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EVALUATION OF AN ECOLOGICAL NUTRIENT GRADIENT IN THE CENTRAL PINE SECTION OF MINNESOTA

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I. INTRODUCTION

This study is part of a larger project on the characteristics of forest ecosystems and the foundations of forest productivity in Minnesota. The basic premise of the project is that ecosystems can be characterized by their positions in a four dimensional space with moisture, nutrients, heat and light as coordinate axes.

The first phase of the project involved a preliminary reconnaissance of Minnesota. Species lists, cover estimates and site descriptions were compiled. The second phase, of which this study is a part, involves the quantitative description of the multi-dimensional ecosystem space by means of field instrumentation, and analysis of soils and plants.

The purpose of this study was to define an ecological nutrient gradient in terms of synecological coordinates and to evaluate the relationship between mineral soil and humus nutrients, foliar nutrients in herbaceous plants and synecological coordinates along the chosen gradient. Three hypotheses were formulated. First, synecological coordinates are positively correlated with humus, soil and foliar nutrients. Second, the species that segregate at the lower end of a nutrient gradient have a lower average foliar nutrient concentration than those at the upper end. Third, plants of a species growing in an infertile stand have a lower foliar nutrient concentration than plants of the same species growing in a fertile, nutrient-rich stand.

It was hoped that this study would lead to a better understanding of the relationship between synecological coordinates and the nutrient relation of forest ecosystems. This would enable foresters and silviculturists to assess rapidly the fertility or potential productivity of forest sites without having to rely solely on site index or costly chemical analysis of soil and plant material.

II. BACKGROUND OF THE STUDY

1. Synecological Coordinates, Ecological Groups and Environmental Gradients

The synecological coordinate method is part of the general method of ecological groups. According to the definition of Ellenberg (1956), an ecological group is a group of species which are similar in their relationships to major site factors, such as moisture, light, etc.

Ellenberg constructed his ecological groups in the following manner: First, a relative value between one and five was assigned to each species for each factor, based on the predominant occurrence of the species. The community value was then computed for each factor by taking the average of the individual values of the species present. The value for each species was adjusted according to the average of the stands in which it occurs. The community values were then recomputed and the community assigned a relative position along a qualitative environmental gradient.

The method of Bakuzis (1959) is similar to that of Ellenberg. Bakuzis, however, considers all species, including ubiquitous plants, whereas Ellenberg considers only the species that appear to respond to effective environmental factors.

An example will illustrate the method of synecological coordinates. According to literature sources, Pinus banksiana[1], Gaultheria procumbens and Maianthemem canadense occur on infertile, acid sites and are therefore assigned a nutrient coordinate value of one. If only these three species occurred on a plot, then the unadjusted synecological nutrient coordinate for that plot would be one. The adjusted value for each species, however, is taken from an extensive regional survey as the average of the plots on which that species occurred. Since Maianthemem canadense in Minnesota also occurs frequently with species characterizing rich sites, the adjusted nutrient coordinate is close to two. Thus the adjusted value for each species is based on its association with all other species. It is important to note that the coordinate values do not necessarily reflect the physiologic requirements of the species; rather they reflect the occurrence of the species under competition.

Rowe (1956) used a method similar to that of Bakuzis to develop a vegetation moisture index. Understory species were classified according to position in the vegetation strata and common occurrence along a moisture gradient. The plants were assigned to ecological moisture groups on a basis of frequency and dominance data and given values (wet to dry) of 1, 2, 4, 8 and 16. The geometric increase was used because of the narrower

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[1] The botanical names follow the Latin nomenclature as given in the eighth edition of Gray's Manual of Botany (Fernald, 1950).

ecological amplitude of species on wet sites. Ubiquists were omitted and the value assigned to each species was not adjusted as was done by Bakuzis.

The method of environmental gradients is closely related to the method of ecological groups. This approach is based on quantitative measurement of effective environmental factors, coupled with vegetation analysis. The term "gradient" usually refers to a ranking of stands or sites on a basis of some environmental factor, although in some cases variation along a transect is implied. Once the factor gradient has been defined, then either individual species or ecological groups can be ordinated along it.

A number of authors have constructed synthetic regimes for expressing environmental factors. Whittaker (1960), for example, defined a moisture gradient in terms of topographic position. He then grouped species into four different moisture classes on a basis of the maximum population levels along the moisture gradient and used the moisture class of each species to compute a weighted average for each stand. This was done separately for each parent material and elevation class. Whittaker's method is thus basically floristic; the moisture classes are not based on quantitative environmental measurements.

Loucks (1962) developed synthetic gradients for moisture, nutrients and local climate. Each gradient or "scalar" was constructed from several different effective components. The synthetic nutrient regime, for example, was constructed separately for organic and inorganic soils. For inorganic soils the parameters used were thickness of the A_1 horizon, depth of the solum and percentage of silt and clay. The nutrient regime for organic soils was based on organic constituents, depth of decomposition and run-off. Each of these factors was found to correspond to a species composition gradient. Having constructed these three synthetic factor gradients, Loucks then plotted the importance values of individual species with moisture, nutrients and local climate as coordinate axes.

A more quantitative approach to environmental gradients was used by Waring and Major (1964) in the Coast Range of northern California. They developed moisture, nutrient, heat and light gradients on a basis of field and laboratory measurements. The environmental moisture gradient was based on the minimum value of available soil moisture during one year. The environmental nutrient gradient was based on exchangeable calcium per m^2 x 30 cm. This variable was selected for its high correlation with redwood and barley yield in pot tests. Soil samples were also analyzed for nitrogen, phosphorus, potassium and magnesium. These nutrients were also significantly related to fertility, but given the calcium concentration they did not add much information.

Light was measured over a one-day period using anthracene, and the ecological light gradient was based on percent of full sunlight. Heat was not measured directly but was evaluated from temperature records for weather station occurring in vegetation zones that corresponded to the zones covered in the study.

With the environmental gradients thus defined, the segregation of individual competing species along the respective gradients was shown. Species were then placed in ecological groups according to their relative positions along the four factor gradients, and an index number was assigned to each group. On a basis of the index values for each species, the average moisture, nutrient, heat and light values for each stand were computed. This method is similar to that of Bakuzis, except that the ecological groups of Waring and Major are based on field instrumentation, whereas those of Bakuzis are based on plant associations. An environmental nutrient gradient may be defined as a ranking or gradation of stands on a basis of soil fertility. An ecological nutrient gradient is thus defined as a ranking or gradation of plant response to an environmental or soil nutrient gradient. Plant response in this case includes presence or absence, growth and development under competition and uptake of nutrients. Response may be defined in terms of individual species or ecological groups.

In the previous work on environmental gradients investigators have seldom used the chemical composition of trees, shrubs or herbaceous plants to characterize or define a nutrient gradient. It was hoped that this study would shed light on this possibility and provide detailed information on the effective variables that comprise an ecological nutrient gradient.

2. Foliar Analysis

a. Foliar analysis in general. The technique of using the nutrient concentration of plants as an index of their nutritional status is old and widespread. The advantage of foliar analysis over soil analysis is based on the fact that the growth of plants is related not to the concentration of nutrients in the soil, but rather to the concentration of nutrients in the plant (Lundegårdh, 1951). Thus the plant itself rather than the investigator does the extracting from the soil. This overcomes the problem of choosing a technique that will measure the nutrients actually available for plant growth.

As work on foliar analysis has accumulated, however, the pitfalls and complications have become increasingly clear. First, the concentration of a given nutrient in plant tissue is a function not of the supply of that one element but rather of the total supply of all elements (Goodall and Gregory, 1947). With an increase of one or more nutrients, the growth of the plant may increase, thus decreasing the foliar concentration of one or more nutrients. This is the so-called "dilution effect." This principle applies not only to nutrients, however, but to other growth factors as well. Thus if the growth of a plant is depressed by lack of available water, heat or light, the concentration of nutrients may be increased. Furthermore, if a given element is available in excess relative to other factors, the uptake and foliar concentration may exceed the physiologic requirements of the plant. This is commonly called "luxury consumption."

Aside from direct environmental effects, the internal concentration of nutrients is strongly influenced by the growth and developmental cycle of the plant. During the period of vegetative growth, the concentration of nutrients generally decreases whereas the absolute weight in a given organ increase. Mitchell (1936), for example, found a decrease over time in the foliar concentration of nitrogen, phosphorus, and potassium in oak, maple and hickory leaves. The concentration of calcium, however, increased during the growth period.

The processes of flowering and fruiting result in a decrease in foliar nutrient concentration. Lundegårdh (1951), for example, found a decrease in foliar potassium during flowering of clover. Goodall and Gregory (1947) reported numerous similar examples.

Most of the research on foliar analysis has been concerned with agricultural problems. Foliar analysis is frequently used for assessing fertilizer requirements of crop plants, either by sampling crops from the field or growing crop plants in soil samples under controlled conditions. Less frequently has foliar analysis been used in ecological situations.

b. Ecological applications of foliar analysis. The ecological applications of foliar analysis fall into two groups. The first of these is concerned with the role of forest litter and subordinate forest plants in mineral cycling. Scott (1955), for example, analyzed the subordinate forest plants and leaves of forest trees for thirteen elements. He found that the litter from subordinate plants contained almost twice the concentration of potassium as the litter of tree species. He concluded that understory plants play an important role in the mineral cycle of a forest.

Madgwick (1965) analyzed 19 understory species in a Fraxinus woodland and expressed nutrients on both a percent and area basis. He found that the foliage of understory plants contained between 37 and 44 percent of the potassium, calcium, magnesium, phosphorus and nitrogen of the total for all of the foliage in the stand.

P'yavchenko (1960) measured the nutrient content of mosses, shrubs and grass in a bog forest. He found that these understory plants cycled a larger quantity of calcium and nitrogen annually than did the overstory of spruce, fir and pine.

Whereas mineral cycling is concerned primarily with the effect of herbaceous and tree litter on forest soils, some research has been devoted to the effect of soil differences on nutrient uptake by trees and herbs. Bard (1945) investigated the nutrient content of several tree species growing on three different soil types. He found that the calcium content of the leaves was a function more of species than of soil type. Phosphorus, however, was related both to species and soil acidity; trees on the more acid soils had a higher foliar concentration of phosphorus. This was attributed to the greater availability of phosphorus in the acid soils. The potassium content also seemed to be positively correlated with supply in the soil as well as species. Nitrogen content of the foliage, however, was a function only of species.

In 1949, Bard followed up this study with a similar investigation of herbaceous species. The general pattern for the herbaceous species followed that of the trees. Calcium concentration was controlled by species rather than soil type, whereas phosphorus concentration in the foliage was correlated with available soil phosphorus. No clear trends were shown for potassium and nitrogen, although plants with high moisture requirements had the highest potassium concentrations.

The findings of Ovington (1956) tend to contradict those of Bard. Ovington found that plants on calcareous soils were higher in calcium than those on acid soils. He did not, however, consider individual species, but lumped all herbaceous species on each plot. Forest plants had a higher percentage nutrient content than plants growing in the open; Ovington attributed this to enrichment of the forest floor rather than differences in light or moisture.

Ovington found no significant differences in the nutrient content of plants associated with hardwood and conifer forests on the same soil type. In some instances, however, the overstory species seemed to exert a strong influence on the chemical composition of the ground flora. For example, the Urtica growing beneath Alnus was high in nitrogen, potassium, calcium and magnesium.

Although most of the studies on the nutrient content of forest plants have been largely descriptive, some authors have used this technique to study plant distribution or to assess gradients in nutrient availability and forest productivity. Pigott and Taylor (1964), for example, studied the distribution of *Urtica dioica* in competition with other herbs. They found a high foliar concentration of both phosphorus and nitrogen in *Urtica* foliage. With fertilizer and plot studies they showed that the distribution of *Urtica* was controlled by the amount of available soil phosphorus; that is, under competition, *Urtica* segregated out at the upper end of a gradient of soil phosphorus.

Olsen (1961) analyzed soils and foliage along a transect from a Danish beech-wood into a chalk barren. He found an increase in foliar calcium and decreases in phosphorus, nitrogen, potassium and iron. He concluded that competition for the limited nutrient supply was responsible for the exclusion of beech from the glades.

Gagnon *et al.* (1958), working in Canada, attempted to relate the nutrient content of understory forest plants and humus layers to forest site quality. They analyzed two herbs, four shrubs and four mosses for calcium, potassium, phosphorus, magnesium, iron and manganese. They also analyzed humus samples for the same elements. The results of the foliar analysis were disappointing; no significant differences were found in nutrient content within species among sites. Large differences among species were found. The nutrient content of the humus layer, however, was found to be highly correlated with site index. This was explained in part by the dominance of *Oxalis* and *Cornus* on the better sites. These species have a higher cation content than the shrubs and mosses and thus form a more base-rich humus.

3. General Description of the Area

Data for this study were collected during the summer of 1966 in and around Itasca State Park, in the Central Pine Section of Minnesota (Bakuzis, 1961).

The present upland vegetation of the Itasca region is a mosaic of hardwood and conifer stands, consisting chiefly of northern hardwoods, aspen-paper birch, red pine and jack pine. Both fire and logging have played important roles in the history of these stands.

Itasca Park lies within 40 miles of the prairie-forest border. This suggests that moisture stress on upland sites is probably an important limiting factor in the distribution of vegetation. This is especially likely in view of the history of the climate and vegetation of the region.

The Itasca area was glaciated in late Wisconsin time, the last ice having left the area 12,000 to 13,000 years B. P. (before present). From about 12,000 B. P. to 8,500 B.P. the region was dominated by a Picea-Populus boreal forest. This was replaced by oak savanna, which in turn was succeeded by a mesic deciduous forest about 4,000 B.P. This forest was invaded by pine about 1,000 to 2,000 years ago (McAndrews, 1966).

The present climate is characterized by warm humid summers and cold dry winters (see Figure 1). The mean annual precipitation is 26.3 inches and the mean annual temperature is 38.7°F

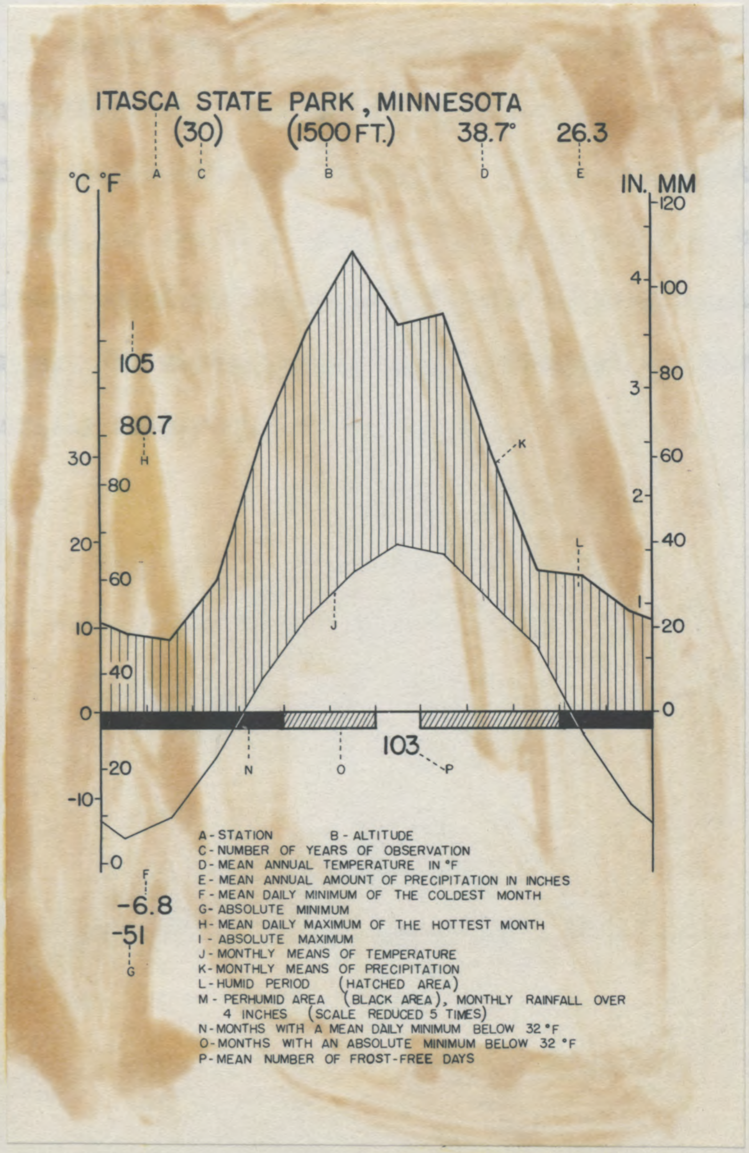


Figure 1. Walter's (1961) climatic diagram for Itasca State Park, Minnesota. The diagram was compiled and constructed by Kurmis (1967).

(Kurmis, 1967).

The role of soil as a controlling factor in the distribution of vegetation in and around Itasca State Park can hardly be over-emphasized. The upland soils are all derived from glacial or water-deposited material, varying in texture from coarse sand and gravel to loam. Different textural classes are often interbedded with one another, and extreme local variation is common. The minerology is mixed, although the parent material is generally calcareous.

III. METHODS

1. Experimental Design

Six stands were selected, two in each of three forest types: jack pine (*Pinus banksiana*), red pine-balsam fir (*Pinus resinosa-Abies balsamea*) and northern hardwoods. Stands were selected on a basis of uniformity of soils and vegetation and lack of dominance of a shrub layer. An attempt was made to find stands that represented a broad range of nutrient conditions as approximated by the synecological nutrient coordinates. The defined gradient in this case represented a ranking of stands rather than a continuous gradation. Since the "gradient" included both hardwood and conifer stands, large discontinuities in plant response were expected.

Table 1 shows the location and code name for each plot. The names were arbitrarily taken from local place names or geographic features. The two jack pine stands are located in the Lake George Township; otherwise all of the plots are in Itasca State Park. Figures 2-1 through 2-6 show the general aspects of the stands chosen for this study.

Within each stand a plot four chains by two chains (264 feet by 132 feet) was delineated. Eight subplot centers were then located systematically within each plot and marked with stakes. Each stake became the center of a nest of concentric

TABLE 1

PLOT LOCATIONS AND FOREST TYPES

Plot Name	Location	Forest Type
Woodlot	S.E. $\frac{1}{4}$ N.W. $\frac{1}{4}$ Sec. 16, T143N, R34W	jack pine
Scott's	S.E. $\frac{1}{4}$ N.W. $\frac{1}{4}$ Sec. 21, T143N, R34W	jack pine
Mary Lake	N.E. $\frac{1}{4}$ S.W. $\frac{1}{4}$ Sec. 19, T143N, R36W	red pine-balsam fir
Wilderness Sanctuary	S.W. $\frac{1}{4}$ S.E. $\frac{1}{4}$ Sec. 16, T143N, R36W	red pine-balsam fir
Campground	S.W. $\frac{1}{4}$ N.W. $\frac{1}{4}$ Sec. 12, T143N, R36W	maple-basswood
Bearpaw Point	S.W. $\frac{1}{4}$ N.E. $\frac{1}{4}$ Sec. 11, T143N, R36W	basswood-elm

subplots with areas of 1, 2, 4, 8, 16, 32, 64, and 128 square meters. This method was chosen to maintain consistency with the method used by Bakuzis (1961).

Species presence was noted for each subplot through eight square meters. These data were used for computing the synecological coordinates for each subplot. Species cover percent was estimated for the eight square meter subplots. Synecological coordinates on a dominance basis were computed by weighting each species with its assigned cover estimate; the weighting factors used were 0.1, 0.5, 1.0, 17.5, 37.5, 62.5 and 87.5. Shrubs were counted and classified according to species, age and height on each subplot through eight square meters. Live trees, dead trees and stumps were counted for all subplots. Diameters of trees one inch or greater were measured on all subplots through 32 square meters; diameters of trees four inches or greater were measured for the 64 and 128-square meter rings. The tree data were used for volume computations.

