

Final Report  
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and Ecosystems.

Institution to which the  
contract was awarded:

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This final report will be divided into three categories. The first will report on work which was in progress during the final contract year and which is not yet completed. The second will review research completed during the final year of the contract. The third will review accomplishments of the ten years of research under this contract. Throughout the ten years of this contract, research was conducted almost entirely by graduate students under the direction of and in collaboration with the principal investigator. Benefits of A.E.C. support went far beyond the students directly involved and the research published by these students. The Department of Botany, the University of North Carolina and the science of ecology benefited immeasurably from the availability of equipment supplies and from the educational process which was so strongly supported by the A.E.C. Other A.E.C. programs, including those at the Savannah River Plant, Oak Ridge National Laboratory, the Puerto Rico Nuclear Center, Brookhaven National Laboratory and the U.S. Forest Service Enterprise Radiation Site all benefited from the participation of our students during and after their graduate research.

#### I. Research Still in Progress

Two research projects remain uncompleted. (1) Recovery of a tropical rain forest following exposure to ionizing radiation.

As early as 1964 we began studies in the El Verde rain forest in Puerto Rico. The objectives and results of most of the studies are included in; A Tropical Rain Forest, Edited by H. T. Odum. A chief objective of the rain forest project was to determine the stability of the rain forest ecosystem when

exposed to gamma radiation. There are several criteria with which one might estimate ecosystem stability. These include resistance to stress persistence in the presence of stress, avoidance of stress and resiliency following stress. Almost all research at El Verde was focused upon analysis of resistance. Most radiation effects studies were terminated within a year or two following irradiation of the forest. This project is concerned with resiliency following irradiation and covers the 12 year period from 1964 to the present. As stated in previous annual reports the chief objectives have been:

- (A) to describe secondary succession (recovery) following irradiation.
- (B) to identify plant species which play a dominant role in recovery.
- (C) to describe the physiological and ecological processes responsible for the dominance of certain species and the exclusion of others.

At present the research is nearly completed. Mrs. Maria Luz Lebron Luteyn is in the rain forest conducting the final experiments. She will complete her research by May, 1976 and will receive the Ph.D. in June or August, 1976. A copy of the dissertation will be sent to the A.E.C. (ERDA) at that time. Thus far, quantitative descriptions of the recovery pattern are complete. Essentially what happened was that typical pioneer and successional species invaded the irradiated forest immediately. Populations of these species, including Palicourea and Cecropia grew rapidly under conditions of high light and moisture and low competition. After approximately five years the first group of pioneer species was replaced by a group of species characteristic of the mature rain forest. Apparently pioneer species so modified the microenvironment that conditions became favorable for the establishment of climax species.

Palicourea was selected as the species for detailed analysis of the physiological processes and ecological relationships which might be responsible for its initial invasion, rapid growth and eventual replacement. Studies conducted in the Duke University phytotron are now completed. Rates of growth, photosynthesis, respiration and transpiration are well defined for environmental conditions simulating those of the post radiation forest, the successional forest and the climax forest.

Presently similar studies are being conducted "in situ" in the rain forest. Within a few months you will receive a copy of Mrs. Luteyn's dissertation which will add an analysis of resiliency to previous studies of resistance. Hopefully this will contribute to a more complete understanding of rain forest stability as well as a detailed analysis of the population dynamics and physiological ecology of a successional species.

Progress since September 1, 1974 is summarized as follows:

#### Field Research:

During the month of January a short trip was taken to Puerto Rico. The meteorological and growth data that had accumulated since August of 1974 was retrieved at that time and it is in the process of being analyzed. At that time a meeting was held with Dr. R. G. Clements, from the Puerto Rico Nuclear Center, during which logistic support for the upcoming season was obtained.

In view of the problems encountered from November of 1974 through April of 1975 with the different Infrared Gas Analyzers used it was decided that such equipment would not be suitable for field use. The alternative of using  $^{14}\text{CO}_2$  was discussed with Dr. J. F. McCormick and it was concluded that this

would be a more appropriate technique for the field experiments. The equipment needed for such a method will be obtained mostly as a loan from The University of Tennessee.

Future field work will be started during the month of October and

barring any unforeseen problems it should not extend past March of 1976.

#### Laboratory Research:

During the month of October of 1974 a grant proposal was prepared and submitted to the Southern Regional Education Board to obtain funds to defray the costs of the use of Duke University's Phytotron facilities. The period of time to be covered by this grant was from November of 1974 through January of 1975 with an extension until the month of February if it was deemed necessary. This grant was partially approved for \$1,064.00.

Work was started immediately on the equipment and set-up. Four Infrared Gas Analyzers were tried with the system, none of which, as it turned out, functioned properly. During April of 1975 a functional Beckman 215-A Infrared Gas Analyzer was obtained on loan from Dr. J. Wuenscher, from the Duke School of Forestry. This instrument was incorporated into the system and is the one being used currently.

In view of these unexpected problems with the Infrared Gas Analyzers, a grant renewal was requested from the Southern Regional Education Board. Due to the stipulations of the Small Grants Program which funds this type of activity, this request was not approved.

As of mid-May, the whole set-up was calibrated and experimentation was started. Presently the baseline studies are nearing completion, both the light and temperature curves as well as the short-term acclimation areas. The long-term acclimation studies will be started within the next three weeks.

# $^{14}\text{CO}_2$ Field Chamber Design

1/2 in

Figure 1-A TOP VIEW - cover  
(drawn to scale 1:1)

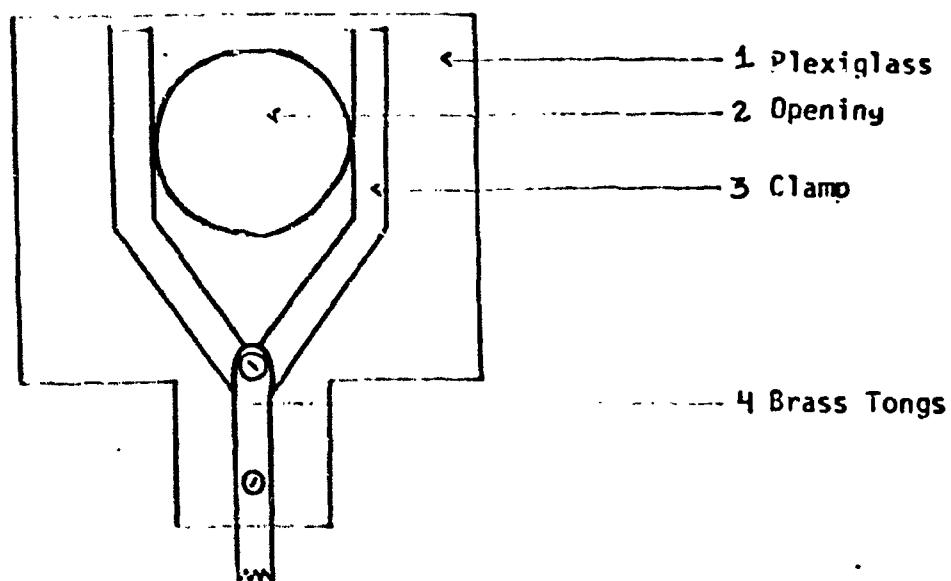


Figure 1-B top view - baseplate  
(drawn to scale 1:1)

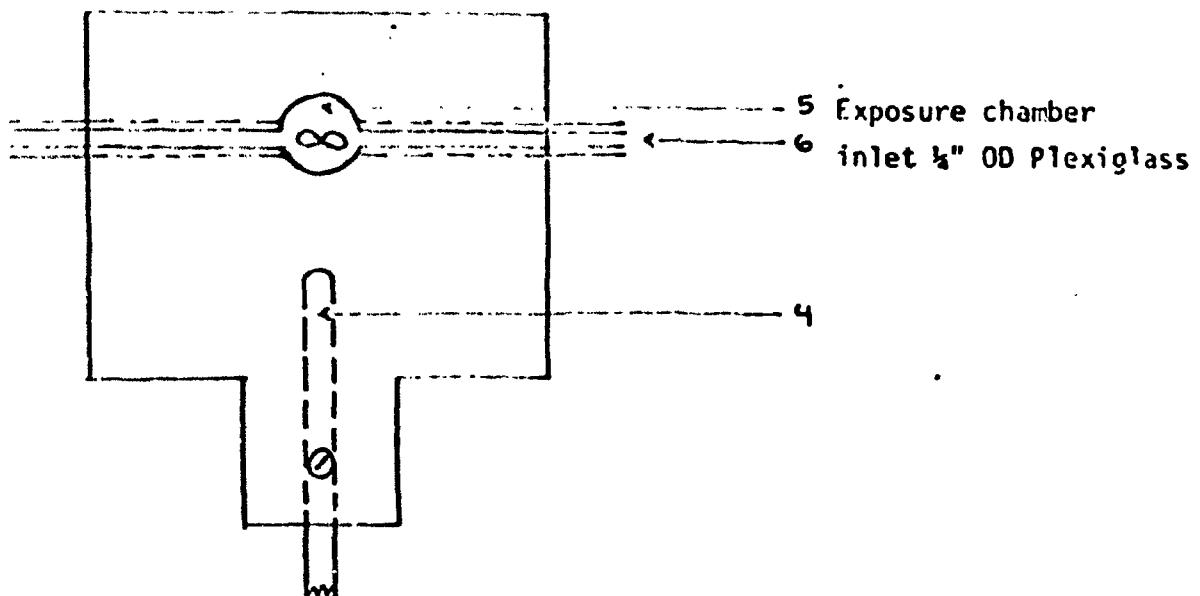


Figure 2-A X.S. Front View  
(drawn to scale 1:1)

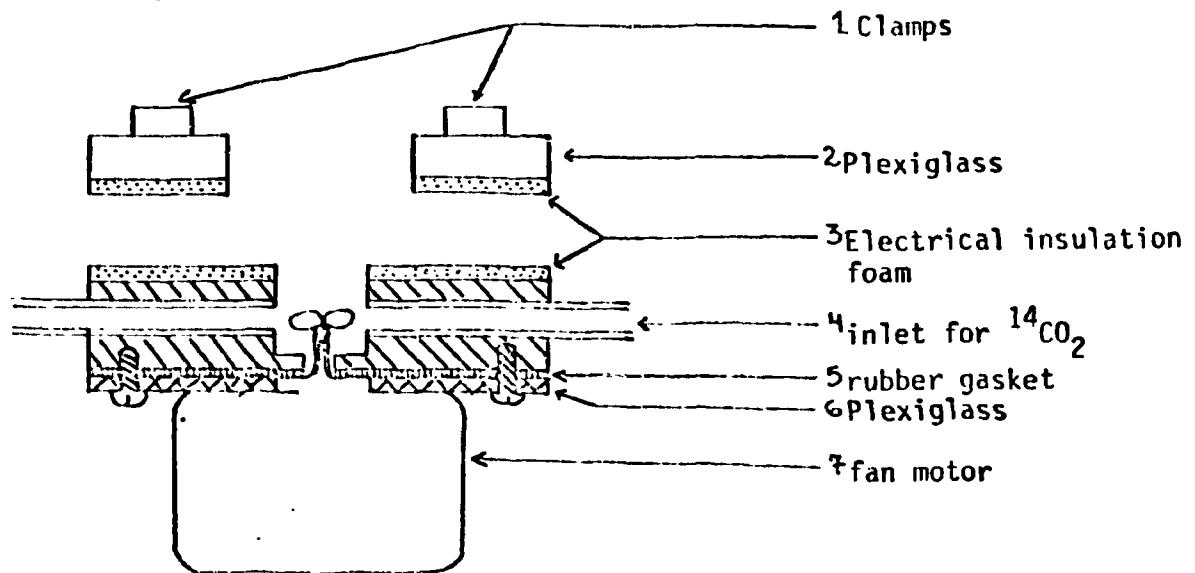
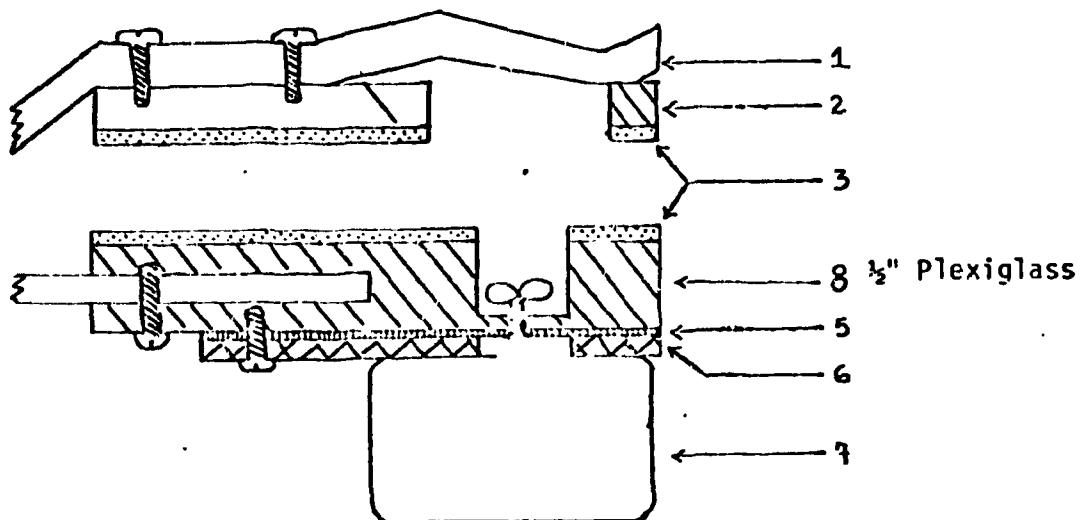


Figure 2-B X.S. Side View  
(drawn to scale 1:1)



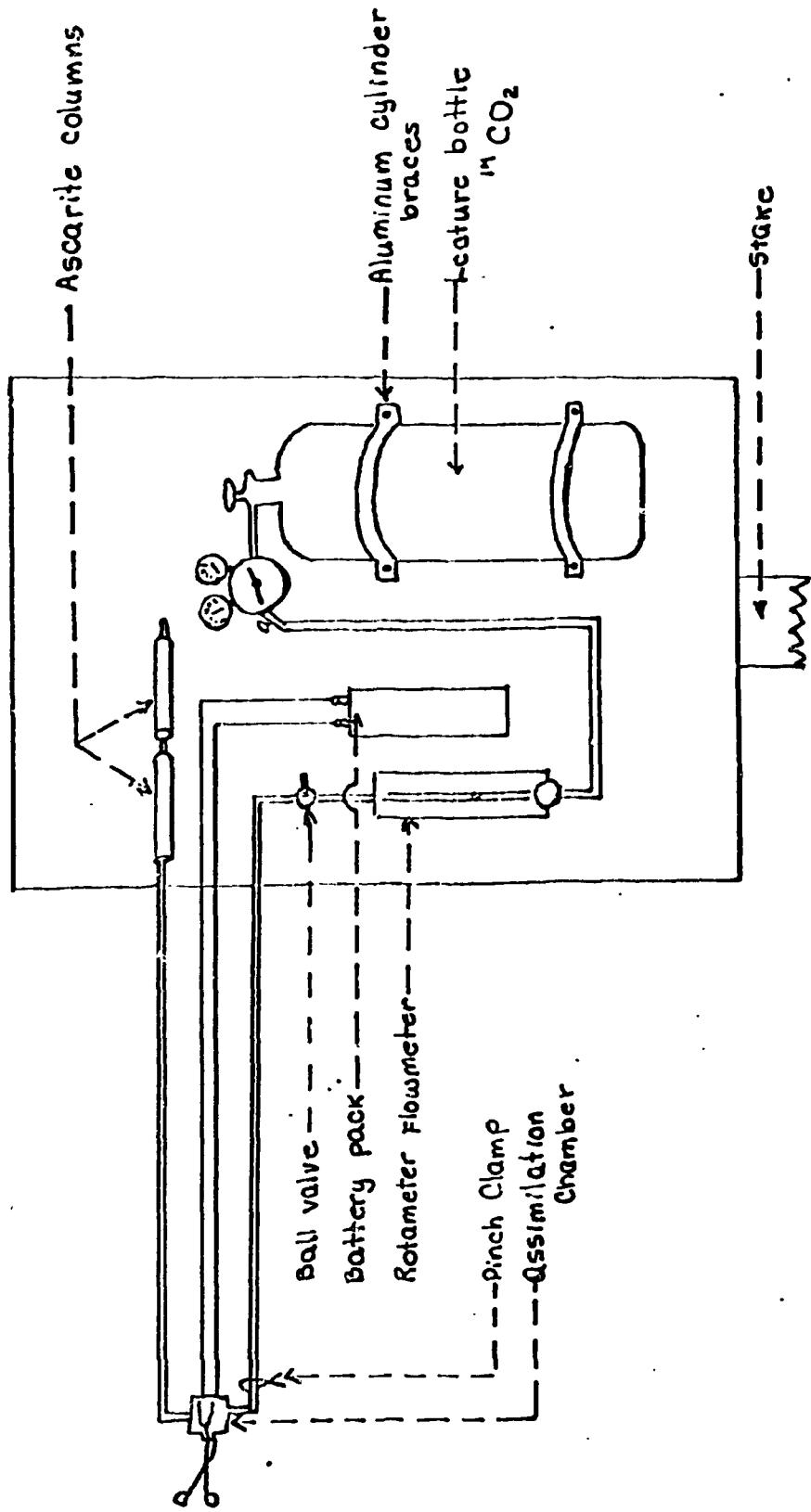


Figure 3 - Panel Board  
(not drawn to scale)

Progress since June 1975 through September 1976 is summarized as follows:

Field Work:

1. Census of the vegetation:

The vegetational data available from the literature corresponds to the following years: 1964, 1966 and 1967..Drury's 1971 data is on field notebooks at the Nuclear Center and this data is available to me. During the months of November and December I will conduct a census of the areas. This should complete the 10 years cycle after the disturbance.

2. Seedling seasonality:

The records for the permanent seedling quadrats have been kept for three full years now. The data for all the species has been partially analyzed while that for Palicourea has been analyzed in more detail. So far, Palicourea seedlings do not show differences in seasonality patterns between the radiation sites except for the winter of 1974.

3. Growth and Phenology of individuals in situ:

The data in this section is somewhat scanty because the poachers got into my open area and tampered pretty badly with my populations. It is difficult to put any weight or make any definite conclusions from this information.

4. Seed germination and seedling growth:

The salient points in the data collected so far are the following:

a. Germination and seedling growth are always higher in the open vs. the closed canopy area.

- b. The season during which the seeds are sown has a marked effect on the germination of those sown in the closed canopy area but not on those sown in the open canopy area.
- c. Seedling survival is highest in the open canopy area than in the closed canopy area.

5. Reciprocal transplants:

These have been kept track of since their start during the summer of 1973. The variability found is great but in general, those individuals transplanted to the open area are taller than those transplanted to the closed area. There is some slight indication of a possible ecotypic differentiation between populations but it is still too early to make any definite conclusions about this.

6. Field gas exchange studies:

These will be conducted during January and February of 1976 using  $^{14}\text{CO}_2$ .

Laboratory Work:

1. Gas exchange studies:

The main question asked was: What effect or effects, do changes in light and temperature have on the gaseous exchange of Palicourea that enable it to play such a dominant role in recovery? As a corollary to this, the following question was also asked: How does the gaseous exchange of Palicourea adjust through time to these changes?

As of this date, the baseline, short term, three days and seven days

acclimation studies have been completed. The preliminary analysis of this data do not show any statistically significant differences between the baseline, three days and seven days acclimation studies, based on standard errors of the means. The twenty one days acclimation studies are under way now and once these are finished and the data is analyzed as a whole, I'll be able to make some definite conclusions about it.

2. The nature of radiation sensitivity in pines.

This research was conducted by Lloyd Willis. He has completed the research and all other requirements for the Ph.D. He is presently writing his dissertation and a copy will be sent to you upon completion. The following summary and tentative conclusions are presented for your use in the meantime.

The hypothesis was proposed that the responses of pines to ionizing radiation are the product of high sensitivity to both radiation and ozone. To test this hypothesis, a three-phase investigation has been undertaken: 1) preliminary laboratory study, 2) field study, and 3) primary laboratory study.

Preliminary Laboratory Study. A series of preliminary studies were conducted with plants grown from seeds using the below described or similar treatments. The main purposes of these experiments were to develop an experimental procedure and to test the reliability of the equipment.

Also in the preliminary laboratory study, one-year-old Pinus taeda seedlings were taken from cold storage, potted in gallon containers, and placed in controlled environmental chambers at UNC. After the plants had broken dormancy and had well established new flushes of growth, they were given the experimental treatment

at the Radiation Biophysics Laboratory. The plants were then returned to the growth chambers for an extended period of observation after which they were removed and planted in a natural setting for further observations. There were a total of eight experimental treatments with eight plants per treatment. The pines received ozone and radiation simultaneously in doses of 0, 125, 375, and 625 R each paired with both 0 and 6 ppmm O<sub>3</sub>.

Results. Several characteristics of the plants were observed. Using plant height, a significant difference between all radiation levels was noted except between 0 R and 125 R. When comparing the plant heights for the two ozone levels at each radiation level, no significant difference was found. Using the number of lateral branches produced, there was a significant difference between the two ozone levels at both the 125 and 625 R levels and the same trend (increase in number of branches with ozone) existed at the 375 R level. It was also noted that bud mortality only occurred at the 625 R level with no significant differences between ozone treatments and that there was little or no needle growth with both ozone treatments at the 375 and 625 R levels. Average lateral branch growth appeared to be depressed on both ozone levels at the 125, 375, and 625 R levels. Average lateral branch growth for new flushes was greater at 125 and 375 R and depressed at 625 R for both ozone levels. The number of plants showing no increase in height in the three one-month periods following treatment increased with each level of radiation; however, this appears to be significant only at the 375 and 625 R levels with no difference according to ozone level.

Conclusions. 1) It appears there are interactions or trends toward interactions in a radiation plus ozone environment. 2) The number of plants per treatment should be increased.

Field Study. In the field study one-year-old Pinus taeda seedlings were taken from cold storage and planted in the Radiation Experiment Field located at the Savannah River Ecology Laboratory, Aiken, South Carolina. Nine experimental groups of 20 pines each were planted along a calculated isodose line in the gamma exposure field. An additional eight control groups of 15 pines each were planted outside the gamma exposure field and shielded from the source. Due to the natural mortality of some groups, the size of the experimental groups were reduced to 12 each.

During treatments, portable ozone chambers were placed over each experimental group. It was decided to use a constant level of radiation and vary the ozone level. The treatments were 0 and 375 R each with 0, 6, 12, 20, 35 pphm  $O_3$ , and ambient air.

Results. Preliminary data has been collected on each of the experimental groups using plant height, branch number and length, bud mortality, and needle growth and damage as the indicators of response to treatment. Since all final data has not yet been taken, this data has not been subjected to statistical analysis; however, using average plant height per group at one year after treatment, some tentative statements can be made. Treatments of 0, 20, 35 pphm  $O_3$ , and ambient air for 10 hours did not appear to result in any significant difference in growth between groups. Visible ozone damage to the secondary needles (chlorotic mottling) was present only at 35 pphm  $O_3$  level and again when this level was used in combination with 375 R. During gamma radiation exposures, three experimental groups were treated simultaneously each day. Comparisons were made between the groups run on a given day. When treatments of 6, 12, and 35 pphm  $O_3$  each with a 375 R level were compared, the 6 pphm  $O_3$  showed a

significant difference from the other two groups by having a greater increase in average plant height. When treatments of 0, 20 pphm  $O_3$ , and ambient air each with 375 R were given, no significant difference was noted between groups. When treatments of 0, 35 pphm  $O_3$ , and ambient air each with 375 R and a high heat stress were given, the 35 pphm  $O_3$  showed a significant difference from the other two groups based on needle damage and apparent mortality rate.

Conclusions. 1) There are indications of interaction occurring in the radiation plus ozone environment. 2) In order to more clearly define these interactions, a controlled environment study with a larger number of plants should be conducted.

Primary Laboratory Study. The equipment necessary for ozone generating and monitoring was reassembled at the Radiation Biophysics Laboratory following use in the field experiments. Thirty-day-old seedlings were used in order to compare different age response and to allow an increase in sample size. The smaller plant size allowed a greater number of plants to be placed in the experimental chamber at one time. For these seedlings, height, biomass, and visible damage were some of the characteristics used to ascertain the response to the ozone and radiation environment.

The first treatments were for high level effect - 35 pphm  $O_3$  with 0, 125, and 375 R. Each treatment group contained a minimum of 15 pines. The experiment was repeated three times. In all three experiments there was a trend towards an interaction only at the 375 R level with 35 pphm  $O_3$ . One of the three showed a significant difference between the 375 R with 0 pphm  $O_3$  and the

375 R with 35 pphm  $O_3$ ; the latter had a lower percent increase in height.

Since a definite interaction appeared at least once at the 375 R level, it was decided to use this as the constant radiation level and vary the ozone by using 0, 6, 12, and 35 pphm  $O_3$  for the second treatments. There was an increase to a minimum of 30 pines in each treatment group. As above there was a trend towards an interaction only at the 35 pphm  $O_3$  level.

For the third set of treatments, exposure time was lengthened from approximately 3 hours to 10 hours. This would be equal to the field exposure times. The levels of radiation and ozone and the sample size remained the same as in the second treatment. 0 R - 0 pphm  $O_3$  and 0 R - 35 pphm  $O_3$  treatment groups were added. The experiment was repeated three times. In each run there was a definite interaction at the 35 pphm  $O_3$  - 375 R level. On the other ozone levels with radiation, there was a trend in the direction of a decrease in plant height as the amount of ozone was increased. Again, the high level of ozone (35 pphm) by itself did not result in a decrease in height as compared to the 0 R - 0 pphm  $O_3$ .

**Conclusions.** 1) It appears an interaction exists between ozone and radiation at 35 pphm  $O_3$  and 375 R levels. 2) A complete statistical analysis is needed to establish the significance of the trends.

**Summary.** During the course of the investigation, Pinus taeda has been exposed at different ages (30, 45, 90-day-old, 15, and 20 months), to different levels of ozone (0, 1.5, 3, 6, 12, 16, 20, and 35 pphm), for different lengths of time (1, 3, 5, and 10 hours) and under different light intensities (600, 800, 1,000, 1,600, and 2,500 foot candles).

Some tentative conclusions can be made:

- 1) The younger the seedlings the more sensitive they are to ozone.
- 2) The higher the light intensity the more sensitive the seedlings are to ozone.
- 3) The longer the length of exposure to ozone at a given level, the greater the sensitivity to ozone. This has only been clearly demonstrated at the 20 pphm  $O_3$  level and above.
- 4) Seedlings usually develop visible damage (chlorotic mottling) only at relatively high ozone levels (20 pphm and higher) for exposure in excess of two hours.
- 5) Seedlings of the same age vary in their sensitivity to ozone. Usually around 25% showed visible damage at the highest ozone levels in the lab study.
- 6) In the field study a higher percentage of seedlings showed damage at the highest ozone level but the light intensity was greater.
- 7) Seedling groups exposed to ozone (at all levels tested) did not differ significantly from control groups in height or biomass.
- 8) Groups of individual seedlings each showing visible damage from ozone did not appear to differ significantly from control groups in height or biomass.
- 9) Primary needles of 30-day-old seedlings appear to be more sensitive to ozone than the cotyledons of the same plants.
- 10) The primary needles of 30-day-old seedlings appear to be more sensitive to ozone than the secondary needles on older plants.

11) Chlorotic mottling of cotyledons, primary and secondary needles was the most common form of visible damage due to ozone.

Also, Pinus taeda seedlings of the above ages, exposure times, and light intensities have received different gamma radiation levels (125, 375, 625 R).

Some tentative conclusions can be made:

- 1) The younger the seedlings the more sensitive they are to gamma radiation.
- 2) The various light intensities and exposure times used did not appear to affect sensitivity of the seedlings to the gamma radiation.
- 3) A radiation level of 375 R or higher will severely retard or stop elongation of secondary needles for all ages tested.
- 4) A radiation level of 125 R will retard but not stop elongation of secondary needles in 30-day-old seedlings with little or no effect on secondary needle development of one-year and older seedlings.
- 5) Elongating primary needles on 30-day-old seedlings exposed to 125 R showed no or slight twisting, at the 375 R level a severe twisting of needles in all plants, and at 625 R elongation stopped in most plants.
- 6) Radiation levels of 375 R and higher resulted in reduced growth as measured by plant height. Those seedlings treated at the 125 R level were not significantly different in height from the control.
- 7) Biomass studies of seedlings treated when 30 days old indicated a reduction in biomass at the 125, 375, and 625 R levels when compared to controls.
- 8) No mortality occurred in the 30-day-old seedlings at the 125 R level; the mortality rate was approximately 1-3% at 375 R for a four month period following treatment. One year and older seedlings showed no mortality.

at these levels.

- 9) Radiation level of 625 R resulted in a premature loss of secondary needles approximately five months after treatment of the 20-month-old pines.
- 10) Seedlings within a treatment group show a relatively constant response to gamma radiation.

In addition, Pinus taeda seedlings have received ozone and radiation simultaneously at the above doses, ages, exposure times, and light intensities.

Some tentative conclusions can be made:

- 1) Interaction between ozone and radiation was most easily seen at the 375 R level.
- 2) Interaction was most easily seen at the highest ozone levels given over the longest exposure time.
- 3) Interaction may be occurring at lower ozone levels over long exposure time but further statistical analysis of the data is needed.
- 4) The mortality rate of 30-day-old seedlings increased to as high as 25% at the highest ozone levels given over the longest exposure time (indicating a synergism).
- 5) Seedlings of the same age show varying sensitivity to the ozone-radiation treatments.

Four subprojects have been completed. The first two appear as sub-projects in previous proposals. The third was approved for funding as a sub-

project and then after we had devoted considerable effort to the project support was withdrawn. Even though the A.E.C. encouraged us to develop the research and then withdrew support, you may find the results of some interest. The final report did not appear as a proposal subproject but because the research was so dependent upon previous research support by this contract the A.E.C. should be acknowledged for the motivation and research facilities which made the study possible.

#### Subproject 1

Interactions of ionizing radiation and other environmental stresses upon plant populations (A) Ecology of Cornus canadensis and Aster macrophylla, two species important to recovery of a northern hardwood forest exposed to gamma radiation. This research was conducted by Dr. Tom Armentano as a part of this Ph.D. program.

(2.) Composition and structure of communities colonizing a swamp hard-wood forest receiving thermal and radioactive effluent. This research was conducted by Ms. Julie Irwin as a part of her M. S. program.

IRWIN, JULIE ENGLISH. Structure of stump communities in a stream  
affected by thermal effluent (Under the direction of J. F. MCCORMICK.)

In a swamp stream on the Energy Research and Development Administration's (formerly Atomic Energy Commission) Savannah River Plant, structure of communities in four different temperature areas, three thermally affected sites (I, II and III with approximate water temperatures of 50° $C$ , 45° $C$ , and 40° $C$  respectively) and one ambient site (IV approximately 20° $C$ ) was described and compared by sampling an equal number of randomly selected communities within each site. Comparisons were made of species composition and importance; species diversity ( $H$ ) and evenness ( $J$ ); species similarity; substrate temperature; and soil nutrients and pH. Species composition varies from site to site with no species dominant in more than one area. Diversity ( $H$ ) is highest in the ambient area; evenness is lowest in area III. Sites I and II are the most similar in species composition. Stump substrate temperature in the ambient site is 13° $C$  below that in the coolest thermal site (site III). Soil nutrients and pH are not significantly different in all four sites.

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## INTRODUCTION

In some swamp forests of the southern U.S., distinct plant communities develop on floating logs and stumps of dead trees (Hall and Penfound, 1943; Dennis and Batson, 1974). The vegetation supported by this type of substrate is primarily herbaceous, but several woody species, including small trees are also present. Lemon (1945) reported that although decaying wood is not considered a favorable substrate for vascular plant growth, the growth of the species he recorded on stumps in the southeastern coastal plain appeared to be normal.

Stump and log communities are widely scattered throughout undisturbed areas of the Santee Swamp on the South Carolina coastal plain, but they occur more frequently in disturbed areas (Dennis and Batson, 1974). Disturbance in the Santee Swamp is due to flooding following construction of a hydroelectric dam. In addition, logging operations left many stumps and logs which function as a substrate for an unusual community type. Hall and Penfound (1943) also reported this unusual type of community in Blue Girth Swamp in Alabama. This community type is also found in Pen Branch, a swamp stream flooded by thermal effluent from a nuclear production reactor on the Energy Research and Development Administration's (formerly Atomic Energy Commission) Savannah River Plant in South Carolina. In this case however, the stumps and logs are not just an additional habitat in which vascular plants are able to grow; but the only one which affords a means of survival in the hot stream.

The objectives of this study are to describe the structure of the stump communities and to determine whether community structure is significantly different in areas of the stream having different water temperatures.

## SITE DESCRIPTION

Pen Branch, a swamp stream located on the Energy Research and Development Administration's Savannah River Plant, receives thermal effluent from a nuclear production reactor which has been in operation for over 20 years. Aerial photographs show that before the reactor began operating, the flood-plain forest at Pen Branch was floristically typical of mixed hardwood swamp forests in the coastal plain of the southeastern United States (Sharitz, Gibbons and Gause, 1974). Such forests have a closed canopy dominated by Acer rubrum L., Planera aquatica Walt ex Gmelin, Fraxinus pennsylvanica Marsh, F. caroliniana Mill, Nyssa aquatica L. and Taxodium distichum (L.) Richard (Sharitz, Irwin and Christy, 1974).

The release of a large volume of reactor effluent into Pen Branch increased the water temperature and flow rate downstream from the reactor, causing flooding and heavy silting. The release of effluent also slowed the flow rate upstream from the discharge, thus causing flooding and deposition of large amounts of organic matter in the stream bed above the reactor input. This combination of factors totally destroyed the forest above and below the reactor discharge so that only stumps, fallen logs and dead standing trunks remain as evidence of the previously existing forest. Downstream from the reactor, temperatures in the stream and associated sediments are too high for the survival of vascular plants. The present flora is restricted to substrates which remain above the water level, such as

rotting logs and stumps around which debris has accumulated. In the upstream ambient area, some submerged aquatic plants occur in the stream sediments, but most of the vegetation grows on the stumps and logs. The stump and log habitats are separated from one another so that the stream appears to contain a large number of small scattered island communities. In the delta region where Pen Branch enters the major swamp forest along the Savannah River, 56% of the area consists of these islands (Sharitz, Irwin and Christy, 1974). Annual and perennial herbs make up 80% of the vegetation of the islands, most being weedy invaders. A few woody species including Rhus radicans L., Ampelopsis arborea (L.) Koehne, Myrica cerifera L., and Acer rubrum L. are present. Species composition is similar on both stumps and logs (Sharitz, Irwin and Christy, 1974).

## METHODS

Four sampling sites corresponding to water temperatures of approximately 50°C (site I) 45°C (site II) 40°C (site III) and 20°C (site IV) were selected. The ambient site (site IV) is the farthest upstream, above the entrance of thermal effluent into Pen Branch. The 50°C site (site I) is the closest to the reactor discharge, and the 45°C site (site II) is approximately 900 meters downstream from site I. The 40°C site (site III) is near the swamp delta, approximately 975 meters below site II.

Within each site, 45 stump communities were numbered and marked and 15 communities from each site were randomly selected for sampling. Nine from each of the thermal sites were sampled during the summer of 1973 and the remaining six from each thermal site as well as all 15 from the ambient area were sampled during the summer of 1974. For the purpose of data analysis, each stump community was treated as a sampling unit.

Habitat availability as determined by stump density per acre was calculated by the quarter method (Phillips, 1959). Twenty-five quarter-points were taken within each site using the direction of the stream channel rather than a compass bearing as a line of orientation. The area of each stump was estimated from its approximate diameter.

Substrate temperature was determined for five randomly selected communities from each site. Thermistors were inserted 12 cm into the center of each stump community. Wires attached to the thermistors ran

from each stump to a common point on shore. A probe was attached to the shore end of each wire, and connected to a bridge circuit specifically designed to match the probes. The readout was in micro-amps and was converted to temperature by means of a calibration curve. Readings were recorded in the morning on 15 sunny, cloud-free days.

Substrate cores were taken with a metal soil corer from eight of the 15 sampled communities within each site. Samples were analyzed for pH; concentration of P, K, Mg, Ca and N; and per cent organic matter by the University of Georgia Soil Testing Laboratory.

Plants of each community were identified (Radford, Ahles and Bell, 1968; Kral, 1971; Horton, 1972) and counted by species. Above-ground portions were collected and dried to a constant weight at 105° C. The number of individuals per species was used to calculate density; dry weight of above-ground biomass was used as a measure of dominance. Species importance values for each site were calculated from the relative density, dominance and frequency values of each species (Curtis and McIntosh, 1950). Density of individuals and amount of biomass per square meter were calculated for each site. Mean species diversity, using the Shannon-Weaver index (Margalef, 1958) ( $\bar{H} = -\sum P_i \log P_i$ ) and evenness ( $\bar{J} = \bar{H}/\log S$ ) were calculated for each site based on biomass and numbers of individuals. A similarity index based on the number of species in common was calculated for the sites according to the following formula:  $S = 2c/ab$ , where  $c$  = number of species common to both areas;  $a$  = total number of species in area  $a$ ;  $b$  = total number of species in area  $b$  (Odum, 1971).

## RESULTS

Relatively few species occur on the stumps in Pen Branch (Table 1). Twenty-six of the 35 species are herbaceous - a combination of old-field plants, roadside weeds and aquatics. Of the nine woody species, only three are trees.

Mineral composition of the substrates of all four sites are similar. There is no significant difference in pH (Table 2) nutrient levels (Table 3) or organic matter (Table 3) among the sites except that site I substrate has significantly less phosphorous than the other sites (ANOVA,  $\alpha = .05$ ) and the substrates of sites III and IV have significantly more nitrogen than sites I and II (ANOVA,  $\alpha = .05$ ). The phosphorous concentration of site I is 3.34 ppm compared with an average of 5.5 ppm in the other sites. The nitrogen level of sites III and IV is 0.42% compared with 0.14% of sites I and II.

Species composition differs from site to site. Species similarity indices (Table 5) show sites I and II to be most similar in species composition with 68% of their species in common, while sites III and IV are the least similar, sharing only 29% of their species. Although species diversity varies among sites, there is no significant difference in species evenness (Table 4). Most of the other parameters vary from site to site without any pattern definitely attributable to temperature differences. Therefore, results are given for each site separately.

Stump communities at site I, located nearest the reactor, contain more species than any other site. Importance values (Table 6) indicate

that four species share dominance: Fimbristylis spadicea, Eupatorium capillifolium, Eupatorium sp., and Paspalum dilatatum. Although site I has the greatest number of species, it has the lowest biomass per meter squared (Table 7). Species diversity calculated using biomass (Table 4) is not significantly different from the biomass diversity of site II (ANOVA,  $\alpha = .05$ ). It is, however, significantly lower than that of site IV, and significantly greater than that of site III. Stump density is 180 per acre, and mean substrate temperature is  $42.9^{\circ}\text{C}$ .

In contrast to the shared dominance in the communities of site I, the communities of site II are dominated by a single species, Ludwigia leptocarpa (Table 6). There is also a much greater standing crop in site II than in site I; however, biomass diversity (Table 4) as well as mean substrate temperature is not significantly different from those of site I. Stump density is 159 per acre.

Mean substrate temperature of site III (Table 2) is  $4^{\circ}\text{C}$  lower than that of sites I and II. Biomass diversity and evenness are lower (Table 4) as is the density of individuals (Table 7). Site III has fewer species than any of the other sites and is dominated by a single species, Panicum anceps (Table 6). Stump density, 216 per acre, is higher than that of the other sites.

The density of stumps at site IV, the ambient area, is 173 per acre. The mean substrate temperature is  $13^{\circ}\text{C}$  below the mean substrate temperature of site I and II. The greatest density of individuals, the greatest biomass per meter squared, and the highest diversity based on biomass and numbers occur in this site. The density of individuals (Table 7) is four times that in site I, twice that in site II, and nine times that in site III. The standing crop of site IV is

approximately three times that of the three thermal sites. The diversity at site IV is significantly greater than that of the other sites (ANOVA,  $\alpha = .05$ ). Of the 19 species present in site IV, Hypericum walteri is the obvious dominant with an importance value 40 points above that of Lycopus sp., the species second in importance (Table 6). Approximately one-third of the plants in the ambient area are not found in any of the thermal areas.

Table 1. Species occurring on stumps in Pen Branch

1. *Acer rubrum* L.
2. *Alnus serrulata* (Aiton) Wild
3. *Ambrosia artemisiifolia* L.
4. *Ammannia coccinea* Rottboell
5. *Ampelopsis arborea* (L.) Koehne
6. *Andropogon virginicus* L.
7. *Bidens frondosa* L.
8. *Boehmeria cylindrica* (L.) Schwartz
9. *Cassia nictitans* L.
10. *Cephalanthus occidentalis* L.
11. *Cicuta mexicana* C. and R.
12. *Cuscuta* sp.
13. *Cyperus strigosus* L.
14. *Eclipta alba* (L.) Hasskarl
15. *Eupatorium capillifolium* (Lam.) Small
16. *Eupatorium* sp.
17. *Fimbristylis spadicea* (L.) Vahl
18. *Galium tinctorium* L.
19. *Hydroclea quadrivalvis* Walter
20. *Hypericum walteri* Gmelin
21. *Ilex opaca* Aiton
22. *Itea virginica* L.
23. *Juncus marginatus* Rostk.
24. *Lespedeza cuneata* (Dumont) G. Don
25. *Liquidambar styraciflua* L.
26. *Lobelia cardinalis* L.

Table 1. (continued) Species occurring on stumps in Pen Branch

27. *Ludwigia decurrens* Walter
28. *L. leptocarpa* (Nuttall) Hara
29. *Lycopus* sp.
30. *Myrica cerifera* L.
31. *Panicum anceps* Michaux
32. *Paspalum dilatatum* Poiret
33. *Polygonum hydropiperoides* Michaux
34. *Ptilimnium capillaceum* (Michaux) Raf.
35. *Rubus* sp.

Table 2. Mean substrate temperature ( $n = 5$ ) and pH ( $n = 9$ ) of stump communities in Pen Branch

Site	Temperature $^{\circ}\text{C}$		pH	
	$\bar{x}$	s.d.	$\bar{x}$	s.d.
I	42.90	3.22	5.55	0.47
II	42.80	1.58	5.48	0.15
III	38.90	0.70	5.46	0.24
IV	24.70	0.82	5.42	0.14

Table 3. Mean substrate nutrient concentrations. P, K, Ca and Mg expressed as ppm. N and organic matter expressed as % (n = 9).

Site	P*	K	C	Mg	N**	O.M.
I	3.34 $\pm$ 1.25	30.84 $\pm$ 10.48	596.57 $\pm$ 291.25	55.94 $\pm$ 23.09	0.29 $\pm$ 0.18	15.31 $\pm$ 9.89
II	6.00 $\pm$ 0.66	33.10 $\pm$ 10.51	602.07 $\pm$ 248.88	54.32 $\pm$ 25.77	0.23 $\pm$ 0.35	14.80 $\pm$ 14.18
III	4.69 $\pm$ 1.07	28.75 $\pm$ 9.11	899.94 $\pm$ 329.16	73.44 $\pm$ 34.42	0.81 $\pm$ 0.18	29.83 $\pm$ 7.05
IV	5.67 $\pm$ 0.64	33.16 $\pm$ 16.58	781.81 $\pm$ 241.79	59.35 $\pm$ 19.13	0.84 $\pm$ 0.17	16.43 $\pm$ 7.05

\*  $\alpha = .05$ , significantly less P in site I

F = 9.65

P = 0.0023

\*\*  $\alpha = .05$ , significantly more N in sites III and IV

F = 11.89

P = 0.0011

Table 4. Species diversity ( $\bar{H}$ ) and evenness ( $\bar{J}$ ) calculated using biomass and number of individuals ( $n = 15$ ).

Site	Biomass		Numbers	
	$\bar{H}$	$\bar{J}$	$\bar{H}$	$\bar{J}$
I	1.51 $\pm$ 0.63	0.73 $\pm$ 0.17	1.61 $\pm$ 0.76	0.83 $\pm$ 0.14
II	1.68 $\pm$ 0.53	0.68 $\pm$ 0.17	1.89 $\pm$ 0.56	0.76 $\pm$ 0.13
III	0.98 $\pm$ 0.67	0.43 $\pm$ 0.22	1.73 $\pm$ 0.57	0.82 $\pm$ 0.14
IV	2.12 $\pm$ 0.39	0.78 $\pm$ 0.11	2.09 $\pm$ 0.61	0.76 $\pm$ 0.13

Shannon-Weaver Index

$$\bar{H} = -\sum P_i \log P_i \quad \text{where } P_i = \text{probability of each species}$$

Evenness

$$\bar{J} = \bar{H}/\log S \quad \text{where } S = \text{number of species}$$

Table 5. Indices of similarity\* between sites.

Sites	Number of Species Shared	S
I & II	15	.68
I & III	11	.55
I & IV	12	.56
II & III	12	.66
II & IV	9	.46
III & IV	5	.29

$$S = \frac{2c}{a+b}$$

a = number species in area a

b = number species in area b

c = number species common to a&b (Odum, 1971)

Table 6. Importance values of each species at each site. Importance value = relative density + relative frequency + relative dominance (Curtis and McIntosh, 1950) \* = importance less than 10; - = species absent.

Species	I	II	III	IV
<i>Eupatorium capillifolium</i>	38	*	-	-
<i>Eupatorium</i> sp.	43	26	*	*
<i>Ludwigia leptocarpa</i>	17	63	35	-
<i>Fimbristylis spadicea</i>	45	*	-	-
<i>Andropogon virginicus</i>	19	*	-	41
<i>Ilex opaca</i>	*	-	-	-
<i>Acer rubrum</i>	*	-	*	-
<i>Cyperus strigosus</i>	12	32	32	25
<i>Ambrosia artemisiifolia</i>	*	*	-	*
<i>Hydrolea quadrivalvis</i>	*	-	-	-
<i>Juncus marginatus</i>	*	-	-	-
<i>Paspalum dilatatum</i>	36	35	39	-
<i>Galium tinctorium</i>	22	*	-	*
<i>Myrica cerifera</i>	*	-	-	*
<i>Itea virginica</i>	*	-	-	11
<i>Lycopus</i> sp.	10	45	-	22
<i>Boechmeria cylindrica</i>	*	10	*	*
<i>Ludwigia decurrens</i>	*	13	*	-
<i>Ptilimnium capillaceum</i>	11	*	-	*
<i>Polygonum hydropiperoides</i>	*	*	-	-
<i>Lespedeza cuneata</i>	*	-	*	10

Table 6. (continued) Importance values of each species at each site.

value = relative density + relative frequency + relative dominance (Curtis and McIntosh, 1950) \* = importance less than 10; - = species absent.

Species	I	II	III	IV
<i>Ammannia coccinea</i>	*	14	23	-
<i>Panicum anceps</i>	-	*	51	-
<i>Cassia nictitans</i>	-	10	14	-
<i>Cephaelanthus occidentalis</i>	-	*	*	13
<i>Liquidambar styraciflua</i>	-	*	-	-
<i>Alnus serrulata</i>	-	*	-	11
<i>Ampelopsis arborea</i>	-	-	28	-
<i>Eclipta alba</i>	-	-	*	-
<i>Lobelia cardinalis</i>	-	-	-	*
<i>Cicuta mexicana</i>	-	-	-	*
<i>Hypericum walteri</i>	*	-	-	85
<i>Bidens frondosa</i>	-	-	-	40
<i>Cuscuta</i> sp.	-	-	-	*
<i>Rubus</i> sp.	-	-	-	*

Table 7. Biomass ( $\text{g/m}^2$ ) and density (individuals/ $\text{m}^2$ ) at each site  
(n = 15).

Site	Biomass	Density
I	621.80	306.70
II	733.70	515.90
III	643.30	162.50
IV	2032.90	1196.90

## DISCUSSION

The differences in community structure of the four sites are due not only to the differences in water and substrate temperatures, but also to a combination of temperature and other factors related to the location of the sites in the stream. A temperature effect is indicated by a significantly lower biomass per square meter in the thermal sites than in the ambient site and by a significantly lower diversity in the thermal sites. However, the greatest differences in species composition, biomass diversity and density occur between the ambient site (IV) and the 40°C thermal site (III) rather than between site IV and the 50°C site (I). The location of site III near the swamp delta may affect the community structure because the delta is subject to higher flood levels than is the stream itself. The communities of site III, therefore, may be affected by flooding as well as by substrate temperature.

Of the species found on Pen Branch stump and log communities, 34% were also reported by Dennis and Batson (1974) from the Santee Swamp stump and log communities. Two-thirds of these species occur in the ambient area of Pen Branch, and all but one occur in the thermal areas. The species common to both Pen Branch and the Santee Swamp are not of the same rank in importance in the two swamps, however. The stump communities of the Santee are dominated by Boehmeria cylindrica which occurs infrequently in all four sites in Pen Branch, and by Hypericum walteri which occurs in two sites in Pen Branch but is important in

only one location. Several of the species of intermediate importance in the Santee Swamp, including Ludwigia leptocarpa, are dominants in the thermal sites in Pen Branch. Of the species common to both the Santee Swamp and Pen Branch, approximately 30% are described by Dennis and Batson (1974) as occurring in a natural swamp only on stumps or logs rather than on the swamp floor.

Some of the species in Pen Branch, including Lespedeza cuneata and Andropogon virginicus are not typically found in swamps, but are normally characteristic of old-field communities. The substrate of the stump communities in Pen Branch is much richer than the soil of South Carolina coastal plain old fields, and supports a much larger standing crop of herbaceous vegetation. Soil nutrient levels for an old-field on the Savannah River Plant are very low (J. E. Pinder, personal communication). P, K, Ca, and Mg levels in the old-field soils are below the minimum quantities measureable by the Soil Testing Laboratory. (The minimum measureable levels are 3.5 ppm for P; 23.5 ppm for K; 59.5 ppm for Ca; and 19.5 ppm for Mg.) The mean % N was 0.0395% and mean organic matter was 0.925%. These values are all considerably lower than those obtained for the stump substrates in Pen Branch. The largest standing crop reported by Odum (1960) for a three year old field in South Carolina was  $202.5 \text{ g/m}^2$ . In contrast, the smallest standing crop of the communities in Pen Branch is  $621.8 \text{ g/m}^2$  (site I); the largest is  $2032.9 \text{ g/m}^2$  (site IV).

In comparison with an undisturbed southeastern mixed hardwood swamp, similar to that which originally occupied the Pen Branch areas, the substrates of the present communities in Pen Branch are rather poor. Nutrient levels (ppm) reported by Monk (1966) for soils in a

mixed hardwood swamp are much higher those of the Pen Branch stumps. There is 19 times as much phosphorous, six times as much potassium, 10 times the amount of calcium and 14 times the amount of magnesium in the undisturbed swamp soils as is present in the stump substrates in Pen Branch.

The species composition in Pen Branch is completely different from that of an undisturbed swamp forest. Pen Branch is dominated by herbaceous species and contains few woody species, whereas a natural swamp forest is dominated by trees and contains very few herbaceous species. Species diversity ( $\bar{H}$ ) in an undisturbed swamp is higher (2.28; Monk, 1967) than diversity in Pen Branch where it ranges from 1.69 in the hottest site to 2.09 in the ambient site.

The vegetation of the stump communities in Pen Branch is a combination of old-field species, roadside weeds and aquatic herbs. Other parameters, including species diversity, evenness, standing crop and soil nutrient content are intermediate between the values reported for old-field communities and undisturbed mature swamp systems (Odum, 1960; Monk, 1966 and 1967; Pinder, personal communication). The community structure of stumps is that of a once mature system which was destroyed stress, has recovered to the point of an early successional stage, and is maintained at that stage by the stress.

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(3). The following report includes the experimental design, partial results, and description of a new conceptual approach to the evaluation of environmental quality. This work is the basis for a M. S. thesis by Kevin Summer, conducted under my direction. Similar research was to have been supported by this contract.

An Ecological Land Use Plan for the Shearon Harris Nuclear Power Plant  
Suitability and Alternatives Analysis

Introduction

The Research Problem

The problem to be discussed involves the investigation of several hypothetical ecological constructs and principles and their applicability to land use planning and land use problems. There are three general objectives of this study.

- (1) To discuss the theoretical effects of ecological diversity, spatial heterogeneity and successional state on the community stability of the five vegetational communities described at the Shearon Harris Nuclear Power Plant site; namely, the (a) old field, (b) pine, (c) hardwood, (d) scrub, and (e) mixed pine-hardwood communities.
- (2) To provide insight into the use of these ecological principles and perspectives in land use planning in order to determine their applicability in land use methodology. This objective involves the organization of a conceptual framework relevant for the analysis of ecological principles in relation to land use planning and policy formulation.
- (3) To apply this theoretical orientation to a specific land use problem, the Shearon Harris Nuclear Power Plant site, producing ecological conclusions in the form of an ecological component of a land use plan in an attempt to ascertain

(a) the best use(s) for the site area, (b) possible alternative land uses for the site and (c) the "best" ecological use(s) for the surrounding area in light of the construction of the Shearon Harris Nuclear Power Plant.

#### The Importance of the Problem

The vast majority of research concerning the relationship of ecological concepts and environmental quality to land use planning has been conducted by professionals other than ecologists. Hill (1968) and Michelson (1970) are representative of sociologists, who have taken an interest in ecology's relationship to land usage. Political scientists, such as Eyerson and Banfield (1955), have also been concerned with planning policy.

The major input into the study of relationships among ecological principles, environmental quality and land use planning has come from land use planners. Achard (1971), Ignire and Patri (1971), O'Riordan (1971) and Kaiser (1974) have attempted to analyze ecological relationships in accordance with resource management in terms of formal planning methodologies.

The method used in this thesis involves a review and evaluation of the interdisciplinary literature concerning ecological principles, environmental quality and land use planning, some of which have been mentioned above. The ecological literature relating ecological principles, and environmental quality assessment to land usage is relatively limited (McCormick, 1972; Neunscher, 1972; Inhaber, 1974)

#### Background

Since the beginning of civilization, when man began to settle in

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larger groups, he began altering the land to meet his needs. Domestication of animals and selection of crop plants began the progressively intensive management of ecosystems which culminated in western industrialized agriculture.

As a result of this process of increasing independence from environmental conditions, man developed a conceptualization of the environment as being separate from himself and imagined himself apart from it. This capacity of human thought and perception has characterized western religion, philosophy and technology and effectively set man apart from the natural environment.

As man is both part and product of his environment, and while his very existence as a biological creature is dependent upon environmental conditions, man needs not only a better understanding of his effect on nature, but there is also a need to change the behavior of man as he affects nature.

Although the natural environment is essential to man to sustain life, conflicting arguments over environmental policies have often failed to adequately consider this dependency. As a result, the resolution of such conflicts has generally resulted in short-term individual benefits, but with long-term common ecological losses.

It is therefore increasingly apparent that whatever form man's activities take, he is part of a large and exceedingly complex system. It is a mistaken view which tries to separate the activities of man and nature or of ecologists and planners, for in essence, they are part of the same system, however large and complex this system may be. The following pages will discuss some important elements of such a system as a conceptual tool in structuring the land use process.

The best management of our resources (inclusive of land) depends, among other factors, upon a sound understanding of the structure and function of ecological systems. To date, narrow approaches such as specialized agriculture and industrial strategies, designed to maximize production of food, power, and other products, have dominated our management of resources and have invariably led to imbalances and instabilities in ecosystems.

When man simplifies an ecosystem he creates numerous ecological problems. Whenever man or nature perturbs an ecosystem he forces that system back in ecological time to a former state, reducing its stability through simplification (Margalef, 1968). Perturbations, such as these, are so much a part of our technology and culture that many think it is questionable whether the problems creating the "environmental crisis" can be controlled.

... In more recent years, an emphasis on environmental quality objectives has initiated a search for appropriate criteria on which to base resource usage. Environmental resources analyses are the result of a growing field of research in planning, where environmental and ecological processes are studied and established as constraints on land usage.

If a harmonious juncture is to be reached between natural ecosystems and man's developmental interests, land use techniques must be developed to match natural systems with suitable developmental practices. At this time there are no land use methodologies which solidly integrate ecological principles and land use management practices. There is a definite need for just such an integrated approach if we are to enjoy both good environmental quality and developmental progress. If such a land use methodology is to be realized, a solid basis in ecological

theory is absolutely necessary. No planning method can claim to be ecological or environmental, unless it has a theoretical basis in the science concerned with the interrelationships of organisms and their environments, ecology.

Before mentioning the various methodologies which have been used in an attempt to narrow the gap between ecology and land use planning, three terms, which will be used throughout this thesis, must be re-emphasized. Ecology is a science and as a science it conforms to the restraints of scientific method and investigation. Environmental quality is a description of the state of existence of a natural system. It is not a science, simply a description. Land use planning is an art representing the planner's attempt to project the "best" overall utilization of an area's natural resources through a formalized plan. The three are in no way synonymous and must not be confused but as a group the three can serve as a bridge between the science of ecology and that science's application in a "real world" problem, land use planning. Ecological principles and methods can be used in defining, discussing and measuring environmental quality and ecological relationships; and consequently, these findings can be directly or indirectly applied to land use planning problems giving a needed ecological input to the program of the planner.

Attempts by planners and landscape architects to incorporate ecological systems into land use planning are discussed by Kaiser, et.al. (1974) and are epitomized by Ian McHarg (1969a, 1969b, 1971, 1972), and Thomas Ingmire and Tito Patri (1971). Attempts by scientists to add sound ecological principles to land use planning procedures are exemplified by the ecologists, J. Frank McCormick (1972) and J.E. Wuenscher (1972), the

geologist, Luna Leopold and the Canadian government's environmental office (Inhaber, 1971).

#### Materials and methods

The basic materials necessary to begin an ecological investigation of a land use problem are all those materials and literature related to the specific land area and the specific proposed usage in question. The specific application of the conceptual framework to be developed in this thesis is to formulate an ecological component of a land use plan for the Shearon Harris Nuclear Power Plant located in southwestern Wake County, northwestern Harnett County and southeastern Chatham County, North Carolina. All materials available were gathered in relation to this specific area and the ecological and siting problems of nuclear power plants, as well as their effluents. These included:

- 1) Aerial photographs of the site area taken by the United States Department of Agriculture in February, 1972.
- 2) Environmental impact statement of the Carolina Power and Light Company for the Shearon Harris Nuclear Power Plant project, as well as, similar environmental impact statements; for example, the impact statement for the Prairie Island Nuclear Generating Plant.
- 3) Stream Classification maps for region J, North Carolina.
- 4) Soil surveys for Wake, Chatham, and Harnett counties, North Carolina.
- 5) Topographic maps for Wake, Chatham, and Harnett counties, North Carolina.
- 6) Various literature concerning nuclear power plant siting, safety and thermal and radioactive effluents.
- 7) Literature concerning basic land use planning techniques and

their relation to ecological principles and environmental quality.

The methods involved in this investigation fall into three categories; conceptualization of the problem, confirmation of primary data and field work, and an evaluative process. The conceptualization phase consists primarily of 1) the assimilation of all materials accumulated with reference to the Shearon Harris Nuclear Power Plant project, 2) the construction of a 20'-by-18' aerial photograph map and 3) the development of a conceptual framework for dealing with land use problems employing the ecological concepts of community diversity, spatial heterogeneity, successional state and stability. The confirmation and field work phase involves the corroboration of very rough basic data taken from the aerial photo map and the expansion of that data using a complete vegetational survey, measuring those parameters deemed necessary by the conceptual framework already devised. The evaluative process calls for a complete evaluation of all data drawn from field studies and their formulation into an ecological component of a land use plan.

The first step in the conceptualization phase is self-explanatory. The construction of the aerial photograph map consisted of the formation of a collage map using the 12"-by-18" photographs provided by the USDA of the site area using an 18'by-20' backboard as backing. These photographs were then interpreted as to vegetational communities of which five were deduced; a) old field, b) pine, c) hardwood (includes bottomland as well as upland communities), d)scrub (cutover areas in various stages of recovery) and, e) mixed pine-hardwood. Each community type was then color-coded and the estimated community boundaries were outlined. The map was overlaid

with acetate plastic and the vegetational community-types were color-coded solidly, on the acetate and each community was identified by type(a,b,c,d,e) and number (1,2,3,4,...). Finally a draftsman's plenometer was used to roughly quantify the area of each individual community and the percentage of the total site area occupied by each community type. The results of this quantification are shown in Appendix 1. The method involved in the development of a conceptual framework to investigate the applicability of the ecological concepts of diversity, heterogeneity, successional state, and stability to the land use planning process involved first, a literature search of previous ecological research in order to determine the ecosystem mechanisms involved in the concepts of diversity, successional state, spatial heterogeneity, and stability; and secondly, a literature search in an attempt to discover appropriate policy pathways and principles in land use planning which might aid in determining the role of these concepts in land use methodology. The method involves an investigation of all pertinent interdisciplinary literature pertaining to land use policy perception and the relation between the afore mentioned ecological concepts and these policy formulations. In this manner the most feasible and equitable manner(s) of fusing ecological concepts and land use principles into a conceptual framework might be determined.

