DYNAMICS OF ADVANCE REPRODUCTION IN UPLAND FOREST COMMUNITIES IN ITASCA STATE PARK, MINNESOTA

A THESIS

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL

OF THE UNIVERSITY OF MINNESOTA

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

March, 1969

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ACKNOWLEDGEMENTS

I wish to express my sincere appreciation to Dr. Henry L. Hansen, my adviser, and to Dr. Egolfs V. Bakuzis for their generous help and encouragement during the entire study, and to other members of my Graduate Committee, Dr. Harold F. Arneman, Dr. Rouse S. Farnham, and Dr. Conrad J. Weiser, for valuable suggestions concerning the project and constructive comments on the manuscript.

I sincerely thank Dr. Frank H. Kaufert for the several research funds provided me by the School of Forestry which made this study possible, and to other faculty and staff members of the School of Forestry for their general interest and encouragement.

Special thanks are due Mr. Darwin D. Ness for fine cooperation in the field work and stimulating exchange of ideas.

1. INTRODUCTION

Itasca State Park is one of the most intensively investigated areas in Minnesota where ecological research and other biological studies have been conducted for many years, taking advantage of natural conditions of the park and the facilities of the University of Minnesota Forestry and Biological Station.

In general, the vegetation of Itasca Park shows the interaction of elements of mixed conifer-hardwood, deciduous, and boreal forests and the prairie. Closeness of the prairie is particularly indicated by the frequent summer drought periods.

The origin of present upland forest stands in the park was largely associated with past fires. These stands have been subject to the process of post-fire stabilization in which fire protection has become an important factor in determining the future forest composition.

Mature and overmature stands of red pine (*Pinus resinosa* Ait.) and white pine (*Pinus strobus* L.) occupy a considerable part of the entire range of the upland forest complex. Young pine stands are almost absent. The mortality rate of overmature pines is high due to windthrow and other causes. It has been apparent that pine seedlings, especially red pine, are present in extremely small numbers and rarely succeed in competition with other plants under existing stand and site conditions. Red and white pine stands were an important component of the presettlement forest and are of great aesthetic value for the park. Their continuity into the future is of concern to management and the public.

This study will examine the advance reproduction in the upland forests in relationship to stand and site characteristics with emphasis on pine reproduction.

The first part of the study will deal with vegetation and environment analyses of the forest ecosystems and construction of a framework in which the forest ecosystems will be organized. Advantage will be taken of a combination of ordination and classification approaches. The method of synecological coordinates will be used to locate the forest ecosystems along moisture-nutrient and heat-light coordinate axes. At the same time, the four-dimensional space will be divided into classification units -- forest types, adjusting the type boundaries to the clustering pattern of ecosystem distribution and certain properties of the ecosystems. Such an approach groups functionally similar ecosystems into forest types suitable for mapping and management purposes, and for making conclusions about reproduction in a more general way. The forest types will provide the basic information about the stand and site conditions which is a prerequisite for prediction of reproduction occurrence and its development.

The second part of this study will deal with an analysis of the existing reproduction conditions and ecological factors determining the failure or success of advance reproduction. Presence, abundance, composition, distribution, and growth pattern of advance reproduction will be studied as related to motherstands, moisture-nutrient gradients, and forest types. The change in reproduction abundance and composition will be examined over a period of time. The role of shrubs and ground cover in competition with pine reproduction will be stressed.

Besides the data from the general study area, records from permanent plots will be used to study and compare the trends in development of pine reproduction under different stand and site conditions.

The reproduction data in this study, except for permanent study areas, are based on one-year measurements. Conclusions about the change in reproduction pattern and abundance in the general study area are indirect, based on abundance, height, and age estimation of the present advance reproduction.

Fire protection, great abundance of shrubs, and excessive deer population prior to 1945, have been cited as the main factors preventing adequate pine establishment. This study attempts to shed additional light on the nature and dynamics of the reproduction processes.