Within each stand, heights and diameters were measured on a sample of trees. These data were used to prepare height-diameter curves for volume estimates. Borings for age determinations were taken from dominant and codominant conifers for site index calculations (Gevorkiantz, 1957).

Two soil pits were dug in each stand. The profiles were described according to the procedures of the Soil Survey Manual (Soil Survey Staff, 1951). Samples from each horizon were collected, air-dried and stored for future analysis. Bulk density

Figure 2-1. Woodlot jack pine stand. Note the uniformity of the stand and lack of a shrub layer.

Figure 2-2. Scott's jack pine stand. The canopy of this stand is more open than that of the Woodlot stand. The well developed shrub layer is chiefly Corylus cornuta.

Figure 2-3. Mary Lake red pine-balsam fir stand. Note the windthrow in the background and the discontinuous distribution of the herb layer.

Figure 2-5. Campground maple-basswood stand. Note the single red pine in the background, right.

Figure 2-6. Bearpaw Point basswood-elm stand. One of the soil pits appears at the right.

measurements were taken in each horizon with a core sampler. It was planned that data from the soil analysis would be converted to an area basis. One quarter cubic foot samples were taken from three profiles so that the gravel fraction could be estimated.

Foliage samples were collected twice. The first sampling was done in the middle of July. Approximately one kilogram (wet weight) of plant foliage was collected for each of four ubiquitous species in each stand. The species collected were Aster macrophyllus, Aralia nudicaulis, Maianthemum canadense and Corylus cornuta. Because of a scarcity of material, no Maianthemum was collected from the Bearpaw Point Stand, and neither Aralia nor Corylus were collected from the Woodlot stand. All samples were collected along the margins of the delineated plots. The plant material was dried within 4 hours of collection at 90° C and stored in paper bags.

The major sampling was done during the third week of August. In most cases, plant material was collected on the eight square meter subplots. For a few species, however, not enough material was available on the subplots, and so additional material was collected elsewhere in the stand. The amount collected for each species ranged from about twenty grams to one kilograms, depending largely on the quantity available. The samples collected in August were dried at 65° within 4 hours of collection.

Table 2 shows the species sampled in each plot, the stage of development at the time of the second sampling and the part taken. It should be noted that the same species was sometimes in

TABLE 2

FOLIAGE SAMPLING METHOD

Species	Developmental Stage	Part Taken
	1. Bearpaw Point	
Aralia nudicaulis	past fruiting	stems broken at base; stems and leaves (lvs) collected
Maianthemum canadense	healthy; most plants senescent	lvs and petioles above 3rd node; lvs adjacent to fruit not taken
Celastrus scandens	small, heavily browsed	lvs only collected
Dirca palustris	yellow spots on some lvs	lvs only were collected
Corylus cornuta	nuts ripening	lvs from top of canopy
Actea rubra	fruit ripening	lvs and petioles above 2nd node
Aster macrophyllus	not yet flowering	basal lvs from sterile plants
Thalictrum dioicum	past fruiting	lvs and petiols above 3rd node
Amphicarpa bracteata	healthy	lvs only
Asarum canadensis	healthy	stems and lvs above base
Uvularia grandiflora	capsules broken	lvs and stem above lowest leaf; capsules not taken
Sanguinaria canadensis	some plants senescent	healthy plants only; stems and lvs above ground level
Smilacina racemosa	fruit ripe	lvs only; fruit not taken
	2. Campground	
Uvularia grandiflora	capsules broken; some plants senescent	lvs and stem above lowest leaf; mostly healthy plants

TABLE 2--*Continued*

Species	Developmental Stage	Part Taken
Hepatica americana	healthy	lvs and petioles above ground level
Maianthemum canadense	healthy, mostly sterile	as above
Aster macrophyllus	not flowering; some lvs chewed by insects	basal lvs only; broken at ground level
Dirca palustris	healthy	lvs only
Clintonia borealis	healthy; berries ripe	lvs above base
Corylus cornuta	healthy, sterile	as above
Ostrya virginiana	healthy	lvs from top of trees 6 ft high
Acer saccharum	healthy	lvs from reproduction 4.5 ft high
	3. Wilderness Sanctuary	
Maianthemum canadense	many plants senescent; past fruiting	healthy lvs, mostly from sterile plants
Aster macrophyllus	some plants flowering	basal lvs from sterile plants only
Aralia nudicaulis	healthy; past fruiting	as above
Corylus cornuta	healthy	as above
Parthenocissus inserta	healthy; still growing	mature lvs only
Lonicera canadensis	healthy; past fruiting	lvs only
Clintonia borealis	berries ripe; some lvs senescent	lvs above base; sterile plants only
Cornus canadensis	berries ripe	lvs and stems above ground level; sterile plants only
Hepatica americana	healthy	as above

TABLE 2--Continued

Species	Developmental Stage	Part Taken
	4. Mary Lake	
Maianthemum canadense	most plants senescent	mostly healthy plants taken
Aralia nudicaulis	healthy	as above
Aster macrophyllus	damaged by insects, otherwise healthy	as above
Corylus cornuta	brown spots on some lvs	as above
Clintonia borealis	healthy; berries ripe	as above
Cornus canadensis	berries ripe	sterile plants only; lvs and stems
Hepatica americana	healthy	as above
Pteridium aquilinum	healthy	fronds only; no stems
Fragaria virginiana	damaged by insects	leaflets only
	5. Scott's	
Maianthemum canadense	berries ripe; many plants senescent	mostly healthy plants; no berries
Aralia nudicaulis	some plants senescent	healthy plants only
Gaultheria procumbens	both fruit and flowers present	lvs from non-fruiting plants only
Arctostaphylos uva-ursi	fruit ripe	lvs only
Hepatica americana	healthy	as above
Aster macrophyllus	healthy	as above
Corylus cornuta	healthy	as above
Pyrola elliptica	healthy	lvs above base of plant
Diervilla lonicera	healthy; fruiting	lvs only

TABLE 2--Continued

Species	Developmental Stage	Part Taken
Epigea repens	healthy	mature lvs
Pteridium aquilinium	healthy	fronds only
Cladonia sp.	healthy	picked clean of litter
Pleurozium schreberii	healthy	picked clean of litter
	6. Woodlot	
Lithospermum canescens	fruit mature	whole plants; no fruit
Maianthemum canadense	mostly healthy	as above
Aralia nudicaulis	healthy but small, mostly sterile	as above
Aster macrophyllus	mostly sterile	as above
Frageria virginiana	psat fruiting	as above
Gaultheria procumbens	fruit and flowers present	lvs only, mostly from sterile plants
Arctostaphylos uva-ursi	healthy	as above
Pyrola elliptica	past fruiting	as above
Epigea repens	healthy	sterile plants only
Pleurozium schreberii	healthy	living parts only; litter removed
Cladonia sp.	healthy	as above
Apocynum androsaemifolium	chlorotic; declining	leaflets and petioles

a different stage of development in different stands. This no doubt contributed to the sampling error but it cannot be helped.

It was hoped that all samples could be collected between storms. The collection of samples in the Bearpaw, Wilderness and Woodlot plots, however, was followed by three days of rain. This could have leached nutrients from the foliage, particularly potassium. Also, there could have been an increase in soil nitrification following the storm. There is no way to evaluate this; the effect must be lumped with the variability within types.

Since light is one major variable affecting nutrient uptake, integrative light measurements were taken on each plot using the ozalid paper method of Friend (1961). A more detailed discussion of the technique appears in the appendix.

2. Analysis of Soils and Plant Material

The air dry soil samples were screened through a 2 mm sieve and the gravel fraction was discarded. Exchangeable soil and humus cations were extracted with neutral 1 N ammonium acetate according to the method of Black (1965). Calcium, magnesium and potassium were analyzed on a Beckman DU flame spectrophotometer. The interference of calcium at the magnesium wave-length used was corrected for by running calcium standards at the same setting and subtracting the appropriate amount.

Exchangeable hydrogen was analyzed by equilibrating soil and humus samples with 1 N ammonium acetate at a pH of 7.00, according to the method of Brown (1943). The pH of the humus was measured in the laboratory with a Beckman pH meter.

Available soil phosphorus was extracted with Bray's No. 1 solution (0.03N NH_4F in 0.025N HCL). The concentration was determined spectrophotometrically with the molybdate blue method, according to the procedures used in the University of Minnesota Soil Testing Laboratory (Grava, 1962).

Mechanical analysis was done with the hydrometer method (Black, 1965). The sand fractions from the jack pine stands were separated by screening, but this was later abandoned because of the time required. Correction for the organic fraction in the A_1 horizons were made by burning ten gram samples at 300°C for two days. It was hoped that this would eliminate the organic matter without a concommitant loss of the water of crystallization.

Nitrogen in both the soil and plant samples was determined by the macro-Kjeldahl method; the soil samples were not ground prior to digestion. Selenium was added as a catalyst.

All other plant nutrients were analyzed on a Jarrell-Ash model 66-000 direct reading emission spectrograph. Material was prepared for analysis by grinding in a wiley mill, dry-ashing at 525° C, and dissolving in hydrochloric acid containing 0.5 percent lithium.

IV. RESULTS AND DISCUSSION

1. Soil Descriptions

Table 3 contains the profile descriptions for each stand; Table 4 contains the mechanical analysis data. These data illustrate the complexity and diversity of the local upland soils.

The Menahga series supporting the two jack pine stands is derived from glacial outwash sands. Since the percentage of silt and clay gives little useful information about this soil, the sand fraction has been subdivided (Table 5). The differing proportions of fine sand in the two Menahga soils appears to be correlated with the jack pine site index.

The A_2 of the Menahga soils is dark, possibly reflecting a residual prairie influence. Horizon development below seven inches is negligible.

The red pine-balsam fir stands are supported by soil derived from stratified sand, silt and gravel. These soils are part of the Marquette series, although extreme local variability makes them difficult to classify. Both stands have a gravelly layer within fourteen inches of the surface, although this is absent from one of the horizons in the Mary Lake stand. These soils are characterized by well developed A_2 horizons and weakly developed sub-horizons.

TABLE 3

SOIL PROFILE DESCRIPTIONS

Bearpaw Point, Profile 1

Horizon	Thickness	Color, moist	Structure	Consistence	pH	Miscellaneous
A_{11}	4"	10YR 2/1	single grain	soft, friable	6.8	
A_{12}	17"	10YR 3/1	single grain	"	6.8	shows signs of degradation
A_{13}	3-8"	10YR 3/1	weak crumb	"	6.4	high in organic matter
B_3	10-15"	10YR 4/3	weak crumb	loose	6.2	bands of organic matter
IIB_3	4"	10YR 5/3	single grain	"	5.6	very fine sand
IIIC	xx	xx	"	"	6.8	stratified fine and coarse sand; lumps of organic matter
Bearpaw Point, Profile 2						
A_{11}	2"	7.5YR 2/3	weak crumb	soft, friable	6.4	
A_{12}	9"	10YR 3/1	" "	"	6.2	
B_3	6"	10YR 3/2	single grain	loose	6.6	motteling from organic matter

TABLE 3--Continued

Horizon	Thickness	Color, moist	Structure	Consistence	pH	Miscellaneous
C_1	15"	10YR 4/4	single grain	loose	6.4	iron bands and mottling from organic matter
			Campground, Profile 1			
A_1	3"	10YR 3/1	crumb	friable	5.8	
A_{21}	3"	10YR 4.5/3	platy	firm	5.6	
A_{22}	10"	"	"	"	"	
A_2B_2	9"	10YR 4/3 rubbed	angular blocky	friable	5.4	A_2 tounging into B_2; possible gleying
B_2	11"	5YR 4/8-10YR 5/4	angular blocky	slightly sticky; plastic	5.4	contains fragments of decomposed rock
C_1	6"	10YR 4/2	weak ang. blocky	slightly plastic	7.2	much rotten rock; free $CaCO_3$
C_2	x	x	x	x	x	much free lime; rotten rock
			Campground, Profile 2			
A_1	2"	10YR 3/2	crumb	friable	5.0	
A_2	14"	10YR 5/4	platy	very fr.	5.2	
A_2B_2	16"	10YR 4/3-10YR 5/4	med. sub-ang. blocky;	friable	5.4	smells bad; gleyed upper 4" free of rock fragments

TABLE 3--Continued

Horizon	Thickness	Color, moist	Structure	Consistence	pH	Miscellaneous
B_2	11"	10YR 4/3 rubbed	med. sub-	slightly sticky, plastic	5.6	many rotten rocks, clear clay flow surfaces
C	x	x	x	x	7.2	free $CaCO_3$
			Wilderness, Profile 1			
A_{12}	2.5"		single grain	loose		
A_2	3"	10YR 3/3	"	"	4.8	
C_1	7-9"	10YR 4/3	"	"	5.2	
IIC	6-8"	10YR 4/3	"	"	5.4	approx. 54 percent gravel; color variable
IIIC	16"	10YR 4/3	"	"	5.8	underlain by stratified sands and gravel
			Wilderness, Profile 2			
A_{12}	2"		single grain	loose		thin and discontinuous
A_2	5-11"	10YR 4/2	"	"	4.6	

TABLE 3--Continued

Horizon	Thickness	Color, moist	Structure	Consistence	pH	Miscellaneous
C_1	7"	10YR 3/4	single grain	loose	5.2	A_2 tounging into C_1
IIC	11"	10YR 4/3	"	"	5.2	depth varies from 11 to 20 in.
IIIC	6"	10YR 4/4	"	"	5.7	underlain by stratified sand, gravel and discontinuous till
Mary Lake, Profile 1						
A_1	1/2"	10YR 3/1	single grain	very friable	6.6	
A_2	14"	10YR 4/3	"	loose	5.0	
A_2C	6"	10YR 4/3- 10YR 4/4	"	"	5.6	A_2 tounging into C, iron stain in C; 37 percent gravel
C	5"	10YR 4/4	"	"	5.6	37 percent gravel
IIC	3"	10YR 5/4	weak subangular blocky	very friable	5.6	some clay flow surfaces; iron banding; underlain by stratified sand & gravel

TABLE 3--Continued

Horizon	Thickness	Color, moist	Structure	Consistence	pH	Miscellaneous
Mary Lake, Profile 2						
A_1	0.5"	10YR 3/2	single grain	loose	5.2	thin and discontinuous
A_{21}	5"	10YR 4/3	"	very friable	5.0	
A_{22}	5"	10YR 4/3	"	"	5.0	
C_1	17"	10YR 4/4	"	loose	5.6	variable in depth
IIC	5"	10YR-2.5Y 4/4	weak sub-ang. blocky	firm	5.8	some clay flow surfaces; underlain by stratified sand and silt with iron bands
Scott's, Profile 1						
A_1	1"	10YR 3/1	single grain	loose	5.4	thin, discontinuous
A_2	5"	10YR 3/2	"	"	5.6	
C_1	6"	10YR 3/3	"	"	5.7	
C_2	11"	10YR 4/3	"	"	5.7	
C_3	17"	10YR 4/4	"	"	6.2	

TABLE 3—Continued

Horizon	Thickness	Color, moist	Structure	Consistence	pH	Miscellaneous
			Scott's Profile 2			
A_1	1"	10YR 2/1	single grain	loose	5.0	
A_2	4"	10YR 2/2	"	"	5.4	
C_1	11"	10YR 3/3	"	"	5.8	
C_2	13"	10YR 4/3	"	"	5.8	
C_3	17"	10YR 4/3	"	"	5.9	
			Woodlot, Profile 1			
A_2	5-7"	10YR 3/2	single grain	loose	5.4	
C_1	8-10"	10YR 4/3	"	"	5.4	
C_2	6"	10YR 5/6	"	"	5.6	
C_3	7"	10YR 5/4	"	"	5.8	
			Woodlot, Profile 2			
A_2	3-7"	10YR 3/4	single grain	loose	5.6	
C_1	13-17"	10YR 4/4	"	"	5.6	
C_2	6"	10YR 5/6	"	"	5.6	
C_3	11"	10YR 5/4	"	"		

TABLE 4

PARTICLE SIZE ANALYSIS OF SOIL SAMPLES

Profile	Horizon	Percent Sand	Percent Silt	Percent Clay
1. Bearpaw Point				
1	A_{11}	75.2	21.6	3.2
1	A_{12}	81.8	15.2	3.0
1	A_{13}	73.4	17.4	9.2
1	B_3	89.0	8.0	3.0
1	IIB_3	62.0	31.0	7.0
1	IIIC	91.0	6.0	3.0
2	A_{11}	83.0	13.8	3.2
2	A_{12}	85.8	10.1	4.1
2	B_3	93.0	5.0	2.0
2	C_1	97.0	1.0	2.0
2	IIC	98.0	1.0	1.0
2. Campground				
1	A_1	50.8	40.6	8.6
1	A_{21}	57.0	36.0	7.0
1	A_{22}	62.0	31.0	7.0
1	A_2B_2	55.0	28.0	17.0
1	B_2	51.0	27.0	22.0
1	C_1	61.0	24.0	15.0
2	A_1	39.7	48.7	11.6
2	A_2	45.0	44.0	11.0
2	A_2B_2	71.0	16.0	13.0
2	B_2	57.0	25.0	20.0
2	C	66.0	27.0	7.0

TABLE 4--*Continued*

Profile	Horizon	Percent Sand	Percent Silt	Percent Clay
		3. Wilderness		
1	A_1	73.3	17.4	4.6
1	A_2	86.0	10.0	4.0
1	C_1	86.0	10.0	4.0
1	IIC	90.0	6.0	4.0
2	A_{12}	70.0	25.0	5.0
2	A_2	82.0	14.0	4.0
2	C_1	86.0	9.0	5.0
2	IIC	95.0	3.0	2.0
		4. Mary Lake		
1	A_1	73.3	23.4	3.3
1	A_2	83.0	13.0	4.0
1	A_2C	94.0	4.0	2.0
1	C_1	96.0	1.0	3.0
1	IIC	82.0	12.0	6.0
1	IIIC	80.0	17.0	3.0
2	A_1	71.5	23.0	5.5
2	A_{21}	84.0	12.0	4.0
2	A_{22}	90.0	7.0	3.0
2	C_1	98.0	1.0	1.0
2	IIC	57.0	32.0	11.0
2	IIIC	97.0	trace	3.0

TABLE 4--*Continued*

Profile	Horizon	Percent Sand	Percent Silt	Percent Clay
		5. Scott's		
1	A_1	92.8	4.1	3.1
1	A_2	93.0	5.3	2.2
1	C_1	95.0	2.8	2.2
1	C_2	96.0	2.8	1.2
2	A_1	94.6	1.8	3.6
2	A_2	94.1	3.5	2.4
2	C_1	95.6	1.0	3.4
2	C_2	96.7	0.0	3.3
		6. Woodlot		
1	A_2	85.4	11.2	2.4
1	C_1	86.6	9.0	4.4
1	C_2	94.2	4.4	1.4
1	C_3	98.2	1.8	0.0
2	A_2	85.5	9.0	4.5
2	C_1	87.0	6.6	6.4
2	C_2	100.0	0.0	0.0
2	C_3	100.0	0.0	0.0

TABLE 5

SAND FRACTIONS FOR MENAHGA SOIL, AS PERCENT OF TOTAL SAND

1. Woodlot

Profile	Horizon	v. coarse	Coarse	Med.	Fine	v. fine
1	A_2	8.5	26.8	33.6	27.9	3.4
1	C_1	12.2	26.6	29.2	28.6	3.1
1	C_2	15.7	25.6	27.6	38.2	3.0
1	C_3	7.0	20.0	34.6	35.0	2.2
2	A_2	9.3	29.9	32.0	26.0	2.8
2	C_1	11.5	32.0	28.9	25.0	2.7
2	C_2	10.8	23.2	31.8	30.0	3.4
2	C_3	27.9	29.0	23.9	18.2	0.9
2. Scott's						
1	A_{11}	1.4	19.9	42.3	34.0	2.3
1	A_{12}	1.1	14.2	40.9	40.5	3.2
1	C_1	1.0	15.0	40.9	40.4	3.2
1	C_2	0.8	12.9	37.2	45.8	3.1
2	A_{11}	1.0	17.7	40.1	38.1	3.1
2	A_{12}	1.4	16.3	37.1	40.7	3.7
2	C_1	0.7	14.4	39.4	42.4	3.0
2	C_2	0.8	13.6	37.3	44.4	3.8

The soil supporting the Campground maple-basswood stand is in the Beltrami series, belonging to the Gray Wooded great soil group. It is derived largely from calcareous till, but is overlain locally by water-deposited silt. A few large boulders are present in the zone below the silt-cap. The humus is a well developed mull, in contrast with the mor humus of the conifer stands. Both the A_2 and subhorizons are well developed. The soil is poorly drained and shows evidence of gleying in the A_2B_2 horizon and below.