The confirmation and field work phase consists of the confirmation of the community-types elucidated from the aerial photographs and the conduction of a vegetational survey of the site area. The confirmation of the aerial map's representation of the vegetational community-types was undertaken by randomly choosing twenty individual communities, locating them in the field, and ascertaining whether or not they conformed to our preconception of the general vegetational structure of the five community-types (Appendix 2). The

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field work consisted primarily of gathering information concerning the structural attributes of individual communities and determining the parameters of diversity, heterogeneity and successional status in community stability; namely, species lists, density distributions, frequency distributions, dominance values and importance values as well as general physical descriptions.

These parameters were determined by using vegetational transects employing the quarter-point sampling procedure. An overview of the sampled area (Appendix 3) shows that approximately 43% of the total site area was sampled. All transects were randomly located by using individual community numbers and matching these letter-number combinations to a seed generation of random numbers by a Tektronix computer.

Community sampling consisted of from one to ten transects per individual community with a minimum of twenty points located ten meters apart travelling along a random compass line (maximum number of points was forty). At each point the nearest canopy and sub-canopy tree species in each compass quadrat were identified, counted, their distance from the central point measured in meters and their diameter-at-breast-height (DBH) measured in centimeters. Presence lists of all shrub, vine, and herb species were made. One hundred-thirty-four transects comprising 4025 points were used in the pine, hardwood, scrub and mixed pine-hardwood communities. From these measurements, relative density, relative frequency, relative dominance and importance values were computed for each tree species and presence lists were compiled for all shrubs, vines and herbs. Diversity values will be determined for each individual community and general diversity values will be determined by community-type.

Plot sampling was undertaken to gather information concerning the old field communities. A minimum of five and a maximum of ten one-square-

meter plots per individual community were employed. The items denoted were number, presence and dry biomass weight. The parameters computed are identical to those previously discussed.

As the dimensions of the environment are space and time, parameters related to these dimensions and relating these dimensions to biologic interaction were sought. The structural components described above are examples of parameters of the space dimension as is spatial heterogeneity, descriptions of which were undertaken for each sampled community and possibly numeric representations will be attempted. The temporal dimension is represented by the use of descriptions of the successional state on all individually sampled communities and temporal heterogeneity in these communities.

The evaluative process will comprise a major portion of the thesis and constitutes the synthesis of all gathered information from the field studies and their organization according to the conceptual framework derived in the initial phase. The evaluation will consist of approximately seven sections discussing: a) an evaluation of the effects of spatial heterogeneity and successional state on the community stability of the five vegetational communities located at the Shearon Harris Nuclear Power Plant site, b) a discussion of the theoretical effects of diversity, spatial heterogeneity and successional status on the stability of the five vegetational communities located there, c) a description of the patterns detected and/or relatedness deduced among the physical and biological factors at the Shearon Harris site, d) a discussion of the best use(s) for the site area in light of the discussion of the physical-biological factors found there and possible alternatives, e) a discussion of the site's suitability for the construction of the Shearon Harris Nuclear Power Plant, and f) a discussion of the "wisest" ecological uses for the

contingent areas of the Shearon Harris plant in the light of its eventual construction in order to formulate ecological suggestions for land usage in the form of an ecological component of a land use plan which would be readily utilizable by a planner, and f) finally a general review of the overall applicability of the present state of ecological knowledge and concepts for a specific land use problem (Shearon Harris Nuclear Power Plant site) in a basic and simple manner.

### Conclusion

Ecologists must learn to understand that land use decisions made on a local basis may and usually are fragmentary and often inappropriate when considered on a regional scale. But it must be also realized that this regional data, although satisfying some needs at the local level, cannot satisfy them all. To produce the necessary data for an entire region requires more effort than regional planners deem justifiable. Ecologists who are willing to search for patterns along the complex gradients of disturbance often characterized by developed areas may contribute to a much needed ecological management of systems. Legally, the upcoming land use legislation (both national and state level) requires an inductive base. Does the present state of ecological research provide it? I think not.

Here, then, is the challenge for ecologists. It is necessary to conduct research in and understand the mechanisms of altered communities. It will be necessary to develop innovative methods which will yield reproducible results, applicable over extensive areas. The approach to this research, however, remains the same: a strong conceptual framework, testable hypotheses and the application of scientific method. It is from this format that the present work begins, exploring a variety of ecological

concepts, discerning their applicability to land use problems, the development of a conceptual framework relating the two which is necessary to initiate field studies, projecting hypotheses concerning the relationship among these ecological principles, constructs and concepts and land use decision making, and finally the application of the framework to a "real world" land use problem; namely, the suitability of the Seearon Harris site for a Nuclear power plant and alternative uses from an ecological viewpoint.

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## An Ecological Index of Environmental Quality

In order that a harmonious juncture might be reached between natural ecosystems and man's developmental interests, land-use planning techniques are necessary which can match developmental practices with natural systems suitable for those practices. At this time, there are no land-use planning procedures which solidly integrate sound ecological principles with developmental methodology. There is a definite need for just such an integrated procedure if we are to enjoy both good environmental quality and developmental progress. Attempts must be made to match developmental desires to already existent natural communities and ecosystems, not vice versa. However, if such a land-use methodology is to be realized, a solid basis in ecological theory is necessary.

Before proceeding further into methodologies whereby the gap between ecology and land-use planning may be narrowed, the clarification of some basic and important terminology is necessary. Ecology is a science and as a science, it conforms to scientific method and practice. Environmental quality is not a science but simply a description of the state of existence of a natural system. Land-use planning is also not a science but an art representing the attempt to utilize available natural resources in as wise a manner as possible through a formalized plan. The three must not be in any way confused; they are in no way synonymous. Ecology is not land-use planning nor is it environmental quality, but the three may serve as an effective

bridge to close the existing gap between the art of planning and the science of ecology. The science of ecology can be used to determine environmental quality and thus, environmental quality can become an input into land-use planning. The primary purpose of this work is to determine the methodology and mechanism whereby this gap can be narrowed and an objective ecological input into land-use planning can be made available as a tool for the planner.

Attempts by planners to incorporate ecological systems into land-use planning are discussed by Kaiser (Kaiser, et.al., 1974) and are epitomized by Ian McHarg's work (1969a, 1969b, 1971, 1972); whereas attempts by ecologists to add sound ecological practices to land-use planning procedures are exemplified by Dr. J. Frank McCormick's work on the wetlands of Mystic Islands, New Jersey (McCormick, 1972).

The primary objective of McHarg's natural systems inventory approach is the development of an information base to be used as a rationale in land-use planning. McHarg's central notion is that certain uses of the land conform to natural systems more suitably than others. McHarg's studies appear to be a good start at trying to integrate ecological principles into land-use planning techniques but his approach does not adequately assess the natural environmental quality of the original ecosystems. His approach to ecosystem inventory is lacking in that it tends to emphasize only one or two ecosystem components; usually area hydrology, virtually

ignoring all other ecological perspectives such as vegetational structure or successional state. McCormick's ecosystem analysis approach, on the other hand, has a solid basis in field sampling, an absolute necessity if one is to project uses for a land area. This ecosystem analysis approach differs from McHarg's natural systems inventory primarily in the degree of its integration of components and its stress on biological components (Kaiser, 1974). In short, an ecosystem is complex of interrelated systems; thus, an ecosystem approach to planning would stress that interrelatedness rather than attempting to examine individual phenomenon separately. An ecosystem analysis is primarily based on biotic components in a community because these components tend to be a fairly accurate reflection of the total effect of most environmental influences. For example, knowing the stage of succession of a particular plant community, an ecologist can tell a good deal about the length of time since the system's last disturbance, its productivity, its ecological diversity and its stability. These in turn indicate the community's role in the totality of the ecosystem. It is this approach that will be utilized as a basis for the development of an Ecological Index of Environmental Quality which can be utilized as a tool by land-use planners. This mathematical index uses a complete ecosystem analysis as its base in conjunction with a Successional Continuum Index, to be discussed further under methods. Using this approach, one will be enabled to determine an area's suitability for and susceptibility to disruption by varying land uses.

### Objectives

The primary objective of the proposed work is the generation of an ecological index of environmental quality using the 24,000-acre area surrounding the Shearon Harris Nuclear Power Plant now undre construction in southwestern Wake County, North Carolina as a test area. Secondary objectives, essential to the realization of the primary goal, include, (1) the construction of a community successional continuum index for the piedmont region of North Carolina and (2) a complete ecosystem inventory of the vegetational communities surrounding the plant site. Both secondary objectives have been completed. It is the opinion of both Dr. J. Frank McCormick and myself that the completion of these secondary objectives sufficiently satisfies the thesis requirement for a Master's degree at the University of North Carolina, but it is my wish to continue and complete the primary objective of generating an ecological index of environmental quality and applying it to the contingent areas of the Shearon Harris Nuclear Power Plant producing the ecological component necessary to formulate a land-use plan. This ecological index of environmental quality and the sucesional continuum index will serve as the research materials to be utilized for the compilation of a Master's thesis, partially fulfilling the requirements for that degree. Presently, this study is under consideration for funding by the Carolina Power and Light Company and if approved, the ecological component of a land-use plan would be required.

## Materials and Methods

Materials: Any attempt at land-use planning generation must begin with an accumulation of all materials pertinent to the area under investigation. These materials may include maps, surveys, impact statements, or other printed data either directly or indirectly related to the area in question. In conjunction with the Shearon Harris Nuclear Power Plant site, the following materials have been assembled.

(a) An 18-foot by 12-foot aerial photo collage of the 24,000 acre research area with the vegetational communities delineated by color variation on an acetate overlay. (The 24,000-acre figure does not include the area to be inundated by a reservoir or area to be cleared for the plant site proper, but these areas are included in the photo collage.) The community typology is as follows:

- (1) Old field community - green
- (2) Pine community - blue
- (3) Hardwood community - orange
- (4) Scrub community - purple
- (5) Mixed pine-hardwood community - yellow

Using a draftman's planimeter, individual communities were measured to determine their areas and the total areas for community types. These totals are shown in Appendix 1 and a description of the vegetation of each of the community types is shown in Appendix 2 (Summers, 1974a, 1974b).

(b) Two maps (hand-drawn) comparing the vegetational

distribution as shown by the Carolina Power and Light Company's environmental impact statement and the distribution as described by the map described in A.

(c) Soil surveys for Wake County, North Carolina (Soil Conservation Service, 1970)

(d) Stream classification map for Region J (North Carolina State Planning Commission, 1972)

(e) General and specific research papers and data concerning nuclear power plant siting, operation, safety, thermal discharge, radioactive discharge, land-use planning, and environmental monitoring.

(f) The Carolina Power and Light Company's environmental impact statement as well as other impact statements for similar nuclear power plants previously constructed (Carolina Power and Light Company, 1971; Northern States Power Company, 1971)

(g) A bibliography compiled for the purpose of bridgeing the gap between ecological theory and land-use planning procedures. (Appendix 3)

(h) A successional continuum index of plant species for the piedmont region of North Carolina compiled using major successional research works (Braun, 1964; Daubenmire, 1968; Keever, 1950; Oosting, 1942, 1956).

This index ranks herbs, vines, shrubs, sub-canopy and canopy species with values ranging from 1 to 10 where a value of 1 indicates an early successional species and 10 describes late successional species.

(Summers, 1974c)

Methods: Essential to all land-use planning, from the perspective of the ecologist, is that the planner be able to describe what constitutes his study region. In short, it is not possible to objectively plan land-use unless one knows the materials he is planning with. This can be accomplished by conducting a vegetational inventory within each of the community types. Quarter-point sampling was conducted in a randomly selected 10% of each of the community types beginning in May, 1974 and continuing until August, 1974. During the same period, plot sampling was conducted at the old field sites. Relative density, relative frequency, relative dominance, and importance values are being computed for each of the tree species and presence lists were compiled for shrubs, vines and herbs in the pine, hardwood, scrub and mixed pine-hardwood communities. Dry biomass weight was used as an indicator of relative dominance in the old field site sampling.

The dimensions of the environment are space and time, a concept with which all ecologists are familiar (Odum, 1971). These dimensions are continuous and it was the notion of a continuous space dimension which prompted J.T. Curtis to develop the continuum theory of community composition (Curtis and McIntosh, 1951; Curtis, 1955).

This method looks at the arrangement of community populations along a uni or multi-dimensional environmental gradient or axis with community recognition based on frequency distributions, similarity coefficients or other statistical comparisons. The term ordination is frequently used to designate the ordering of species and communities along gradients and the term continuum to designate the gradient containing the ordered communities.. In general, the steeper the environmental gradient, the more distinct or discontinuous are communities, not only because of the greater probability of abrupt physical environment changes, but because boundaries are sharpened by competition and co-evolutionary processes.

Using the Curtis-McIntosh community continuum as a guide, I suggest that we proceed a step further incorporating the second environmental dimension; namely, time, in a similar continuum approach. It is generally accepted among ecologists that the effect of disturbance or disruption within a natural ecosystem is to set that system back in time if the system is terrestrial or push it forward in time if the system is aquatic. Examples of this concept can be seen in a multitude of areas ranging from random lightning fires to waste-water pollution of varying water bodies. Combining this notion with the continuum idea enables us to suggest an index which quantitatively describes successional continuum. This successional continuum index (Appendix 4) ranks vegetational species most frequently found in various successional states using values ranging from 1 through 10. This approach as stated earlier is based primarily on frequency and similarity data supplied by early successional works (Keever, 1950; Oosting, 1942, 1956).

A value of 1 represents early successional species and a value of 10 represents a late successional species. The next step is then to ordinate this continuum scale in order to identify individual communities as to successional stage; in short, what we have then identified is what I will call an Ecological Index of Environmental Quality.

Using the importance values generated from the field sampling already mentioned, an ecological index of environmental quality will be generated for each site. These values are first computed for individual species within a site by multiplying the species' importance value by their successional continuum number. The ecological index of environmental quality (EIEQ) value for a community is then computed by summing the index values for all species present in the community and then dividing that sum by a spacing coefficient of structure. The spacing coefficient is added to the equation here in order to incorporate community structure as well as community composition into the methodology. Both forest density and strata development levels are included in this structural coefficient, which takes the form of:

$$S' = \bar{D}^2 / L \text{ where,}$$

S = spacing coefficient of structure

$\bar{D}$  = mean distance between tree species

L = number of fully developed strata within a community.

Overall, the equation representing the computed EIEQ values would be as follows:

$$\text{EIEQ}(t) = \sum \text{EIEQ}(c) + \sum \text{EIEQ}(sc) + \sum \text{EIEQ}(s) + \sum \text{EIEQ}(v) + \\ \sum \text{EIEQ}(h) / S', \text{ where,}$$

EIEQ(t)= Ecological Index of Environmental Quality  
Number for Community

EIEQ(c)= Ecological Index of Environmental Quality  
Number for Canopy species

EIEQ(sc)=Ecological Index of Environmental Quality  
Number for Sub-canopy species

EIEQ(s) =Ecological Index of Environmental Quality  
Number for shrub species

EIEQ(v)= Ecological Index of Environmental Quality  
Number for vine species

EIEQ(h)= Ecological Index of Environmental Quality  
Number for herbal species

EIEQ(x)= Ecological Index of Environmental Quality  
Number for Community component x or the  
Importance values of species x' multiplied..  
by the successional continuum index (SCI)  
value of species x' + importance value of  
species x'' multiplied by SCI value of species  
x''' + ...

S' = Spacing coefficient of structure

These Community EIEQ index values will range from 1 to 10,000 with the lower values representing communities in lower successional states and with lower over-all environmental quality.

Having computed these EIEQ values for each community, a color-coded map will be constructed showing the value (EIEQ value) of each of the communities. The map will show any clustering effects which might prevail and should prove useful in ascertaining the types of permissible uses for a particular locale. Finally, an ecological component of a land-use plan will be formulated for the 24,000 Shearon Harris Nuclear Power Plant site designating suggested uses and placement of specific developments for that area. These usages will take four different perspectives;

- (1) Protection: The preservation and protection of some of all the community types is necessary and advised.
- (2) Recreation: Community areas would be set aside, relegating their use for leisure time usage by the nearby populous for such activities as camping, hiking, fishing, boating, swimming, hunting, etc.
- (3) Production: Communities designated for the purposes of agriculture, forestry or wildlife propagation.
- (4) Urbanization: Communities designated as areas for commercial, residential or institutional development.

This land-use plan component will in no way claim to be an all-encompassing plan as such important inputs as population distribution, economic motivations, political and legal arguments, and other such pertinent information will not be utilized. The plan will simply be incorporating a new method of mathematically indexing natural communities in order to match the utilization of the site area land to a good ecological perspective.

#### Justification

In closing, it is believed that new ecological inputs are necessary in land-use planning if we are to enjoy good environmental quality in conjunction with developmental progress. This system of indexing communities by successional states in relation to their environmental quality may prove useful in areas other than land-use planning. It could prove to be helpful in the formulation of legislation whereby legislators would have a tool to use in formulating land-use laws.

Primarily, any impact that might be felt from this project would take the form of bridging the gap now separating ecology and land-use planning; a gap whose existence at least partially nullifies the separate work of both the planner and the ecologist. If a tool can be formulated whereby this rift no longer exists or is at least narrowed; where a land-use plan utilizes the best methods environmentally and developmentally, truly a step forward in planning methodology will have taken place. In all, the projected benefits from such an undertaking appear to far outweigh any negative output. Thus, the project appears to be an adequate and worthwhile undertaking for a Master's degree.

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## SUMMARY

ENCLOSURE  
II

## Community Acreage/ Sector

Communities

<u>Sector</u>	Old Field	Pine	Hardwoods	Scrub	Mixed Pine-Hardwoods	Totals
1	404.24	322.80	254.34	81.25	2,414.00	3,476.60
2	1,000.31	1,164.91	2,283.64	189.84	3,351.27	7,989.96
3	326.18	3,494.65	1,072.83	255.26	3,391.47	8,540.40
4	794.44	752.82	1,797.59	446.07	2,898.12	6,689.05
5	828.78	1,509.29	1,076.46	113.16	3,203.72	6,731.41
6	142.11	419.54	323.61	235.13	1,532.58	2,653.00
7	59.39	179.26	88.95	5.97	1,833.60	2,167.20
Totals	3,555.45	7,843.27	6,897.42	1,326.68	18,624.76	38,247.58

## Percentage Community/Sector

Communities

<u>Sector</u>	Old Field	Pine	Hardwoods	Scrub	Mixed Pine-Hardwoods
1	11.37%	4.12%	3.69%	6.12%	12.96%
2	28.13%	14.85%	33.11%	14.31%	14.31%
3	9.17%	44.56%	15.55%	19.24%	18.21%
4	22.34%	9.60%	26.06%	33.62%	15.56%
5	23.31%	19.24%	15.61%	8.53%	17.20%
6	4.00%	5.35%	4.69%	17.72%	8.23%
7	1.67%	2.29%	1.29%	0.45%	9.84%

## Percentage Community

<u>Sector</u>	Old Field	Pine	Hardwoods	Scrub	Mixed Pine-Hardwoods	Totals
Computed	9.30%	20.51%	18.03%	3.47%	48.70%	100.01
Statement* <sup>8.2-21.99%</sup> <sup>1</sup>	19.12%	3.52% <sup>2</sup>	13.79% <sup>3</sup>	55.47% <sup>4</sup>		100.10

## CP&amp;L IMPACT STATEMENT

\* Percentage values taken from Environmental Impact Statement of Shearon Harris Nuclear Power Plant; Volume 1; p. 3.6-42.

<sup>1</sup> Combined values of Field and Cut-over

<sup>2</sup> Combined Hardwoods and Bottomland Hardwoods

<sup>3</sup> Value is for Cut-over areas

<sup>4</sup> Combined Pine-Hardwoods and Hardwoods-Pine

Explanation of Communities

(1) Old Field (A): Includes fields presently under cultivation as well as successional old fields; Predominated by grasses and herbs.

Old field areas concentrated in northern acreage of CP&L site (Sectors 1, 2, and 4) comprising nearly 62% of total old field acreage. Also a smaller concentration in central western region (approaching town of Corinth) (Sector 5) and accounting for about 23% of old field acreage.

(2) Pine (B): Included cultivated plantation pine as well as natural pine forest; dominantes are Pinus sp.

Pine communities concentrated in north western portion of CP&L site (sectors 3 and 5) accounting for nearly 64% of total pine acreage.

(3) Hardwoods: (C): Natural forests dominated by deciduous hardwoods species such as Quercus sp. and Carya sp.

Hardwood communities in central region of CP&L site and primarily in southcentral region (Sectors 2,4). South-central area comprises 59% of total hardwood acreage and entire central region (Sectors 2,3,4,5) account for 90% of acreage.

(4) Scrub: (D): Characterized as natural and/or man-induced combination of flora dominated by shrubs and having relatively few trees.

These communities are spread fairly evenly throughout site.

(5) Mixed Hardwoods-Pine (E): Natural Forests having Hardwoods and Pines as Co-dominates.

Easily the most dominant community on CP&L site acreage, comprising over 48% of all vegetational communities. Highly uniform throughout site.

*Enclosure II*

(A) Old Field : Natural old fields are communities which can be characterized temporally as falling into three distinct yearly stages. Almost without exception, abandoned fields follow a distinct and easily recognizable series of stages of dominance which fall in a regular succession. Fields abandoned for one year are dominated by Ericorone canadensis (horseweed) and Digitaria sanguinalis (crabgrass). In the second year Aster ericoides (Oosting, 1942) is dominant with a mixture of Ambrosia artemisiifolia (ragweed). But a literature search a taxonomic references fails to show Aster ericoides for the area in question, but dominance of an aster is expected in the second year. Here primary suspects for dominance would be Aster dumosus, A. pilosus, and/or A. patens in conjunction with Ambrosia artemisiifolia. By the third year, Andropogon virginicus, A. elliotii, and/or A. ternarius have assumed dominance and this final third year community is maintained until it is shaded out by Pinus taeda (long-leaf pine) or Pinus echinata (short-leaf pine). Pine seedlings may be found in this community as early as the third year. (Oosting, 1942, 1956; Keever, 1950; Daubenmire, 1968)

(B) Pine : Pinus taeda and/or Pinus echinata (primarily Pinus taeda) overtops the Andropogon species of the mature old field community usually by the fifth year and tends to form closed stands in 10-15 years. Neither of these pines can reproduce in their own shade but several hardwood species do. A middle-aged pine community is approximately forty years of age and is predominated almost exclusively by an overstory of primarily Pinus taeda. Normally it has developed a distinct understory of subordinate species such as Liquidambar styraciflua (sweet gum), Nyssa sylvatica (black gum), Cornus florida (dogwood), Juniperus virginiana (red cedar) and Oxydendron arboreum (sourwood). Several transgressives of Quercus species (oaks) and Carya species are present signaling the structure of the climax forest. In some lowland fields, Rubus cuneifolius (blackberry) is important in pre-pine stages and is gradually eliminated after pine comes to dominance. In addition, in some bottomland pine communities some Fagus grandifolia (beech) and Acer saccharum ssp. floridanum (southern sugar maple) is present. (Oosting; 1942, 1956; Keever, 1950; Daubenmire; 1956; Odum, 1971)

(C) Hardwoods: This community, the climax forest of this region, is dominated by a combination of oaks and hickories. The commonest upland oaks are Quercus alba (white oak), Quercus velutina (black oak), Quercus rubra (red oak), Quercus falcata (southern red oak), Quercus stellata (post oak) and Quercus coccinea. Two types of oak communities generally arise in this region (1) the white-black-red oak complex and (2) the white-post oak complex. The region in question is most likely dominated by the first community. The dominant overstory tree in this community is Quercus alba. Often as co-dominant species in these communities are found several species of hickories; primarily, Carya cordiformis (bitternut hickory), Carya ovata (shagbark hickory), Carya glabra (pignut hickory) and Carya tomentosa (mockernut hickory). These species of oaks and hickories by far contribute most of the individuals of both the overstory and understory of the hardwood community. Bottomland hardwood communities are often characterized in the earlier stages by Betula nigra (river birch) and Platanus occidentalis (sycamore) with a associated understory of Diospyros virginiana (persimmon), Fraxinus pennsylvanica (red ash), Fraxinus pennsylvanica var. subintegerrima (green ash), Ulmus americana (American elm), Ulmus rubra (slippery elm), Ulmus alata (winged elm), Nyssa sylvatica (black gum), Liquidambar styraciflua (sweet gum), and Liriodendron tulipifera (tulip poplar). Bottomland hardwood communities eventually progress to an ultimate lowland oak-hickory community. (Braun; 1964; Oosting, 1942,1956; Daubenmire, 1968; Odum, 1971)

(d) Scrub: This is a community that is primarily man-induced through the process of clear cutting. Few if any overstory trees still exist and dominance in the community is then shifted to a wide variety of understory species. These species consist of Liquidambar styraciflua, Oxydendron arboreum, Cornus florida, Juniperus virginiana, Nyssa sylvatica, Acer rubrum, and Diospyros virginiana. Some species of oaks or hickories may be present if the logging was for a pine species. (Odum, 1971; Oosting 1942,1956; Daubenmire, 1968)

(E) Mixed Pine-Hardwood: This community is successional a transitional stage between the Pine Forest (B) and Hardwood Forest (C) characterized by a co-dominance of Pine (primarily Pinus taeda) and oaks (primarily Quercus alba) although some hickories may share in that dominance.

Associated species in the understory of this community are Pinus echinata, Quercus rubra, Carya tomentosa, Acer rubrum, Quercus stellata, Quercus velutina, Carya ovata, Carya cordiformis, Quercus falcata, Quercus coccinea and occasionally Fagus grandifolia.  
(Oosting 1942, 1956; Braun; 1964; Daubenmire, 1968; Odum, 1971)

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Sector 1:

Unit Number	Plenometer Units	Square Inches	Square Feet	Acres
A-1	0.444	4.434	709,476.48	16.287
A-2	1.689	16.868	2,698,886.88	61.958
A-3	0.102	1.019	162,987.84	3.742
A-4	0.027	0.270	43,143.84	0.990
A-5	0.903	9.018	1,442,921.76	33.125
A-6	0.046	0.459	73,504.32	1.687
A-7	0.039	0.389	62,318.88	1.431
A-8	0.036	0.340	57,525.12	1.321
A-9	0.019	0.190	30,360.48	0.697
A-10	1.498	14.961	2,393,684.16	54.951
A-11	0.022	0.220	35,154.24	0.807
A-12	0.015	0.150	23,968.80	0.550
A-13	0.049	0.489	78,298.08	1.797
A-14	0.042	0.419	67,112.64	1.511
A-15	1.105	11.036	1,765,701.60	40.535
A-16	0.291	2.906	464,994.72	10.675
A-20	0.040	0.399	63,916.80	1.467
A-35	0.185	1.848	295,615.20	6.786
A-36	1.561	15.590	2,494,353.12	57.262
A-37	0.139	1.388	222,110.88	5.099
A-38	0.064	0.639	102,266.88	2.348
A-39	0.985	9.837	1,573,951.20	36.133
A-40	1.719	17.168	2,746,824.48	63.058
B-8	1.208	12.064	1,930,287.36	44.313
B-9	0.065	0.649	103,864.80	2.384
B-10	0.700	6.991	1,118,544.00	25.678
B-11	0.393	3.925	627,982.56	14.416
B-12	0.227	2.267	362,727.84	8.327
B-13	0.743	7.420	1,187,254.56	27.256
B-14	0.024	0.240	38,350.08	0.860
B-15	0.065	0.649	103,864.80	2.384
B-16	0.120	1.198	191,750.40	4.402
B-17	0.205	2.047	327,573.60	7.520
B-18	0.219	2.186	349,839.36	8.031
B-19	0.133	1.328	212,523.36	4.879
B-20	0.039	0.389	62,318.88	1.431
B-21	0.950	9.488	1,518,024.00	34.849
B-22	0.041	0.409	65,514.72	1.504
B-23	0.071	0.709	1,113,452.32	2.605
B-24	0.020	0.200	31,958.40	0.734
B-25	0.358	3.575	572,055.36	13.133
B-26	0.454	4.534	725,455.68	16.654
B-27	0.053	0.529	84,689.76	1.944
B-28	0.006	0.060	9,584.64	0.220
B-29	0.656	6.551	1,048,235.52	24.064
B-30	0.240	2.397	383,500.80	8.804
B-31	0.616	6.152	984,318.72	22.597
B-32	0.989	9.877	1,580,342.88	36.280

Unit Number	Plenemeter Units	Square Inches	Square Feet	Acres
C-1	0.813	8.119	1,299,108.96	29.823
C-2	0.340	3.396	543,292.80	12.472
C-3	0.060	0.599	95,875.20	2.201
C-4	0.422	4.215	674,322.24	15.480
C-5	0.249	2.487	397,882.08	9.134
C-6	0.070	0.699	111,854.40	2.568
C-7	4.377	43.714	6,994,095.84	160.562
D-1	0.085	0.849	135,823.20	3.118
D-2	1.037	10.357	1,657,043.04	38.040
D-3	0.225	2.247	359,532.00	8.254
D-4	0.408	4.077	651,951.36	14.967
D-5	0.009	0.090	14,381.28	0.330
D-6	0.018	0.180	28,762.56	0.660
D-7	0.027	0.270	43,143.84	0.990
D-8	0.015	0.150	23,968.80	0.550
D-9	0.274	2.737	437,830.08	10.051
D-10	0.117	1.168	186,956.64	4.292
E-1	65.800	657.200	105,154,445.80	2,414.000

Community Type	Percentage of Sector 1	Square Feet	Acres
Old Field	11.62%	17,609,078.40	404.24
Pine	9.28%	14,061,587.46	322.80
Hardwoods	7.31%	11,079,431.52	254.34
Scrub	2.33%	3,539,392.80	81.25
Mixed Pine-Hardwood	69.43%	105,154,445.80	2,414.00
Totals	99.97%	151,443,936.00	3,476.60

### Sector 2:

Unit Number	Plenemeter Units	Square Inches	Square Feet	Acres
A-41	0.020	0.020	31,958.40	0.734
A-42	0.335	3.346	535,303.20	12.289
A-43	0.328	3.276	524,117.76	12.032
A-44	0.082	0.819	131,029.44	3.008
A-45	0.312	3.116	498,551.04	11.445
A-46	1.002	10.007	1,601,115.84	36.757
A-47	2.873	28.693	4,590,824.16	105.391
A-48	0.219	2.187	349,944.48	8.034
A-49	0.306	3.056	488,963.52	11.225
A-50	0.255	2.547	407,469.60	9.354
A-51	0.038	0.380	60,720.96	1.394
A-52	0.264	2.637	421,850.88	9.684
A-53	0.066	0.659	105,462.72	2.421
A-54	1.144	11.425	1,828,020.48	41.966
A-55	1.471	14.691	2,350,540.32	53.961

## Sector 3: (Cont'd)

Unit Number

Plenometer  
Units

Square Inches

Square Feet

Acres

A-56	0.050	0.499	79,896.00	1.834
A-57	0.127	1.268	202,935.84	4.659
B-1	5.178	51.713	8,274,029.76	189.946
B-2	0.159	1.588	254,043.84	5.832
B-3	40.477	404.214	64,679,007.84	1,484.823
B-4	0.050	0.499	79,896.00	1.834
B-5	0.816	8.150	1,303,902.72	29.933
B-8	11.755	117.697	18,831,487.20	432.311
B-34	0.309	3.985	637,570.08	14.637
B-35	0.142	1.418	226,904.64	5.209
B-36	0.182	1.818	290,821.44	6.676
B-37	0.015	0.150	23,968.80	0.550
B-38	0.067	0.669	107,060.64	2.458
B-39	0.061	0.609	97,473.12	2.238
B-40	0.259	2.587	413,861.28	9.501
B-41	0.636	6.352	1,016,277.12	23.331
B-42	21.361	213.332	34,133,169.12	783.590
B-43	2.028	20.254	3,240,581.76	74.394
F-44	1.867	18.646	2,983,316.64	68.488
B-45	0.120	1.198	191,750.40	4.402
B-46	0.357	3.565	570,457.44	13.096
B-47	0.251	2.507	401,077.92	9.207
B-48	0.065	0.649	103,864.80	2.384
B-49	1.610	16.079	2,572,651.20	59.060
B-50	0.201	2.007	321,181.92	7.373
B-51	0.152	1.518	242,883.84	5.576
B-52	1.000	9.987	1,597,920.00	36.683
B-53	0.432	4.314	690,301.44	15.847
B-54	0.054	0.538	86,287.68	1.981
B-55	3.209	32.048	5,127,725.28	117.716
B-56	0.154	1.538	246,079.68	5.649
B-57	0.849	8.479	1,356,634.08	31.144
B-58	0.037	0.369	59,123.04	1.357
B-59	0.002	0.020	3,195.84	0.073
B-60	0.052	0.519	83,091.84	1.908
B-61	0.068	0.679	108,658.56	2.494
B-62	0.008	0.080	12,783.36	0.293
B-63	0.464	4.634	741,434.88	17.021
B-64	0.385	3.845	615,199.20	14.123
B-65	0.314	3.135	501,596.16	11.515
C-7	2.823	28.193	4,510,928.16	103.557
C-8	0.503	5.023	803,753.76	18.452
C-9	1.482	14.801	2,368,117.44	54.364
C-10	0.346	3.455	552,803.20	12.697
C-11	0.225	2.247	359,532.00	8.254
C-12	23.867	238.360	38,137,554.64	875.518
D-11	0.042	0.419	67,112.64	1.541
D-12	2.409	24.059	3,849,389.28	88.370
D-13	0.175	1.748	279,636.00	6.420
D-14	0.043	0.129	68,710.56	1.577
D-15	0.051	0.509	81,493.92	1.871
D-16	0.181	1.808	289,223.52	6.640
D-17	0.112	1.119	177,367.04	4.072

Sector 3: (Cont'd)

Unit Number	Plenemeter Units	Square Inches	Square Feet	Acres
D-18	0.434	4.334	693,497.28	15.921
D-19	1.235	12.339	1,974,313.28	45.324
D-20	1.939	19.365	3,098,366.88	71.129
D-21	0.184	1.838	294,017.28	6.750
D-22	0.154	1.538	246,079.68	5.649
E-1	14.053	140.347	22,455,569.76	515.509
E-2	0.329	3.326	525,715.53	12.069
E-3	0.164	1.638	262,058.88	6.016
E-4	0.276	2.756	441,025.92	10.125
E-5	11.388	113.732	18,197,112.96	417.748
E-6	0.056	0.559	89,483.52	2.054
E-7	0.544	5.433	869,268.48	19.956
E-8	1.210	12.084	1,933,483.20	44.387
E-9	20.217	201.907	32,305,148.64	741.624
E-10	3.410	34.056	5,448,907.20	125.090
E-11	0.255	2.547	407,469.60	9.354
E-12	15.392	153.720	24,595,184.64	564.628
E-13	0.900	8.988	1,438,128.00	33.015
E-14	0.917	9.158	1,465,292.64	33.638
E-15	1.515	15.130	2,420,848.80	55.575
E-16	0.317	3.166	506,540.64	11.629
E-17	5.254	52.472	8,395,471.68	192.734
E-18	3.239	32.348	5,175,662.88	118.817
E-19	0.200	1.997	319,584.00	7.337
E-20	12.613	125.966	20,154,564.96	462.685
E-21	0.204	2.038	325,975.68	7.483

Community Type	Percentage of Sector 3	Square Feet	Acres
Old Field	3.81%	14,208,704.64	326.18
Pine	40.91%	152,227,270.56	3,491.65
Hardwoods	12.56%	46,732,691.20	1,072.83
Scrub	2.98%	11,119,207.36	255.26
Mixed Pine-Hardwoods	39.71%	147,732,497.76	3,391.47
Totals	99.97%	372,020,371.60	8,540.40

Sector 5:

Unit Number	Plenemeter Units	Square Inches	Square Feet	Acres
A-58	0.105	1.049	167,781.60	3.852
A-59	0.064	0.639	102,266.88	2.348
A-60	0.322	3.216	514,530.24	11.812
A-61	3.601	35.963	5,754,109.92	132.096
A-62	0.120	1.198	191,750.40	4.402
A-63	0.168	1.678	268,450.56	6.163
A-64	0.462	4.614	738,239.04	16.948

Sector 5 (Cont'd)

Unit Number	Plenometer Units	Square Inches	Square Feet	Acres
A-65	0.356	3.555	568,859.52	13.059
A-66	4.059	40.537	6,485,957.28	148.897
A-67	0.039	0.389	62,318.88	1.431
A-68	0.043	0.429	68,710.56	1.577
A-69	0.699	6.981	1,116,946.08	25.642
A-70	2.695	26.915	4,306,394.40	98.861
A-71	0.136	1.358	217,317.12	4.989
A-72	2.488	24.848	3,975,624.96	91.268
A-73	0.069	0.689	110,256.48	2.531
A-74	0.209	2.087	333,965.28	7.667
A-75	0.020	0.200	31,958.40	0.734
A-76	0.009	0.090	14,381.28	0.330
A-77	0.920	9.188	1,470,086.40	33.749
A-78	0.182	1.818	290,821.44	6.676
A-79	0.042	0.419	67,112.64	1.541
A-80	0.007	0.070	11,185.44	0.257
A-81	0.306	3.056	488,963.52	11.225
A-82	0.030	0.300	47,937.60	1.100
A-83	0.065	0.649	103,864.80	2.384
A-84	0.079	0.789	126,235.68	2.898
A-85	5.162	51.553	8,248,463.04	189.359
A-86	0.069	0.689	110,256.48	2.531
A-87	0.067	0.669	107,060.64	2.458
B-3	13.852	138.340	22,134,387.84	508.136
B-6	2.870	28.663	4,586,030.40	105.281
B-7	0.554	5.533	885,247.68	20.322
B-66	3.788	37.831	6,052,920.96	138.956
B-67	0.091	0.909	145,410.72	3.338
B-68	0.068	0.679	108,658.56	2.494
B-69	1.100	10.986	1,757,712.00	40.352
B-70	0.864	8.629	1,380,602.88	31.694
B-71	0.965	9.637	1,541,992.80	35.399
B-72	0.079	0.789	126,235.68	2.898
B-73	8.741	87.296	13,967,418.72	320.648
B-74	0.370	3.695	591,230.40	13.573
B-75	0.153	1.528	244,481.76	5.613
B-76	2.574	25.707	4,113,046.08	94.423
B-77	0.375	3.745	599,220.00	13.756
B-78	0.095	0.949	151,802.40	3.485
B-79	0.025	0.250	39,948.00	0.917
B-80	0.370	3.695	519,230.40	13.573
B-81	0.249	2.487	397,882.08	9.134
B-82	0.968	9.667	1,546,786.56	35.509
B-83	1.168	11.665	1,866,370.56	42.846
B-84	0.114	1.139	182,162.88	4.182
B-85	0.115	1.149	183,760.80	4.219
B-86	0.076	0.759	121,441.92	2.788
B-87	0.097	0.969	154,998.24	3.558
B-88	0.020	0.200	31,958.40	0.734
B-89	0.141	1.408	225,306.72	5.172
B-90	1.307	13.053	2,088,481.44	47.945

**Sector 5(Cont'd)**

Unit Number	Plenometer Units	Square Inches	Square Feet	Acres
C-1C-12	7.037	70.279	11,244,563.04	258.140
C-13	8.195	81.843	13,094,954.40	300.619
C-14	3.108	31.040	4,966,335.36	114.011
C-15	0.540	5.393	846,876.80	19.442
C-16	1.669	16.668	2,666,928.48	61.224
C-17	0.850.	8.489	1,358,232.00	31.181
C-18	3.137	31.329	5,012,675.04	115.075
C-19	0.341	3.406	544,890.72	12.509
C-20	0.512	5.113	818,135.04	18.782
C-21	0.675	6.741	1,078,596.00	24.761
C-22	3.291	32.867	5,258,754.72	120.724
D-23	0.115	1.149	183,760.80	4.219
D-24	2.647	26.436	4,229,694.24	97.100
D-25	0.195	1.947	311,594.40	7.153
D-26	0.052	0.519	83,091.84	1.908
D-27	0.036	0.360	57,525.12	1.321
D-28	0.018	0.180	28,762.56	0.660
D-30	0.022	0.220	35,154.24	0.807
E-9	7.177	71.677	11,468,271.84	263.275
E-20	59.926	598.481	95,756,953.92	2,198.277
E-22	1.663	16.608	2,657,340.96	61.004
E-23	5.287	52.801	8,448,203.04	193.944
E-24	11.432	114.171	18,267,421.44	419.362
E-25	0.051	0.509	81,493.92	1.871
E-26	1.799	17.967	2,874,658.08	65.993

Community Type	Percentage of Sector 5	Square Feet	Acres
Old Field	12.31%	36,101,806.56	828.78
Pine	22.42%	65,744,726.88	1,509.29
Hardwoods	15.99%	46,890,941.60	1,076.46
Scrub	1.68%	4,929,583.20	113.16
Mixed Pine-Hardwoods	47.59%	139,554,343.20	3,203.72
Totals	99.99%	293,220,219.60	6,731.41

**Sector 7:**

Unit Number	Plenometer Units	Square Inches	Square Feet	Acres
A-89	0.225	2.247	375,532.00	8.621
A-90	0.229	2.287	365,923.68	8.400
A-91	0.045	0.449	71,906.40	1.651
A-92	0.043	0.429	68,710.56	1.577
A-93	0.174	1.738	278,038.08	6.383
A-94	0.249	2.187	397,882.08	9.134
A-95	0.180	1.798	287,625.60	6.603

Sector 7 (Con'td)

Unit Number	Plenometer Units	Square Inches	Square Feet	Acres
A-96	0.015	0.150	23,968.80	0.550
A-97	0.056	0.559	89,483.52	2.054
A-98	0.053	0.529	84,689.76	1.944
A-99	0.090	0.899	143,812.80	3.301
A-100	0.034	0.340	54,329.28	1.247
A-101	0.059	0.589	94,277.28	2.164
A-102	0.157	1.568	250,873.44	5.759
B-91	0.256	2.557	409,067.52	9.391
B-92	0.287	2.866	458,603.04	10.528
B-93	0.621	6.202	992,308.32	22.780
B-94	0.325	3.246	519,324.00	11.922
B-95	0.304	3.036	485,767.68	11.152
B-96	0.441	4.404	704,682.72	16.177
B-97	0.429	4.284	685,507.68	15.737
B-98	0.175	1.748	279,636.80	6.420
B-99	0.127	1.268	202,935.84	4.659
B-100	0.071	0.709	113,452.32	2.605
B-101	0.074	0.739	118,246.08	2.715
B-102	0.106	1.059	169,379.52	3.888
B-103	0.032	0.320	51,133.44	1.174
B-104	0.072	0.719	115,050.24	2.641
B-105	1.225	12.234	1,957,452.00	44.937
B-106	0.040	0.399	63,916.80	1.467
B-107	0.302	3.016	482,571.84	11.078
C-23	0.457	4.564	730,249.44	16.764
C-24	0.333	3.326	532,107.36	12.216
C-25	0.427	4.264	682,311.84	15.664
C-26	0.138	1.378	220,512.96	5.062
C-27	0.235	2.347	375,511.20	8.621
C-28	0.125	1.248	199,740.00	4.585
C-29	0.655	6.541	1,046,637.60	24.027
C-30	0.021	0.210	33,556.32	0.770
C-31	0.034	0.340	54,329.28	1.247
D-31	0.051	0.509	81,493.92	1.871
D-32	0.087	0.869	139,019.04	3.191
D-33	0.010	0.100	15,979.20	0.367
D-34	0.015	0.150	23,968.80	0.550
E-20	37.459	374.103	59,856,485.28	1,374.116
E-27	10.934	109.198	17,471,657.28	401.094
E-28	0.044	0.439	70,308.48	1.614
E-29	0.106	1.059	169,379.52	3.888
E-30	1.267	12.653	2,024,564.64	46.478
E-31	0.131	1.308	209,327.52	4.805
E-32	0.044	0.439	70,308.48	1.614

Sector 7 (Cont'd)

Community Type	Percentage of Sector 7	Square Feet	Acres
Old Field	2.74%	2,587,053.04	59.39
Pine	8.27%	7,808,835.04	179.26
Hardwoods	4.10%	3,874,956.00	88.95
Scrub	0.27%	260,460.96	5.97
Mixed Pine-Hardwoods	84.60%	79,872,031.20	1,833.60
<b>Totals</b>	<b>99.98%</b>	<b>94,403,336.24</b>	<b>2,167.20</b>

Sector 6:

Unit Number	Plenometer Units	Square Inches	Square Feet	Acres
A-103	0.069	0.689	110,256.48	2.531
A-104	0.064	0.639	102,266.88	2.348
A-105	0.096	0.959	153,400.32	3.522
A-106	0.113	1.129	180,564.96	4.145
A-107	0.723	7.221	1,155,296.16	26.522
A-108	0.280	2.796	477,417.60	10.271
A-109	0.477	4.764	762,207.84	17.498
A-110	0.182	1.818	290,821.44	6.676
A-111	0.027	0.270	43,143.84	0.990
A-112	0.296	2.956	472,984.32	10.858
A-113	0.245	2.447	391,490.40	8.987
A-114	0.163	1.628	260,460.96	5.979
A-115	0.150	1.498	239,688.00	5.502
A-116	0.516	5.153	824,526.72	18.929
A-117	0.473	4.724	755,816.16	17.351
B-108	0.302	3.016	482,571.84	11.078
B-109	0.210	2.097	335,563.20	7.703
B-110	0.180	1.798	287,625.60	6.603
B-111	0.526	5.253	840,505.92	19.295
B-112	1.250	12.484	1,997,400.00	45.854
B-113	1.083	10.816	1,730,547.36	39.728
B-114	1.650	16.479	2,636,568.00	60.527
B-115	0.576	5.753	920,401.92	21.130
B-116	0.451	4.504	720,661.92	16.544
B-117	2.256	22.531	3,604,907.52	82.757
B-118	0.341	3.406	544,890.72	12.509
B-119	0.187	1.868	298,811.04	6.860
B-120	0.111	1.109	177,369.12	4.072
B-121	0.382	3.815	610,405.44	14.013
B-122	1.932	19.295	3,087,181.44	70.872
C-12	1.710	17.078	2,732,443.20	62.728
C-16	2.978	29.741	4,758,605.76	109.243
C-32	0.557	5.563	890,041.14	20.433
C-33	0.862	8.609	1,377,407.04	31.621
C-34	2.075	20.723	3,315,684.00	76.118
C-35	0.640	6.392	1,022,668.80	23.477

**Sector 6: (Cont'd)**

Unit Number	Plenometer Units	Square Inches	Square Feet	Acres
D-35	0.678	6.771	1,083,389.76	24.871
D-36	0.137	1.368	218,915.04	5.026
D-37	5.311	53.041	8,486,553.12	194.824
D-38	0.284	2.836	453,809.28	10.418
E-23	40.749	406.960	65,113,642.08	1,494.804
E-33	0.135	1.348	215,719.20	4.952
E-34	0.058	0.579	92,679.36	2.128
E-35	0.660	0.659	105,462.72	2.421
E-36	0.155	1.548	247,677.60	5.686
E-37	0.174	1.738	278,038.08	6.383
E-38	0.442	4.414	706,280.84	16.214

Community Type	Percentage of Sector 6	Square Feet	Acres
Old Field	5.35%	6,190,342.20	142.11
Pine	15.81%	18,275,411.04	419.54
Hardwoods	12.19%	14,096,850.24	323.61
Scrub	8.86%	10,242,667.20	235.13
Mixed Pine-Hardwoods	57.76%	66,759,499.68	1,532.58
<b>Totals</b>	<b>99.97%</b>	<b>115,564,770.24</b>	<b>2,653.00</b>

**Sector 4:**

Unit Number	Plenometer Units	Square Inches	Square Feet	Acres
A-118	0.320	3.196	511,334.40	11.739
A-119	0.651	6.502	1,040,245.92	23.881
A-120	0.284	2.836	453,809.28	10.418
A-121	0.314	3.136	501,746.88	11.519
A-122	0.045	0.449	71,906.40	1.651
A-123	0.271	2.706	433,036.32	9.941
A-124	0.029	0.290	46,339.68	1.064
A-125	0.102	1.019	162,987.84	3.742
A-126	0.322	3.216	514,530.24	11.812
A-127	0.093	0.929	148,606.56	3.412
A-128	0.063	0.629	100,668.96	2.311
A-129	0.035	0.350	55,927.20	1.284
A-130	0.032	0.320	51,133.44	1.174
A-131	0.149	1.488	238,090.08	5.466
A-132	0.055	0.549	87,885.60	2.018
A-133	0.057	0.569	91,081.44	2.091
A-134	0.057	0.569	91,081.44	2.091
A-135	0.621	6.202	992,308.32	22.780
A-136	0.126	1.258	201,337.92	4.622
A-137	0.328	3.276	524,117.76	12.032
A-138	0.099	0.989	158,194.08	3.632
A-139	0.628	6.272	1,003,493.76	23.037

Sector 4: (Cont'd)

Unit Number	Plenometer Units	Square Inches	Square Feet	Acres
A-140	0.045	0.449	71,906.40	1.651
A-141	0.121	1.208	193,348.32	4.439
A-142	0.139	1.388	222,110.88	5.099
A-143	0.087	0.869	139,019.04	3.191
A-144	0.069	0.689	110,256.48	2.531
A-145	0.334	3.336	533,705.28	12.252
A-146	0.150	1.498	239,688.00	5.502
A-147	0.037	0.370	59,123.04	1.357
A-148	0.445	4.444	711,074.40	16.324
A-149	5.722	57.146	9,143,298.24	209.901
A-150	0.143	1.428	228,502.56	5.246
A-151	0.256	2.557	409,067.52	9.391
A-152	0.054	0.539	86,287.68	1.981
A-153	0.241	2.407	385,098.72	8.841
A-154	0.210	2.097	335,563.20	7.702
A-155	3.096	30.920	4,947,160.32	113.571
A-156	3.721	37.162	5,945,860.32	136.498
A-157	0.129	1.288	206,131.58	4.732
A-158	0.149	1.488	238,090.08	5.466
A-159	0.073	0.729	116,648.16	2.678
A-160	0.140	1.398	223,708.80	5.136
A-161	0.602	6.012	961,947.84	22.083
A-162	0.256	2.557	409,067.52	9.391
A-163	0.221	2.207	353,140.32	8.107
A-164	0.248	2.477	396,284.16	9.098
A-165	0.056	0.559	89,483.52	2.054
A-166	0.143	1.428	228,502.56	5.246
A-167	0.215	2.148	343,552.80	7.887
 B-57	 1.887	 18.845	 3,015,275.04	 69.221
B-123	3.946	39.409	6,305,392.32	144.752
B-124	0.999	9.977	1,596,322.08	36.647
B-125	0.289	2.886	461,798.88	10.601
B-126	0.182	1.818	290,821.44	6.676
B-127	0.123	1.228	196,544.16	4.512
B-128	0.276	2.756	441,025.92	10.125
B-129	0.069	0.689	110,256.48	2.531
B-130	0.106	1.059	169,379.52	3.888
B-131	0.357	3.565	570,457.44	13.096
B-132	0.454	4.534	725,455.68	16.64
B-133	0.169	1.688	270,048.48	6.199
B-134	3.038	30.341	4,854,480.96	111.444
B-135	0.340	3.396	543,294.08	12.472
B-136	0.052	0.559	89,483.52	2.054
B-137	0.059	0.589	94,277.28	2.164
B-138	0.596	5.952	952,360.32	21.863
B-139	0.013	0.130	20,772.96	0.477
B-140	0.106	1.059	169,379.52	3.888
B-141	0.367	3.665	586,436.64	13.463
B-142	0.249	2.487	397,882.08	9.134
B-143	0.143	1.428	228,502.56	5.246
B-144	0.135	1.348	215,719.20	4.952
B-145	0.079	0.789	126,235.68	2.898
B-146	1.236	12.344	1,975,029.12	45.340
B-147	0.454	4.534	725,455.68	16.654
B-148	0.476	4.754	760,609.92	17.461

Sector 4: (Cont'd)

Unit Number	Plenometer Units	Square Inches	Square Feet	Acres
B-149	1.375	13.732	2,197,140.00	50.439
B-150	0.056	0.559	89,483.52	2.054
B-151	0.341	3.406	544,890.72	12.509
B-152	0.237	2.367	378,707.04	8.694
B-153	0.101	1.009	161,389.92	3.705
B-154	0.064	0.639	102,266.88	2.348
B-155	0.217	2.167	346,748.64	7.960
B-156	0.245	2.447	391,490.40	8.987
B-157	0.316	3.156	504,942.72	11.592
B-158	0.467	4.664	746,228.64	17.131
B-159	0.820	8.189	1,310,294.40	30.080
C-7	9.211	91.990	14,718,441.12	337.889
C-12	11.625	116.099	18,575,820.00	426.442
C-36	3.843	38.380	6,140,806.56	140.974
C-37	0.471	4.704	752,620.32	17.278
C-38	0.556	5.553	888,443.52	20.396
C-39	1.314	13.123	2,099,666.88	48.202
C-40	0.754	7.530	1,204,831.68	27.659
C-41	1.723	17.208	2,753,216.16	63.205
C-42	1.302	13.003	2,080,491.84	47.762
C-43	0.151	1.508	241,285.92	5.539
C-44	0.054	0.539	86,287.68	1.981
C-45	0.174	1.738	278,038.08	6.383
C-46	0.696	6.951	1,112,152.32	25.532
C-47	2.570	25.667	4,106,654.40	94.276
C-48	0.198	1.977	316,388.16	7.263
C-49	0.497	4.964	794,166.24	18.232
C-50	0.057	0.569	91,081.44	2.091
C-51	5.371	53.640	8,582,428.32	197.025
C-52	8.436	84.250	13,480,051.52	309.459
D-35	2.848	28.443	4,550,876.16	104.474
D-39	1.421	14.192	2,270,644.32	52.127
D-40	0.719	7.181	1,148,904.48	26.375
D-41	0.076	0.759	121,441.92	2.788
D-42	0.545	5.443	870,866.40	19.992
D-43	0.332	3.316	530,509.44	12.179
D-44	0.191	1.908	305,202.72	7.006
D-45	0.375	3.745	599,220.00	13.756
D-46	0.375	3.745	599,220.00	13.756
D-47	0.823	8.219	1,315,088.16	30.190
D-48	0.102	1.019	162,987.84	3.742
D-49	0.055	0.549	87,885.60	.018
D-50	0.045	0.449	71,906.40	1.651
D-51	0.454	4.534	725,455.68	16.654
D-52	0.814	8.129	1,300,706.88	29.860
D-53	3.284	32.797	5,247,569.28	120.468
E-15	7.359	73.494	11,759,093.28	269.952
E-23	64.897	643.133	102,901,254.24	2,362.288
E-39	0.132	1.318	210,925.44	4.842
E-40	0.267	2.667	426,644.64	9.794
E-41	0.316	3.156	504,942.72	11.592
E-42	0.096	0.959	153,400.32	3.523

Sector 4: (Cont'd)

Unit Number	Planimeter Units	Square Inches	Square Feet	Acres
E-43	0.157	1.568	250,873.44	5.759
E-44	0.169	1.688	270,048.48	6.199
E-45	0.063	0.629	100,668.96	2.311
E-46	0.325	3.246	519,324.00	11.922
E-47	0.042	0.419	67,112.64	1.541
E-48	0.266	2.657	425,046.72	9.758
E-49	0.455	4.544	727,053.60	16.691
E-50	3.122	31.179	4,988,706.24	114.525
E-51	0.423	4.225	675,920.16	15.517
E-52	0.641	6.402	1,024,266.72	23.514
E-53	0.182	1.818	290,821.44	6.676
E-54	0.391	3.905	624,786.72	14.343
E-55	0.041	0.409	65,514.72	1.504
E-56	0.118	1.178	188,554.56	4.329
E-57	0.042	0.419	67,112.64	1.541

Community Type	Percentage of Sector 4	Square Feet	Acres
Old Field	11.88%	34,606,153.44	794.44
Pine	11.25%	32,792,999.04	752.82
Hardwoods	26.87%	78,302,872.16	1,797.59
Scrub	6.67%	19,430,707.20	446.07
Mixed Pine-Hardwoods	43.33%	126,242,071.68	2,898.12
<b>Totals</b>	<b>100.00%</b>	<b>291,374,803.52</b>	<b>6,689.05</b>

Sector 2:

Unit Number	Planimeter Units	Square Inches	Square Feet	Acres
A-17	0.091	0.909	145,410.72	3.338
A-18	0.123	1.228	196,544.16	4.512
A-19	0.038	0.390	60,720.96	1.394
A-21	0.109	1.089	174,173.28	3.998
A-22	0.026	0.260	41,545.92	0.954
A-23	0.115	1.149	183,760.80	4.219
A-24	0.771	7.700	1,231,956.32	28.283
A-25	0.057	0.569	91,081.44	2.091
A-26	0.349	3.485	557,674.08	12.802
A-27	0.289	2.886	461,798.88	10.601
A-28	2.160	21.572	3,451,507.20	79.236
A-29	0.044	0.439	70,308.48	1.614
A-30	0.067	0.669	107,060.64	2.458
A-31	0.096	0.959	153,460.32	3.522
A-32	0.011	0.110	17,577.12	0.404
A-33	1.424	14.221	2,275,438.08	52.237
A-34	1.285	12.833	2,053,327.20	47.138
A-167	0.846	8.449	1,351,840.32	31.034
A-168	0.114	1.139	182,162.88	4.182
A-170	0.059	0.589	94,277.28	2.164
A-171	0.096	0.959	153,400.32	3.522
A-172	0.251	2.507	401,077.92	9.207

## Sector 2: (Cont'd).

Unit Number	Perimeter Units	Square Inches	Square Feet	Acres
B-169	2.534	25.307	4,049,129.28	92.955
B-170	0.102	1.019	162,987.84	3.742
B-171	0.074	0.739	118,246.08	2.715
B-172	0.046	0.459	73,504.32	1.687
B-173	0.051	0.509	81,493.92	1.871
B-174	0.055	0.549	87,885.80	2.018
B-175	0.058	0.579	92,579.36	2.128
B-176	0.187	1.868	298,811.04	6.860
B-177	0.225	2.247	359,532.00	8.254
B-178	3.413	34.086	5,453,700.96	125.200
B-179	0.042	0.419	67,112.64	1.541
B-180	0.028	0.280	44,741.76	1.027
B-181	0.026	0.260	41,545.92	0.954
B-182	0.035	0.350	55,927.20	1.284
B-183	0.101	1.009	161,389.92	3.705
B-184	0.077	0.769	123,039.84	2.825
B-186	0.119	1.168	190,152.48	4.365
B-187	0.128	1.278	204,533.76	4.695
B-188	0.050	0.499	79,896.00	1.834
B-189	0.094	0.939	150,204.48	3.448
B-190	0.031	0.310	49,535.52	1.137
B-191	0.022	0.220	35,154.24	0.807
B-192	0.031	0.310	49,535.52	1.137
B-193	0.082	0.819	131,029.44	3.008
B-194	0.016	0.160	25,566.72	0.587
B-195	0.087	0.869	139,019.04	3.191
B-196	0.094	0.939	150,204.48	3.448
B-197	0.417	4.165	666,332.64	15.297
B-198	0.026	0.260	41,545.92	0.954
B-199	0.046	0.459	73,504.32	1.687
B-200	1.395	13.932	2,229,098.40	51.173
B-201	0.114	1.139	182,162.88	4.182
B-202	0.009	0.090	14,381.28	0.330
B-203	0.143	1.428	228,502.56	5.246
B-204	0.058	0.579	92,679.36	2.128
B-205	0.155	1.548	247,677.60	5.685
B-206	0.109	1.089	174,173.28	3.998
B-207	0.862	8.609	1,377,407.04	31.621
B-208	0.053	0.529	84,689.76	1.944
B-209	0.241	2.407	385,098.72	8.841
B-210	3.324	33.197	5,311,486.08	121.935
B-212	0.115	1.149	183,760.80	4.219
B-213	0.062	0.619	99,071.04	2.274
B-214	0.085	0.849	135,823.20	3.118
B-215	0.111	1.109	177,369.12	4.072
B-216	2.336	23.330	3,732,741.20	85.692
B-217	2.871	28.673	4,587,628.32	105.317
B-218	0.511	5.103	816,537.12	18.745
B-219	0.122	1.218	1,949,462.40	44.753
B-220	5.659	56.516	9,042,629.28	207.590
B-221	0.138	1.378	220,512.96	5.062
B-222	0.117	1.168	186,956.64	4.292
B-223	0.301	3.006	480,973.92	11.042
B-224	0.125	1.248	199,740.00	4.585
B-225	0.019	0.190	30,360.48	0.697
B-226	0.314	3.136	501,745.88	11.519
B-227	0.527	5.263	842,103.84	19.332

