. Two-way analyses of variance between ephemeral pond physical factors.

Water Temperature

Source	df	MS	F
Dates	6	1032.3226	1121.2244***
Ponds	2	308.4287	334.9901***
Dates X Ponds	12	10.0361	10.9004***
Error	231		

Pond Volume

Source	df	MS	F
Dates	5	.5184	5.1226**
Ponds	2	.1919	1.8963^{ns}
Dates X Ponds	10	.0579	0.5722^{ns}
Error	18	.1012	

Log Oxygen Concentration

Source	df	MS	F
Dates	4	.0692	230.6667***
Ponds	2	.0466	155.3334***
Dates X Ponds	8	.0010	3.3334*
Error	45	.0003	

Insolation at the Surface of the Pond

Source	df	MS	F
Dates	6	24,963,265.5	2.095^{ns}
Ponds	2	123,314,441.0	10.345***
Dates X Ponds	12	11,459,085.8	0.962^{ns}
Error	147	11,919,220.4	

* = 0.05; ** = 0.01; *** = 0.001. Original values are given in Appendix i.

Figure 9.   Mean water temperature recorded on the pond bottom and

monthly mean air temperature (open triangles). Forest

ponds = closed circles; grassland ponds = open circles.

Data for the pond temperatures are recorded in Appendix

i.
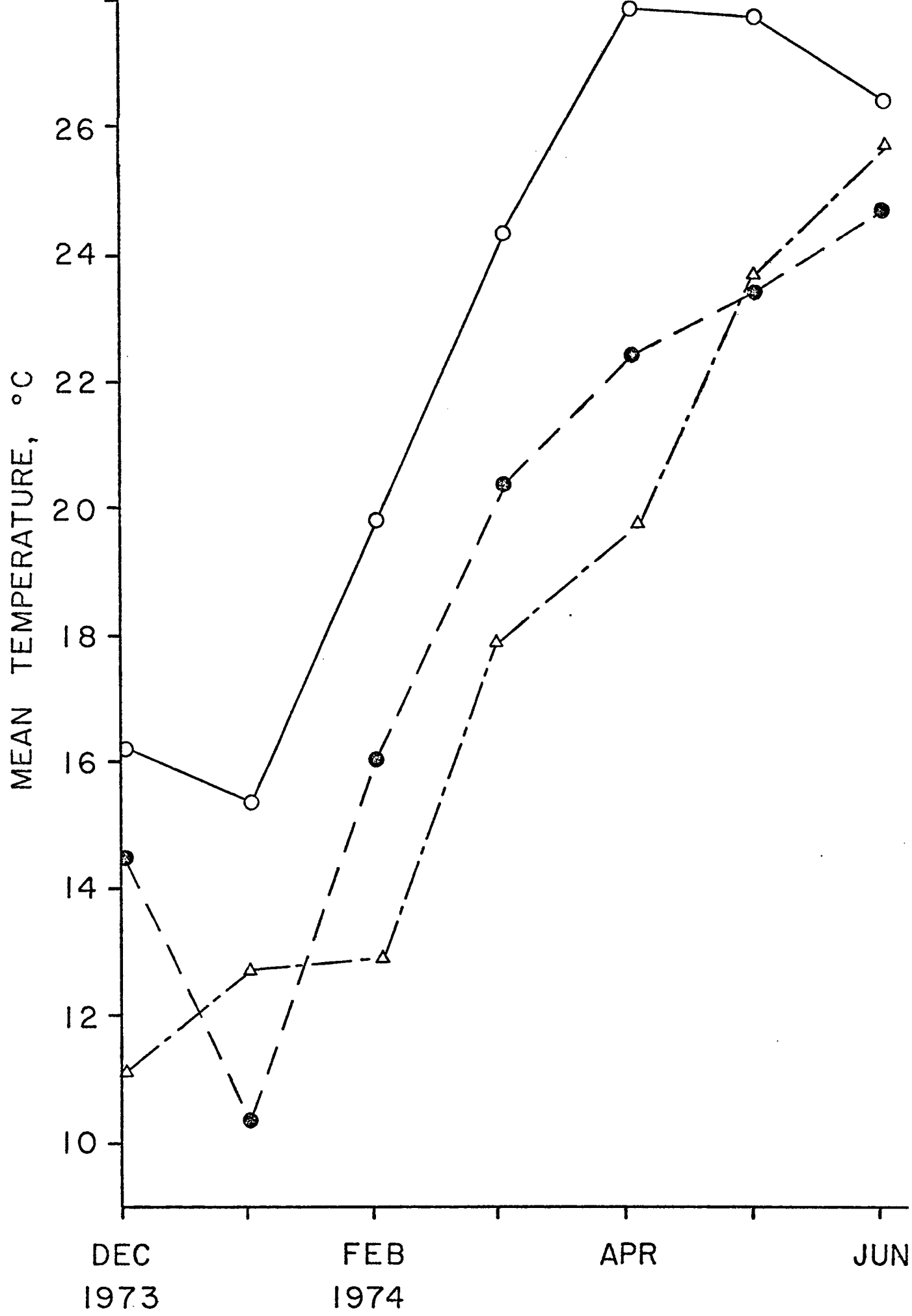
Figure 10. Total monthly rainfall for the University of

Houston Coastal Center.
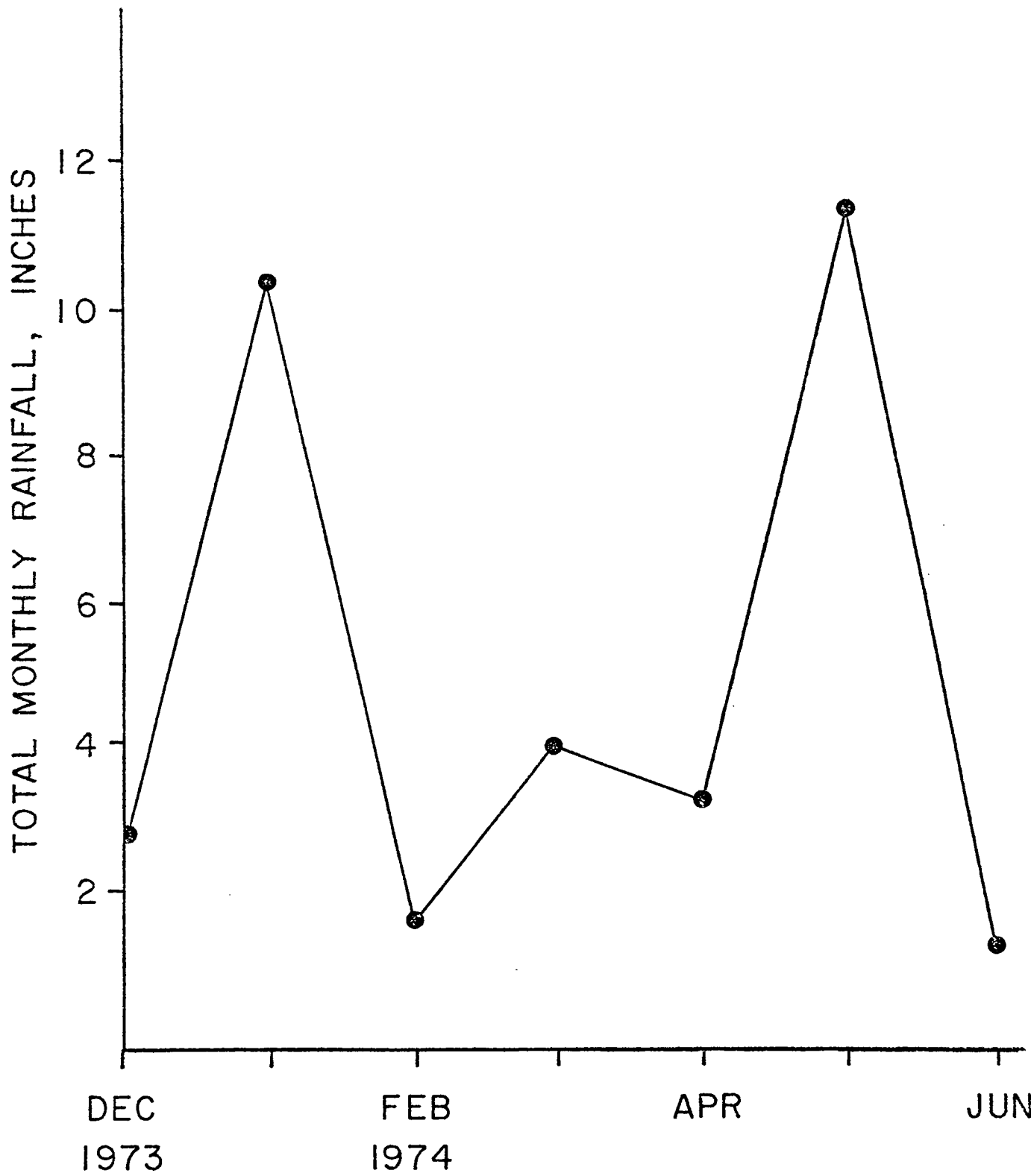
Figure 11. The mean pond volumes for the combined covered and

uncovered forest ponds (closed circles) and the

grassland ponds (open circles). Pond volume

data are recorded in Appendix i.
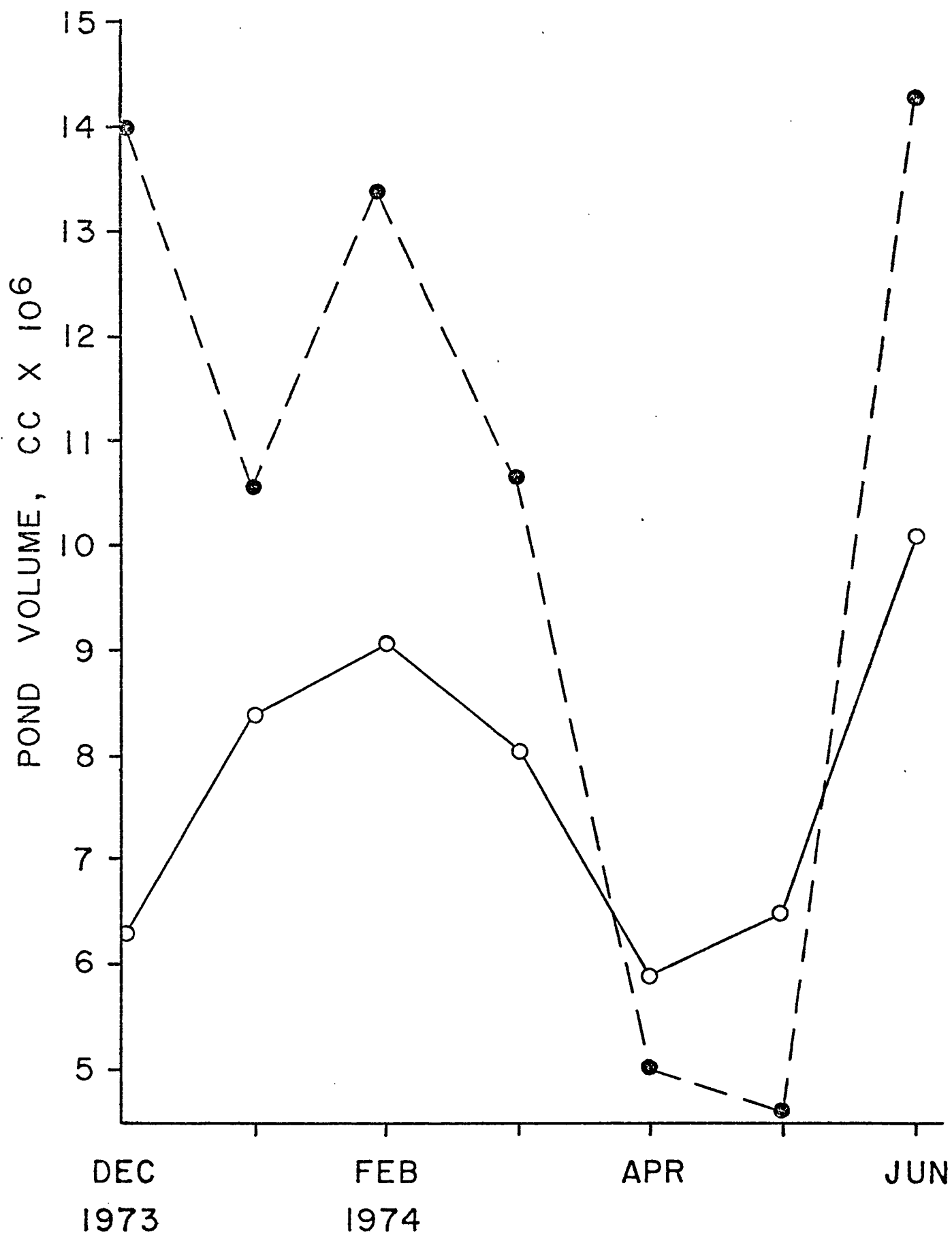
than two inches on the 31st of May, three days before the ponds were sampled. All the ponds were dry after the 15th of June, 1974.

The oxygen concentration differed significantly ($F_{2,45}$ = 155.33, p = 0.001) between the grassland and forest ponds (Table 9 and Fig. 12). The higher values in the grassland habitat could result from three factors: (1) an increased circulation and mixing in the ponds; although I did not measure the wind velocity, there was invariably a breeze over the surface of the grassland ponds while the forest was dense enough to inhibit wind movement. A constant wind blowing over the grassland can partially account for the increased oxygen concentrations. (2) Another factor could be the presence of an unidentified algae found growing upon the grass litter in the grassland ponds; no such algae was observed in the forest ponds. Oxygen concentration was measured during the early afternoon hours when the bryophytes were photosynthesizing and producing oxygen. Aquatic plants in shallow lakes and ponds can often account for a super-saturation through daytime photosynthesis (Ruttner, 1953). (3) A third factor possibly causing low values within the forest ponds could be a potentially greater organic content. Generally, net productivity is higher in forests than in grassland-shrub areas within a given climatic zone (Whittaker, 1971); this may be reflected by a higher biomass being passed to decomposers. If such is the case in the forest ponds, an increase in microbial (and other) decomposition would create an oxygen demand, lowering the oxygen concentration. The seasonal trend in both habitats reflected a general decrease in oxygen concentration because of the seasonal rise in temperature.