The soil of the Bearpaw point basswood stand may be classified as a Poppelton or N~~y~~ymore loamy sand. The presence of mesic-rich vegetation on loamy sand presents an interesting anomaly. This is explained, however, by the thickness of the A_1 horizon, which varies from 30 to 12 inches throughout the stand. Probably this plot, which lies within one hundred yards of Lake Itasca, was formerly dominated by lake-shore or bog vegetation. With the recession of the Lake, the organic deposits decomposed and worked downward into the stratified sands. Subsequent encroachment of the forest appears to have furthered the degradation of the organic matter and may eventually produce an A_2 horizon.

The A_o horizon in this stand is also somewhat unique. Although the humus resembles a mor humus morphologically, the base saturation is almost 100 percent. According to the classification scheme of Duchaufour (1961), this could probably be called a sandy moder.

2. Soil Chemical Analysis

Table 6 shows the results of the soil chemical analysis for each horizon. Because only two profiles were examined in each stand, a statistical treatment of the soil nutrient data would be meaningless. Some qualitative conclusions, however, are possible.

a. Nitrogen. There is an increase in percent total nitrogen in the soil profile from the jack pine stand to the hardwood stands, particularly in the surface horizons. An exact ranking is difficult to assign on a percentage basis, however, since the volume of gravel and bulk density are not considered. The highest concentration of total nitrogen was found in the Poppelton soil, due to the high organic matter content. The decrease with depth here was rapid as compared with the Beltrami, due to the sandy parent material.

Pluth and Arneman (1963) found a significant correlation between the plot synecological nutrient coordinate and percent total nitrogen in the O1, O1 and A_1 horizons of soils in the central pine section. Bakuzis (1961) also reported a significant correlation between total soil nitrogen and synecological nutrient coordinate, but found that the moisture coordinate was more highly correlated with percent nitrogen.

b. Phosphorus. The distribution pattern for "available" phosphorus is somewhat anomalous. In most horizons, available phosphorus was low in the surface horizon. It generally increased

TABLE 6

SOIL CHEMICAL ANALYSIS

Profile	Horizon	Ca^{++}	Mg^{++}	K^{+}	H^{+}	Per- cent Base Sat.	Percent N	PPM P
1. Bearpaw Point								
1	A_{11}	10.19	1.66	0.35	2.0	86	0.200	65.7
1	A_{12}	4.30	0.66	0.21	2.5	68	0.042	67.5
1	A_{13}	7.05	0.50	0.31	3.0	72	0.101	131.1
1	IIB_3	3.50	0.33	0.12	3.0	57	0.024	52.6
1	B_3	1.50	0.27	0.08	1.5	55	0.019	48.2
2	A_{11}	10.90	1.90	0.30	2.0	87	0.247	29.7
2	A_{12}	3.87	0.58	0.28	1.5	76	0.056	79.6
2	B_3	1.44	0.25	0.08	2.0	47	0.019	45.2
2	C	1.75	0.29	0.11	1.5	59	0.009	50.7
2	IIC	2.06	0.16	0.08	1.5	60	0.010	50.7
2. Campground								
1	A_1	7.57	1.75	0.22	5.0	66	0.167	46.8
1	A_{21}	1.62	0.41	0.12	3.0	41	0.029	43.7
1	A_{22}	1.20	0.41	0.09	3.0	36	0.014	36.9
1	A_2B_2	4.32	1.32	0.14	3.0	66	0.019	15.5
1	B_2	6.71	3.50	0.22	3.0	78	0.023	10.1
1	C_1	5.26	3.38	0.15	0.0	100	0.020	10.5
2	A_1	4.07	1.68	0.51	12.0	34	0.269	50.0
2	A_2	1.87	0.66	0.13	2.5	52	0.024	26.0
2	A_2B_2	4.07	1.57	0.15	2.5	70	0.021	14.0
2	IIA_2B_2	4.40	1.66	0.13	2.5	71	0.019	11.5
2	B_2	5.63	3.80	0.14	3.0	76	0.027	8.2
2	C	4.41	2.56	0.05	0.0	100	0.010	5.0

TABLE 6--Continued

Profile	Horizon	Ca^{++}	Mg^{++}	K^{+}	H^{+}	Percent Base Sat.	Percent N	PPM P
		3. Wilderness						
1	A_{12}	3.03	0.92	0.17	5.3	44	0.097	44.3
1	A_2	0.94	0.33	0.06	2.5	35	0.057	38.4
1	C_1	1.18	0.41	0.08	1.5	53	0.013	42.8
1	IIC	1.06	0.37	0.06	1.5	50	0.011	30.9
2	A_{12}	3.59	1.41	0.26	9.0	37	0.144	37.0
2	A_2	0.88	0.41	0.06	3.0	31	0.029	35.8
2	C_1	0.93	0.45	0.08	5.0	23	0.019	50.0
2	IIC	0.74	0.30	0.05	3.0	27	0.008	43.7
		4. Mary Lake						
1	A_1	7.18	1.16	0.30	6.0	59	0.194	14.6
1	A_2	0.31	0.21	0.13	2.5	21	0.020	57.9
1	AC_1	0.81	0.33	0.08	1.0	52	0.006	13.9
1	C_1	1.18	0.24	0.07	2.0	43	xxxx	11.9
1	IIC	2.17	0.27	0.09	3.0	45	0.010	12.0
1	IIIC	2.00	0.41	0.07	2.0	56	0.006	10.9
2	A_1	11.10	2.67	0.56	4.0	79	0.184	11.1
2	A_{21}	0.95	0.31	0.13	4.0	26	0.040	56.4
2	A_{22}	0.63	0.21	0.08	3.0	23	xxxx	55.9
2	C_1	1.06	trace	0.06	1.5	53	0.006	33.3
2	IIC	3.68	0.78	0.16	2.5	65	0.013	27.3
2	IIIC	0.81	trace	0.04	2.0	42	0.0	7.2

TABLE 6--Continued

Profile	Horizon	Ca^{++}	Mg^{++}	K^{+}	H^{+}	Per-cent Base Sat.	Percent N	PPM P
		5. Scott's						
1	A_{11}	1.18	0.12	0.06	2.2	39	0.054	12.4
1	A_2	1.99	0.45	0.19	2.0	57	0.027	35.9
1	C_1	0.75	trace	0.05	1.5	35	0.010	71.5
1	C_2	0.69	trace	0.03	1.5	32	0.006	62.2
1	C_3	0.50	trace	0.04	1.0	33	0.001	38.5
2	A_{11}	3.06	0.70	0.24	5.5	38	0.109	17.1
2	A_2	1.18	0.16	0.08	3.3	30	0.031	25.5
2	C_1	0.81	trace	0.07	5.3	14	0.010	80.0
2	C_2	0.69	trace	0.06	1.0	43	0.006	63.5
2	C_3	0.69	0.21	0.06	xxx	xx	0.004	70.9
		6. Woodlot						
1	A_2	2.01	0.58	0.12	2.5	51	0.041	20.2
1	C_1	1.44	0.58	0.16	1.5	60	0.013	41.2
1	C_2	0.81	0.16	0.08	1.5	39	0.001	124.9
1	C_3	0.44	trace	0.04	1.0	33	0.002	127.4
2	A_2	2.20	0.66	0.11	2.5	55	0.034	23.1
2	C_1	1.88	0.66	0.09	2.0	57	0.020	38.4
2	C_2	0.81	0.16	0.04	1.5	40	0.021	105.6
2	C_3	0.31	trace	0.01	1.0	24	0.0	50.0
2	C_4	0.37	trace	0.03	xx	xx	0.001	28.9

to a maximum value in the A_2 or C_1 horizon and then decreased with depth. Thus some of the highest values were from the subhorizons of the Menahga profiles. Only in the Beltrami profiles did phosphorus decrease continuously from the A_1 to the C horizon. There appears to be no relationship between stand synecological coordinate and ppm of "available" soil phosphorus in the stands and profiles sampled.

These somewhat negative results may be due to the variation in the chemical state of phosphorus among horizons and soil types. For example, in the acid subhorizons of the Menahga, most phosphorus is probably bound with iron or aluminum, whereas in the Beltrami subhorizons, it is probably present as calcium phosphates. In the surface horizons and humus layer, however, it is probably tied up in organic compounds. Thus it is unreasonable to expect one extraction method to approximated the available phosphorus for a wide range of soil types, horizons and plant species.

The lack of a direct relationship between soil phosphorus and forest soil fertility or productivity has long been known. Valmari (1921), in fact found an inverse relationship between forest productivity and kilograms per hectare of P_2O_5 extracted with 0.2 N HCl. Viro (1952) measured total clay phosphorus as well as extracting with Ca lactate, Na zeolite, acid NH_4F and neutral NH_4F. When a broad range of forest stands were considered, none of these methods gave values which were correlated with fertility of the forest soil. When all measurements above a certain limit were discarded, however, then the lactate-soluble, flouride-soluble and total clay phosphorus values were well correlated with forest soil fertility. Thus he concluded that the fertility of forest soil does depend on the phosphate content.

The lack of a direct relationship between soil phosphorus and synecological coordinates has been reported for Minnesota. Pluth and Arneman (1963) using the dilute acid flouride extracting method, found no significant correlation between plot synecological nutrient coordinate and available phosphorus in the humus, A_1, A_2 or C horizons. They did, however, report a negative correlation with available phosphorus in the B_2 horizon. Bakuzis (1961) also found no clear distribution of available phosphorus in moisture-nutrient coordinates. Thus it is possible that phosphorus is not a limiting factor in forest productivity in the Central Pine Section. Further studies on the phosphorus problem should involve different extraction methods and fertilizer experiments.

c. Exchangeable Bases. Given the broad range of soil types selected for this study, it is not surprising that there appears to be a good relationship between exchangeable bases and stand synecological nutrient coordinate. The concentration of calcium, potassium and magnesium within a given profile, however, appears to be closely related to the percentage of silt plus clay. Between profiles, the degree of profile development is an important controlling factor. For example, the A_2 horizons of the Marquette profiles are much lower in calcium than the A_2 horizons of the Menahga profiles, although the surface layer of the Marquette is higher in calcium.

In the subhorizons of the Campground maple-basswood stand and at least two of the profiles under the red pine stands, the concentration of exchangeable bases increases with depth. This is due in part to soil development and in part to parent material. Thus in the Beltrami, the calcium profile is the result of leaching of the A_2, accumulation in the B_2 horizon and presence of free calcium in the parent material. In the Marquette, particularly at Mary Lake, the increase of calcium with depth reflects the presence of layers of silt and very fine sand with a higher exchange capacity that the coarse sand above.

3. Vegetation Analysis

Table 7 shows the total cubic foot volume by species on each 128 square meter subplot. These data show the relative dominance of different species within each stand. They also illustrate the irrelevance of total volume or biomass as a measure of productivity.

Table 8 shows the basal area and the site index by species within each stand. Red pine site index for the Woodlot stand was measured on trees outside of the plot. The site index reported for red pine in the Campground stand is unreliable, since the three trees measured were probably suppressed during part of their development. For the other stands, however, the site index is based on adequately large samples.

The plot synecological coordinates are given in table 9. These values are based on species presence in the eight square

TABLE 7

TOTAL CUBIC FOOT VOLUME ON 128 m^2 SUBPLOTS

Species	Subplot Number 1	2	3	4	5	6	7	8
				1. Campground				
Acer saccharum	3.0	12.4	9.5	2.1	30.4	1.5	3.8	2.2
Quercus rubra	40.5	23.8	x	23.8	54.0	42.7	x	x
Populus tremuloides	51.4	x	x	80.0	x	x	45.2	4.4
Tilia americana	4.4	x	25.0	20.5	42.6	8.4	4.4	x
Betula papyrifera	7.3					27.0	14.4	11.2
Pinus strobus	284.					160.		
Pinus resinosa								169.
Acer rubrum			9.2			3.2		
Quercus macrocarpa							7.5	
				2. Bearpaw Point				
Tilia americana	135.2	138.6	47.5	46.0	147.7	29.1	127.2	69.9
Betula papyrifera	9.7	22.0			16.3			
Ulmus americana			12.1	13.3	3.0	32.5		18.1

TABLE 7--Continued

Species	Subplot Numbers 1	2	3	4	5	6	7	8
	3. Wilderness							
Pinus resinosa	333	371	438	297	328	269	258	286
Abies balsamea	2.8	5.3	3.8	10.9	1.8	15.8	2.9	10.5
Betula papyrifera	3.2	5.8		1.6	4.5		1.6	
	4. Mary Lake							
Pinus resinosa	67.0		78.0		124.5	106.5	157.5	
Abies balsamea	22.7	28.1	78.9	10.4	12.3	15.8	7.8	32.6
Betula papyrifera	19.2			46.2	18.8	7.0	7.4	4.5
	5. Scott's							
Pinus banksiana	97.4	54.0	110.3	40.0	85.8	125.3	83.3	111.2
Betula papyrifera				16.6				
	6. Woodlot							
Pinus banksiana	64.9	76.4	72.6	74.8	89.1	60.9	65.8	60.8

TABLE 8

BASAL AREA AND SITE INDEX

Stand	Species	Basal Area, sq. ft./acre	Site Index
Woodlot	jack pine	109	49
Scott's	red pine		35[*]
Scott's	jack pine	113	68
Mary Lake	red pine	48	45
Mary Lake	balsam fir	22	
Mary Lake	paper birch	35	
Mary Lake	white pine	2	
Wilderness	red pine	155	53
Wilderness	balsam fir	15	
Wilderness	white pine	2	
Bearpaw Point	basswood	91	
	American elm	17	
	paper birch	7	
	bur oak	4	
Campground	sugar maple	30	
	quaking aspen	10	
	bigtooth aspen	4	
	red oak	19	
	white pine	28	
	red pine	6	51
	paper birch	10	
	hop hornbeam	2	
	basswood	6	

[*] Measured outside of the plot.

TABLE 9

SYNECOLOGICAL COORDINATES, PRESENCE BASIS

Subplot	Moisture	Nutrients	Heat	Light
		1. Bearpaw Point		
1	2.4	3.4	3.2	2.5
2	2.2	3.1	3.1	2.8
3	2.2	2.9	2.9	2.9
4	2.5	3.5	3.2	2.4
5	2.6	3.3	2.8	2.3
6	2.2	3.0	2.9	2.4
7	2.3	3.1	2.9	2.9
8	2.4	3.4	3.1	2.5
		2. Campground		
1	2.2	3.1	2.6	2.2
2	2.3	3.0	2.6	2.2
3	2.3	3.0	2.7	2.5
4	2.1	3.5	2.8	2.1
5	2.0	3.2	3.1	2.4
6	2.1	3.4	3.9	2.3
7	2.6	2.8	2.5	2.5
8	2.2	3.2	2.8	2.2

TABLE 9--*Continued*

Subplot	Moisture	Nutrients	Heat	Light
		3. Wilderness		
1	2.5	2.3	2.2	2.9
2	2.4	2.3	2.1	2.5
3	2.5	2.3	2.2	3.2
4	2.9	2.1	1.9	2.8
5	2.2	2.2	1.8	2.8
6	2.6	2.1	1.9	2.4
7	2.6	2.1	2.0	2.7
8	2.5	2.3	2.0	2.5
		4. Mary Lake		
1	2.4	2.1	1.9	2.6
2	2.3	2.1	2.0	2.8
3	2.0	2.0	2.1	3.1
4	2.1	2.3	2.1	3.5
5	2.3	2.2	2.0	3.3
6	2.5	2.0	2.0	3.5
7	1.9	2.0	2.1	4.0
8	2.0	2.1	1.9	3.6

TABLE 9--Continued

Subplot	Moisture	Nutrients	Heat	Light
		5. Scott's		
1	1.6	2.0	2.5	4.1
2	1.5	1.9	2.2	4.1
3	1.7	1.9	2.2	4.0
4	1.6	2.0	2.2	3.8
5	1.6	1.8	2.1	4.3
6	1.7	1.8	2.2	4.1
7	1.6	1.8	2.2	4.2
8	1.4	1.8	2.2	4.4
		6. Woodlot		
1	1.3	1.6	2.3	4.2
2	1.7	1.8	2.2	4.3
3	1.5	1.7	2.2	4.3
4	1.6	1.9	2.3	4.4
5	1.6	1.9	2.2	4.2
6	1.5	1.7	2.2	4.4
7	1.5	1.9	2.4	4.3
8	1.6	1.8	2.3	4.3

meter plots. Coordinate values for nutrients and light were also computed on a dominance basis for the herb layer. These data are presented in Table 10.

Figure 3 shows the position of each plot in the edaphic field with moisture and nutrients as coordinate axes. The two jack pine stands fall somewhat below the moisture-nutrient coordinates for the jack pine stands sampled by Bakuzis (1961). The red pine stands are roughly centered in the edaphic field with respect to moisture, but the nutrient coordinates are somewhat low. The hardwood stands have roughly the same moisture coordinates as the red pine stands, but the nutrient coordinates are in the upper portion of the edaphic field for Minnesota.

4. Light Measurements

The integrative light measurements showed a high correlation between percent of full sunlight and synecological light coordinates. The results are plotted in Figure 4. On a presence basis the correlation coefficient is +0.86, but on a dominance basis it is only +0.66. A more detailed discussion of the results of the light measurements appears in the appendix.