## Sector 2: (Cont'd).

Unit Number	Planimeter Units	Square Inches	Square Feet	Acres
A-173	0.082	0.819	131,029.44	3.008
A-174	0.339	3.386	541,694.88	12.436
A-175	0.040	0.399	63,916.80	1.467
A-176	0.578	5.772	923,597.76	21.203
A-177	0.073	0.729	116,648.16	2.678
A-178	0.040	0.399	63,916.80	1.467
A-179	0.102	1.019	162,987.84	3.742
A-180	0.200	1.997	319,584.00	7.337
A-181	0.780	7.790	1,246,377.60	28.613
A-182	0.351	3.505	560,869.92	12.876
A-183	0.456	4.554	728,651.52	16.728
A-184	0.090	0.899	143,812.80	3.301
A-185	1.366	13.642	2,182,758.72	50.109
A-186	0.061	0.609	97,473.12	2.238
A-187	0.055	0.549	87,885.60	2.018
A-188	0.065	0.649	103,864.80	2.384
A-189	1.295	12.933	2,069,306.40	47.508
A-190	1.638	16.359	2,617,392.96	60.087
A-191	0.040	0.399	63,916.80	1.467
A-192	0.024	0.240	38,350.08	0.880
A-193	0.031	0.310	49,535.52	1.137
A-194	0.289	2.886	461,798.88	10.601
A-195	0.007	0.070	11,185.44	0.257
A-196	0.819	8.179	1,308,696.48	30.044
A-197	0.023	0.230	36,752.16	0.844
A-198	0.104	1.039	166,183.68	3.815
A-199	0.157	1.568	250,873.44	5.759
A-200	0.111	1.109	177,369.12	4.072
A-201	0.104	1.039	166,183.68	3.815
A-202	0.113	1.129	180,564.96	4.145
A-203	0.161	1.608	257,265.12	5.906
A-204	0.118	1.178	188,554.56	4.329
A-205	0.106	1.059	169,379.52	3.888
A-206	1.988	19.854	3,176,664.96	72.926
A-207	0.314	3.136	501,746.88	11.519
A-208	0.096	0.959	153,400.32	3.522
A-209	0.117	1.158	186,956.64	4.292
A-210	0.112	1.119	178,967.04	4.109
A-211	0.251	2.507	401,077.92	9.208
A-212	0.105	1.049	167,781.60	3.852
A-213	0.214	2.137	341,954.88	7.850
A-214	0.114	1.139	182,162.88	4.182
A-215	0.098	0.979	156,596.16	3.595
A-216	0.103	1.029	164,585.76	3.778
A-217	0.108	1.079	172,575.36	3.962
A-218	0.101	1.009	161,389.92	3.705
A-219	3.057	30.530	4,884,841.44	112.141
B-160	0.013	0.130	20,772.96	0.477
B-161	0.072	0.719	115,050.24	2.641
B-162	1.169	11.675	1,867,968.48	42.883
B-163	0.052	0.519	83,091.84	1.908
B-164	0.032	0.320	51,133.44	1.174
B-165	0.089	0.889	142,214.88	3.265
B-166	0.245	2.447	391,490.40	8.987
B-167	0.161	1.608	257,265.20	5.906
B-168	0.260	2.597	415,459.20	9.538

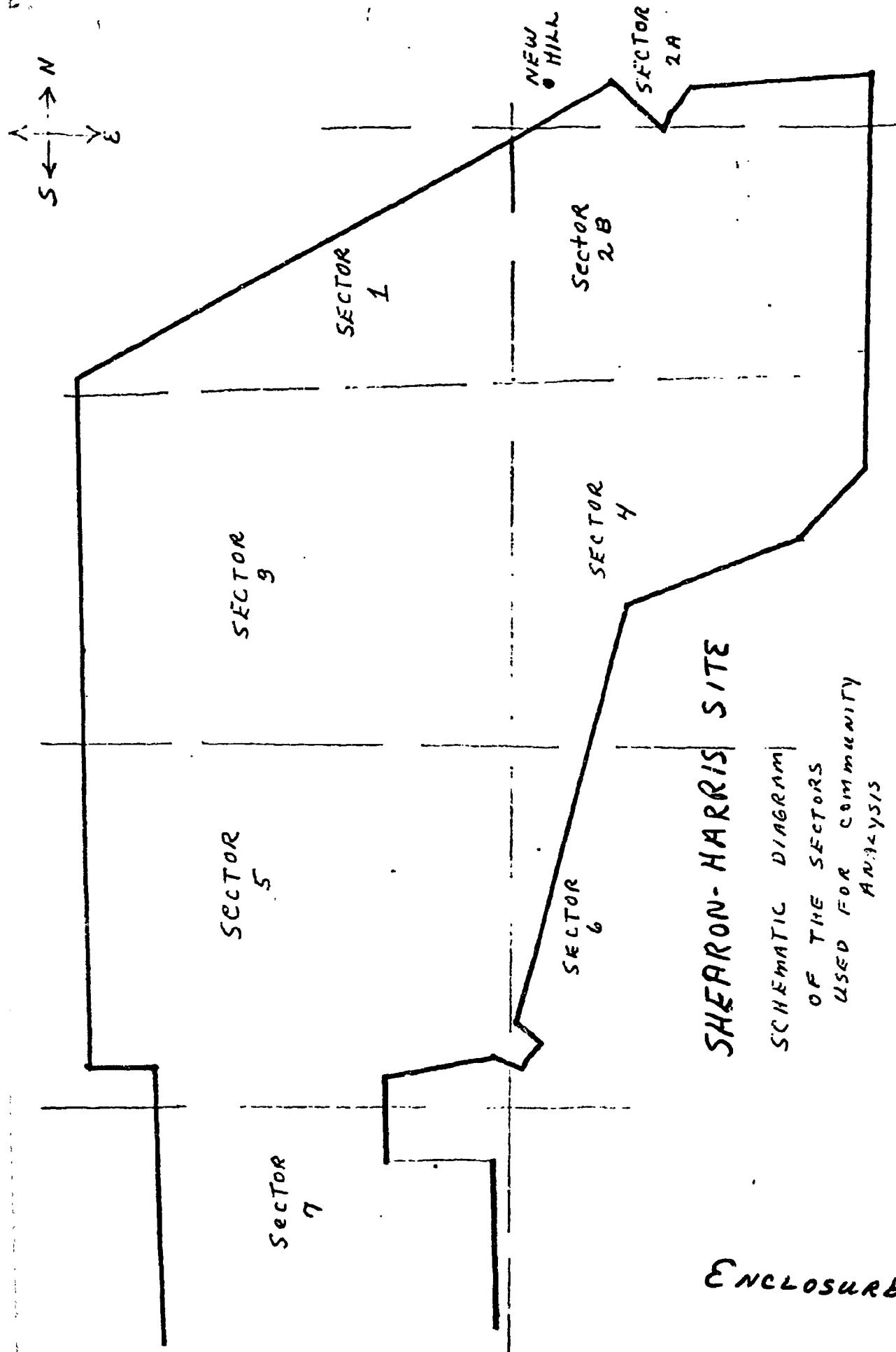
## Sector 2: (Cont'd)

Unit Number	Plenometer Units	Square Inches	Square Feet	Acres
B-228	0.411	4.105	656,745.12	15.077
B-229	0.012	0.120	19,175.04	0.440
C-7	40.929	408.758	65,401,267.68	1,501.407
C-53	1.199	11.974	1,915,906.08	43.983
C-54	0.738	7.370	1,179,264.96	27.072
C-55	1.116	11.145	1,783,278.72	40.938
C-56	0.315	3.146	503,251.04	11.553
C-57	1.437	14.351	2,296,211.04	52.714
C-58	0.096	0.959	153,400.32	3.522
C-59	0.089	0.889	112,214.89	3.265
C-60	0.092	0.919	147,008.64	3.375
C-61	0.094	0.939	150,204.48	3.448
C-62	3.029	30.251	4,840,099.68	111.113
C-63	0.394	3.935	629,580.48	14.453
C-64	1.330	13.283	2,125,233.60	48.789
C-65	3.746	37.411	5,985,808.32	137.415
C-66	0.297	2.966	474,582.24	10.895
C-67	0.329	3.286	525,715.68	12.069
C-68	2.607	26.036	4,165,777.44	95.633
C-69	1.695	16.928	2,708,474.40	62.178
C-70	0.211	2.107	337,161.20	7.740
C-71	0.450	4.494	719,064.00	16.507
C-72	0.411	4.105	656,745.12	15.077
C-73	1.649	16.469	2,634,970.08	60.491
D-52	0.655	6.541	1,046,637.60	24.027
D-54	0.073	0.729	116,648.16	2.678
D-55	0.094	0.939	150,204.48	3.448
D-56	0.094	0.939	150,204.48	3.448
D-57	0.041	0.409	65,514.72	1.504
D-58	0.113	1.129	180,564.96	4.145
D-59	0.032	0.320	51,133.44	1.174
D-60	0.202	2.017	322,779.84	7.410
D-61	0.011	0.110	17,577.12	0.404
D-62	0.142	1.418	226,904.64	5.209
D-63	0.029	0.290	46,339.68	1.064
D-64	0.023	0.230	36,752.16	0.844
D-65	0.065	0.649	103,864.80	2.384
D-66	0.157	1.568	250,873.44	5.759
D-67	0.094	0.939	150,204.48	3.448
D-68	0.100	0.999	159,792.00	3.668
D-69	0.071	0.709	113,452.32	2.605
D-70	0.089	0.889	142,214.88	3.265
D-71	0.187	1.868	298,811.04	6.860
D-72	0.099	0.989	158,194.08	3.632
D-73	0.043	0.429	68,710.56	1.577
D-74	1.115	11.136	1,781,680.80	40.902
D-75	0.705	7.041	1,126,533.60	25.862
D-76	0.019	0.190	30,360.48	0.697
D-77	0.038	0.380	60,720.96	1.394
D-78	0.570	5.693	910,814.40	20.909
D-79	0.200	1.997	319,584.00	7.337
D-80	0.049	0.489	78,298.08	1.797
D-81	0.065	0.649	103,864.80	2.384
E-23	2.345	23.420	3,747,122.40	86.022

Sector 2: (Cont'd)

Unit Number	Plenometer Units	Square Inches	Square Feet	Acres
E-50	0.799	7.980	1,270,733.08	29.310
E-58	0.337	3.366	538,499.04	12.362
E-59	0.328	3.276	524,117.76	12.032
E-60	0.409	4.085	653,549.28	15.003
E-61	0.305	3.046	487,365.60	11.188
E-62	0.066	0.659	105,462.72	2.421
E-63	19.327	193.019	30,882,999.84	708.976
E-64	0.155	1.548	247,677.60	5.686
E-65	0.209	2.087	333,965.28	7.667
E-66	4.751	47.448	7,591,717.92	174.282
E-67	1.537	15.350	2,456,003.04	56.382
E-68	0.024	0.240	38,350.08	0.880
E-69	0.716	7.151	1,144,110.72	26.265
E-70	0.144	1.438	230,100.48	5.282
E-71	0.082	0.819	131,029.44	3.008
E-72	0.095	0.949	151,802.40	3.485
E-73	0.051	0.509	81,493.92	1.871
E-74	0.069	0.689	110,256.48	2.531
E-75	0.052	0.519	83,091.84	1.908
E-76	0.081	0.809	129,431.52	2.971
E-77	0.199	1.987	317,986.08	7.300
E-78	0.124	1.230	198,142.08	4.549
E-79	0.021	0.210	33,556.32	0.770
E-80	0.157	1.568	250,873.44	5.759
E-81	0.043	0.429	68,710.56	1.577
E-82	0.224	2.237	357,934.08	8.217
E-83	1.199	11.974	1,915,906.08	43.983
E-84	9.829	98.162	15,705,955.68	360.559
E-85	43.899	438.419	70,147,090.08	1,610.356
E-86	1.831	18.286	2,925,791.52	67.167
E-87	1.522	15.200	2,432,034.24	55.832
E-88	0.217	2.167	346,748.64	7.960
E-89	0.068	0.879	140,616.96	3.228
E-90	0.122	1.218	194,946.24	4.475

Community Type	Percentage of Sector 2	Square Feet	Acres
Old Field	12.52%	43,573,617.00	1,000.313
Pine	14.58%	50,743,547.52	1,164.912
Hardwoods	28.58%	99,475,220.00	2,287.637
Scrub	2.38%	8,269,236.00	189.836
Mixed Pine-Hardwoods	41.94%	145,981,177.44	3,351.267
<b>Totals</b>	<b>100.00%</b>	<b>348,042,797.96</b>	<b>7,989.963</b>



SCHEMATIC DIAGRAM  
OF THE SECTORS  
USED FOR COMMUNITY  
ANALYSIS

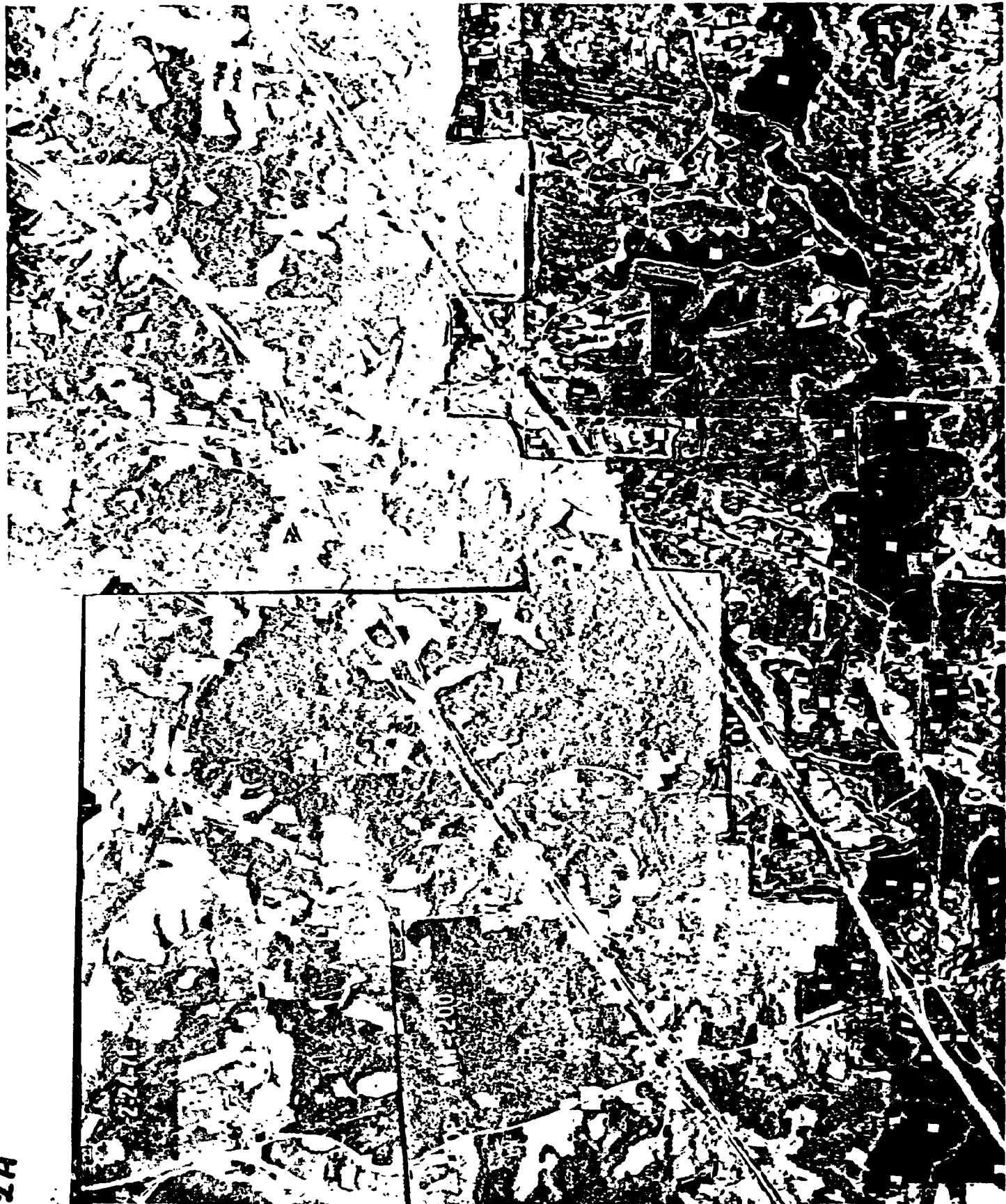
Legend:

PINE Forest - BLUE  
1/2 abandoned Fields GREEN  
HARDWOOD Forest - ORANGE  
SHARB-COTTOVER Community - PURPLE  
WILDED PINE - HARDWOOD - YELLOW

ENCLOSURE H



1



2A













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with Dr. J. Frank McCormick

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INDICATOR  
SPECIES

ENCLOSURE IV

LOWLAND

1

Herbs

*Digitaria sanguinalis*  
*Rumex acetosella*  
*Fimbristylis autumnalis*  
*Leptilon canadense*  
*Hypericum gentianoides*  
*Polygonum pensylvanicum*  
*Eragrostis pilosa*  
*Cyperus compressus*

2

Herbs

*Sporobolus poiretii*  
*Setaria lutescens*  
*Solidago caroliniana*  
*Eragrostis refracta*  
*Plantago lanceolata*  
*Gymnopogon brevifolius*  
*Lactuca canadensis*  
*Croton glandulosa*  
*Gnaphalium purpureum*  
*Ambrosia artemisiifolia*  
*Juncus tenuis*

*Allium vineale*  
*Diodia teres*  
*Plantago aristata*  
*Panicum dichotomum*  
*Euphorbia nutans*  
*Solanum carolinense*  
*Hypericum drummondii*  
*Ipomoea lacunosa*  
*Cassia chameacrista*  
*Aristida dichotoma*  
*Aster ericoides*

*Daucus sarota*

Herbs

*Oxalis stricta*  
*Polypodium procumbens*  
*Xanthium canadense*  
*Gnaphalium obtusifolium*  
*Helenium tenuifolium*  
*Andropogon spp.*  
*Eragrostis pectinacea*  
*Eupatorium capillifolium*  
*Pyrrhopappus carolinianus*  
*Panicum anceps*  
*Sorghastrum nutans*  
*Holcus lanatus*  
*Anthoxanthum odoratum*  
*Setaria geniculata*  
*Triodia flava*  
*Paspalum laeve*

3

*Paspalum circulare*  
*Paspalum floridanum*  
*Carex lurida*  
*Juncus effusus*  
*Scirpus atrovirens*  
*Panicum stipitatum*  
*Panicum clandestinum*  
*Leersia oryzoides*  
*Glyceria striata*  
*Zephyranthes atamasco*  
*Eupatorium perfoliatum*  
*Vernonia noveboracensis*  
*Chrysanthemum leucanthemum*  
*Fragaria virginiana*

Shrubs and Vines

*Alnus rugosa*  
*Cephalanthus occidentalis*

Herbs

*Panicum microcarpon*.  
*Ascyrum hypercoides*  
*Desmodium laevigatum*  
*Strophostyles umbellata*  
*lespedeza virginiana*

Trees

*Pinus taeda*  
*Pinus echinata*  
*Pinus virginiana*  
*Betula nigra*  
*Platanus occidentalis*  
*Salix nigra*  
*Diospyros virginiana*  
*Alnus serrulata*  
*Oxydendrum arboreum*  
*Sassafras officinale*

Shrubs and Vines

*Vitis labrusca*  
*Vitis cordifolia*  
*Rhus copallina*  
*Smilax bona-nox*  
*Viburnum rufidulum*  
*Tecoma radicans*  
*Viburnum affine v. hypomalacum*  
*Polycodium neglectum*  
*Polycodium stamineum*  
*Vitis aestivalis*  
*Hamamelis virginiana*  
*Ilex monticola*

Herbs

*Potentilla canadensis*  
*Eupatorium hyssopifolium*  
*Diodia virginiana*  
*Fluchea petiolata*  
*Galium pilosum*  
*Hieracium gronovii*

*Prunella vulgaris*  
*Galactis regularis*  
*Cassia nictitans*

Trees

*Liquidambar styraciflua*  
*Ostrya virginiana*  
*Ulmus fulva*

Shrubs and Vines

*Vitis rotundifolia*  
*Erythronium americanum*  
*Viburnum acerifolium*

Herbs

*Boehmeria cylindrica*  
*Chimaphila maculata*

## ?

Trees*Nyssa sylvatica*Shrubs and Vines

*Crataegus spp.*  
*Lonicera japonica*  
*Parthenocissus quinquefolia*

Herbs*Eupatorium aromaticum*

## 8

Trees

*Liriodendron tulipifera*  
*Cornus florida*  
*Juglans nigra*

Shrubs and Vines

*Smilax glauca*  
*Ilex decidua*  
*Viburnum nudum*  
*Amelanchier canadensis*  
*Sassafras officinale*  
*Ilex opaca*  
*Rhus toxicodendron*  
 var. *radicans*

Herbs

*Impatiens biflora*  
*Ambrosia trifida*  
*Tiarella cordifolia*  
*Hypericum punctatum*  
*Galium aparine*  
*Ceum canadense*

*Verbesina occidentalis*  
*Asplenium platyneuron*  
*Epigaea repens*  
*Elephantopus tomentosus*  
*Botrychium virginianum*  
*Onoclea sensibilis*

*Hypericum muticum*

## 9

Trees

*Ulmus alata*  
*Ulmus americana*  
*Fraxinus pennsylvanica*  
 var. *subintegerrima*  
*Fraxinus pennsylvanica*  
*Acer rubrum*

Shrubs and Vines

*Rosa palustris*  
*Sambucus canadensis*  
*Cercis canadensis*

Herbs

*Phryma leptostadrya*  
*Verbena urticaefolia*  
*Agrimonia parviflora*  
*Saururus cernuus*  
*Ranunculus hispidus*

*Ranunculus abortivus*  
*Osmorrhiza claytoni*  
*Rumex conglomeratus*  
*Rudbeckia laciniata*  
*Equisetum praelatum*

Trees

*Fagus grandifolia*  
*Acer floridanum*  
*Carya ovata*  
*Quercus phellos*  
*Quercus alba*  
*Quercus rubra* var.  
    *pagodaefolia*  
*Ilex decidua*  
*Carpinus caroliniana*  
*Morus rubra*  
*Fraxinus americana*  
*Prunus serotina*  
*Celtis occidentalis*

Shrubs and Vines

*Vaccinium* spp.  
*Bignonia capreolata*  
*Smilax rotundifolia*  
*Gelsemium sempervirens*

Herbs

*Galium tinctorium*  
*Asarum virginicum*  
*Anemonella thalictroides*  
*Asarum arifolium*  
*Goodyera pubescens*  
*Scutellaria serrata*  
*Arisaema triphyllum*  
*Zizea aurea*  
*Podophyllum peltatum*  
*Scutellaria integrifolia*

*Luzula carolinae*  
*Aristolochia serpentaria*  
*Ruellia caroliniensis*  
*Ranunculus recurvatus*  
*Hystrix patula*  
*Pilea pumila*

UPLAND

1

Herbs

*Digitaria sanguinalis*  
*Leptilon canadense*  
*Hypericum gentianoides*  
*Cyperus compressus*  
*Eragrostis pilosa*  
*Polygonum pensylvanicum*  
*Fimbristylis autumnalis*

2

Herbs

*Rumex acetosella* (1)  
*Gnaphalium purpureum*  
*Ambrosia artemisiifolia*  
*Juncus tenuis*  
*Allium vineale*  
*Diodia teres*  
- *Plantago aristata*  
*Solidago* spp.  
*Antennaria* spp.  
*Panicum dichotomum*  
*Euphorbia nutans*  
*Solanum carolinense*  
*Hypericum drummondii*  
*Ipomoea lacunosa*  
*Cassia chamaecrista*

*Aristida dichotoma*  
*Aster ericoides*  
*Daucus carota*  
*Sporobolus poiretii*  
*Setaria lutescens*  
*Eragrostis refracta*  
*Plantago lanceolata*  
*Gymnopogon brevifolius*  
*Lactuca canadensis*  
*Croton glandulosa*

3

Herbs

*Oxalis stricta*  
*Polygonum procumbens*  
*Gnaphalium obtusifolium*  
*Helenium tenuifolium*  
*Andropogon* spp.

*Eragrostis pectinacea*  
*Eupatorium capillifolium*  
*Pyrrhopappus carolinianus*

4

Herbs

*Cynodon dactylon*  
*Gymnopogon ambiguus*

Herbs (cont.)

*Chrysanthemum leucanthemum*  
*Oenothera fruticosa*  
*Physalis virginiana*  
*Erigeron ramosus*

Trees

*Pinus taeda*  
*Pinus virginiana*  
*Pinus echinata*  
  
*Sassafras officinale*

Shrubs and Vines

*Tecoma radicans*  
*Smilax glauca*  
*Rubus spp.*  
*Lonicera japonica*  
*Rhus glabra*  
*Rhus copallina*  
*Ascyrum hypericoides*

Herbs

*Elephantopus tomentosus*  
*Eupatorium hyssopifolium*  
*Lobelia puberula*  
*Galium pilosum*  
*Lespedeza repens*  
*Galium pilosum*  
*Desmodium obtusum*  
*Galactia regularis*

*Stylosanthes biflora*  
*Clitoria mariana*  
*Prenanthes spp.*  
*Cunila origanoides*

Trees

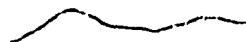
*Liquidambar styriflua*  
*Oxydendrum arboreum*  
*Diospyros virginiana*  
*Liriodendron tulipifera*  
*Prunus serotina*  
*Ulmus alata \**  
*Cercis canadensis*

Shrubs and Vines

*Crataegus spp.*  
*Viburnum rufidulum*  
*Rhus toxicodendron var. radicans*

Herbs

*Desmodium canescens*  
*Sanicula marilandica*



7

Trees

*Nyssa sylvatica*

Shrubs and Vines

*Ilex opaca*

Herbs

*Chimaphila maculata*

8

Trees

*Cornus florida*  
*Fraxinus americana*

Shrubs and Vines

*Viburnum prunifolium*  
*Erythronium americanum*  
*Amelanchier canadensis*

Herbs

*Desmodium nudiflorum*  
*Hieracium gronovii*

9

Trees

*Acer rubrum*

Shrubs and Vines

*Viburnum affine* var. *hypomalacum*  
*Polycodium* spp.  
*Rosa virginiana*

Herbs

*Hieracium venosum*

10

Trees

*Quercus alba*  
*Carya* spp.  
*Quercus velutina*  
*Quercus stellata*  
*Quercus borealis*  
*Quercus rubra*  
*Quercus coccinea*  
*Ilex decidua*  
*Quercus marilandica*

Shrubs and Vines

*Chionanthus virginica*  
*Styrax grandifolia*  
*Ceanothus americanus*  
*Vaccinium* spp.  
*Viburnum acerifolium*  
*Azalea nudiflora*  
*Vitis aestivalis*  
*Parthenocissus quinquefolia*  
*Vitis rotundifolia*  
*Smilax rotundifolia*  
*Vitis labrusca*  
*Lonicera sempervirens*  
*Bignonia capreolata*

Herbs

*Agrimonia gyposepala*  
*Aristolochia serpentaria*  
*Aureolaria flava*  
*Panicum microcarpon*  
*Prunella vulgaris*  
*Asarum virginicum*  
*Galium circaeans*  
*Pyranthemum flexuosum*

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(4.) The following thesis research was conducted by Richard Olson under my direction.. The experimental systems used were made available by funds under this contract.

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Appendix 5:

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RICHARD KENNETH OLSON. The Effects of Simulated Acid Precipitation on Nutrient Cycling in Granite Outcrop Ecosystems. (Under the direction of J. FRANK MCCORMICK).

Simulated acid rain of pH 2.0, 3.0, and 4.0 was applied to groups of granite outcrop ecosystems over an eleven week period. Analyses of nutrient inputs and outputs from these ecosystems showed significant increases in nutrient losses from the ecosystems correlated with increases in the acidity of simulated rain. Studies of the effects of acid precipitation on nutrient retention by the litter, vegetation, and soil components of the outcrop ecosystem were also conducted. Sensitivities of the components to acid leaching varied, but combined were greater than that of the complete ecosystem. Nutrient conservation in granite outcrop ecosystems thus appears to be an ecosystem level process. Other responses of the ecosystems to increased precipitation acidity included reduction in species diversity, tissue damage to plants, and redistribution of nutrients within the ecosystem.

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## INTRODUCTION

Acid precipitation <sup>1</sup> is a recent world phenomenon which represents a possible source of disruption to ecosystem structure and function. Distilled water in equilibrium with CO<sub>2</sub> at normal atmospheric pressures has a pH of approximately 5.7 (Barrett and Brodin 1955) resulting from the formation of carbonic acid. Precipitation samples from unpolluted regions have a pH close to 5.7. Precipitation samples collected during 1963-1964 in the forests of coastal Oregon ranged in pH from 5.7-6.3 (Tarrant et. al. 1968). Snow samples collected from Devon Island, Canada, in 1974 gave pH values of 5.7 (Miller <sup>2</sup> pers. comm.), and the pH of glacial ice from the Cascade Mountains was determined to be 5.6 (Reynolds and Johnson 1972).

Evidence exists that precipitation acidity over large portions of the earth's surface is no longer controlled by the CO<sub>2</sub>-carbonic acid equilibrium (weakly acid, strongly buffered), but is instead controlled by stronger, unbuffered acids. According to Likens et. al. (1972), the acidity of rain in some parts of Scandinavia has increased 200-fold since 1956, with values as low as 2.8 reported. At Hubbard Brook

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<sup>1</sup> Precipitation characterized by levels of acidity significantly greater than normal.

<sup>2</sup> N.G. Miller, Department of Biology, Harvard University, Cambridge, Massachusetts.

Experimental Forest in New Hampshire, the average weighted pH of precipitation for the years 1965-1971 ranged from 4.03 to 4.19 with a low single measurement of 3.0. Likens (1972) found the weighted average pH for 1970-1971 in the Finger Lakes Region of New York to be approximately 4.0. Average weighted pH values for Mt. Moosilauke, N.H. in 1974 were 3.8 (Vitousek <sup>3</sup> pers. comm.). Precipitation samples collected from 1971 to 1973 at a site thirty-two kilometers from Chapel Hill, N.C. had a mean pH of 4.28 (Wells <sup>4</sup> unpublished data). The lowest reported pH of rainfall in the U.S. is 2.1 for a single storm in Connecticut (Likens and Bormann 1974).

Apparently, these increases in precipitation acidity are the result of atmospheric pollution. Combustion of fossil fuels in the United States releases approximately  $3.74 \times 10^6$  tons of sulfur into the atmosphere annually (Bertine and Golberg 1971). In 1968, atmospheric emissions in this country alone equalled  $3.22 \times 10^7$  tons of sulfur oxides and  $2.07 \times 10^7$  tons of nitrogen oxides (Massachusetts Institute of Technology 1970). Sulfur and nitrogen oxides are oxidized and hydrolyzed in the atmosphere at varying rates to form sulfuric and nitric acids (Sethi 1971, Likens et. al. 1972). Since rainwater is a very dilute solution of ions, a small amount of acid is sufficient to greatly reduce its pH (Likens 1972).

The widespread nature of the acid precipitation phenomenon is due to the atmospheric transport of polluted air masses. Since the average

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<sup>3</sup> P.M. Vitousek, Department of Zoology, University of Indiana, Bloomington, Indiana.

<sup>4</sup> C.G. Wells, USDA Southeastern Forest Experimental Station, Research Triangle Park, North Carolina.

residence time for sulfur in the atmosphere is 2-4 days (Likens 1972), sulfur compounds may fall out hundreds of miles from their source. Thus, acid rain falling on New England may have its primary sources in the midwest and mid Atlantic states (Johnson et. al. 1972).

Future trends in acid precipitation are difficult to predict, but indications are that the problem may worsen. Yearly anthropogenic emissions of sulfur oxides in the United States are projected to increase 2-5 fold by 2000 A.D.. This increase, combined with the building of taller smokestacks which increase the dispersal range of pollutants and the use of stack precipitators to control emissions of basic fly ash particles, may lead to increases in the acidity of precipitation and the areas affected (Likens and Bormann 1974).

#### Ecological Effects of Acid Precipitation

The effects of acid precipitation on ecosystem structure and function are incompletely understood. Likens et. al. (1972) suggest the following as possible ecological consequences of acid precipitation:

- 1) increases in leaching rates of nutrients from soils
- 2) increases in leaching rates of nutrients from plant foliage
- 3) acidification of lakes and rivers
- 4) effects on the metabolism of organisms

The effect of acid precipitation on soils is most closely related to cation exchange capacity. Cation exchange capacity refers to the degree to which a soil holds cations by adsorption on the surfaces of colloidal micelles. Micelles are particles whose surfaces contain

negative charges that attract and hold cations. Cations adsorbed on colloidal surfaces exist in equilibrium with free cations in solution around the colloidal particles. In a normal soil, approximately 99 cations are adsorbed for every cation in solution (Thompson and Troeh 1973).

Cations are exchangeable if they can be replaced on the micelles with other cations in solution. The strength with which a cation is adsorbed on a colloidal surface is dependent on several factors such as the charge of the cation and the degree to which the cation is hydrated (Thompson and Troeh 1973). In general, the major cations can be placed in a preferential adsorption series known as the lyotropic series:



Cation exchange sites will adsorb more of an ion found early in the series than of one found later in the series if both are present in equal amounts. For example, unless a solution percolating through a normal soil contains at least three milliequivalents<sup>5</sup> of sodium for each milliequivalent of calcium, almost no sodium will be adsorbed (Black 1957). The exact order of cations in the lyotropic series may vary depending on soil type, interactions between adsorbed cations, and

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<sup>5</sup> A milliequivalent is defined as one milligram of hydrogen or the amount of any other ion that will combine with or displace it (Buckman and Brady 1969). When discussing cation-exchange processes, measurement of amounts of cations in milliequivalents allows direct comparison of numbers of different cations.

other factors (Kelly 1948). The position of hydrogen ion in the series is often disputed. Based on its valence and high state of hydration, it should lie close to sodium. But, the tendency of acids to flocculate clay suspensions as does calcium suggests that  $H^+$  should occupy a position close to calcium (Thompson and Troeh 1973).

In light of these principles of soil chemistry, the possibility of increased soil nutrient leaching due to acid precipitation becomes apparent. Increased acidity of precipitation increases the amount of hydrogen ions in the soil solution and alters equilibria between adsorbed cations and free cations. The result is the replacement of basic cations (Ca, Mg, K, Na) on the micelles by excess hydrogen ions in solution until new equilibria are established. Increased numbers of basic cations in solution are then more susceptible to leaching and possible loss from the system. Correlations between increased loss of calcium from forest soils and increased acidity of precipitation have indeed been demonstrated (Smith 1974). Since cation exchange capacity is also a property of humus (Hesse 1971), litter (Wells and Davey 1966), and vegetation, the basic principles presented above apply to these materials as well. Additional soil alterations could include a lowering of soil pH with a subsequent decrease in nutrient availability to plants, changes in soil microorganism populations (Buckmann and Brady 1969), and reduced rates of mineralization (Quraishi and Cornfield 1973).

The effects of acid precipitation upon vegetation are quite varied. Direct foliar leaching of nutrients may be enhanced by increases in the acidity of precipitation (Mecklenburg et. al. 1966, Eaton et. al. 1973). Precipitation with a low pH may directly injure vegetation. Symptoms

include necrosis of leaf tissue and reduction of pollen germination (Likens and Bormann 1974), dwarfing of needles (Likens 1972) and acid hydrolysis of chlorophyll a and b (Sheridan and Rosenstreater 1973).

Erosion of leaf cuticle by acid rain could increase plant susceptibility to pathogens, herbivores, and foliar leaching (Likens and Bormann 1974). Reduction of soil fertility by acid precipitation may lead to a reduction in plant growth. Such a reduction has been postulated for forests in New England (Likens and Bormann 1974) and Scandinavia (Likens 1972).

Responses of aquatic ecosystems to acid precipitation include acidification of lentic and lotic waters (Oden and Ahl 1972, Likens and Bormann 1974), extinction and reduction of fish populations (Schofield in press), and shifts in phytoplankton composition (Stokes and Hutchinson in press). Disruption of nutrient cycling and energy flow in aquatic systems may result from acidification. Grahn (in press) suggests that acidification in Swedish lakes causes long-term biological perturbations at all trophic levels. Relative dominances of macrophytes are altered with a resulting expansion of Sphagnum mats along the lake bottoms. The acidifying effects of the Sphagnum then induce further acidification of lake waters. Nutrient cycling is disrupted due to the accumulation of large amounts of nutrient ions in the moss mats and to the prevention of nutrient regeneration from bottom sediments covered by the mats. The acidification of lake waters inhibits decomposition of organic matter (Wright et. al. in press) and leads to a build-up of detritus (Hultberg in press). Increases in the solubility and availability of toxic heavy metals may also occur (Stokes and Hutchinson in press).

### Granite Outcrop Ecosystems

Experimental determination of the effects of acid precipitation at the ecosystem level requires an ecosystem that is: 1) clearly defined and easily manipulated, and 2) thoroughly characterized as to structure and function. Granite outcrop ecosystems meet both these criteria (Platt and McCormick 1964, McCormick et. al. 1974) and are therefore excellent systems for this purpose.

Granite outcrop ecosystems are small communities which occur in shallow, circular soil-filled depressions on exposed granite outcrops. The outcrops are found in a band approximately 120 miles wide extending north and west of the intersection of the Coastal Plain and Piedmont from North Carolina to Alabama (McVaugh 1943). Composition of the outcrops is primarily granite and granitic gneiss (Hermann 1954).

Characteristic species of granite outcrop ecosystems have been described by Harper (1929, 1939), McVaugh (1943), Baker (1956), Burbank and Platt (1964), and McCormick, Bozeman, and Sponberg (1971). Species distributions within the community parallel soil depth gradients (McCormick 1959, Sharitz and McCormick 1973, McCormick et. al. 1974), soil moisture gradients (Cumming 1969, Mellinger 1972, Sharitz and McCormick 1973) and soil nutrient gradients (Meyer 1972).

Environmental conditions of outcrop ecosystems and species adaptations to them were studied by Cotter and Platt (1959), Wiggs and Platt (1962), McCormick and Platt (1964), Murdy (1968), Lugo (1969), Mellinger (1972), and Sharitz and McCormick (1973). Outcrop successional patterns were characterized by Oosting and Anderson (1937, 1939), Keever, Oosting

and Anderson (1951), Burbank and Platt (1964), and Sharitz and McCormick (1973). The energy balance of granite outcrop ecosystems was thoroughly studied by Lugo (1969) and Murphy (1970). Water relations in the system were the concern of Lugo (1969), Sharitz and McCormick (1973), and McCormick et. al. (1974), while nutrient compartmentalization, distribution, availability, and cycling were examined by Braun (1971) and Meyer (1972).

Platt and McCormick (1964) and McCormick et. al. (1974) describe the characteristics of granite outcrop ecosystems that make these systems highly manipulatable. Because the ecosystems are isolated and rest on granite, they have clearly defined boundaries. Their closed granite basins simplify water and nutrient flow measurements. Since large numbers of very similar outcrop ecosystems exist, replication of sampling and treatments is possible. Their small size and shallow depths allow transportation of entire outcrop ecosystems to sites where environmental conditions may be controlled or modified.

Thus, it is evident that granite outcrop ecosystems are small, easily manipulated systems that have been thoroughly characterized with regard to structure and function, including internal nutrient cycling. As a consequence, they lend themselves to immediate experimental manipulation.

The only previously existing data concerning effects of precipitation acidity on granite outcrop ecosystems is found in Meyer (1972). For a single storm, the pH of run-on entering the ecosystem was determined to be 4.68. Concentrations of Ca, Mg, K,  $\text{NO}_3$ -N and  $\text{NH}_4$ -N were only slightly higher in runoff from the ecosystem than in the run-on. This indicates that precipitation of pH 4.68 is not acid enough to cause short-term

disruption of nutrient conservation by the granite outcrop ecosystem.

Objectives of Research

The following research was designed to analyze the effects of acid rain on nutrient cycling in granite outcrop ecosystems. Its main objectives were:

- 1) To test the hypothesis that increased acidity in simulated rainfall will lead to a reduction in the efficiency of these ecosystems in retaining nutrients in internal nutrient cycles.
- 2) To determine the effects of acid rain on nutrient losses from specific compartments in the system: soil and soil solution, litter, and vegetation.

## MATERIALS AND METHODS

### Field Studies

#### Site description

During April of 1968 and April of 1969, nine granite outcrop ecosystems were transplanted from Mt. Arabia, Georgia, to simulated granite outcrops in the North Carolina Botanical Gardens (Murphy and McCormick 1971). These simulated granite outcrops contained nine circular depressions in sloping (8°) concrete pads. Each depression was approximately two meters in diameter and increased gradually in depth from the outer edge to a maximum central depth of 20 centimeters. A shallow drainage channel left each depression at its lower edge.

Cumming (1969) demonstrated that granite outcrop communities in simulated granite outcrops in the North Carolina Botanical Gardens paralleled natural communities with regard to both structure and function. The transplanted granite outcrop communities selected for use in this research have existed under simulated granite outcrop conditions for 6-7 years. Major outcrop species Viguiera porteri (A. Gray) Blake, Senecio tomentosus Michaux, and Polytrichum commune Hedw. still dominate these communities and species composition and distribution are similar to that of communities on natural outcrops.

These transplanted ecosystems have also retained the normal soil profile and moisture gradients.

#### Alteration of Field Sites

In order to control the acidity and volume of precipitation entering the experimental ecosystems, transparent plastic domes were erected over each simulated outcrop. The domes, made of two sheets of 6 mil clear polyethylene stretched over chicken wire were 2.1 meters in height at their center ridge and 2.4 meters in width. Length varied in relation to the lengths of the simulated outcrops from 2.5 meters to 10 meters. Each dome was open at the sides to a height of one meter to reduce the greenhouse effect (Fig. 1A).

A drainage channel funneled runoff from each community. Each channel was lined with plastic to form a catch-basin for runoff following simulated rain (Fig. 1B).

#### Experimental Manipulations

Simulated acid rain (tap water, acidity adjusted with sulfuric acid) was applied to each community with a 7.4 liter plastic sprinkling can. A comparison of the nutrient content of the simulated rain with that of natural precipitation in this area is given in Table 1. Rain was applied directly to the ecosystem and not to the surrounding concrete platform. Each 7.4 liter application was applied evenly over the surface of the community with a fifteen minute interval between applications. Applications were continued until runoff from the

**Figure 1 (A).** One of three plastic domes erected over the experimental granite outcrop ecosystems.

This dome is approximately 10 meters in length and 2 meters at its peak.

**(B).** A single experimental outcrop ecosystem.

The runoff collection basin is visible in the foreground. The large flowering plants are Viguiera porteri (A. Gray) Blake.



A



B

**Table 1.** Comparison of the mean nutrient concentrations of simulated rain applied to the experimental ecosystems with that of natural precipitation. Data for natural precipitation are from Wells (unpublished data) for southeastern Alamance County, N.C. Natural precipitation values are weighted means for samples collected June 1, 1971, to May 31, 1973. All values in mg/l.

<u>Precipitation type</u>	<u>Ca</u>	<u>Mg</u>	<u>K</u>	<u>NH<sub>4</sub>-N</u>	<u>NO<sub>3</sub>-N</u>	pH
Simulated	3.57	2.92	2.13	0.02	0.02	--
Natural	0.21	0.06	0.16	0.14	0.19	4.28

ecosystem commenced. An average of 55.6 liters were applied to each ecosystem per treatment. This is approximately equal to 1.77 cm of simulated rain falling on each ecosystem over a two hour period. All runoff was collected sequentially in one liter plastic bottles and refrigerated along with samples of the simulated rain. 50 ml subsamples of runoff and simulated rain were later analysed for nutrient content and pH.

All nine ecosystems initially received two treatments with pH 4.0 simulated rain. Measurements of nutrient losses from the ecosystems could then be used as baseline data to detect inherent differences between ecosystems. Any differences could then be accounted for when the nine experimental ecosystems were divided into treatment groups.

Experimental treatments for this research included the application of pH 2.0, 3.0 or 4.0 simulated rain to each of the ecosystems within each of the treatment groups. These three acidity levels were chosen to represent a range of natural values from the average for Chapel Hill, N.C. of 4.28 (Wells unpublished data) to the lowest recorded value for a natural storm of 2.1 (Likens and Bormann 1974). The data of Meyer (1972) suggests that precipitation of pH 4.68 was not disruptive to the granite outcrop ecosystem examined by him. The precipitation acidities selected for this experiment represent a range falling below pH 4.68.

Thus, for the remainder of the field studies each of three groups of three ecosystems received simulated rain of either pH 2.0, 3.0 or 4.0 as their sole water source. Initial treatments of all communities with pH 4.0 rain were conducted on July 1, 1974 and July 8, 1974. A total of seven treatments using the three concentrations of acid rain

were then conducted from July 21, 1974 to October 3, 1974 at approximately two week intervals.

Nutrients selected for analysis were calcium, magnesium, potassium, ammonium and nitrate. Nutrients were selected on the basis of several criteria. First, all of these nutrients may limit the growth of different outcrop species in various habitats within the outcrop ecosystem (McCormick et. al. 1974). Due to this, they are important components of outcrop ecosystem nutrient cycles. Second, the four cations selected represent a wide range along the lyotropic series. If acid rain causes increased leaching due to increased cation exchange, increases in leaching of cations located early in the series may be less than increases for cations located later in the series. To test this, calcium, a relatively unexchangeable cation and magnesium, an intermediate cation were selected along with potassium and ammonium, two relatively exchangeable cations. Finally, nitrate was selected to examine the effect of acid rain on anion exchange and cycling in these ecosystems.

#### Vegetation Analysis

Species presence lists were compiled for the nine experimental ecosystems. Identifications were performed both in summer 1974 and spring 1975 (Table 2).

#### Soil Sampling

Soil samples were collected from each community on October 14, 1974

Table 2. Species present in the experimental granite outcrop communities.

Herbs:

*Agave virginica* L.  
*Allium canadense* L.  
*Allium vineale* L.  
*Arabidopsis thaliana* (L.) Heynhold  
*Barbarea verna* (Miller) Ascherson  
*Bulbostylis capillaris* (L.) Clarke  
*Cardamine hirsuta* L.  
*Cerastium glomeratum* Thuillier  
*Crotonopsis elliptica* Willd.  
*Digitaria sanguinalis* (L.) Scopoli  
*Geranium carolinianum* L.  
*Hordeum pusillum* Nuttall  
*Houstonia pusilla* Schoepf  
*Linaria canadensis* (L.) Dumont  
*Minuartia uniflora* (Walt.) Mattfeld  
*Oenothera laciniata* Hill  
*Opuntia compressa* (Salisbury) Macbride  
*Oxalis dillenii* Jacquin  
*Portulaca smallii* P. Wilson  
*Ranunculus abortivus* L.  
*Rumex hastatus* Baldwin ex Ell  
*Schoenolirion croceum* (Michaux) Gray  
*Sedum acre* L.  
*Senecio tomentosus* Michaux  
*Talinum teretifolium* Pursh  
*Trifolium campestre* Schreber  
*Veronica arvensis* L.  
*Vicia lathyroides* L.  
*Viguiera porteri* (A. Gray) Blake  
*Vicia rafinesquii* Greene

Mosses and Lichens:

*Cladonia caroliniana* (Schwein.) Tuck  
*Crimmia laevigata* (Brid.) Brid.  
*Polytrichum commune* Hedw.

at the completion of the field experiments. Fifteen five centimeter diameter cores were taken at random from each community. They were thoroughly mixed, and then subsampled. Soil pH and organic matter content were then determined. Additional samples were collected December 15, 1974 for nutrient analysis. Cores were taken from the soil surface to the basin floor in two distinct zones in each ecosystem. Soils with a depth of fourteen centimeters or more were sampled in the center of each system. Soils up to eight centimeters deep were sampled around the edge of each ecosystem. Thirty cores were taken from each outer zone, mixed and subsampled. Twenty cores were taken from each central zone, mixed and subsampled. Samples were then analyzed for available potassium, calcium, and magnesium.

#### Ecosystem Compartment Studies

The total nutrient content of an ecosystem is divided between a number of different nutrient compartments within the ecosystem (Bormann and Likens 1967). In the granite outcrop ecosystem, these include litter, soil and soil solution, and living vegetation. In order to determine the influence of acid rain on these specific nutrient compartments, additional field and laboratory experiments were coordinated with the main field program. The following experiments utilized transplanted granite outcrop ecosystems not involved in the main nutrient cycling study.

Vegetation

Simulated rain of pHs 2.0, 3.0 and 4.0 was applied to three similar stands of Viguiera porteri on October 3, 1974. Four liters of rain were applied with a sprinkling can to one square meter areas of Viguiera. Throughfall was collected in glass fingerbowls placed under the vegetation on the soil surface. 50 ml subsamples of throughfall and simulated rain were then analysed for calcium, magnesium, potassium, ammonium, nitrate, and pH.

Litter

Litter was collected from several granite outcrop communities in April, 1975. Litter was defined as both standing and fallen dead vegetation whose origin was not yet obscured by decomposition. For these communities, most of the litter consisted of remains of Viguiera porteri. The litter was thoroughly mixed and 30 gram subsamples were placed in each of 15 plastic pots. Each pot has a diameter of 15.5 centimeters and a depth of 18 centimeters. Drainage holes in each pot were plugged with cotton and cheesecloth to contain particulate matter.

The fifteen pots were then evenly divided into three groups and the litter samples treated with simulated rain of either pH 2.0, 3.0 or 4.0. Simulated rain was applied with a small sprinkler bottle. Each litter sample was leached three times with 200 ml simulated rain per treatment for a total of fifteen replications per pH. Runoff from each pot was collected and 50 ml samples taken along with samples of simulated rain for the standard nutrient and pH analysis.

Soil

Soil was collected from a single granite outcrop ecosystem in the 2-15 cm depth zone of the community. Vegetation and litter were excluded. The soil was thoroughly mixed and 1500 gram subsamples were then placed in each of twelve plastic pots whose drainage holes were also plugged with cotton and cheesecloth. Groups of four pots were then treated with pH 4.0, 3.0 or 2.0 simulated rain. The acid rain was poured onto the soil surface and allowed to percolate to the bottom where it drained into a glass fingerbowl. Each of the four pots in a treatment group received four applications of 250 ml acid rain. 50 ml samples each of simulated rain and runoff were collected for the standard nutrient and pH determinations.

Pot leaching

The possibility existed that for the litter and soil leaching experiments, the plastic pots were leaching nutrients into the runoff. To determine if this was so, nine pots were plugged with cotton and cheesecloth, but left empty. Three pots were then treated at each pH level. Each pot was given three treatments of 150 ml of acid water and allowed to drain. Runoff was collected and 50 ml samples each of leachate and simulated rain analysed for nutrient content.

### Analytical Procedures

#### Sample Collection and Storage

Water samples were collected with a plastic baster and stored in one liter or 50 ml plastic bottles at 7°C for 1-3 weeks before analysis. Sample bottles and other hardware used for sampling were acid washed (HCl) and detergent washed, then rinsed five times with tap water and three times with distilled water.

#### Analytical Techniques

Water samples were analysed for calcium, magnesium, and potassium with a Perkin-Elmer Model 303 atomic absorption spectrophotometer. Nitrate-nitrogen and ammonium-nitrogen analyses of water samples were made with a Technicon Autoanalyzer. The pH of water and soil samples was determined with a Beckman Zeromatic II pH meter and a Fisher Accumet Model 520 Digital pH/Ion Meter. Soil pH techniques followed Black (1965). Soil organic matter content was determined by weight loss during ignition (Andrews 1973). Nutrient analyses of soil samples were conducted by HCl-H<sub>2</sub>SO<sub>4</sub> extraction by the North Carolina Department of Agriculture, Soil Testing Division.

## RESULTS

### Species Composition

A total of 33 plant species were identified in the nine experimental outcrop communities (Table 2). These included thirty herbaceous species, two mosses and one lichen. Species commonly dominant in natural outcrop communities were present in the experimental systems, including Viguiera porteri (A. Gray) Blake, Senecio tomentosus Michaux, Minuartia uniflora (Walt.) Mattfield, Sedum acre L., and Polytrichum commune Hedw..

### Baseline Data

Initial treatments of all nine experimental ecosystems with pH 4.0 simulated rain yielded a range of responses among the ecosystems as measured by the concentrations of nutrients lost from each system in runoff (Table 3). To clearly quantify differences in ecosystem responses, the concentrations of calcium, magnesium, ammonium, and nitrate in runoff were summed for each ecosystem to serve as an index of total nutrient loss (Table 4). Potassium was excluded from these calculations to prevent the high potassium concentrations from obscuring the differences in the other nutrients.

As Table 4 illustrates, the nine ecosystems fell into three groups on the basis of nutrient loss in runoff. Nutrient loss rates of each

Table 3. Average nutrient losses from the experimental outcrop ecosystems following the application of pH 4.0 simulated rain. Averages are based on two treatments per ecosystem. A negative loss means a net gain of a nutrient by the ecosystem. All values except pH are in mg/liter of runoff.

<u>Ecosystem</u>	<u>Net nutrient losses from ecosystems</u> <sup>1</sup>					<u>Mean pH</u>
	<u>Ca</u>	<u>Mg</u>	<u>K</u>	<u>NH<sub>4</sub>-N</u>	<u>NO<sub>3</sub>-N</u>	
A	-1.89	1.63	12.47	0.66	1.36	5.4 (5.4--5.5) <sup>2</sup>
B	-1.86	0.42	17.68	0.66	0.65	5.9 (5.7--6.1)
C	-1.96	0.42	9.42	0.25	0.11	6.0 (5.9--6.1)
D	2.35	0.86	12.62	0.19	0.35	6.7 (6.6--6.8)
E	-1.82	-0.08	23.76	0.12	0.15	6.9 (6.8--7.0)
F	2.96	1.06	21.80	0.40	3.07	6.9 (6.7--7.1)
G	0.20	0.10	21.09	0.28	1.24	6.6 (6.6--6.7)
H	-0.35	0.13	21.29	0.15	0.56	6.5 (6.5--6.6)
I	2.94	0.29	23.55	0.19	2.01	6.6 (6.5--6.8)

<sup>1</sup>Corrected for nutrient input from simulated rain.

<sup>2</sup>Range of treatment means.

Table 4. Average combined nutrient losses from granite outcrop ecosystems following two applications of pH 4.0 simulated rain.

Ecosystem	<u>Net nutrient loss (mg/l. runoff)</u> <sup>1</sup>	Loss Rate
	Ca + Mg + NH <sub>4</sub> -N + NO <sub>3</sub> -N	
F	7.49	High
I	5.43	High
D	3.75	High
G	1.82	Medium
A	1.76	Medium
H	0.49	Medium
B	-0.13	Low
C	-1.18	Low
E	-1.63	Low

<sup>1</sup>Corrected for nutrient input from simulated rain.

group were classified as high, medium, or low relative to the other groups. To insure that inherent differences in nutrient retention between ecosystems was not a variable in this experiment, a complete random block design was utilized (Platt and Griffiths 1964). One ecosystem was selected at random from each baseline group to form each experimental group. As a result, the following treatment groups were designated:

pH 4.0; D-A-C

pH 3.0; E-F-G

pH 2.0; B-H-I

#### Ecosystem Responses to Acid Precipitation

Cation concentrations in runoff from the experimental ecosystems increased as the acidity of the simulated rain applied to the ecosystem increased (Table 5). Potassium displacement significantly increased with each single pH unit decrease of the simulated rain. Calcium, magnesium and ammonium showed no significant differences in runoff concentrations between pH 4.0 and pH 3.0, but increased greatly from pH 3.0 to pH 2.0. Nitrate concentrations in runoff did not follow the cation pattern. Ecosystem losses of nitrate were highest at pH 3.0 and lowest at pH 2.0.

Table 6 illustrates the influence of three months of acid rain on soil pH and soil organic matter content of the outcrop ecosystems. Soil pH was 1-2 units lower in ecosystems treated with pH 2.0 rain than in the other ecosystems. Amounts of soil organic matter showed no

Table 5a. Mean nutrient losses from granite outcrop ecosystems subjected to simulated rain of different acidities. Each treatment mean based on seven simulated rain applications with three replicates per application.

Simulated rain pH	Net nutrient losses from ecosystems (mg/l. runoff) <sup>1</sup>					
	Ca	Mg	K	NH <sub>4</sub> -N	NO <sub>3</sub> -N	Mean pH
pH 2.0	51.88	36.32	174.02	7.44	0.70	2.6 (2.1--3.8) <sup>2</sup>
pH 3.0	13.95	5.10	98.39	0.83	2.11	6.1 (5.8--7.0)
pH 4.0	7.45	5.60	30.81	1.25	1.18	5.3 (5.1--6.7)

<sup>1</sup>Corrected for nutrient input from simulated rain.

<sup>2</sup>Range of treatment means for individual communities.

Table 5b. Significance levels for the Newman-Keuls test of differences among means. \*\* =  $P < .01$ ; \* =  $P < .05$ , ns = not significant.

means compared	Ca	Mg	K	NH <sub>4</sub> -N	NO <sub>3</sub> -N
2.0 v. 3.0	**	**	**	**	**
3.0 v. 4.0	ns	ns	**	ns	*
2.0 v. 4.0	**	**	**	**	ns

Table 6. Mean soil pH and soil organic matter content for ecosystem treatment groups. Soil samples taken 10-14-74 at the completion of acid rain treatments.

<u>Treatment Group</u>	<u>Mean Soil pH</u>	<u>% Organic Matter</u>
pH 2.0	4.1 (3.9--4.5) <sup>1</sup>	9.0
pH 3.0	5.8 (5.6--6.3)	7.3
pH 4.0	5.2 (5.0--5.5)	10.0

<sup>1</sup>Range of means for individual ecosystems within each treatment group.

correlation with precipitation acidity.

Nutrient concentrations in the soil of the granite outcrop ecosystems at the completion of the study are presented in Table 7. Nutrient concentrations were significantly higher than those reported for outcrop ecosystems by Meyer (1972). Nutrient distribution was correlated with simulated rain acidity and will be discussed. Only qualitative analyses were conducted on the direct effects of acid rain on vegetation in the outcrop communities. Vegetation in communities treated with pH 4.0 or 3.0 rain showed no visible signs of acid effects. In the pH 2.0 communities, several changes occurred. Individuals of Viguiera porteri exhibited chlorosis and necrosis of leaf tissues. All individuals of Polytrichum commune were killed. The other moss in these communities, Grimmia laevigata (Brid.) Brid., showed no obvious signs of damage.

#### Compartment Studies

In both the litter and soil leaching studies, increases in the amounts of cations leached from these nutrient compartments were directly correlated with increases in the acidity of the simulated rain (Tables 8,9). The one possible exception may be the loss of ammonium from litter (Table 8). While ammonium losses from litter increased with increasing rain acidity, differences between the pH levels were not statistically significant. Nitrate losses from these compartments showed no correlation with pH.

Leaching experiments on outcrop vegetation showed significant correlations between increased precipitation acidity and increased losses of calcium (Table 10). Magnesium and potassium followed this

Table 7. Distribution of available soil nutrients within the granite outcrop ecosystems of each acid rain treatment group. Soil samples taken December 15, 1974 after completion of treatments. All values in ppm. Values given are means for all ecosystems in each treatment group. Soils 1-8 centimeters deep occupy the outer edges of the ecosystems. Soils greater than 14 centimeters deep occur in the center of each ecosystem.

<u>Treatment Group</u>	<u>Soil Depth Zone</u>	<u>Ca</u>	<u>Mg</u>	<u>K</u>
pH 4.0	1-8 cm	417.6	61.8	87.7
pH 4.0	>14 cm	354.9	37.5	106.0 <sup>a</sup>
pH 3.0	1-8 cm	647.9	44.4	114.9
pH 3.0	>14 cm	626.2	56.5 <sup>a</sup>	131.4 <sup>a</sup>
pH 2.0	1-8 cm	426.5	16.9	99.3
pH 2.0	>14 cm	631.8 <sup>a</sup>	133.6 <sup>a</sup>	120.4 <sup>a</sup>

<sup>a</sup>Nutrient present in greater concentration in deep soil zone than in shallow soil zone.

Table 8a. Mean nutrient losses from litter subjected to simulated rain of three different acidities. Each treatment mean based on three simulated rain applications with five replicates per application.

Simulated Rain pH	Net nutrient losses from litter (mg/l runoff) <sup>1</sup>					Mean pH
	Ca	Mg	K	NH <sub>4</sub> -N	NO <sub>3</sub> -N	
pH 2.0	23.26	4.38	6.51	1.39	0.39	2.1 (2.0--2.1) <sup>2</sup>
pH 3.0	6.09	1.36	3.16	1.07	0.37	2.3 (3.2--3.5)
pH 4.0	1.36	0.50	2.54	0.98	0.40	4.6 (4.5--4.9)

<sup>1</sup>Corrected for nutrient input from simulated rain and container leaching.

<sup>2</sup>Range of individual samples.