Insolation at the surface of the ponds (Fig. 13) differed significantly

Figure 12. The mean oxygen concentration, in parts per million,

for the combined covered and uncovered forest

ponds (closed circles) and the grassland ponds

(open circles). Oxygen data are tabled in Appendix

i.
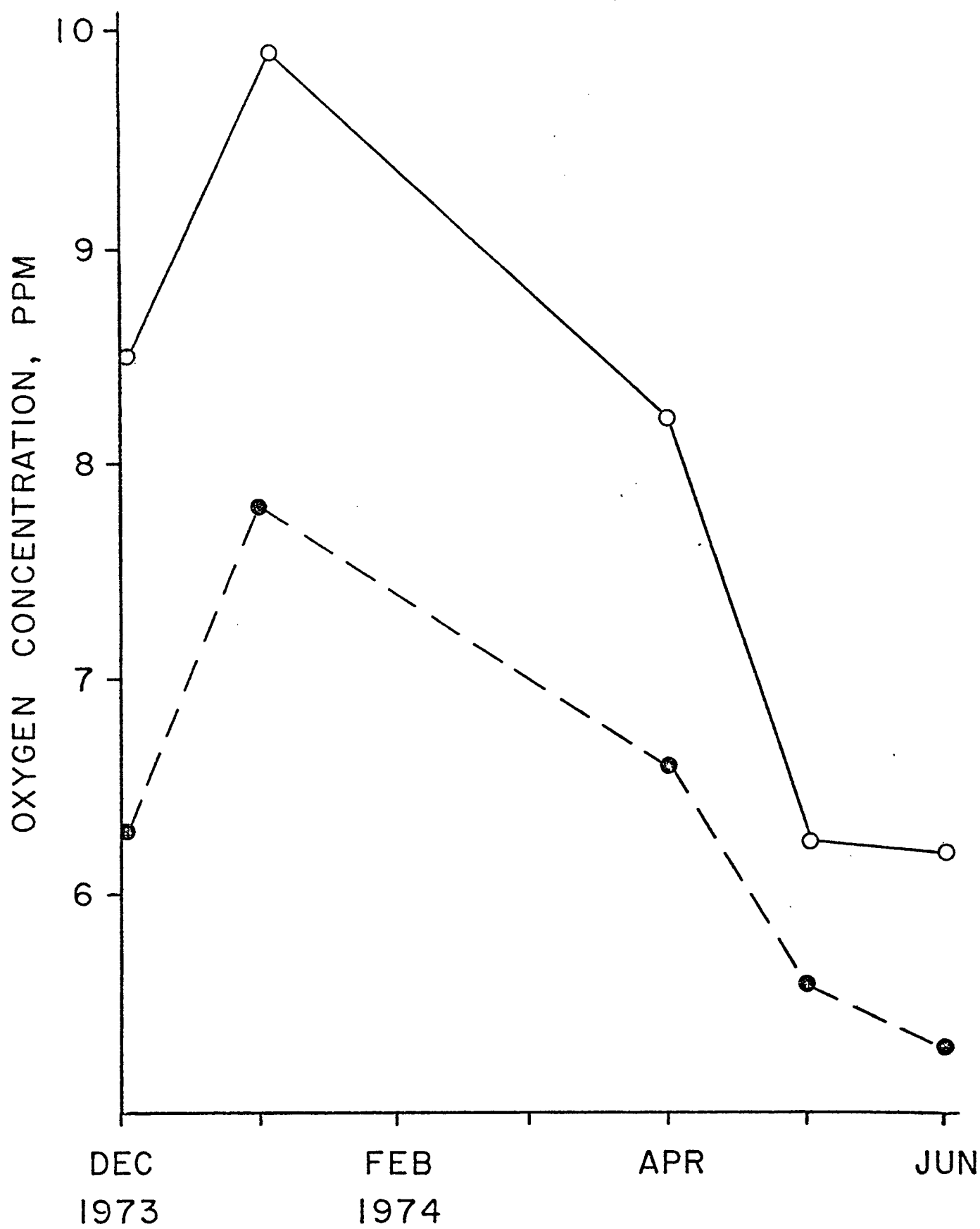
Figure 13. The mean insolation in foot-candles X 10^3 at the

surface of the ponds for the combined covered and

uncovered forest ponds (closed circles) and the

grassland ponds (open circles). Insolation data

are tabled in Appendix i.
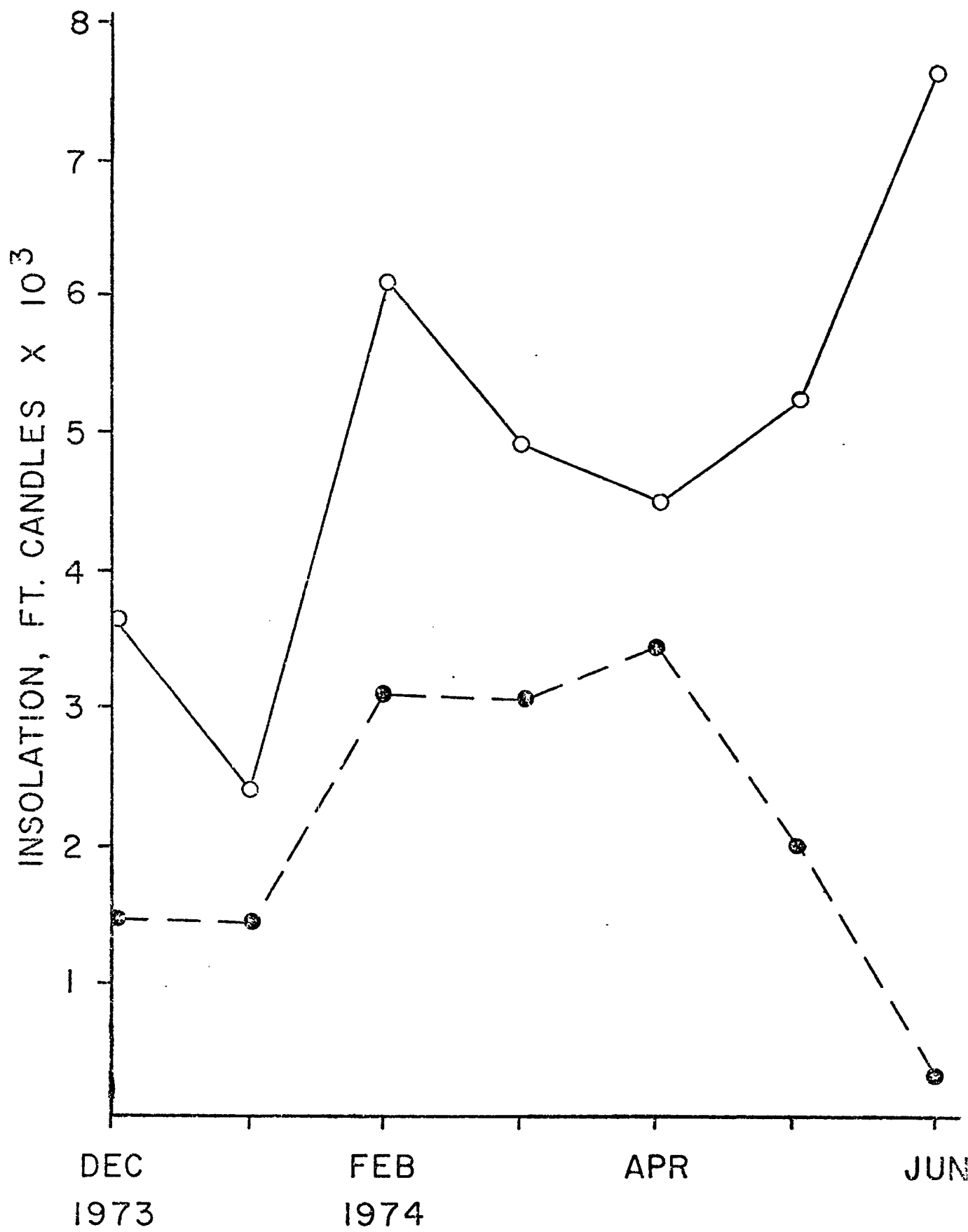
$(F_{2,147} = 10.34$, p = 0.001) between the forest and grassland ponds (Table 9). However, there is no difference between sample dates because of a large measurement error. The measurement error stems from the sensitivity of the light meter to such effects as passing clouds and moving tree branches, which increases the error mean square. It can be seen from Figure 13 that the leaves began to fully develop and form a dense canopy from the middle of March through June.

Tannin content in the hand-picked leaves of S. sebiferum varied linearly from 0.71% tannin per gram dry weight in the spring to 4.3% tannin per gram dry weight in the fall (Fig. 14). Tannin content in leaves which were shaken down from the trees in the fall was less than that in leaves picked off of the trees (dotted line, Fig. 14). This would be expected because tannins and other polyphenols may often be withdrawn from the leaf before abscission; also, there may be some leaching from the leaves before they fall from the tree. The major leaf fall in 1973 was during late October, November and through December. The heavy rains did not come until January, 1974. It is not known how much the rain contributed to the smaller tannin content in the dead leaves on the trees; however, nutrients leached by rainfall from the canopy of forests have an important role in the complete circulation of minerals and nutrients in forests (Jensen, 1974). No seeds or husks of S. sebiferum were found to contain tannin.

In an attempt to elucidate the factors which influence the diversity and the numbers of species present in the two habitats, a linear, forward-selection, stepwise regression analysis was performed on the physical data using H' and the number of species as dependent variables in separate

Figure 14. Percent tannin per gram dried S. sebiferum leaf, expressed as catechin equivalents, in leaves hand picked off of trees (solid line) and in leaves shaken off the trees (dashed line).
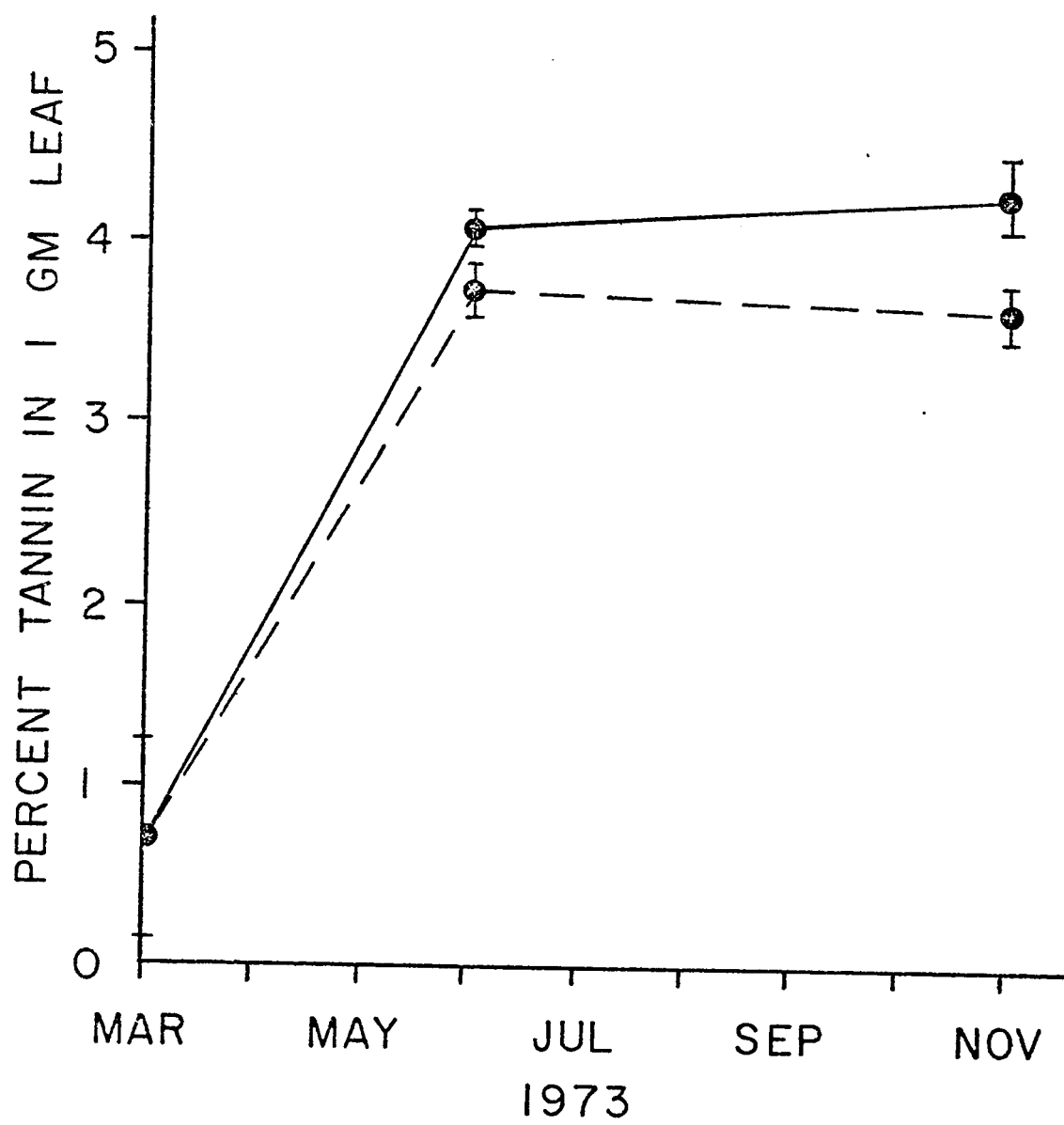
runs, with both time-lag and immediate responses (Table 10). Most of the variation of H' in the forest ponds was significantly explained by a linear combination of pond volume and rainfall. The decrease in volume and rainfall accounts for the decrease in H' in the forest ponds. The same variables utilized in a one-month time lag analysis did not account for variation in either H' or the number of species. The variation in H' for the grassland ponds cannot be explained by a linear combination of the variables in either immediate or time-lag analyses (Table 10). There may be a synergistic effect between decreasing volume, decreasing oxygen concentration and increasing temperature on diversity. Rainfall alone explains 42.3% of the variation in the number of species in the forest ponds (Table 10). Rainfall and pond volume may explain the wide variance obtained in the forest ponds; sudden rains may wash in new species most of which do not survive well and soon die. Of particular importance to my study is the fact that no variation in either the diversity or the number of species can be accounted for by an increasing tannin concentration in the leaves of the Chinese tallow tree. The fact that decreasing oxygen content and pond volume in the grassland ponds accounts for the observed increase in the number of species appears to be somewhat anomalous; this can be explained by the fact that the increase in the number of species in the grassland ponds is largely a result of transient species being caught.