5. Analysis of Humus Samples

The humus samples collected at each subplot were leached with ammonium acetate and analyzed for exchangeable calcium, magnesium, potassium and hydrogen. The results show that the relationship between these four cations varies from one end of the nutrient

TABLE 10

SYNECOLOGICAL COORDINATES, DOMINANCE BASIS

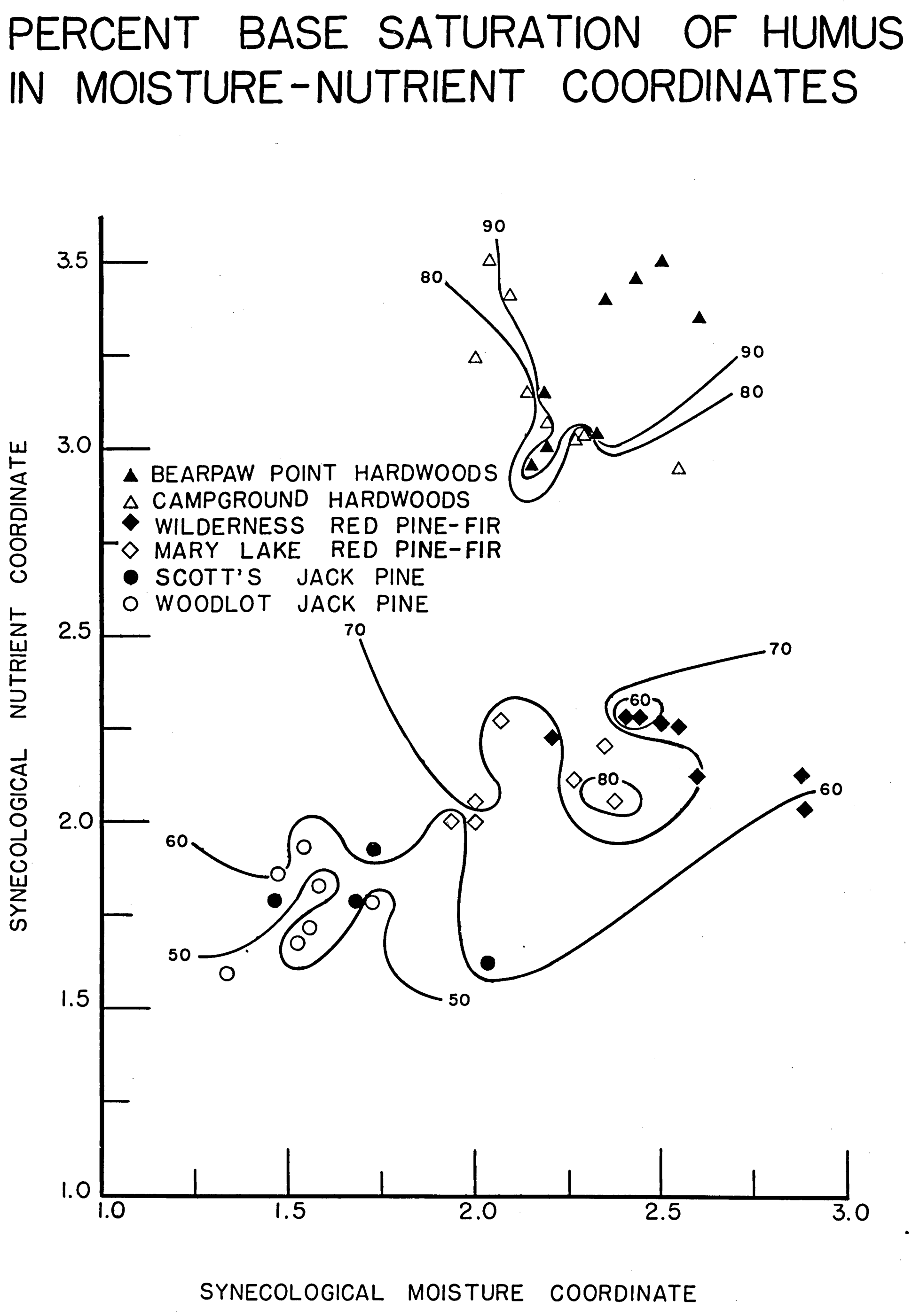
Subplot	Nutrients	Light
	1. Bearpaw Point	
1	3.4	2.5
2	3.2	2.6
3	4.0	2.1
4	4.1	2.1
5	3.9	1.5
6	3.0	2.4
7	3.7	2.0
8	2.9	2.5
	2. Campground	
1	3.6	2.0
2	3.3	2.1
3	4.4	1.5
4	3.5	2.4
5	2.6	3.2
6	4.8	1.2
7	4.3	1.5
8	4.3	1.5

TABLE 10--Continued

Subplot	Nutrients	Light
	3. Wilderness	
1	2.0	3.7
2	2.0	3.1
3	1.9	3.5
4	2.0	3.3
5	1.9	3.4
6	2.0	3.0
7	1.8	2.5
8	2.0	3.0
	4. Mary Lake	
1	2.0	3.0
2	2.2	2.0
3	2.2	3.3
4	2.0	3.2
5	2.0	3.9
6	1.7	3.7
7	2.0	3.4
8	2.0	3.2

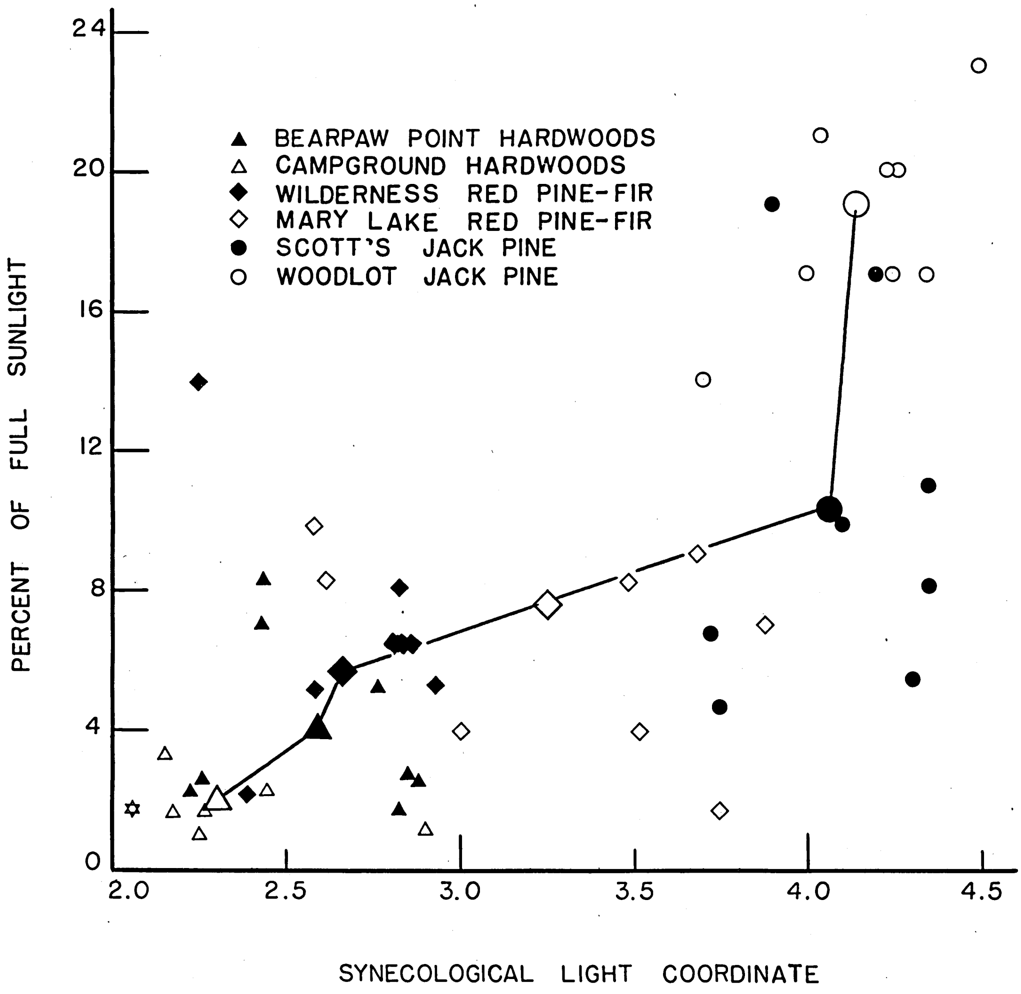
TABLE 10—Continued

Subplot	Nutrients	Light
	5. Scott's	
1	1.9	3.6
2	1.7	4.4
3	1.7	3.4
4	2.0	3.3
5	1.7	4.3
6	1.6	4.0
7	1.2	4.8
8	1.3	4.8
	6. Woodlot	
1	1.5	3.7
2	1.7	3.3
3	1.7	3.5
4	1.9	4.4
5	1.7	4.7
6	2.0	4.1
7	1.8	3.8
8	1.8	3.8



PERCENT BASE SATURATION OF HUMUS IN MOISTURE-NUTRIENT COORDINATES

Figure 3. The distribution of subplots in moisture-nutrient coordinate axes and horizontals showing the percent base saturation of the humus collected at each subplot. Well developed humus was absent from some subplots; the points were omitted from the diagram.



RELATIONSHIP BETWEEN LIGHT INTENSITY AND SYNECOLOGICAL LIGHT COORDINATES IN AN UPLAND FOREST GRADIENT

Figure 4. The relationship between integrated light intensity for one day and synecological light coordinates in six forest stands. Light intensity was measured with ozalid paper. The large symbols connected by the solid line represent stand averages.

gradient to the other.

On the assumption that the exchange capacity can be approximated by the sum of the exchangeable cations, the percent base saturation of each sample was calculated (see Table 11). This value shows a high degree of correlation with plot synecological nutrient coordinate; the linear correlation coefficient obtained was +0.83 on a presence basis and +0.73 on a dominance basis. Both values are highly significant.

Figure 3 shows the percent base saturation as contours in the moisture-nutrient coordinate field. The greatest variation occurs in the red pine-balsam fir stands. This may be due to the heterogeneous ground flora or the influence of scattered birch trees. The Campground maple-basswood stand also shows considerable variation; this appears to be related to the presence of isolated red pine and white pine trees in the stand. In contrast, the jack pine stands show relatively little variation. The humus layer in the Bearpaw Point basswood stand is the least variable and is practically saturated with bases, chiefly calcium.

In order to explore the relationships between these exchangeable cations along the nutrient gradient, triangular coordinates were used. This involves grouping the cations three at a time and mathematically adjusting the values so that the sum of the three cations (e.g. calcium, magnesium and potassium) is equal to 100 percent (see Table 12 for sample computations). In this computation, the average of all points is exactly at the center of the triangle. Thus each sample is expressed in relation to the average of a given cation for all samples, and each of the three

TABLE 11

EXCHANGEABLE CATIONS IN HUMUS, MEQ. PER 100 GRAMS

Subplot	H^{+}	Ca^{++}	K^{+}	Mg^{++}	Percent Base Sat.
		1. Bearpaw Point			
1	1.1	51.4	1.57	14.4	98.4
2	0.6	63.3	1.77	10.6	99.2
3	0.2	51.6	1.43	9.8	99.7
4	1.1	51.6	1.58	12.1	98.3
5	3.0	52.0	1.75	10.9	95.6
6	2.0	61.5	1.12	11.0	97.4
7	0.9	77.9	1.93	13.6	99.0
8	4.4	51.5	2.19	14.2	93.9
		2. Campground			
1	2.6	8.7	0.25	2.3	81.3
2	11.8	20.3	0.98	7.7	71.1
3	6.4	13.9	0.46	4.3	74.5
4	2.6	12.4	0.38	2.6	85.6
5	5.4	11.3	0.55	3.5	74.0
6	1.0	11.8	0.37	3.5	94.0
7	7.8	14.9	0.64	5.2	72.6
8	9.8	16.4	1.04	7.1	71.4

TABLE 11--Continued

Subplot	H^+	Ca^{++}	K^+	Mg^{++}	Percent Base Sat.
		3. Wilderness			
1	15.0	24.5	0.88	6.2	67.8
2	18.2	15.1	1.14	5.1	53.9
3	20.5	19.8	1.42	6.0	57.0
4	14.8	22.2	1.12	4.9	65.6
5	11.8	20.2	0.81	3.6	67.6
6	14.8	26.4	1.02	7.1	70.0
7	16.0	17.8	1.09	4.4	59.3
8	17.7	20.5	0.83	6.1	60.8
		4. Mary Lake			
1	6.0	36.9	1.37	12.6	89.5
2	12.1	36.8	1.04	7.4	78.9
3	15.5	20.7	0.94	4.4	64.1
4	12.1	20.0	1.02	6.1	69.1
5	11.8	26.6	1.20	6.2	74.2
6	xxx	xxx	xxx	xxx	xxx
7	20.5	17.0	1.63	5.1	53.6
8	10.2	25.7	1.02	7.6	77.1

TABLE 11--Continued

Subplot	H^{+}	Ca^{++}	K^{+}	Mg^{++}	Percent Base Sat.
		5. Scott's			
3	10.6	11.9	0.61	4.3	61.3
4	14.0	16.9	0.66	4.1	60.8
6	12.1	10.4	0.51	3.8	54.9
8	11.5	11.1	0.54	3.1	56.1
		6. Woodlot			
1	8.5	5.1	0.28	1.9	46.2
2	11.0	7.4	0.75	2.5	49.3
3	11.0	10.6	0.45	2.7	55.8
4	9.8	8.06	0.46	2.3	52.4
5	9.2	8.7	0.46	3.0	56.2
7	8.6	9.2	0.66	3.0	60.0
8	8.2	5.5	0.43	2.0	49.1

TABLE 12

SAMPLE CALCULATION FOR CENTERING NUTRIENT CONCENTRATIONS IN TRIANGULAR COORDINATES

1. The following values were assumed as original data:

sample number	percent N	percent P	percent K
1	2.28	0.314	1.68
2	1.83	0.237	1.88
3	0.67	0.063	0.27
Column totals:	4.78	0.614	3.83

2. Average values were computed for each of the nutrients.

$$\bar{N} = \frac{4.78}{3} = 1.59$$

$$\bar{P} = \frac{.614}{3} = 0.205$$

$$\bar{K} = \frac{3.83}{3} = 1.28$$

3. The original values were divided by the respective nutrient averages, giving the following values:

sample number	N	P	K	row total
1	1.43	1.53	1.31	4.27
2	1.15	1.16	1.47	3.78
3	0.42	0.31	0.21	0.94

4. Each value was then divided by the total for the row in which it occurred, giving the final adjusted values:

sample number	N	P	K
1	0.335	0.358	0.307
2	0.304	0.307	0.389
3	0.446	0.330	0.223

cations taken is given equal weight. For example, one plot had a K:Mg:Ca ratio of 1:5:15, but the adjusted values for that plot are 45.0 percent for potassium, 31.5 percent for magnesium and 23.5 percent for calcium. The data were adjusted for plotting by an IBM 360 computer.

Table 13 shows the average exchangeable cations for the 42 samples analyzed. Given this population, any sample containing these proportions of cations would fall at the center of the triangular coordinates. For example, a humus sample containing 8.1 meq. of calcium per 100 gm., 2.05 of magnesium and 0.32 of potassium would fall in the center of the Ca-Mg-K coordinates.

The four possible combinations of calcium, magnesium, potassium and hydrogen in forest humus have been plotted in Figure 5. In Figure 5-1, calcium, magnesium and potassium are plotted. The different configurations for the jack pine, red pine-fir and hardwood stands suggests that the ratios of calcium to potassium and magnesium to potassium are higher for the hardwood stands than for the pine stands.

This trend is illustrated in greater detail by the other three combinations. Given the high correlation between synecological nutrient coordinates and percent base saturation, it is natural that the points are well spread out along the H^+ axis in these three diagrams. In the H-Ca-Mg coordinates (Figure 5-2) there is only a slight and inconclusive slant toward calcium with respect to the H-axis. In the H-K-Mg coordinates (Figure 5-3), however, the distribution is slanted toward the potassium side of the H-axis at the low end of the nutrient gradient and toward

TABLE 13

AVERAGE VALUES FOR NUTRIENTS PLOTTED IN TRIANGULAR COORDINATES

1. Humus Samples

Element	Average for 42 plots, meq. per 100 gm.
calcium	24.40
magnesium	6.14
potassium	0.961
hydrogen	9.33

2. Foliar Samples

Nutrient	Average for 94 samples, percent ovendry weight
nitrogen	2.01
phosphorus	0.312
potassium	2.45
calcium	1.23
magnesium	0.340

EXCHANGEABLE HUMUS CATIONS IN TRIANGULAR COORDINATES

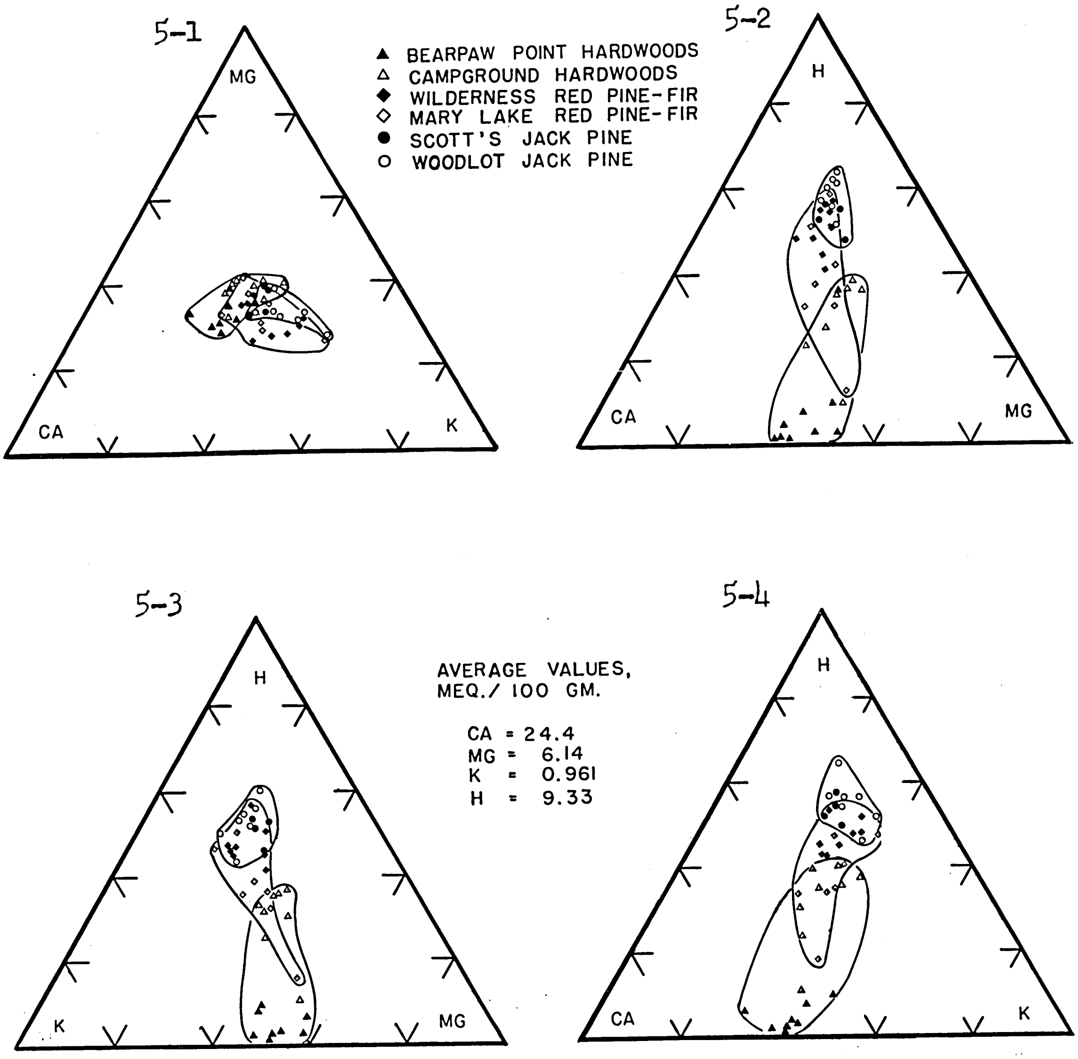


Figure 5. The relationship between exchangeable humus cations from six forest stands. The data were transformed prior to plotting so that the average of all points in each set of coordinates falls at the center of the graph. Lines have been drawn around the points from each forest type. The configurations indicate that the K: Ca plus Mg ratio decreases toward the upper end of the nutrient gradient.

the magnesium side at the upper end. In the H-K-Ca coordinates (Figure 5-4) the pattern is clearest. The Bearpaw Point plots fall almost entirely on the calcium side of the H-axis and the Woodlot plots are entirely on the potassium side.