Table 8b. Significance levels for the Newman-Keuls test of differences among means. \*\* = P < .01; \* = P < .05.

means compared	Ca	Mg	K	NH <sub>4</sub> -N	NO <sub>3</sub> -N
2.0 v 3.0	**	**	**	ns	ns
3.0 v 4.0	**	**	ns	ns	ns
2.0 v 4.0	**	**	**	ns	ns

Table 9a. Mean nutrient losses from soil subjected to simulated rain of three different acidities. Each treatment mean based on four simulated rain applications with four replicates per application. A negative loss means a net gain of nutrient by the soil.

Simulated Rain pH	Net nutrient losses from soil (mg/l runoff) <sup>1</sup>					
	Ca	Mg	K	NH <sub>4</sub> -N	NO <sub>3</sub> -N	Mean pH
pH 2.0	6.08	2.80	30.09	0.19	-0.04	2.3 (2.2--2.5) <sup>2</sup>
pH 3.0	1.44	0.28	14.08	0.01	-0.01	4.0 (3.8--4.2)
pH 4.0	-1.58	-0.26	5.25	-0.16	-0.02	5.2 (4.9--5.4)

<sup>1</sup>Corrected for nutrient input from simulated rain and container leaching.

<sup>2</sup>Range of individual samples.

Table 9b. Significance levels for the Newman-Keuls test of differences among means. \*\* = P < .01; \* = P < .05

means compared	Ca	Mg	K	NH <sub>4</sub> -N	NO <sub>3</sub> -N
2.0 v 3.0	**	**	**	*	**
3.0 v 4.0	**	**	**	ns	ns
2.0 v 4.0	**	**	**	**	*

Table 10a. Mean nutrient losses from vegetation subjected to simulated rain of three different acidities. Each treatment mean based on five replicates.

Simulated Rain pH	<u>Net nutrient losses from vegetation (mg/l runoff)</u> <sup>1</sup>					Mean pH
	Ca	Mg	K	NH <sub>4</sub> -N	NO <sub>3</sub> -N	
pH 2.0	1.11	1.64	3.79	0.40	0.20	2.0
pH 3.0	1.25	1.26	2.86	0.12	0.06	3.1 (3.0--3.1) <sup>2</sup>
pH 4.0	0.18	0.76	2.16	0.32	0.17	4.2 (4.1--4.3)

<sup>1</sup>Corrected for nutrient input from simulated rain.

<sup>2</sup>Range of individual samples.

Table 10b. Significance levels for the Newman-Keuls test of differences among means. \*\* = P < .01; \* = P < .05.

means compared	Ca	Mg	K	NH <sub>4</sub> -N	NO <sub>3</sub> -N
2.0 v 3.0	ns	ns	ns	ns	*
3.0 v 4.0	**	ns	ns	ns	*
2.0 v 4.0	**	ns	ns	ns	ns

trend, but differences were not statistically significant. Ammonium and nitrate showed no correlation with pH.

Plastic pots used to hold the litter and soil samples were tested for leaching and found to release appreciable amounts of the nutrients under study (Table 11). Nutrient concentrations in soil and litter runoff were corrected for this extraneous input.

Table 11. Nutrient losses from litter and soil containers leached with simulated rain of three different acidities.

Simulated Rain pH	Net nutrient losses from containers (mg/l runoff) <sup>1</sup>				
	Ca	Mg	K	NH <sub>4</sub> -N	NO <sub>3</sub> -N
pH 2.0	1.28	0.20	0.20	0.08	0.02
pH 3.0	1.08	0.22	0.13	0.10	0.02
pH 4.0	0.85	0.10	0.08	0.07	0.02

<sup>1</sup>Corrected for nutrient input from simulated rain.

## DISCUSSION

Increases in the acidity of simulated precipitation significantly increase leaching losses of basic cations from granite outcrop ecosystems (Table 5) and their major nutrient compartments (Tables 8-10). The increased cation leaching could be due to:

- 1) hydrogen ion exchange with adsorbed cations, and/or
- 2) acid induced weathering of soil minerals (Wood and Bormann in press)

It is unlikely that for the period of this experiment and the range of precipitation acidities studied that increased rates of weathering could totally account for the increased cation losses. Wood and Bormann (in press) conducted leaching experiments on a sandy loam soil. Their results suggest that at precipitation pHs of 4.0 or higher, weathering inputs keep pace with leaching losses and plant uptake. As the precipitation becomes more acid, total exchangeable cations in the soil decrease, indicating that weathering rates fall behind leaching rates. While changes in exchangeable cations were not measured directly in this study, a decrease is indicated by measurements of soil pH made at the conclusion of the study. As shown in Table 6, the mean soil pH of the ecosystem group receiving pH 2.0 simulated rain is 4.1, a level 10 to 100 times as acidic as that of the other treatment groups. The pH of

a soil is closely related to the relative amounts of acidic and basic cations held on its cation exchange sites (Thompson and Troch 1973). The percentage of total exchange sites filled by basic cations is known as the percent base saturation. A decrease in the percent base saturation of a soil results in a decrease in soil pH. Thus, the low soil pH values of the pH 2.0 treatment group may result from a net decrease in exchangeable basic cations. At least for this treatment group, replacement of leached cations by weathering may not equal leaching losses.

Increases in cation leaching due to acid precipitation could also be the result of hydrogen ion exchange with exchangeable cations. The importance of this mechanism within the ecosystem and its components is suggested by pH measurements of simulated rain, outcrop ecosystem soils (Table 6), and leachate from the ecosystem and its components (Tables 5, 8-10). In all cases, the pH of leachate was higher than that of the simulated rain from which it was derived. The decrease in the acidity of the rain as it passed through soil, litter, or vegetation could be due to:

- 1) uptake of  $H^+$  by the soil, litter, and vegetation through cation exchange, with the concurrent release of basic cations to the leachate, and/or
- 2) neutralization of acids by organic bases (Wood and Bormann in press)

Since concentrations of basic cations in the leachate do increase as rain acidity increases, hydrogen ion exchange is most likely involved in the leaching process. Replacement of basic cations by hydrogen ions would lower the percent base saturation of the soil and reduce

soil pH as discussed earlier. The low soil pH of the ecosystems receiving pH 2.0 simulated rain (Table 6) supports hydrogen ion exchange as one mechanism involved in acid leaching.

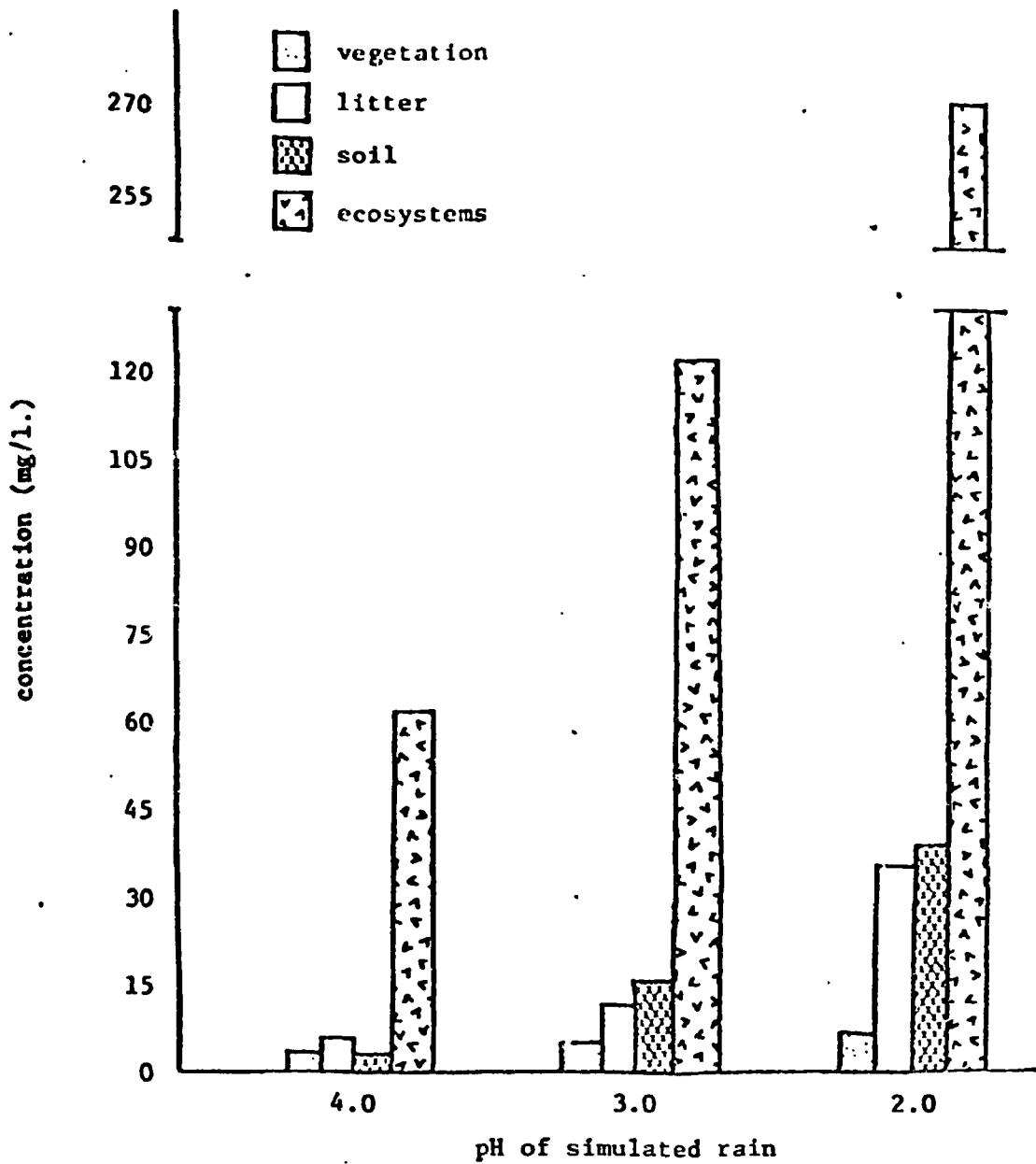
The net effects of acid precipitation on nutrient losses from the experimental granite outcrop ecosystem and its nutrient compartments are summed up in Figure 2. Mean ecosystem and nutrient compartment losses of calcium, magnesium, potassium, ammonium, and nitrate are plotted against the three experimental pHs of simulated rain. Nutrient losses from the ecosystems as well as the litter, vegetation, and soil nutrient compartments making up the ecosystems increase significantly as precipitation acidity increases.

#### Simulation of Rain

Concentrations of calcium, magnesium and potassium in the simulated acid rain were considerably higher than concentrations of these ions in natural precipitation (Table 1). This is due to the use of tap water in preparing the simulated rain. The large volumes of water required (approximately 500 liters for each treatment) prohibited the use of distilled water for a more accurate simulation of natural rain. The high cation concentrations of the simulated rain could have influenced the experimental results. High cation inputs in the simulated rain could have obscured significant differences in nutrient losses between acid treatment levels in cases where the total concentrations of cations involved was small (T. Wood pers. comm.)<sup>6</sup>. Examples of this are mag-

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<sup>6</sup>T. Wood, School of Forestry, Yale University, New Haven, Conn.



**Figure 2.** Nutrient losses from the experimental granite outcrop ecosystems and their nutrient compartments as a function of the pH of simulated rain. Values are the sum of the average concentrations of Ca, Mg, K,  $\text{NH}_4^-\text{N}$ , and  $\text{NO}_3^-\text{N}$  in the leachate from ecosystems or compartments. The scale on the vertical axis is broken.

nesium losses from the ecosystem at pHs 4.0 and 3.0, and cation losses from vegetation at all pH levels. The absolute amounts of cations leached from the systems may have been altered by the application of cation-rich simulated rain. The total losses of potassium could have been increased by replacement of adsorbed potassium ions by calcium ions in the simulated rain. Hydrogen ion exchange was probably not the only ion exchange process occurring when the simulated rain was applied. But since only the concentration of hydrogen ions varied between acid treatment levels, differences in nutrient losses between treatment levels should be due solely to hydrogen-ion exchange.

#### Ecosystem Processes

The data demonstrate that acid precipitation acts as a stress on normal nutrient conservation and cycling processes of the granite outcrop ecosystem. Meyer (1972) has pointed out that nutrient conservation is of critical importance to the granite outcrop ecosystem due to:

- 1) the exposed position of the ecosystem on granite which causes large inputs of water proportional to the soil volume of the ecosystem. This creates a high potential for leaching losses.
- 2) the low initial amounts of nutrients in the ecosystem whose soils have a low cation-exchange capacity and are relatively infertile.
- 3) the possible limiting effects of nutrients, particularly calcium and nitrogen, on growth of plant populations within the ecosystem.
- 4) the limited nutrient inputs into these systems.

Data from this research (Table 12) suggest that nutrient conservation in the granite outcrop ecosystem is not simply a function of the

**Table 12.** Relative sensitivities of the granite outcrop ecosystem and its nutrient compartments to acid leaching. Combined losses of Ca, Mg, K, and NH<sub>4</sub> from each compartment are normalized at each pH level with the losses at pH 4.0 as the standard. Losses were originally calculated as miliequivalents per liter.

pH of simulated rain	soil	litter	ecosystem	vegetation
2.0	13.02	6.59	6.01	2.03
3.0	5.10	2.17	2.50	1.60
4.0	1.00	1.00	1.00	1.00

properties of each nutrient compartment, but is an ecosystem level process.

Table 12 presents the total cation losses (milliequivalents/liter) from each compartment at each pH treatment level as a proportion of the losses at pH 4.0. The compilations allow comparison of the responses of the individual nutrient compartments and the ecosystem to increases in the acidity of precipitation. They also allow comparison of the relative sensitivities of each compartment and the ecosystem to the stress of acid rain. The greater the increase in nutrient losses from a compartment caused by a one unit (pH 4.0-3.0) or two unit (pH 4.0-2.0) decrease in pH, the greater is its sensitivity.

The compartment experiments were designed to examine the relative responses of individual nutrient compartments to different precipitation acidities. This design may incorporate a source of error in comparisons of responses between different nutrient compartments. The amounts of simulated rain applied to the ecosystems or to the soil, litter and vegetation samples were not equivalent based on the volume or weight of sample treated. Direct comparison of the sensitivities of different compartments is based on the assumption that the proportional increase in nutrients lost from a compartment at pH 2.0 compared to pH 4.0 will remain constant regardless of the amount of acid rain applied. The amount of simulated rain applied to a sample at each acid level must, of course, be the same. If different 1500 gram samples of soil were leached with pH 4.0 and pH 2.0 water, the relative amounts of nutrients lost at pH 2.0 would be approximately 13 times greater (based on Table 12) whether 250 ml or 500 ml of water were applied. Only the

absolute amounts of nutrients lost would vary with the volume of water applied.

This assumption may not be entirely correct, especially if extremely large or small volumes of simulated rain are applied. Within a moderate range of simulated rain volumes, it may be upheld. With these qualifications in mind, the three nutrient compartments and the entire ecosystem may be arranged in order of decreasing sensitivity to acid precipitation as follows:

soil > litter = granite outcrop ecosystem > vegetation

The soil compartment is the most sensitive unit studied, over twice as sensitive as the entire ecosystem. The litter component has an acid precipitation sensitivity about equal to that of the ecosystem, while vegetation is about one-third as sensitive as the whole ecosystem.

The relative sensitivities of the nutrient compartments are understandable. Almost all of the available cations in the soil compartment are held as adsorbed ions at cation-exchange sites. Since acid precipitation operates to increase leaching largely through the mechanism of hydrogen ion exchange, most of the nutrients in the soil compartment are susceptible to displacement by increased hydrogen ion concentrations in precipitation. Litter may have as high or higher a cation-exchange capacity as many soils (Wells and Davey 1966). Many of the cations held in litter, however, are bound in organic compounds and protected from the direct effects of acid leaching. The sensitivity of litter to acid leaching is high, but not as high as that of soil. Living vegetation is well protected against acid leaching by structures such as the cuticle,

and the containment of most cations bound in organic compounds or held inside living cells. Still, the sensitivity value given for vegetation in Table 12 may not be representative of outcrop vegetation as a whole. Only Viguiera porteri was tested for leaching. Polytrichum commune, a moss lacking a heavy protective cuticle, might be much more sensitive to acid leaching than Viguiera. Other species could be less sensitive.

The ecosystem as a whole is less sensitive (based on nutrient retention) to acid precipitation than would be predicted from a knowledge of its components alone. Distribution of calcium, magnesium, and potassium in nutrient compartments in a granite outcrop ecosystem is given in Table 13. Soil is by far the largest reservoir, holding 70.83% of these cations. Vegetation and litter hold lesser amounts. These percentages may be used to formulate a weighted average of the sensitivities of the litter, soil and vegetation components to acid leaching (Appendix 1). Based on this weighted average, an increase in cation losses of 1024% is predicted for the granite outcrop ecosystem following an increase in rain acidity from pH 4.0 to 2.0. The experimental value is only 601%. The ecosystem as a whole proves to be about half as sensitive to disturbances by acid precipitation than are its components.

As is often the case, the whole is more than the sum of its parts. It is the relationships between components and the constraints imposed by these relationships that determine the ultimate functioning of the system. As an example, Patten and Witkamp (1967) examined cesium cycling in a series of successively more complex microcosms. In a system composed only of leaves labeled with radioactive cesium, cesium was lost

Table 13. Nutrient distribution in granite outcrop ecosystem compartments. Data from Meyer (1972) for granite outcrop ecosystems on Mt. Arabia, Georgia in June.

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<u>Nutrient compartment</u>	<u>% total Ca + Mg + K</u>
Soil	70.83
Vegetation	19.83
Litter	9.34

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from the leaves by leaching at a rate of 3.7% per day. When system complexity was increased to include soil, cesium was lost from the leaves to the leachate at a rate of only 0.1% per day. The remaining 3.6% per day was retained in the soil and not lost. Similarly, in the granite outcrop ecosystems, nutrients leached from vegetation and litter are not directly lost to the environment, but must pass first through the soil. They may be retained in this compartment and not lost. The inter-relationships between the litter and vegetation compartments, and the soil compartment place constraints on total nutrient losses from the ecosystem. To quote Patten and Witkamp (1967), "...transfers of energy and matter in ecosystems are functions of networks which define inter-compartmental interactions; internal coupling should be considered a significant variable in investigations of ecosystem processes."

Nutrient conservation mechanisms cited by Meyer (1972) for granite outcrop ecosystems include:

- 1) storage of large percentages of nutrients in vegetation and litter
- 2) the retention of the bulk of the soil nutrients and litter nutrients in the center of the ecosystem where they are less susceptible to erosion or leaching
- 3) the bowl-shaped granite basin which directs water flow and the nutrients it carries into the ecosystem, not out of it

These nutrient conservation mechanisms are ecosystem properties. For example, distribution of nutrients in different compartments is an ecosystem property because these nutrient compartments exist together only at the ecosystem level. Processes involving all the nutrient compartments must be ecosystem level processes. Reice (1974) defines

an ecosystem process in terms of a community level process. "A community level process involves the actions and interactions of several populations, mediated by physical factors. If the process is determined by the physical factors, then it is an ecosystem process."

Nutrient conservation in the granite outcrop ecosystem certainly involves interactions between plant populations including competition for nutrients, but the nutrient conservation process is dominated by physical factors. The short, simple nutrient pathways of the granite outcrop ecosystem intimately link all the ecosystem components, abiotic and biotic, together. Loss of nutrients from one compartment rapidly affects all other compartments. The largest nutrient compartment, soil, is a physical factor and exerts a large influence on ecosystem response to acid precipitation. Two other physical factors also dominate. The functioning of the granite depression containing the ecosystem has already been discussed. The acid precipitation itself is a physical factor whose dominance is shown by the high correlation between ecosystem nutrient loss and precipitation acidity.

These three physical factors predominantly determine granite outcrop ecosystem responses to acid precipitation as measured by nutrient losses. Nutrient conservation within the granite outcrop ecosystem is therefore an ecosystem level process.

#### Redistribution of Nutrients

Since the response of the granite outcrop ecosystem to acid precipitation is an ecosystem process, what will the effects of acid rain on the structure and function of this ecosystem be? Increased

nutrient losses from the ecosystem have already been demonstrated (Table 5). The ecosystem is protected to a high degree against increases in nutrient losses by its ability to trap and hold water. Meyer (1972) investigated an outcrop ecosystem with a surface area of  $11.6 \text{ m}^2$ , a maximum depth of 18 cm, and a watershed of  $61.2 \text{ m}^2$ . Meyer found that it required 0.5 cm of rain to produce runoff from the ecosystem. For a rain of 1.2 cm, only 85.2 liters of runoff resulted from 616 liters run-on to the ecosystem. Obviously, many rain storms will cause no nutrient loss from the basin. Only during large rains will the nutrient leaching due to acid precipitation result in increased ecosystem nutrient losses. In contrast, every acid rain will cause water movement and therefore increased leaching from the edges of the ecosystem inward and from the soil surface downward. This would result in movement of nutrients to the deep soil zone in the center of the ecosystem. Therefore, a more important granite outcrop ecosystem response to acid precipitation than nutrient loss may be nutrient redistribution within the ecosystem.

Table 7 illustrates the distribution of available soil calcium, magnesium, and potassium within the three granite outcrop ecosystems of each acid rain treatment group. Concentrations of each nutrient are given for shallow (1 cm to 8 cm deep) soils around the edges of the systems and deep (greater than 14 cm deep) soils located in the center of the systems. Ecosystems receiving pH 4.0 simulated rain experienced the least acid leaching. For these systems, only one nutrient, potassium, was found in greater concentrations in deep soils than in shallow soils. At pH 3.0, both potassium and magnesium had

greater concentrations in deep soils than in shallow soils. In those ecosystems receiving pH 2.0 rain and thus being subjected to the most intense acid leaching, all three cations were found in greater concentrations in the center of the ecosystems than at its edges.

A redistribution of nutrients within the granite outcrop ecosystem as a result of increasing acidity of precipitation is evident. Two different consequences of this redistribution seem possible:

- 1) the interrelationships between the nutrient compartments will serve to maintain the relative sizes of the compartments. This will be accomplished by an increase in the rate of flux between compartments
- 2) an enlargement of the soil compartment and a decrease of the vegetation and litter compartments will occur

The first alternative could result from an increase in deep soil fertility due to increases in nutrient concentrations. Deep soil plant populations could respond with increased growth rates and increased nutrient uptake. Increased plant growth would in turn increase litter production. Increased inputs to the vegetation and litter nutrient compartments could offset the increased losses from these compartments due to acid leaching. The result would be a faster flow of nutrients through these compartments, but a maintenance of compartment size. The effect on ecosystem structure would be an increase in plant biomass and litter toward the center of the ecosystem and a decrease in biomass and litter on the basin edges due to loss of shallow soil fertility.

Several factors tend to counter this first alternative. It is questionable whether increased growth of deep soil species such as Viguiera porteri and Senecio tomentosus could entirely compensate for

reduction in growth of shallow soil populations. Increased concentrations of nutrients in the deep soil zone might not result in increased nutrient availability to plant populations under acid conditions.

After eleven weeks of pH 2.0 simulated rain, three ecosystems had a mean soil pH of 4.1 (Table 6). Soil pH has little or no direct effect on plant growth (Thompson and Troeh 1973). However, nutrient availability to plants may be greatly affected by soil pH. Below pH 6.0, availability of calcium, magnesium, and potassium declines as soil acidity increases (Buckman and Brady 1969). Aluminum solubility increases with increasing acidity and may reach toxic levels in low pH soils (Pierre et. al. 1932, Blevins et. al. 1970). Soil at pH 4.0 often contains enough soluble aluminum to be detrimental to most plants (Thompson and Troeh 1973). Both low nutrient availability and aluminum toxicity could counteract increases in plant nutrient uptake and facilitate decreases in the litter and vegetation nutrient compartments.

Another factor possibly contributing to changes in the relative sizes of the nutrient compartments is direct damage to plant tissues caused by acid precipitation. Granite outcrop ecosystems receiving pH 2.0 simulated rain suffered mortality of all individuals of Polytrichum commune. Individuals of Viguiera porteri developed necrosis of leaf tissues. Polytrichum, a moss, lacks a thick cuticle and depends upon direct precipitation unbuffered by soil reactions for much of its water absorption. It is particularly sensitive to acid precipitation and can suffer severe physiological damage including acid hydrolysis of chlorophyll a and b (Sheridan and Rosenstreter 1973). Tissue necrosis similar to that seen in Viguiera was reported

by Wood and Bormann (1974) for yellow birch seedlings misted with pH 3.0 or pH 2.0 simulated rain.

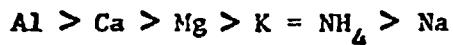
Vegetation damage in the pH 2.0 treatment ecosystems could substantially alter nutrient flow through the ecosystem. In outcrop communities studied by Meyer (1972), Polytrichum commune accounted for 39% of the total plant uptake of calcium, magnesium, and potassium during a ten week period in mid-summer. Polytrichum was second only to Viguiera porteri in total uptake. Reduction of photosynthetic tissue in Viguiera by tissue necrosis may cause reductions in growth and nutrient uptake of this species.

When these factors are considered, it seems probable that increased precipitation acidity will lead to an increase in the size of the soil nutrient compartment and a corresponding decrease in the vegetation and litter nutrient compartments of the granite outcrop ecosystem.

#### Cation Sensitivities

Table 7 not only illustrates an overall redistribution of nutrients within the experimental ecosystems, but exposes a pattern of redistribution. Potassium is found in greater concentrations in deep soils than in shallow soils in all three treatment groups. Magnesium shows higher central concentrations only in those ecosystems receiving pH 3.0 or 2.0 simulated rain. Calcium has higher concentrations in deep soils only in the ecosystem group receiving the highest acidity treatment. This pattern suggests that potassium is more easily leached by acid rain than magnesium or calcium and that calcium is the most resistant to acid leaching of the three cations. This would correlate well

with the positions of the three nutrients in the lyotropic series:



The ratios of the concentrations of each cation, shallow soil zone/ deep soil zone (Table 7), suggest a different conclusion. In the ecosystems receiving pH 4.0 rain, the concentration of magnesium in the shallow zone is almost twice that in the deep soil zone. The ecosystems receiving pH 2.0 rain have a shallow soil concentration of magnesium that is only one-tenth the concentration in the deep soil zone. Of the three cations, magnesium shows the greatest redistribution between acid treatment levels. Calcium is less sensitive than magnesium, while the relative concentrations of potassium in the shallow and deep soil zones do not change with increasing acidity, suggesting that potassium is the least sensitive of the three cations to acid leaching. This would place potassium much earlier in the lyotropic series than it is reported to be.

Possibly, the high acidity of the natural precipitation to which these ecosystems were exposed caused sufficient leaching of potassium prior to the experimental treatments to limit the effects of the increased acidities of the simulated precipitation. Potassium is leached in much higher concentrations at pH 4.0 than calcium or magnesium (Table 5), thus supporting this idea.

#### Nitrate

Acid precipitation may also influence cycling and loss of nutrient

anions in these granite outcrop ecosystems. Soil micelles and various organic materials including humus and litter have on their surfaces anion exchange sites as well as cation exchange sites. Anion exchange sites can result from:

- 1) amine groups in humus
- 2) bonding terminating with a cation at the edge of a silicon clay particle
- 3)  $\text{OH}^-$  ionizing from materials such as  $\text{Al}(\text{OH})_3$  or  $\text{Fe}(\text{OH})_3$   
(Thompson and Troeh 1973)

The anion exchange capacity of a soil increases as soil acidity increases, primarily due to increased ionization of  $\text{OH}^-$ . Acid precipitation could reduce losses of anions from outcrop ecosystems by increasing the ability of the soil to bind anions through anion exchange.

Measurements of nitrate losses (Tables 5, 8-10) show no correlation between nitrate concentrations in leachates from each compartment, and the pH of simulated rain applied to the outcrop ecosystems, litter, soil, or vegetation. Nitrate losses from the ecosystems (Table 5) do correlate with soil pH (Table 6). An increase in soil acidity corresponds with a decrease in nitrate losses.

The results suggest that nitrate losses are not controlled directly by the influence of acid rain on anion exchange, but indirectly through the effect of soil pH on nitrification. Nitrification and nitrogen fixation occur at normal rates only at pHs considerably higher than 5.5 (Buckman and Brady 1969). Rates of mineralization of nitrogen compounds decrease below pH 6.0 (Thompson and Troeh 1973). Thus, as soil pH declines, the rate of nitrate production drops and the amounts

of nitrate available to be leached is reduced. Since ammonium is converted to nitrate through nitrification, a reduction in the rates of nitrification should lead to an increase in ammonium concentrations. As Table 5 reveals, ecosystem losses of ammonium are inversely correlated with ecosystem losses of nitrate. Losses of ammonium, a cation, appear to be controlled not by the direct influence of acid rain on cation exchange, but through the influence of acidity on nitrification.

It is not surprising that anion exchange does not play a major role in regulating nitrate losses. Nitrates are capable of only slight anion exchange under acid conditions, and almost no exchange under more neutral conditions (Donahue 1965). The anion exchange capacity of most soils is much lower than their cation exchange capacity (Thompson and Troeh 1973). A percentage increase in the anion exchange capacity of a soil could be too small in absolute terms to cause a noticeable effect on nitrate retention. Most nitrogen compounds, including nitrate, are highly water soluble at any pH and are subject to rapid leaching (Thompson and Troeh 1973). Wood and Bormann (in press) examined leaching effects of simulated acid precipitation on soil samples. After several months of leaching, they were unable to detect nitrate-nitrogen in any soil samples regardless of the pH of the simulated rain applied. Apparently, all the nitrate was leached from the soil samples by the simulated rain.

#### Ecosystem Responses to Perturbations

Changes in ecosystem nutrient cycling parallel ecosystem succession (Vitousek and Reiners 1975). For terrestrial systems undergoing secon-

dary succession, nutrient outputs exceed inputs only for a short period immediately following the perturbation which initiates the new successional sequence. Likens et. al. (1970) reported large increases in the concentrations of nutrients in a stream following clear-cutting of the watershed. Concentrations increased by a factor of 57 for nitrate, 15.6 for potassium, 4.2 for calcium and 4.1 for magnesium. Nutrient losses rapidly decline as the rate of biomass accumulation increases until outputs of essential nutrients may reach zero. The rate of biomass accumulation and nutrient uptake then declines as succession continues resulting in an increase in nutrient outputs. At maturity or steady-state, the ecosystem will have no net biomass increase and nutrient inputs will equal nutrient outputs.

The only period during ecosystem development that nutrient outputs exceed inputs follows a perturbation of the ecosystem. Short-term nutrient cycling studies conducted by Meyer (1972) showed the granite outcrop ecosystem to have equal inputs and outputs of essential nutrients when the pH of run-on entering the system was 4.68. The present study demonstrated that increases in the acidity of simulated rain greatly increased nutrient losses from outcrop ecosystems (Table 5). The results indicate that acid precipitation represents a perturbation to these ecosystems.

Margalef (1968) stated that when subjected to a perturbation, ecosystems of higher maturity regress and acquire properties similar to those of an earlier successional stage. Odum (1969) has compiled a list of trends to be expected in ecosystem development. Margalef's theory may be tested by comparing the responses of the experimental outcrop

ecosystems to acid precipitation with the trends suggested by Odum. If ecosystem response to perturbation actually entails a regression to an earlier successional state, the experimental outcrop ecosystems should have acquired some of the properties characterized by Odum as less mature.

Many of Odum's parameters were not considered in this study and cannot be used for comparison. Appropriate trends include:

- 1) species diversity increases with succession
- 2) the nutrient exchange rate between organisms and the environment slows as the system matures
- 3) nutrient conservation by the system improves
- 4) total organic matter increases
- 5) inorganic nutrients are primarily extrabiotic in developing systems, primarily intrabiotic in mature systems
- 6) the role of detritus in nutrient regeneration increases with succession

Based on these successional indices, outcrop ecosystems do respond to the perturbation of increased precipitation acidity by regressing to an earlier successional state. Species diversity declined with the elimination of Polytrichum commune from those ecosystems receiving pH 2.0 rain. Long term effects of reduced nutrient availability and possible metal toxicity could further reduce diversity over longer time periods. Nutrient exchange rates between plants and the environment increased as a result of acid leaching (Table 10). Nutrient conservation by the entire ecosystem became less efficient as evidenced by increased losses in runoff (Table 5). A decrease in plant biomass, an increase in the percentage of total nutrients located in the soil

compartment, and a decrease in litter are all probable outcrop ecosystem responses discussed earlier in this section.

Verhoff and Smith (1971) have modelled a theoretical ecosystem whose properties are very similar to those of the granite outcrop ecosystem. They define their system as "conservative nutrient-controlled." A conservative nutrient system lacks a constant source of nutrients, and so the total amounts of nutrients present are quite constant. The granite outcrop ecosystem meets this criteria with its limited inputs and outputs. In a nutrient conservative system, the nutrient studied must meet two criteria: 1) it must be limiting plant growth or the primary producer growth; thus it affects the entire ecosystem, 2) the concentration of the nutrient must change significantly in the resource storage (soil or water) as the plants grow, i.e. the plants must use enough of the nutrient to change its concentration. The nutrients examined in this research fit these criteria. Calcium and nitrogen are frequently limiting in outcrop ecosystems (McCormick et. al. 1974). In outcrop ecosystems studied by Meyer (1972), soil solution concentrations of calcium, magnesium, potassium, and ammonia decreased by a minimum of 50% of each nutrient during the growing season. Granite outcrop ecosystems meet the criteria of nutrient conservative systems, and the simulations of Verhoff and Smith's (1971) model may be used to examine outcrop ecosystem responses to perturbations.

Verhoff and Smith's model of a nutrient conservative system predicts that as the total amount of a limiting nutrient decreases, the percent of the nutrient held in plants will decrease, and the percent contained in the soil compartment will increase. This is exactly what was

predicted earlier for the distribution of nutrients in outcrop ecosystems subjected to acid precipitation. For the outcrop systems, it is the total availability to plants of the nutrients as well as the total amount of nutrients in the system that declines. Verhoff and Smith also predict that an increase in the death rate will decrease the amount of nutrients in plants and increase the amount in the soil. This redistribution of nutrients was predicted for the outcrop ecosystems based on the increased death rate of Polytrichum commune.

Verhoff and Smith (1971) determined that their theoretical system could only exist for a certain range of total nutrient concentration. Above or below this range, the present ecosystem disappeared and was replaced by a new system. Should acid precipitation reduce the total nutrient concentration or availability in an outcrop ecosystem to a critical level, that ecosystem could conceivably be altered to form a new system with a different species composition, structure, and function. In the terminology of Holling (1973), the system would shift from one domain of attraction to another domain of attraction. A domain of attraction may be described as a range of values for the parameters of a system. As long as the parameters or state-variables of a system remain within these ranges, the system is stable and can withstand varying amounts of perturbations. Should one or more of the state-variables exceed their range, the system becomes unstable and shifts to a new domain of attraction, within which it is stable until random fluctuations or external perturbations drive it to a new domain.

An example of this shift is described by Glendening (1952). In semi-arid regions of the southwestern United States, grazing and fire control allow invasion of grasslands by shrubs and trees such as

mesquite and cholla. If grazing has not been too intense or prolonged, its cessation allows the ecosystem to return to grassland. Once the invading trees reach a large enough size and density to outcompete the grasses for moisture, the grasses don't return even if grazing is stopped. Once a system state-variable (tree size and density) exceeds its range in the grassland domain as a result of an external perturbation (grazing), the system shifts to a new and stable domain of attraction.

The shifting of a granite outcrop ecosystem to a new domain of attraction due to the perturbation of increased precipitation acidity is possible but unlikely. Acid rain acts primarily as a stress upon the nutrient cycling of the outcrop ecosystem. Nutrients, however, are only secondarily limiting in these systems. Moisture is the primary limiting factor (Sharitz and McCormick 1973). A decrease in nutrient availability in the outcrop ecosystem could increase the competitive edge of certain outcrop species, but they would be prevented from outcompeting and eliminating other species by the primary limiting factor. Moisture gradients in the outcrop systems restrict species to distinct zones, thus normally preventing interspecific competition for nutrients (McCormick et. al. 1974). Invasion of the system by non-outcrop species better able to compete in low nutrient, higher acid conditions would be prevented by their lack of tolerance for high water stresses. Thus, the perturbation of the ecosystem caused by acid rain seems more likely to cause a reduction in the growth of existing populations than an actual shift to a new domain of attraction. In this case, a stress regularly applied to the system (limiting moisture) acts to stabilize the system in its present domain of attraction in the face of a new perturbation.

## CONCLUSIONS

- A. Increases in the acidity of simulated rain applied to nine granite outcrop ecosystems caused increases in the total amounts of calcium, potassium, and magnesium lost from these ecosystems and their individual nutrient compartments.
- B. Losses of ammonium and nitrate from the outcrop ecosystems are controlled indirectly by acid precipitation through its effect on soil pH which in turn influences rates of nitrification.
- C. Increases in precipitation acidity correlate with a redistribution of nutrients within the outcrop ecosystem.
- D. Nutrient conservation by the granite outcrop ecosystem is an ecosystem level process.

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## APPENDIX 1

Calculation of the weighted average of ecosystem compartment sensitivities  
to acid leaching.

<u>compartment</u>	<u>% nutrients in compartment (Table 13)</u>		<u>normalized nutrient losses at pH 2.0 (Table 12)</u>	
soil	70.83	X	13.02	= 922.21
vegetation	19.93	X	2.03	= 40.25
litter	9.34	X	6.59	= <u>61.55</u> 1024.01

$$\frac{1024.01}{100} = 10.24$$

The third section of this report is a summary of ten years of research activity under this contract. An incomplete, but perhaps useful summary is as follows:

1. Publications of the principal investigator which were supported by this contract:

Effects of ionizing radiation on natural ecosystems. FUNDAMENTAL NUCLEAR RESEARCH. U.S. Atomic Energy Commission, 1965.

A portable radiation facility for ecological studies. On site ecological research of the Division of Biology and Medicine at the Savannah River Ecology Laboratory. January, 1965. U.S. Atomic Energy Commission TID-21713, McCormick, Golley and Monk.

Irradiation of natural vegetations Experimental facilities, procedures, and dosimetry. On site ecological research of the Division of Biology and Medicine at the Savannah River Ecology Laboratory. McCormick and Golley, January, 1965. U.S. Atomic Energy Commission TID-21713.

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2. Graduate Students who received M.S. or Ph.D. degrees working under this contract:

Barbara Bannister: The Ecological Life Cycle of Euterpe globosa (Gaertn). M.A., 1967. (Research conducted in Puerto Rico). Currently employed as research associate in tropical ecology program at U.P.R.

Fairman Cumming: Experimental Analysis of Community Structure. M.A., 1969. Employed as research assistant. Laboratory of Radiation Ecology, Savannah River Plant.

Bruce Dayton: Accumulation and Transfer of Radiostrontium by Young Loblolly Pines. Ph.D. June 1968. Associate Professor of Biology, New York State College, Oneonta, N.Y.

Ron Dillon: Distribution and Production of the Macrofauna Flora of a North Carolina Estuary. M.A., June, 1968. Ph.D. completed June, 1971. (Research conducted at our Institute of Marine Sciences.)

Ron Dillon cont.: Associate Professor of Botany, Dean of Faculty, Clemson University.

Ariel Lugo: Energy,  $CO^2$  and water Budget of a Natural Ecosystem. Ph.D. August, 1969. Associate Professor of Botany, Univ. of Florida. Currently Deputy Secretary of Natural Resources, Government of Puerto Rico.

Clair Mellinger: Causes of Endemism in Viguiera porteri. Ph.D. June 1971. Associate Professor, Eastern Mennonite College.

Pete Murphy: Effects of Beta Radiation and Simulated Fallout on a Natural Ecosystem. Ph.D., August, 1970. Assoc. Prof. Michigan State Univ.

Ken Meyer: Seasonal Fluctuation of Phytoplankton Composition, Diversity, and Production in a Freshwater Lake. M.A. January 1969. Ph.D. August, 1972. Influence of Nutrient Availability and Nutrient Cycles on Ecosystem Structure and Stability. Asst. Professor Mansfield State Univ.

Gary Lee Miller: The Influence of Season on the Radiation Sensitivity of an Old Field Community. Ph.D., August 1968. Assoc. Professor of Biology, Eisenhower College.

Rebecca Sharitz: Life Tables as a Means of Describing the Ecology of Two Plant Species. M.A. 1969, Ph.D. August 1970

Sharitz cont.: Asst. Professor University of Georgia Institute of Ecology. Presently, ERDA, Technical Representative, Washington, D.C.

Lloyd Willis: Physiological Basis of Radiation Sensitivity in Pines. Ph.D. to be completed August, 1976.

Tom Armentano: Population Dynamics of Aster macrophylla and Cornus canadensis Under Varying Intensities of Environmental Stress. Ph.D. completed December 1973. Post-Doctoral Research Fellow, Brookhaven National Laboratory.

Julie Irwin: Structure and Composition of island Communities in a Stream Receiving Thermal Effluent from a Nuclear Reactor. M.A. 1974.

Maria Lebron: Recovery of a Tropical Rain Forest Following Irradiation, Ph.D. 1975.

Richard Olson: Effects of Acid Rain on a Natural Plant Community, M.A. 1975.

Kevin Summers: Ecological Basis for Land Use Planning at the Shearon Harris Nuclear Power Plant, Wake County, North Carolina. 1975.

3. Selected papers presented at scientific meetings:

Association of Southeastern Biologists - 1966, "An Ecological Study of the Radiation Sensitivity of Euterpe globosa."

American Institute of Biological Sciences - 1966, Symposium on Current Research in Two Tropical Rain Forest Areas. (1) "Effects of Radiation on Dominance and Diversity;" (2) "The Microdosimetry of the Forest."

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Ecological Guidelines for Environmental Impact Analysis. Savannah Georgia. ASB Meeting 1974.

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4. Appointments and activities directly related to work conducted under this contract:

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Consultant, Oak Ridge National Laboratories.

Consultant, U.S. Forest Service, Institute of Forest Genetics.

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2. Ecological Effects of Ionizing Radiation.
3. Inquiries into the Structure, Function and Evolution of a  
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National Research Council, National Academy of Sciences, Panel Chairman, Committee on Arms Control and Disarmament. Published report entitled, "Long term world wide effects of Multiple Nuclear Weapons Detonations."

United Nations and World Health Organization (PAHO), Consultant on Environmental Quality. Consultant to the government of Mexico with responsibility to design and evaluate environmental monitoring and safety program for the nation's first nuclear power facility.

Summary

This being a final report, it is appropriate that it is comprised almost entirely of results. For ten years the science of ecology, the University of North Carolina, my students and I have benefited from the generous support of the A.E.C.

### Abstract

THOMAS VINCENT ARMENTANO. Population Ecology and Response to Stress of Aster macrophyllus and Cornus canadensis  
(Under the direction of J. FRANK McCORMICK.)

Aster macrophyllus and Cornus canadensis, two herbaceous perennials of northern Wisconsin, were found to be adapted to both undisturbed forest habitats and to recently disturbed sites. Both species are capable of maintaining populations in forests by vegetative propagation, but require disturbance for colony expansion. Disturbance stimulates flowering, greater plant vigor, and higher caloric content in Aster, but only vegetative propagation in Cornus.

Both species are primarily asexual in forest habitats, with seedling establishment rare. The bottomland habitat of Cornus subjects the species to late frosts after flowering begins, with signs of frost damage to flowers common. Flowering in Aster increased with increasing light intensity of its habitat.

Seasonal changes in aerial shoot density were similar in all populations of both species over two years, in that population density increased in June and early July during

the time of vegetative propagation and then decreased in September as recruitment declined. Effects of an August 1970 drought were minimal probably because most life history events were completed before then.

Seasonal variation in caloric values were similar in undisturbed populations of both species except for some unexplained fluctuations in Aster which occurred during the August 1970 drought. Canopy removal did not disrupt typical seasonal trends in either species, but caused an increase of 300-500 cal/g in Aster shoots. Overall leaf chlorophyll concentrations were inversely related to incident light intensity in both species and involved June maxima during the time of maximum growth and September minima. Canopy removal caused only small reductions in chlorophyll levels, with no photo-oxidation noted in either species.

Gas exchange studies show that both species can acclimate to changes in microclimate such as can result from forest disturbance by increasing photosynthetic efficiency when exposed to a given microclimate regime. Plants acclimated to a cool regime (22 C days, 12 C nights) had higher respiration rates at all temperatures than plants acclimated to a warm regime (30-35 C days and 20 C nights). Cool preconditioning caused a depression in net photosynthetic rates at all temperatures in Aster, and at temperatures exceeding

25C in Cornus. Warm acclimated plants had higher net photosynthesis: dark respiration ratios at all temperatures. In both species, plants grown under 7000 lux exhibited greater photosynthetic efficiencies at light intensities up to 15000 lux, and had lower light compensation points than plants grown under 20,150 to 50,000 lux. Aster macrophyllus maintained relatively higher rates of CO<sub>2</sub> uptake at lower leaf water potentials and lower relative water content than did Cornus canadensis.

Soil shielding enhanced survival under gamma radiation stress. A dose of 2.2 kR over 44 days stimulated flowering and leaf caloric content in Aster, and doses of 2.2 - 44 kR stimulated rhizome caloric values in Cornus. Above ground: below ground biomass ratios decreased under radiation stress.

It is predicted that the hemicryptophytic life form of both species would enable them to survive the direct effects of ionizing radiation, and that colonies of both species would expand in response to the increased light intensity which would likely be a secondary effect of radiation stress.

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## INTRODUCTION AND LITERATURE REVIEW

Although there are many studies of forest herbs in the literature, comparatively few are concerned with the temporal and spatial variations of populations and their response to disturbance.

Several studies on the response of herbs and shrubs to disturbance indicate that certain species are well adapted to disturbed conditions, while other species which lack these adaptations, are selectively eliminated by environmental stress. Preliminary observations and a literature review suggest that Aster macrophyllus and Cornus canadensis, two prominent hemi-cryptophytes found in the understory of northern Wisconsin forests may not only be adapted to undisturbed conditions, but may also be pre-adapted to disturbed forest conditions.

Raunkaier (1934) has indicated that the hemicryptophyte life form of herbaceous perennials is prevalent in climates such as that in northern Wisconsin. Hemicryptophytes have perennating buds near the soil surface, with perennial rhizomes (which also have buds) and roots within the soil. That the location of buds at or beneath the soil surface

results in protection from above-ground stresses is shown by several studies. Brayton and Woodwell (1966) found that frequent burning increased the cover of Carex pensylvanica in New York. Bud sprouts of Vaccinium vacillans helped this species increase in importance in the same habitat in New Jersey (Buell and Cantlon 1954). Wagner (1966) found Carex pensylvanica greatly increased its cover and density in areas of the Brookhaven oak-pine forest in which the canopy was opened by chronic gamma irradiation. Because of its capacity for vegetative propagation, its shielded buds and its radioresistance, the sedge was less inhibited by radiation than other species. McCormick (1969) found that Campsis radicans dominated the inner zone of a southern pine forest which was exposed to doses exceeding 3 kR of gamma radiation for over 200 hours. The radiation stress eliminated competition and altered the microclimate. Chappell (1963) showed that subterranean perennating buds of greenbriar (Smilax) survived gamma irradiation because of soil shielding even though aerial parts had a relatively high sensitivity to ionizing irradiation compared to other flowering plants.

Woodwell (1970) has pointed out that even though ionizing radiation could not have played a major role in the evolutionary selection of adaptive characters, species and

community responses to ionizing radiation are paralleled by their response to other stresses such as fire, overgrazing, sulfur dioxide pollution, and herbicides, as well to environmental extremes such as occur on mountain tops and high latitudes.

One of the main objectives of this study is to evaluate the response of Aster macrophyllus and Cornus canadensis populations to forest disturbance and to compare population characteristics under disturbed conditions with those in undisturbed habitats. Since both species occur in several different undisturbed habitats, an additional objective is to determine the spatial and temporal variations in intact populations over two growing seasons, and to determine the adaptations which enable Aster and Cornus to persist in a wide range of environments.

There are few reported studies in the literature concerned with the physiological ecology and population ecology of forest herbs in both disturbed and undisturbed habitats. Most investigations cover only one or the other of these subjects, and a brief review of these papers follows.

Tamm (1956) counted marked individuals of three species of herbs in permanent plots for 13 years and found that although the populations were fairly constant, there was a rapid turnover of individuals involving losses of seedlings

and mature plants and recruitment by sexual and asexual reproduction. Harper (1967) expressed Tamm's data logarithmically and found a linear relationship indicating a constant mortality rate similar to decay of radioisotopes. From this relationship, he calculated a "half-life" for each species. A short half-life characterized a senescent population and a longer half-life characterized a more vigorous population.

Struik and Curtis (1962) sampled herbaceous distribution patterns in a southern Wisconsin Acer saccharum forest and found that most species were homogeneously distributed with some degree of aggregation, and that herbs as a whole were randomly distributed. Perennial species were less homogeneously distributed than annuals since they were primarily dependent upon vegetative propagation for dispersal. Whitford (1949) analyzed the spatial patterns of clonal perennials in forest stands of different successional status and concluded that the later the position of the stand in the sere, the more uniform the distribution and that the degree of departure from a random distribution was related to stand age. Rabotnov (1969) reported that great plasticity in reproduction and growth typifies the responses of herbaceous perennials to environmental variation. He also noted that many individuals may be capable of producing seeds for 20 to 30 years or more. Kerster (1968) determined the population

age structure for the prairie herb Liatris aspera by counting growth rings of the corm. The size of the age class was related to seed germination and survival levels which in turn varied with spring moisture availability. Individuals flowered after age nine and the oldest individual lived 34 years.

The importance of the ecological life cycle approach to research into population dynamics of herbs was cited by Pelton (1953) who provided a basic study outline. Such investigations have been made by several authors including Pelton (1961), Martin (1965), Kawano, Ihara and Suzuki (1968), and Whigham (1971). The latter found that the microenvironment of early successional old field and pine forest habitats significantly reduced growth and reproduction of transplanted individuals of Uvularia perfoliata in comparison to naturally occurring populations in climax hardwood stands. Vezina and Grandtner (1965) correlated the initiation of several life history stages with soil temperature and solar radiation for spring geophytes of Ontario. Kieckhefer (1962, 1963) followed temporal changes in phenology and energy content of Illinois forest herbs and found that trends vary with species, time of flowering and season of maximum growth. Bazzaz and Bliss (1971) found that the chlorophyll content and leaf area index of an Illinois forest herb community during a cool year

may be only 50% and 35% respectively, of the total during a warm year. The seasonal trend in light compensation point of several species of forest herbs was correlated with canopy closure according to Lieth and Ashton (1961). Sparling (1967) divided 30 species of woodland herbs into three groups based on light saturation point, and related this to prevailing solar radiation of the species' habitat during time of maximum growth. The light saturation point of a given species increased with increasing light intensity prevailing throughout critical phases of the ecological life cycle. But Bazzaz and Bliss (1971) point out that certain species can belong to all three of Sparling's categories depending upon their state of maturity. Randall (1953) studied Wisconsin forest herbs from different stands and found that stands with higher continuum indices supported herbs with higher chlorophyll content on an area and dry weight basis, higher dry weight to leaf area ratio and herbs which lost less water before wilting. Evans and Hughes (1961) used experimental techniques to demonstrate the effects of artificial shading upon morphology and physiology, and obtained results similar to those reported in the field in other papers. Struik (1965) examined the growth patterns of southern Wisconsin forest herbs and studied the changes in energy content and biomass in sexual and asexual organs

throughout the growing season. When compared to annuals, perennials allocated less biomass and energy to above-ground parts and sexual reproductive organs, were less succulent, and wilted more slowly. Anderson, Loucks and Swain (1969) used regression techniques to show that the canopy of a northern Wisconsin pine forest exerts a greater limiting effect upon the leaf area index of herbs through its reduction in throughfall than in its reduction of light intensity.

Northern Wisconsin is an optimum location to study both the impact of disturbance upon forest herb populations and to examine population behavior under different environmental conditions. The forests of northern Wisconsin have been subjected to extensive logging and frequent fires during the past century, especially in the years 1860 to 1920 (Brown and Curtis, 1952). Because of these disturbances, and the Pleistocene glaciation which created many abrupt topographic variations (Curtis, 1959), northern Wisconsin is occupied by a mosaic of vegetative types, mostly successional in nature. Thus within a 1440 acre area (the Enterprise Radiation Site), there are aspen, white birch, and northern hardwood stands, as well as a variety of bottomland habitats and recently disturbed sites. This fact, along with the availability of field and laboratory facilities of the U. S. Forest Service make the site an ideal location to carry out a study of the

response of populations of herbaceous perennials to forest disturbance.

#### Site Characteristics

Study Site. All field work was completed at the Enterprise Radiation Site, a 1440 acre tract in Oneida County (T35N, R9E) Wisconsin. This is the study location for a joint project of the Atomic Energy Commission and the United States Forest Service (North Central Forest Experimental Station) entitled the Radiobiology of Northern Forest Communities. The area supports a mosaic of forest types which vary with topography and drainage (Fig. 1) and which are largely of second growth origin. A Cesium 137 gamma source was positioned at the confluence of three forest types before the 1972 growing season. The three forest types are aspen (Populus tremuloides), white birch (Betula papyrifera), and northern hardwoods (Acer saccharum, Tilia americana, Acer rubrum, Quercus borealis and others).

Brown and Curtis (1952) studied northern Wisconsin forests and found Populus tremuloides to be important in stands of low continuum indices (pioneer forests). These stands usually were burned over, had open canopies, and were initiated on mineral soil. Betula papyrifera is important in stands of medium low to intermediate continuum indices

with denser canopies than the Populus stands. It is more shade tolerant than the Populus species, but is also dependent upon disturbance for reproduction. Quercus borealis and Acer rubrum are trees of greater shade tolerance than the two previously mentioned and both regenerate after fire. Acer rubrum may be found in almost any stand but is usually only of secondary importance. Quercus borealis is quite long lived and thus often occurs in mesic stands as large trees. Tilia americana is important but not dominant in stands of medium high and high continuum indices which may persist under Acer saccharum primarily by sucker sprouts. Acer saccharum is the dominant of stands with high continuum indices, and the only species that reproduces well under its own canopy, but a pure stand is rarely attained due to the frequency of disturbances.

climate. The regional climate is classified as humid and cold. (Walter and Lieth, 1960). According to data from the Rhinelander, Wisconsin Weather Station, about 20 miles away, the average January mean temperature is 13 F and the average July temperature is 68.2 F. Winter minimums between -30 and -40 F are not infrequent and summer highs around 95 F can be expected each summer. Night temperatures in confined openings and bogs can be expected to go below 32 F in all summer

months. The frost-free season at Rhinelander is 123 days. The annual precipitation of 32 inches is well-distributed throughout the year with 60% falling from May 1st to October 1st. The mean annual snowfall is about 54 inches and an uninterrupted snow cover from December 1st to March 1st is average.

Soils and Topography. Strelow (1968) described and mapped the soils of the study site. The soils of the area are of glacial origin with silt loams and sandy soils prevailing. The forest communities are found on well drained to excessively drained soils on rolling and undulating uplands. The soils are formed from acid sandy, stony tills (Eldron Series), silty material over sandy loam to heavy loam acid till (Goodmar Series), or a thinner silty layer over acid sandy glacial till (Iron River Series). All upland soils are weak or medially podzolic in nature. Bog elevation is 1640 feet with highest upland sites reaching 1720 feet.

The Species. The following is a description of the species modified from Gleason (1952). Aster macrophyllus, a member of the Asteraceae, is a perennial with creeping rhizomes, and sometimes with a short, branched caudex producing abundant clusters of basal leaves on short, sterile shoots. The stem is two to 12 dm tall, glandular in the inflorescence or some-

times throughout, and often more or less spreading hairy. The cordate leaves are thick and usually firm, scabrous-hirsute above and villous-hirsute beneath, sometimes glandular, crenate or serrate with usually mucronulate teeth. The inflorescence is corymbiform, flat or round-topped. This is a highly variable species from which numerous segregates have been proposed. It flowers from July to October. It ranges from New Brunswick and Quebec to Wisconsin and Minnesota, south to Pennsylvania, Indiana, and in the mountains to Georgia. The habitat is described as "woodlands."

Gleason (1952) describes Cornus canadensis: a member of the Cornaceae, as a perennial forming colonies with horizontal rhizomes. The stem is erect, one to two dm tall, bearing clusters of four to six apparently whorled leaves at the summit, and below them, one or two pairs of scales or smaller foliage leaves. Leaves are lanceolate to oblanceolate or obovate, four to seven cm long and acute at both ends. The flower cluster is solitary on a peduncle one to three cm long. There are four ovate-lanceolate to broadly ovate, white bracts subtending the inflorescence. Fruits are red, globose drupes, about eight mm in diameter. It flowers in June and July. It ranges from Greenland to Alaska, south to New Jersey, Pennsylvania, Indiana, and

Minnesota, in the Appalachians to West Virginia, in the west to California, and also in eastern Asia. The habitat is described as moist acid woods and bogs.

At Enterprise, aerial shoot development of vegetative individuals of both species is initiated in the beginning of the growing season and completed by the middle of June. Bolting shoots of Aster macrophyllus continue to elongate until the latter half of July when flowering commences. Flowering stems range upward to 70 cm in height.

At what age individuals first flower is not known since there is no way of aging herbaceous perennials except by growing plants over several years and correlating age with some constant morphological feature (Dr. Katharine Esau and Dr. Sherwin Carlquist - personal communications). Also in Aster macrophyllus, rhizome connections are too short-lived to correlate clone size with age as can be done with some herbaceous perennials (Dr. Philip B. Whitford, personal communication). But there is considerable population variation in caudex diameter, and flowering shoots originate from caudices that average thicker than those of the vegetative shoots (Figure 5). Also, inspection of new asexual shoots of the year indicate that these never flower.

By September, most heads of Aster macrophyllus contain mature fruits. Vegetative shoots consist of a stem from

0.3 - 0.8 cm tall which bears two to four long-petioled leaves. Canopy removal results in the production of six to 12 leaves with shorter petioles (Figure 6). Greenhouse and growth chamber plants also have numerous leaves.

Flowering shoots of Cornus canadensis emerge simultaneously with asexual shoots, and flower buds open while leaves are expanding. The two-seeded fruits are mature by August, and in shoots with a full complement of fruits their weight may bend the plant to the ground. In the individuals in which the flowers abort, axillary buds produce secondary shoots which extend above the original shoot, and include two to six leaves.

By the middle of July both species have distinctive perennating buds which will produce next year's shoot. In Aster the buds are 0.8 to 2.0 cm long and terminate the caudex. There is no terminal perennating bud in Aster shoots that bolt. Instead, an axillary bud develops into next year's shoot. In Cornus, perennating buds, which may contain pre-formed floral primordia, are 0.2 to 0.4 cm long, and develop from the basal node of the current year's shoot (Figure 7). Typically in Cornus, dead stems remain attached two to three years, usually without leaves after the first year. No thickened caudex develops in Cornus as it does in Aster. Vegetative propagation and colony expansion in both

species result from axillary buds beneath the soil surface.

No individual studies of Aster macrophyllus or Cornus canadensis have been reported in the literature but both species are cited in several papers which provide some insight into the ecological requirements of the species.

Wilde and Leaf (1955) classified the soils of central Wisconsin into five types and reported that Aster macrophyllus was found only on sandy podzols with a mean pH of 3.5. This soil is the second highest of the five types in moisture, organic matter content and cation exchange capacity. Cornus canadensis was restricted to sandy gley podzols with an average pH of 3.7 and the highest ranking in the three categories just mentioned.

Both species were present in the boreal forest study of LaRoi (1967), with Cornus canadensis having the highest presence values of all herbs in black spruce stands and the second highest in white spruce stands. Aster macrophyllus was present in both stand types but with much lower presence values. According to Christensen (1963) both species are present in the prime winter habitat of white-tailed deer of northern Wisconsin - white cedar swamps and deciduous swamps. Both species increase in frequency under heavy browsing pressure. Levy (1970) found that both species are components of one of three types of northern Wisconsin woodland openings

maintained by fire and repeated cutting. This community is dominated by weedy exotics, and Aster and Cornus are of secondary importance. Aster macrophyllus was called "almost ubiquitous" by Buell and Cantlon (1951) in their study of Itaska Park, Minnesota, along the prairie-forest margin. Flaccus and Ohmann (1965) cited Aster macrophyllus as an important species in early successional forest stands in Minnesota.

Cornus canadensis is found in a wide variety of habitats in northern Alberta (Ritchie 1956) including open jack pine forests subject to heavy fire frequency, and open heath stands. Moss (1955) considered Cornus canadensis one of two characteristic herbs of the Populus tremuloides consociation and of the white spruce association in Alberta. It is also found throughout the coniferous forest types that merge into the Boreal-Cordilleran forests of the Canadian Rockies. Mueller-Dombois (1964) cited Cornus canadensis as a moisture-indicating species which grows very densely in the oligotrophic, moist margins of spruce bogs on gley podzols of southeastern Manitoba. In contrast, Jeglum (1971) found Cornus canadensis to be most characteristic of very eutrophic peatlands at Candle Lake, Saskatchewan.