C. Tallow Leachate Experiment

The field experiment initiated during the late fall, 1974, showed that there were no significant differences in the relative leachate concentration between the dates (Table 11 and Fig. 15) after I added the leachate solution to pond number 11; this indicates that the leachate added to the

Table 10. Stepwise linear regression analysis on the diversity and

number of species in ephemeral ponds on the Coastal Center.

FOREST - IMMEDIATE RESPONSE

	Variable	Reg. Coef.	Computed T	Beta Coef.
H'	Volume	.40519	5.004^{***}	.88642
R = .870	Rainfall	.03800	4.297^{**} $(0.1 \ p \ 0.05)$	.76211
	Insolation	.04981	2.011	.31767
# species	Rainfall	.00026	2.421^{*}	.57692
R = .651	Oxygen Conc.	.00578	1.241^{ns}	.25848

FOREST - LAG PERIOD

	Variable	Reg. Coef.	Computed T	Beta Coef.
H'	Volume	.21399	1.762^{ns}	.49433
R = .544	Tannin Conc.	.35011	$.955^{ns}$	.26783
# species	Rainfall	-.00026	1.965^{ns}	-.52700
R = .528				

GRASSLAND - IMMEDIATE RESPONSE

	Variable	Reg. Coef.	Computed T	Beta Coef.
H'	Temperature	-.01129	-1.358^{ns}	-.35814
R = .487	Rainfall	-.01431	-1.342^{ns}	-.35394
# species	Oxygen Conc.	-1.77935	-3.469^{**}	-.71119
R = .733	Volume	-2.73392	-0.949^{ns}	-.19448

GRASSLAND - LAG PERIOD

	Variable	Reg. Coef.	Computed T	Beta Coef.
H'	Oxygen Conc.	1.04158	1.445^{ns}	.73168
R = .501	Insolation	.06577	1.394^{ns}	.59890
# species	Temperature	.05943	3.317^{**}	.95351
R = .789	Oxygen Conc.	.00790	$.935^{ns}$	.26877

Table 11. Two-way ANOVA of relative tallow leaf leachate concentration in ponds on the Coastal Center. Winter, 1974-75.

Source	df	MS	F
Dates	5	138.6831	2.2227^{ns}
Ponds	4	145.6256	54.2347^{***}
Dates X Ponds	20	62.3941	23.2372^{***}
Error	90	2.6851	

Table 12. Two-way ANOVA on the diversity and the number of species present during the tallow leaf leachate experiment. Winter, 1974.

	Source	df	MS	F
H'	Dates	5	.0518	5.3369^{**}
	Ponds	2	.0247	2.5448^{ns}
	Dates X Ponds	10	.0166	1.7103^{ns}
	Error	18	.0097	
# species	Dates	5	2.9333	1.60^{ns}
	Ponds	2	1.0833	$.591^{ns}$
	Dates X Ponds	10	2.1167	1.15^{ns}
	Error	18	1.8333	

Figure 15. Mean relative pond tallow leachate concentration. Each point represents a mean of four samples from each pond (data are tabled in Appendix ii), read at 335 mμ. The ponds are as follows:

△ = #11 (leaf leachate added) ⎫
○ = #12 (well water added)   ⎬ Grassland ponds
✕ = #13 (nothing added)   ⎭

◉ = # 3 ⎫
▣ = # 8 ⎬ Forest ponds
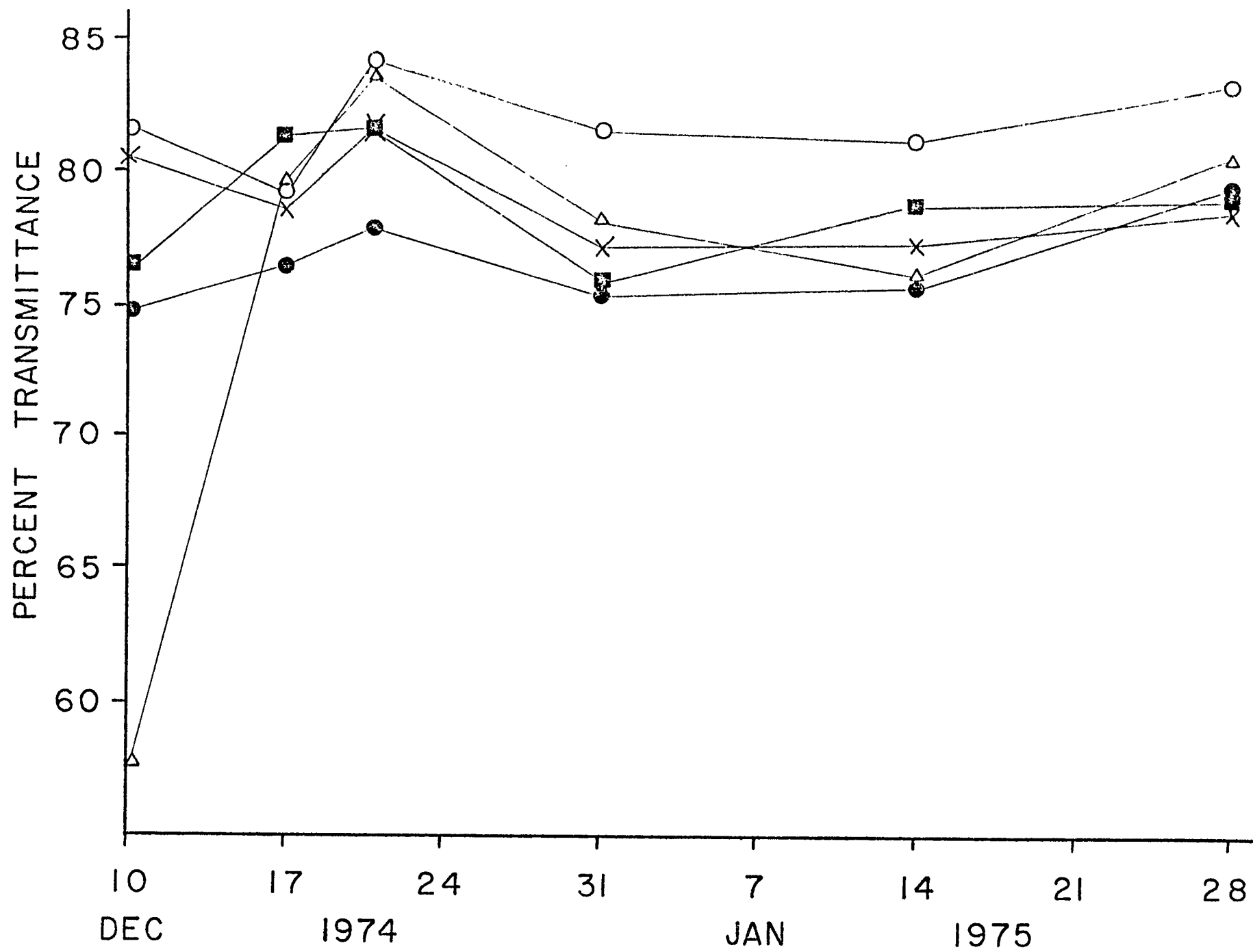
experimental pond did not remain for any length of time. Heavy rains, on the 11th and 13th of December, flooded the ponds and reduced the leach-ate concentration. There were significant ($F_{4,90}$ = 54.24, p = 0.001) differences between habitats in relative leachate concentration (Table 11); an SNK test indicated that the forest ponds numbers 3 and 8 contained significantly higher amounts of leachate than any of the grassland ponds. Ponds 11 and 12 (to which tallow leaf leachate and well water had been added, respectively) were intermediate in concentration and pond number 13 (to which nothing had been added) had the lowest leachate concentration. The slight, but measurable, relative leachate concentrations of the grass-land ponds may stem from the sparse stands of S. sebiferum which invariably border the ditches or they may stem from tannins in certain grasses which may exist on the Coastal Center.

Species diversity was not significantly different between ponds; but did differ ($F_{5,18}$ = 5.34, p = 0.01) between dates (Table 12 and Fig. 16). Diversities were higher on November 30, January 14 and January 28; December 17, 21 and 31 show lower diversities. There were no significant differences between the number of species occurring over the dates or between the ponds (Table 12 and Fig. 17). Comparisons of the numbers of Asellus, Crangonyx and Procambarus individuals show that there were no significant differences between dates in the numbers of these three species (Table 13). There are significant ($F_{2,18}$ = 8.47, p = 0.01) differences between ponds 12 (fewest), 11 (intermediate) and 13 (most individuals) for Asellus indivi-duals (Fig. 18). Crangonyx numbers differed significantly ($F_{2,18}$ = 41.56, p = 0.001) between ponds, with fewest in pond 12, and greater numbers in ponds 13 and 11 (Table 13 and Fig. 19). The differences seen in these

Figure 16. Mean species diversity (H') for grassland ephemeral
        ponds on the Coastal Center, winter, 1974-75.
        Each point is a mean of two replicate samples
        from each pond (data are tabled in Appendix ii).
        The ponds are as follows:

        ● = #11
        ○ = #12
        □ = #13
        ✕ = # 3
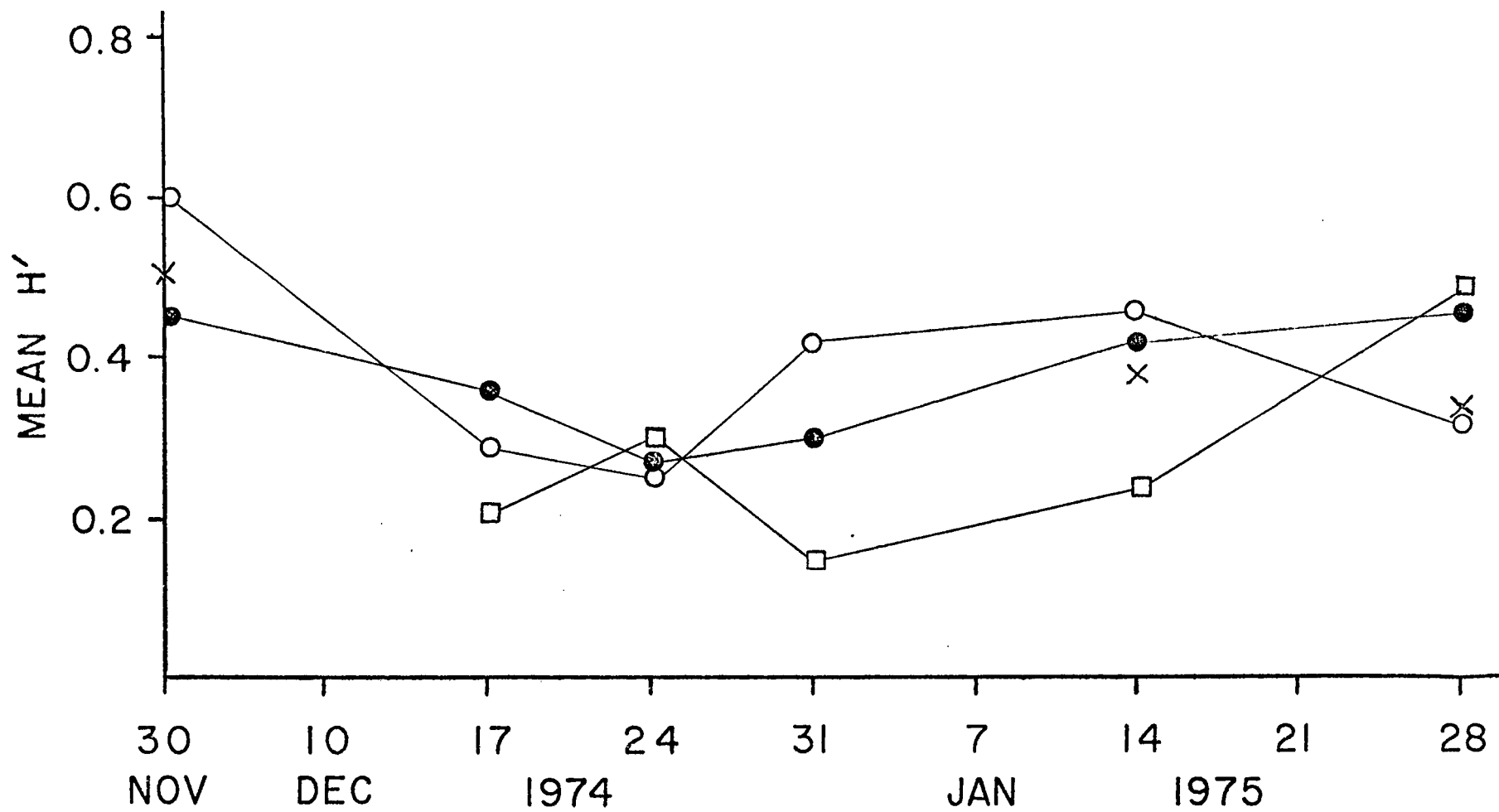
Figure 17. The mean number of species captured for grassland

ephemeral ponds on the Coastal Center, winter, 1974-75.