This relationship is further illustrated in Figure 6, which shows the distribution of synecological nutrient coordinates in K-Ca-Mg coordinates. The high coordinate values are associated with low relative potassium values. Thus it appears that the proportions of calcium and magnesium in the humus exchange complex increase relative to potassium from the lower end of the gradient, dominated by jack pine, to the upper end of the gradient, dominated by northern hardwoods.

In order to evaluate the relationship between the relative and absolute values for exchangeable cations, simple correlations were run between the absolute values, relative values and synecological nutrient coordinates (presence basis). Tables 14 and 15 show the simple correlation coefficients obtained. A comparison of these data further supports the previous conclusions. For example, the correlation coefficient between nutrient coordinates and exchangeable hydrogen is -0.69, whereas for calcium, magnesium and potassium it is respectively +0.54, +0.55 and +0.32 (Table 14). This implies that the sum of the exchangeable bases is more important than any one alone, but calcium and magnesium are both more closely related to the defined gradient than is potassium.

This relationship is shown more strongly by a comparison of the correlation coefficients between nutrient coordinates and

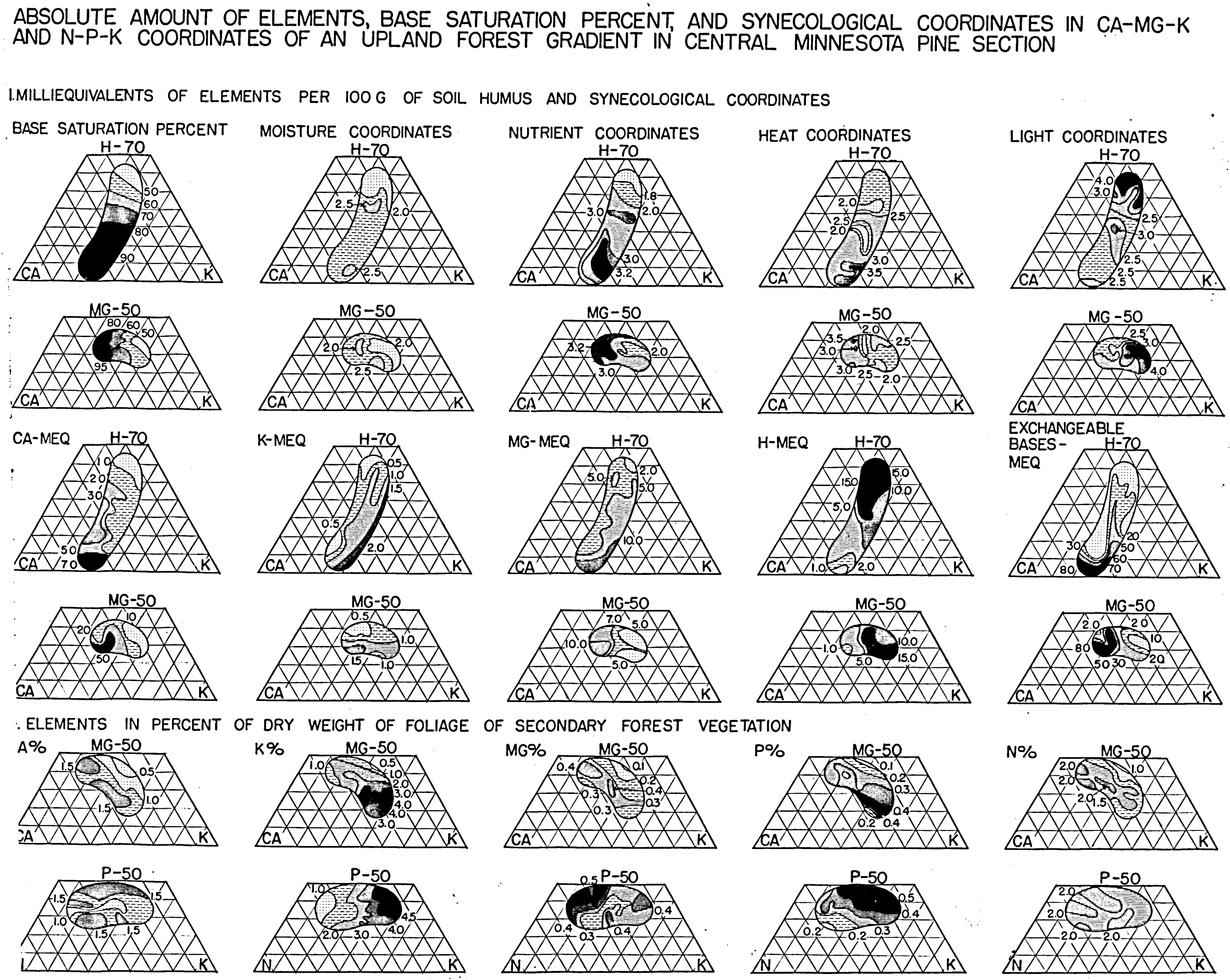


Figure 6. The relationship between relative and absolute humus cation concentrations in Ca-Mg-K and Ca-H-K coordinates and the relationship between humus cations and synecological coordinates. Foliar nutrient concentrations are shown in Ca-Mg-K and N-P-K coordinates.

TABLE 14

ECOSYSTEM CORRELATION COEFFICIENTS

	Ca	K	Mg	H	pH	Base Sat. Percent	Synecological Coordinates Moisture	Nutrient	Heat	Light
Ca		.7029**	.9074**	.5040**	.8291**	.8113**	.4785**	.5362**	.4449**	-.4092**
K			.7758**	-.0912	.4380**	.5076**	.5642**	.3281*	.1942	-.3421*
Mg				-.4043**	.7450**	.7689**	.5488**	.5511**	.4313**	-.4878**
H					-.8207**	-.7695**	.0081	-.6888**	-.7292**	.3272*
pH						.9447**	.3181*	.7519**	.6859**	-.5272**
Base saturation percent							.4963**	.8260**	.6659**	-.6884**
Moisture coordinate								.4946**	.1548	-.8174**
Nutrient coordinate									.7333**	-.7853**
Heat coordinate										-.4092**
Light coordinate										

*Significant at the 5 percent level

**Significant at the 1 percent level

TABLE 15

RELATIONSHIP BETWEEN RELATIVE AND ABSOLUTE VALUES IN CA-K-MG AND CA-K-H COORDINATES

Relative Values, Ca-K-Mg Coordinates

Absolute Value	Ca	K	Mg
Ca	+0.719**	-0.517**	-0.170
K	+0.245	-0.075	-0.223
Mg		+0.084	+0.551*
Nutrient Coordinate	+0.503**	-0.584**	+0.237

Relative Values, Ca-K-H Coordinates

Absolute Value	Ca	K	H
Ca	+0.845**	+0.608**	-0.847**
K	+0.454**	+0.672**	-0.570**
H	-0.787**	-0.507**	+0.769**
Nutrient Coordinate	+0.763**	+0.685**	-0.810**

*Significant at the 5 percent level

**Significant at the 1 percent level

relative cation values (Table 15). In the Ca-K-Mg coordinates, for example, the correlation coefficient with synecological nutrient coordinates is +0.50 for calcium, +0.24 for magnesium and -0.58 for potassium.

The correlation coefficient between the relative and absolute value for a given element indicates the degree to which the absolute value is changed by the transformation. With a high positive correlation between three variables, there must be a negative correlation between the relative and absolute value for at least one element. Intuitively, it appears that the element with the highest variance in concentration will be best correlated with the corresponding adjusted value, whereas the least variable element will be the least correlated. In the Ca-K-Mg coordinates, the correlation coefficients between relative and absolute values decrease in the order Ca > Mg > K; the variances of these cations decreases in the same order. If at least one element is inversely related to the other two, however, (as with the Ca-K-H coordinates) then there may be a high correlation between the relative and absolute value for all three elements.

Figure 6 shows the absolute values of calcium, potassium, magnesium and hydrogen in Ca-K-Mg and Ca-K-H coordinates. These illustrations show graphically that the effect of the transformation on a single variable is determined by the variance of each element and the degree of correlation between them. If this triangular transformation is used in the future, then the effect of unequal variances and correlation between elements should be solved rigorously.

Duchaufour (1961) suggested that the ecological group on a given site is closely related to the humus type, and that ecological groups should be defined together with humus types. Because of the key position occupied by the humus layer in the nutrient cycle of a forest, a detailed study of the chemical and biological properties of the humus should be part of any future study on the characteristics of an ecological nutrient gradient.

6. Foliar Analysis

The elements in the foliage samples that were analyzed by the emission spectrograph are phosphorus, potassium, calcium, strontium, sodium, iron, magnesium, zink, copper, molybdenum, manganese and boron. The levels of sodium and molybdenum, however, were too low to be measured accurately. Also, the iron values may represent contamination from the Wiley mill or muffle furnace liner. The original data are reported in Tables 16 and 17. The stand numbers in Tables 16 and 17 refer to the stands in the following order: 1) Woodlot jack pine, 2) Scott's jack pine, 3) Mary Lake red pine-balsam fir, 4) Wilderness red pine-balsam fir, 5) Campground hardwoods and 6) Bearpaw Point hardwoods.

A comparison of these data with previously reported concentrations shows a general consistency within species. For example, Gerloff (1964) reported very high potassium concentrations for Clintonia borealis and Aster macrophyllus and low potassium concentrations for Corylus cornuta and Ostrya virginiana (see Table 18). These findings are consistent with the data

TABLE 16-1

PERCENT FOLIAR CONCENTRATION OF NITROGEN, DRY WEIGHT BASIS

Code No.	Species	Stand Number					
		1	2	3	4	5	6
01	Lithospermum canescens	1.61					
02	Fragaria virginiana	2.28	2.21	2.37			
03	Pteridium aquilinum	1.83	1.92	1.93			
04	Cladonia sp.	0.67	0.74				
05	Epigaea repens	1.47	1.49				
06	Maianthemum canadense	1.73	1.69	1.86	2.01	1.97	1.93
07	Gaultheria procumbens	1.27	1.31				
08	Aster macrophyllus	1.66	1.91	1.83	2.23	1.87	1.93
09	Aralia nudicaulis	1.17	1.88	2.07	2.43	1.69	1.88
10	Arctostaphylos Uva-ursi	1.29	1.41				
11	Pyrola elliptica	1.60	1.66				
12	Pleurozium schreberii	1.17	1.17				
13	Apocynum androsaemifolium	2.31					
14	Corylus cornuta		2.33	2.30	2.56	2.14	2.28
15	Hepatica americana		1.81	1.84	1.94	1.86	
16	Diervilla lonicera		2.03				
17	Thalictrum dioicum			2.46		2.17	2.53
18	Cornus canadensis			1.73	1.69		
19	Clintonia borealis			2.04	2.16	1.91	
20	Parthenocissus inserta				3.51		2.87
21	Lonicera canadensis				1.88		
22	Uvularia grandiflora					2.07	2.38
23	Dirca palustris					2.38	2.38
24	Acer saccharum					1.86	
25	Ostrya virginiana					2.21	
26	Amphicarpa bracteata						4.27
27	Caulophyllum thalictroides						2.41
28	Celastrus scandens						3.21
29	Actaea rubra						2.70
30	Smilacina racemosa						2.24
31	Sanguinaria canadensis						1.81
32	Asarum canadense						1.03

TABLE 16-2

PERCENT FOLIAR CONCENTRATION OF PHOSPHORUS, DRY WT. BASIS

Code No.	Species	Stand Number 1	2	3	4	5	6
01	Lithospermum canescens	0.167					
02	Fragaria virginiana	0.314	0.316	0.376			
03	Pteridium aquilinum	0.237	0.303	0.248			
04	Cladonia sp.	0.063	0.080				
05	Epigaea repens	0.132	0.166				
06	Maianthemum canadense	0.264	0.314	0.332	0.309	0.296	0.410
07	Gaultheria procumbens	0.133	0.137				
08	Aster macrophyllus	0.300	0.312	0.347	0.267	0.329	0.393
09	Aralia nudicaulis	0.269	0.319	0.454	0.380	0.386	0.369
10	Arctostaphylos Uva-ursi	0.155	0.174				
11	Pyrola elliptica	0.192	0.178				
12	Pleurozium schreberii	0.162	0.209				
13	Apocynum androsaemifolium	0.304					
14	Corylus cornuta		0.300	0.384	0.289	0.282	0.309
15	Hepatica americana		0.241	0.255	0.204	0.239	
16	Diervilla lonicera		0.454				
17	Thalictrum dioicum			0.280		0.257	0.327
18	Cornus canadensis			0.367	0.234		
19	Clintonia borealis			0.445	0.393	0.500	
20	Parthenocissus inserta				0.318		0.369
21	Lonicera canadensis				0.235		
22	Uvularia grandiflora					0.291	0.338
23	Dirca palustris					0.438	0.517
24	Acer saccharum					0.280	
25	Ostrya virginiana					0.241	
26	Amphicarpa bracteata						0.278
27	Caulophyllum thalictroides						0.517
28	Celastrus scandens						0.632
29	Actaea rubra						0.582
30	Smilacina racemosa						0.445
31	Sanguinaria canadensis						0.526
32	Asarum canadense						0.530

TABLE 16-3

PERCENT FOLIAR CONCENTRATION OF POTASSIUM, DRY WT. BASIS

Code No.	Species	Stand Number 1	2	3	4	5	6
01	Lithospermum canescens	3.01					
02	Fragaria virginiana	1.68	1.59	1.96			
03	Pteridium aquilinum	1.88	2.27	2.37			
04	Cladonia sp.	0.27	0.31				
05	Epigaea repens	0.66	1.03				
06	Maianthemum canadense	3.27	2.70	3.36	3.19	2.79	1.94
07	Gaultheria procumbens	0.79	0.73				
08	Aster macrophyllus	3.61	3.94	4.59	3.54	4.37	3.96
09	Aralia nudicaulis	1.38	1.76	2.36	2.08	2.79	2.94
10	Arctostaphylos Uva-ursi	0.77	1.01				
11	Pyrola elliptica	1.08	0.86				
12	Pleurozium schreberii	0.87	1.18				
13	Apocynum androsaemifolium	1.85					
14	Corylus cornuta		0.84	1.30	1.14	1.11	1.04
15	Hepatica americana		2.90	3.03	2.31	2.76	
16	Diervilla lonicera		2.86				
17	Thalictrum dioicum			2.97		3.21	3.56
18	Cornus canadensis			1.78	1.33		
19	Clintonia borealis			4.53	4.55	4.83	
20	Parthenocissus inserta				1.83		1.94
21	Lonicera canadensis				1.66		
22	Uvularia grandiflora					2.91	3.08
23	Dirca palustris					2.10	1.88
24	Acer saccharum					0.85	
25	Ostrya virginiana					0.77	
26	Amphicarpa bracteata						2.17
27	Caulophyllum thalictroides						3.21
28	Celastrus scandens						3.46
29	Actaea rubra						4.17
30	Smilacina racemosa						3.52
31	Sanguinaria canadensis						4.72
32	Asarum canadense						4.47

TABLE 16-4

PERCENT FOLIAR CONCENTRATION OF MAGNESIUM, DRY WT. BASIS

Code No.	Species	Stand Number 1	2	3	4	5	6
01	Lithospermum canescens	0.226					
02	Fragaria virginiana	0.458	0.439	0.570			
03	Pteridium aquilinum	0.240	0.226	0.282			
04	Cladonia sp.	0.045	0.053				
05	Epigaea repens	0.228	0.270				
06	Maianthemum canadense	0.227	0.258	0.311	0.297	0.319	0.278
07	Gaultheria procumbens	0.290	0.314				
08	Aster macrophyllus	0.185	0.331	0.365	0.361	0.381	0.303
09	Aralia nudicaulis	0.272	0.283	0.377	0.394	0.352	0.329
10	Arctostaphylos Uva-ursi	0.193	0.210				
11	Pyrola elliptica	0.253	0.237				
12	Pleurozium schreberii	0.140	0.154				
13	Apocynum androsaemifolium	0.339					
14	Corylus cornuta		0.354	0.384	0.400	0.398	0.377
15	Hepatica americana		0.439	0.362	0.372	0.378	
16	Diervilla lonicera		0.398				
17	Thalictrum dioicum			0.430		0.427	0.365
18	Cornus canadensis			0.584	0.563		
19	Clintonia borealis			0.384	0.423	0.441	
20	Parthenocissus inserta				0.443		0.394
21	Lonicera canadensis				0.435		
22	Uvularia grandiflora					0.436	0.407
23	Dirca palustris					0.623	0.533
24	Acer saccharum					0.239	
25	Ostrya virginiana					0.384	
26	Amphicarpa bracteata						0.452
27	Caulophyllum thalictroides						0.235
28	Celastrus scandens						0.391
29	Actaea rubra						0.300
30	Smilacina racemosa						0.322
31	Sanguinaria canadensis						0.234
32	Asarum canadense						0.467

TABLE 16-5

P.P.M. FOLIAR CONCENTRATION OF MANGANESE, DRY WT. BASIS

Code No.	Species	Stand Number 1	2	3	4	5	6
01	Lithospermum canescens	100					
02	Fragaria virginiana	264	227	268			
03	Pteridium aquilinum	146	232	241			
04	Cladonia sp.	49	46				
05	Epigaea repens	334	342				
06	Maianthemum canadense	167	138	168	177	116	39
07	Gaultheria procumbens	231	237				
08	Aster macrophyllus	177	170	171	158	124	66
09	Aralia nudicaulis	450	389	373	412	233	117
10	Arctostaphylos Uva-ursi	28	34				
11	Pyrola elliptica	65	50				
12	Pleurozium schreberii	172	146				
13	Apocynum androsaemifolium	104					
14	Corylus cornuta		360		364	262	141
15	Hepatica americana		101	112	143	98	
16	Diervilla lonicera		124				
17	Thalictrum dioicum			98		66	48
18	Cornus canadensis			110	90		
19	Clintonia borealis			258	307		
20	Parthenocissus inserta				246		121
21	Lonicera canadensis				223		
22	Uvularia grandiflora					79	53
23	Dirca palustris					179	130
24	Acer saccharum					215	
25	Ostrya virginiana					272	
26	Amphicarpa bracteata						120
27	Caulophyllum thalictroides						93
28	Celastrus scandens						68
29	Actaea rubra						50
30	Smilacina racemosa						54
31	Sanguinaria canadensis						48
32	Asarum canadense						76

TABLE 16-6

PERCENT FOLIAR CONCENTRATION OF CALCIUM, DRY WT. BASIS

Code No.	Species	Stand Number 1	2	3	4	5	6
01	Lithospermum canescens	1.38					
02	Fragaria virginiana	1.53	1.26	1.63			
03	Pteridium aquilinum	0.48	0.56	0.60			
04	Cladonia sp.	0.08	0.08				
05	Epigaea repens	0.53	0.64				
06	Maianthemum canadense	0.77	0.91	1.20	1.13	1.15	1.05
07	Gaultheria procumbens	1.11	1.18				
08	Aster macrophyllus	1.39	1.38	1.46	1.35	1.49	1.30
09	Aralia nudicaulis	1.18	1.01	1.56	1.16	1.15	1.33
10	Arctostaphylos Uva-ursi	0.68	0.79				
11	Pyrola elliptica	1.02	1.02				
12	Pleurozium schreberii	0.38	0.37				
13	Apocynum androsaemifolium	1.06					
14	Corylus cornuta		1.35	1.56	1.41	1.56	1.64
15	Hepatica americana		1.27	1.36	1.24	1.31	
16	Diervilla lonicera		1.19				
17	Thalictrum dioicum			1.55		1.59	1.56
18	Cornus canadensis			2.20	2.02		
19	Clintonia borealis			1.43	1.41	1.40	
20	Parthenocissus inserta				1.72		1.76
21	Lonicera canadensis				1.75		
22	Uvularia grandiflora					1.27	1.28
23	Dirca palustris					2.22	1.89
24	Acer saccharum					1.27	
25	Ostrya virginiana					1.61	
26	Amphicarpa bracteata						1.61
27	Caulophyllum thalictroides						1.20
28	Celastrus scandens						1.83
29	Actaea rubra						1.80
30	Smilacina racemosa						1.36
31	Sanguinaria canadensis						1.29
32	Asarum canadense						1.23