## METHODS AND MATERIALS

### Objectives

The specific aims of this study were as follows:

- 1) To determine the response of populations of Aster macrophyllus and Cornus canadensis to canopy removal, thus evaluating the capacity of populations already adapted to undisturbed forest environments to adjust to sudden forest disturbance. Parameters studied included density, standing crop biomass, asexual and sexual reproduction, seasonal variation in caloric content and leaf pigment concentration and leaf area loss to herbivores.
- 2) To determine the response of the species to gamma radiation administered in an experimental gamma field, and in conjunction with other data, to predict the response of intact populations to irradiation of the forests of Enterprise.
- 3) To examine the metabolic response of the two species to laboratory manipulation of light, temperature and moisture conditions. This helps answer the following questions: What environmental factors limit species populations in the field? What adaptations permit these species to occur over a wide range of microclimates?
- 4) To study the spatial and temporal

differences in populations of the two species in undisturbed habitats, and thus furnish a comparison to the response of the species to forest disturbance. Populations from the six forest stands were studied seasonally over two years and the characteristics studied were the same as those of the disturbed site population.

#### Experimental Design

Field Sampling Design. The sampling scheme established by the U.S. Forest Service for the Radiobiology of Northern Forest Communities project was used to sample forest populations of Aster macrophyllus and Cornus canadensis for data on density and reproduction trends. Two stands of each of the following forest types were sampled: aspen (Populus tremuloides), white birch (Betula papyrifera) and northern hardwoods (Acer saccharum, Tilia americana, Quercus borealis, and others). One stand of each of the forest types was exposed to gamma radiation in the summer of 1972, and these stands are designated as "experimental." The second set of stands was located several hundred meters from the radiation source and were considered the "control" stands. Both control and experimental stands were sampled in 1970 and 1971.

In the experimental stands, the sampling scheme consisted of 20 paired  $1/4 \text{ m}^2$  quadrats between 5 and 10 m from

the source, and 44 paired 1 m<sup>2</sup> quadrats from 10 to 150 m from the source. In the control stands, 20 paired 1 m quadrats spaced every 10 m were sampled. In addition, a transect consisting of 28 1 m quadrats were sampled along a logging trail which was cordoned off in 1969. The effect of the removal of trampling stress was thereby evaluated (Figure 1). To study populations of Cornus canadensis where its colonies are best developed, a 1 m wide transect 20 m long was established along the periphery of a spruce-tamarack bog adjacent to a logging road (Figure 1). Scattered aspen trees comprise an open canopy here. Cornus does not occur in the bog itself. This colony is designated as the "bog-edge population."

To investigate the effect of canopy removal upon intact populations of Cornus canadensis and Aster macrophyllus, 10 quadrats each 1 m<sup>2</sup> were laid in the logged portion of the control white birch stand and in the control aspen - bog ecotone. Logging occurred in April 1971 before aerial shoots of herbs were produced, and the perennating organs were undamaged. All other plants were removed initially. The plots were located in the center of a 20 m wide swath, thus exposing them to full insolation throughout the day.

### Population Structure

Seasonal variation in density of vegetative and reproductive shoots. To study seasonal variation in shoot density, all forest quadrats were sampled over a several day period beginning on the following dates: 1970-May 31, July 12, Sept. 3; 1971-May 29, July 17, Aug. 29. Quadrats in the disturbed sites were sampled on the 1971 dates and on June 15, 1972.

The following data were taken from all plots:

- a) the number of shoots/m<sup>2</sup>
- b) the number of flowering shoots/m<sup>2</sup>
- c) the number of fruiting shoots/m<sup>2</sup>
- d) the number of fruits/m<sup>2</sup>
- e) the number of seedlings/m<sup>2</sup>

Also, the number of flowering shoots producing fruits after being bagged was determined by bagging 15 shoots of each species.

Standing crop biomass. In order to determine the standing crop biomass of the various populations of Aster macrophyllus and Cornus canadensis, estimates were made of below-ground and above-ground biomass on an area and mean shoot basis in the three control stands in July 1970. Similar data were obtained from the bog-edge population of Cornus and the

disturbed site populations of both species in July 1971. In the control forests, all below-ground biomass was collected down to 25 cm from 40 plots. Plot area was  $1/4 \text{ m}^2$  in the aspen stand,  $1 \text{ m}^2$  in the birch stand, and  $2 \text{ m}^2$  in the hard-wood stand. Ten  $1/4 \text{ m}^2$  quadrats were excavated in the bog-site and disturbed site. The number of aerial shoots of the current year (which could be distinguished by the lack of bud scale scars) and the number of young shoots still below-ground were also tallied. An attempt was made to quantitatively determine *Cornus canadensis* root biomass, but because of the organic substrate (often old stumps or rotting logs) and the very fine texture of the roots, this was abandoned and below-ground biomass reported is principally rhizome biomass. In the case of *Aster macrophyllus* which occurred primarily in well-drained mineral soil, and which has coarse roots, careful removal of soil with running water in the laboratory provided a satisfactory estimate, although undoubtedly fine rootlets were lost. Aerial shoot biomass was obtained from the same quadrats.

Leaf Area and Herbivory. To find the leaf area index of populations of both species, and leaf area : leaf weight ratios, collections of 50 leaves from each habitat for each population were made. Seasonal collections of 50 leaves were

used to assess the impact of herbivores by tracing leaves and determining the area of leaf holes (Odum, 1970).

Phenology. On May 29, July 19, and August 27, 1971, the following observations were made on 15 marked shoots of Aster macrophyllus growing in the white birch control forest, and 15 marked shoots of Cornus canadensis in the experimental aspen stand:

- 1) length of aerial stem
- 2) length and width of first and second pair of leaves
- 3) presence or absence of flowers
- 4) presence or absence of fruits and their developmental stage
- 5) presence or absence of perennating bud and its size

Timing of asexual reproduction was estimated by counting the number of new above and below ground shoots which originated from rhizome extensions. These represent the number of shoots added to the population during the current year. This data was taken from plots excavated for biomass determination.

#### Seed Germination Studies

Laboratory seed germination studies were made by scarifying 900 fruits of Cornus canadensis in concentrated

sulfuric acid for 15 minutes, and then stratifying them in moist peat at 5 C in the dark, as recommended by the Woody Plant Seed Manual. Stratification of 1900 Aster macrophyllus seeds was identical but scarification was omitted. Seven months later, seeds were transferred to environmental chambers with a photoperiod of 13 hours and a thermoperiod of 26 C days and 12 C nights. Seeds were watered until November and the percent germination tallied. Ungerminated seeds were over-wintered in North Carolina. Second year germination was noted the following year.

#### Seasonal Variation in Caloric Content

In order to study seasonal variation in caloric content of aerial and subterranean plant organs, samples of the two species from each habitat were collected, oven-dried at 90 C for 24 hours (48 hours in the case of rhizomes) and stored in sealed plastic bags for transport to the University of North Carolina Ecology Laboratory. Here the samples were ground in a Wiley Mill with a 40 mesh screen. Energy values were determined from 0.8 to 1.0 g pellets in a Parr adiabatic oxygen-bomb calorimeter. The procedure outlined in the Parr Manual (1960) was followed except that the acid correction step was omitted since this was shown by Leith (1968) to

amount to less than a 0.1% error. Means are expressed on an ash-free dry weight basis assuming complete ashing by the calorimeter. The combustion procedure was repeated up to six times to obtain duplicate (1970) or triplicate (1971) values that agreed to within one percent. Occasionally, it was necessary to accept variation up to 1.25%, but in many the variation is as low as 0.1%.

Caloric equivalents of leaf, rhizome and root samples were determined for Aster macrophyllus, and of aerial shoots and rhizomes for Cornus canadensis, on a seasonal basis for each of the habitats. Additional values for reproductive structures and certain vegetative structures were also obtained.

#### Seasonal Variation in Leaf Pigment Content

To determine the seasonal variation in leaf pigment content of populations in disturbed and undisturbed habitats, leaf samples of the two species from the various habitats were collected for pigment extraction and analysis during the regular census periods, beginning in July 1970. Leaves of 20 individual shoots were collected along a transect, stored in plastic on ice in the dark until return to the U.S. Forest Service laboratory where extraction was usually begun within

three hours of collection. Ten samples, each composed of one mature leaf from two plants were ground in 90% acetone and added  $\text{CaCO}_3$  with a mortar and pestle. Optical densities were determined with a Hitachi-Perkin Elmer 139 UV-VIS Spectrophotometer in 1970 and with a Unicam SP 1800 Ultraviolet Spectrophotometer in 1971, at the following wave lengths: 665, 645, 630, 510, 480, and 430 nm. Chlorophyll a concentration was calculated using the formula of Parsons and Strickland (1963). The yellow to green pigment ratio (Margalef, 1968) was found from the ratio of the optical densities at 430 and 665 nm.

#### Gas Exchange Studies

To study metabolical response to temperature, light intensity and moisture variations, rates of net photosynthesis and dark respiration of the two species were determined in the ecology laboratory of the University of North Carolina. Plants were collected at the Enterprise Radiation Site, overwintered at 5 C and then grown under two different environmental regimes. The "cool" regime consisted of a 13 hour photoperiod with 22 C days and 12 C nights, and light intensities of 7050 lux. The "warm" regime was that of a greenhouse. Conditions varied, but daytime temperatures

regularly exceeded 30 C, and sometimes reached 35 C, while nighttime minima always exceeded 20 C, sometimes reaching 24 C. Greenhouse light intensities, measured with a Weston photometer at plant level, ranged from about 20,150 lux on cloudy days, to 50,350 lux on clear days.

Plants were sealed in the base of a single-walled plexiglas chamber using Apiezon (Type Q) sealant. The chamber (Figure 2) consisted of two compartments, one containing a motor-driven fan and a small radiator. The other compartment received the plant through a tongue and groove slot in the base plate. Gas exchange was measured with a Beckman 215 A infra-red gas analyzer as the main unit of a laboratory gas analysis system (Figure 3).

The analyzer was calibrated at least once daily using research grade gases from The Matheson Company. Flow rates were generally maintained at 2 liters/minute through the system, but for respiration determinations, a 1 liter/minute flow rate was sometimes used. To keep cuvette air CO<sub>2</sub> concentration within 30 ppm of ambient air, the flow rate was often increased to 4 liters/minute for photosynthesis studies of Aster macrophyllus. The relative humidity of the incoming air was maintained above 60%, by bubbling it through flasks of water when required. An open system was used, and rates of gas exchange in mg CO<sub>2</sub>/dm<sup>2</sup> leaf surface/hour were

calculated from an equation given in Brown and Rosenberg (1968). Extra Aster macrophyllus leaves were removed at least one hour before measurement so that only two or three leaves remained in the cuvette and there was no shaded leaf surface. In the case of Cornus canadensis, a shoot included four to eight leaves and some self-shading occurred. This was estimated by removing the cuvette top and visually tracing leaf overlap from a vertical position, and found to be generally less than 10%, although in one plant it reached 20% of total upper leaf surface.

Studies included analysis of the effect of different leaf temperatures, light intensities, and relative water content upon gas exchange rates. A Haake FK2 controlled temperature circulator regulated the temperature of a 1:1 methanol-water coolant which circulated through the cuvette radiator. As measured with a YSI surface thermistor attached to the leaf underside, leaf temperature could be maintained within 1 C indefinitely. Environmental chamber light sources were an even mixture of Sylvania GroLux VHO and Westinghouse Cool White SHO fluorescent lamps plus incandescent bulbs, with an output of 17,250 lux. For light intensities up to 38,750 lux, chamber lights were augmented with GE 150 watt flood lamps. The spectral energy distribution curve of the lighting as determined with an Isco

spectral radiometer, is given in Figure 45. For lower light intensities, cheesecloth was placed between the cuvette and the light source. Dark respiration was determined by darkening the chamber.

In a typical run, plants were exposed to temperatures at 5 C intervals between 5 and 40 C. A given leaf temperature was maintained for at least one hour with the first half hour reserved for equilibration. Then an average net exchange of CO<sub>2</sub> was determined by analyzing cuvette air for ten minute periods, alternating with a five minute analysis of ambient air. To determine the effect of water stress upon CO<sub>2</sub> uptake, net photosynthesis rates were obtained at 17,250 lux from plants rooted in soil at field capacity. Water was then withheld and CO<sub>2</sub> uptake determined at least once daily until no further uptake was detected. Relative water content of leaves was determined by following the method of Slatyer and Barrs (1965) and water potential of selected plants was estimated by the Shardakov dye method as described by Knippling (1967). In the relative turgidity experiment, leaf discs 0.6 cm in diameter were floated in water for four hours at a light intensity of 650 lux- near the compensation of the two species. In the dye method, whole leaves of Corinus and cut sections of Aster were allowed to equilibrate overnight.

The study of plant metabolism through the use of cuvettes may be subject to errors caused by the artificial environment within the enclosure (Larcher, 1969). These errors include increase in relative humidity, differential transmissivity of cuvette material, low or high wind effect depending upon flow rate, and CO depression of CO ambient  $\text{CO}_2$  concentration resulting in inhibition of photosynthesis. Through the manipulation of flow rates, use of humidifying flasks and the use of "transparent" plexiglas, some of these effects were hopefully minimized.

#### Response to Gamma Radiation Stress

To study the effects of radiation stress upon survival, flowering, biomass and caloric content of Aster and Cornus, plants of both species were transferred from Enterprise to an irrigated experimental gamma field in Rhinelander on July 21, 1971. Rhizome sections with aerial shoots and intact roots in soil blocks were transplanted into one quart plastic containers, held over in a greenhouse several weeks and then transferred to the gamma field at different distances from the Cesium-137 source. Plants were sunk to pot level and shaded with cedar shingles. Twenty-five individuals of each species were transplanted in arcs giving daily

dose rates of 1000 R, 300 R, 50 R, and 6 R in addition to a control series. Total counts of survival, rates of flowering and fruiting and assessment of morphological changes were made on September 2, 1971, and on June 12, 1972. Aerial shoots were considered living if intact green leaves remained, while rhizomes were considered living if intact buds with living tissue were found. Plants were then harvested, and energy and biomass determination made of the above and below-ground parts for both species at the different doses.

#### Distribution and Community Relationships

The composition of the herbaceous layer of the six forest stands was determined by finding the density and frequency of all vascular plant species below one meter in height except Carex pensylvanica in one transect in each stand in July 1970. In the case of clonal forbs, individual shoots were counted as individuals. Density of Carex pensylvanica stems was estimated using a line intercept technique (Philips, 1959). Importance Values were calculated using cover data of the United States Forest Service.

Interspecific association between Aster macrophyllus and Cornus canadensis was tested by calculating Cole's Index as revised by Hurlbert (1969).

Dispersion of the two species was examined from abundance:frequency ratios calculated from the transect data (Whitford, 1949).

#### Soils and Microclimate

To characterize the soils at the site, three soil pits were dug in each habitat and the samples from 2 to 5 cm combined. Mechanical textural analysis was made by the Bouyoucos hydrometer method (Bouyoucos 1936) with Calgon as the dispersing agent. Percentage of sand (2.0 to 0.05 mm diameter particles), silt (0.05 to 0.002 mm), clay (less than 0.002 mm), were calculated. Wilting point and field capacity were determined using a pressure plate apparatus at 15 and 1/3 atmospheres respectively. Analysis of Ca, Mg, K, P, Mn and organic matter were made by the North Carolina Department of Agriculture-Soil Testing Division. Extractable nutrients were analyzed using HCl - H<sub>2</sub>SO<sub>4</sub> extractions. Organic matter was determined using H<sub>2</sub>SO<sub>4</sub> - Na<sub>2</sub>CrO<sub>4</sub> digestion procedures.

The United States Forest Service has set up microclimate stations throughout the experimental and control forests and an open field to collect the following data: air temperature, soil temperature, soil moisture, precipitation, relative

humidity, and solar radiation at the three foot level. The latter is being monitored using a chlorophyll extract system calibrated with a solar radiometer. Other instruments employed include wet bulb thermisters, thermister temperature probes, and soil thermisters. There are 18 stations in the treatment area, nine in the control area and one in an open field adjacent to the disturbed site.

## RESULTS

### Population Structure

Seasonal variation in shoot density over two years. Seasonal variation in density of aerial shoots of Aster macrophyllus were similar in all six forest stands (Figures 13, 14). All population densities were lowest in September 1970 and all except the experimental birch stand (prior to radiation) returned to 1970 densities by June 1971. All populations decreased more sharply from July to September 1970 during the drought than during the same period in 1971 except the pre-radiation experimental aspen stand.

The disturbed site population density differed from the forest populations in that it declined sharply from July to September 1971 (Figure 13).

The density of aerial shoots of Aster was greatest in July 1970 in the control aspen stand where there were 56.10 shoots/m<sup>2</sup> (Figure 13). The lowest value was 3.80 shoots/m<sup>2</sup> in the control hardwood stand.

Seasonal variation in density of Cornus canadensis aerial shoots was similar in 1970 bog-edge, trail and aspen populations, with June minima and July maxima (Figures 15,16).

In 1971, the trail population declined continuously from the July 1970 peak, unlike the other populations which repeated their 1970 patterns. The birch and hardwood densities were low, with more clustering and the density trends were close to that of the trail population. Absolute shoot density varied from a maximum of 171.70 shoots/m<sup>2</sup> in the bog-edge colonies to 0.80 shoots/m<sup>2</sup> in the hardwood stand.

The disturbed site population of Cornus was distinctly different than all other populations of both species in that there was a continual increase in density (from 30.00 to 94.00 shoots/m<sup>2</sup>) from June 1971 to June 1972, including a rapid surge in numbers from June to July 1971 (Figure 15).

Cornus populations other than the disturbed site contrasted with all Aster populations in that minima occurred in June rather than September. This is a consequence of the differences in the phenophase timing of the two species (Figure 4). Vegetative propagation in Cornus largely occurs after the shoot elongation and flowering stages of early June. In Aster, propagation begins earlier, during shoot elongation. Thus, by the first census date in the first week of June, new aerial shoots of Aster have already appeared, but those of Cornus do not emerge until later.

Density of flowers, fruits, and seedlings. Flowering of

Aster macrophyllus on an area basis (Figures 17, 18) and on a mean individual basis (Table 9) was greatest in the disturbed-site population in which all bolting shoots flowered. In other stands, not all bolting shoots flowered. The control aspen population had the highest density of flowering shoots/ $m^2$ , but the control birch population had the highest flowering rate on a per individual basis.

In general, bolting and flowering of Aster shoots increased with prevailing light intensity at the forest floor level. Highest numbers occurred in the control aspen forest where a two year average of 0.83 shoots/ $m^2$  bolted and 0.50 shoots/ $m^2$  completed flowering. Light here in July 1971 averaged 981 Langleys/month. In the stands receiving 580-600 Langleys/month insolation, flowering shoots occurred at densities of 0.15 and 0.38 shoots/ $m^2$  (experimental aspen and control birch stands), and in the remaining stands which received 300-420 Langleys/month, the densities were 0.01 - 0.62 shoots/ $m^2$ . Canopy removal greatly stimulated flowering in Aster, with 12.90 shoots/ $m^2$  flowering. This included a mean of 44% of all shoots averaged over 1970 and 1971 - compared to 1% in the control aspen population, and only 0.2% in the experimental hardwood population.

Flowering of Cornus canadensis was almost completely suppressed in forest populations. In the trail population,

0.77 flowering shoots/m<sup>2</sup> occurred, equivalent to 15.14% of all shoots. This compares to 11.20% and 15.64% of all shoots flowering in the bog-edge and disturbed site populations respectively (Table 10).

It is of interest to compare flowering densities for 1970 and 1971, since the two years differed significantly in microclimate. Flowering in Aster was reduced in all stands during 1971. Also fewer bolting shoots completed flowering in 1971, a year with less insolation (28.5% less in the open), and higher soil moisture than 1970 (Figures 39, 40). In contrast, flowering in Cornus populations increased in 1971 except in the bog-edge populations. This suggests that available light limits the flowering in Aster, but not Cornus (to be discussed later).

The seedling search in the control forests, disturbed sites and bog-edge site show that sexual reproduction provided few new individuals of either species (Table 11).

Aster macrophyllus seedlings found in the control aspen and birch forests were located in July 1971, but remained suppressed throughout the remainder of the growing season. When re-examined in June 1972, only four of thirteen seedlings in the aspen stand remained, but none in the birch stand.

Bagging results show that Cornus canadensis requires

cross-pollination in order to set seed (Table 11). In Aster macrophyllus, bagging reduced seed germinability by nearly 75 percent, but some self-fertility exists.

Standing crop biomass. The below-ground biomass of the Aster macrophyllus population in the control aspen stand totalled  $70.97 \text{ g/m}^2$  dry weight - more than six times the biomass of the control birch population and more than thirty times the biomass of the control hardwood population (Figure 8). The above-ground biomass of  $29.96 \text{ g/m}^2$  for the control aspen population was nearly five times greater than that of the control birch population and more than twelve times that of the control hardwood population.

The relative contribution of the caudex, rhizome and root tissues to the below-ground standing crop differed with forest type (Figure 9). On a mean individual shoot basis, rhizomes contributed the greatest proportion in the aspen stand, and the caudex contributed the greatest relative amount in the hardwood stand.

Individuals of Aster from the disturbed site averaged 1.42 g -- more than three times greater than any of the forest populations which had means ranging from 0.26 to 0.50 grams. Mean below ground biomass in the disturbed site was 0.93 g, compared to a range of 0.53 to 0.76 g for the forest

populations. The above-ground : below-ground ratio was highest at the disturbed site, followed closely by the other populations (Figure 9). Reproductive structures added greatly to the aerial portion in the disturbed population.

The bog-edge population of Cornus canadensis had nearly six times the below-ground biomass and seven times the above-ground biomass of the aspen population on an area basis (Figure 10). The mean individual aerial shoot from the disturbed site was 27% smaller than that of the aspen population and 76% smaller than that of the bog site. In contrast to Aster macrophyllus, canopy removal resulted in reduction of the above ground : below ground ratio in Cornus canadensis (Figure 11). This is attributed to two factors. First, there was no sharp increase in flowering in Cornus as there was in Aster. Also flowering does not involve production of extensive additional biomass in Cornus as it does in Aster in which a tall stem, cauline leaves and many heads are produced. Secondly, in Cornus there was a surge in asexual reproduction (Figure 15) in response to canopy removal. Since the new aerial shoots of the year average smaller than older shoots, the overall population mean is reduced. Asexual reproduction also increased the below ground biomass by adding many new rhizome extensions.

Leaf area and herbivory. The leaf area index (LAI) of Aster macrophyllus in the aspen forest was 0.52, indicating that slightly over one-half of the ground surface was covered by leaf surface, in contrast to the much lower values in the other two stands (Figure 12). Since the LAI was calculated from traced leaves the estimate is probably high due to leaf overlap and leaf orientation, but inspection in the field showed these to be minor sources of error.

At the bog site, the LAI of Cornus canadensis was four times that of the forest population and was greater than the LAI of Aster macrophyllus in the birch and hardwood stands, even though the mean individual leaf area of Cornus canadensis is only about 25% that of a mean shoot of Aster macrophyllus (Figure 12). The LAI within dense colonies of both species may approach or even exceed one (based on observation).

The leaf dry weight to area ratio, indicate that the open sites with greater radiant energy, support plants of both species with much thicker leaves than the forest sites (Figure 12).

The leaf area per individual shoot varied inversely with incident radiant energy in Aster macrophyllus (Figure 12). The effect of canopy removal is to reduce the leaf area of the mean individual in Aster macrophyllus but this

had no apparent effect upon Cornus canadensis leaf area.

Losses to herbivores increased seasonally in both species. Greater losses occurred in 1970 than in 1971, and greater losses occurred in the disturbed area than in the undisturbed area, especially in the case of Cornus canadensis (Table 14).

Phenology. The seasonal progression of life history events is presented in the phenological spectrum for 1971 (Figure 4). In Aster macrophyllus, vegetative propagation begins while aerial shoot development is occurring (late May and early June) and is largely completed by the time the flowering phenophase begins (late July), even though most of the forest individuals do not flower. In Cornus canadensis vegetative propagation does not begin until after flowering has occurred (no new shoots arising from rhizome buds were found on May 29 and June 8) and is largely completed by the second census date in the third week of July.

No variations in the nature and sequence of the various phenophases were discovered in the disturbed populations of either species, although quantitative differences, which are discussed under various headings, did occur.

Data from marked shoots indicates that from 61.7 to 84.0% of the shoots that were counted in June are still

present in September. Most recruitments occurred by the July sampling date and most losses are between the July and September sampling dates in both species. The control aspen Aster macrophyllus population and the bog-edge Cornus canadensis population gained in absolute numbers during the season while the other populations showed a net loss. This data does not correlate directly with the aerial shoot density data presented elsewhere because different quadrats were used for each study. Of the total number of new shoots produced, most of them are from new rhizome extensions rather than from axillary buds of the long-lived caudex in Aster macrophyllus. In Cornus canadensis, all vegetative recruitment is, of course, from rhizome branches since no caudex develops.

#### Seed Germination Studies

Seed germination studies indicate that viability is low in Cornus. After the first year, 1.33% of the seeds germinated, and after overwintering an additional 1.55% of the same lot germinated. From a sample of 25 seeds, 96% were found to empty when sectioned. Aster seeds germinated quickly over a several week period beginning two days after the end of the cold treatment and at higher rates (35.3%)

than those of Cornus.

#### Seasonal Variation in Caloric Content

Within each species, variations in caloric content of aerial and subterranean organs were broadly similar between the various undisturbed populations, with some exceptions (Figures 21, 22). Aster macrophyllus leaf values were similar in June and July of both years, but a sharp drop in the birch and hardwood stands that occurred by September 1970 did not occur in the aspen stand in 1970 nor in any of the stands in 1971. Only the aspen population showed a similar trend both years. Rhizome values varied less between populations (extremes differed by 140 calories over two years) and from year to year than the other organs. Extreme caloric values of roots varied 320 cal/g over two years. There was no similarity in root caloric values in 1970 and 1971. The sharp September 1970 increase in aspen and birch populations was not found in September 1971 in any population or in the hardwood population in either year.

In Cornus canadensis variations in aerial shoot energy content were similar in 1970 and 1971 in all populations, and also resembled trends in Aster macrophyllus leaves in 1971. Aerial shoot values are rather low, but when leaf and stem

values are determined separately it is found that Cornus canadensis leaf energy content is similar to that of Aster macrophyllus (Table 12) and the aerial shoot means are lower because stem energy levels are lower. Rhizome values have similar patterns both years in aspen and bog-edge populations, but seasonal differences are more pronounced in 1970 than in 1971, with nearly 400 cal/gm variation between June and July. Peak rhizome caloric content in Cornus canadensis occurred in July both years, whereas in Aster macrophyllus it was in June both years. In both species these peaks coincide with time of maximum rhizome elongation and production of new aerial shoots. For both species, peak above-ground values occurred in June, the time of maximum shoot growth.

Based on the caloric values presented in Table 12, reproductive organs and the structures that support them are high in calories and thus must represent an energy sink. The energy content of the food storage and food producing organs in flowering shoots were similar or higher than the same organs in vegetative individuals. This is also true of flowering Aster from the disturbed site (Figure 23) where leaf values exceeded 5000 cal/g. A possible source of some of this energy may have been Aster roots which were lower in flowering than in vegetative individuals.

Canopy removal affected energy relationships of the

two species differently. The much greater leaf caloric values of the disturbed site Aster macrophyllus compared to the forest populations (about 300 cal/g higher in June 1971, a highly significant difference at the 99% level using a "t" test), indicates that the Aster populations were converting some of the additional solar energy of the open site into stored foods. This is also shown by the greater biomass of the disturbed population as shown earlier (Figure 9). Most of these additional storage compounds appear to be stored in leaf rather than rhizome and root tissue since caloric values of subterranean organs are similar in forest and disturbed sites (no significant difference at the 95% level). The seasonal variation in rhizome energy content of open site Aster includes a June minimum (4405 cal/g) and a July maximum (4590 cal/g) that is lacking in the forest populations. Disturbed site roots also show this trend. This may result from an early translocation of stored foods from below ground storage organs to expanding aerial shoots in June, and a reverse translocation of current photosynthate in July. This can also explain the variation in root values of the birch and aspen populations which have patterns similar to the disturbed site, but leaves unexplained the small drop in hardwood root values from June to July.

Variation in caloric values of above and below ground

organs are similar in undisturbed and disturbed Cornus canadensis populations. Actual energy content of leaves and rhizomes are essentially identical in disturbed and undisturbed conditions in contrast to Aster macrophyllus. Disturbed site leaf caloric values of Cornus also differ from that of Aster in being much lower (maximum of 4540 cal/g) suggesting several possibilities. Cornus may have been less able to utilize the high levels of solar energy, or they may have had higher respiration rates due to solar heating of leaves (lower net photosynthetic efficiency in Cornus than in Aster is indicated by metabolism studies [Figure 30, Table 13]). The very high rates of vegetative propagation exhibited by the disturbed site Cornus population may also have channelled energy from storage sites to active growth sites.

#### Seasonal Variation in Leaf Pigment Content

Chlorophyll "a" concentrations for the three forest populations of Aster macrophyllus were similar with highest values early in the season followed by a slow decline (Figure 24). The northern hardwoods population, which received the lowest incident radiant energy, had the most chlorophyll a and the disturbance population, which received

the highest incident radiant energy, had the lowest. Chlorophyll concentrations increased late in the growing season in the disturbed site, unlike the other populations. One observable trend is the greater negative slope between the July and September sampling dates in 1970 than in 1971, perhaps related to early senescence brought on by the 1970 drought.

The aspen population of *Cornus canadensis* is similar to the forest *Aster* populations in absolute value and in seasonal changes (Figure 25). It differs from the bog-site population in both respects, and from the disturbance population in absolute value. The bog-site population shows a fall concentration increase like the *Aster* disturbance population.

The Margalef Ratios for the *Aster macrophyllus* populations were highest in 1971, then dropped before partially recovering in September of both years. The aspen population, however, continued to decline further by the end of the growing season. The very small change in Margalef Ratio from July to September, 1970, contrasts with the sharp drop in chlorophyll a concentration, indicating that carotenoids dropped similarly over the same time period (Figure 26).

Plants exposed to canopy removal follow a pattern similar to the other populations but ratios were higher

throughout the season.

All populations of Cornus canadensis showed a mid-season minimum in 1971 as did the non-aspen populations of Aster macrophyllus, but the late season recovery resulted in ratios higher than those in June, indicating a net decrease in carotenoid pigment concentration (Figure 27). This is especially so in the disturbed site Cornus canadensis plants in which there was no change in chlorophyll a, but a significant increase in the Margalef Ratio.

The full sun of the disturbed site did not reduce the chlorophyll concentration of Cornus leaves below that of leaves from undisturbed populations. Nor did full sun alter the seasonal variation of chlorophyll concentrations.

#### Gas Exchange Studies

The environmental regime to which plants were preconditioned was found to influence the metabolic response of both species to variations in temperature and light intensity.

In both species, cool-acclimated plants exhibited greater photosynthetic efficiency at lower temperatures and warm-acclimated plants exhibited greater photosynthetic efficiency at higher temperatures (Figures 28-31). It should be pointed out that these differences were only significant (at the 95% level)\* at 35 and 40 C in Aster and at 35 C in Cornus.

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\* according to a "t" test

Acclimation caused a shift in the optimum temperature for net photosynthesis towards the preconditioning temperature in Cornus canadensis (Figure 30), as reported for other species (Mooney & West 1964, Strain and Chase 1967). But this shift was not observed in Aster macrophyllus for which the optimum temperature for all plants was 20 C. The reason for the lack of shift may be that the optimum temperature for Aster actually lay between the temperatures selected for study. The two species also differed in that cool pre-conditioning caused an overall depression of net photosynthesis rates in Aster at all temperatures, but in Cornus this was true only at temperatures of 25 C and above.

In Cornus, cool-acclimated plants had higher respiration rates at all temperatures, although only at 35 and 40 C were differences between the warm and cool-acclimated plants statistically significant (95% level) (Figure 28). Differences caused by pre-conditioning regimes were greatest at 40 C where cool-acclimated Cornus plants had a respiration rate 70% greater than warm-acclimated plants. In Aster no significant difference in dark respiration rate was found as a result of preconditioning at any temperature.

Aster macrophyllus maintained a net photosynthesis: dark respiration ratio in excess of one at all temperatures except 40 C (Table 13). Warm preconditioned plants had higher P:R ratios at all temperatures - a reflection of the fact that they had higher photosynthetic rates throughout the temperature range and generally lower respiration rates. At

5 C the respiration rate of the warm-acclimated plants was extremely low, resulting in a very high ratio. At 40 C the photosynthetic rate of the cool preconditioned plants was only about 15% of the warm regime plants resulting in a very low P:R ratio.

Warm preconditioning of Cornus canadensis enabled the plant to maintain a P:R ratio of 1.02 at 35 C as opposed to 0.62 for the cool regime plants. Both groups had ratios well below one at 40 C. As in the Aster, warm-acclimated Cornus canadensis plants had higher P:R ratios throughout the temperature range. This seems to be due principally to the higher respiration rates of the cool-acclimated plants.

In both species, preconditioning to a lower light intensity in the cool regime resulted in greater relative light utilization at lower light intensities, although in Aster macrophyllus the effect was observed only below 15,000 lux (Figures 32, 33). Also in Cornus canadensis, plants grown under low light intensities were light-saturated at 17,200 lux (1600 foot-candles), and those grown under high light intensities were saturated at 22,600 lux (2100 foot-candles), the next experimental level. In Aster macrophyllus there was no observed shift in light saturation. The light compensation point varied from 540 lux to about 320 lux in warm and cool preconditioned Cornus

ca.adensis, respectively, and from about 1080 lux to about 320 lux in warm and cool-acclimated Aster macrophyllus. There were no photo-inhibitory effects observed at 38,750 lux, the highest intensity used.

There is some doubt as to whether water potential ( $\psi$ ) or relative water content (RWC) is the more important parameter affecting plant growth (Barrs, 1968). Each describes a different aspect of the internal water status of a plant. Whereas RWC expresses the actual quantity of water present in a leaf relative to the water quantity when the leaf is turgid,  $\psi$  defines the chemical potential of the cell water compared to that of pure free water. Units of  $\psi$  are those of pressure (bars) and since the chemical potential of pure water is given as 0, values for plant systems are nearly always negative (Slatyer 1967). Although it is doubtful which parameter best describes plant water deficits, it is clear that water absorption from the soil, water movement within the plant and transpiration loss result from water potential gradients, and that water content declines indirectly with declining water potential.

The relative turgidity method is considered the best method for determining relative water content of most species (Barrs 1968). Knipling (1967) points out that as determined by the dye method is an estimate of true  $\psi$ ,

but that comparisons between species must be made with caution. Thus interpretations of the relative drought resistance of two species based on water potential - relative water content curves can be questioned, although Slatyer (1967) has showed that the drought resistant Acacia neura has a lower  $\Psi$  at a given RWC than does the mesophytic tomato.

Results indicate that over the range of water stress studied, Aster macrophyllus maintains a lower  $\Psi$  for a given RWC than does Cornus canadensis. Differences are greater with higher RWC. For example at a RWC of 80%, the  $\Psi$  of Aster is just under -7 bars, while for Cornus  $\Psi$  is about -4 bars. At the  $\Psi$  at which complete inhibition of photosynthesis occurs (about -16 bars), RWC is 47% for Aster and 55% for Cornus.

There was a greater inhibition of net  $\text{CO}_2$  uptake at a given RWC or  $\Psi$  in Cornus than in Aster. Maximum photosynthesis was maintained down to a RWC of 80% and down to a  $\Psi$  of -7 bars in Aster; and in Cornus down to a RWC of 90% and a  $\Psi$  of -2.7 bars (Figure 34).

#### Response to Gamma Radiation Stress

After 44 days of exposure of fully mature aerial shoots

to gamma radiation there was nearly complete survival of both species (Figures 35, 36). It was not until the following year when active meristematic tissues were irradiated, that radiation effects became obvious.

The response of both species indicates that soil-shielding of below-ground rhizomatous buds, characteristic of hemi-cryptophytes, increases the apparent exposure that the individual plant can tolerate, as has been reported by Chappell (1963) for Smilax.

Aster macrophyllus, the most sensitive of the two species on the basis of interphase chromosome volume (Zavitkowski & Rudolph 1971), suffered complete death of above-ground parts at 1000 R/day but 44% of the individuals had living rhizomatous buds which could produce viable leafy shoots upon cessation of radiation stress. Survival of below-ground parts also increased the survival rate from 68% to 80% at 300 R/day, whereas complete survival of aerial shoots occurred at 50 R/day and at 6 R/day.

Cornus canadensis, predicted to be the second most radio-resistant angiosperm present at the Enterprise Radiation Site (Zavitkowski and Rudolph 1971), had 40% more aerial shoots surviving at 1000 R/day than did the control. Plants from the 1000 R/day arc had chlorotic areas, were smaller, and had less chlorophyll than the controls.

Survival of rhizomes increased total survival at 1000 R/day from 40% to 64% of the control. Survival of below-ground organs also increased the total survival at the other exposure rates. At 300 R, total survival exceeded that of the controls and aerial shoot survival was greater than at the lower dose rates, thus suggesting a stimulatory effect of radiation as has been reported by McCormick (1962). Unfortunately interpretation of the Cornus data is confounded by the loss of individuals to factors other than radiation after the September 1971 census as evident by the 56% survival of the controls and the low survival of aerial shoots receiving 6 and 50 R/day. Stimulatory effects are also suggested for Aster macrophyllus, since the rate of bolting was greatest at 50 R/day, and the rate at 6 R/day also exceeded that of the control.

No flowering by Cornus canadensis occurred at any exposure rate and in only eight percent of the controls.

Although plants of Aster macrophyllus receiving 50 R/day had significantly higher leaf caloric content (95% level) using a "t" test, and plants receiving 300 R had significantly higher root caloric values than did the controls, when data for whole plants were compared, there was no significant increase (95% level) resulting from any of the dose rates (Figure 37). There was, in fact, a highly significant

decrease (99% level) in total caloric content of plants receiving 6 R/day. Rhizomes of Cornus canadensis had caloric values significantly higher than the controls at 50 R/day, 300 R/day, and 1000 R/day, as did the shoots exposed to 1000 R/day. Only whole plants receiving 1000 R/day had significantly greater caloric values than the controls, although growth was inhibited (Figure 38).

Daily doses of 300 R and 1000 R in Aster and 1000 R in Cornus caused a decrease in above ground : below ground biomass ratio resulting from growth inhibition of unshielded shoots (Figure 38).

#### Distribution and Community Relationships

Importance value data show that Aster macrophyllus is among the most important herb in all six forest stands, whereas Cornus canadensis is present in only the experimental aspen and birch stands. Aster is the second most important species in all but the control birch and experimental aspen stands where it ranks third (Tables 2-7).

In the control hardwood and control birch stands, which are upland stands, the herbaceous layer is of low diversity and standing crop, with Carex pensylvanica forming a continuous matrix in which other species are dispersed. The many

fine stems of the sedge give it very high density values which bias its importance value. Here the concentration of dominance in Carex pensylvanica is great and it has far higher cover values and importance values than Aster macrophyllus. In the two aspen stands, which are higher in species richness and have the highest herbaceous layer standing crop, dominance is spread more equitably and Aster macrophyllus has higher cover values than Carex pensylvanica, although the sedge still has the highest importance value as a result of its high density.

Cornus canadensis is present only in bottomland stands, but in one of these, the control aspen stand, it is too rare to appear in any of the quadrats, although some individuals have been found on or at the base of old tree stumps.

The abundance/frequency ratio of the distribution of an herbaceous perennial changes in relationship to the length of time the species has occupied a given stand (Whitford 1949). A high ratio (maximum=1) indicates clustering during stages of colonization, with a low value (minimum value=0) resulting from an equitable distribution, and a secondary high index occurring again when relict status is attained. The abundance/frequency ratios obtained for the stands in which the two species occurred are presented in Table 8.

The coefficient of interspecific association is a

measure of the degree to which the number of joint occurrences of two species differ from that based on chance alone. A coefficient of 0 indicates no association with +1 indicating complete positive association with -1 complete disassociation (Cole 1949; Hurlbert 1969). Only relatively high absolute numbers indicate a definite positive or negative relationship. There appears to be no significant interaction between the species.

#### Soils and Microclimate

Texture of the soils at Enterprise is sandy, with only small differences between habitats (Table 1). It can be noted, however, that experimental aspen and bog-sites, the principal habitats of *Cornus canadensis*, have the lowest sand content and the highest silt, clay and colloid content. At field capacity (-0.33 bars) there is only a 3.46% difference in water content by weight between the extreme stands, and at the permanent wilting point (-15 bars), there is only a 2.43% difference between extreme stands. Soil from the experimental aspen stand is lower in organic matter and all elements analyzed except for manganese and calcium. The other soils are quite similar to each other.

Microclimate data indicates that environmental differences between the years 1970 and 1971 were greater than

between habitats within either year (Figures 39-42). A late summer drought developed in 1970 which resulted in soil moisture depletion in all stands (Table 15, Figure 40). In 1971, soil moisture remained above the permanent wilting point in all habitats throughout the growing season except in the aspen stand in the first week of August. Associated with the greater rainfall in 1971 (Table 15), was greater cloudiness which depleted incident solar energy. Total energy in the open was 12,763 Ly for July 1971, and 17,884 Ly for July 1970. Differences between stands were similar in both years although all totals were reduced in 1971. In general, the aspen stands had the most open canopy resulting in greatest light penetration, with the birch stands intermediate, and the hardwood stands the most shaded. Air temperatures within the herb layer were similar in all forest stands with slightly greater extremes in the aspen stands, and slightly higher overall temperatures in 1970 than in 1971 (Figures 41, 42). The base station, situated adjacent to the bottomland disturbed site of the Cornus canadensis population, had greater extremes than all forest stands, but of greater significance is the high frequency of freezing temperatures recorded here. For example, during the flowering and late bud phenophase of Cornus (May 27-June 20), the base station recorded over nine

hours of below freezing temperatures in 1970 while none were recorded in the forest stations. During the same period in 1971, 18 hours of below freezing temperatures occurred at the base station compared to a maximum of six in the forest stations. These late frosts are believed to contribute to the low fruit set in Cornus.

## DISCUSSION

### Response to Disturbance

The two species differed in response to forest disturbance although reproductive processes were enhanced in both. Full sun stimulated vigorous top growth in Aster macrophyllus in the form of greater basal leaf number per plant and greater leaf thickness plus the production of more aerial stems and caulin leaves associated with bolting. Root and rhizome biomass increased to a lesser extent. The result was a much higher above ground : below ground ratio in comparison to forest populations.

Mean aerial shoot biomass of Cornus canadensis actually decreased upon canopy removal since the increased asexual reproduction which occurred produced many small, young shoots. Below ground growth was increased probably from the combination of increased rhizome production associated with propagation, and increased vigor resulting from greater radiant energy availability as seen in pines by Kramer and Decker (1944). There was no change in leaf size, leaf number or leaf thickness in Cornus compared to the bog-edge population. The net result of canopy removal was to

reduce the above ground : below ground ratio (Figure 11).

Disturbance greatly stimulated bolting and flowering in Aster macrophyllus. The result was an increase of from 4.3 seeds per plant in the aspen population (1970) to 33.0 seeds per plant in the disturbed site population. The number of heads per flowering shoot was 41.8 in the disturbed site and only 14.1 in the aspen population. In Cornus only 8.18% of the shoots flowered compared to 9.31% in the bog-edge population. This was undoubtedly due partly to the fact that because of enhanced asexual reproduction, the disturbed site population was younger and thus had fewer shoots able to flower. In addition over 95% of the inflorescence aborted, resulting in very low fruit production. The reasons for this have already been discussed, and involve late frosts which occur well into June in bottomland areas.

In the disturbed site seasonal variations in caloric content were much like those in the forests in both species, indicating that the full light intensity of an open site did not disrupt normal seasonal patterns.

The high leaf energy values of Aster macrophyllus leaves in the disturbed site (300 to 500 cal/g higher than forest leaves) indicate that more high energy compounds were synthesized in response to the increased radiant energy (Figure 23). In Cornus no such spectacular increase occurred, perhaps because Cornus was less able to use the additional energy. Caloric value trends may also be related to population trends. Thus canopy removal stimulated a rapid increase in density in

the Cornus canadensis population with recruitment exceeding mortality even into September, in sharp contrast to populations from undisturbed sites (Figures 15-16). The additional available radiant energy may have been channelled into asexual propagation rather than into storage.

In Aster macrophyllus, rates of asexual reproduction were much more modest and the negative slope of the disturbed site population density late in the growing season was sharper than in undisturbed populations (Figure 13). At the same time, canopy removal promoted a surge in flowering of Aster. Apparently the additional energy available in the disturbed site was channelled into sexual reproduction rather than into maintenance of non-flowering shoots or asexual propagation.

The fact that direct exposure to full sunlight of leaves of forest established plants did not cause bleaching or excessive pigment breakdown is another indication that Cornus and Aster are adapted to forest disturbance (Figures 24 and 25). Yellowing as a result of exposure to intense light has been reported for shade tolerant herbs (Whigham, 1971; Curtis, 1959). Salisbury and Ross (1969) report that certain carotenoids help reduce photo-oxidation of chlorophyll in high light intensities by acting as anti-oxidants. The opening of the canopy did result in higher Margalef Ratios in Aster but this resulted largely from reduced chlorophyll concentration.

The seasonal pattern in Margalef Ratios and chlorophyll concentration were similar in all populations of Aster indicating that carotenoid levels rose and fell with chlorophyll levels (Figures 26-27). No response to increased light intensity was apparent in the pigment ratio of Cornus canadensis.

Zavitkowski and Rudolph (1971) predict that in the portion of the Enterprise Radiation Site receiving a growing season exposure of 250 to 500 R/day surviving vegetation would include scattered individuals of Carex pensylvanica, Lycopodium obscurum and perhaps Cornus canadensis. Their predictions are based primarily on the inverse relationship between interphase chromosome volume and radioresistance (Sparrow and Woodwell, 1962), and do not consider the importance of soil-shielding or species response to micro-climate changes. But gamma field data indicate that soil shielding would enable rhizomatous buds of Aster macrophyllus and Cornus canadensis to survive and that these would produce new aerial shoots as soon as radiation stress ceased and growing conditions permitted (Figures 35-36). The fact that rhizomes from the 1000 R arc maintained high caloric equivalents with no photosynthetic tissue present indicates that there would be sufficient stored food for rhizomes to survive without shoots for a considerable time. Subterranean buds would likely survive in the 500 to 1500 R/day zone even

though only cryptograms would survive direct exposure. Although shoot biomass was reduced by higher levels of radiation stress, below-ground biomass was relatively unaffected and the plants were able to tolerate reduction of photosynthetic surface and still maintain or even increase caloric content (Figures 37-38). Stimulatory effects of radiation have long been known (McCormick and Platt, 1962; Sax, 1963), but the mechanism behind it is unknown. The increase in caloric equivalents at the intermediate exposure levels at which stimulation of flowering and survival occurred (Figure 37) suggests that further investigations should be made into the possible inter-relationship between radiation intensity gradients and metabolic responses. The data suggest that radiation can stimulate plants to synthesize increased quantities of high energy storage compounds similar to the effect of opening the canopy or imposing a drought stress (Malone, 1968).

Experimental gamma field studies cannot provide information on the role of competition in regulating post-exposure community dynamics, but can predict species behavior under radiation stress. Combined with data on species dynamics under disturbed and undisturbed forest conditions, such studies can provide insight into the probable response to forest irradiation. Distribution and density trends show that at dose rates which opened the canopy but did not inhibit other forest herbs, competition for light and nutrients would limit *Cornus canadensis*. On the other hand, under

higher dose rates, Cornus' radioresistance and hemi-cryptophytic growth habit would permit it to survive while most competitors would be eliminated. Where competition was reduced and micro-climate was favorable, enhanced vegetative propagation and colony expansion would result.

Although more radiosensitive, the large size and rapid growth of Aster macrophyllus would make it an important understory species in a post-irradiation forest or at low dose rates in a chronically irradiated forest. Radiation-caused microclimate changes would greatly stimulate Aster macrophyllus growth and flowering (Figures 9 and 18). The importance of sexual reproduction would depend upon seedbed conditions, but there would probably be an ample supply of seeds both from within and outside the radiation site. The presence of rhizomes with their stored food and shielded buds would put both Cornus and Aster at a competitive advantage with any invading species which would colonize the area by seed.

### Physiological Adaptations

Metabolism studies indicate that both Aster macrophyllus and Cornus canadensis can adjust their rates of net photosynthesis and dark respiration to changes in microclimate (Figures 28-33). This acclimation enables Cornus and Aster to adapt their metabolism to seasonal change in temperature as well as to the greater temperature extremes characteristic of disturbed sites.

Acclimation effects were clearly demonstrated at the high temperatures (35 and 40 C in Aster and 35 C in Cornus), with mean net photosynthetic rates of warm-acclimated plants significantly higher (95% level) than cool-acclimated plants. Warm acclimation enables Cornus to reduce respiration rates significantly at 35 and 40 C; and enables both species to increase relative net photosynthetic rates at high temperatures thereby maintaining more favorable P:R ratios during summer hot spells especially in the higher light intensities of disturbed sites. Although air temperatures seldom reach 35 C, in full sunlight leaf temperatures often heat up to 10 C or more above air temperatures due to radiational heating (Gates, 1965). Adaptation to warm temperatures is especially important in herbs which retain aerial shoots throughout the summer.

The P:E ratios of the two species indicate that Aster is better adapted to high temperatures than is Cornus. Even at 35 C warm-acclimated plants of Cornus had a P:R ratio barely above one, in contrast to a P:R ratio of 1.82 for Aster. High temperatures perhaps interacting with other factors may play a role in restricting the local distribution of Cornus to cool bottomland sites and also help in fixing the southern limits to the range of the species. Supporting this is the observation of Curtis (1959) that Cornus is most frequent in the boreal forests of Wisconsin fifty miles to the north. There the proximity of Lake Superior, reduces summer highs 12 to 15 F or more. Wherry (1933) also suggested that Cornus was limited to soil temperatures below 65 F, thus explaining the southern limits to its distribution. That high temperatures can limit species distribution is suggested for some montane and alpine species (Rochow, 1970; Mooney, Wright and Strain, 1964). The more favorable P:R ratio of Aster macrophyllus at 30 and 35 C is consistent with the more southerly range of the species.

The optimum temperature for net photosynthesis of 20 C found in Aster and Cornus is typical of temperate zone plants (Larcher, 1969; Tranquillini, 1964). The rates at this temperature are also within the range commonly found in temperate zone species (Talling, 1961; Tranquillini, 1964).

According to Zelitch (1972), most species which have a carbon dioxide fixation pathway involving organic acids such

as oxaloacetic and malic acids ( $C_4$  pathway) are adapted to high light intensities in hot climates. No literature reference has been found which indicates that forest herbs possess this pathway. Thus although no investigation was made, it is assumed that Cornus and Aster possess the  $C_3$  pathway of carbon dioxide fixation.

Both species have the capacity to increase their survival potential in shaded habitats by increasing their photosynthetic efficiency at lower light intensities. This includes a downward shift in light compensation point as observed in other species (Bohning and Burnside, 1956; Sparling, 1967). Sparling reports that the light compensation points of forest herbs are correlated with the time of leaf development. But he did not account for adaptive shifts of species in different habitats. Thus the shift in light compensation point of Aster would result in a switch from Sparling's shade-intolerant category (leaves develop before canopy expansion) to the semi-shade tolerant group (leaves develop during canopy expansion), whereas the light saturation point of Aster and Cornus would place them in the shade intolerant category. In fact, leaves develop during canopy development in undisturbed habitats for both species, but can develop in full sun.

Jarvis and Jarvis (1963) hypothesize that a plant for which a decline in relative water content brings a relatively

small drop in tissue water potential has less survival capacity under drought stress than one for which a greater drop in water potential occurs. This is because the first plant will lose more water in maintaining a favorable gradient from soil to leaf as the soil dries and the critical water content at which cell damage occurs will be reached rapidly. But if either or both species is capable of drought adaptation, this hypothesis might not hold. Based on this interpretation, however, limited data suggest that Cornus would have less drought resistance than Aster. Thus water stress might partly explain the restriction of Cornus to bottomlands. The absence of Cornus from the control aspen stand may be due to limiting soil water as a result of root competition, as much as to shading effects. Greater drought resistance on the part of Aster is also suggested by the fact that it maintains higher net photosynthetic rates at lower relative water content and lower water potentials than does Cornus.

#### Population Patterns in Undisturbed Sites

Seasonal variation in aerial shoot populations of Aster macrophyllus was similar in all habitats although density varied from 56 shoots/m<sup>2</sup> in the control aspen stand to less

than 4 shoots/m<sup>2</sup> in the control hardwood stand. Vegetative propagation occurs in June, resulting in highest densities by July. By the end of August, densities drop, as recruitment declines, and mortality increases. In 1970, the negative slope from July to September was sharper, and senescence was earlier, probably a response to the late summer drought. Densities recovered to early 1970 levels by 1971, indicating that the drought had little permanent effect upon the populations probably because the chief growth period is early in the growing season before the drought developed.

Seasonal variation in Cornus populations of undisturbed sites resembled those of Aster, but the trail population differed. The trail population continuously declined in 1971, indicating that the vegetative propagation phenophase which typically occurs in June and July was suppressed. The trail site was cordoned off in late 1969, and by 1971 was dominated by large aggressive species like Aster umbellatus and Solidago graminifolia which invaded after trampling stress was eliminated. In 1970, the trail population seasonal pattern was still similar to other habitats.

Other lines of evidence from distribution and population data support the hypothesis that competition for light and nutrients is an important factor limiting the range of Cornus canadensis. Although Cornus is restricted to

bottomland sites at Enterprise, it is rare in the control aspen stand which borders a muskeg. This stand has a very well developed understory with a total biomass of  $176 \text{ g/m}^2$  which is at the upper end of the range of 100 to  $200 \text{ g/m}^2$  reported for rich forests (Bazazz and Bliss 1970). Cornus, which is shallow-rooted and less than 2 dm tall has escaped the considerable competition and shading that undoubtedly occurs here by maintaining itself on upright tree stumps where it is often the only plant. In the experimental aspen stand the forest in which Cornus reaches its greatest importance, ground layer biomass is considerably lower ( $92.4 \text{ g/m}^2$ ). The sites in which the highest Cornus densities are found (bog-edge) has a ground layer of low stature in which Cornus, Lycopodium sp., Trientalis borealis and mosses predominant. In the lowland hardwood and birch forests no decline in density is evident, although densities are so low as to suggest a declining population. This is supported by the abundance:frequency ratios of 0.498 and 0.451 in the birch and hardwood forests - ratios that may represent a relict population (Whitford 1949). The nearly complete lack of sexual reproduction in these stands also suggests a declining population. Thus Cornus is capable of maintaining asexual populations in shaded habitats for some time. These populations can then expand rapidly if the canopy is opened as

seen in the disturbed site, but may be inhibited by the presence of other species.

Low seedling production makes both species primarily asexual in undisturbed habitats, although suppressed seedlings of Aster were located in birch and aspen stands. The low seed production of Cornus in all environments means that sexual reproduction is uncommon in this portion of its range. The lower densities and low rates of sexual reproduction in hardwood stands indicate that both species are not climax species but require disturbance for long-term maintenance of populations in a given habitat.

Even though the forest habitats studied include a range of successional stages from a young pole stage aspen stand to near-climax hardwood stands, none of the population patterns of either species separate out according to the successional status of the habitat. If as Whitford (1949) suggested, an herbaceous-perennial reaches a peak in colony development in a certain forest type and then declines in the stand that replaces it, both species should be declining in the northern hardwood stands. That this hasn't occurred probably results from several facts. First, as Rabotnov (1969) and Whitford (1951) indicate, the longevity of herbaceous perennials is considerable with individuals living 20 to 30 years or more, and clones lasting 40 to 400 years depending on the species.

Thus, as in trees, temporal trends may occur on a greater time scale than it is possible to detect in several years.

The mean age of the trees at Enterprise was only 24 years suggesting that the canopy closed only recently in the hard-wood forests and there is still a lag in population response of Aster and Cornus.

In forest habitats there are differences in the biomass allocation between above and below ground parts resulting from population age differences and environmental effects.

A greater proportion of below ground biomass of Aster macrophyllus in the aspen population consists of rhizome tissue because the population is young with many new shoots which are produced from rhizome extensions of several dm or more. Also caudex biomass is smaller because caudices increase by radial increments over time and younger shoots always have smaller caudices. New caudices of the year are distinguishable by the lack of leaf scars and are always under 2 mm in diameter as opposed to older ones which range up to 9 mm in diameter. Since new shoots have smaller leaves than mature plants, at least in July, mean leaf area of the aspen population averages smaller than the older hard-wood population, even though the most vigorous mature shoots in the aspen site have greater leaf area than the largest shoots from the hardwood site. In Cornus canadensis,

bog-edge plants have larger, thicker leaves and shoots and more below ground biomass per shoot than plants from the aspen site, a relationship believed to be a response to the very open canopy of the bog-edge habitat.

The number of flowering shoots in forest habitats of Aster was significantly less (95% level) in 1971 when compared to 1970, when 40.2% more light energy reached the forest canopy in July. Other data show flowering to be proportional to available light energy. This includes the high proportion of flowers in the disturbed site which received direct sunlight, and the inverse relationship between the number of bolting shoots and the available solar energy in the forest habitats. As pointed out by E. J. Salisbury (1942), for a forest herb, producing sexual offspring requires more energy than producing asexual ones. Hamner (1940) demonstrated that there was a threshold light intensity below which floral-primordia were not initiated in barley, even with the correct photoperiod. Curtis (1959) reported that some shade herbs of Wisconsin rely primarily on asexual reproduction, and Kawano, et al (1968) indicate that Maianthemum biflorum and M. dilatatum have a very low fruit set in Japanese forests. Martin (1965) has shown that Geranium maculatum, when transplanted from a shaded forest habitat into a well-watered, competition-free sun garden, greatly increased its flowering

and fruiting rate as well as its vegetative development. The presence of cauline leaves in Aster suggests that successful bolting is dependent upon a continued input of energy above that supplied by the basal leaves. The presence of shoots that bolt to various heights but never flower in the forest stands (with a greater proportion of these in 1971) indicates that sometimes the necessary energy input is not maintained.

Since the floral primordia of Cornus canadensis are initiated the previous year, factors regulating flowering may occur in the preceding year, as reported for tundra plants by Holway and Ward (1965). In 1972, there were two to three times as many individuals flowering as in 1971, when there was ample soil moisture throughout the growing season. In 1971, flowering percentage was the lowest and in 1970 there was a late summer drought. The low fruit set which occurred in both years may be caused by several factors. The restriction of Cornus to lowland sites subjects it to late frosts that occur well into June. This is especially true in the disturbed site, but also pertains to the other sites which would be subject to cold-air drainage. A weather station 20 m away from the disturbed site in a location similar to the other Cornus populations recorded 25 hours of below freezing temperatures after June 1, 1970. Flower buds had already expanded by June 1, 1970 and June 8, 1971, and

already blackened, dead inflorescences with no sign of insect or fungus damage were apparent. Bog-edge and trail populations had extensive inflorescence damage and they occur in similar locations. Further north where Cornus may be found in a variety of habitats (Moss 1955; Ritchie 1956) there is some indication that fruiting is more successful. Porsild (1951) found Cornus common and widespread in the south-eastern Yukon Territory, with flowering beginning on June 22 in a location which was "practically" free from frost in valley bottoms from May 25 to August 25. Calder and Taylor (1968), who considered the closely related Cornus umalasch-kensis to be the sub-species Cornus canadensis intermedia, found it to be wide-ranging in the Queen Charlotte Islands from sea-level to sub-alpine meadows with abundant fruit set observed on most mature plants. Plants growing in bogs were "more depauperate" than those in adjacent regions.

A second contributing factor is that introgressed genes from closely related taxa may have reduced fertility. Hulten (1943) indicates that in the western and eastern coastal regions of Canada, Cornus canadensis intergrades with C. suecica and the resultant hybrid, C. c. intermedia, has much lower production of normal flowers and fruits. Even though Cornus canadensis is transcontinental and C. suecica is coastal in distribution, some hybrid strains should be

expected even in the mid-continental regions since C. succica occupied these areas along with Cornus canadensis in the recent past (Hulten 1943).

Energy content of aerial and subterranean organs of Cornus canadensis are similar in the different habitats even though there is a large difference in available light energy. One way Cornus can maintain levels of stored food in shaded habitats is by curtailing sexual reproduction. Caloric values of reproductive structures of Cornus are high, especially fruits and seeds. These structures are a significant energy sink and reduced flowering in a shaded habitat would result in a more favorable energy balance. The leaf values generally complement the rhizome values indicating that translocation of stored reserves was involved. In the spring the rapidly developing aerial shoot increased in energy content as it received storage compounds from rhizome storage sites. This pattern is found in fast-developing alpine species as well (Rochow, 1968; Mooney and Billings, 1960). By mid-season current year photosynthate was translocated down to the rhizomes, resulting in a decline in shoot energy content. The shoots by now were fully mature which means lower respiration rates and lower energy demand (Smillie, 1962). The September data suggest a reverse of the trend (in both species), the basis for which is not clear.

