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# Structural Organization of Forest Ecosystems

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# STRUCTURAL ORGANIZATION OF FOREST ECOSYSTEMS*

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An ecosystem is defined as a functional unit of organisms and environment. An ecosystem is a particular kind of physical system (Tansley, 1935). "A system is a structure in which all processes are connected functionally in a more or less complicated way, and the rules which assert something about single processes occurring in the system apply only conditionally". The term "system" implies the principle of "wholeness" (Mainx, 1955).

The forestry viewpoint restricts the inquiry to forest ecosystems and emphasizes the utilitarian values.

## GENERAL METHODOLOGY

Matter-energy balance is considered to be the central problem of ecosystems, and methods have been proposed for such investigation (Lindeman, 1942; Sukachev, 1954). Other methods with more restricted aims have been developed historically, and new methods are currently being added.

Structural organization of ecosystems is a fundamental problem; its investigation requires methods which permit generalizations. It can be approached in two ways. The most common is from induction to deduction; less frequently the reverse method is used.

The inductive-deductive method is closely associated with the classification of environmental factors according to their origin, such as climatic, edaphic, and biotic factors and the many subfactors of these groups. Difficulties in generalizing are very great. Recently some new, interesting, and effective methods have been proposed (Jenny 1941, 1946, 1958).

When greater emphasis is placed on deduction, the matter-energy complex involved can be subdivided into smaller complexes: moisture, nutrients, air, heat, light, and mechanical force. This method of separating the environmental factors has been designated the classification of factors by their mode of action or the physiological approach (Livingston and Shreve, 1921, cited from Toumey and Korstian, 1947). The field methods are mostly designed to measure factors ac-

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cording to their origin. The physiological approach to factors is gradually gaining greater attention particularly among agronomists and foresters. Search for new methods of direct measurement of biotically effective environmental factors is going on. Vegetational and physiographic indication methods must also be directed to the estimation of the biotically effective part of the moisture, nutrient, heat and light regimes.

The advantage of the deductive-inductive approach lies in the ability to arrive more easily at generalizations.

## RECONNAISSANCE OF SOME CHARACTERISTICS OF FOREST ECOSYSTEMS IN MINNESOTA

In 1957, there was an opportunity to carry out a brief reconnaissance of forest ecosystems in Minnesota along the lines of the deductive-inductive approach. A vegetational indication method based on species presence was used. The field work consisted in listing the species in 356 systematically chosen forest communities. In addition, the percentage of tree, shrub, reproduction, and ground cover was estimated. Brief soil descriptions for each stand were added. From literature data for each species observed in the survey, relative moisture, nutrient, heat and light requirements were evaluated on a scale from 1 to 5. Community requirements were computed as unweighed averages from the component species requirements. Community requirements for the essential factor complexes—moisture, nutrients, heat and light—were selected as the basic coordinate axes ("synecological coordinates") to which other phenomena observed could be referred. The pattern of community response simultaneously to two or more factor complexes is considered as a major element in the structural organization of forest ecosystems.

## DISCUSSION AND RESULTS

The four basic factor complexes (moisture, nutrients, heat, and light) produce six bivariate combinations. Distribution of the 356 Minnesota forest communities in these combinations is shown in Fig. 1.

It can be noted that forest communities are distributed in a certain characteristic "synecological field". Synecological fields with moisture as one of the coordinate axes show a rather typical triangular shape, the others are elliptical or nearly circular.

The pattern of the edaphic field (moisture-nutrient axes) resembles closely the primary successional schemes presented by the American ecological school. The agreement becomes more obvious when the ecographs or the distribution pattern of individual forest species (Fig. 2) are compared. The ordinate axis in primary succession schemes is supposed to represent a chronological sequence. However, it should be noted that at least with some types of soil formation processes nutrients increase with the passing of time and the influence of the vegetation on the soil. The authors of the classical American ecological school (Weaver and Clements, 1938 and others) have noted the enrichment of forest soils under both xeric and hydric types