TABLE 16-7

P.P.M. FOLIAR CONCENTRATION OF STRONTIUM, DRY WT. BASIS

Code No.	Species	Stand Number 1	2	3	4	5	6
01	Lithospermum canescens	47.4					
02	Fragaria virginiana	55.0	37.2	48.9			
03	Pteridium aquilinum	29.9	44.5	41.9			
04	Cladonia sp.	1.8	1.5				
05	Epigaea repens	11.0	8.5				
06	Maianthemum canadense	26.4	21.0	29.4	17.7	27.4	16.3
07	Gaultheria procumbens	15.8	14.2				
08	Aster macrophyllus	49.0	33.5	36.5	27.5	33.9	18.3
09	Aralia nudicaulis	44.2	21.6	43.7	18.7	26.6	22.1
10	Arctostaphylos Uva-ursi	30.9	20.1				
11	Pyrola elliptica	38.0	23.7				
12	Pleurozium schreberii	10.2	6.2				
13	Apocynum androsaemifolium	65.0					
14	Corylus cornuta		34.4	41.6	28.1	40.2	28.2
15	Hepatica americana		39.9	45.3	37.8	43.2	
16	Diervilla lonicera		36.1				
17	Thalictrum dioicum			32.0		32.1	21.1
18	Cornus canadensis			60.0	59.5		
19	Clintonia borealis			44.0	26.9	31.3	
20	Parthenocissus inserta				36.8		33.4
21	Lonicera canadensis				37.6		
22	Uvularia grandiflora					29.5	20.4
23	Dirca palustris					53.0	32.9
24	Acer saccharum					31.0	
25	Ostrya virginiana					41.6	
26	Amphicarpa bracteata						24.7
27	Caulophyllum thalictroides						16.0
28	Celastrus scandens						35.6
29	Actaea rubra						32.2
30	Smilacina racemosa						24.5
31	Sanguinaria canadensis						22.5
32	Asarum canadense						47.7

TABLE 16-8

P.P.M. FOLIAR CONCENTRATION OF ZINC, DRY WEIGHT BASIS

Code No.	Species	Stand Number 1	2	3	4	5	6
01	Lithospermum canescens	39.5					
02	Fragaria virginiana	48.7	40.1	35.6			
03	Pteridium aquilinum	31.8	35.5	30.1			
04	Cladonia sp.	43.2	42.9				
05	Epigaea repens	37.2	39.2				
06	Maianthemum canadense	47.3	37.8	32.1	62.9	41.6	55.3
07	Gaultheria procumbens	30.7	29.1				
08	Aster macrophyllus	84.9	64.5	57.2	72.3	69.5	69.5
09	Aralia nudicaulis	82.5	70.3	60.9	80.0	63.3	68.0
10	Arctostaphylos Uva-ursi	70.7	86.9				
11	Pyrola elliptica	49.6	36.9				
12	Pleurozium schreberii	68.6	71.4				
13	Apocynum androsaemifolium	33.8					
14	Corylus cornuta		30.5	31.5	34.7	33.6	31.5
15	Hepatica americana		48.5	38.2	52.2	51.0	
16	Diervilla Lonicera		109.6				
17	Thalictrum dioicum			44.2		50.5	50.8
18	Cornus canadensis			29.6	46.1		
19	Clintonia borealis			21.7	32.3	44.1	
20	Parthenocissus inserta				26.2		33.0
21	Lonicera canadensis				64.8		
22	Uvularia grandiflora					56.6	40.3
23	Dirca palustris					63.9	39.6
24	Acer saccharum					41.3	
25	Ostrya virginiana					25.8	
26	Amphicarpa bracteata						43.0
27	Caulophyllum thalictroides						35.2
28	Celastrus scandens						39.3
29	Actaea rubra						33.6
30	Smilacina racemosa						22.0
31	Sanguinaria canadensis						40.0
32	Asarum canadense						107.8

TABLE 16-9

P.P.M. FOLIAR CONCENTRATION OF COPPER, DRY WT. BASIS

Code No.	Species	Stand Number 1	2	3	4	5	6
01	Lithospermum canescens	8.50					
02	Fragaria virginiana	8.20	5.67	6.86			
03	Pteridium aquilinum	5.56	5.18	5.45			
04	Cladonia sp.	3.60	3.71				
05	Epigaea repens	6.00	7.18				
06	Maianthemum canadense	4.97	4.69	4.75	5.62	4.58	4.86
07	Gaultheria procumbens	5.07	4.75				
08	Aster macrophyllus	8.63	6.86	8.15	7.51	6.81	7.13
09	Aralia nudicaulis	5.73	5.56	7.24	6.48	5.40	5.24
10	Arctostaphylos Uva-ursi	5.56	6.10				
11	Pyrola elliptica	6.64	5.51				
12	Pleurozium schreberii	6.05	6.54				
13	Apocynum androsaemifolium	7.34					
14	Corylus cornuta		6.10	7.40	7.61	5.83	5.89
15	Hepatica americana		6.75	7.45	7.29	6.00	
16	Diervilla lonicera		6.00				
17	Thalictrum dioicum			6.64		5.78	6.54
18	Cornus canadensis			4.15	3.87		
19	Clintonia borealis			5.67	5.56	5.07	
20	Parthenocissus inserta				8.09		9.27
21	Lonicera canadensis				5.89		
22	Uvularia grandiflora					6.16	6.48
23	Dirca palustris					6.48	5.56
24	Acer saccharum					4.91	
25	Ostrya virginiana					6.05	
26	Amphicarpa bracteata						6.05
27	Caulophyllum thalictroides						6.10
28	Celastrus scandens						7.29
29	Actaea rubra						7.51
30	Smilacina racemosa						5.18
31	Sanguinaria canadensis						5.40
32	Asarum canadense						5.35

TABLE 16-10

PPM FOLIAR CONCENTRATION OF BORON, DRY WEIGHT BASIS

Code No.	Species	Stand Number 1	2	3	4	5	6
01	Lithospermum canescens	31.3					
02	Fragaria virginiana	24.0	21.5	27.6			
03	Pteridium aquilinum	10.6	15.8	13.8			
04	Cladonia sp.	12.5	3.0				
05	Epigaea repens	18.4	22.7				
06	Maianthemum canadense	12.1	14.7	16.3	16.3	15.7	17.6
07	Gaultheria procumbens	17.5	12.4				
08	Aster macrophyllus	31.1	33.8	45.9	41.8	41.3	42.7
09	Aralia nudicaulis	24.3	20.6	25.2	18.5	19.2	19.4
10	Arctostaphylos Uva-ursi	15.5	15.6				
11	Pyrola elliptica	16.0	9.6				
12	Pleurozium schreberii	31.5	5.3				
13	Apocynum androsaemifolium	12.9					
14	Corylus cornuta		33.9	40.7	41.8	27.6	48.0
15	Hepatica americana		21.4	22.0	22.5	20.8	
16	Diervilla lonicera		30.8				
17	Thalictrum dioicum			27.7		20.4	25.9
18	Cornus canadensis			38.0	25.6		
19	Clintonia borealis			13.6	14.2	14.7	
20	Parthenocissus inserta				19.1		22.9
21	Lonicera canadensis				32.3		
22	Uvularia grandiflora					12.4	16.8
23	Dirca palustris					33.4	30.1
24	Acer saccharum					27.0	
25	Ostrya virginiana					16.0	
26	Amphicarpa bracteata						34.4
27	Caulophyllum thalictroides						23.8
28	Celastrus scandens						27.5
29	Actaea rubra						24.0
30	Smilacina racemosa						20.2
31	Sanguinaria canadensis						38.0
32	Asarum canadense						18.2

TABLE 17-1

FOLIAR CONCENTRATION OF MACROELEMENTS FROM JULY SAMPLING

		Stand Number					
No.	Species	1	2	3	4	5	6
		Percent Nitrogen					
06	Maianthemum canadense	1.84	1.96	1.94	1.81	1.98	
08	Aster macrophyllus	1.86	1.86	2.00	2.01	1.97	1.93
09	Aralia nudicaulis		2.01	1.96	2.31	1.77	1.71
14	Corylus cornuta		2.56	2.54	2.74	2.33	2.58
		Percent Phosphorus					
06	Maianthemum canadense	0.345	0.336	0.332	0.276	0.370	
08	Aster macrophyllus	0.280	0.312	0.266	0.300	0.369	0.358
09	Aralia nudicaulis		0.300	0.340	0.307	0.323	0.307
14	Corylus cornuta		0.285	0.273	0.300	0.309	0.312
		Percent Potassium					
06	Maianthemum canadense	2.41	3.16	3.61	3.06	3.50	
08	Aster macrophyllus	4.01	4.70	3.62	4.16	4.60	4.27
09	Aralia nudicaulis		1.86	2.17	1.86	2.61	2.21
14	Corylus cornuta		0.97	1.02	1.61	1.24	1.33
		Percent Calcium					
06	Maianthemum canadense	0.79	0.78	0.94	0.82	1.13	
08	Aster macrophyllus	1.18	1.20	1.16	1.23	1.36	1.26
09	Aralia nudicaulis		0.85	0.82	0.80	0.83	0.85
14	Corylus cornuta		1.26	1.30	1.31	1.69	1.58
		Percent Magnesium					
06	Maianthemum canadense	0.280	0.285	0.296	0.246	0.328	
08	Aster macrophyllus	0.266	0.329	0.377	0.330	0.399	0.345
09	Aralia nudicaulis		0.305	0.257	0.333	0.310	0.306
14	Corylus cornuta		0.430	0.411	0.395	0.497	0.421

TABLE 17-2

FOLIAR CONCENTRATION OF MICROELEMENTS FROM JULY SAMPLING

No.	Species	Stand Number 1	2	3	4	5	6
		Parts Per Million Manganese					
06	Maianthemum canadense	161	117	134	126	102	
08	Aster macrophyllus	130	115	105	142	105	59
09	Aralia nudicaulis		272	219	260	170	107
14	Corylus cornuta		392	393	357	360	181
		Parts Per Million Strontium					
06	Maianthemum canadense	31.4	17.4	23.3	15.7	25.3	
08	Aster macrophyllus	43.7	30.3	24.3	31.6	30.4	20.5
09	Aralia nudicaulis		15.8	18.6	14.8	17.0	14.4
14	Corylus cornuta		31.5	31.9	28.7	45.1	34.8
		Parts Per Million Zinc					
06	Maianthemum canadense	56.5	37.8	38.3	47.0	47.5	
08	Aster macrophyllus	57.5	55.0	50.2	72.7	72.6	69.4
09	Aralia nudicaulis		48.7	42.6	47.8	41.0	42.4
14	Corylus cornuta		32.5	29.6	38.9	34.9	31.5
		Parts Per Million Copper					
06	Maianthemum canadense	5.29	4.80	5.29	4.69	5.45	
08	Aster macrophyllus	7.08	6.81	7.88	6.21	6.75	6.43
09	Aralia nudicaulis		6.48	5.67	6.16	5.83	5.18
14	Corylus cornuta		6.98	6.91	8.42	7.18	7.99
		Parts Per Million Boron					
06	Maianthemum canadense	12.5	14.6	13.4	13.7	16.2	
08	Aster macrophyllus	43.2	32.1	31.4	34.8	40.6	42.9
09	Aralia nudicaulis		20.2	18.0	17.4	16.7	17.3
14	Corylus cornuta		34.9	32.9	36.0	34.7	45.9

TABLE 18

COMPARISON OF NUTRIENT CONCENTRATIONS IN FOLIAGE WITH PREVIOUSLY REPORTED DATA

Species	Source[1]	N	P	K	Ca	Mg
Acer saccharum	S	0.44	0.14	0.52	1.66	
"	G	0.73	0.12	0.39	1.01	0.45
"	C	1.86	0.28	0.85	1.27	0.24
Apocynum androsaemifolium	G	1.45	0.28	2.12	0.81	0.27
"	G	1.35	0.33	2.43	0.78	0.18
"	C	2.31	0.34	1.85	1.06	0.34
Aralia nudicaulis	G	1.66	0.29	2.53	0.83	0.33
"	G	2.06	0.29	1.51	0.94	0.43
"	G	1.97	0.32	2.07	1.13	0.26
"	S	0.56	0.22	0.79	1.83	
"	C	1.71	0.27	1.38	1.18	0.27
"	C	1.88	0.32	1.76	1.01	0.28
"	C	2.07	0.45	2.36	1.56	0.38
"	C	2.43	0.38	2.08	1.16	0.39
"	C	1.69	0.39	2.79	1.15	0.35
"	C	1.88	0.37	2.94	1.33	0.33
Caulophyllum thalictroides	G	1.83	0.31	2.09	0.82	0.30
"	C	2.41	0.52	3.21	1.20	0.24
Diervilla lonicera	G	1.31	0.23	2.18	0.73	0.26
"	C	2.03	0.45	2.86	1.19	0.40

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[1] "G" indicates Gerloff, 1964; "S" indicates Scott, 1955; "C" indicates the present study.

TABLE 18--Continued

Species	Source	N	P	K	Ca	Mg
Cornus canadensis	G	1.52	0.25	1.14	0.85[1]	0.68
"	C	1.73	0.37	1.78	2.20	0.58
"	C	1.69	0.23	1.33	2.02	0.56
Epigaea repens	C	1.47	0.13	0.66	0.53	0.23
"	C	1.49	0.17	1.03	0.64	0.27
"	G	1.02	0.10	0.52	0.44	0.27
Gaultheria procumbens	G	0.87	0.09	0.46	0.96	0.46
"	C	1.27	0.13	0.79	1.11	0.29
"	C	1.31	0.14	0.73	1.18	0.31
"	S	1.38	0.12	1.23	1.06	
Clintonia borealis	G	1.76	0.31	5.54	1.19	0.28
"	C	2.04	0.45	4.53	1.43	0.38
"	C	2.16	0.39	4.55	1.41	0.42
"	C	1.91	0.50	4.83	1.40	0.44
Smilacina racemosa	G	1.82	0.33	3.57	1.32	0.22
"	C	2.24	0.45	3.52	1.36	0.32
"	S	1.91	0.17	3.73	1.82	
Uvularia grandiflora	G	1.87	0.28	3.09	1.11	0.24
"	C	2.07	0.29	2.91	1.27	0.44
"	C	2.38	0.34	3.08	1.28	0.41

---

[1] This value appears disproportionately low.

TABLE 18--Continued

Species	Source	N	P	K	Ca	Mg
Sanguinaria canadensis	G	1.49	0.33	5.73	1.77	0.12
"	S	1.96	0.18	2.70	2.45	
"	C	1.81	0.53	4.72	1.29	0.23
Pteridium aquilinum	G	2.00	0.25	1.76	0.26	0.22
"	G	1.56	0.24	2.50	0.42	0.28
"	G	1.78	0.25	2.68	0.26	0.17
"	C	1.83	0.31	1.88	0.48	0.24
"	C	1.92	0.32	2.27	0.56	0.23
"	C	1.93	0.38	2.37	0.60	0.28
Hepatica americana	G	1.71	0.25	3.36	1.15	0.33
"	C	1.81	0.24	2.90	1.27	0.44
"	C	1.84	0.26	3.03	1.36	0.36
"	C	1.94	0.20	2.31	1.24	0.37
"	C	1.86	0.24	2.76	1.31	0.38
Fragaria virginiana	G	1.44	0.33	1.74	1.02	0.50
"	G	1.29	0.35	1.26	1.22	0.32
"	C	2.28	0.31	1.68	1.53	0.46
"	C	2.21	0.32	1.59	1.21	0.44
"	C	2.37	0.38	1.96	1.63	0.57
Aster macrophyllus	G	1.78	0.24	4.74	1.00	0.39
"	G	1.76	0.25	5.78	1.48	0.23
"	G	1.90	0.29	4.82	1.41	0.26

TABLE 18--Continued

Species	Source	N	P	K	Ca	Mg
Aster macrophyllus	C	1.66	0.30	3.61	1.39	0.19
"	C	1.91	0.31	3.94	1.38	0.33
"	C	1.83	0.35	4.59	1.46	0.37
"	C	2.23	0.27	3.54	1.35	0.36
"	C	1.87	0.33	4.37	1.49	0.38
"	C	1.93	0.39	3.96	1.30	0.30
Maianthemum canadense	S	1.61	0.26	2.68	1.46	
"	C	1.73	0.26	3.27	1.05	
"	C	1.69	0.31	2.70	1.15	
"	C	1.86	0.33	3.36	1.13	
"	C	2.01	0.31	3.19	1.20	
"	C	1.97	0.30	2.79	0.91	
"	C	1.93	0.41	1.94	0.77	
Corylus cornuta	G	1.52	0.17	0.65	1.08	0.23
"	C	2.33	0.30	0.84	1.35	0.35
"	C	2.30	0.38	1.30	1.56	0.39
"	C	2.56	0.29	1.14	1.41	0.40
"	C	2.14	0.28	1.11	1.56	0.40
"	C	2.28	0.31	1.04	1.64	0.38
Ostrya virginiana	G	1.49	0.16	0.64	1.06	0.54
"	G	1.44	0.17	0.43	1.03	0.58
"	C	2.21	0.24	0.77	1.61	0.38

collected for this study. In general, however, the values reported by Gerloff are slightly lower than the values reported here. This is particularly true for nitrogen, phosphorus and calcium. The values reported by Scott (1955), however, are frequently higher. These differences may be due to time of sampling, method of sampling or geographic variables.

There is no simple correlation of nutrient concentration in a given species with synecological nutrient coordinates. There appears, however, to be an optimum range for nitrogen accumulation occurring near the center of the edaphic field (see Figure 7). For the ubiquitous species, the nitrogen concentration is low in the jack pine stands, increases in the red pine-fir stands and again drops in the hardwood stands. This suggests that the importance of nitrogen as a factor in the growth of understory plants varies between stands. It is not possible, however, to infer exactly how the role of nitrogen varies. For example, it is possible that available nitrogen was a limiting factor in the jack pine stands, but was in ample supply in the red pine stands, particularly the Wilderness stand. The soil analysis data show a relative increase of nitrogen in the surface horizon. If soil moisture did not increase concomittantly, the foliar nitrogen content could have increased. Moving to the hardwood stands, an increase of available moisture could again make nitrogen the limiting factor, thus resulting in a decrease in foliar nitrogen concentration. Obviously many other factor combinations could have resulted in the observed pattern.