The possibility exists that the aerial shoots become an energy drain in late season because post-mature leaves have a respiration increase and a photosynthesis decrease (Smillie, 1962), but retaining these leaves would seem to be non-adaptive. Further study of this problem is needed, and in particular, more frequent sampling extended to the time of frost (several weeks beyond the September sampling date) would be required.

The variations in caloric value of Aster macrophyllus in 1971 are similar to that in Cornus, suggesting that the same processes are occurring. In Aster the roots are large and fleshy and apparently are involved in storage and translocation of reserves. The relatively small changes in energy content of the rhizomes, especially between June and July, may mask short-term trends that could only be recognized with more frequent sampling. In 1970, widely divergent values occurred in roots and leaves of the three populations of Aster suggesting that the August drought disrupted typical patterns. Leaves from the hardwood and birch population dropped sharply in caloric content, reflecting early senescence. In contrast, energy content of the above and below ground organs of the aspen population increased, responding to drought in a way similar to that reported by Malone (1968) for old-field herbs.

Aster leaves in the hardwoods stand were the largest and thinnest on a mean shoot basis although the leaf area index was considerably lower than the aspen and birch population. Canopy removal resulted in the production of thicker, smaller leaves than in the forest stands. It has long been considered that shade adaptation included the production of thinner, larger leaves with more chlorophyll (Bohning and Burnside, 1957; Oosting, 1956; Whittaker and Garfine, 1962) and this seems to apply here. The leaves of Cornus canadensis show the species to have less plasticity in that the mean leaf area per shoot was essentially similar in the disturbed and undisturbed habitats. Leaf thickness also did not vary along a light intensity gradient as in Aster macrophyllus.

Talling (1961) reports that shade adapted leaves may not always have higher chlorophyll concentrations on an area basis because of leaf thinness, but do usually on a weight basis. There was an inverse relationship between chlorophyll concentration of Aster macrophyllus leaves in 1971, and ground level light intensity. The chlorophyll peak in June occurred just after canopy closure and coincided with the middle of the vegetative growth phenophase. A decline in chlorophyll a from July to August also occurs in Corylus cornuta, a common shrub associate of Aster, in Minnesota

(Sanger, 1971). The sharp negative slope in the chlorophyll concentration curve in late 1970 coincided with the developing drought whereas there was a very gradual decline over the same period in 1971. Seasonal trends in Cornus canadensis were generally similar to those of Aster except for the bog-edge colony which increased its chlorophyll concentration slightly in the latter half of both seasons.

Although herbivore activity has been implicated in limiting the lower elevational limits of alpine species (Rochow, 1970) there is no indication that herbivores are important in affecting the distribution or response to canopy removal in Aster macrophyllus or Cornus canadensis. The percent of leaf area consumed by herbivores is in line with the value of eight percent reported by Odum (1970) for temperate forests.

#### Conclusions

The following conclusions can be drawn from this study.

1. Canopy removal stimulates flowering and fruiting, individual plant biomass and increased caloric values in Aster macrophyllus, but enhanced primarily asexual reproduction in Cornus canadensis. No disruption of the timing or sequence of phenophases occurred in either species when the canopy was

removed from above intact populations. Exposure to full sunlight did not cause excessive photo-oxidation of leaf pigments nor alter the seasonal pattern in caloric values of above and below ground organs of either species.

2. The hemicryptophytic growth habit of Aster macrophyllus and Cornus canadensis enabled these species to benefit from soil shielding of rhizome buds, thereby allowing plants to survive dose rates as high as 1000 R/day in an experimental gamma field. Also, radiation actually stimulated flowering in Aster, increased caloric content of plants of both species, and increased rhizomatous bud survival in Cornus. These responses plus the responses of the two species to canopy removal outlined above, indicate that both species would play an important role in the recovery of a forest to stress, such as ionizing radiation, which would destroy or open the canopy.

3. Laboratory studies indicate that both species have the potential to acclimate to microclimate changes which accompany forest disturbance. These adaptations include a shift in the optimum temperature of net photosynthesis towards the preconditioning temperature in Cornus canadensis and a lower rate of dark respiration at 35 and 40 C in warm-acclimated plants of Cornus. Aster macrophyllus maintained higher P:R ratios at higher temperatures, and had relatively higher rates of net photosynthesis at given leaf water potentials, characteristics consistent with the more southerly distribu-

tion and upland habitat of this species.

4. Both species persist in undisturbed habitats but require forest disturbance for flowering, fruiting and long-term maintenance of populations. Seedling establishment is rare in Aster and Cornus and they maintain themselves chiefly by vegetative propagation in forests. In Aster the proportion of flowering shoots in a population increased with increasing light intensity, but in Cornus flowering was low in all populations. The bottomland habitat of this species exposes it to frosts during the flowering and fruit development phenophases, and this at least partly explains the low fruit set. In spite of a wide range in aerial shoot densities of populations of both species in undisturbed habitats, seasonal variations in density were similar, except for the Cornus trail population which declined continuously as other species invaded the site. Other populations showed little net change in density over the two year period of this study.

## SUMMARY

The population ecology of Aster macrophyllus and Cornus canadensis at the Enterprise Radiation Site in northern Wisconsin was studied with emphasis upon the response of the two species to forest disturbance and a consideration of their potential role in the recovery of the forest to radiation stress. Spatial and temporal variations in populations in undisturbed habitats and certain physiological adaptations were also examined. The following are the salient facts brought out by this study:

1. Canopy removal greatly stimulated flowering (from 5.3 to 49.7% of the aerial shoots bolting), leaf caloric values (300-500 cal/g increase) and individual plant vigor in Aster macrophyllus. Canopy removal stimulates primarily asexual reproduction in Cornus canadensis, with a consequent decrease in biomass of the mean individual shoot. The above-ground: below-ground ratio in disturbed site populations shifts toward above-ground production in Aster due to mass bolting but shifts toward below-ground production in Cornus because vegetative propagation rather than flowering is stimulated. Canopy removal did not cause excessive photo-oxidation of

chlorophyll in either species as has been reported for some herbs. It did cause the production of an increased number of leaves, smaller and thicker in texture in Aster. Canopy removal did not disrupt normal seasonal trends in caloric content, leaf chlorophyll content or timing of phenophases in either species.

2. Soil shielding of rhizomatous buds enables both species to survive in zones receiving doses that would be lethal to directly exposed tissues. In an experimental gamma field, 50 R/day stimulated flowering and increased caloric values in Aster macrophyllus, and 300 R/day stimulated below-ground survival and increased caloric values of Cornus canadensis. A shift in biomass allocation occurs toward below-ground parts at high dose rates.

3. It can be predicted that the hemicryptophytic life form of both species would enable them to survive short-term radiation stress because of shielding of below ground buds. Radioresistance would further pre-adapt Cornus to survival in bottomland locations where competition for light and nutrients was reduced by irradiation or other stress. The increased light intensity which would result from canopy opening would stimulate vegetative propagation in Cornus canadensis but low fruit set would limit the potential for establishing new colonies. Increased light intensity would

increase the vigor and extent of established colonies of Aster and increase the probability of new colony establishment by greatly enhancing seed production.

4. Acclimation, the phenotypic adjustment of metabolic rates in response to preconditioning environment, was found in both species, although statistically significant adjustment in photosynthetic rates were found only at 35 and 40 C in Aster and 35 C in Cornus. But the overall patterns of photosynthesis and respiration in Cornus and of photosynthesis in Aster are similar to that reported for other species in which acclimation has been demonstrated (Mooney & West, 1964; Mooney & Shropshire, 1968). These adaptations include an upward shift in optimal temperature for net photosynthesis in warm acclimated Cornus canadensis, and lower rates of respiration at 35 and 40 C in Cornus. Relative rates of net photosynthesis were greater at higher temperatures and lower at lower temperatures in warm-acclimated plants of both species. Of the two species, Aster macrophyllus has a more favorable P:R ratio at higher temperatures and has a faster decline in water potential with decreasing relative water content, characteristics that explain its more southerly range and more widespread local distribution. Acclimation is seen as an important adaptation to a changing environment such as occurs when disturbance suddenly produces a new microclimate.

5. More chlorophyll is synthesized as incident light intensity decreases in Aster macrophyllus populations. In

Cornus canadensis the forest population had the highest concentration but canopy removal did not reduce pigment levels below that of the bog-edge site. Leaf chlorophyll a concentrations varied from 3.50 to 7.98 mg/g dry weight in Aster, and 2.60 to 7.20 mg/g dry weight in Cornus. Variations were greater between populations than between seasons except in the 1970 Aster populations. In both species there were June maxima and late season minima except that an increase occurred in the September disturbed site population of Aster and the bog-edge population of Cornus. Sharp late season declines in all the forest populations of Aster and Cornus coincided with the 1970 drought, but in the Cornus bog-edge population an actual increase occurred. There was no correlation between carotenoid concentration or carotenoid:chlorophyll ratios and light intensity of habitat.

6. Aster macrophyllus is second or third in importance value in all six forest stands studied, whereas Cornus canadensis is present only in bottomland stands but is most common in lowland, open areas adjacent to bogs.

7. Total biomass of Aster ranged from 29.9 g/m<sup>2</sup> above-ground biomass and 71.0 g/m<sup>2</sup> below-ground biomass in the control aspen stand to 2.0 g/m<sup>2</sup> above-ground biomass and 3.5 g/m<sup>2</sup> below-ground biomass in the treatment birch stand. Total biomass of Cornus ranged from zero in three stands to

12.2 g/m<sup>2</sup> above-ground biomass and 13.8 g/m<sup>2</sup> below-ground biomass in the bog-edge site.

8. Seasonal patterns in population density from year to year were similar in both species in all undisturbed habitats except in the trail site where Cornus declined in density as competing species increased in importance. Competition for light and nutrients is probably also limiting Cornus in the control aspen stand where Cornus is restricted to tree stumps. In both species, population recruitment occurred primarily in June and early July, when highest densities occurred, and density then declined, with earlier senescence occurring in the August drought of 1970. Since most growth was completed before the drought, the effect on population density of both species was negligible.

9. Both species are primarily asexual in forest habitats with 0 to 3.70% of aerial shoots of Aster macrophyllus flowering, and 0 to 19.88% of aerial shoots of Cornus canadensis flowering. Seedling establishment in undisturbed habitats is rare in both species. Flowering and fruit set in Aster increases with increased light intensity of its habitat. Flowering and fruit set in Cornus is low in all populations, even in the disturbed site. Its bottomland habitat subjects it to late frosts and many inflorescences show signs of frost damage.

10. Variations in caloric values were similar in undisturbed populations of both species. Translocation of stored food from below-ground storage sites to rapidly growing aerial parts in spring is followed by reverse translocation of current photosynthate later in the season. Cornus canadensis caloric values were similar in both years, but Aster populations differed in July and September between the years possibly because of differential response to the 1970 drought.

Figure 1 Map of Enterprise Radiation Site and location of transects studied. The transects are coded as follows (1 inch = 100 meters):

A - <u>Cornus canadensis</u> , treatment aspen	C-H - control northern hardwood stand
B - <u>Cornus canadensis</u> , bog-edge site	E-A - experimental aspen stand
D - disturbed site	E-W - experimental white birch stand
C-A - control aspen stand	E-H - experimental northern hardwoods
C-W - control white birch stand	T - trail

The map symbols are coded as follows:

- - - Logging road	NH - northern hardwood
● water	RP - red pine
—+— abandoned railroad	SF - white spruce - balsam fir
A - aspen	Sp - black spruce
G - grasses and/or sedges	T - tamarack
LH - lowland hardwood	Wb - white birch

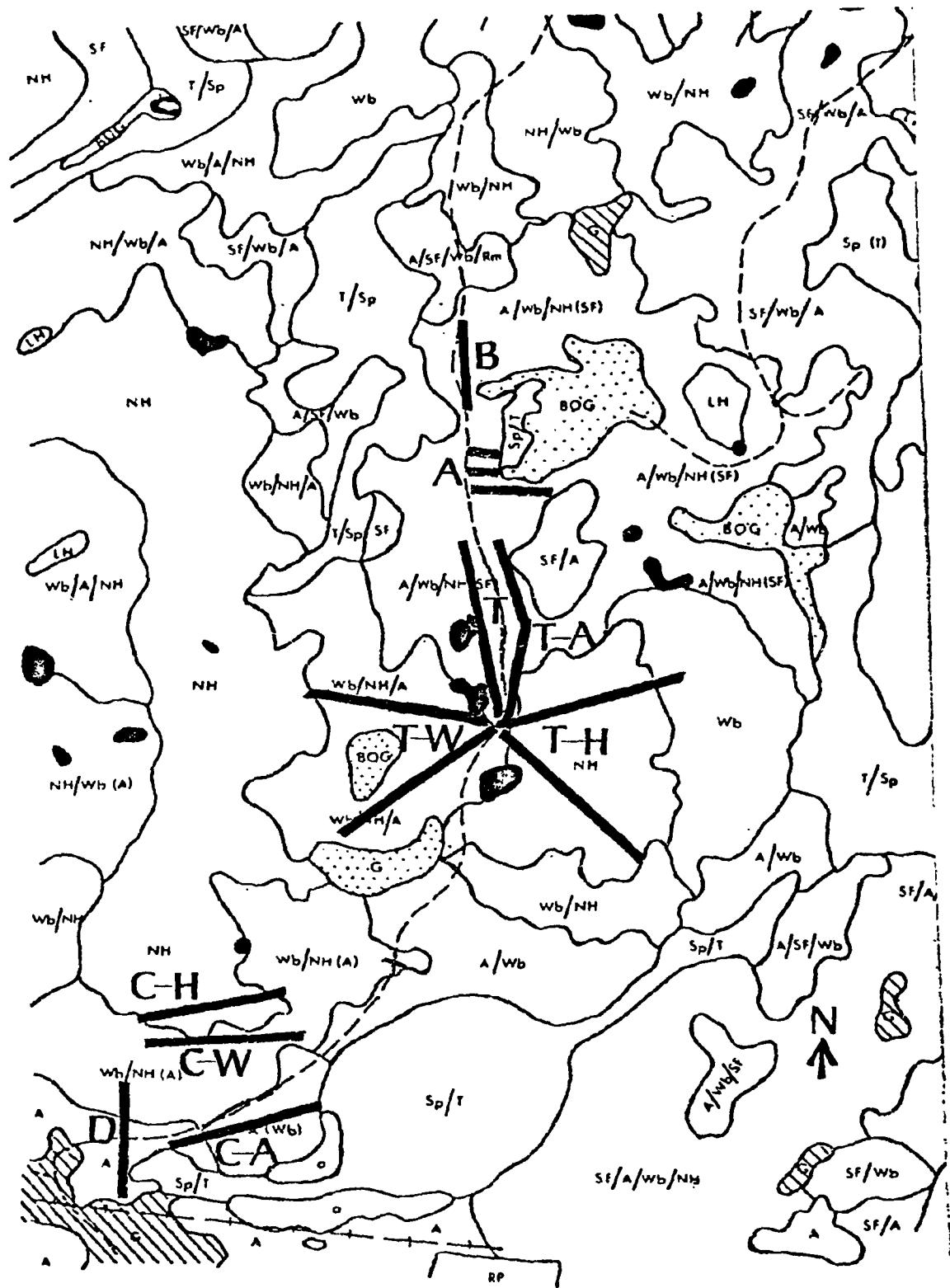
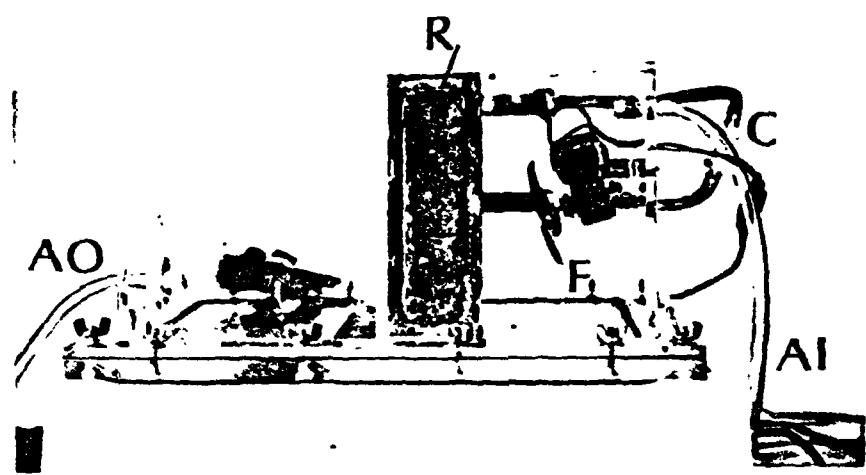


Figure 2 Cuvette used in gas analysis. Visible are the radiator (R), fan (F), air inlet and outlet (AI, AO), and coolant circuit (C).



**Figure 3** Diagram of laboratory system used for gas exchange studies. The following symbols are used:

**Hu** - humidifier

**CTC** - controlled temperature circulator

**AR** - air reservoir

**Hy** - hygrometer

**F** - fan

**Ra** - radiator

**T-T** - telethermometer

**FW** - flowing water heat shield

**FM** - flow meter

**P** - diaphragm pump

**D** - desiccant

**DF** - dust filter

**IRGA** - Infra-red gas analyzer

**R** - recorder

Single lines represent air pathway and double lines represent coolant pathway.

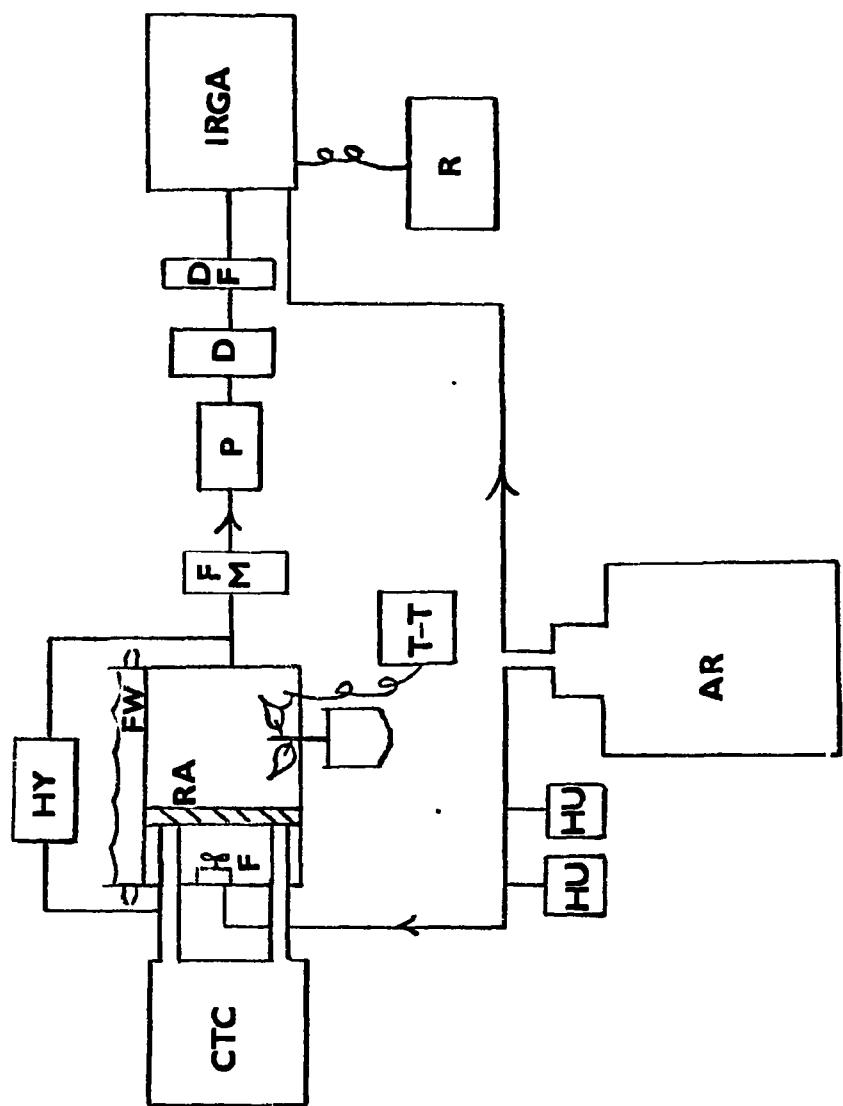
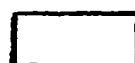
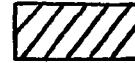
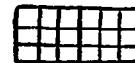
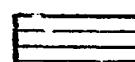
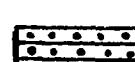
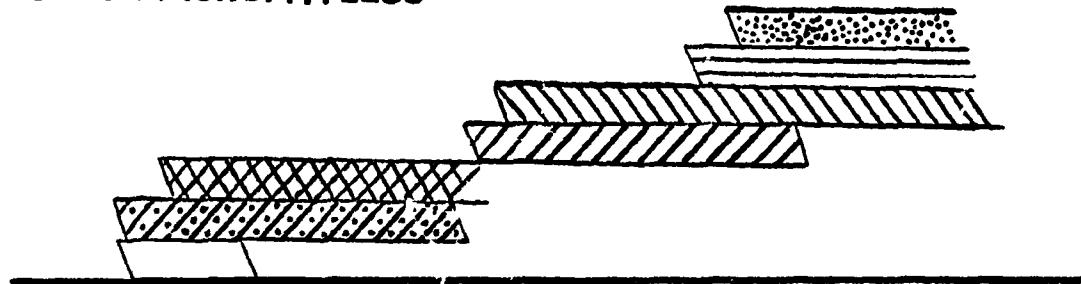


Figure 4 Phenological spectrum. The length of time occupied by each phenophase is indicated by the length of the bars which are identified according to the code below. The period of canopy closure is indicated by the black bar.

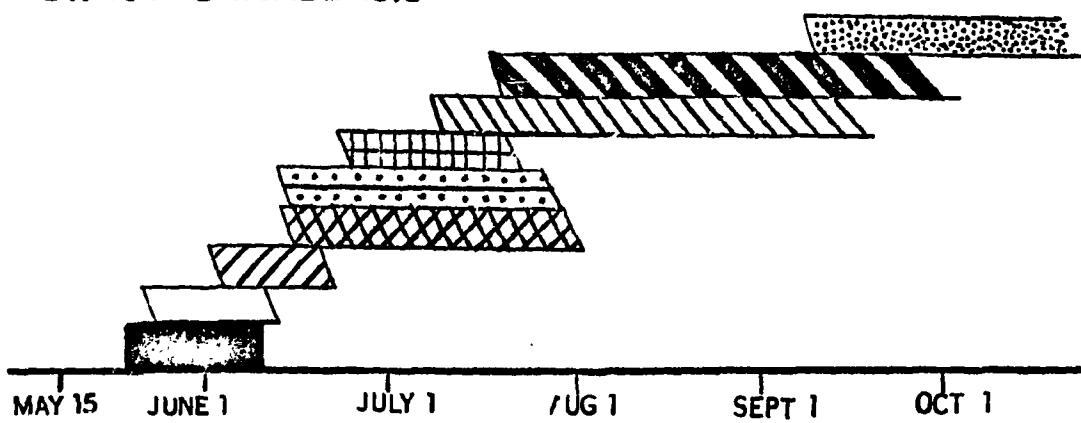
-  Vegetative shoot elongation
-  Bolting (Aster macrophyllus)
-  Flowering
-  Secondary shoot development (Cornus canadensis)
-  Perennating bud mature (vegetative shoots)
-  Vegetative propagation
-  Fruit maturation and dissemination (Aster macrophyllus)
-  Fruit maturation (Cornus canadensis)
-  Fruit abscission (Cornus canadensis)
-  Leaf abscission

Open-ended bars represent phenophases without definitely determined end points.

**ASTER MACROPHYLLUS**



**CORNUS CANADENSIS**



MAY 15

JUNE 1

JULY 1

AUG 1

SEPT 1

OCT 1

Figure 5 Distribution of Aster macrophyllus individuals in the three control forests according to caudex diameter. The large bar indicates the number of vegetative individuals in each class and the small bar the number of flowering individuals in each size class.

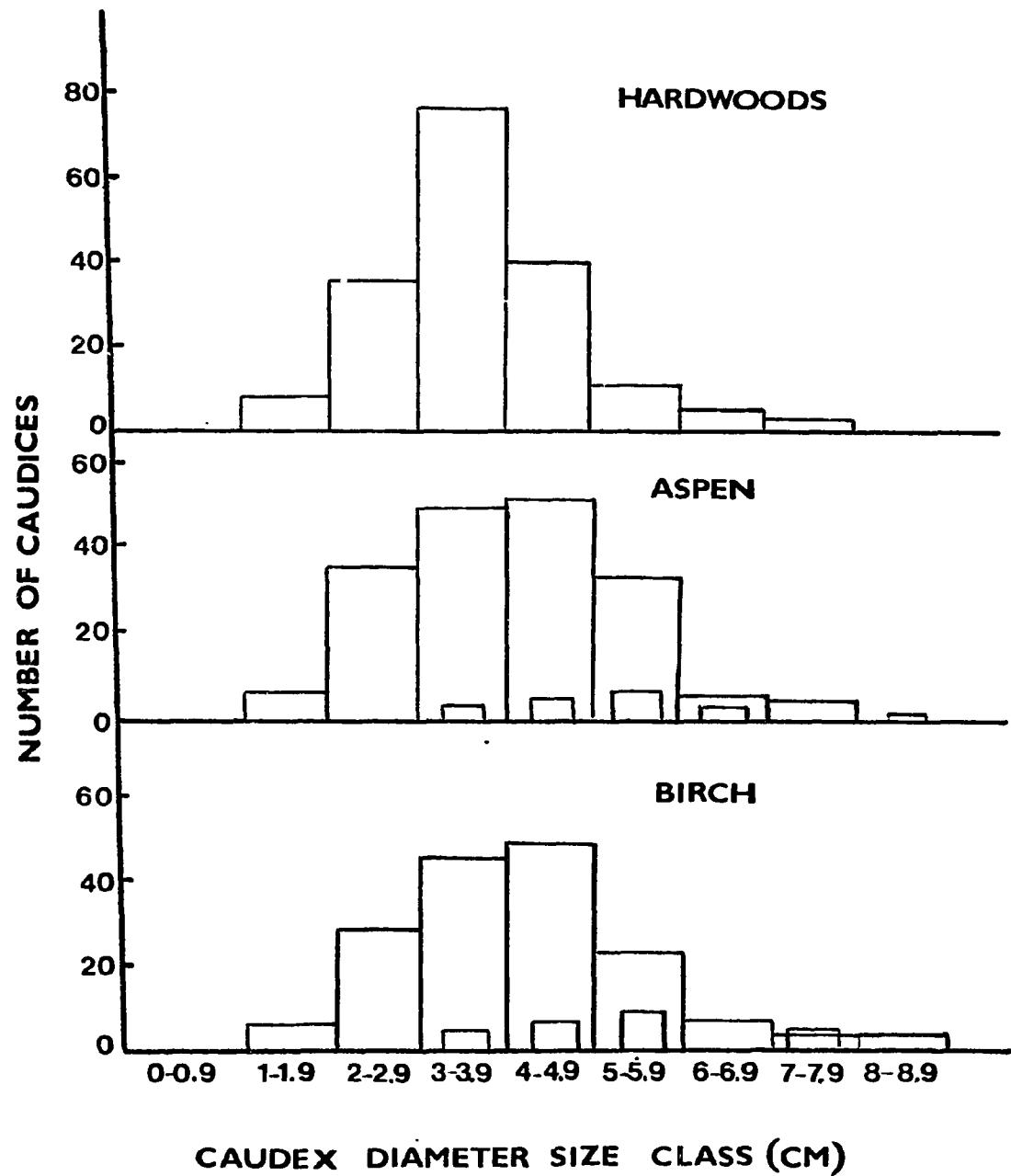


Figure 6 Aster macrophyllus from birch forest (left) and disturbed site (right). Visible are the roots, leaves, caudex (c), mature rhizomes (r), new rhizomes of the year (yr), and bolting stem on the forest plants.

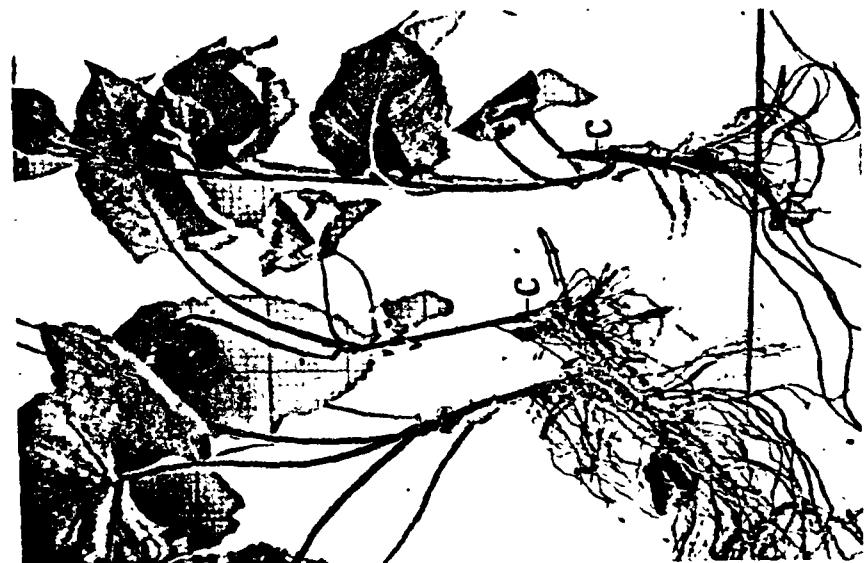


Figure 7 *Cornus canadensis* from aspen forest (left) and disturbed site (right). Leaves removed in forest plant. Visible are the roots, aerial shoot (as), perennating bud (pb), rhizome bud (rb), shoot primordia (s), young rhizome (yr), old rhizome (or), and shoot of the current year (ns).

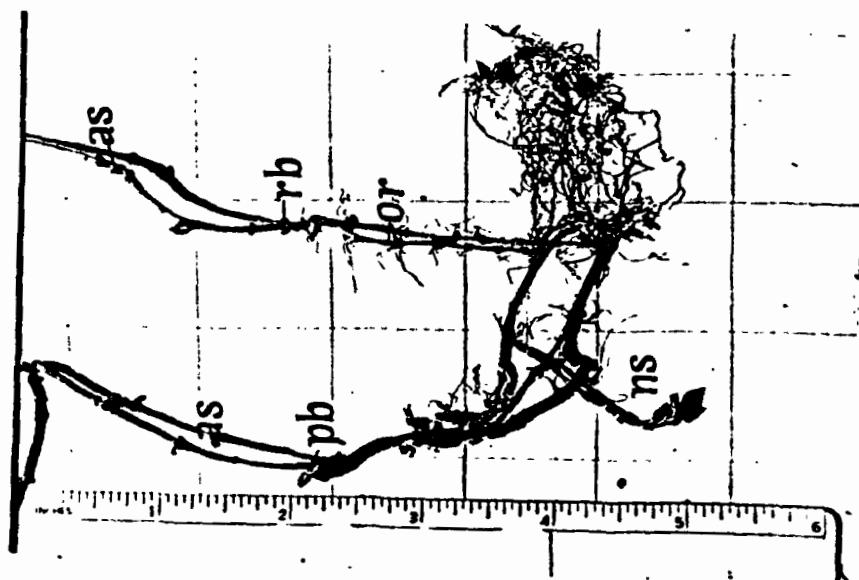
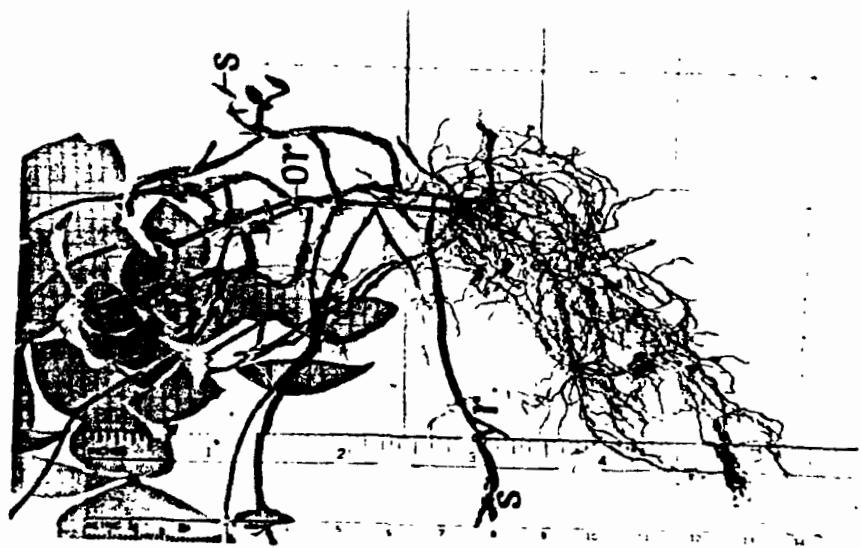


Figure 8 Above and below-ground biomass/ $m^2$  of Aster macrophyllus. The numbers above the above-ground figures represent the percentage of the total ground layer biomass for 1971. Below-ground biomass is separated into root (cross-hatched), rhizome (lined) and caudex (clear). Note that control aspen below-ground data is on a different scale than the other populations.

The populations are coded as follows:

C-A - control aspen

C-W - control white birch

C-H - control hardwoods

E-A - experimental aspen

E-W - experimental white birch

E-H - experimental hardwoods

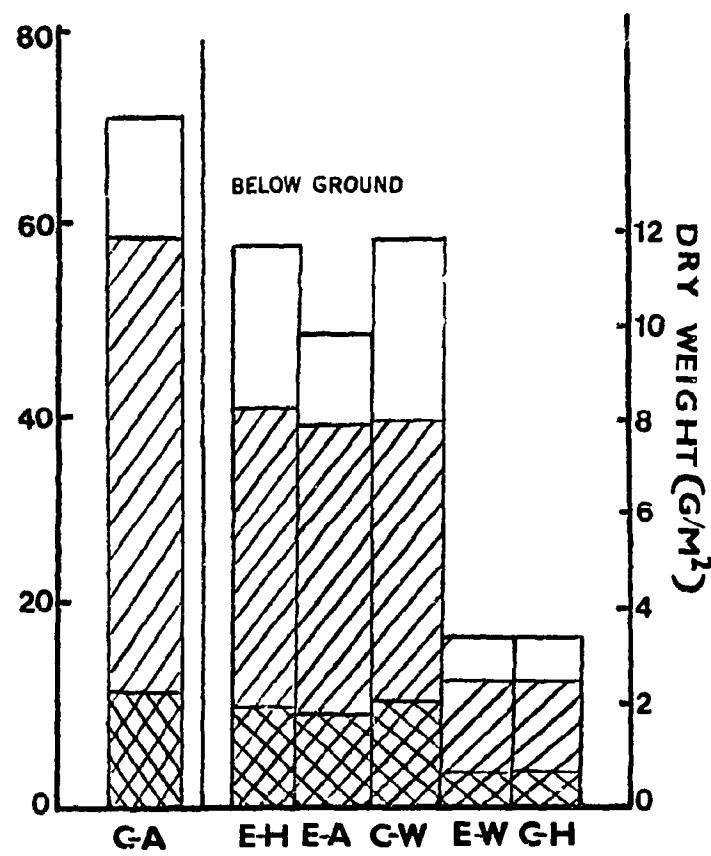
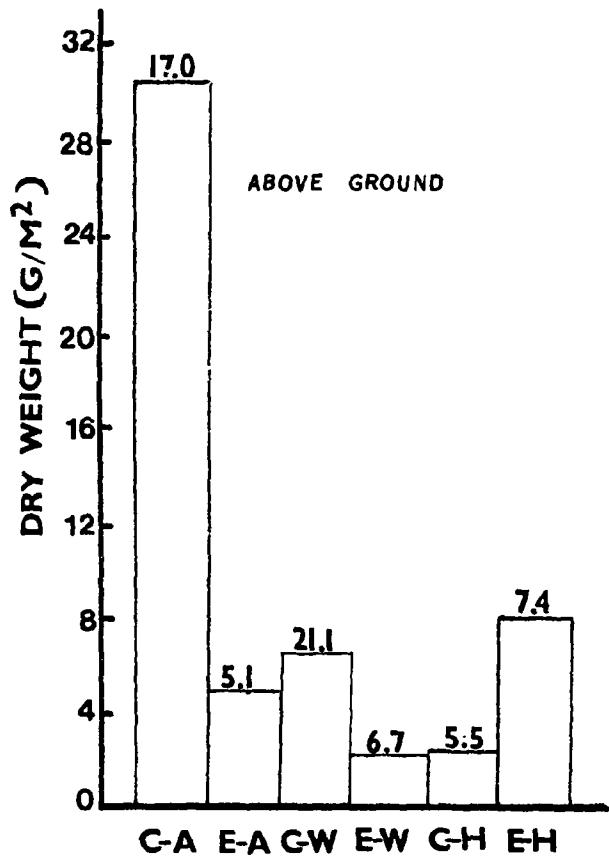


Figure 9 Mean individual biomass of Aster macrophyllus in the control forests and disturbed site ( $\pm 1$  standard error). Shown are the mean above-ground shoot biomass, the mean below-ground biomass per aerial shoot and the ratio of the two. Below-ground biomass is separated into root (cross-hatched), rhizome (lined), and caudex (clear). The populations are coded as follows:

C-A - control aspen

C-W - control white birch

C-H - control hardwoods

D - disturbed site

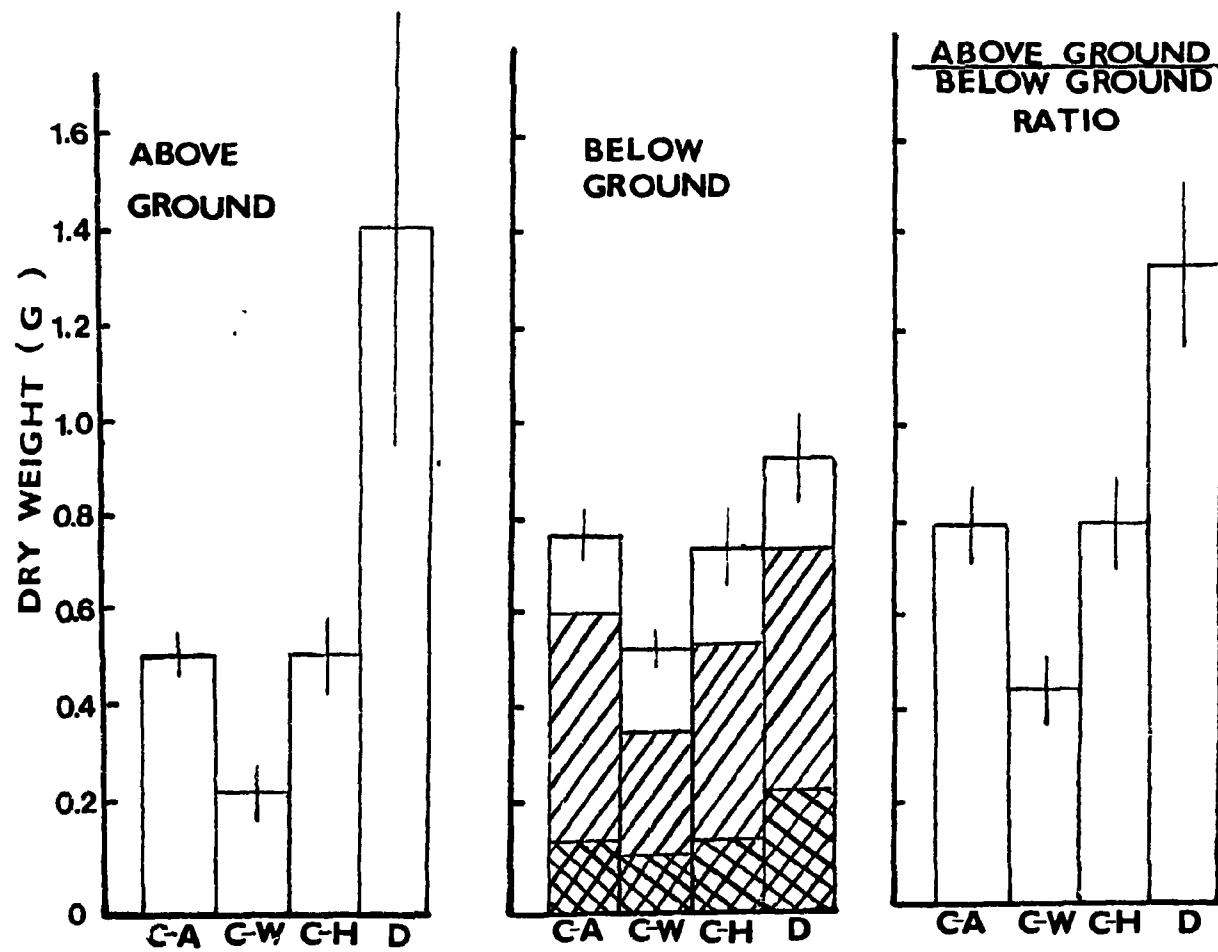


Figure 10 Above and below-ground biomass/m<sup>2</sup> of Cornus canadensis. The numbers above the above-ground figures represent the percentage of the total ground layer biomass for 1971. The populations are coded as follows:

C-A - control aspen

E-A - experimental aspen

C-W - control white birch

E-W - experimental white birch

C-H - control northern hardwood

E-H - experimental northern hardwoods

B - bog-edge site

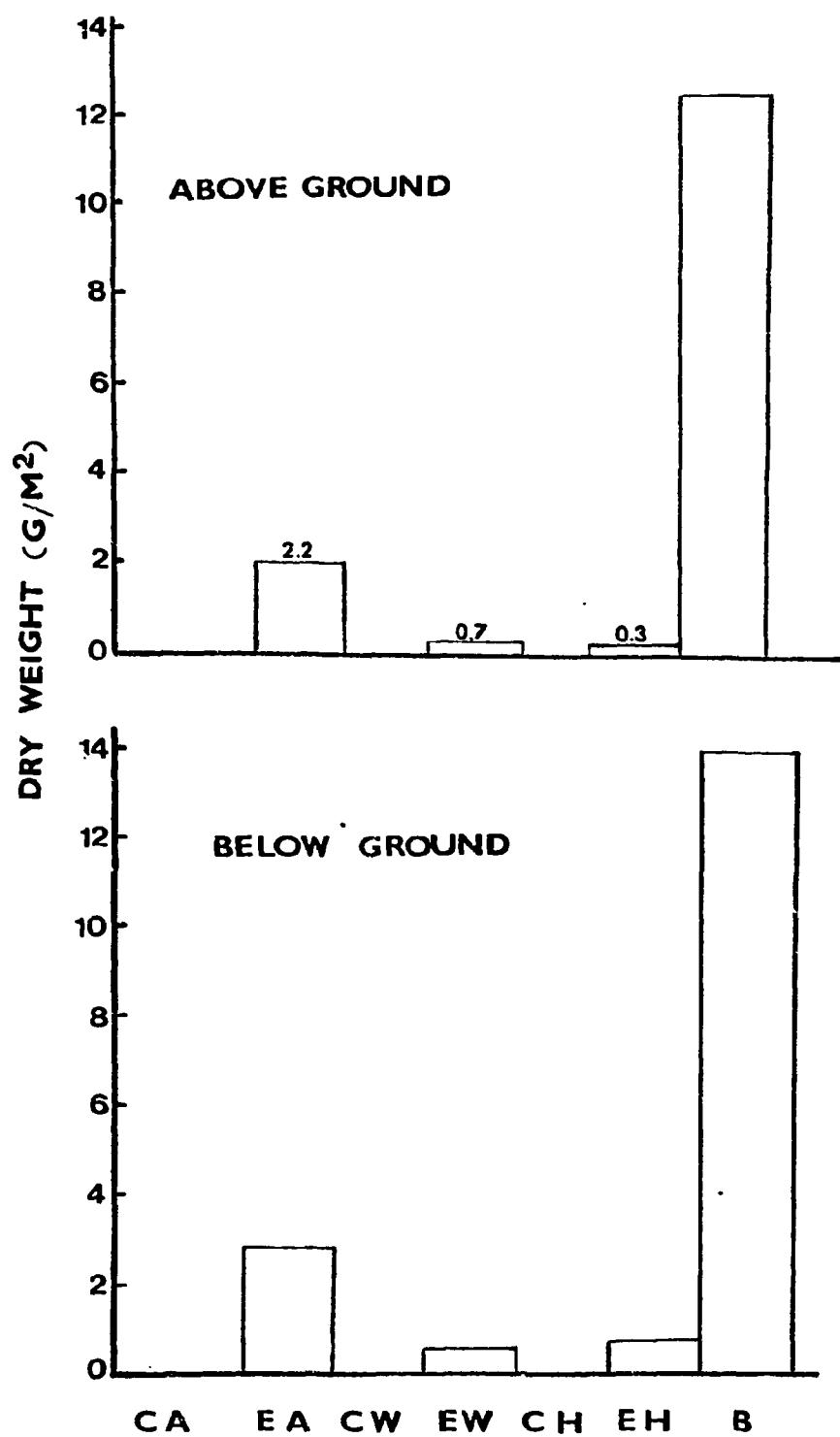


Figure 11 Mean individual biomass of Cornus canadensis.

Shown are the mean aerial shoot biomass, the mean below-ground biomass per aerial shoot and the ratio of the two. Roots are not included. The populations are coded as follows:

E-A - experimental aspen

B - bog-edge site

D - disturbed site

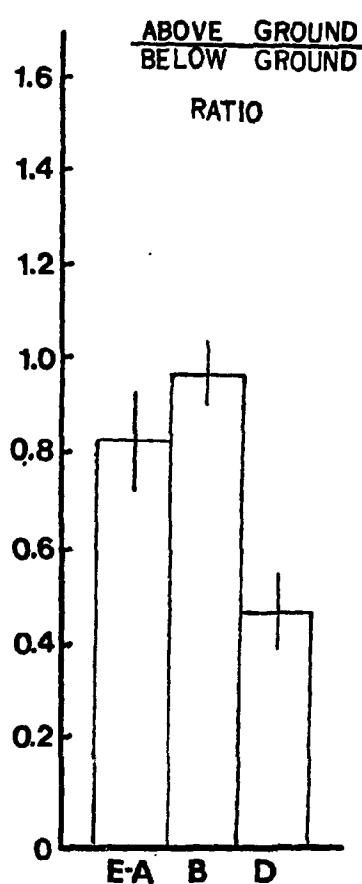
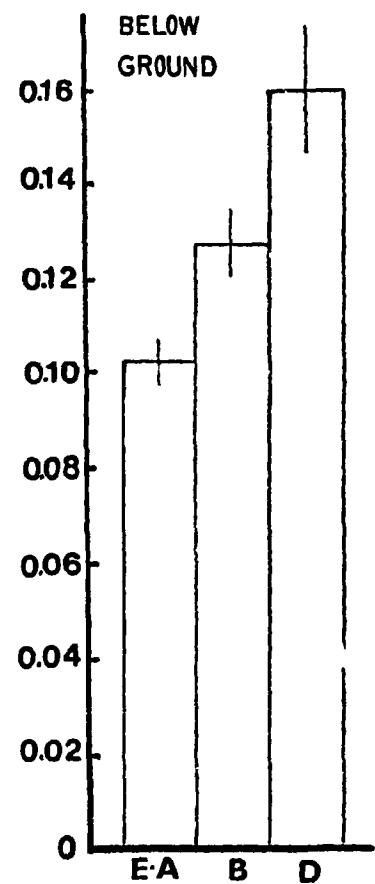
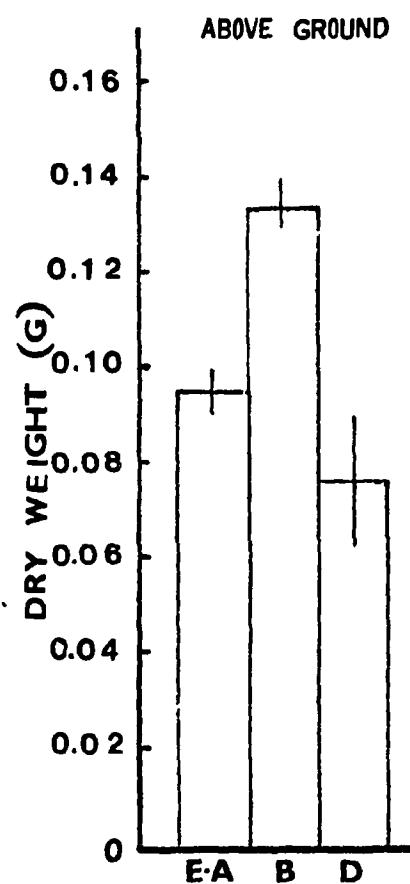


Figure 12 Leaf characteristics of Aster macrophyllus and Cornus canadensis. Shown are (A) mean leaf area per shoot, (B) leaf area index, and (C) mean ratio of leaf dry weight to leaf area. The populations are coded as follows:

C-A - control aspen (Aster macrophyllus)

E-A - experimental aspen (Cornus canadensis)

C-W - control white birch

C-H - control northern hardwoods

B - bog-edge site

D - disturbed site

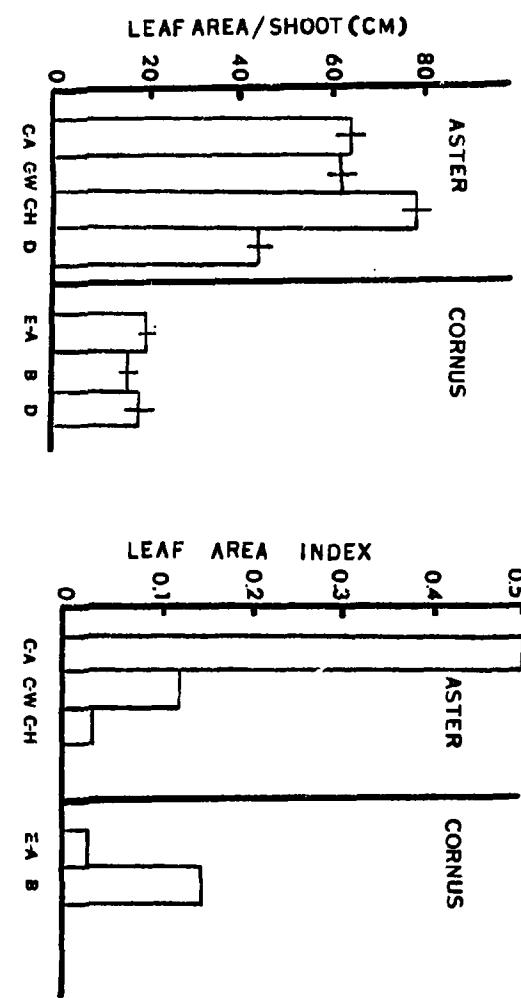
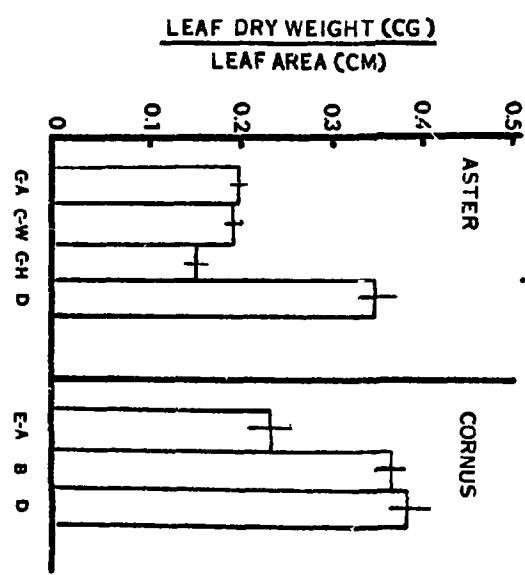


Figure 13 Seasonal variation in aerial shoot density  
of Aster macrophyllus in control forests  
and disturbed site, 1970 - 72. The  
populations are coded as follows:

- control aspen
- △ control white birch
- control hardwoods
- × disturbed site

The aspen population is on a different scale  
than the other populations.

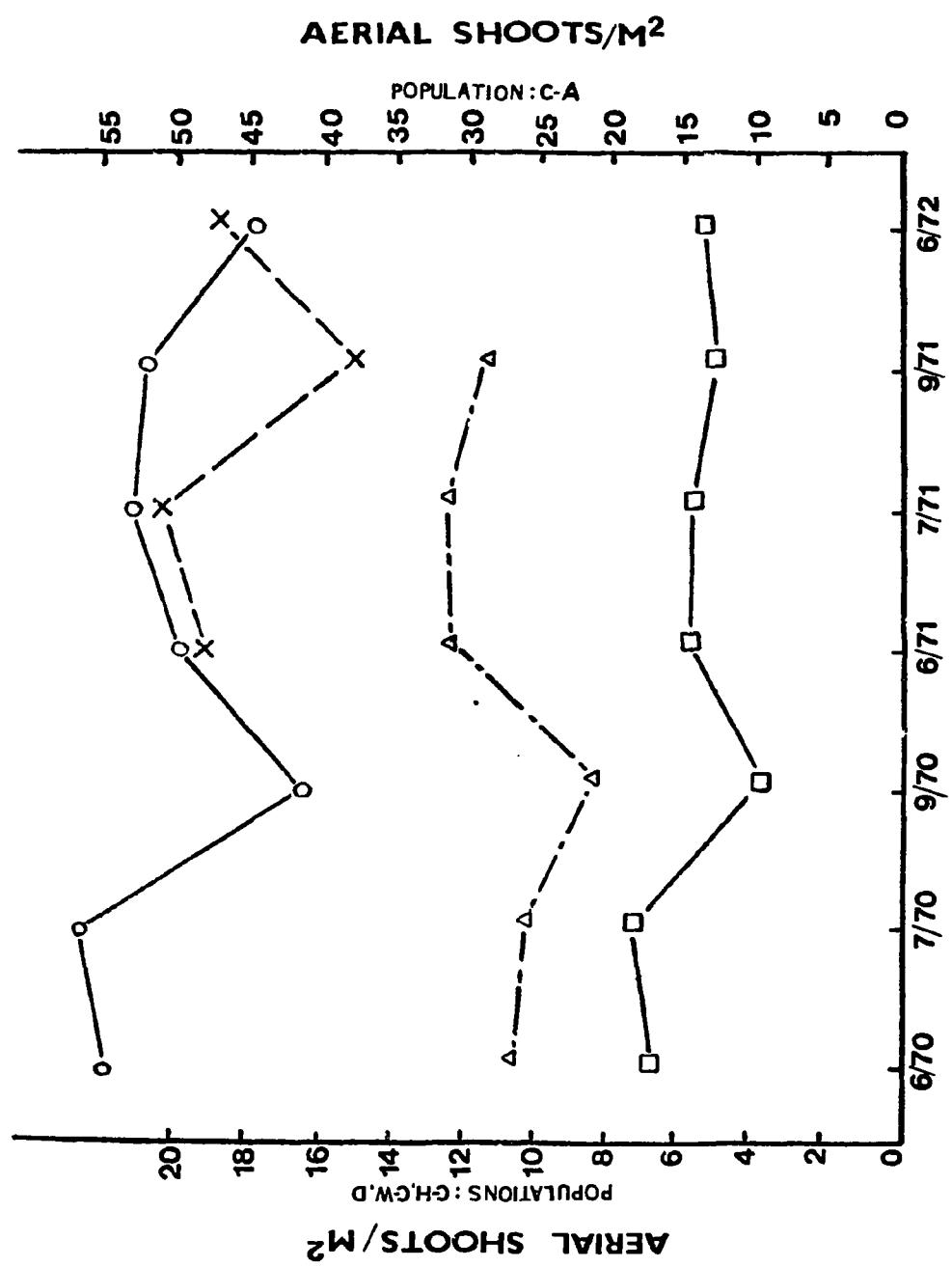


Figure 14 Seasonal variation in aerial shoot density of Aster macrophyllus in experimental forests and trail transect 1970 - 71. The populations are coded as follows:

- experimental hardwoods
- ▲ experimental white birch
- experimental aspen
- ✗ trail transect

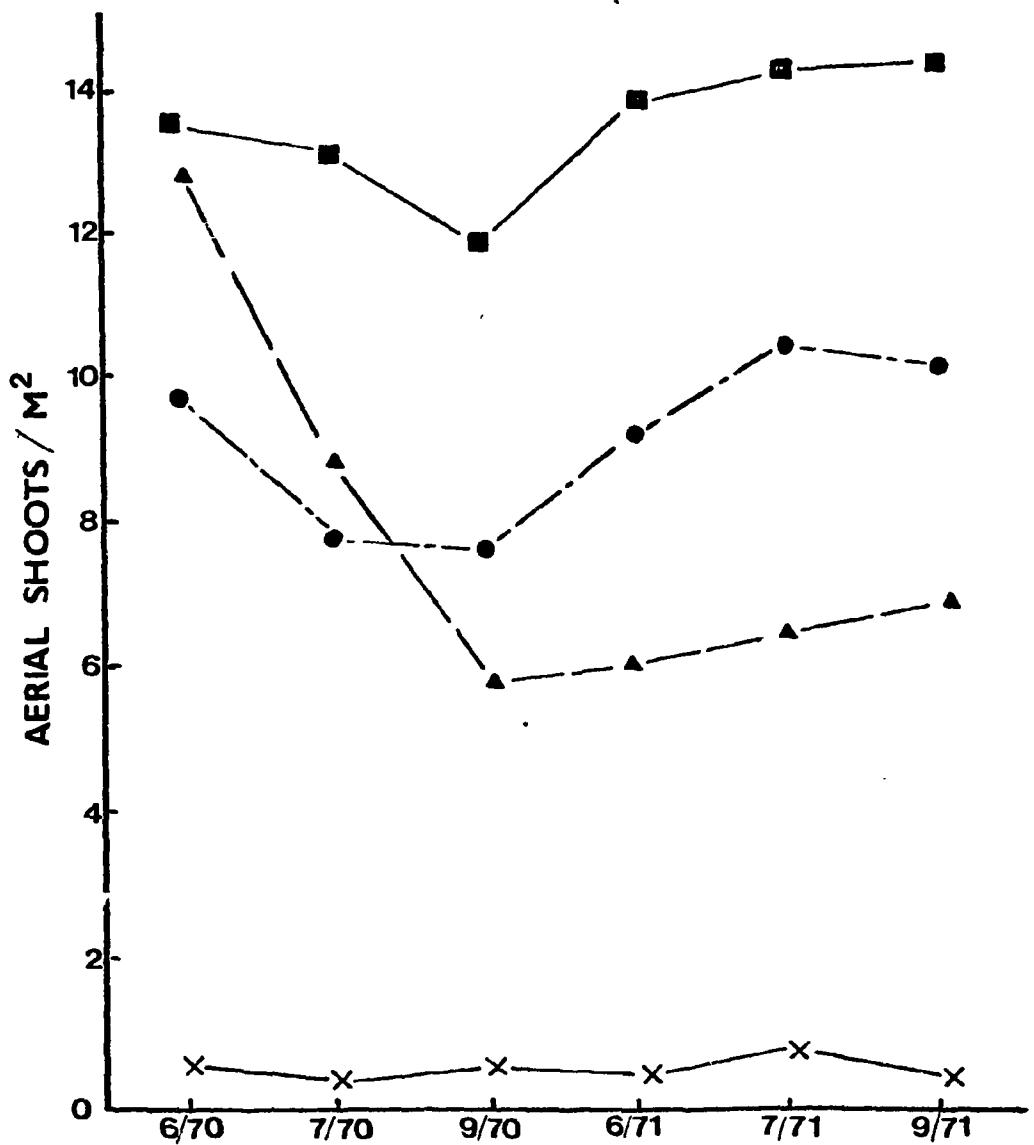


Figure 15 Seasonal variation in aerial shoot density  
of Cornus canadensis habitats from 1970 -  
72. The populations are coded as follows:

- Bog-edge site
- × Disturbed site

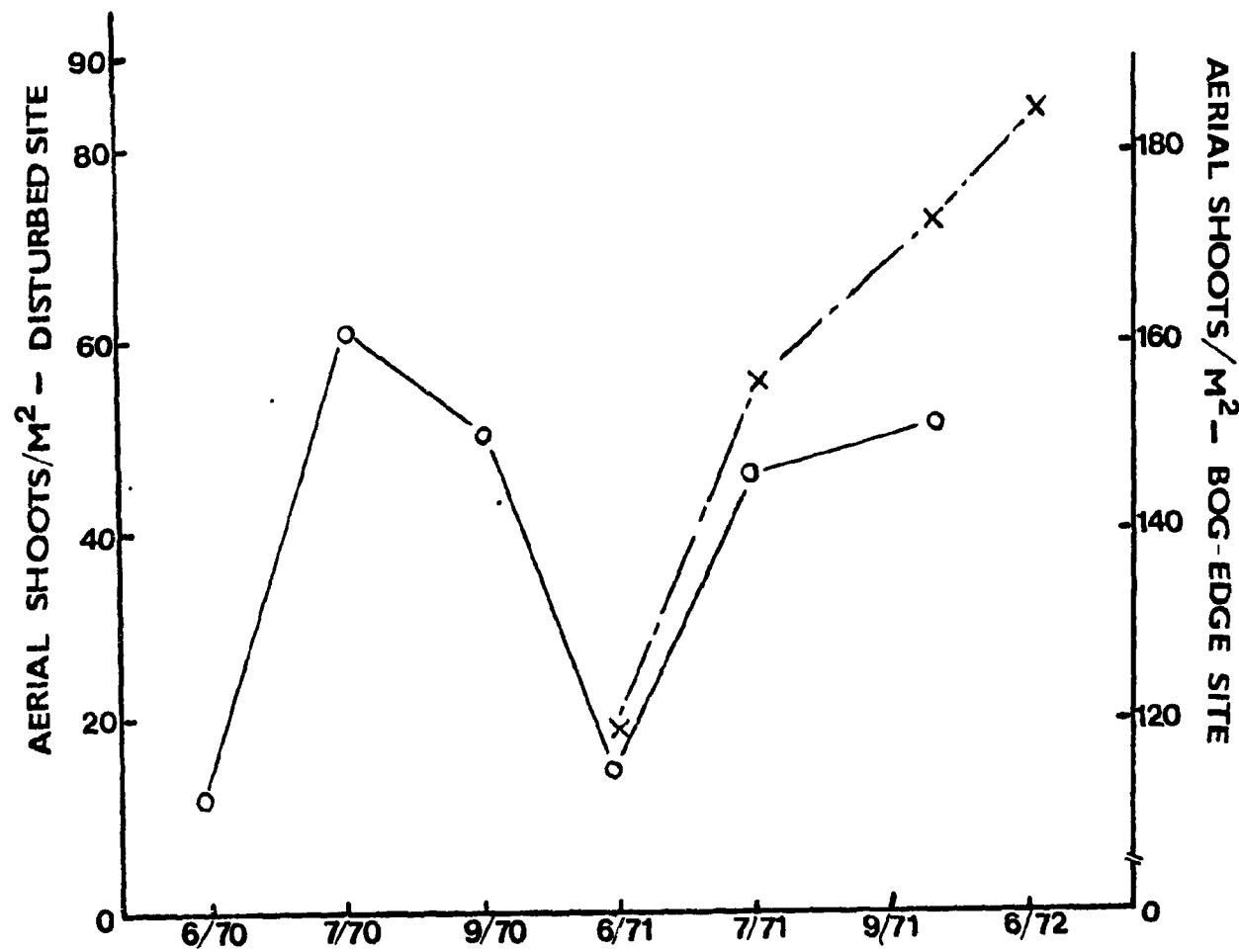


Figure 16 Seasonal variation in aerial shoot density  
of Cornus canadensis habitats from 1970 -  
72. The populations are coded as follows:

- experimental aspen
- ▲ experimental white birch
- experimental northern hardwoods
- ✗ trail transect

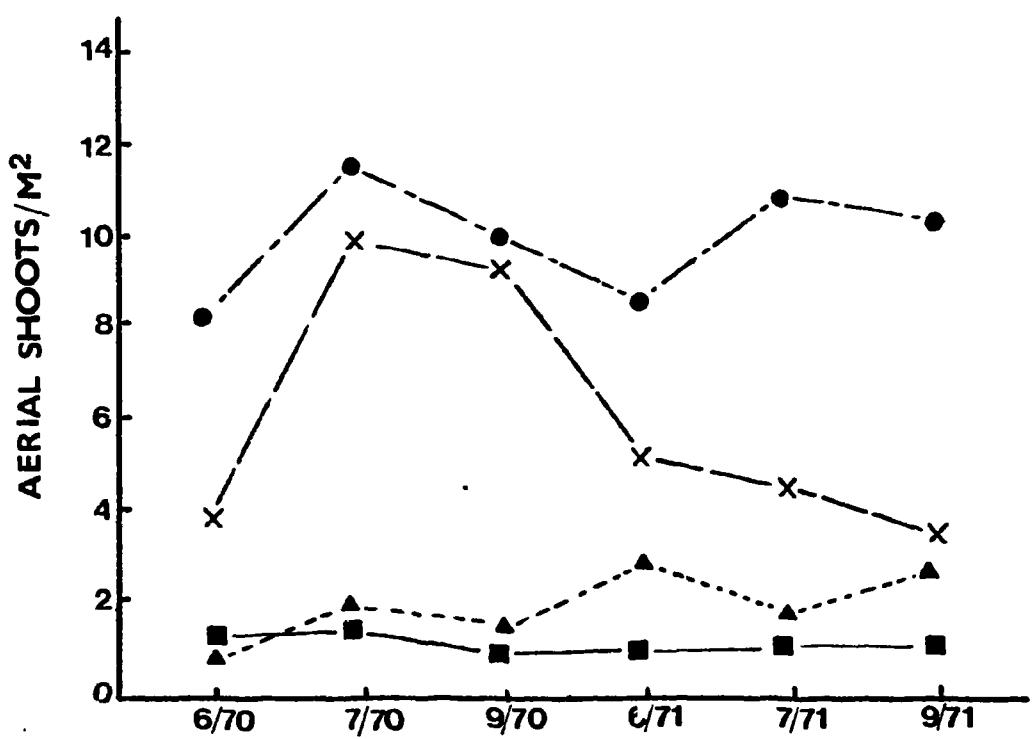


Figure 17 Bolting and flowering of Aster macrophyllus in the experimental and control stands in 1970.