Each point is a mean of two replicate samples

from each pond (data are tabled in Appendix ii).

The ponds are as follows:

● = #11
○ = #12
□ = #13
✕ = # 3

68
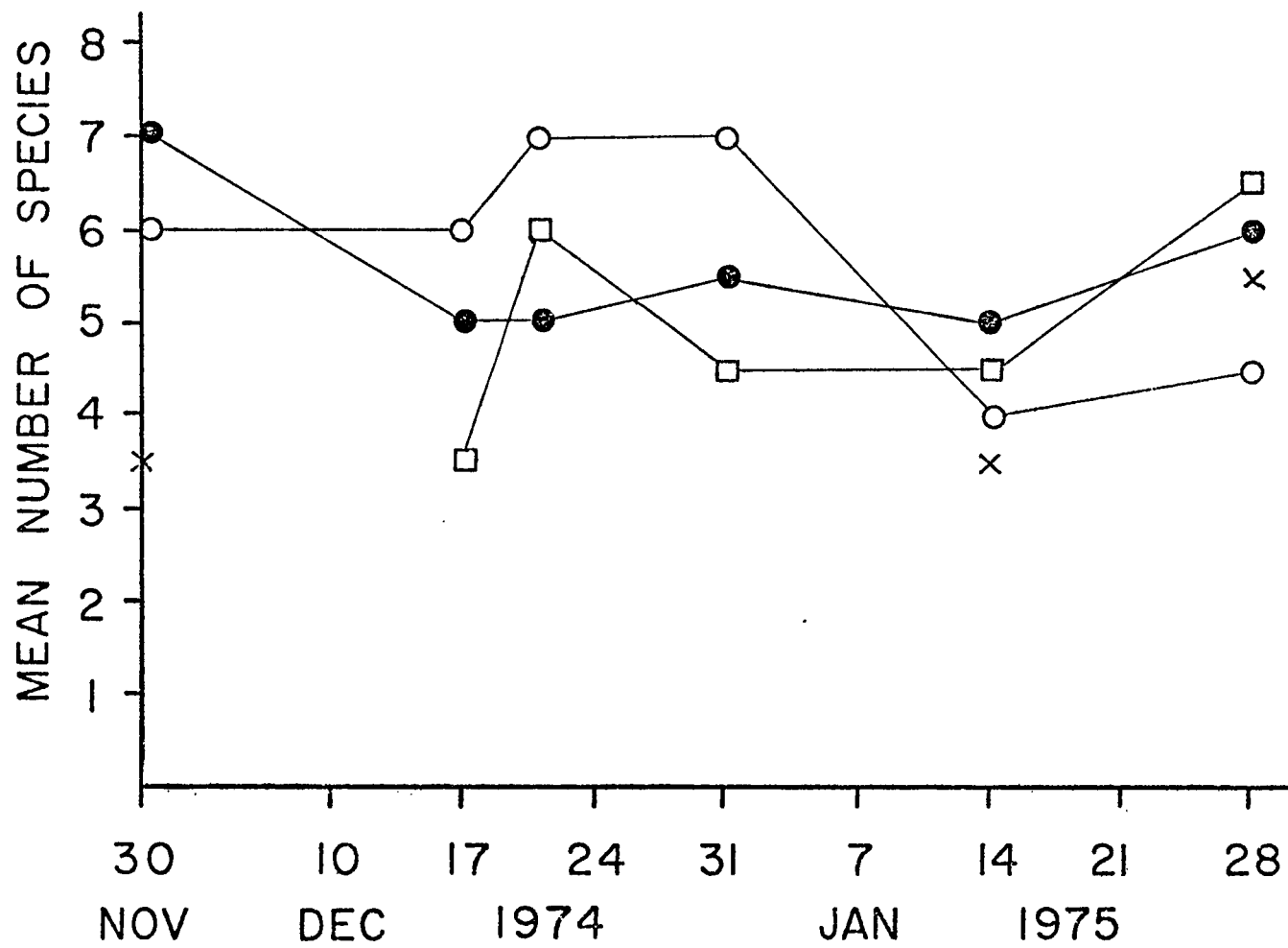
Table 13. Two-way ANOVA between the numbers of individuals of Asellus
and Crangonyx in grassland ponds during the tallow leaf leachate
experiment.

	Source	df	MS	F
Asellus	Dates	5	7844.7110	2.4131^{ns}
	Ponds	2	27525.7776	8.4670^{**}
	Dates X Ponds	10	2805.8111	$.8631^{ns}$
	Error	18	3250.9444	
Crangonyx	Dates	5	142.7167	2.5909^{ns}
	Ponds	2	2289.0833	41.5567^{***}
	Dates X Ponds	10	133.5500	2.4245^{ns}
	Error	18	55.0833	

Figure 18. The mean number of <u>Asellus</u> <u>militaris</u> individuals

captured per sample in grassland ephemeral ponds,

winter, 1974-75. Each point is a mean of two

samples per pond. The ponds are as follows:

    ● = #11

    ○ = #12

    □ = #13
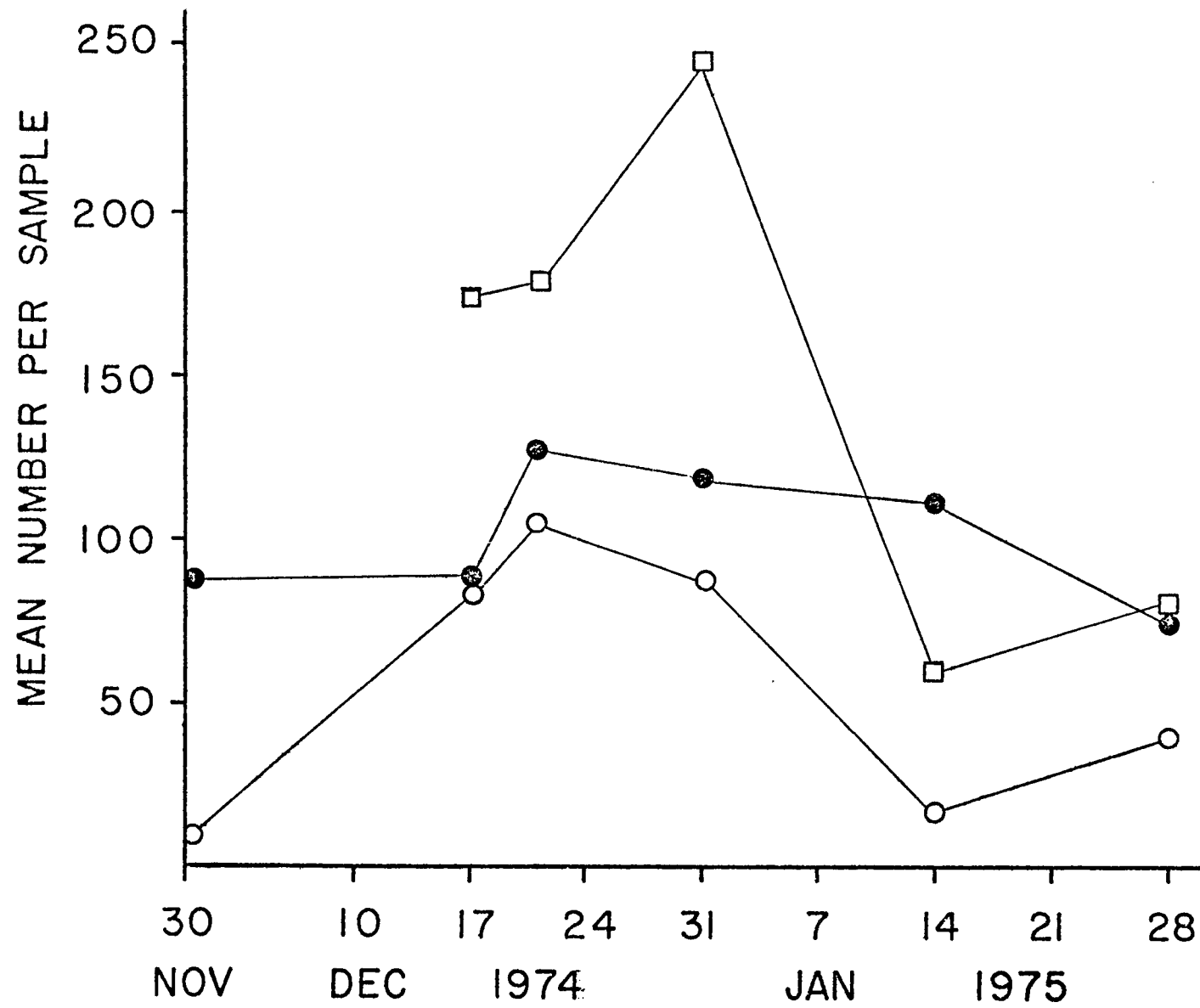
Figure 19. The mean number of *Crangonyx shoemackerii* individuals

captured per sample in grassland ephemeral ponds,

winter, 1974-75. Each point is a mean of two

samples per pond. The ponds are as follows:

    ● = #11

    ○ = #12

    □ = #13
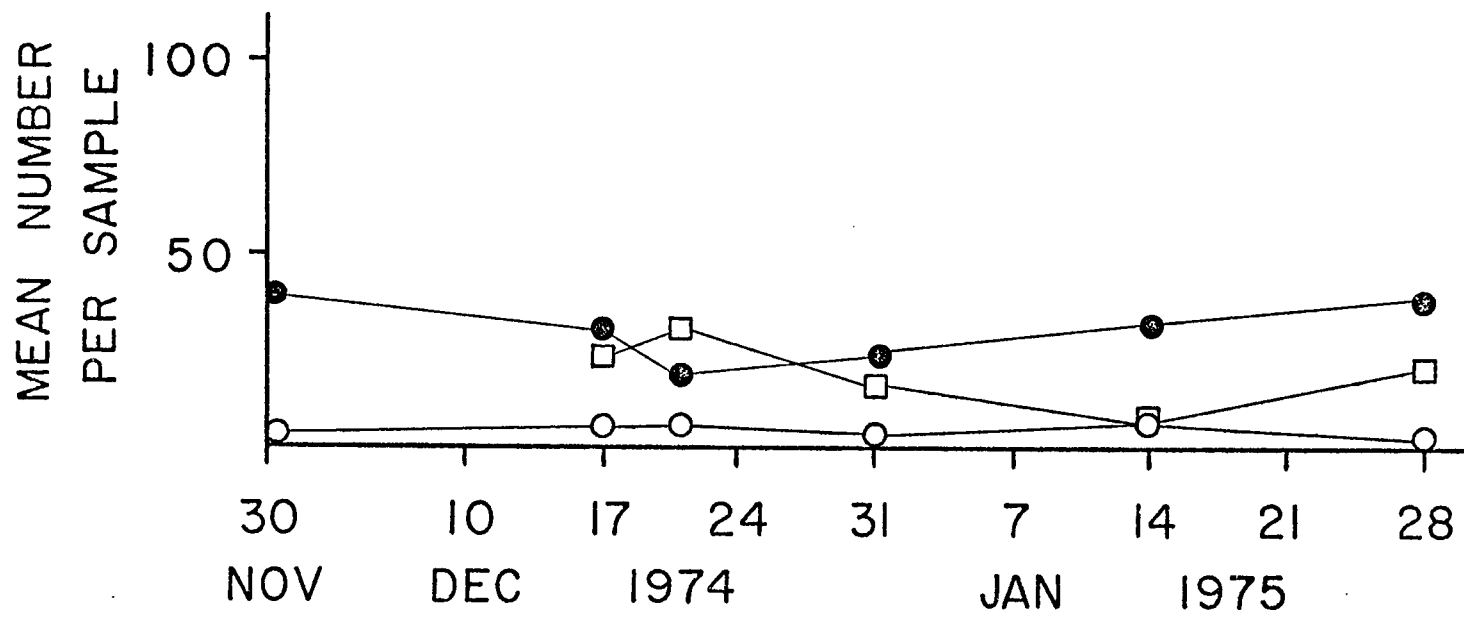
comparisons are not due to the experimental perturbation; rather, they are measures of the variation found in numbers of individuals within the grassland ponds. There were no significant differences between ponds or dates of the numbers of Procambarus individuals (Friedman's two-way analysis of variance; $X^2_{r,\ k=3,\ N=7} = 4.786$, Fig. 20).

A stepwise linear regression was run using pond volume, water temperature, rainfall and leachate concentration to account for the variance observed in species diversity, species number and the number of individuals of Asellus, Crangonyx and Procambarus. The analysis (Table 14) shows 35.2% of the variation in H' is explained by a linear combination of leachate concentration and temperature ($T_{14} = 2.08$, $0.1 > p > 0.05$). The variation in the number of species is explained ($T_{14} = 2.603$, $p = 0.05$) by leachate concentration and volume (Table 14). The variation in the number of individuals of Asellus is explained by tannin concentration and rainfall ($T_{14} = 3.97$, $p = 0.01$; Table 15). In a similar manner, the variation in numbers of Procambarus is explained ($T_{14} = 2.45$, $p = 0.05$) by leachate concentration and pond volume (Table 15). Variation in the numbers of Crangonyx individuals could not be accounted for by the variables measured.