2. DESCRIPTION OF THE STUDY AREA

2.1 Geographic Location

Itasca State Park encompassing 32,054 acres is located in northwestern Minnesota and lies in adjacent portions of Clearwater, Becker, and Hubbard counties.

The square near the center of maps of northwestern Minnesota (Fig. 1), characterizing general climatic, geological, and vegetational conditions indicates the location of Itasca State Park. Figure 1 also shows a map of Itasca State Park. Plot identification numbers (2-90) refer to the locations of the investigated forest ecosystems. Plot 3 is located in an area on which reproduction data have been collected since 1947. Another permanent reproduction study area is designated by "T" (Fig. 1). Appendix Table 1 shows the legal descriptions of plot locations.

2.2 Climate

Minnesota, lying in the center of the North American land mass, is characterized by a typically continental climate. In winter the prevaling northwest winds provide the area with cold dry air, and in summer the prevaling southwest winds carry warm moist air into the area. In addition, the westerly winds provide dry, continential air. Seasonal and annual interaction of these air masses largely determine the weather and climate in Minnesota.

Climatic data in Figure 1 illustrates the mean annual temperature and precipitation from 1926-1955 in northwestern Minnesota (Baker, 1958). Climatogram approach by Walter (1963) was chosen to characterize the climatic conditions in the Itasca State Park area (Fig. 2).