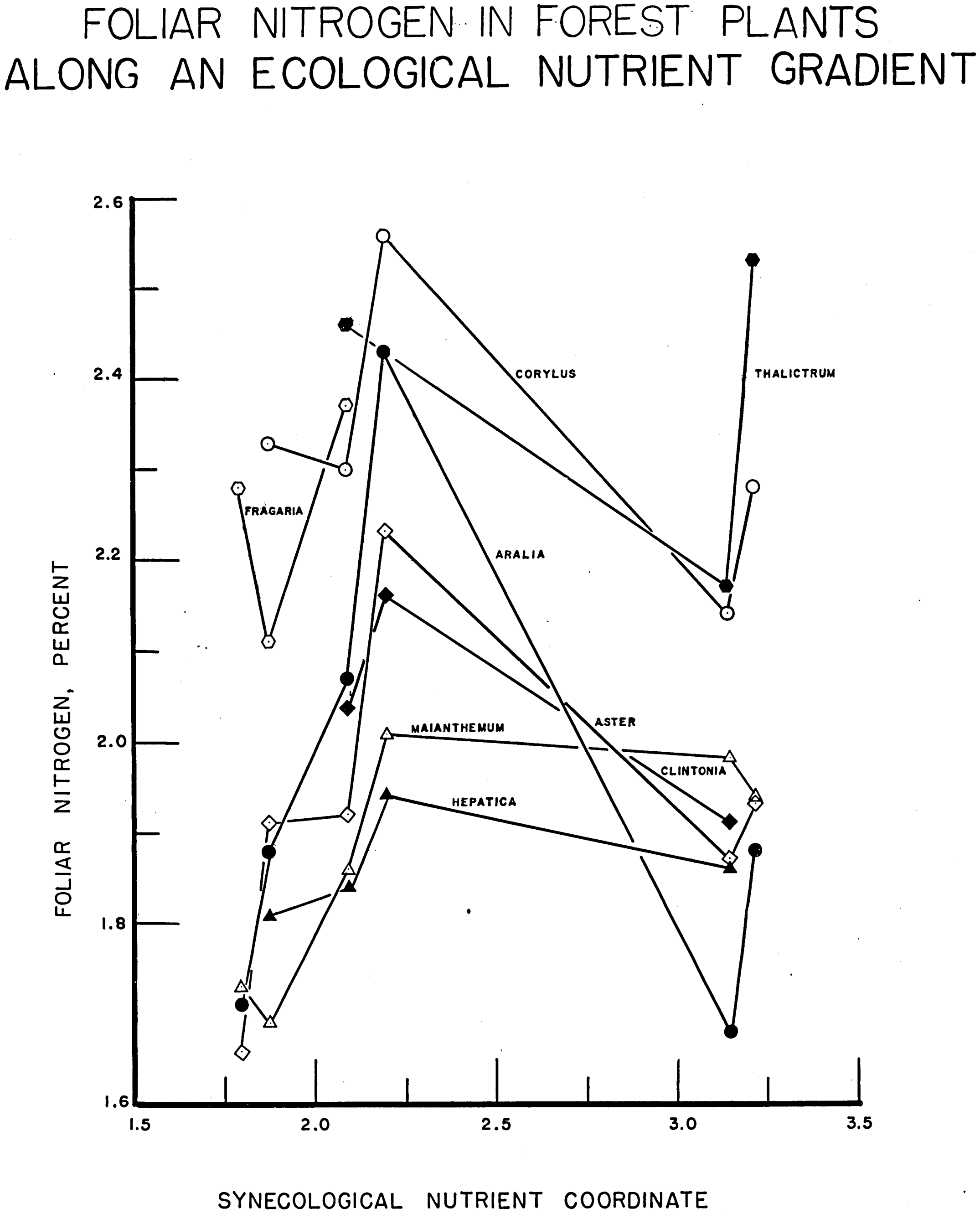


Figure 7. Foliar nitrogen concentration in eight forest plants from six stands. The foliar nitrogen concentration was highest in the red pine-fir stands and lowest in the jack pine and northern hardwood stands. The stands are plotted along the abscissa (from left to right) in the following order: 1) Woodlot jack pine, 2) Scott's jack pine, 3) Mary Lake red pine-fir, 4) Wilderness red pine-fir, 5) Campground maple-basswood and 6) Bearpaw Point basswood-elm.

No consistent site effect was observed for potassium, phosphorus, calcium or magnesium concentrations in the plants sampled.

It appeared on inspection that the species sampled at the upper end of the nutrient gradient had a higher average nitrogen, phosphorus, and potassium content than those at the lower end of the gradient. In order to test this hypothesis, Duncan's new multiple range test (Duncan, 1955) was used. When this test was run on all samples for the nitrogen data, no significant differences between stands were detected. The sampling, however, was designed to include the four ubiquitous species wherever possible. Since the nutrient content of these species does not vary consistently between stands, their inclusion in the multiple range test would mask significant differences in the nutrient content of species that segregate toward the ends of a nutrient gradient. Accordingly, these four species were dropped and the test was re-run for nitrogen, phosphorus and potassium.

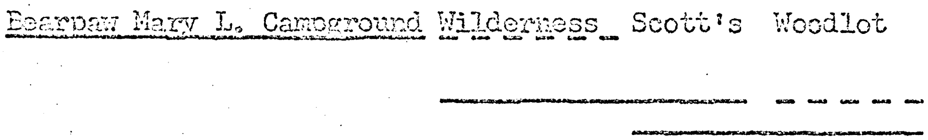
The results indicate that the species confined to nutrient-rich stands in general have a higher foliage nutrient concentration than species confined to poor stands. The difference in this case is greatest between the pure basswood stand on Bearpaw Point and the two jack pine stands.

Figure 8 shows graphically the significant differences between stands. A line under two stands indicates lack of significance. Since an unequal number of species for each stand were used in the multiple range test, two least significant

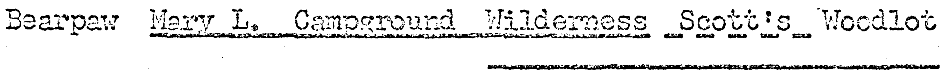
Figure 8

DUNCAN'S NEW MULTIPLE RANGE TEST ON FOLIAR NUTRIENT CONCENTRATIONS

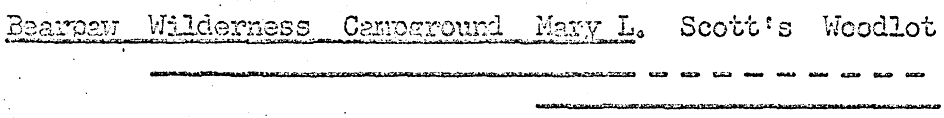
1. Potassium



2. Phosphorus



3. Nitrogen



A solid line under two plots indicates no significant difference between the mean foliage nutrient concentrations for the species sampled on those plots. A dotted line indicates a doubtfully significant difference.

ranges were computed for each comparison. A dotted line in Figure 8 indicates that the observed difference fell between the two computed test statistics and the difference is therefore of doubtful significance. The differences between stands are most pronounced for phosphorus and potassium. The differences in average nitrogen concentrations, although significant, are not as great.

In order to explore the interrelationships between different nutrients and draw conclusions as to their relative importance, the foliar analysis data were plotted in triangular coordinates. The use of triangular coordinates makes it possible to plot simultaneously the relationship between three different nutrients in a given sample. The plotting method is similar to that used by the "foliar diagnosis school." Thomas (1939; 1943) used triangular coordinates to show the effect of fertilizer and weather on the N-P-K coordinates and K-Mg-Ca coordinates. Plants were grown under different conditions and sampled at regular intervals. Rather than sampling whole plants, however, Thomas sampled homologous leaves from different plants on the same plot.

Holland (1966) compared the triangular coordinate method with analysis of variance, ratios of pairs of elements and Principal Component Analysis. Each method was judged by its ability to give consistent results in fertilizer trials from year to year. As a technique for interpreting results, Holland found that triangular coordinates were superior to both the analysis of variance and comparisons of ratios. Since both a statistical analysis and use of more than three elements at a time is impossible with this method, Holland concluded that the method of Principal Component Analysis was preferable to the triangular coordinate method that was used in this study.

In order to plot widely varying values in triangular coordinates, the data from this study were adjusted mathematically. The technique used has been discussed with respect to the humus samples.

When different combination of the nutrients nitrogen, phosphorus, potassium, calcium and magnesium are centered and plotted in triangular coordinates, some interesting relationships are suggested. Although no site effects within species are discernible, individual species occupy different positions within the triangular fields. This is particularly true for combination of N-P-K, K-Ca-Mg, P-K-Ca, and N-K-Ca (Figures 9-1 through 9-4). In each of these cases, most of the spread is along the potassium axis. When potassium is dropped from consideration, as with N-Ca-P, then the species tend to overlap near the center of the triangle (Figure 9-5). The finding that species differences are much stronger than site effects within species is consistent with the results of Scott (1955), Gagnon (1958) and others.

If all species are plotted in triangular nutrient coordinates with potassium as one of the axes, then the points are well spread along the potassium axis, as in Figures 10-1 and 10-2. If potassium is excluded, however, (as in Figure 10-3), then the result is a scatter diagram. Furthermore, species from

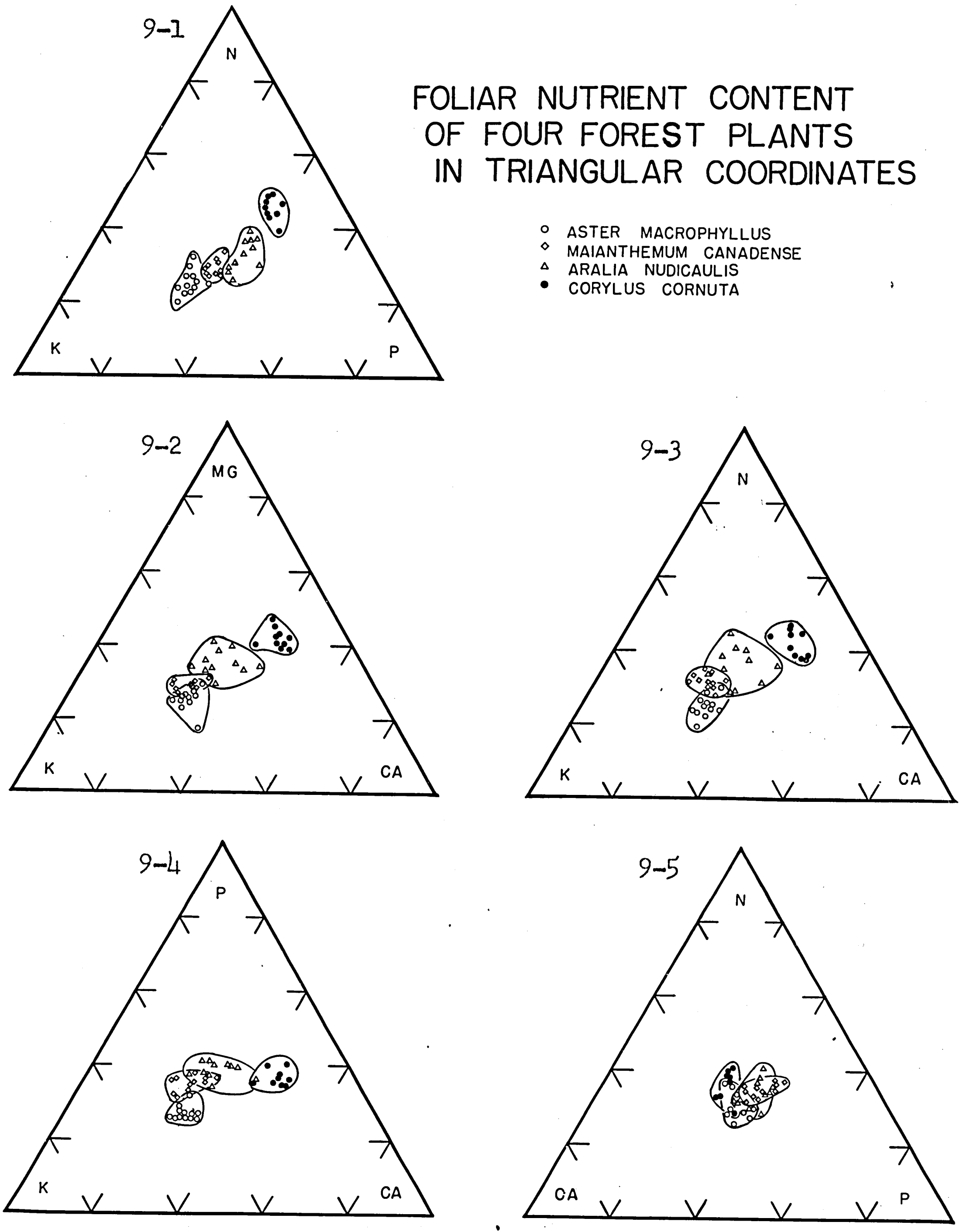


Figure 9. Relative foliar nutrient content of four ubiquitous forest plants in five sets of triangular coordinates. The data plotted here were centered with respect to the 94 foliage samples that were analyzed. Differences between species in triangular nutrient coordinates are most pronounced if potassium is one of the axes.

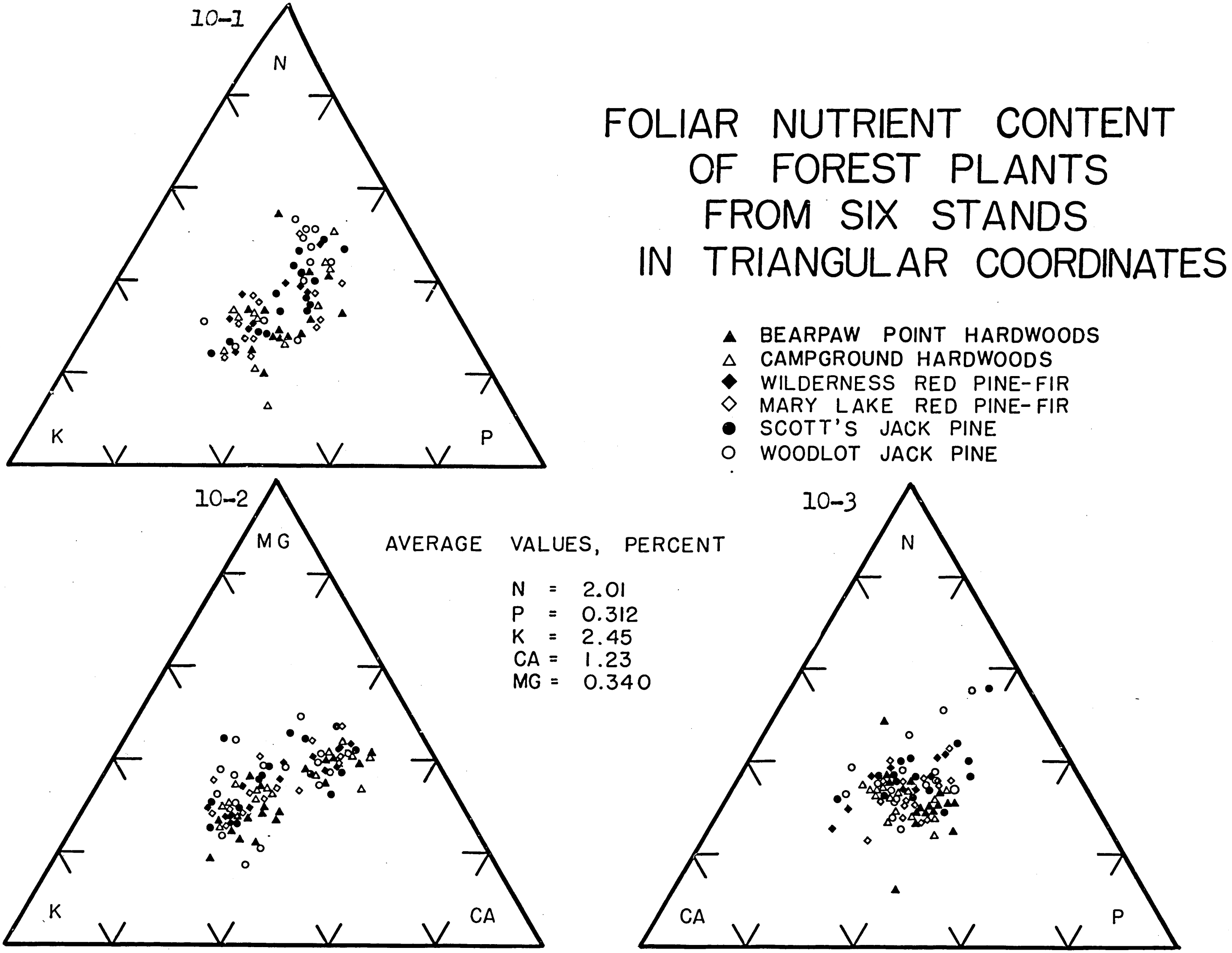


Figure 10. Relative foliar nutrient content of 32 species from six stands centered in three sets of triangular nutrient coordinates. The spread is greatest along the potassium axis.

the hardwood stands appear to be slightly clustered toward the upper end of the potassium axis, whereas species from the jack pine stands are well distributed toward the lower end.

In the N-P-K coordinates, it appears that most of the species fall into two groups along the potassium axis. These groups were arbitrarily divided at 30 percent potassium. The species in each group are listed in Table 19. The high potassium group contains only those species which occur in the middle and upper end of the nutrient gradient, that is, nutrient demanding species, such as *Sanguinaria canadensis*, and ubiquists, such as *Maianthemum canadense* and *Aster macrophyllus*. The only exceptions are *Lithospermum canescens*, which is confined to acid xeric sites and *Aralia nudicaulis*, which falls into both groups. The "low potassium" group, however, contains only species that are confined to the low end of the nutrient gradient, and trees, shrubs and vines. The only exceptions are *Cornus canadensis*, which is confined to the middle range of the nutrient gradient, and *Amphicarpa bracteata*. The low relative potassium value for this leguminous species, however, reflects the high internal nitrogen concentration.

If the species are grouped according to relative phosphorus content, then the same trend appears: species from "rich" stands have a higher relative phosphorus content than species from poor stands. The grouping, however, is not as clear as with potassium. Thus species restricted to rich stands have a higher foliar concentration of nutrients; this difference decreases in the order K > P > N.

TABLE 19

CLASSIFICATION OF SPECIES BY POTASSIUM CONTENT RELATIVE TO PHOSPHORUS AND NITROGEN

K-Coordinate above 30 percent

Lithospermum canescens

Pteridium aquilinium

Maianthemem canadense

Aster macrophyllus

Aralia nudicaulis

Hepatica americana

Thalictrum dioicum

Clintonia borealis

Uvularia grandiflora

Caulophyllum thalictroides

Actea rubra

Smilacina racemosa

Sanguinaria canadensis

Asarum canadensis

K-Coordinate below 30 percent

Fragaria virginiana

Cladonia sp.

Epigea repens

Gaultheria procumbens

Aralia nudicaulis

Arctostaphylos uva-ursi

Pyrola elliptica

Pleurozeum schreberii

Apocynum androsaemifolium

Cornus canadensis

Amphicarpa bracteata

Shrubs, trees and vines

Corylus cornuta

Dirca palustris

Parthenocissus inserta

Ostryavirginiana

Acer saccharum

Lonicera canadensis

It is unclear, however, whether these differences reflect the physiological ability of the different species to concentrate nutrients, or whether they are the result of deficiencies and luxury uptake. Possibly all three factors are involved. The four ubiquitous species generally had high nutrient concentration, regardless of where they were growing. Thus these plants appear to exceed the low-nutrient species in their ability to extract and concentrate nutrients in their foliage. The same may be true for plants that are restricted to rich stands. This does not imply, however, that the supply of nutrients in the jack pine stands was optimal for the plants growing there. More likely the low minimum nutrient requirements of these species allow them to segregate at the low end of the nutrient gradient under competition.