The leachate addition experiment did not work as expected because excessive rainfall, one day after the tallow leaf leachate was added, diluted the ponds' concentration before there was any chance for changes to occur in the biota due to tannin input. The positive association of leachate concentration and the number of species may not be meaningful, for all the grassland ponds (as shown above) did contain a significantly smaller leachate concentration than any of the forest ponds. The stepwise

Figure 20. The mean number of _Procambarus simulans_ individuals

captured per sample in grassland ephemeral ponds,

winter, 1974-75. Each point is a mean of two

samples per pond. The ponds are as follows:

    ● = #11
    ○ = #12
    □ = #13
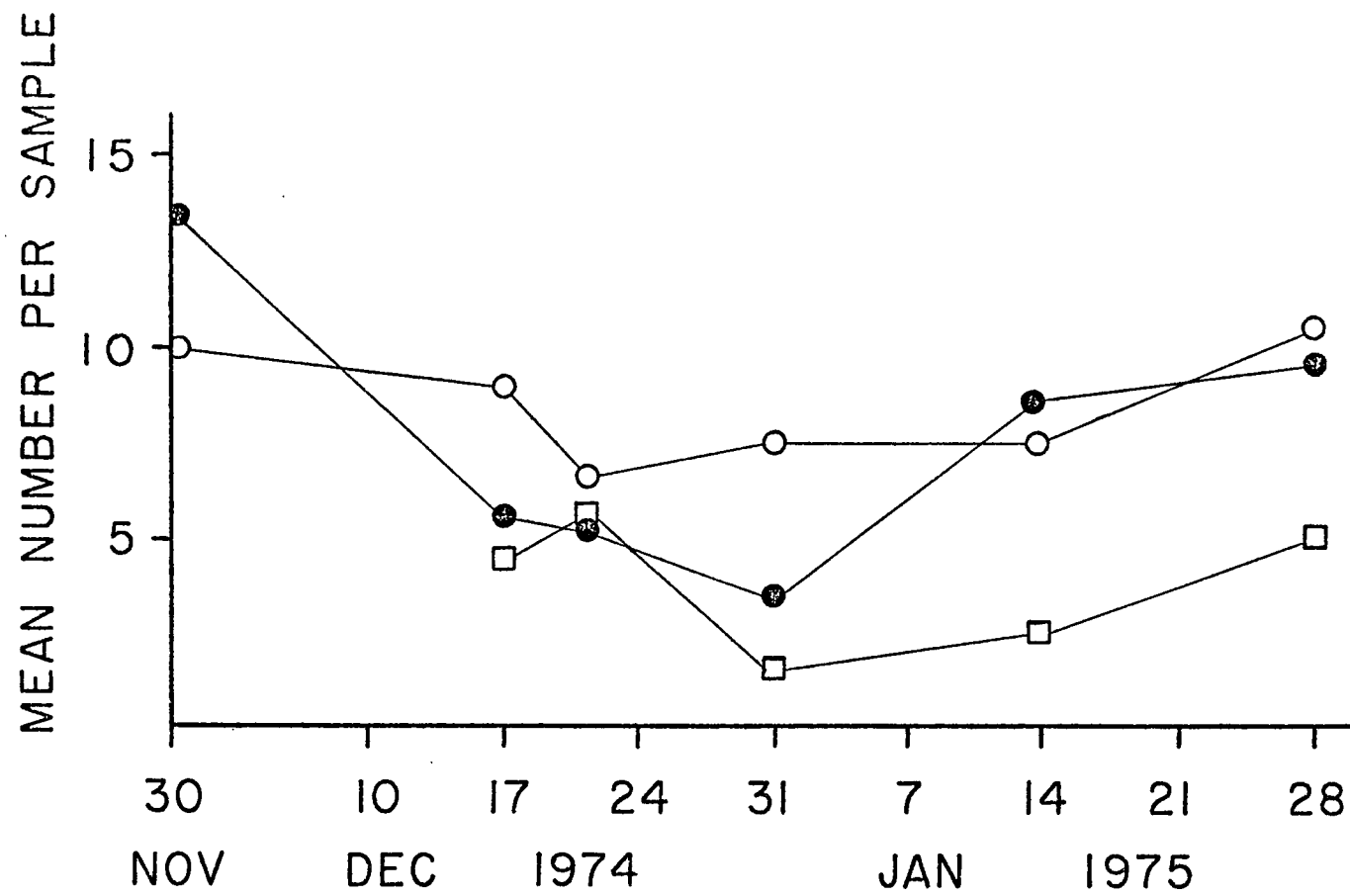
Table 14. Stepwise linear regression analyses on the diversity and number of species in the grassland ponds during the tallow leaf leachate addition experiment.

DIVERSITY

R = .593

Variable	Reg. Coef.	Computed T	Beta Coef.
Tannin Conc.	.00811	$2.077^{(0.1 \quad p \quad 0.05)}$	.45986
Temperature	.02266	1.270^{ns}	.28134

SPECIES

R = .577

Tannin Conc.	.10858	2.603^{*}	.73481
Volume	.18340	1.289^{ns}	.36399

Table 15. Stepwise linear regression analyses on the number of individuals of Asellus and Procambarus species.

ASELLUS

R = .728

Variable	Reg. Coef.	Computed T	Beta Coef.
Tannin Conc.	-6.56467	-3.970**	-.81702
Rainfall	-271.77279	-1.736^{ns}	-.35738

PROCAMBARUS

R = .753

Variable	Reg. Coef.	Computed T	Beta Coef.
Tannin Conc.	.23850	2.448*	.55693
Volume	-.38625	-1.163^{ns}	-.26452

regressions show the importance of volume in determining the diversities and the numbers of species, as well as the number of individuals within species.

D. Chinese Tallow Litter Decomposition Study

The Chinese tallow leaf litter in both the small pore and the large pore bags decayed at the same rate (Table 16); there was a significant ($F_{5,12}$ = 14.76; p = 0.001) increase in the weight lost over the eight week period (Table 16 and Fig. 21). The lack of a significant difference between the large and small pore bags indicates decomposition is occurring largely by fungi and bacteria and leaching of the water soluable components. The presence of reducer organisms (particularly shredders) would have increased the weight loss in the large pore bags. At the end of the eight week period, over 50% of the original dry weight leaf remained (Fig. 21). Litter in the forest ponds will remain for a longer time without many reducer organisms. The weight lost in the small pore bags was consistently (but non-significantly)greater than in the large pore bags. This is the result of more mud, silt and debris settling into the leaf pack of the large pore bags and artificially increasing the weight. Hence, the weight difference is due to experimental error.

The tannin in the litter of both the small and large pore bags leached out rapidly within the first week; there was no difference between the pore sizes and a highly significant ($F_{6,70}$ = 467.06; p > 0.001) difference between the dates (Table 17). Following the initial loss, there was a slow increase in the tannin content (Fig. 22). A portion of this initial loss was attributed to heavy rains that fell on December 11 and 13, just after the initiation of the experiment; however, laboratory tests and

Table 16. Two-way ANOVA of weight loss from litter bags of two different pore sizes over an eight week period of immersion in pond water.

Source	df	MS	F
Weeks	5	316.0968	14.757***
Pore Size	1	.0759	.0036^{ns}
Weeks X Pore Size	5	28.4674	1.3290^{ns}
Error	12	21.4194	

Figure 21. Percent initial dry weight remaining of S. sebiferum

leaves in large pore (closed circles) and small pore

(open circles) litter bags after immersion in the

forest pond. Each point is a mean of two replicate

bags of each pore size (data is tabled in Appendix iii).
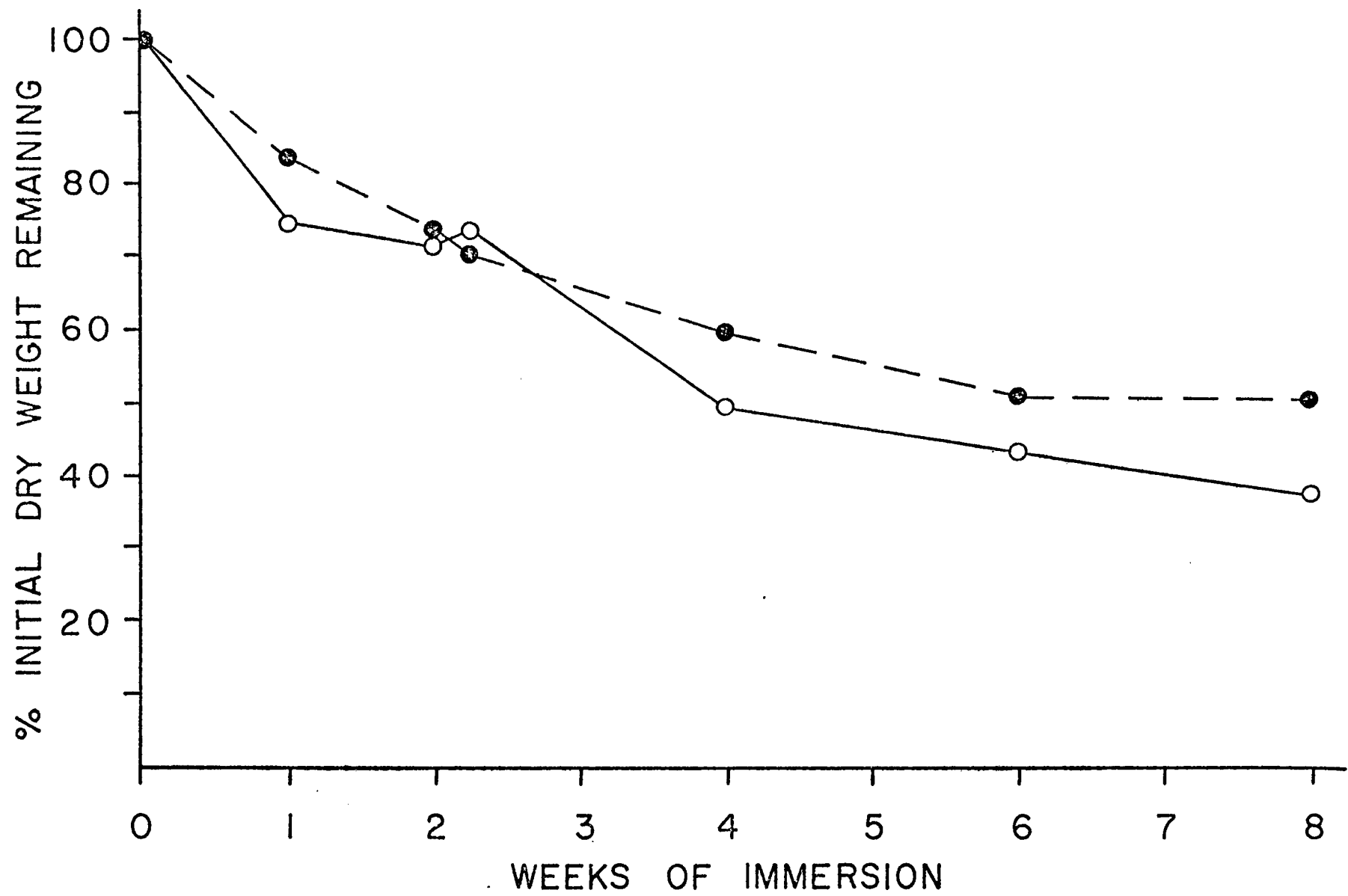
Table 17. Two-way ANOVA of tannin concentration (arcsine transformation of percent transmittance at 500 mμ) between pore sizes over weeks.

Source	df	MS	F
Weeks	6	1034.1130	467.0622***
Pore Size	1	4.0612	1.8343[ns]
Weeks X Pore Size	6	21.7399	9.8189***
Error	70	2.2141	

Figure 22. Mean percent transmittance at 500 mμ for leaves in
large pore (closed circles) and small pore (open
circles) litter bags immersed in a forest pond for
eight weeks. Each point is a mean of six readings
(data are tabled in Appendix iii).
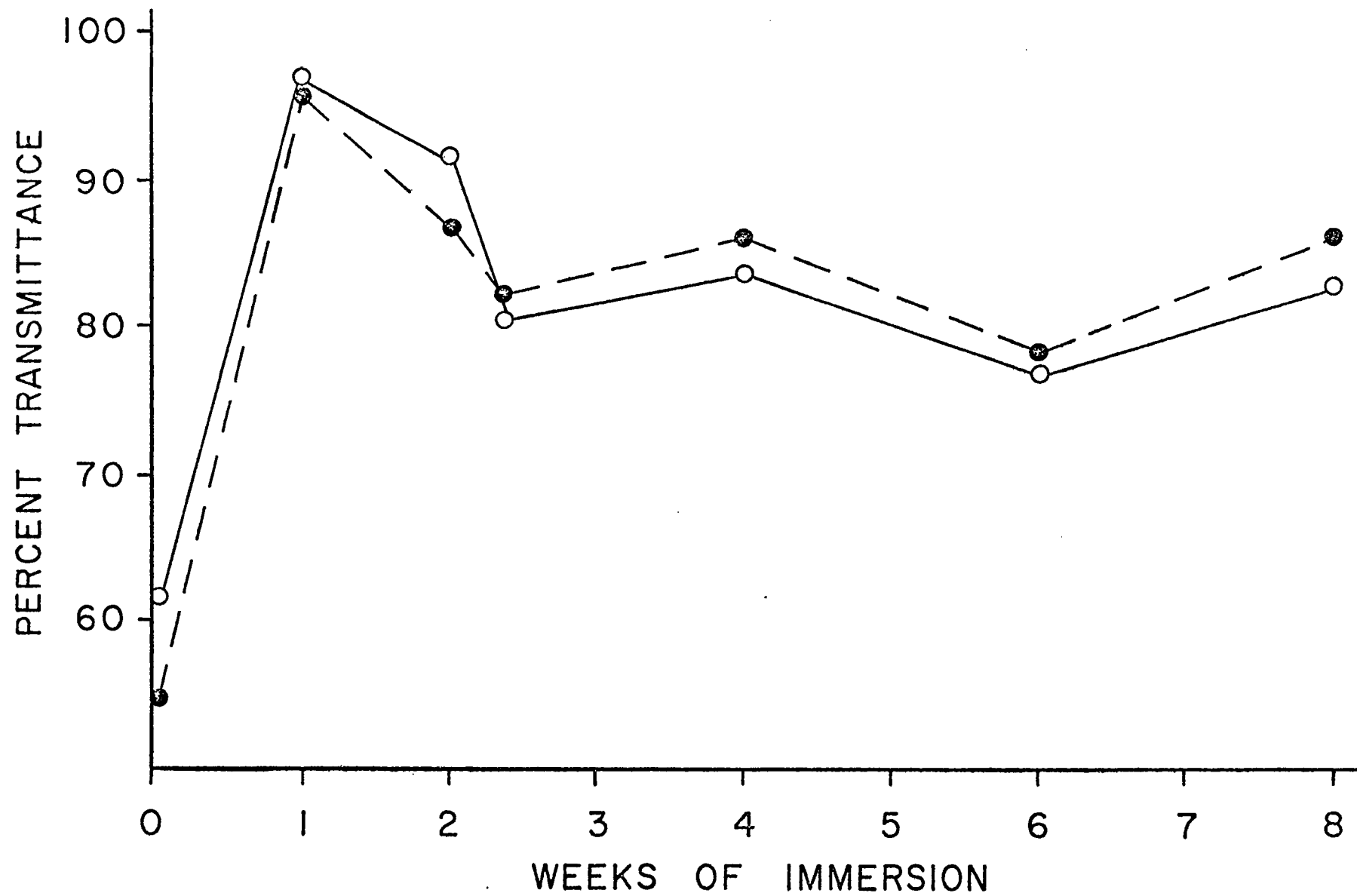
other litter bag studies show that most of the water soluable components will be lost within one week after immersion in water. Subsequent to the initial loss, there may have been an increase in the quantity of polyphenols leached into the ponds from the soil and newly fallen leaves which might "tan" the plant cellulose, an effect noted in forest litter by Bloomfield (1957, cited by Coulson, et al., 1960). Williams and Gray (1974) state that the accumulation of condensed or polymerized polyphenols with very slow decomposition rates in litter is an important phenomenon. The polyphenolic compounds may originate from the litter itself (via adsorption) or be synthesized by microbes. These factors may account for the increase in tannin concentration through the first seven week period after the initial leaching. The loss of tannin in the latter part of January could be due to the heavy rainfall occurring on the 15th and 19th, when there was 3.08 and 3.28 inches of rain, respectively.