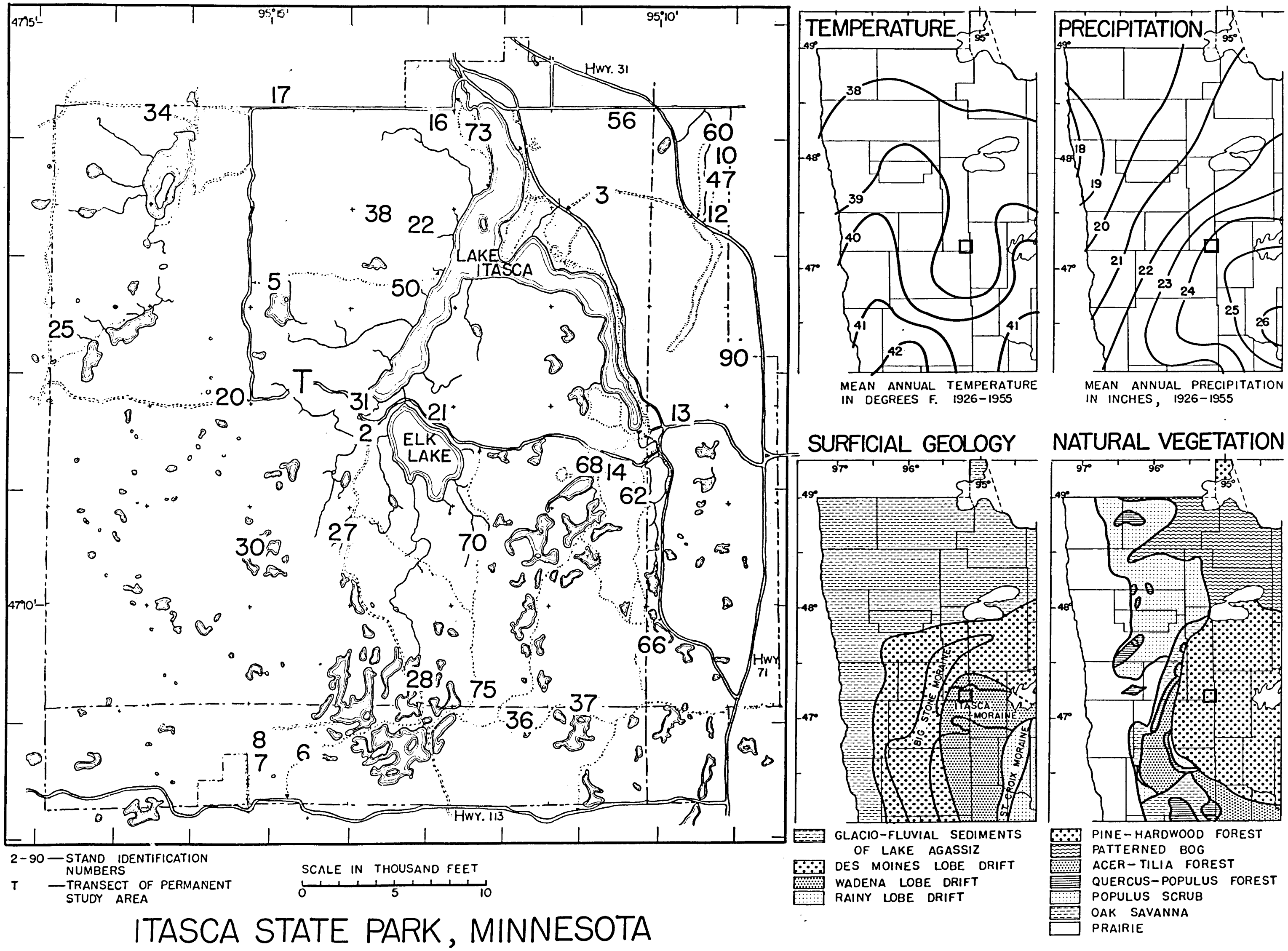

Figure 1. Location of sample areas in Itasca State Park, Minnesota. Maps of northwestern Minnesota (Itasca Park as a square in the center) show temperature and precipitation (Baker, 1958), surficial geology (Wright, 1962 and McAndrews, 1966), and natural vegetation (Marschner, 1930 and McAndrews, 1966).

Climatograms were constructed based on the Itasca station records for the last 30 years (U.S. Weather Bureau, 1936-1965). Diagrams were prepared as used by Walter (1963) on a scale where a temperature of 1^{o}C corresponds to 2 mm precipitation. If the precipitation curve falls under the temperature curve at such a scale, it is an indication of extreme drought conditions. Comparison between the curve of temperature and precipitation is justifiable because evaporation is mostly proportional to temperature. To obtain the water balance it is necessary to know the ratio of evaporation to rainfall. Many authors have used the ratio of precipitation to temperature as an indicator of the water balance (Walter, 1963).

The first diagram in Figure 2 shows the distribution of mean monthly temperature and precipitation and the seasonal rhythm of other most important factors. The extreme difference between the January and July temperatures emphasizes the continentality of the climate. Minnesota has great extremes in temperatures not only from season to season and month to month, but also on a diurnal basis as well. An absolute range of 173^{o}F in Minnesota is only 31^{o}F less than the absolute range measured anywhere in the continental United States (Baker and Strub, 1965). Itasca station shows an absolute range of 156^{o}F for the last 30 years. There is also great variation in precipitation with over half coming during the summer months and a maximum in June. Winter precipitation is meager. According to Baker et al. (1967) the Itasca station had a maximum annual precipitation of 35.51 inches in 1949 and a minimum of 13.93 in 1929 for the period from 1912-1965. Normal precipitation, based on 1931-1960 records, was 25.25 inches.