DISTRIBUTION OF FOREST COMMUNITIES BY ECOTOPES IN MINNESOTA

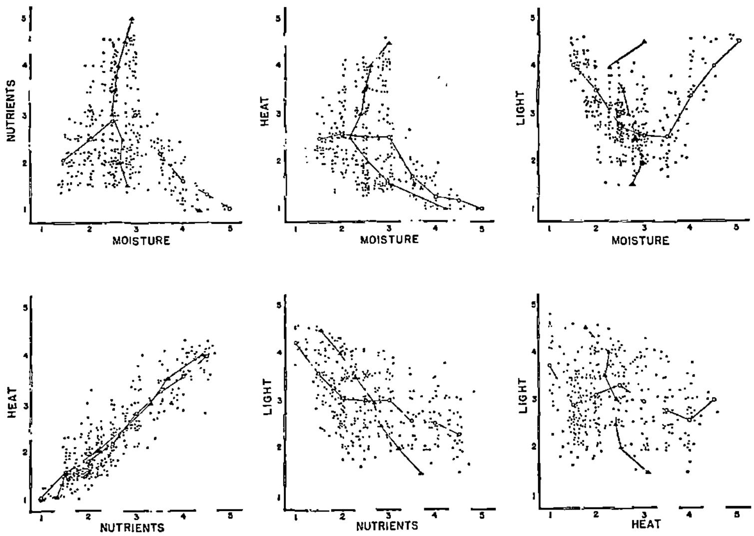


FIGURE 1.

of the primary succession. Thus the time sequence is equated to nutrient levels on the ordinate axis.

Inadvertently the triangular form of the edaphic field has also been demonstrated by other authors whenever a larger forest geographical area has been investigated (Pogrebnjak, 1955; Arnborg, 1958).

The configuration of the moisture-heat field strongly resembles the moisture-nutrient field. The nutrient-heat field shows a strong positive relationship between the community requirements for nutrients and heat.

The moisture—light field is a reversed triangle. It indicates also lack of forest communities with high light requirements under mesic moisture conditions.

Besides the bivariate distributions of forest communities it is also possible to show trivariate distributions, and attempts have been made to develop four dimensional relationships.

Figure 2 shows distribution of tree species in edaphic (moisture-nutrient) and climatic (heat-light) coordinates. Close agreement of jack pine (*Pinus banksiana Lamb.*) and red pine (*Pinus resinosa Ait.*) ecographs in Minnesota conditions can be noted. The ecographs further indicate that jack pine, red pine, and trembling aspen (*Populus tremuloides Michx.*) occurring southwards do not appear to increase their shade tolerance as do white spruce (*Picea glauca* (Moench) (Voss), balsam fir (*Abies balsamea* (L.) Mill), sugar maple (*Acer saccharum* Marsh), red oak (*Quercus rubra* L.) and American elm (*Ulmus americana* L.)

Similar ecographs were prepared for shrub and ground cover

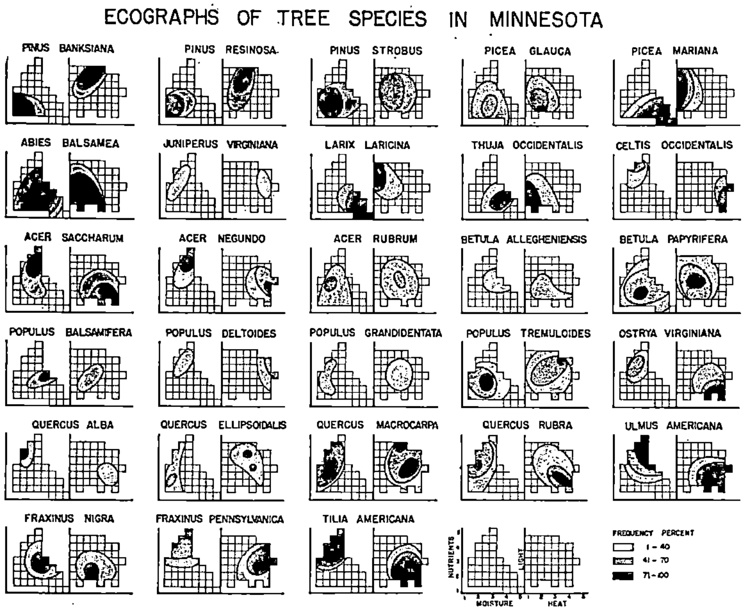


FIGURE 2.