The populations are coded as follows:

E-A - experimental aspen

C-A - control aspen

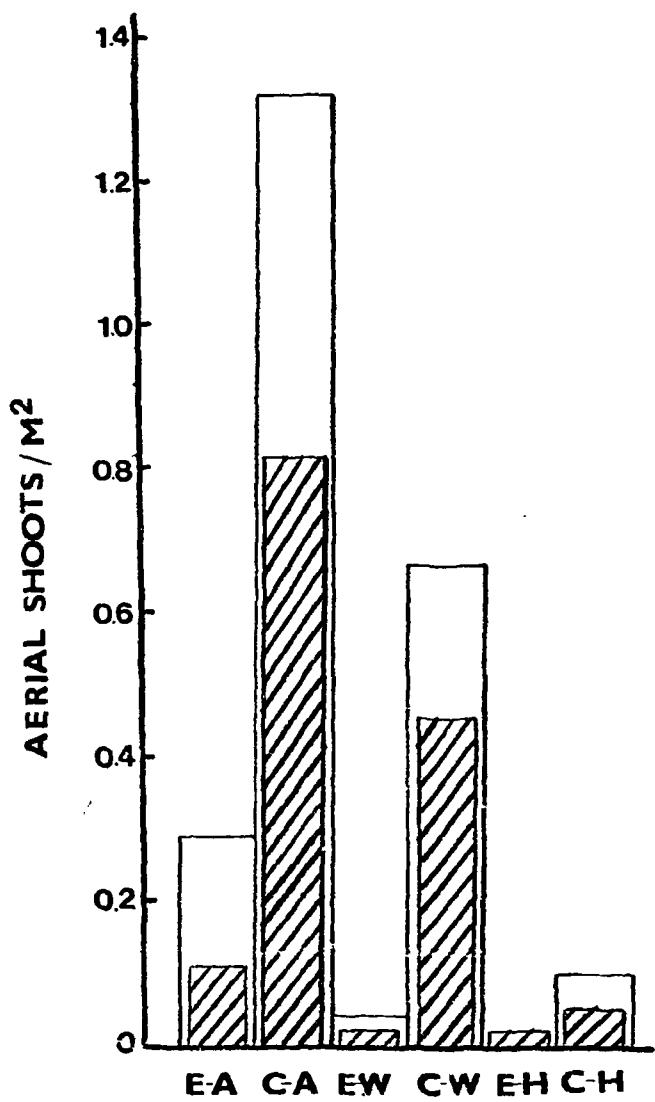
E-W - experimental white birch

C-W - control white birch

E-H - experimental hardwood

C-H - control hardwoods

The outer bar is the number of bolting stems and the inner bar is the number of flowering stems.



**Figure 18** Bolting and flowering of Aster macrophyllus in the experimental and control stands in 1971, and in the disturbed site in 1971 and 1972. The 1972 census was in June, before flowering, thus only bolting data is available. The populations are coded as follows:

E-A - experimental aspen  
C-A - control aspen  
E-W - experimental white birch  
C-W - control white birch  
E-H - experimental hardwoods  
C-H - control hardwoods  
D - disturbed site

The outer bar is the number of bolting stems and the inner bar is the number of flowering stems.

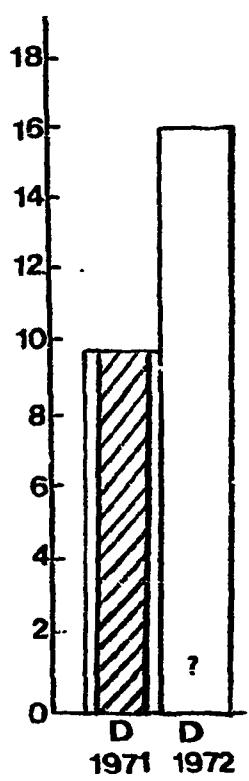
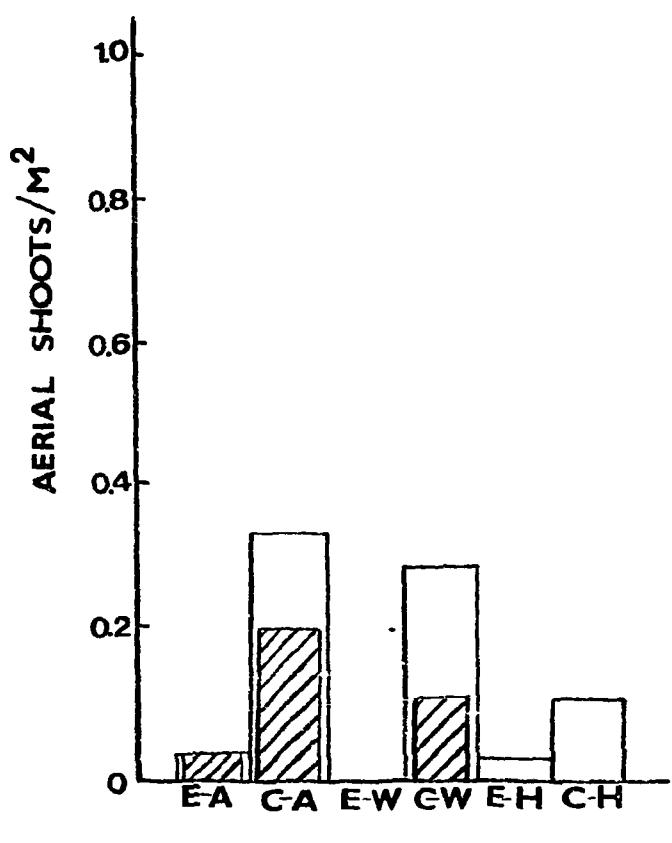


Figure 19 Flowering and fruiting of Cornus canadensis in forest and trail transects in 1970 and 1971.

The outer bar represents the number of flowering shoots/ $m^2$ . The inner bar represents the number of flowering shoots/ $m^2$  that produced at least one fruit. The number above the bar is the number of fruits/ $m^2$ . The populations are coded as follows:

E-A - experimental aspen

E-W - experimental white birch

T - trail transect

There were no flowering or fruiting plants in any of the other habitats.

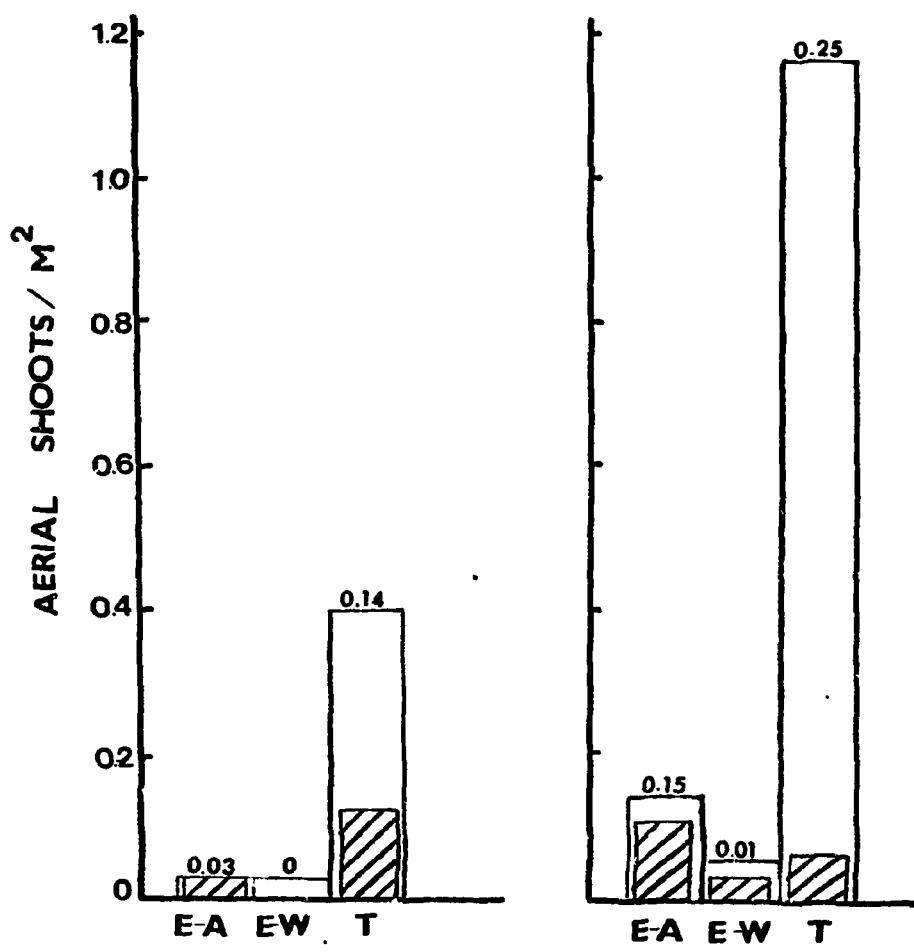


Figure 20 Flowering and fruiting of Cornus canadensis in the disturbed and bog-edge site, 1970 - 72.

The outer bar represents the number of flowering shoots/m<sup>2</sup>. The inner bar represents the number of flowering shoots/m<sup>2</sup> that produced at least one fruit. The number above the bar is the number of fruits/m<sup>2</sup>. The populations are coded as follows:

B - bog-edge site

D - disturbed site

The 1972 census was in June, before fruit development.

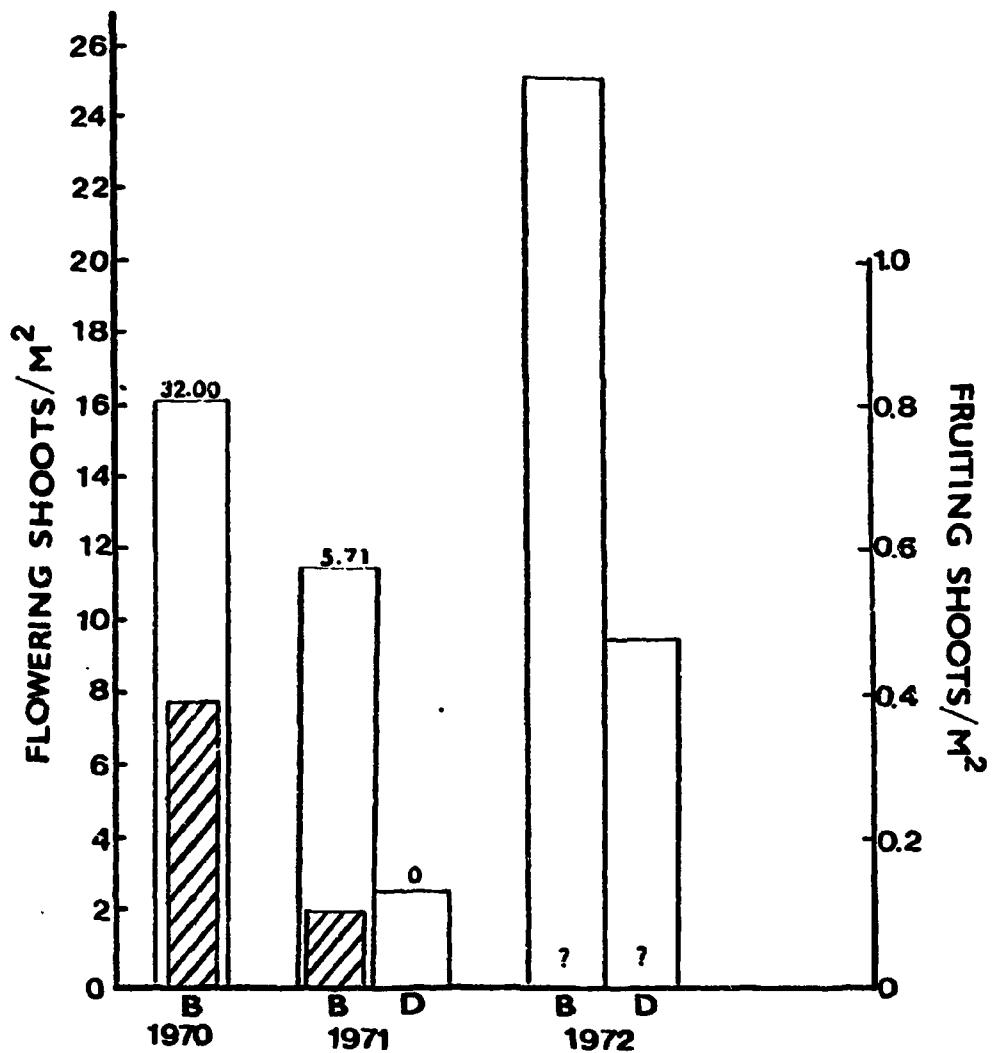


Figure 21 Seasonal change in caloric content of Aster macrophyllus in the control forests in 1970 and 1971. Vertical lines represent range of values. The populations are coded as follows:

- control aspen
- △ control white birch
- control northern hardwoods

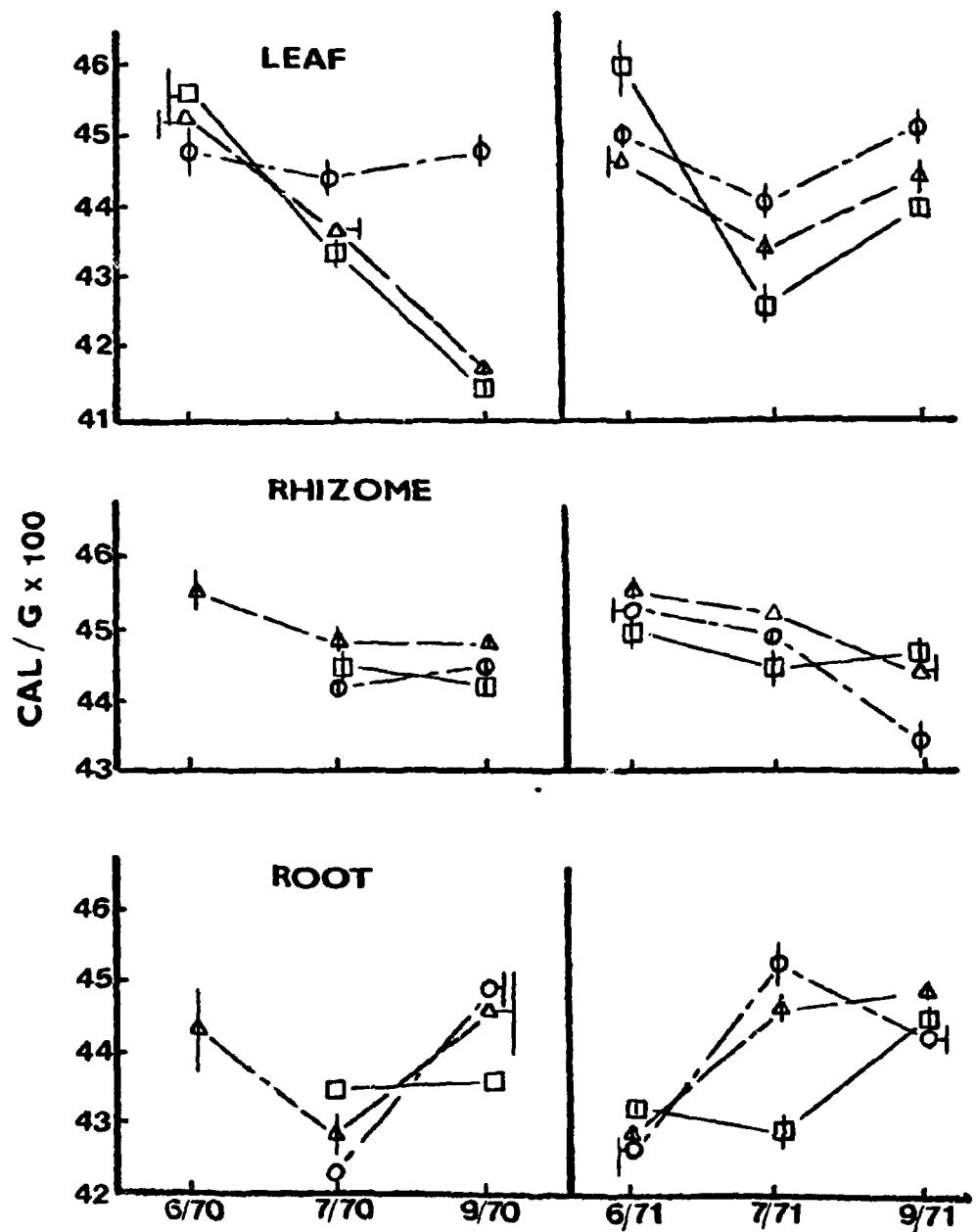


Figure 22 Seasonal change in caloric content of Cornus canadensis in experimental aspen forest and bog-edge site for 1970 and 1971. Vertical lines represent the range of values. The populations are coded as follows:

- experimental aspen
- . bog-edge

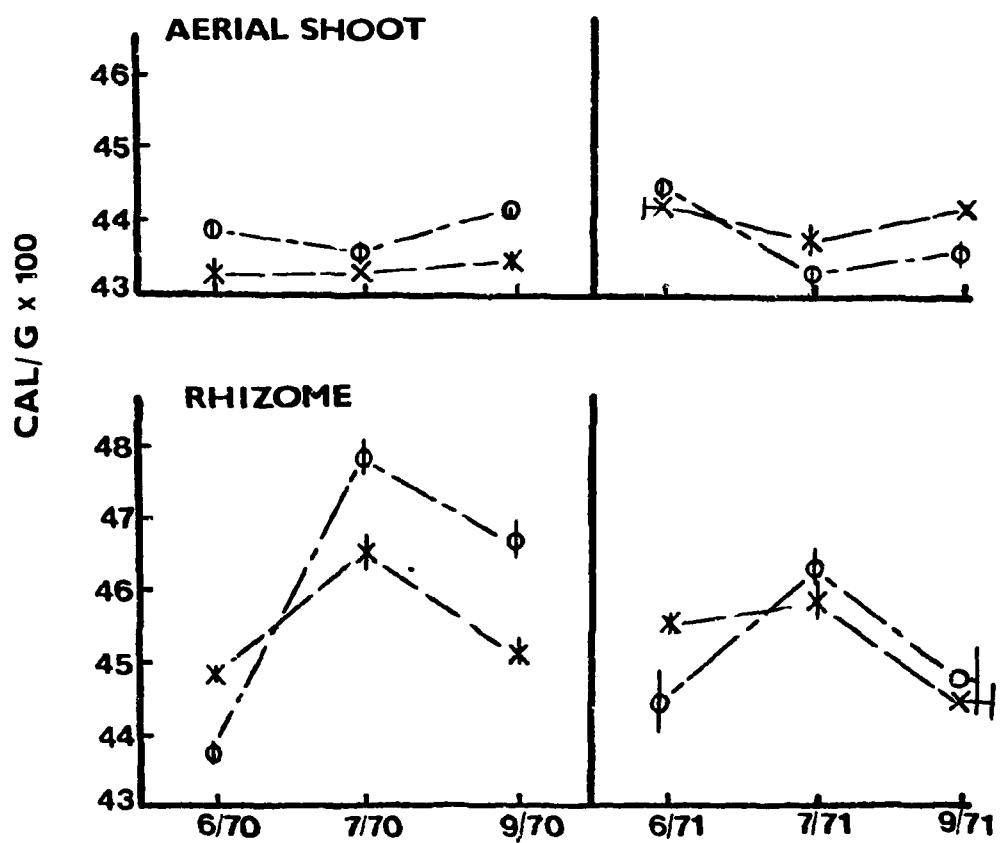


Figure 23 Seasonal change in caloric content of  
Aster macrophyllus and Cornus canadensis in  
disturbed site for 1971.

X Leaf  
□ Rhizome  
Δ Root

Vertical lines represent the range in values.

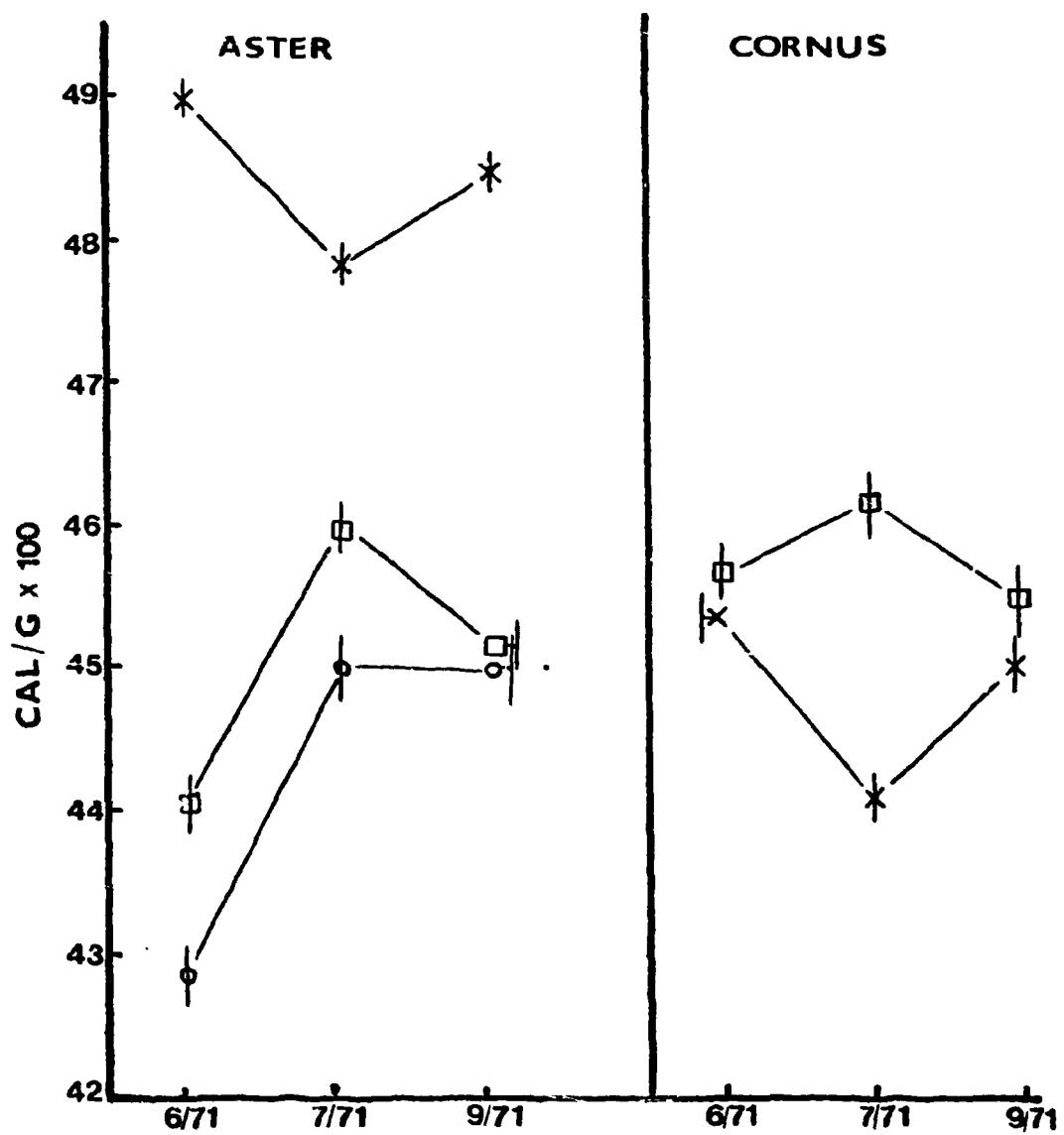


Figure 24 Seasonal variation in chlorophyll a concentration of Aster macrophyllus leaves in control aspen, control white birch, control hardwoods, and disturbed site habitats. Vertical lines represent plus or minus one standard error of the mean. The populations are coded as follows:

- control aspen
- △ control birch
- control hardwoods
- × disturbed site

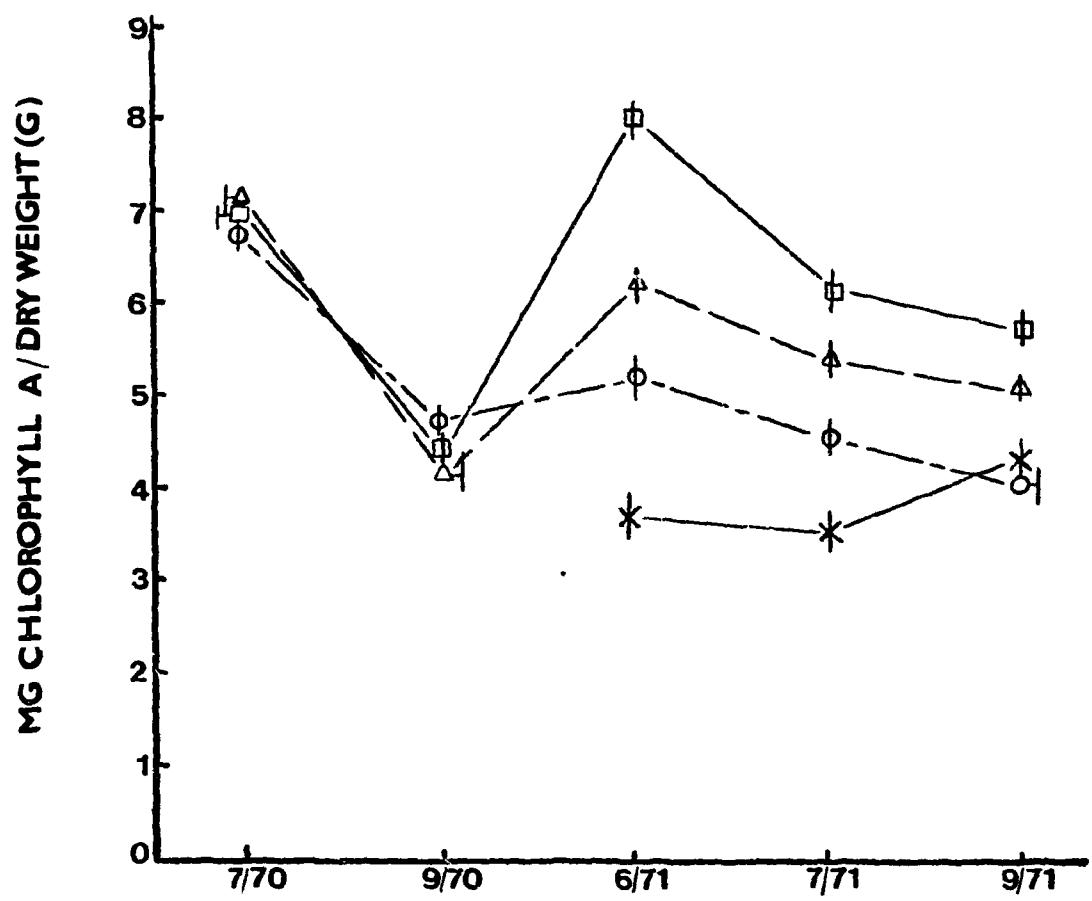


Figure 25 Seasonal variation in chlorophyll a concentration of Cornus canadensis leaves in the experimental aspen stand, bog-edge habitat, and disturbed site. Vertical lines represent plus or minus one standard error of the mean. The populations are coded as follows:

- experimental aspen
- bog-edge site
- ✗ disturbed site

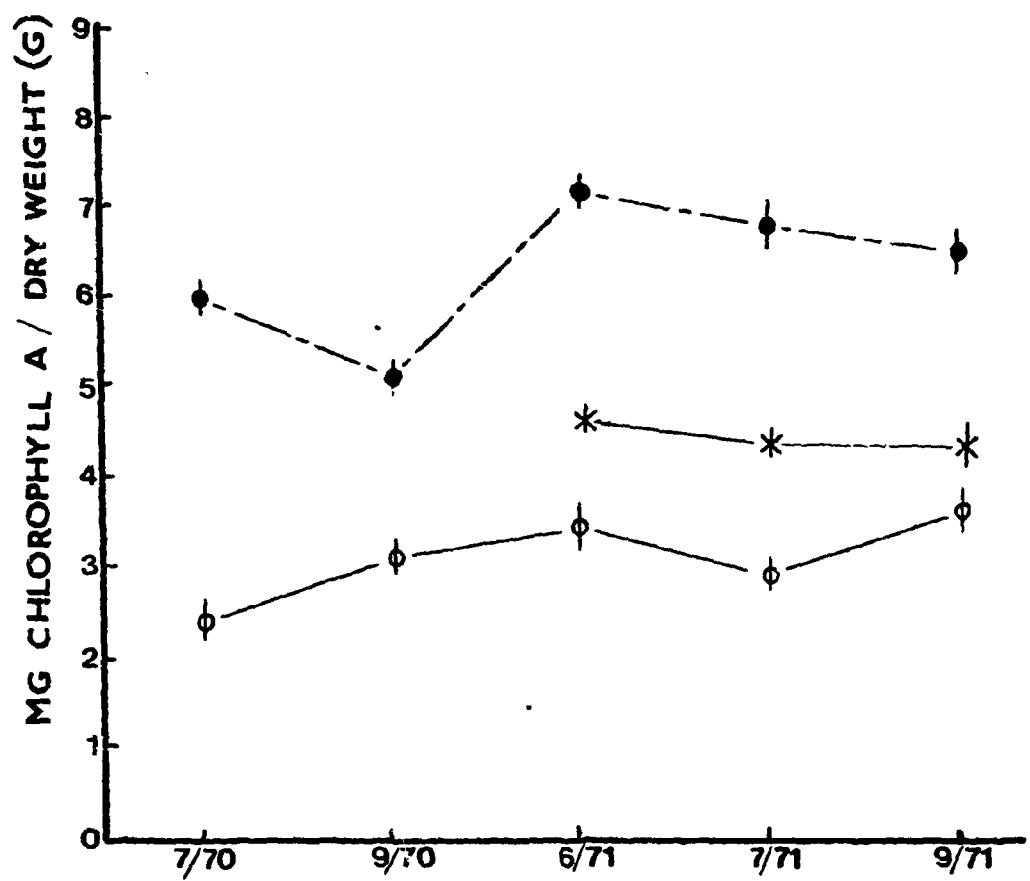


Figure 26 Margalef Ratios for Aster macrophyllus in control forests and the disturbed site in 1970 and 1971. The populations are coded as follows:

- control aspen
- △ control white birch
- control hardwoods
- × disturbed site

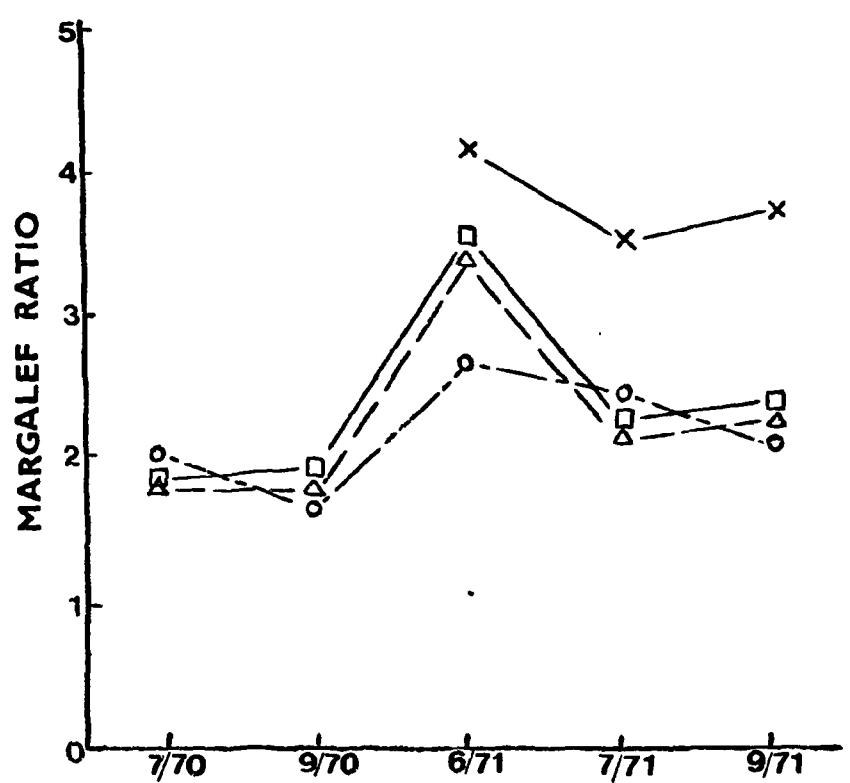


Figure 27 Margalef Ratios for Cornus canadensis in the experimental aspen stand, bog-edge and disturbed sites in 1970 and 1971. The populations are coded as follows:

- experimental aspen
- bog-edge
- ✗ disturbed site

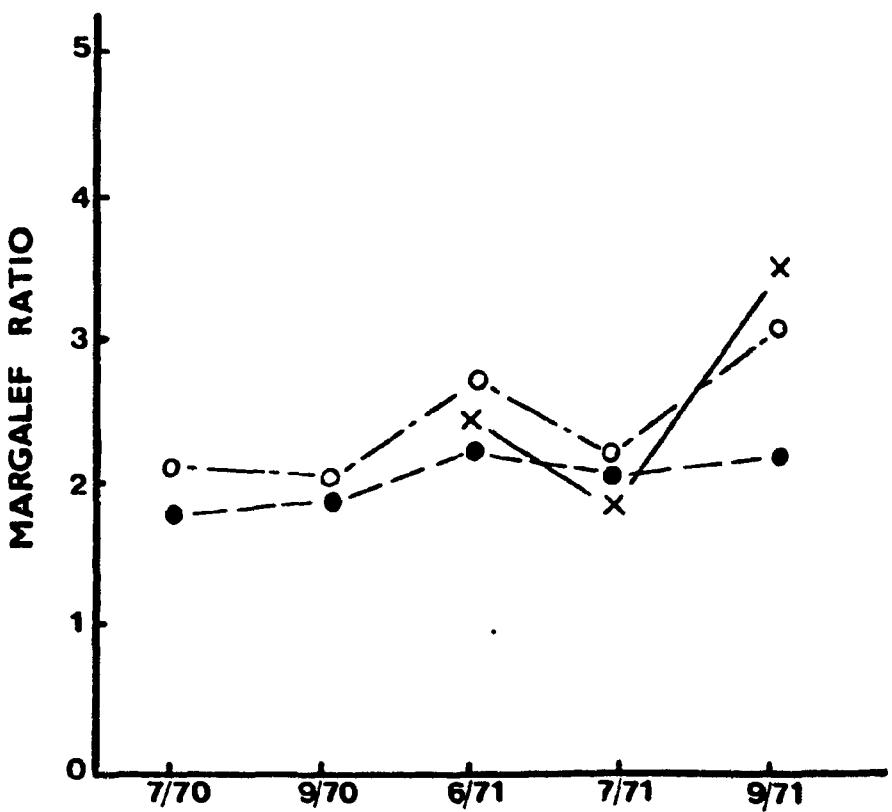
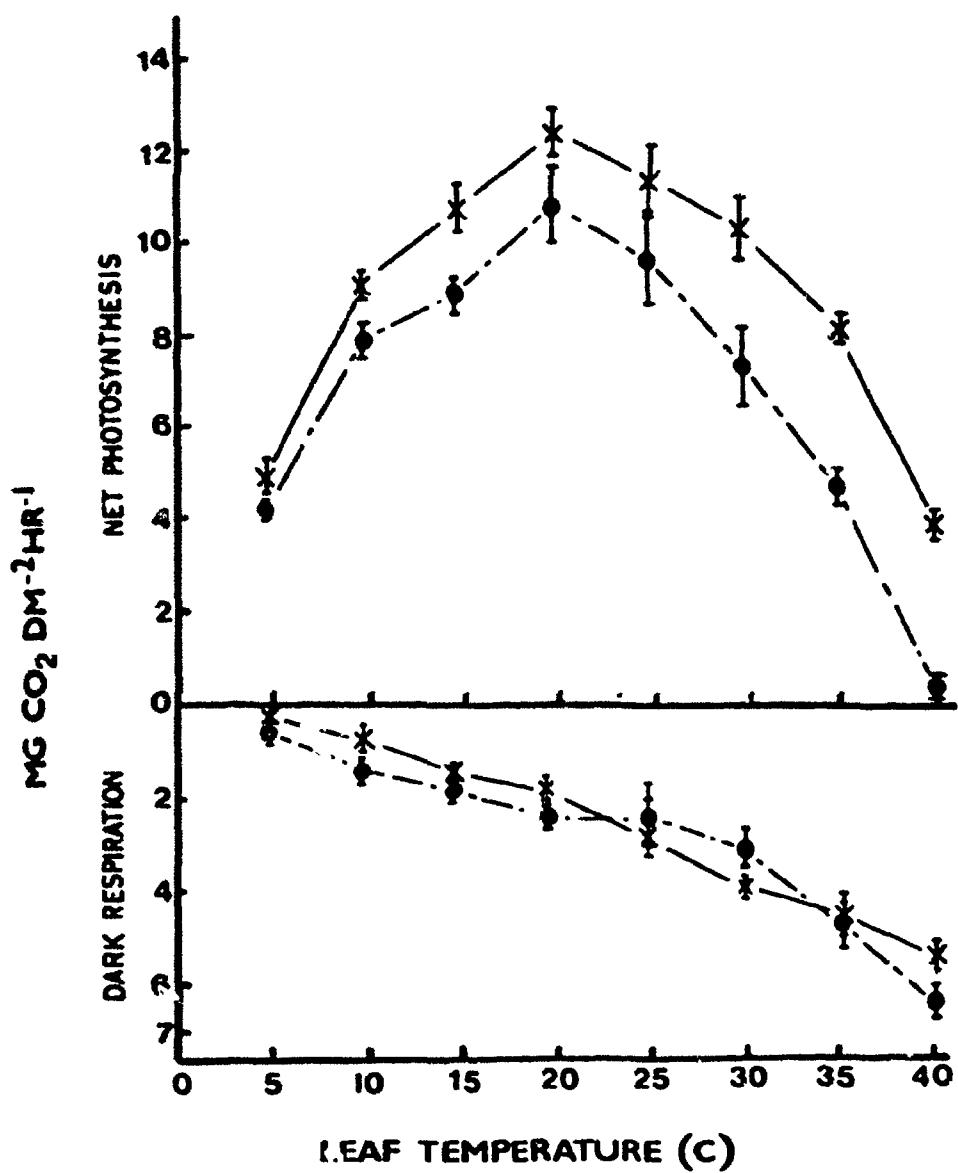


Figure 28 Net photosynthesis and dark respiration of  
Aster macrophyllus grown under two tempera-  
ture regimes. Vertical lines represent plus  
or minus one standard error of the mean.

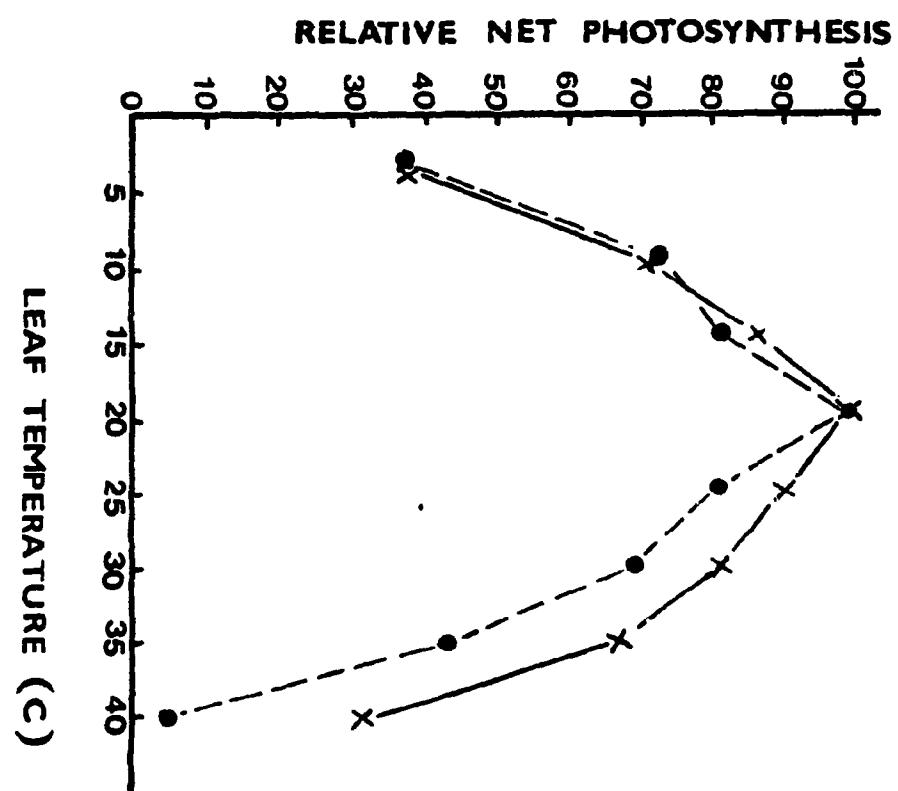
- X warm preconditioning (greenhouse)
- cool preconditioning (18 C days,  
9 C nights)



**Figure 29 Net photosynthesis rates at different temperatures as percent of maximum rate in warm and cool acclimated plants of Aster macrophyllus.**

× warm regime

● cool regime



**Figure 30** Net photosynthesis and dark respiration rates of Cornus canadensis grown under two temperature regimes. Vertical lines represent plus or minus one standard error of the mean.

**X** warm preconditioning (greenhouse)

**●** cool preconditioning (18 C days,  
9 C nights)

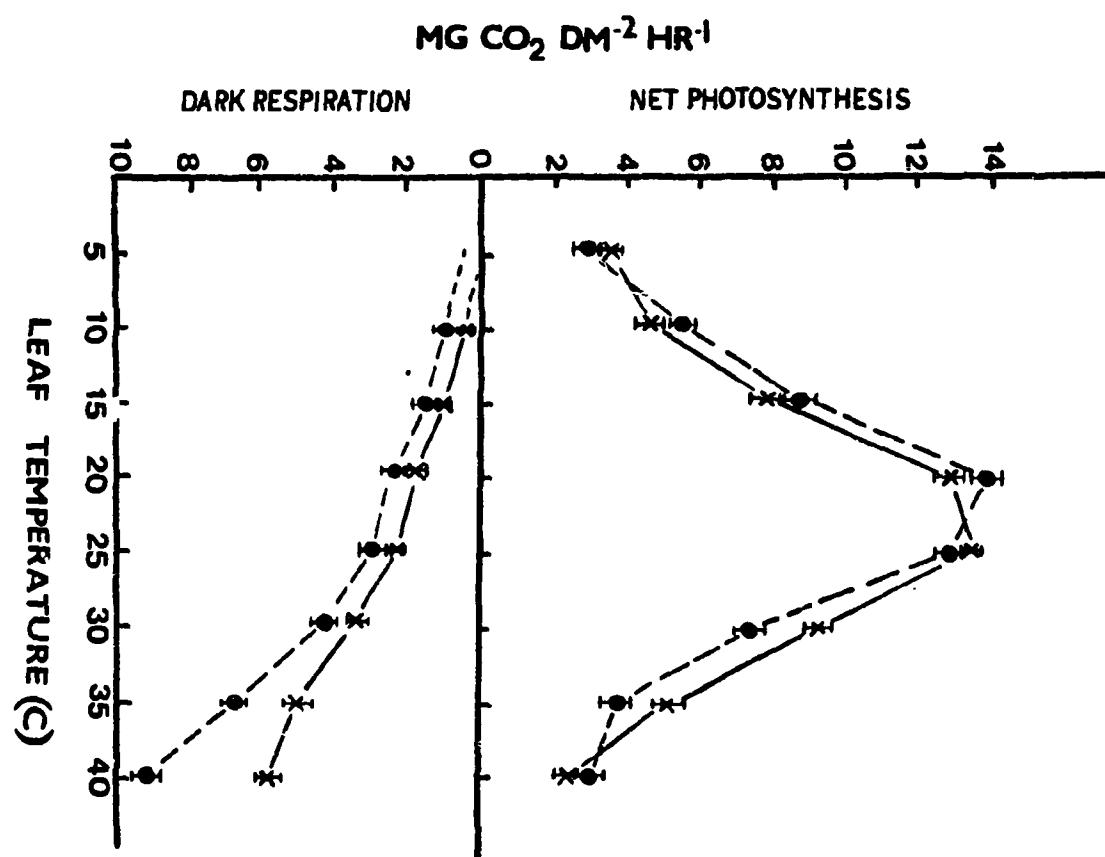


Figure 31 Net photosynthesis at different temperatures  
as percent of maximum rate in warm and cool  
acclimated plants of *Cornus canadensis*.

X warm regime

● cool regime

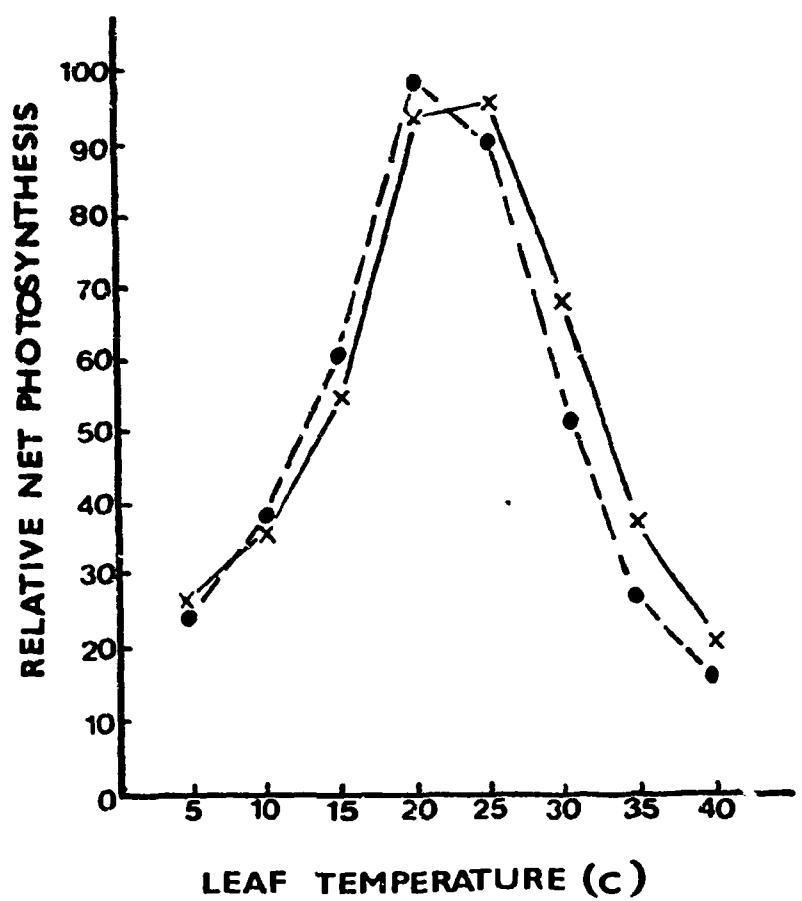


Figure 32 Effect of light intensity upon rate of net photosynthesis in warm (X) and cool (●) acclimated Aster macrophyllus. Data is expressed as percentage of maximum net photosynthesis. Leaf temperature was maintained at  $20 \pm 1$  C.

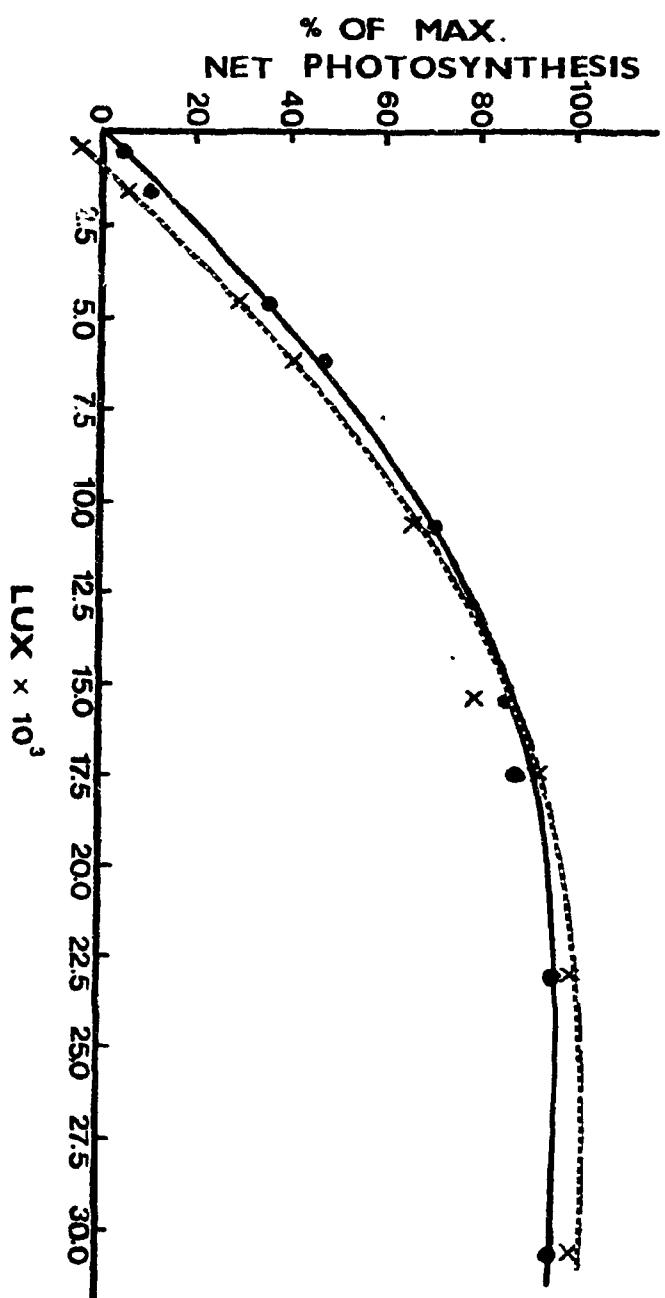


Figure 33 Effect of light intensity upon rate of net photosynthesis in warm (X) and cool (●) acclimated Cornus canadensis. Data is expressed as percentage of maximum net photosynthesis. Leaf temperature was maintained at  $20 \pm 1$  C.

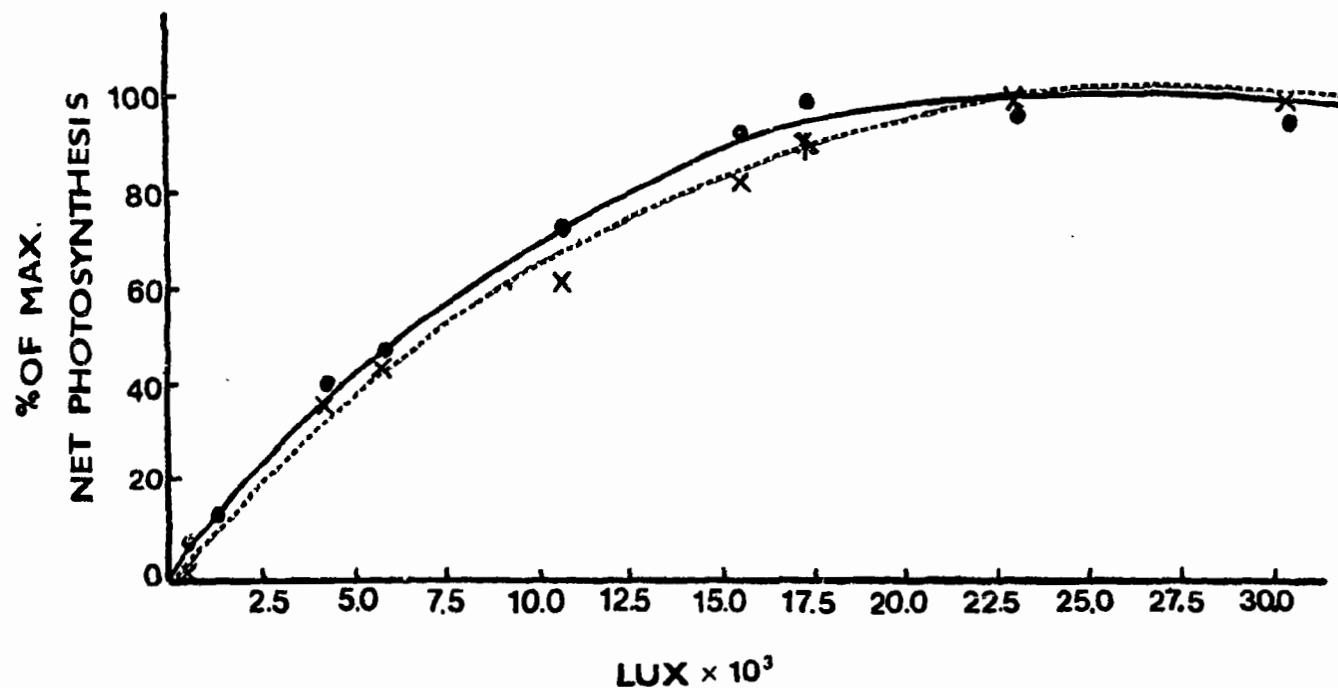
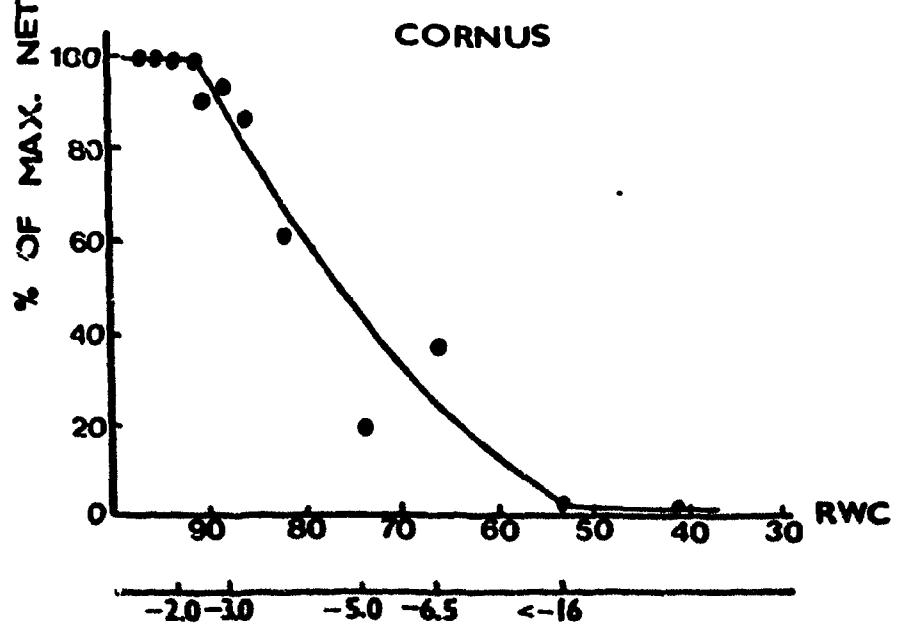
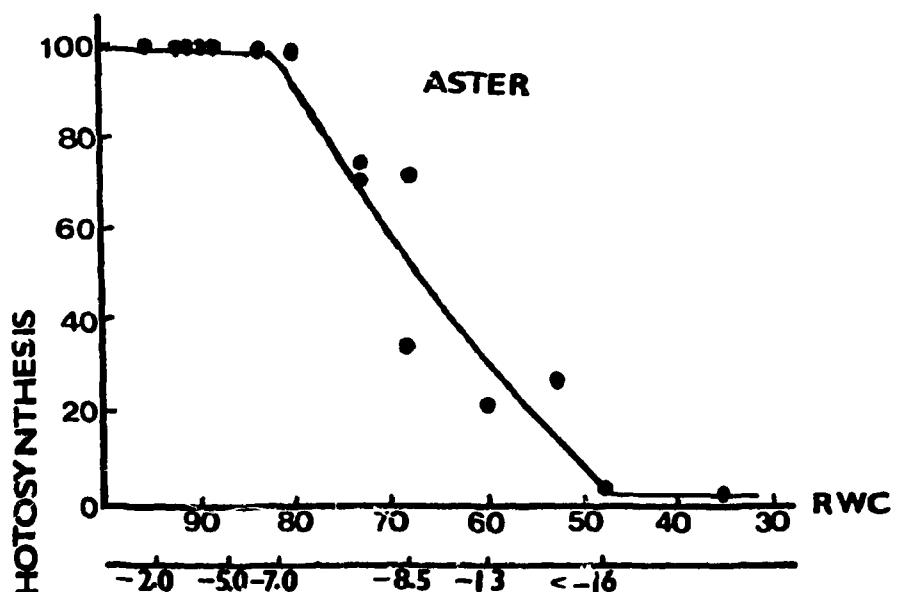
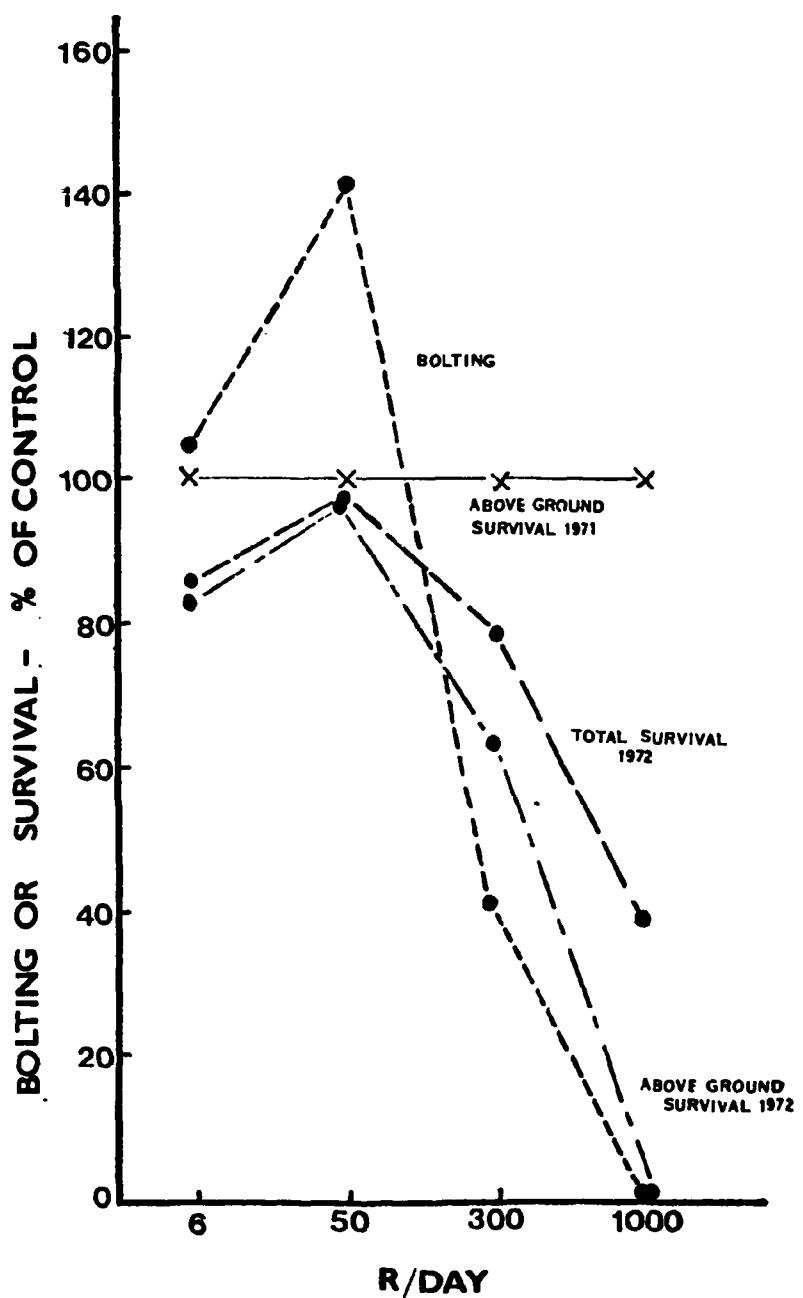


Figure 34 Relationship between net photosynthesis and internal water status of leaves. Relative water content was determined from water uptake of leaf discs, and water potential from the Schardakov dye method. Lines fitted by eye. Leaf temperature was maintained at  $20 \pm 1$  C.