B. Laboratory Experiments

In the laboratory, the tallow leaf leachate experiment (Figs. 23 and 24) showed that fewer individuals of both Asellus and Crangonyx survived at higher concentrations of leachate; however, the leachate concentration in the laboratory bottles was at least three to five times that found in the forest ponds. The animals in this part of the experiment were not fed; the rate at which the organisms died did not differ between the control and the experimental bottles (Table 18). This indicates that the organisms were starving at an equivalent rate and that the tallow leachate had no direct toxic effect upon the organisms.

The second experiment showed that tannins in solution will inhibit the ability of Asellus and Crangonyx individuals to feed on grass litter.

Figure 23. The mean number of <u>Crangonyx</u> <u>shoemackerii</u> remaining

in four solutions of <u>S.</u> <u>sebiferum</u> leaf leachate.

Each point is the mean of four bottles, each of

which initially contained 10 adults. The concen-

trations are as follows:

   O = 0% (= Control)

   ◕ = 16%

   ▲ = 33%

   ▤ = 50%

16% ; Y=.934-.116X

50% ;
Y=.642-.122X

33% ;
Y=.617-.118X

CONTROL ; Y=.833-.084X

Figure 24. The mean number of <u>Asellus militaris</u> remaining in

four concentrations of <u>S</u>. <u>sebiferum</u> leaf leachate.

Each point is the mean of four bottles, each of

which initially contained 10 adults. The concen-

trations are as follows:

    O = 0% (= Control)

    ◐ = 16%

    ▲ = 33%

    ■ = 50%

LOG NUMBER ISOPODS REMAINING

33%;
Y=.882-.108X

CONTROL; Y=1.082-.111X

16%;
Y=.667-.091X

50%;
Y=.870
-.148X

DAYS

Table 18. Comparison of linear regression equations for survival of

organisms in four Chinese tallow leaf leachate concentrations.

ASELLUS

Source	Error df	Reg. Coef.	Dev. from Regression df	MS
0%	24	-.11120	6	.0295
16%	24	-.09073	6	.1641
33%	24	-.10874	6	.0431
50%	24	-.14823	6	.0884

Linear comparison of regression coefficients

Source	df	MS	F
Among b's	3	.0978	1.2032^{ns}
Weighted avg. of deviations	24	.0813	

CRANGONYX

Source	Error df	Reg. Coef.	Dev. from Regression df	MS
0%	24	-.08363	6	.0639
16%	24	-.11647	6	.0998
33%	24	-.11850	6	.2619
50%	24	-.12197	6	.2343

Linear comparison of regression coefficients

Source	df	MS	F
Among b's	3	.0534	$.3234^{ns}$
Weighted ave. of deviations	24	.1650	

The tannin concentrations significantly ($F_{3,24}$ = 10.35, p = 0.001 for

Asellus; $F_{3,24}$ = 2.95, p = 0.05 for _Crangonyx_) inhibited survival (Table

19 and Figs. 25 and 26). The control organisms survived well whereas

feeding was significantly inhibited in the experimental bottles and these

organisms exhibited the same type of survival curve seen in the previous

experimental situation. There appears to be a lack of any direct toxicity

on the part of the Chinese tallow tree leaf leachate; however, leached

tannins can inhibit reducer feeding and may limit the actual food available

for these animals in the forest ponds.

Table 19. Comparison of linear regression equations for survival of organisms in four tannin solutions.

ASELLUS

Source	Error df	Reg. Coef.	Dev. from Regression df	Dev. from Regression MS
0%	24	-.02255	6	.0029
3%	24	-.06900	6	.0239
6%	24	-.10026	6	.0474
10%	24	-.14057	6	.0873

Linear comparison of regression coefficients

Source	df	MS	F
Among b's	3	.41789	10.352***
Weighted avg. of deviations	24	.04037	

CRANGONYX

Source	Error df	Reg. Coef.	Dev. from Regression df	Dev. from Regression MS
0%	24	-.02219	6	.0011
3%	24	-.12421	6	.1473
6%	24	-.09577	6	.2682
10%	24	-.12552	6	.1184

Linear comparison of regression coefficients

Source	df	MS	F
Among b's	3	.39473	2.952*
Weighted avg. of deviations	24	.13374	

Figure 25. The mean number of <u>Asellus militaris</u> remaining
in four concentrations of tannin (d-catechin).
Each point is the mean of four bottles, each of
which initially contained 10 adults. The concen-
trations are as follows:

O = 0% (Control)

◉ = 3%

▲ = 6%

◼ = 10%

CONTROL; $Y = 1.045 - .023X$

$3\%; Y = .931 - .069X$

$6\%; Y = .846 - .100X$

$10\%;$ $Y = .329 - .141X$

Figure 26. The mean number of Crangonyx shoemackerii remaining

in four concentrations of tannin (d-catechin).

Each point is the mean of four bottles, each

of which initially contained 10 adults. The

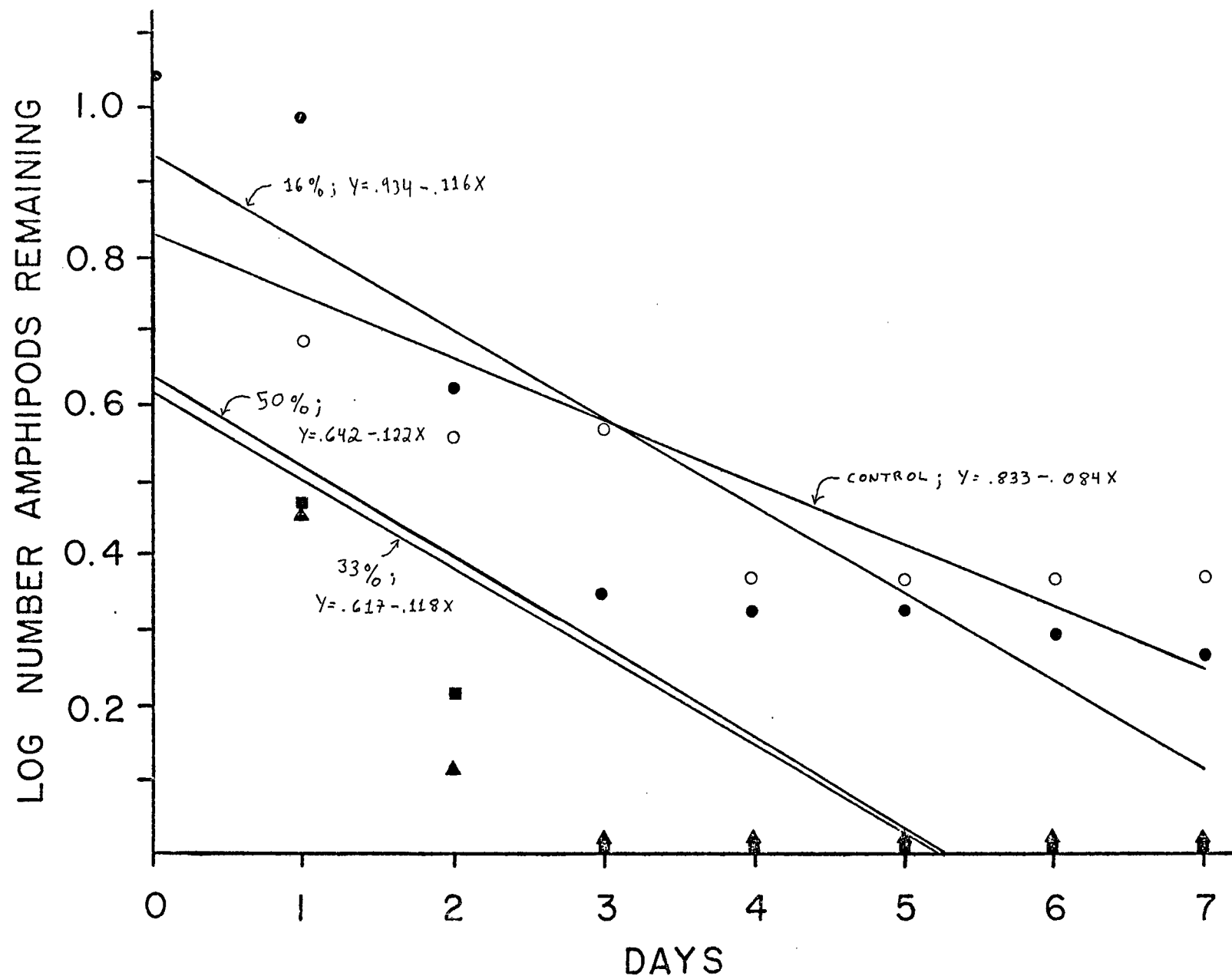concentrations are as follows:

○ = 0% (Control)