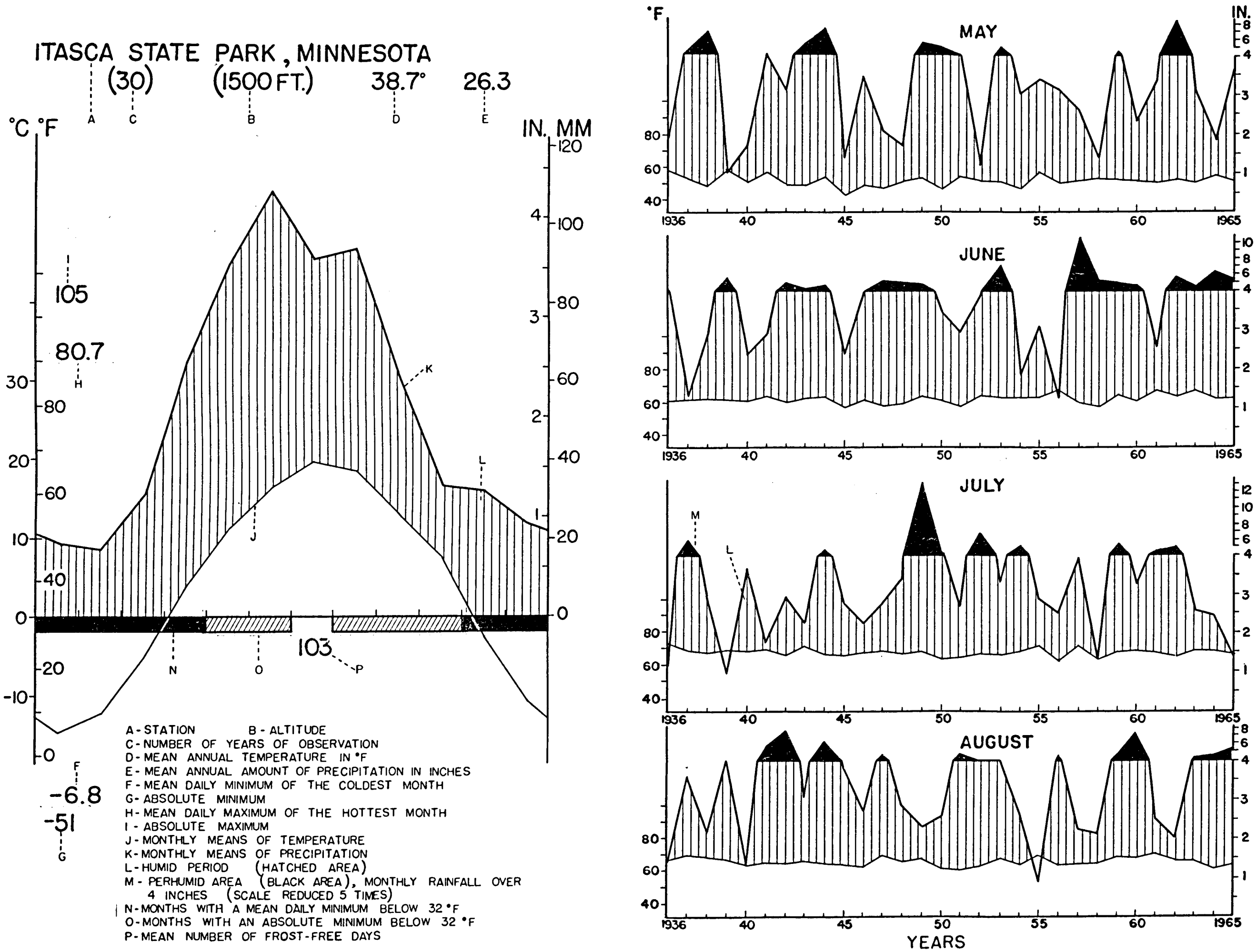

Figure 2. Monthly means of temperature and precipation (Walter's climatic diagram) and monthly temperature and precipication for May, June, July, and August from 1936 to 1965 in Itasca State Park, Minnesota.

The four diagrams (Fig. 2), showing distribution of monthly temperature and precipitation, indicate that there are years with drought conditions during the growing season. The bulk of the precipitation in Minnesota actually is received in a few days of high precipitation, many days have very low precipitation, and an even greater number of days have no recorded precipitation. Irregular drought periods of 10 to 30 days with little or no rainfall are characteristic during the growing season in the area. According to calculations by Blake et al. (1960) for soils in the Itasca Park area having root-zone water-holding capacities of one, three, and five inches per foot, one can expect at least 65, 35, and 17 drought-days per growing season, respectively, 50 percent of the time.

In most cases, the drought periods are not critical for tree growth, but they may cause severe damage to reproduction, especially for conifer seedlings in their early growth under conditions of competition with other plants.