On a basis of commonly reported optimum and minimum foliar nutrient values, however, the nutrient concentration in some plants certainly exceeded the optimum concentration for growth (Goodall and Gregory, 1947). Several species from Bearpaw Point, for example, had phosphorus concentrations in excess of 0.5 percent and potassium concentrations greater than 4.0 percent. These values are greater than any reported by Goodall and Gregory as optimum for agricultural plants and forest trees. The nitrogen values, however, do not greatly exceed the commonly reported values. Possibly nitrogen is the limiting nutrient in the hardwood stands. This is supported by the N-P-K coordinates in Figure 10-1. Species from the hardwood stands are displaced further from the nitrogen vertex than species from the jack pine stands.

In the humus samples the ratio of calcium plus magnesium to potassium increased toward the upper end of the nutrient gradient. This pattern was not observed for the foliar samples. Furthermore, foliar potassium showed the greatest site effect of any nutrients, whereas the humus potassium was only weakly correlated with synecological nutrient coordinates. Thus the chemical structure of the ecosystems sampled is strongly affected by the physiology of the subordinate forest plants.

As with the humus data, a simple correlation analysis was run between the absolute and relative foliar nutrient concentrations (Table 20). Of the five macronutrients correlated, calcium vs. magnesium had the highest correlation coefficient (+0.703). Potassium was better correlated with phosphorus than with any other element. This is consistent with the finding that nutrient concentration differences between sites are strongest for potassium and second strongest for phosphorus.

In the N-P-K coordinates, the correlation between relative and absolute values decreased in the order K > P > N. In the K-Ca-Mg coordinates, the order was K > Ca > Mg. This is probably an effect of differing variances between elements.

Although the four ubiquitous species were sampled twice during the summer, consistent changes in nutrient concentration are hard to detect. This is probably due to sampling error. Three generalizations, however, are possible. First, the calcium

TABLE 20

CORRELATION COEFFICIENTS BETWEEN FOLIAR NUTRIENT VALUES

Absolute, percent	Absolute, percent N	 P	 K	 Ca	 Mg
N		+0.397**	+0.003	+0.338**	+0.552**
P			+0.557**	+0.403**	+0.424**
K				+0.204*	+0.090
Ca					+0.703**

Absolute, percent	Relative values, N-P-K Coordinates N	 P	 K
N	+0.226*	+0.092	-0.243*
P	-0.605**	+0.509**	+0.284**
K	-0.874**	-0.294**	+0.908**

Absolute, percent	Relative Values, K-Ca-Mg Coordinates K	 Ca	 Mg
K	+0.813**	-0.482**	-0.859**
Ca	-0.281**	+0.560**	-0.098
Mg			+0.225*

concentration increased almost uniformly, both in absolute concentration and relative to other nutrients. This is consistent with the findings of Mitchell (1936), Thomas (1967) and others. Second, an increase in concentration was more frequent in the red pine stands than in the hardwood and jack pine stands. Third, the concentration of all nutrients in *Aralia nudicaulis* increased, whereas *Maianthemum canadense*, *Aster macrophyllus* and *Corylus cornuta* were erratic.

7. Factor Interaction

Although this study was primarily concerned with the evaluation of a nutrient gradient, it must be stressed that nutrients do not function alone in ecosystems but rather in interaction with other factors. The relationships and interactions between the moisture, nutrient, heat and light regimes are suggested by the matrix of simple correlation coefficients between the four coordinates and the humus exchangeable cations (Table 14).

The moisture coordinates show a high degree of correlation with the nutrient coordinates and exchangeable bases. Exchangeable potassium, however, is more highly correlated with moisture than any of the other exchangeable bases. This is especially interesting in view of Bard's (1949) observation that plants with the highest moisture requirements also had high potassium requirements. The foliar potassium data from this study suggest a correlation between synecological moisture coordinates and potassium uptake.

The mechanical analysis data from the mineral soil samples suggest conclusions about the moisture regime. On a basis of silt plus clay content, the moisture holding capacity in the profiles sampled decreases in the order: Campground > Bearpaw > Wilderness = Mary Lake > Scott's > Woodlot. The interpretation is complicated, however, by the presence of thin bands of silt and very fine sand in the Marquette profiles and by the high organic matter content of the Poppleton profile. In view of the local variability in the soils that were sampled, a much larger number of samples is needed to adequately assess the moisture regime.

The synecological light coordinates are negatively correlated with nutrients. The negative correlation is highest for the synecological nutrient coordinates and next highest for percent base saturation. Exchangeable potassium was not as highly correlated with light as were calcium and magnesium. This is somewhat disappointing in view of Bergmann's (1958) observation that potassium requirements are higher at low light intensities. It appears, however, that foliar potassium is more strongly negatively correlated with either actual light measurements or light coordinates than is either calcium or magnesium. Thus the high potassium content of plants in the rich stands may be related to both low light intensities and high moisture requirements.

The synecological heat coordinates are positively correlated with the nutrient regime. The correlation is best for the integrative measurements of nutrients, that is, nutrient coordinates, pH, exchangeable hydrogen and percent base saturation. Calcium and magnesium are also positively correlated with heat coordinates but potassium is not. This appears to be related to the increase in the K : Ca+Mg ratio in the nutrient poor (jack pine) stands which have low synecological heat coordinates. It must be stressed, however, that the "heat regime" in this case is based only on the synecological heat coordinates. The coordinates do not necessarily reflect significant differences in effective temperature between stands, since the heat coordinates were developed on a basis of regional distribution of the individual species.

More detailed conclusions on the interactions and relationships between the effective environmental factors are beyond the scope of this study. A complete and integrated picture must await proper field instrumentation.

V. SUMMARY AND CONCLUSIONS

The purpose of this study was to relate the nutrient content of soils and subordinate forest vegetation to an ecological nutrient gradient in the Central Pine Section of Minnesota. The nutrient gradient was defined in terms of synecological coordinates and was described by means of soil and site description, soil chemical analysis and foliar analysis.

Six stands were selected for the study, with two stands in each of three vegetation types: jack pine, red pine-balsam fir and northern hardwoods. Eight subplots were located within each stand.

Humus samples were collected at each subplot and analyzed for exchangeable cations and pH. Percent base saturation was more highly correlated with synecological nutrient coordinates than any of the other humus parameters ($r = +0.83$). The degree of correlation with nutrient coordinates decreased in the order: percent base saturation > pH > exchangeable H > exchangeable Mg = exchangeable Ca > exchangeable K.

The relatively poor correlation between potassium and synecological nutrient coordinates is due to the decrease in the K : Ca plus Mg ratio in the nutrient-rich hardwood stands. This relationship has been illustrated by means of triangular coordinates.

The good correlation between nutrient status of the humus layer and synecological coordinates obtained in this study suggests that the humus layer occupies a key position in the forest ecosystem. It appears to be an important factor in controlling plant distribution and productivity, and its characteristics are determined by the vegetation itself. Future work on ecological nutrient gradients should be focused sharply on the chemical and biological characteristics of the humus layer.

Thirty-two different species from the six stands were analyzed for thirteen different elements. Samples were collected during the third week of July and third week of August. Four ubiquitous species only were sampled during July. The results for the foliar analysis may be summarized as follows:

1. No statistically significant differences between sites were found in the nutrient concentration of a given species, except possibly for nitrogen. In this case the plants growing in red pine-fir stand have a higher foliar concentration of nitrogen than plants of the same species at either end of the nutrient gradient. Probably the relative importance of nitrogen as a limiting factor in the growth of herbaceous plants differs between stands.

2. Between ecological groups on different sites, there are significant differences in the foliar concentration of nitrogen, phosphorus and potassium. This may be due to differing physiologic requirement, luxury uptake or deficiency. The difference decreases in the order $K > P > N$.

3. Although the K : Ca plus Mg ratio in the humus samples decreased in the hardwood stands, a similar trend was not observed in the foliage samples.

4. Consistent changes in foliar nutrient concentration over time were not observed, except for calcium, which consistently increased.

Triangular coordinates provide a useful tool for interpreting data and illustrating relationships. The relative values generated by the transformation, however, appear to be strongly influenced by the variance of each element and the degree of correlation between the three elements. Until this relationship is evaluated rigorously, any inferences based on triangular models should be supported by unadjusted or absolute values.

Many attempts to find significant differences in foliar nutrient concentration within species between sites have, like this one, either failed or yielded ambiguous results. Rather than abandoning all at attempts to find significant differences, it might be useful to combine data on nutrient concentration with information on species productivity or biomass per unit area. The sampling should be designed so that nutrient uptake for a given species can be expressed on a per leaf, per plant or unit area basis. The latter is perhaps the most difficult, since the biomass per unit area for a given species is highly variable within most stands. In any case the number of replications within stands should be greatly increased; at least one sample should be collected on each subplot within each stand.

Given the multiplicity of variables that affect nutrient uptake, however, it would be better to concentrate attention on nutrient uptake by plants grown under controlled conditions, at least until more is known about the physiological requirements of the species being considered.

An explanation for the wide differences in nutrient concentration between ecological groups could be sought by growing these groups of species under controlled conditions in the associated surface soil horizon. Fertilizer trials, associated with productivity and foliar analysis, data might suggest which nutrients are limiting to which ecological groups. An alternative method might be to grow each ecological group on different surface soil horizons. For example, understory plants associated with jack pine might be grown on soil from jack pine, red pine and hardwood stands. The results of such a study might indicate to what degree the species distribution is determined by physiologic requirements rather than ecological requirements.

This study has failed to answer many fundamental questions concerning ecological nutrient gradients in Minnesota. As an exploratory study, however, it has raised new questions and suggested worthwhile areas for future inquiry, and it has revealed some of the advantages and pitfalls of applying foliar analysis of subordinate forest plants to ecological situations. A more detailed evaluation of ecological nutrient gradients must await the results of studies of the humus layer, fertilizer trials and greenhouse experiments.

APPENDIX

INTEGRATIVE LIGHT MEASUREMENTS

In order to provide quantitative data for future studies, light measurements were taken on all subplots. Although these measurements are somewhat incidental to the main purpose of the study, they are relevant in that light is an important variable in the growth and mineral uptake of plants.

Ozalid paper booklets were made according to the method described by Friend (1961). Four masked booklets were taped on each of 48 four-foot laths. On August 18, the laths with the ozalid papers attached were set out and the booklets were unmasked. This was done by centering a lath on top of each stake and nailing it in a horizontal position about 24 inches off the ground. All laths were oriented in a north-south direction to avoid bias. Control papers were set out at three location in the open.

The sun rose at 6:30 A.M.; the last papers were set out before there were many sunflecks on the forest floor. The day was mostly sunny, with no more than two hours of cloudiness. Following collection, the papers were developed over ammonium hydroxide.

According to Friend (1963), the number of papers exposed is a logarithmic function of the total foot-candle minutes. Thus the sample papers could be calibrated by comparison with standards exposed for a known length of time to a known light intensity.

Some of the papers could not be collected until late at night and were therefore discolored by moisture. Within the stands there was no appreciable dew; apparently exposure to 100 percent relative humidity is enough to discolor the papers. For this reason, no attempt was made to subdivide the interval between the last two papers. This results in a considerable loss of accuracy, particularly at the higher light intensities. This loss is tolerable due to the broad range of light intensities involved in the study.

The light measurements with ozalid paper yielded useful information on the environmental light gradient in the stands studied. Figure 5 shows graphically the relationship between the synecological light coordinate for each plot and the percentage of full sunlight received at the herb level in one day.

If only the hardwood stands and jack pine stands are considered, there appears to be a fairly neat curvilinear relationship between percentage of full sun and synecological light coordinate. When the red pine stands are considered alone, however, the relationship is poor. There are several reasons for this. For one, these stands have a discontinuous second story of balsam fir. Some plots fell beneath a dense fir canopy and others fell in relatively open spots. Second, plots in dense shade frequently have very few species. In these cases the synecological coordinate probably does not mean much. Plot 6 at Mary Lake, for example, had only eight species and hence may be discarded. Third, blow-downs are frequent in the fir and hence the herb flora on some plots may be out of equilibrium with light intensity. In the Wilderness stand, plot 3 occurred near the north edge of a 30 year-old clear-cut strip and received much more light than other plots in the stand. Hence this plot may also be discarded.

Figure 5 also shows the average percent of full sunlight against synecological light coordinate. In compiling the averages, plot 6 at Mary Lake and plot 3 in the Wilderness stand were omitted. Averages are designated by the larger symbols in Figure 5.

A linear correlation analysis was run using percent of full sunlight and synecological light coordinate computed on both a presence and dominance basis. The correlation coefficients obtained were +0.86 on a presence basis but only +0.66 on a dominance basis. The two plots mentioned previously were also omitted from the calculation.

Future work on light gradients should involve measurement of light both above and below the shrub layer. Measurements should be taken on sunny and cloudy days and during both spring and summer. Synecological light coordinate should be computed separately for the tree, shrub and herb layers.

Given the low light intensity in the two hardwood stands, it seems likely that growth of the ground flora, particularly the ubiquists, was limited by light intensity. If this were the case, then the foliar concentration of nutrients in the plants sampled should be increased. Without more replication and data on dry-matter weights and leaf size, however, detailed conclusion on the importance of light in mineral uptake are impossible.

LITERATURE CITED

Bakuzis, E. V., 1959. Synecological coordinates in forest classification and in reproduction studies. Ph.D. Thesis, University of Minnesota. Microfilm and Xerox Publ. Univ. Microfilms, Ann Arbor, Mich. 242 pp.

Bakuzis, E.V., 1961. Synecological coordinates and investigation of forest ecosystems. Rep. 13th Cong. Int. Union For. Res. Org. Vienna, Austria. 10 pp.

Bard, G.E., 1945. The mineral nutrient content of the foliage of forest trees on three soil types of varying limestone content. Proc. Soil Sci. Soc. Amer. 10:419-422.

Bard, G.E., 1949. The mineral nutrient content of the annual parts of herbaceous species growing on three New York soil types varying in limestone content. Ecology 30: 384-389.

Bergmann, W., 1958. Methoden zur Ermittlung mineralischen Bedürfnisse der Pflanzen. Encycl. Plant Physiol. 4: 36-86.

Black, C.A., 1965. Methods of Soil Analysis. Agronomy Ser. 9. Amer. Soc. Agron. Madison, Wis. 1572 pp.

Brown, I.C., 1943. A rapid method of determining exchangeable H and total exchangeable bases of soils. Soil Sci. 56: 353-358.

Duchaufour, Ph., 1961. Sites, humus-types and ecological groupings. Scot. For. 15 (2): 55-62.

Duncan, D.B., 1955. Multiple range and multiple F tests. Biometrics 11: 1-42.

Ellenberg, H., 1956. Aufgaben und Methoden der Vegetationskunde. Grundlagen der Vegetations Gliederung. Vol. 4. 136 pp. (In) Einführung in die Phytologie. H. Walter, ed. Ulmer, Stuttgart.

Fernald, M.L., 1950. Gray's Manual of Botany. American Book, New York, N.Y. 1632 pp.

Friend, D.T.C., 1961. A simple method of measuring integrated light values in the field. Ecology 42: 577-580.

Gagnon, D., Laford, A. and Amiot, L.P., 1958. The mineral nutrient content of some forest plant leaves and of the humus layer as related to site quality. Can. J. Bot. 36: 201-220.

Gerloff, G.C., Moore, D.G. and Curtis, J.T., 1964. Mineral content of native plants of Wisconsin. Univ. of Wisconsin Experiment Station. Research Report 14, 27 pp.

Govorkiantz, S.R., 1957. Site index curves for the Lake States. Lake States For. Exp. Sta. U.S. Dept. Agric. For. Serv. Tech. Notes, 463, 484.

Goodall, D.W. and Gregory, J.C., 1947. Chemical composition of plants as an index of their nutritional status. Comm. Bur. of Hort. and Plant Crops. Tech. Comm. 17. 167pp.

Grava, J., 1962. Soil Analysis methods as used in the University of Minnesota Soil Testing Laboratory. Dept. Soil Sci. Univ. Minn. 7 pp.

Holland, D.A., 1966. The interpretation of leaf analysis. J. Hort. Sci. 41: 311-329.

Kurmis, V., 1967. Dynamics of advanced reproduction in upland forest communities in Itasca State Park, Minn. Thesis in preparation.

Loucks, O.L., 1962. Ordinating forest communities by means of environmental scalars and phytosociological indicies. Ecol. Monog. 32: 137-166.

Lundegårdh, H., 1951. Leaf Analysis. Hilger and Watts, London. 176 pp.

Madgwick, H.A., 1965. The weights and nutrient composition of understory species in ashwood. J. Ecol. 53: 335-341.

McAndrews, J.H., 1966. Postglacial history of prairie, savanna and forest in northwestern Minnesota. Memoirs of the Torrey Bot. Cl. 22 (2): 1-72.

Mitchell, H.L., 1936. Trends in the nitrogen, phosphorus, potassium and calcium content of the leaves of some forest trees during the growing season. Black Rock Forest Pap. I (6). 44 pp. Cornwall-on-the-Hudson, New York, N.Y.

Olsen, C., 1961. Competition between trees and herbs for nutrient elements in calcareous soil. Symp. Soc. Exp. Biol. 15: 145-155.

Ovington, J.D., 1956. Studies of the development of woodland conditions under different trees. 5. The mineral composition of the ground flora. J. Ecol. 44: 597-604.

Piggot, C.P. and Taylor, K., 1964. The distribution of some woodland herbs in relation to the supply of N and P in the soil. J. Ecol. Jubilee Symposium Suppl. pp. 175-185.

Pluth, D.J. and Arneman, H.F., 1963. Forest soil and tree growth characteristics related to a synecological coordinate system. (In) Forest-Soil Relationships in North America. C.T. Youngberg, ed. Oregon State Univ. Press. Corvallis, Oregon. pp. 331-351.

P'yavchenko, N.I., 1960. The biological cycle of nitrogen and mineral substances in bog forests. Sov. Soil Sci. 6: 593-602.

Rowe, J.S., 1956. Uses of undergrowth plant species in forestry. Ecology 37: 461-473.

Scott, D.R.M., 1955. Amount and chemical composition of the organic matter contributed by overstory and understory vegetation to forest soil. Yale Sch. For. Bull. 62, 73 pp.

Soil Survey Staff, 1951. Soil Survey Manual. U.S. Dept. Agric. Handb. 18, 503 pp.

Steel, R.G.D. and Torrie, J.H., 1960. Principles and Procedures of Statistics. McGraw-Hill, New York, N.Y. 481 pp.

Thomas, W., 1939. Foliar diagnosis: physiological balance between the bases lime, magnesia and potash. Plant Physiology 14: 699-715.

Thomas, W. and Mack, W.B., 1943. Foliar diagnosis in relation to plant nutrition under different conditions of weather and soil reaction. Soil Sci. 56: 197-212.

Thomas, W.A. Jr., 1967. Accumulation and cycling of calcium by flowering dogwood trees. Ph.D. Thesis. Univ. Minn. 152 pp.

Valmari, J., 1921. Beiträge zur chemischen Bodenanalyse. Acta Forestalia Fennica 20 (4): 1-67.

Viro, P.J., 1952. Nutrient status and fertility of forest soil. I. Pine stands. Comm. Instit. For. Fenn. 39 (4): 1-44.

Walter, H., 1961. Climatic diagrams as a means to comprehend the various climatic types for ecological and agricultural purposes. pp. 3-9. (In) The Water Relations of plants. A.J. Rutter and F.H. Whitehead, Ed. Blackwell, London. 393 pp.

Waring, R.H. and Major, J., 1964. Some vegetation of the California Coastal Redwood Region in relation to gradients of moisture, nutrients, light and temperature. Ecol. Monog. 34 (2): 167-215.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monog. 30: 279-338.