● = 3%

▲ = 6%

■ = 10%
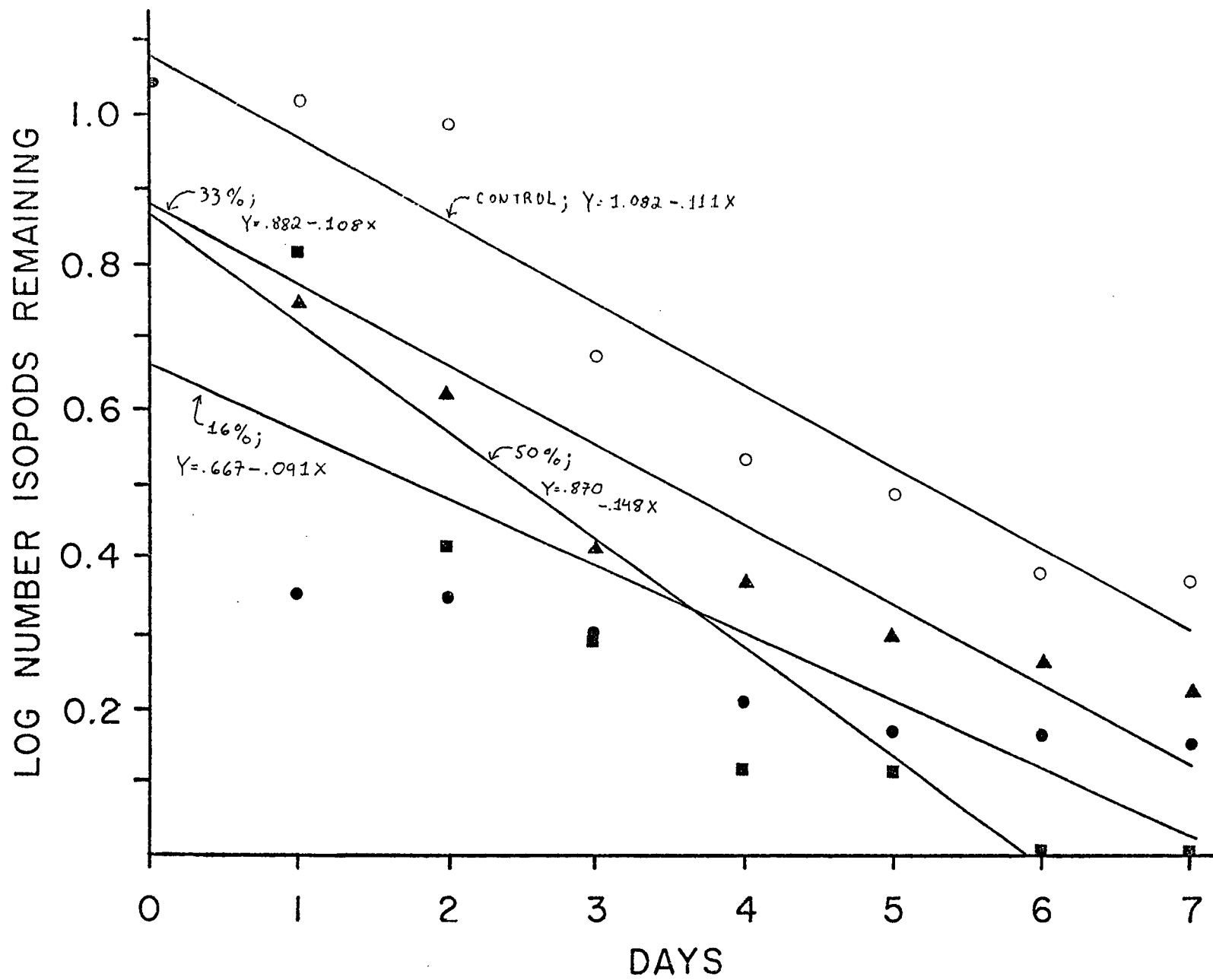
CONTROL; Y= 1.034 - .022X

3%; Y = .704 - .124X

10%; Y = .751 - .126X

6%; Y = .567 - .096X
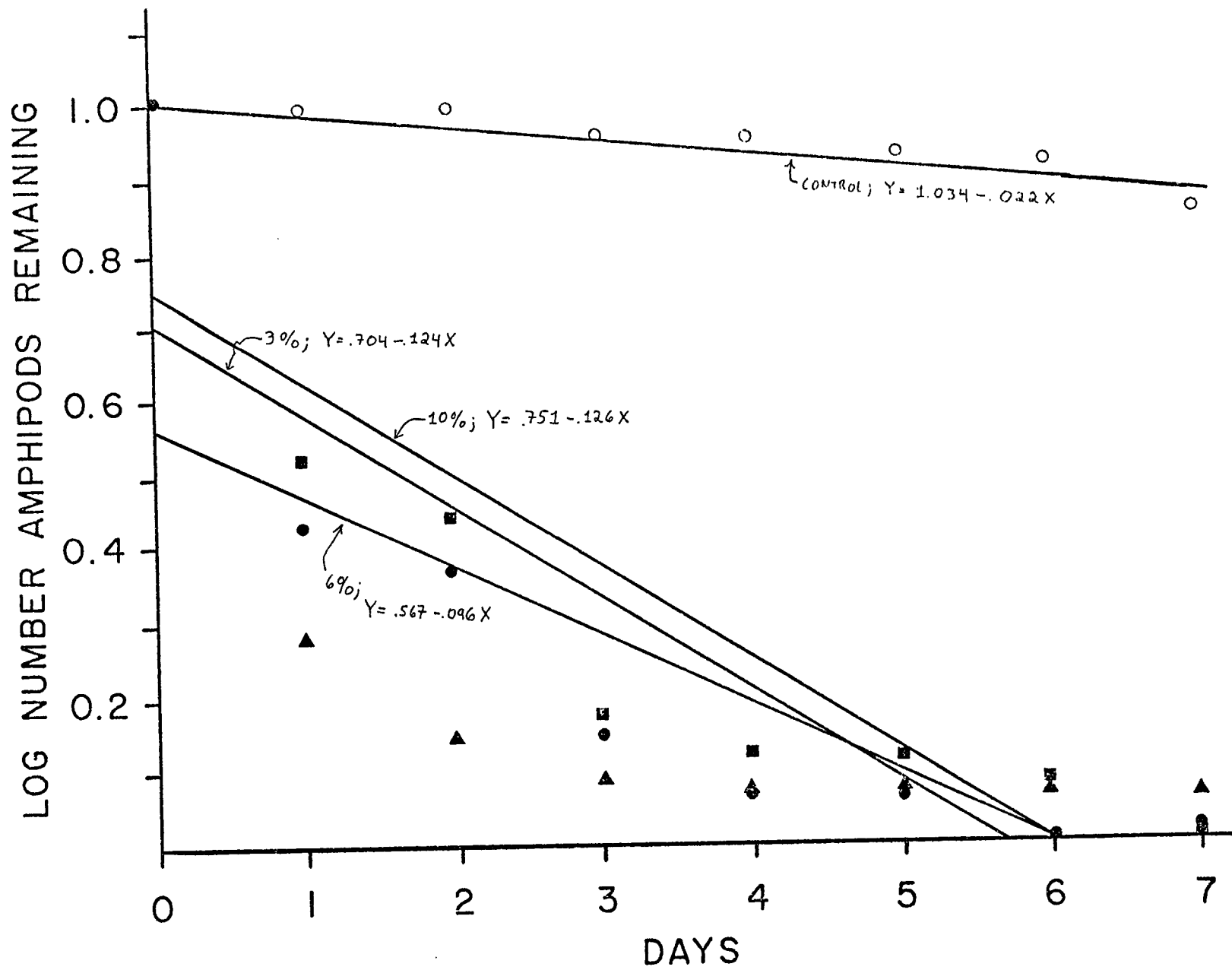
DISCUSSION

Forest detritus, composed largely of leaves, but also including branches, seeds, bark and flowers, is a major source of nutrients and energy for aquatic as well as terrestrial ecosystems. The surrounding terrestrial flora may strongly influence the diversity and productivity of streams and ponds which exist in the same watershed (Ross, 1963; Vannote, 1970). In the forest ponds affected by the Chinese tallow tree on the Coastal Center, the lack of shredder organisms which feed upon large particle litter could be due to an evolutionary response to feeding upon non-tannin containing detritus.

The ponds on the Coastal Center are usually water-filled by the time the leaves begin to fall off the trees in late October and November. The variation in the number and diversity of species in the ponds were by and large the result of pond volume and/or rainfall. This may explain the pulses of diversity and species' numbers in the forest ponds. The rains dilute the leachate concentration in the ponds and simultaneously, if a flooding rain occurs, allow invasion by species from the grassland habitat. Less intense subsequent rains may leach tannins into the ponds from the surrounding soil and from those leaves yet remaining on the trees, slowing the rate at which reducers are able to utilize the allochthonous debris, and hence, their populations decrease. The importance of pond volume (and ultimately precipitation) in determining the numbers of species existing in the ephemeral ponds was evidenced in both the forest and grassland habitats. These effects may overshadow the effects of tannins in solution in the forest ponds. It can be seen that the sizes of the populations in ephemeral ponds on the Coastal Center are the direct result of

physical factors.

There are five methods by which the biota in ephemeral ponds arise: (1) airborne and terrestrial vectors, such as being carried in by birds, racoons, etc., or active overland migration from nearby populations; (2) the entry of individuals into the ponds once they are connected to the large, permanently filled ditch surrounding the Coastal Center; (3) excystment from the sediments once proper conditions arise in the ponds; (4) hatching from eggs buried within the sediments; and (5) by burrowing upwards from the deeper sediments into which they retreat to escape dessication during the ponds' dry periods. Gambusia, Palaeomonetes, Asellus and Crangonyx probably enter the ephemeral ponds from the permanently filled ditch surrounding the Coastal Center. Nematodes, Oligochaeta, Acari and the Tendipedidae probably survive dry periods by burrowing into the substratum; the Culicidae which develop in the ponds may stem from adults which develop from eggs hatching in the few permanent ponds and a small stream near the Coastal Center. Many of the rare species caught in the ponds were transients; these species may be adapted for an aquatic existence but are not able to adapt to the conditions of low pond volume, low oxygen levels and high temperature.

The major Chinese tallow tree leaf fall occurs on the Coastal Center during the months of November, December and January. Several authors report that rates of leaf decomposition, whether on soil or in water, begin rather slowly and increase with age. This rate is determined by temperature and chemical parameters such as pH, calcium, nitrogen, total-ash, lignin and tannins in the soil and in the leaves themselves (Coldwell and DeLong, 1950). Edwards and Heath (1963) used oak leaf discs to show that

the physical condition of the leaves is important in determining the rate and type of breakdown. They observed that some oak discs turned brown, became tanned and remained intact, whereas others that were (or became) yellow were broken up much faster. According to Handley (1961), the polyphenolic material in the leaves which precipitates protein complexes and masks cellulose, making them less digestible, is responsible for the decreased rate of leaf breakup. Other workers have related tannin complexes within the litter to the inhibition of microbial decomposition (Davies, et al., 1964; Benoit and Starkey, 1968a,b; Davies, 1971). Larger animals are also very important in the breakdown of leaf litter (Bocock and Gilbert, 1960; Edwards and Heath, 1963). Reducer organisms which include shredding insects, such as caddis larvae, some Tendipedidae and Chrysomelidae, maintained a large role in the energy and nutrient transfer from terrestrial to aquatic systems (Anderson and Grafius, 1974). Crustaceans (Asellidae, Gammaridae, Astacidae) have been shown to be important in this role also (Minshall, 1967). In addition to converting primary production to animal tissue that will be eaten by aquatic (or terrestrial) predators, shredders also increase the rate of degradation of the allochthonous material. This will increase the microflora which in turn can be food for "scrapers" such as certain Gastropoda and for benthic zooplankton.

Kaushik and Hynes (1971) observed that Gammarus sp. feed preferentially on leaves of elm, maple and alder (non-tannin containing) over leaves of oak and beech which do have tannins. From their study, a general picture of leaf degradation comes to light. A decaying leaf loses weight and total caloric value, but the protein content rises steeply to an asymptotic level where it remains for many weeks. Due to the fungal and bacterial growth,

no nitrogen is lost from the leaves so reducer organisms would obtain no more calories from an old than a fresh leaf, but the older leaf has a higher protein content and so constitutes a better meal. In the autumn, winter and spring, the main growing period for many stream animals, a steady supply of protein-rich food is available. The oak leaves are kept in reserve, as it were, for later months after the more easily decayed leaves are fed upon. In this study, Chinese tallow tree leaves in the forest ponds were slow to decay, with over 50% of their original dry weight left after two months. The unbroken appearance of the leaves in the large pore bags indicated that no shredders had utilized these leaves for food, despite the length of time the leaves were immersed.

Cummins (1973) reported that many aquatic reducers may actually feed upon bacteria and fungi growing on the allochthonous debris rather than the cellulose and protein of the plant. In this respect they resemble herbivores and predators more than detritivores. However, whether these aquatic invertebrates feed upon the leaves themselves or the microflora and fauna which may grow on the leaves, tannins may inhibit feeding by either "tanning" the proteins and the cellulose present within the leaves or, via enzymic inhibition, slow the rate of microbial development on the leaf. Despite the abundance of tallow leaf material in the forest ponds on the Coastal Center, my laboratory tests show that the pond shredder-reducers may not be able to utilize it. Inevitably, microbial action and physical breakup would complete decomposition of the Chinese tallow tree leaves; however, the strenuous seasonal effects of high temperature, decreasing volume and decreasing oxygen concentration in the ephemeral ponds prevent the build-up of large populations of decomposers which

could process the litter.

The fact that tannins are leached out of living plant tissue into soil, and that the death of tannin-containing plants increases the concentration of tannins in the soil (Rice and Pancholy, 1973, 1974) may explain the observed increase in tannin content in the leaf packets which I had placed in the forest ponds for this study. The field experiment showed that tannins can be rapidly leached out of tallow leaves into the ponds. Yet there was a subsequent, slow increase in tannin concentration in the leaves beyond the first week. Since polyphenols are readily leached out of plant material, the potential store of tannins in the soil and litter affected by the tallow tree forest may provide a continual tannin input to the forest ponds after rains. The lack of feeding on the large pore litter bags can be accounted for by the lack of shredder-reducers present in these ponds. Since the majority of freshwater aquatic species tend to be polyphagous (Cummins, 1973), most of the species present in the ponds on the Coastal Center may at some time consume litter. Much of the potential energy in the tallow leaf litter fall may be kept unavailable for use by these animals in the forest ponds.

The laboratory survival experiments show that, at the levels of tallow leaf leachate concentration above those normally found in the ponds, there is no direct toxicity to either Asellus militaris individuals or Crangonyx shoemackerii individuals. However, tannins in solution did inhibit feeding by these organisms on allochthonous litter. Whether the tannins work by enzyme inhibition or by the tanning of proteins, the ultimate effect is the same and the various species which normally utilize detritus may find that this source of nutrients and energy is blocked.

Adding tallow leaf leachate to a grassland pond might have shed some light on whether or not the tannins in S. sebiferum leaves could inhibit the development and maintenance of reducer populations. The addition of the leachate was more than enough to duplicate leachate concentrations found in the forest ponds; however, one day after the addition, the Coastal Center was subject to intense rains which effectively diluted the pond leachate concentration to its original level. The duration of "forest conditions" in the grassland pond was too short to be able to monitor any changes in the biota.