2.3 Glacial Geology

The development of Minnesota's landscape is marked by complex ice movements of late-Wisconsin glaciation which reached its maximum about 13,000 to 14,000 years ago. The surficial geology of northwestern Minnesota with Itasca State Park in the center (Fig. 1) reflects the activities of three ice lobes. Arneman and Wright (1959) and Wright (1962) summarized the ice movements and their deposited materials in the area. The Des Moines Lobe advanced from the northwest and carried a gray or buff generally silty till with

Paleozoic carbonates from the Winnipeg lowland and Cretaceous shale from the Red River Valley. On this calcareous till, a silt loam soil has developed. The Wadena Lobe came from the Winnipeg lowland and moved southeastward into north central Minnesota. This ice lobe carried a gray to buff calcareous sandy till with Paleozoic carbonates but no Cretaceous shale. Sandy loam soils have developed on this calcareous till. The Rainy Lobe advanced from the northeast over the area of gabbro and volcanic rocks north of Lake Superior and produced a gray sandy till in the area. According to Wright and Ruhe (1965), the northwestern part of the St. Croix Moraine is composed of brown sandy till which rests on the Wadena Lobe till with interlamination at the contact. A noncalcareous sandy loam soil has developed from these tills.

Itasca State Park lies in the area of the Itasca Moraine which was formed by a stillstand of the Wadena Lobe. According to Zumberge (1952) the retreat of the ice in the park area was slow, and this resulted in the hilly terminal moraine with numerous kettles, now filled with lakes or bogs. Many local sandy outwash deposits were formed by meltwater in addition to those in drainageways. Most of the smaller lake and pond basins originated from the melting of buried ice blocks (McAndrews, 1966).

2.4 Soils

Repeated glaciation, interaction of ice movements, and meltwater action have deposited materials in the park area with a wide textural range on which soils have developed with rather great variations in moisture and nutrient regimes.

The soils of the park area belong mainly to Nebish-Rockwood and Menahga-Marquette soil associations as classified by Arneman (1963). Figure 5 shows the general soil distribution of the investigated forest ecosystems in moisture-nutrient gradients.

Soils of Nebish-Rockwood group vary texturally from coarse or gravelly sandy loams to loams and clay loams (Rust et al., 1958), and consequently show a variation in internal drainage and profile development. Leaching has removed a part of the lime from the upper soil but, in general, the rooting zone is well supplied with bases. Nebish-Rockwood soils support northern hardwoods and old growth white pine. Extensive areas are covered with aspen-birch stands with different stages of northern hardwood development in the understory or vigorous shrub growth.

Marquette soils are formed in loam materials over calcareous gravel within 18 inches of the surface and are well drained. The old growth red pine stands as well as mixtures of jack pine and red pine grow on these rather coarse-textured soils. Shrub layers with interspersed hardwood reproduction are well developed under pine stands, except for stands with a spruce-fir understory.

Menahga soils have developed on fine to medium outwash sands under influence of conifers, mainly jack pine. Shrub invasion and development are relatively slow as compared to soils with higher moisture and nutrient levels. Scattered pine reproduction may be found under these site conditions, but Menahga soils occupy only a rather small percentage of the total park area.

Baudette soils are lucastrian and have developed on slackwater deposits. They have only a very local significance on upland sites within the park.

2.5 Vegetation

Minnesota is the meeting ground of the Prairie, Lake Forest, and Deciduous Forest formations. The Boreal Forest formation does not reach Minnesota but its elements, such as *Abies* and *Picea*, are present.

The Itasca State Park area constitutes a part of the Pine-Hardwood Forest (Fig. 1). According to Braun (1950) it belongs to the Minnesota Section of Hemlock-White Pine-Northern Hardwoods Region. Under other classification systems Itasca State Park is located in the Lake Forest formation (Weaver and Clements, 1938), in the western portion of the Northern Forest Region (Soc. Amer. For., 1954), and in the Great Lakes Pine Forest according to Küchler (1964).