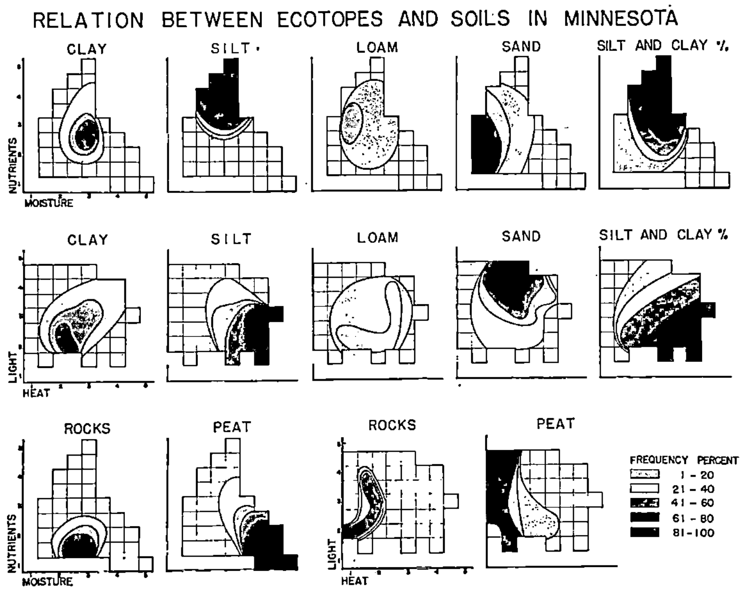


FIGURE 3.

species. A comparison of these ecographs reveals some interesting associations between species. For example, it appears that under some edaphic conditions white pine is not associated with *Ribes* species. This may aid in the identification of sites on which white pine may be grown with reasonable immunity to blister rust. Bimodal distribution of species, as already pointed out by Pogrebnjak (1930), suggests a possible existence of different ecotypes of a species. This may be the case for *Quercus macrocarpa Michx.* and *Quercus ellipsoidalis* E. J. Hill as indicated by the ecographs for those species.

Plots taken in forest stands all over Minnesota were classified both into broad physical soil groups and on the basis of the ecological evaluation of the plant species present. The relationships between the soil groups and their synecological evaluation is shown in Fig. 3. It appears that silty, rocky and peat soils, and to some extent also sandy soils, occupy certain positions in the synecological fields. The situations occupied by clayey and loamy soils are more frequently occupied by other soils.

Figure 4 shows that the densest tree cover is located around the mesic moisture line with an ultimate maximum at the highest nutrient level. Tree cover density decreases with increasing light demands of the community. The smallest variations in tree cover density occur at medium heat level. Variability in tree cover increases and the tree cover becomes more open approaching the prairie conditions.

COVER RELATIONSHIPS IN FOREST COMMUNITIES
IN MINNESOTA

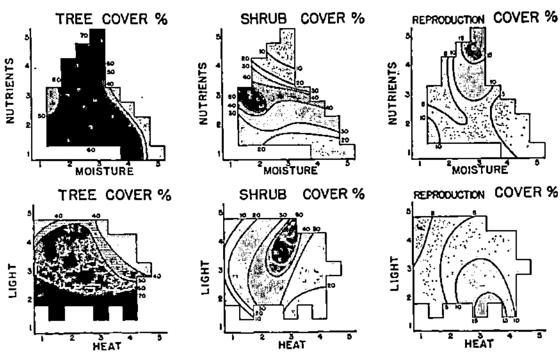


FIGURE 4.

The pattern of shrub cover appears to change at right angles to the changes of tree cover. Maximum shrub cover is located around the medium nutrient level and is more widely spread under drier conditions. Superposition of the tree cover graph on the shrub cover graph reveals more details of the effect of environmental conditions on cover relationships.

The reproduction pattern to some extent resembles the distribution of tree cover, except for small pine-oak and spruce-fir maxima which are located outside the tree cover maximum zone. The impact of shrub cover on reproduction cover appears rather distinctly.

Ground cover is not shown, but in Minnesota forest communities it tends to invade the synecological space from the periphery. Particularly dense ground cover develops at the boundary of the bog vegetation. In the drier forest communities shrub cover prevents a greater prairie ground cover intrusion.

Using secondary coordinate systems together with the fundamental synecological coordinate system (moisture, nutrient, heat, and light axes), a more detailed analysis of cover relationships is possible. By the same practice other problems of forest production and reproduction may be analyzed.

## SUMMARY

The structural organization of forest ecosystems is approached in a deductive-inductive way which requires an estimation of the relative moisture, nutrient, heat, and light requirements for each forest community. As the first step, the requirements of individual species are assessed upon the basis of previous research. Then community values are computed as unweighed averages of the requirements of all its species.

356 forest communities were investigated. The distribution of these communities in bivariate combinations of moisture, nutrient, heat and light requirements show specific patterns. The patterns in moisture-nutrient axes agree well with the primary succession schemes as presented by the American ecological school. The other patterns reflect either previous knowledge or suggest new knowledge.

Species distribution diagrams (ecographs) with respect to community requirements for essential environmental factors (synecological coordinates) demonstrate some individual characteristics of the species and allow for comparisons.

The results obtained by using purely vegetational indicators of environmental factors have been substantiated by physiographic observations.

Cover relationships in forest communities show a characteristically changing pattern under different combinations of environmental factors.

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