What happens to the tallow leaves which fall into the Coastal Center forest ponds? Experiments conducted in our laboratory, and field observations at the Coastal Center, indicate that the leaves which fall into the forest ponds during the three month period of November, December and January lie mostly unutilized by the reducer organisms in the forest ponds. During the time the ponds are extant, the leaves undergo leaching and only minimal physical breakup and microbial and bacterial decomposition (Fig. 27). Figure 27 depicts a tallow leaf as an example of coarse particulate organic matter. Until the leaf has undergone considerable solubilization and physical breakup, it is not utilized by the shredders in the forest ponds. The leaf fall can support the sediment-deposit feeders through the aggregation of fine particulate matter in the water and on the pond floor. Eventually the leaf matter will become fragmented and can further support the sediment-deposit feeders. The lack of shredders in the forest ponds may slow the rate at which the nutrients in leaf litter are recycled and the rate at which sediment-deposit feeders and predators obtain the energy stored in the leaves.
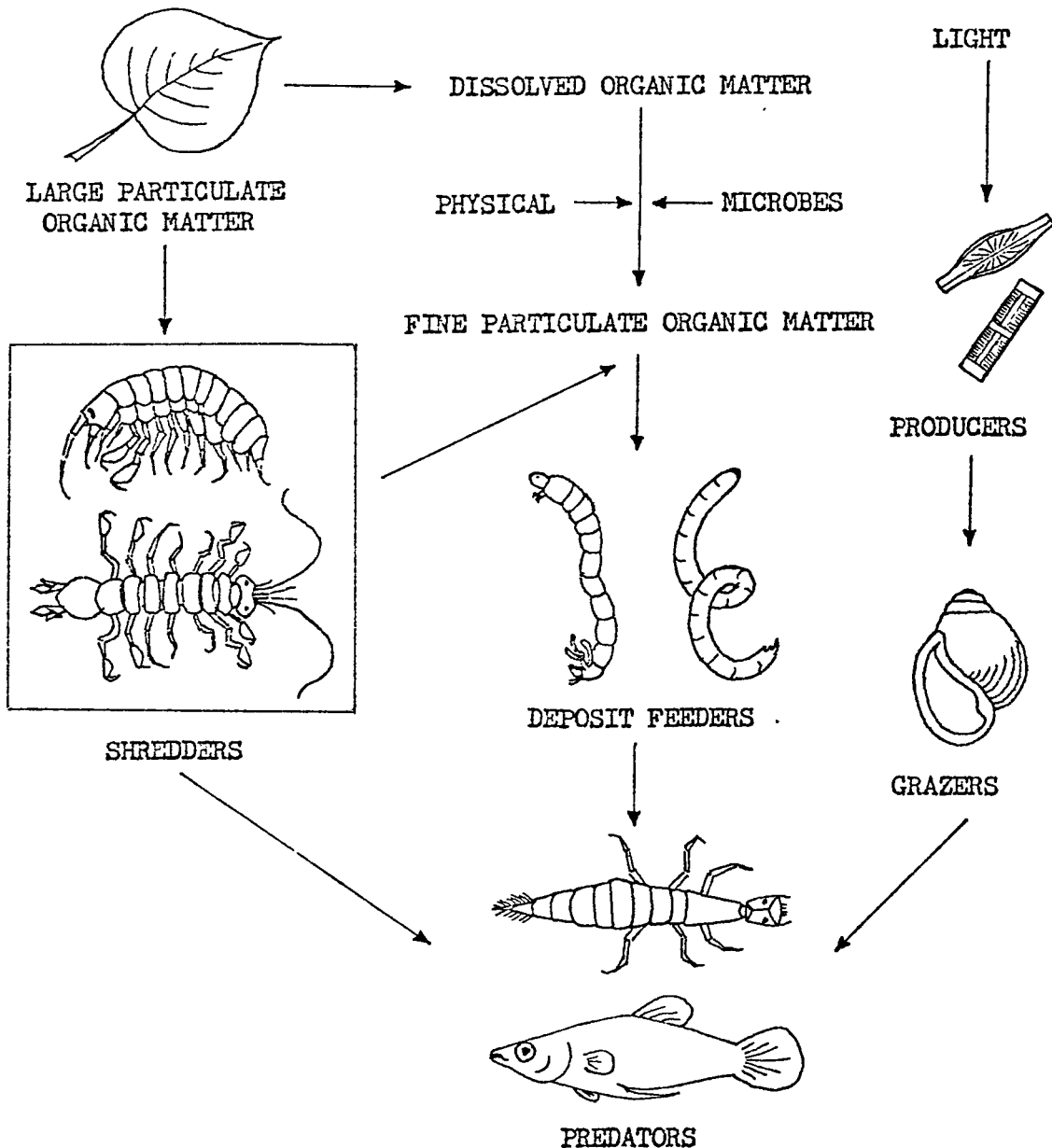
Figure 27. A simplified view of trophic relationships in the ephemeral ponds. Modified from Cummins (1973, 1974). A significant proportion of the energy and nutrients in the leaf litter in the Coastal Center ephemeral ponds may remain unutilizable to the aquatic consumers because of tannin content. Shredders are represented by Crangonyx and Asellus, deposit feeders by Tendipedini and Dero, grazers by Physa, predators by Laccophilus and Gambusia. See text for further details.

There is no apparent buildup of Chinese tallow tree leaf litter
on the forest floor (including the pond floor) at the Coastal Center.
Apparently, when the ponds dry up in the early summer, the terrestrial
isopod, Armadillidium vulgare, may feed upon the leaves and further con-
tribute to their degradation. We have found, through laboratory and field
experiments, that A. vulgare will feed preferentially and is better able
to survive on leached Chinese tallow tree leaves than un-leached leaves;
the preference for leached leaves holds using both entire leaves and
ground-up leaves. Grinding up the leaves eliminates the added factor of
"toughness" in unleached versus leached leaves. Litter bag studies have
shown A. vulgare to be the predominant terrestrial shredder organism in
the Coastal Center forest litter. The increase in litter surface area,
resulting from the comminution of the litter by terrestrial reducer organisms,
is probably the most important contribution to its ultimate breakdown
(Edwards, et al., 1970). In the four month period the ponds are dry on
the Coastal Center, the leaf litter from the previous fall may be utilized
by terrestrial reducer organisms with A. vulgare primarily responsible
for the initial comminution of the leaf litter.

APPENDIX i. Data for the field survey of December, 1973,

through June, 1974.

)

A. The number of species caught in each replicate.

	DEC	JAN	FEB	MAR	APR	MAY	JUN
#3	7	8	9	8	4	9	6
	7	8	5	8	5	9	8
#7	6	9	9	10	8	10	2
	6	11	7	10	9	9	6
#8	6	9	5	9	7	5	6
	11		6	9	5	7	8
#10	11		5	7	11	7	14
	10		7	12	11	8	13
#11	11	7	9	10	10	16	11
	13	11	10	11	12	21	11
#12	10	7	8	10	9	8	12
	4		7	8	14	11	15

B. The Shannon-Weaver diversity index calculated for each replicate.

	DEC	JAN	FEB	MAR	APR	MAY	JUN
#3	.84292	.81602	.88012	.82096	.34031	.71131	.53248
	.56000	.65728	.44277	.80657	.43895	.64912	.42982
#7	.23138	.77854	.28649	.66560	.14692	.41598	.26529
	.54826	.68894	.39194	.57098	.22100	.42606	.59759
#8	.51236	.85019	.44625	.82843	.24719	.40271	.54112
	.75706	.	.29046	.79249	.28830	.51456	.67423
#10	.78765		.62929	.55637	.71170	.26518	.86464
	.69676		.66427	.51555	.76940	.20206	.72673
#11	.88083	.77778	.79650	.76377	.87408	.66465	.57627
	.83027	.84557	.87593	.84142	.87972	.67576	.65912
#12	.88117	.42744	.77014	.86294	.39706	.45952	.47027
	.60205	.	.66000	.65373	.57747	.51414	.53048

APPENDIX 1, CONT.

C. Evenness component for each replicate.

	1973 DEC	1974 JAN	FEB	MAR	APR	MAY	JUN
#3	.84292 .78221	.90359 .72781	.92233 .46400	.90906 .89312	.48687 .62800	.74542 .68025	.58962 .47594
#7	.29735 .70457	.74760 .66156	.30023 .41074	.66560 .57098	.15397 .23160	.41598 .42606	.34092 .76796
#8	.49200 .72697	.89096	.63844 .34370	.86816 .83049	.29250 .34114	.47652 .60887	.59919 .74658
#10	.75634 .66907		.74463 .78603	.51555 .77340	.68341 .73882	.29364 .22374	.75440 .63407
#11	.79073 .74535	.74687 .81196	.79650 .87593	.73341 .80798	.80995 .81517	.50268 .55075	.55337 .63292
#12	.60205 .88117	.50579	.79753 .85278	.65373 .86294	.50384 .34644	.49371 .44126	.45105 .39986

D. Pond volume for each pond, cc X 10^7.

	1973 DEC	1974 JAN	FEB		APR	MAY	JUN
#3	1.5520	1.4933	1.5508		0.6342	0.7137	1.5554
#7	1.1424	0.6890	1.0560		0.4006	0.2633	1.1837
#8	1.3478	1.2116	1.3934		0.7311	0.7023	1.5202
#10	0.7148	0.6886	0.7603		0.2714	0.2520	1.0829
#11	0.5297	0.9882	1.0499		0.4784	0.5933	1.3083
#12	0.6418	0.7202	0.7698		0.6623	0.6955	0.7626

APPENDIX 1, CONT.

E. Oxygen concentration, ppm, for each replicate.

	1973 DEC	1974 JAN			APR	MAY	JUN
#3	5.42	7.44			6.59	5.49	5.26
	6.25	7.40			6.44	5.42	5.04
#7	6.64	8.23			6.72	5.48	5.29
	6.33	8.04			6.68	5.88	5.47
#8	6.29	7.96			6.89	5.76	5.37
	6.30	8.17			6.81	5.68	5.02
#10	6.78	8.12			7.04	5.61	5.30
	6.28	8.28			6.82	5.54	5.23
#11	8.20	9.83			8.25	6.05	6.23
	8.33	9.99			8.16	6.18	6.08
#12	8.46	10.15			8.06	6.53	6.16
	7.92	9.81			8.10	6.32	6.17

F. Mean pond bottom temperature and standard deviation, for each pond. n = 6 measurements.

	1973 DEC	1974 JAN	FEB	MAR	APR	MAY	JUN
#3	14.0 .063	10.0 .476	16.6 .415	21.0 .532	22.9 .117	23.6 .371	25.1 .117
#7	15.0 .187	10.7 .634	15.6 .653	19.8 .194	22.0 .133	23.2 .194	24.2 .117
#8	15.5 .103	11.1 1.039	15.9 .280	24.5 2.656	22.0 .050	23.4 .423	24.2 .105
#10	14.9 .179	11.0 .650	17.8 .258	23.8 .261	23.9 .082	27.9 .446	26.2 .121
#11	16.2 .151	14.9 .358	19.4 .418	25.6 .063	28.4 .431	27.3 1.047	26.3 .172
#12	16.1 .194	16.0 .122	20.3 .361	23.0 .121	27.4 .561	27.9 .413	26.4 .266

APPENDIX i, CONT.

G. Mean insolation at the pond surface and standard deviation; for each pond, n = 4 measurements.

	1973 DEC	1974 JAN	FEB	MAR	APR	MAY	JUN
#3	2200 952.2	1500 115.5	4050 2015.8	3950 2493.3	3975 1405.6	2700 2615.3	504 172.2
#7	825 221.7	1425 236.3	2300 1453.7	2200 812.4	2900 1829.4	1285 1545.4	142 12.6
#8	1100 416.3	1900 529.2	5175 793.2	2425 1150.0	2525 1417.4	725 727.4	685 87.0
#10	438 35.0	1450 435.9	2975 650.0	3200 1460.6	6375 450.0	2450 1258.3	5475 573.7
#11	3900 258.2	2600 816.5	6950 914.7	5025 873.2	5500 2868.2	6450 660.8	7950 378.6
#12	3400 1095.4	2175 170.8	5300 702.4	4800 516.4	3550 2241.3	4025 1167.3	7300 1013.2

APPENDIX ii. Data for the field experiment, winter, 1974-75.

A. The number of species caught in each replicate.

	1974 NOV 30	DEC 17	21	31	1975 JAN 14	28
#11	8 6	3 7	6 4	5 6	5 5	6 6
#12	6 6	6 6	6 8	7 7	5 3	4 5
#13		4 3	7 5	2 7	5 4	6 7

B. The Shannon-Weaver diversity index calculated for each replicate.

	1974 NOV 30	DEC 17	21	31	1975 JAN 14	28
#11	.48500 .41368	.29684 .41878	.27622 .26061	.22993 .36412	.31151 .52703	.48439 .43386
#12	.68026 .53338	.31977 .25498	.26589 .26352	.53182 .30015	.50818 .41506	.24213 .40020
#13		.24277 .17178	.23968 .35306	.06566 .23129	.24159 .23888	.34091 .64329

C. Pond volume for each pond, cc X 10^7.

	1974 NOV 30	DEC 17	21	31	1975 JAN 14	28
#11	0.85186	0.809844	0.920966	0.955500	1.053328	0.984375
#12	0.72364	0.717024	0.768384	0.766080	0.781531	0.723200
#13		1.200960	1.259712	1.232748	1.361520	1.140210

D. Mean pond bottom temperature and standard deviation; for each pond, n = 6 measurements.

	1974 NOV 30	DEC 17	21	31	1975 JAN 14	28
#11	12.9 .432	10.0 .107	9.2 .444	12.6 .682	9.3 .245	12.5 .396
#12	12.9 .192	10.0 .357	9.2 .664	12.6 .478	9.3 .277	12.5 .361
#13		9.8 .638	9.0 .402	11.7 .209	9.3 .075	12.0 .316

E. Mean percent transmittance (335 mu) and standard deviation; for each pond, n = 4 readings.

	1974 DEC 10	17	21	31	1975 JAN 14	28
#3	68.97 0.24	66.35 0.26	61.65 0.57	72.22 0.49	59.92 0.57	58.20 1.48
#8	68.15 0.58	70.10 1.17	58.40 0.57	71.45 1.17	58.50 0.70	60.30 0.37
#11	83.52 0.53	77.87 1.32	77.67 0.72	84.72 1.88	73.27 0.39	74.97 0.15
#12	87.02 0.85	84.55 0.59	85.15 0.35	88.47 1.36	78.60 1.16	87.80 0.37
#13	83.52 0.53	70.42 0.68	66.35 0.75	75.07 0.60	67.65 0.37	75.25 0.65

APPENDIX iii. Data for the large and small pore litter bags

immersed in a forest pond, winter, 1974-75.

A. Percent initial weight remaining for each replicate bag.

	1974 DEC 10	17	21	31	1975 JAN 14	28
FINE PORE	21.50 28.44	25.64 30.67	18.89 32.38	42.60 58.47	48.98 38.26	56.26 42.96
LARGE PORE	15.61 15.98	24.12 28.25	19.94 38.15	36.11 47.13	47.14 55.33	67.95 58.18

B. Mean percent transmittance (500 mu) and standard deviation; each date, the contents of the two bags were pooled and n = 6 readings taken.

	1974 DEC 3	10	17	21	31	1975 JAN 14	28
FINE PORE	61.23 1.83	97.06 1.54	91.85 1.03	80.28 0.75	83.28 0.52	77.25 1.79	83.25 2.61
LARGE PORE	54.71 1.11	96.70 1.44	87.01 1.43	82.06 1.35	86.33 1.19	78.71 1.31	86.46 2.42

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