**Figure 35 Effect of gamma radiation on bolting and survival of Aster macrophyllus transplants.**  
Experiment was begun on July 20, 1971, and plants were examined on September 2, 1971, for above-ground survival, and on June 15, 1972, for above-ground survival, total survival (survival of aerial or subterranean buds), and bolting.



**Figure 36** Effect of gamma radiation on flowering and survival of *Cornus canadensis* transplants. Experiment was begun on July 20, 1971, and plants were examined on September 2, 1971, for above-ground survival, and on June 15, 1972, for above-ground survival, total survival (survival of aerial or subterranean buds) and flowering.

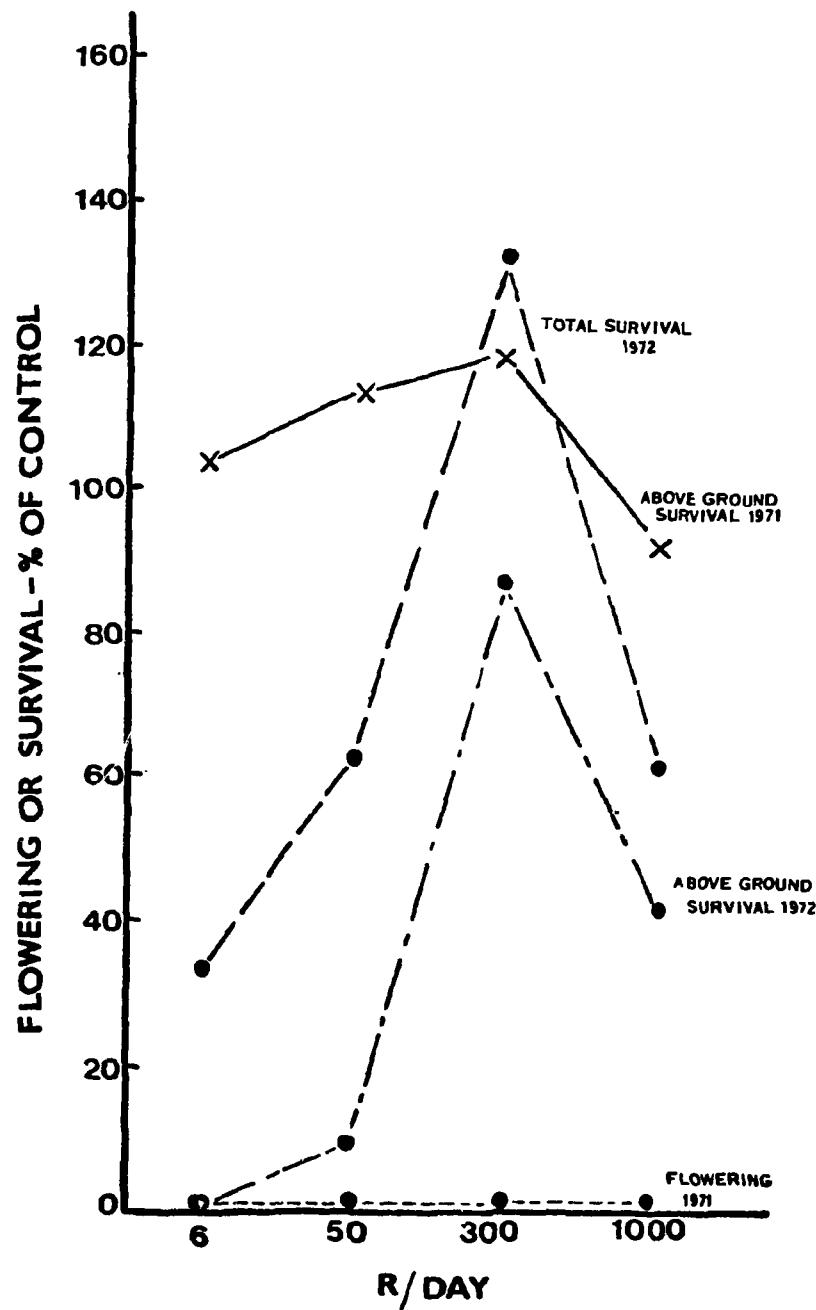


Figure 37 Effect of gamma radiation on caloric content  
of aerial and below-ground parts of Aster  
macrophyllus and Cornus canadensis.

X Leaf

□ Rhizome

△ Root

Vertical line represents the range in values.

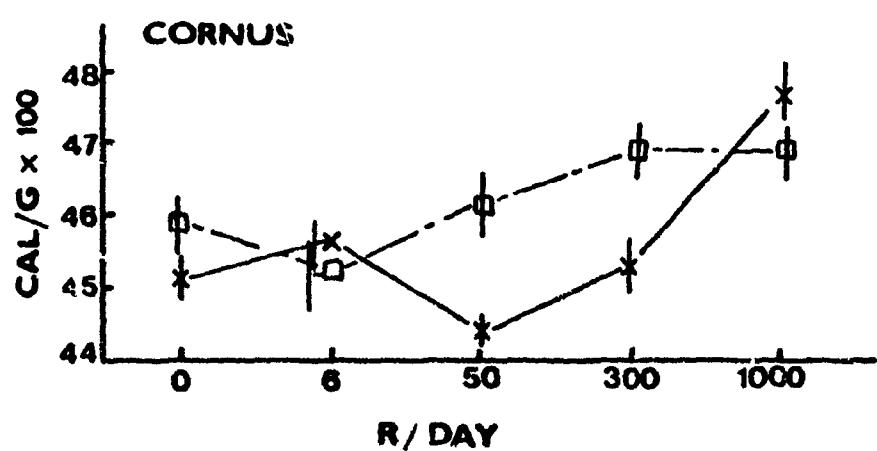
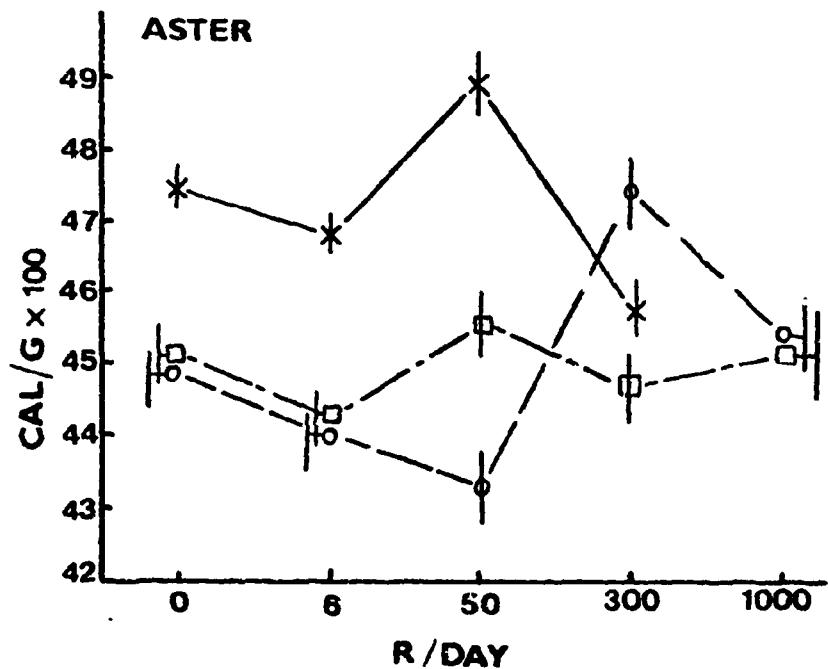
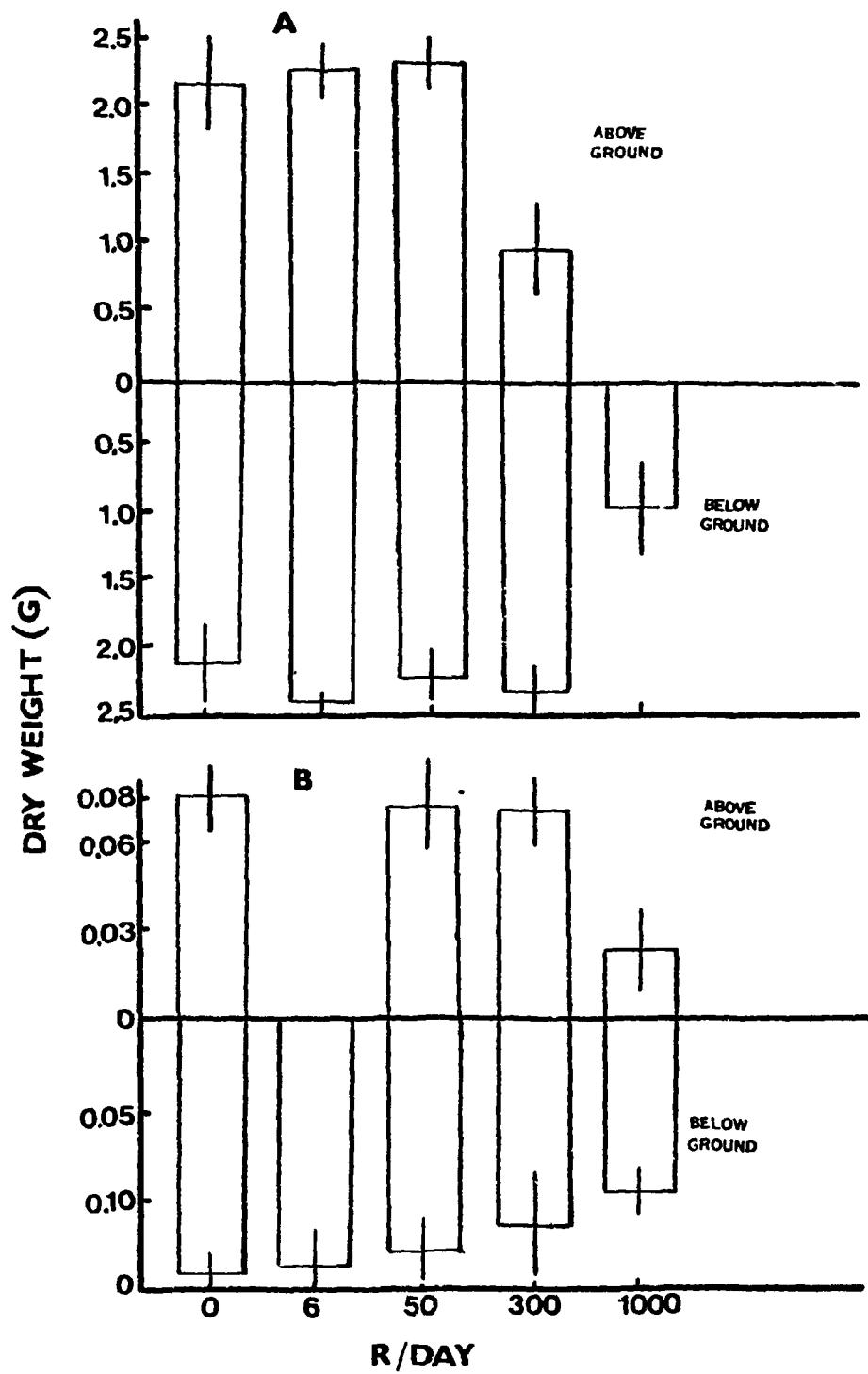


Figure 38 Effect of gamma radiation upon mean biomass  
of above and below ground parts of Aster  
macrophyllus (A) and Cornus canadensis (B).  
No aerial shoots of Cornus canadensis  
survived at 6 R per day. Vertical lines  
represent plus or minus one standard error  
of the mean.



**Figure 39** Summary of understory light intensity measurements in the six stands of the Enterprise Experimental Area. The habitats are coded as follows:

- control aspen stand
- experimental aspen stand
- △ control hardwoods stand
- △ experimental hardwoods stand
- control white birch stand
- experimental white birch stand
- ✗ open site

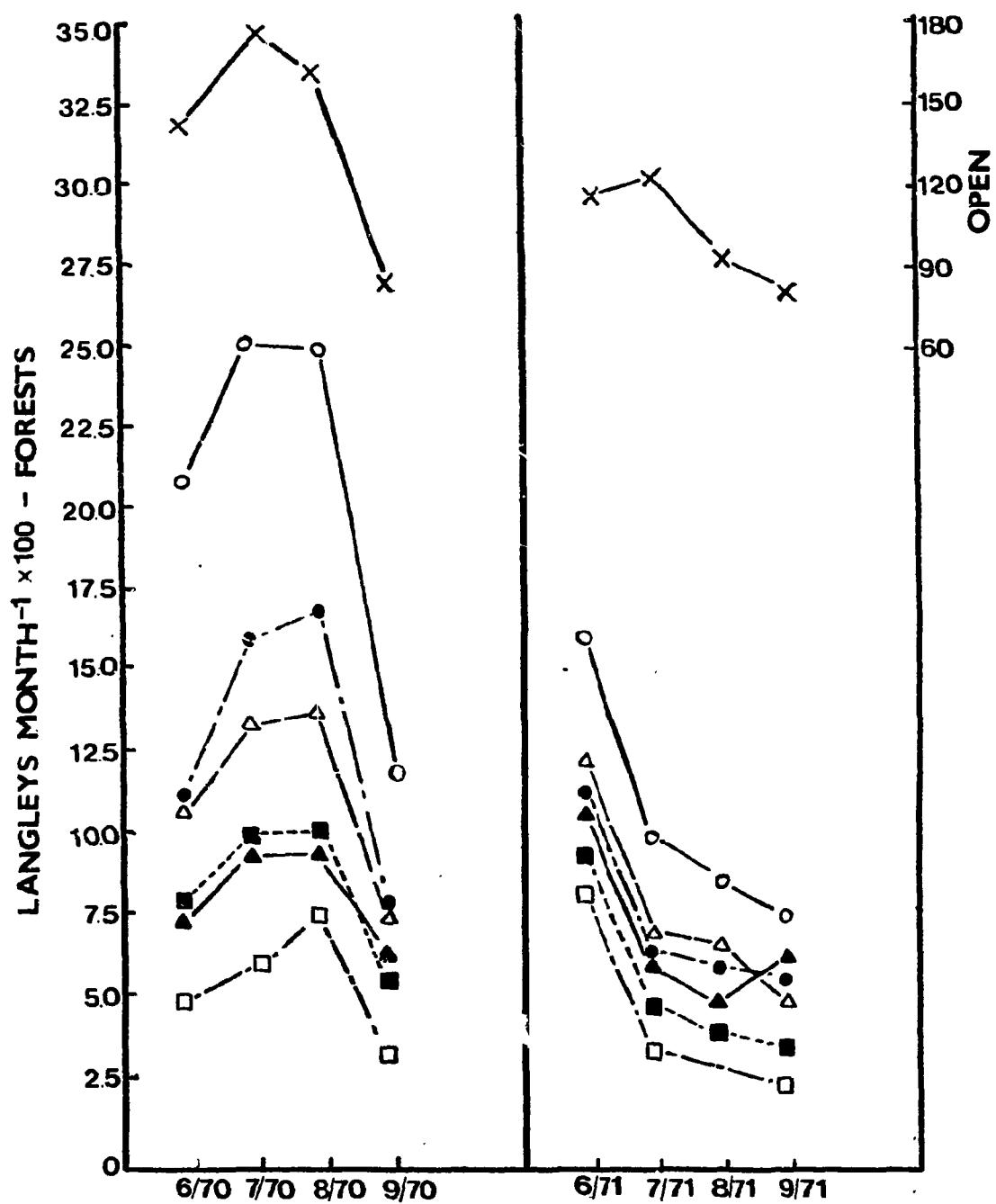
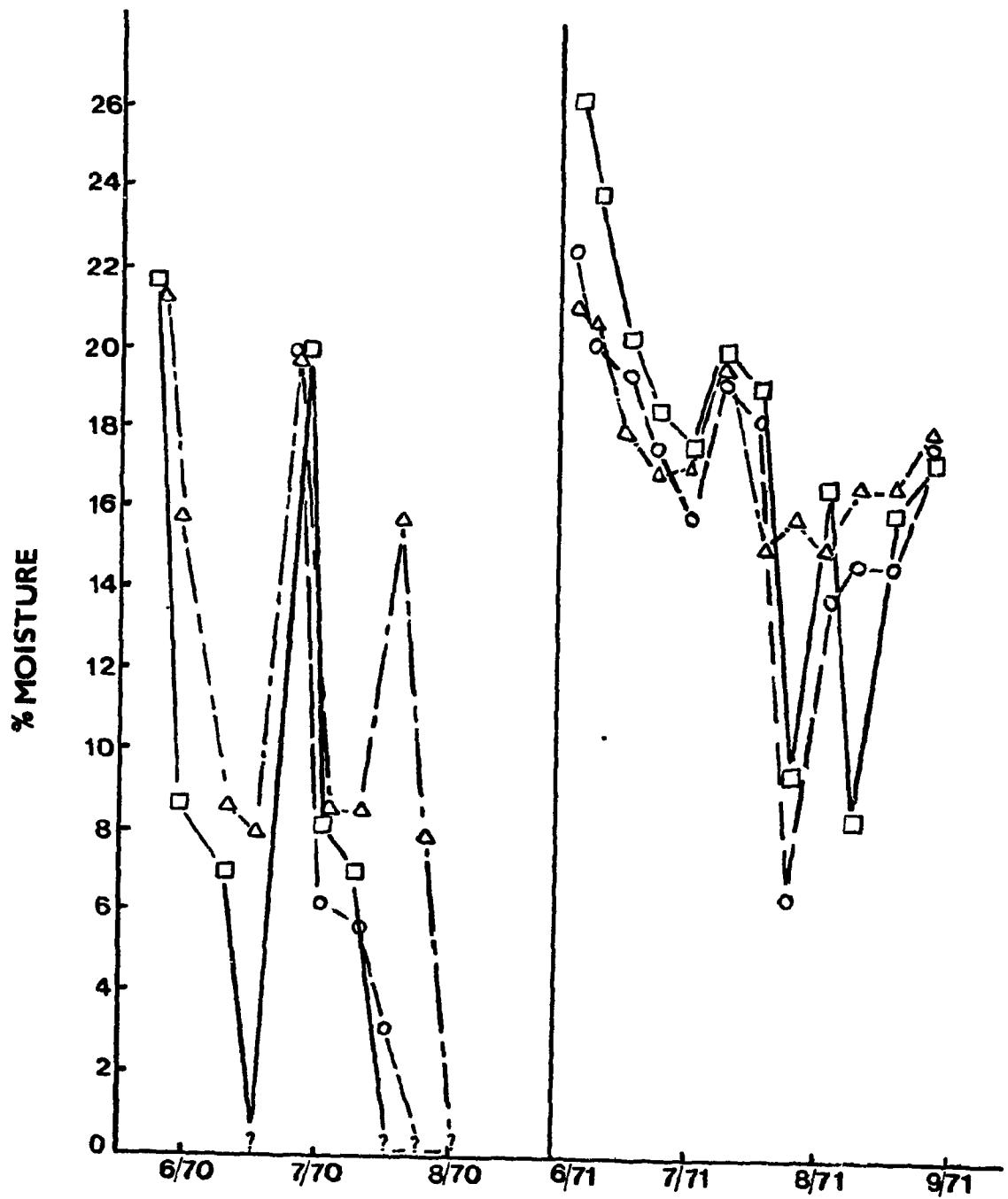
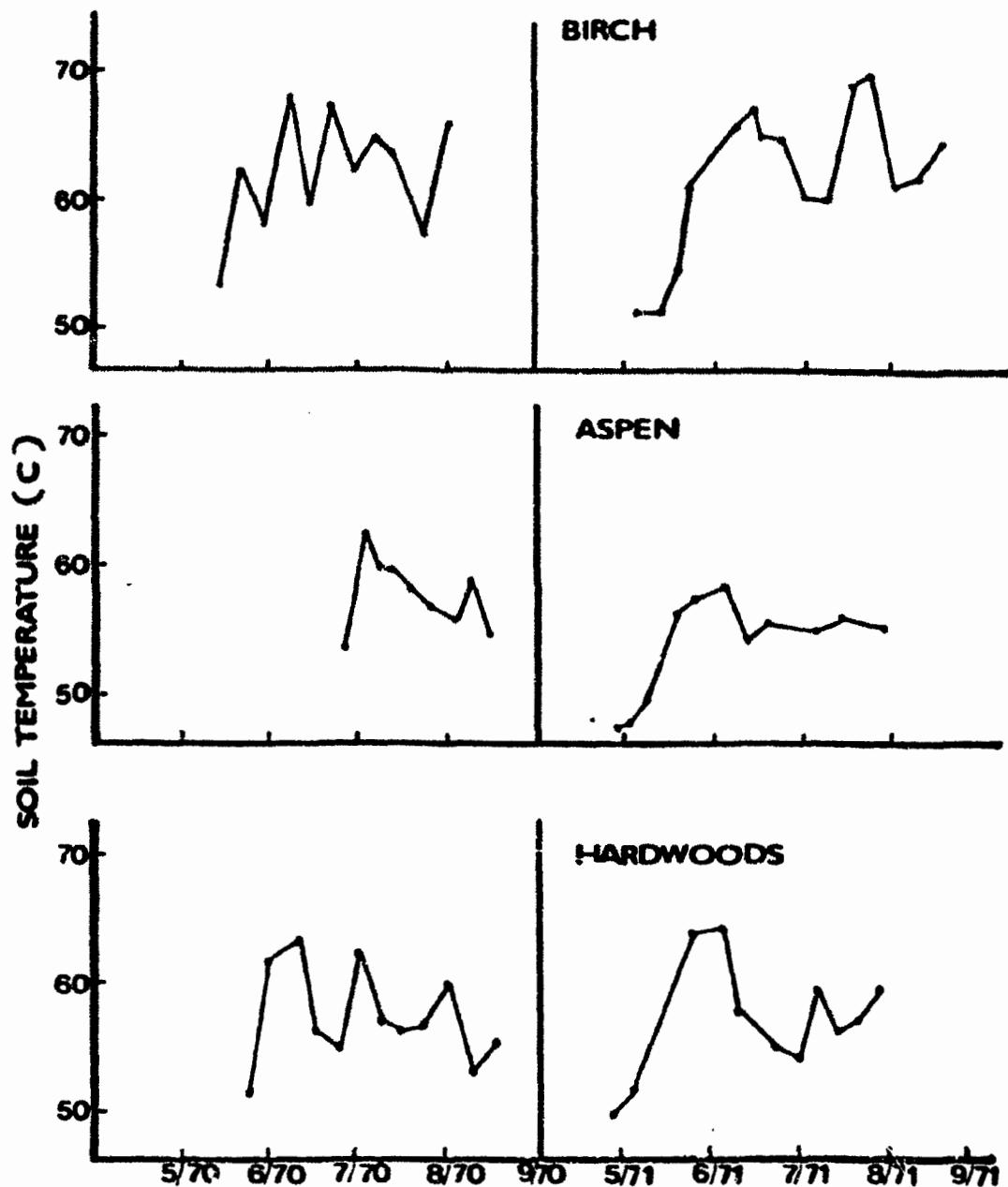


Figure 40 Soil moisture at three-inch depth for the control forests during 1970 and 1971. The habitats are coded as follows:

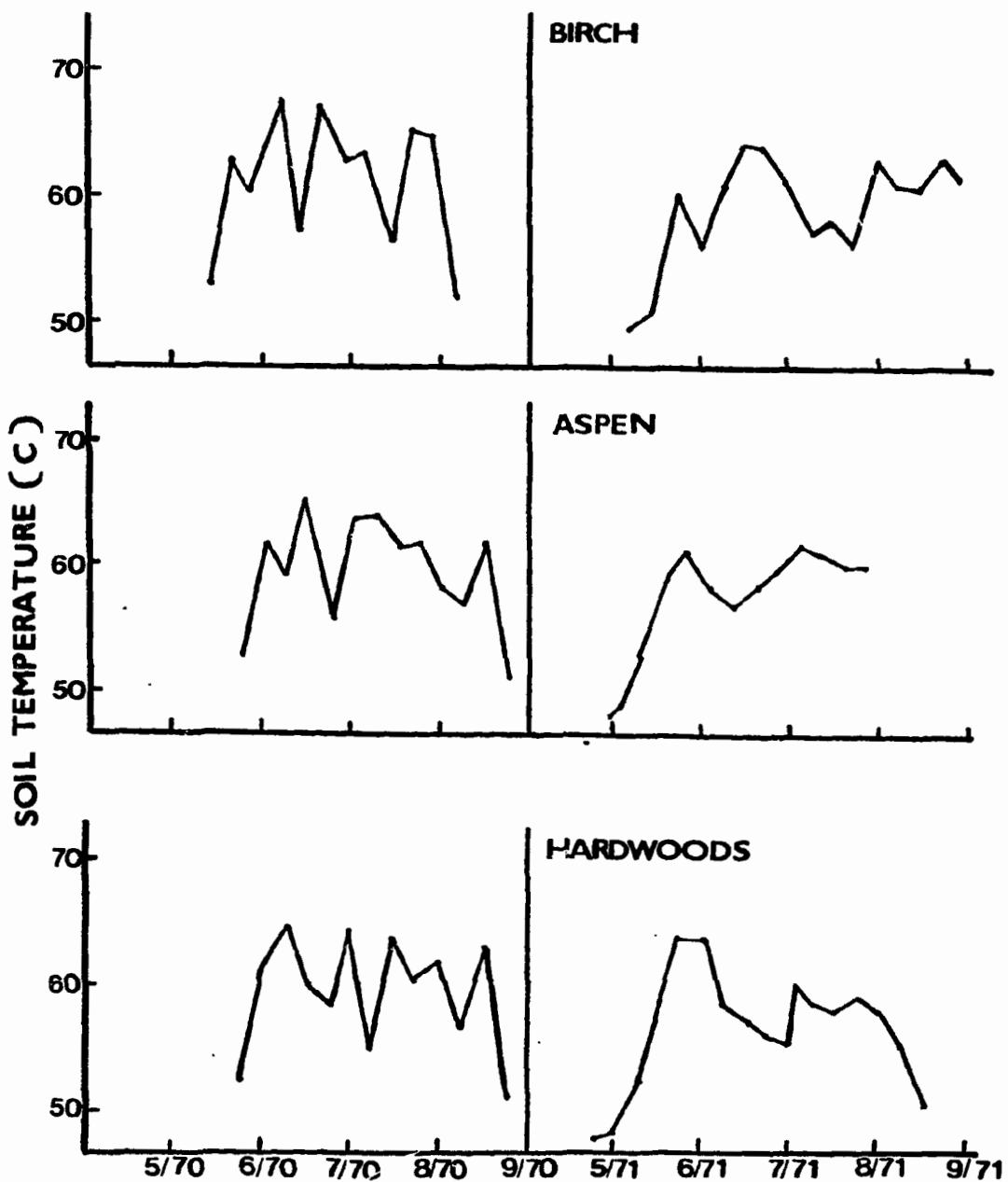
- control aspen stand
- control birch stand
- △ control hardwoods stands



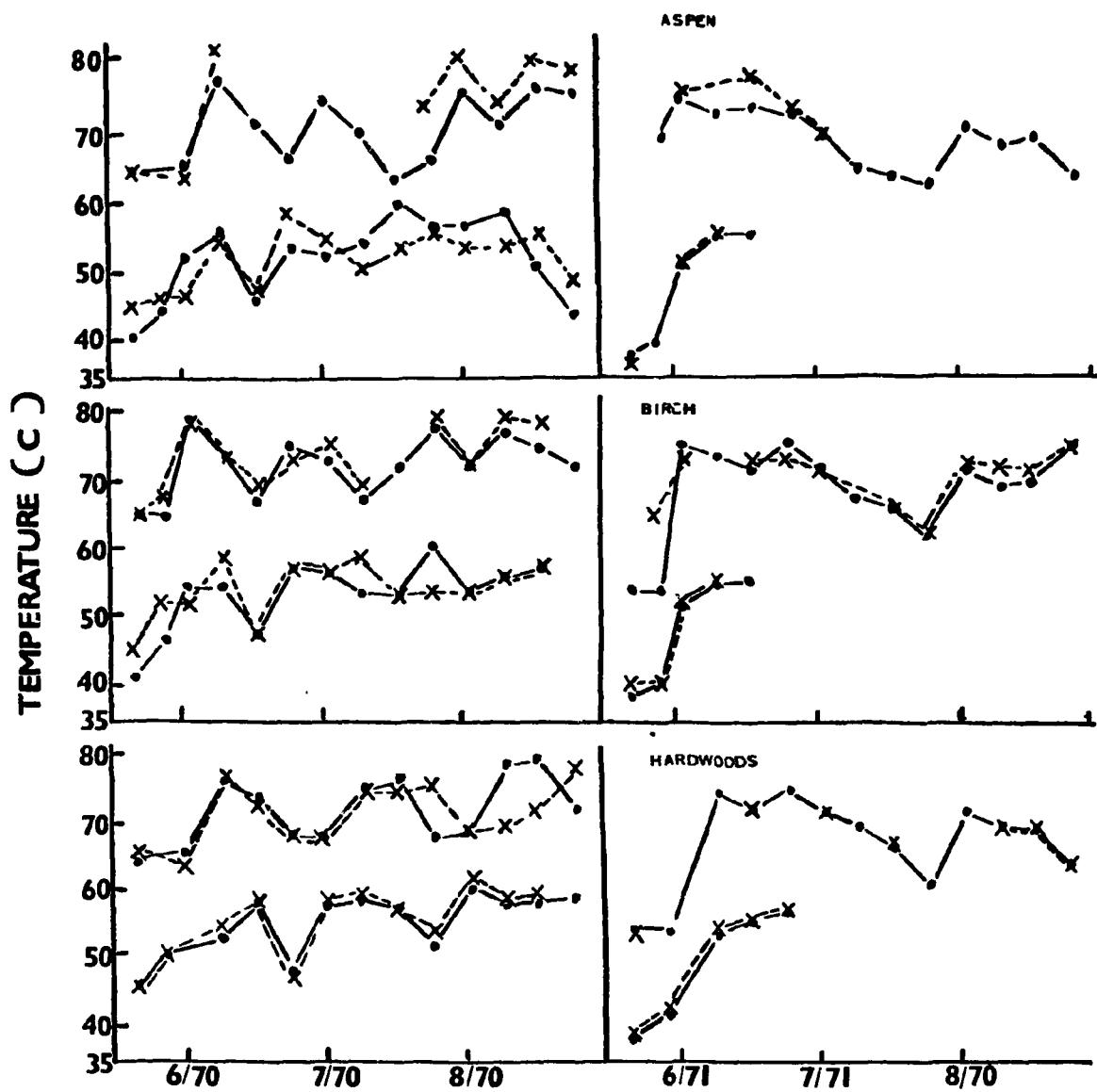
**Figure 41 Weekly mean soil temperature at three-inch  
depth in the control forests for 1970 and  
1971.**



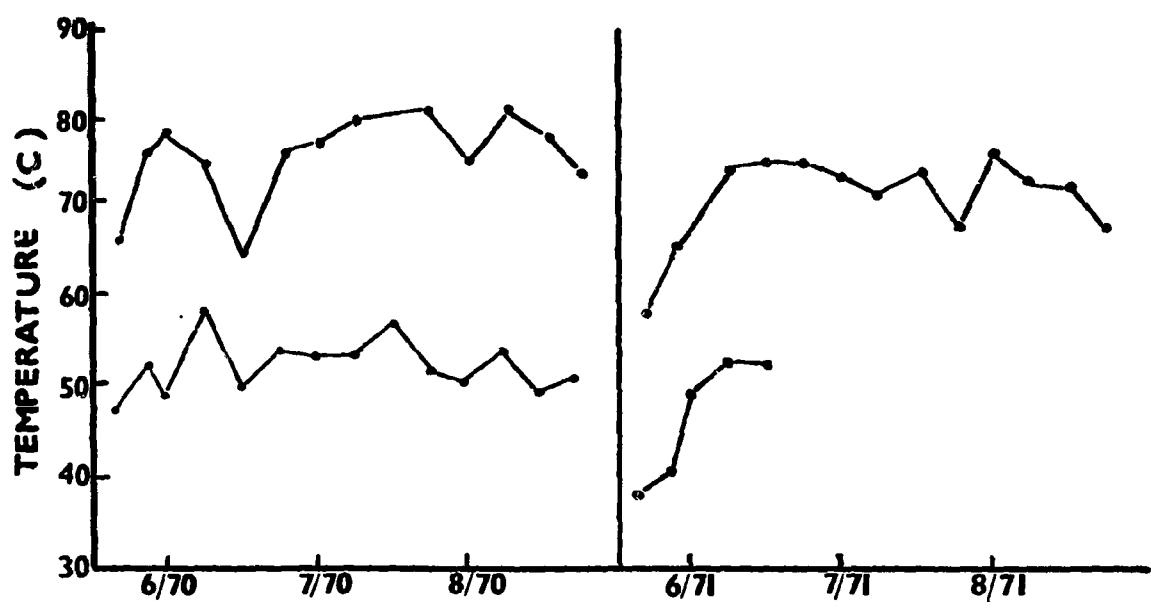
**Figure 42 Weekly mean soil temperature at a three-inch  
depth in the experimental forests for 1970  
and 1971.**



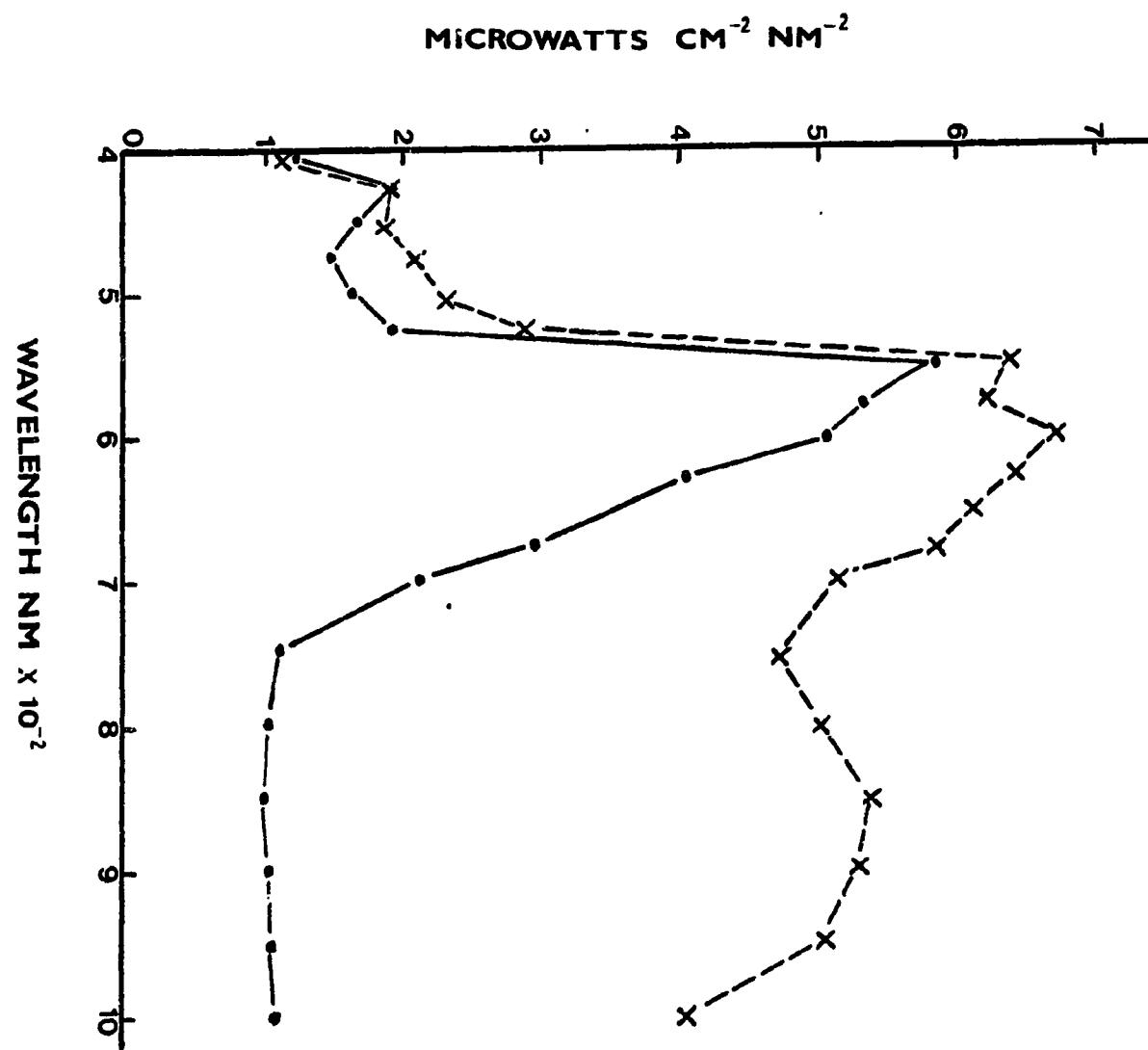
**Figure 43** Maximum and minimum temperatures in the under-story of the six forest stands of Enterprise Radiation Site for 1970 and 1971. Straight lines represent experimental forests, and dotted lines, the control forests.



**Figure 44** Maximum and minimum temperatures in 1970 and 1971 recorded in the open field weather station adjacent to the disturbed site.



**Figure 45** Spectral energy distribution of environmental chamber lights used in gas exchange studies. The solid line represents spectral energy distribution of chamber lights, and the dotted line represents the spectral energy distribution of the chamber lights plus a G.E. 150 watt flood lamp.



**Table 1**      **Analysis of soils of Enterprise Radiation Site.**  
Field capacity and wilting point are in percentage of oven-dry weight. Organic matter is in percentage of air-dry soil. Ca, Mg, and K are in milliequivalents/100 g soil, while P and Mn are in parts per million (ppm).

The habitats are coded as follows:

C-A - control aspen

C-W - control white birch

C-H - control no.thern hardwoods

E-A - experimental aspen (Cornus site)

B - bog-edge site

	C-A	C-W	C-H	E-A	B
<b>TEXTURAL ANALYSIS</b>					
% Sand	79.6	79.9	83.1	68.3	73.8
% Silt	17.4	18.2	15.1	28.5	22.9
% Clay	2.9	2.1	1.0	3.2	3.2
% Colloid	4.6	5.2	4.7	7.9	7.9
<b>MOISTURE PROPERTIES</b>					
-0.33 bars	19.25	17.15	18.86	15.79	18.56
-15 bars	7.09	7.98	7.49	5.55	5.27
<b>SOIL ANALYSIS</b>					
Organic Matter (%)	5.83 $\pm$ .60	5.10 $\pm$ .40	6.10 $\pm$ .90	2.73 $\pm$ 1.20	6.30 $\pm$ .70
Ca(me/100g)	0.23 $\pm$ .01	0.34 $\pm$ .12	0.41 $\pm$ .04	0.53 $\pm$ .10	0.80 $\pm$ .09
Mg(me/100g)	.160 $\pm$ .010	.056 $\pm$ .005	.055 $\pm$ .004	.051 $\pm$ .008	.130 $\pm$ .020
K(me/100g)	.043 $\pm$ .001	.061 $\pm$ .007	.046 $\pm$ .003	.021 $\pm$ .013	.047 $\pm$ .002
P (ppm)	1.10 $\pm$ .30	1.97 $\pm$ .30	2.70 $\pm$ 0	0.80 $\pm$ .30	1.70 $\pm$ .30
Mn (ppm)	2.60 $\pm$ .20	0.93 $\pm$ 1.00	3.27 $\pm$ .10	3.33 $\pm$ .30	2.63 $\pm$ .40

Tables 2-7      Importance values for Aster macrophyllus,  
Cornus canadensis and principal ground  
layer species in the six stands of the  
Enterprise Radiation Site. Only species  
with importance values of 3.00 or more  
are presented.

TABLE 2  
CONTROL ASPEN STAND

Rank	Species	Relative Density	Relative Frequency	Relative Cover	Importance Value
1	<i>Carex pensylvanica</i> Lam.	55.00	10.28	16.85	82.13
2	<i>Aster macrophyllus</i> L.	21.10	10.28	30.69	62.07
3	<i>Pteridium aquilinum</i> (L.)	2.40	8.02	37.70	48.12
4	<i>Maianthemum canadense</i> Desf.	5.40	7.07	0.63	12.53
5	<i>Oryzopsis asperifolia</i> Michx.	0.64	8.02	1.26	9.92
6	<i>Clintonia borealis</i> (Ait.)	2.80	5.19	0.11	8.10
7	<i>Streptopus roseus</i> Michx.	2.41	4.71	0.06	7.18
8	<i>Viola pallens</i> (Banks)	0.75	4.25	0.06	5.06
9	<i>Lycopodium obscurum</i> L.	0.90	2.83	0.50	4.23
10	<i>Gaultheria procumbens</i> L.	0.16	3.77	0.25	4.18
11	<i>Diervilla lonicera</i> Mill.	0.26	2.83	0.57	3.66
12	<i>Corylus cornuta</i> Marsh.	0.24	2.83	0.57	3.64
13	<i>Mitchella repens</i> L.	0.22	2.83	0.01	3.06
37	<i>Cornus canadensis</i> L.	0.075	0.94	0.06	1.08

Total Number of Species 40

Standing Crop of Herbaceous Layer 176.0 g/m<sup>2</sup>

TABLE 3  
EXPERIMENTAL ASPEN STAND

Rank	Species	Relative Density	Relative Frequency	Relative Cover	Importance Value
1	<i>Carex pensylvanica</i> Lam.	44.07	6.28	8.08	58.43
2	<i>Pteridium aquilinum</i> (L.)	1.77	5.98	41.86	49.61
3	<i>Aster macrophyllus</i> L.	4.92	5.00	15.85	25.77
4	<i>Cornus canadensis</i> L.	6.58	5.82	3.94	16.34
5	<i>Aralia nudicaulis</i> L.	0.85	3.22	10.67	14.74
6	<i>Rubus allegheniensis</i> Porter	1.23	6.44	3.32	10.99
7	<i>Maianthemum canadense</i> Desf.	3.87	3.45	0.78	8.10
8	<i>Diervilla lonicera</i> Mill.	0.67	3.91	1.87	6.45
9	<i>Oryzopsis asperifolia</i> Michx.	0.51	3.91	1.45	6.29
10	<i>Viola pallens</i> (Banks)	1.48	3.22	0.26	4.96
11	<i>Hieracium</i> sp.	1.41	2.30	1.14	4.85
12	<i>Gaultheria procumbens</i> L.	1.56	2.99	0.26	4.81
13	<i>Lycopodium clavatum</i> L.	2.77	1.79	0.21	4.77
14	<i>Athyrium filix-femina</i> (L.)	0.32	1.15	2.64	4.11
15	<i>Aster umbellatus</i> Mill.	0.26	1.79	2.02	4.07
16	<i>Corylus cornuta</i> Marsh.	0.48	1.61	1.81	3.90
17	<i>Clintonia borealis</i> (Ait.)	0.68	2.07	0.98	3.73
18	<i>Fragaria virginiana</i> Duchesne	0.48	2.78	0.47	3.73
19	<i>Lycopodium obscurum</i> L.	0.61	2.07	0.73	3.41
20	<i>Vaccinium myrtilloides</i> Michx.	0.77	1.39	0.88	3.04

Total Number of Species 54

Standing Crop of Herbaceous Layer 92.4 g/m<sup>2</sup>

TABLE 4  
CONTROL WHITE BIRCH STAND

Rank	Species	Relative Density	Relative Frequency	Relative Cover	Importance Value
1	<i>Carex pensylvanica</i> Lam.	92.40	16.3	56.16	164.86
2	<i>Pteridium aquilinum</i> (L.)	1.02	12.20	25.19	38.41
3	<i>Aster macrophyllus</i> L.	3.13	15.45	14.13	32.71
4	<i>Oryzopsis asperifolia</i> Michx.	0.80	8.13	2.31	11.24
5	<i>Viola eriocarpa</i> Schw.	0.29	9.76	1.02	11.07
6	<i>Gaultheria procumbens</i> L.	1.72	5.7	0.64	8.06
7	<i>Viola pallens</i> (Banks)	0.76	3.25	1.28	5.29

Total Number of Species 20

Standing Crop of Herbaceous Layer (7/71) 85.0 g/m<sup>2</sup>

TABLE 5  
EXPERIMENTAL WHITE BIRCH STAND

Rank	Species	Relative Density	Relative Frequency	Relative Cover	Importance Value
1	<i>Carex pensylvanica</i> Lam.	70.50	10.35	31.88	112.73
2	<i>Aster macrophyllus</i> L.	6.41	7.47	15.28	29.16
3	<i>Oryzopsis asperifolia</i> Michx.	0.59	5.46	11.74	17.79
4	<i>Maianthemum canadense</i> Desf.	7.62	6.82	0.99	15.43
5	<i>Pteridium aquilinum</i> (L.)	0.11	1.02	13.56	14.69
6	<i>Aralia nudicaulis</i> L.	0.41	4.43	6.78	11.62
7	<i>Gaultheria procumbens</i> L.	2.22	4.78	1.20	8.20
8	<i>Cornus canadensis</i> L.	1.42	4.12	1.42	6.96
9	<i>Corylus cornuta</i> Marsh.	0.98	3.75	1.60	6.33
10	<i>Rubus allegheniensis</i> Porter	0.25	2.05	3.54	5.84
11	<i>Viola pallens</i> (Banks)	2.14	2.05	1.40	5.59
12	<i>Amelanchier</i> sp.	0.63	4.44	0.21	5.28
13	<i>Vaccinium myrtilloides</i> Michx.	0.25	1.02	3.00	4.27
14	<i>Lycopodium obscurum</i> L.	0.61	2.33	0.81	3.75
15	<i>Prenanthes</i> sp.	0.36	2.33	0.61	3.30

Total Number of Species 47

Standing Crop of Herbaceous Layer 29.9 g/m<sup>2</sup>

TABLE 6  
CONTROL NORTHERN HARDWOODS STAND

Rank	Species	Relative Density	Relative Frequency	Relative Cover	Importance Value
1	<i>Carex pensylvanica</i> Lam.	89.10	19.04	77.60	185.74
2	<i>Aster macrophyllus</i> L.	3.83	10.48	7.82	22.13
3	<i>Oryzopsis asperifolia</i> Michx.	3.80	14.28	1.33	19.41
4	<i>Maianthemum canadense</i> Desf.	3.0	10.48	1.62	12.40
5	<i>Viola pensylvanica</i> Schw.	0.52	9.52	1.35	11.39
6	<i>Prenanthes</i> sp.	.78	3.81	0.27	4.86
7	<i>Trillium grandiflorum</i> (Michx.)	.39	2.85	0.81	4.05
8	<i>Streptopus roseus</i> Michx.	.13	2.85	0.54	3.52

Total Number of Species 24

Standing Crop of Herbaceous Layer 45.7 g/m<sup>2</sup>

TABLE 7  
EXPERIMENTAL NORTHERN HARDWOODS STAND

Rank	Species	Relative Density	Relative Frequency	Relative Cover	Importance Value
1	<i>Carex pensylvanica</i> Lam.	75.00	12.8	39.57	127.37
2	<i>Aster macrophyllus</i> L.	7.17	8.41	23.60	39.18
3	<i>Pteridium aquilinum</i> (L.)	0.38	2.93	20.09	23.40
4	<i>Aralia nudicaulis</i> L.	0.71	7.73	12.98	21.42
5	<i>Athyrium filix-femina</i> (L.)	0.62	2.93	15.92	19.47
6	<i>Maianthemum canadense</i> Desf.	2.54	5.87	2.94	11.35
7	<i>Viola pensylvanica</i> Schw.	1.01	3.73	4.02	8.76
8	<i>Lycopodium obscurum</i> L.	1.26	5.60	1.55	8.41
9	<i>Oryzopsis asperifolia</i> Michx.	0.32	3.51	3.86	7.69
10	<i>Lycopus (uniflorus)</i>	1.75	1.33	3.09	6.17
11	<i>Cornus canadensis</i> L.	0.90	2.53	2.10	5.53
12	<i>Rubus allegheniensis</i> Porter	0.81	1.86	2.32	4.99
13	<i>Clintonia borealis</i> (Ait.)	0.62	2.66	1.70	4.98
14	<i>Anemone quinquefolia</i> L.	0.83	3.20	0.77	4.80
15	<i>Diervilla lonicera</i> Mill.	1.49	0.31	2.93	4.73
16	<i>Corylus cornuta</i> Marsh.	0.23	2.66	0.93	3.82

Total Number of Species 63

Standing Crop of Herbaceous Layer 47.4 g/m<sup>2</sup>

Table 8      Abundance:Frequency Ratios and Coefficient  
of Interspecific Association of Aster  
macrophyllus and Cornus canadensis. The  
coefficient of interspecific association  
is presented only for the stands in which  
both species are present.

Abundance : Frequency Ratios

<u>Stand</u>	<u>Aster</u> <u>macrophyllus</u>	<u>Cornus</u> <u>canadensis</u>
control aspen	0.273	
experimental aspen	0.250	0.155
control birch	0.128	
experimental birch	0.175	0.498
control hardwoods	0.200	
experimental hardwoods	0.295	0.451

Coefficient of Interspecific Association

<u>Stand</u>	<u>Coefficient</u>
experimental aspen	-0.03
experimental birch	-0.15
experimental hardwoods	-0.05

Table 9      Sexual reproduction of Aster macrophyllus  
in disturbed and undisturbed sites, 1970 -  
72.

POPULATION	Total Number aerial shoots	% of aerial shoots bolting	% of shoots flowering	# of shoots flowering # of shoots bolting x 100	Mean number of heads/flowering plant	Mean number of seeds per population
1970						
Experimental aspen	712	1.90	0.60	30.80		
Control aspen	1088	2.39	1.47	61.50	14.1	4670
Experimental hardwoods	1212	0.16	0.16	100		
Control hardwoods	140	1.45	1.45	100		
Experimental birch	722	0.42	0.28	66.70		
Control birch	244	5.33	3.70	68.30	16.1	3109
Trail	18	0	0	0	0	0
1971						
Experimental aspen	675	0.17	0.17	100		
Control aspen	1046	0.67	0.38	57.20		
Experimental hardwoods	1234	0.13	0	0	0	0
Control hardwoods	109	1.83	0	0	0	0
Experimental birch	722	0	0	0	0	0
Control birch	251	2.39	0.79	33.30		
Trail	12	0	0	0	0	0
Disturbed site	180	38.40	38.40	100	41.8	5900
1972						
Control aspen	875	0.58				
Control birch	246	0.67				
Control hardwoods	101	0				
Disturbed site	224	49.70				

Table 10      Sexual reproduction of *Cornus canadensis*  
                  in disturbed and undisturbed habitats  
                  1970-72.

Population Location		Total Number of Shoots Counted					
1970							
Bog-edge	855	13.10	3.16	27.00	73.00	3.34	0.52
Experimental Hardwoods	74	0	0	0	0	0	0
Experimental Birch	216	0.46	0	0	100.	0	0
Experimental Aspen	1065	0.26	0.13	50.00	50.00	6.0	0.01
Trail	96	10.41	3.13	30.00	70.00	0.80	0.08
1971							
Bog-edge	870	9.31	0.92	9.90	80.10	10.00	0.09
Experimental Hardwoods	75	0	0	0	0	0	0
Experimental Birch	272	1.15	0.38	33.00	67.00	2.00	0.01
Experimental Aspen	996	2.01	0.68	40.00	60.00	9.00	0.07
Trail	161	19.88	1.24	6.25	93.75	0.44	0.09
Disturbed Site	737	8.18	.03	4.55	95.45	0.08	0.07
1972							
Bog-edge	898	16.48					
Experimental Aspen	1106	6.60					
Disturbed Site	850	23.10					

Table 11      Bagging, seed germination and seedling count.  
Seeds of both species were stratified during  
1970. Ungerminated seeds of Cornus canadensis  
were overwintered in 1971, and germination  
determined the second year as well.

### SEED GERMINATION

Species	Number	Percentage	Germination
<u>Aster macrophyllus</u>	900	<u>1971</u> 35.3	<u>1972</u> -
<u>Aster macrophyllus</u> - Bagged	1000	9.1	-
<u>Cornus canadensis</u>	901	1.33	1.55

### BAGGING

Species	Number of Shoots	Percentage of Shoots Setting Fruit
<u>Aster macrophyllus</u>	15	100
<u>Cornus canadensis</u>	15	0

### SEEDLING DENSITY - 1971

Population	Number of Seedlings per m <sup>2</sup>
<u>Aster macrophyllus</u>	
Control Aspen	0.40
Control Birch	0.25
Control Hardwoods	0
<u>Cornus canadensis</u>	
Bog-edge Site	0
Experimental Aspen	0

Table 12      Caloric values of selected plant organs of  
Aster macrophyllus and Cornus canadensis.

The asterisk indicates flowering or fruiting  
shoots. The populations are coded as follows:

C-A - control aspen

C-W - control white birch

D - disturbed site

The range in values is indicated after the  
mean. In several cases only one determination  
was made.

*Aster macrophyllus*

Date	Population	Leaf	Stem	Rhizome	Root	Caudex	Head
9-70	C-A	*4325 <sup>±</sup> 18	4205 <sup>+</sup> 17	4546 <sup>±</sup> 18	4290 <sup>+</sup> 47		4627 <sup>±</sup> 5
9-70	C-W*	4451 <sup>±</sup> 6	4248 <sup>+</sup> 2	4523 <sup>+</sup> 23	4427 <sup>+</sup> 5	4474 <sup>+</sup> 0	4720 <sup>±</sup> 18
9-71	D-plot*	5045 <sup>+</sup> 7	4541 <sup>±</sup> 14	4585 <sup>±</sup> 25	4556 <sup>±</sup> 3		4610
6-70	C-W					4699 <sup>+</sup> 7	
7-70	C-W					4337 <sup>±</sup> 1	
9-70	C-W					4388 <sup>+</sup> 5	

*Cornus canadensis*

Date	Population	Aerial		Aerial		Inflor- escence	Fruit	Dead Stems
		Shoot	Leaf	Stem	Rhizome			
6-71	Bog-edge*	4532 <sup>±</sup> 20	4552 <sup>±</sup> 21	4512	4586 <sup>+</sup> 4	4437	5101	4475
6-71	Bog-edge			4373 <sup>+</sup> 44				4316
6-71	Aspen		4618 <sup>+</sup> 19	4273 <sup>±</sup> 8				
9-71	Aspen		4425 <sup>+</sup> 2	4279 <sup>+</sup> 53				

Table 13 Mean net photosynthesis/dark respiration ratios of Aster macrophyllus and Cornus canadensis grown under two environmental regimes.

Leaf Temperature (C)

<u>Aster</u> <u>macrophyllus</u>	5	10	15	20	25	30	35	40
Cool Regime	5.90 <sup>+</sup> .48	6.34 <sup>+</sup> .85	5.12 <sup>+</sup> .52	4.41 <sup>+</sup> .13	3.18 <sup>+</sup> .74	2.39 <sup>+</sup> .45	1.22 <sup>+</sup> .23	0.09 <sup>+</sup> .03
Warm Regime	39.23 ±3.89	11.56 ±2.63	7.68 ±1.32	6.35 ±1.38	3.75 <sup>+</sup> .95	2.58 <sup>+</sup> .06	1.82 <sup>+</sup> .09	0.74 <sup>+</sup> .79
<u>Cornus</u> <u>canadensis</u>								
Cool Regime	5.72 <sup>+</sup> .96	4.57 <sup>+</sup> .32	5.52 <sup>+</sup> .78	6.29 ±1.01	4.27 <sup>+</sup> .67	1.59 <sup>+</sup> .23	0.56 <sup>+</sup> .14	0.22 <sup>+</sup> .07
Warm Regime	9.75 ±1.80	14.00 ±2.17	7.19 <sup>+</sup> .32	7.04 <sup>+</sup> .69	4.96 <sup>+</sup> .04	2.61 <sup>+</sup> .44	1.02 <sup>+</sup> .17	0.32 <sup>+</sup> .18

Table 14 Leaf area loss to herbivores as a percent  
of total leaf area of Aster macrophyllus  
and Cornus canadensis for the 1971 growing  
season.

<u>Aster macrophyllus</u>		<u>Percent Leaf Area Consumed</u>		
<u>Population</u>		<u>Date</u>		
		<u>June 6</u>	<u>July 19</u>	<u>Sept. 2</u>
control aspen		0.38	0.81	3.19
control birch		0.84	2.36	3.70
control hardwoods		0.85	3.20	4.08
disturbed site		1.10	1.60	2.85

<u>Cornus canadensis</u>		<u>Percent Leaf Area Consumed</u>		
<u>Population</u>		<u>Date</u>		
		<u>June 6</u>	<u>July 19</u>	<u>Sept. 2</u>
experimental aspen		0.41	1.63	1.90
bog-edge site		1.17	3.28	3.08
disturbed site		1.62	1.10	1.30

Table 15      Precipitation recorded at Hugo Sauer Nursery,  
Rhineland, Wisconsin, during the growing  
season of 1970 and 1971.

PRECIPITATION (INCHES)

MONTH	1970	1971
MAY	5.27	1.44
JUNE	2.10	5.67
JULY	4.14	3.15
AUGUST	.38	3.28
SEPTEMBER	7.18	5.23

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