Bordering the forest-prairie vegetation transition line or being even a part of it, Itasca State Park vegetation exhibits a rather great variation. The pattern of natural vegetation is strongly influenced by physiographic and soil conditions, and local physiographic variations give rise to distinctive microsites with their own characteristic vegetation (McAndrews, 1966). This results in a mosaic of forest types of limited area.

Mature and overmature red pine (*Pinus resinosa*)[1/] and white pine (*Pinus strobus*) are the predominant trees in the park due to

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[1/] Botanical nomenclature of tree species follows Little (1953), that of other species, Fernald (1950).

their size, longevity, and resistance to fire. Red pine occurs in relatively pure stands or mixed with jack pine (Pinus banksiana) and some white pine on coarser-textured mineral soils. White pine is usually present in form of an open overstory of scattered trees in hardwood stands on finer-textured soils. Balsam fir (Abies balsamea) and white spruce (Picea glauca) occur on sites with mesic moisture conditions, mainly along the numerous lake margins. Quaking aspen (Populus tremuloides), paper birch (Betula papyrifera), and bigtooth aspen (Populus grandidentata) are widespread on the many burned areas. Sugar maple (Acer saccharum), American basswood (Tilia americana), and also red oak (Quercus rubra) are the important tree species on the most mesic sites accompanied by aspen, paper birch, bur oak (Quercus macrocarpa), American elm (Ulmus americana), green ash (Fraxinus pennsylvanica), black ash (Fraxinus nigra), and ironwood (Ostrya virginiana).

The frequent fires in the 19th century and before created conditions favorable for establishment of less shade-tolerant species such as pines, aspen, and paper birch. Since the introduction of fire protection in the area, the successional trend according to Buell and Cantlon (1951) has been toward the more shade-tolerant sugar maple or balsam fir. In this post-fire stabilization process, shrubs have played an important role as a forest undergrowth. Lee (1924) indicated that the most striking feature of these forests was the abundant undergrowth of shrubs and ground cover. Kell (1938) pointed out that there was a complete lack of successful pine reproduction under closed forest conditions throughout the park.

Since that time several other studies and observations have resulted in similar statements about the complete absence, scarcity, and poor condition of pine reproduction (Hansen and Duncan, 1954; Hansen, 1955).

In the early studies by Bergman and Stallard (1916) red pine and white pine were considered as climax species in northern Minnesota. Lee (1924) emphasized the importance of fir-spruce in the park area and expected that Acer-Pinus strobus and Abies-Picea forests will develop concurrently. Kell (1938) stated that fir-spruce-birch on coarse-textured mineral soils and maple-basswood on fine-textured mineral soils can be considered as climax communities. In 1939, Buell and Gordon (1945) investigated a spruce-fir and maple-basswood forest contact zone in the park and concluded that spruce-fir is the more aggressive. Later examination of the same area (Buell, 1956) led to the conclusion that both forest types exist side by side with rather sharp boundaries and that it was doubtful that one of these upland forests could have the potential to advance into the other. In 1959, however, the main boundary between the maple-basswood and spruce-fir had shifted at the expense of the spruce-fir; in addition, young islands of maple-basswood had become established in the spruce-fir community. This was a reversal of the situation 20 years before (Buell and Martin, 1961; Westman, 1968). Studies of stand structure and environmental conditions in different forest types are under way at the present time to further clarify the main successional trends in Itasca State Park (Ness, 1969).

According to McAndrews' (1966) pollen studies the present type of vegetation has its origin about 2000 years ago. About this time, white pine migrated in and dominated the forest. Red pine and jack pine joined it about 1000 years later. All the three pines together with hardwoods formed the Pine-Hardwood forest, which persisted until the time of settlement.

Most of the park area was burned over several times during the 19th and 18th centuries and periodic fires were probably common earlier. The fire history of the park has been studied by Spurr (1954) and Frissell (1969), among other workers. The years of fire occurrence were determined by studying annual growth rings of old, fire-scarred trees. The origin of many rather even-aged forest stands has been found to correlate with the fire years.

The major present red pine stands became established after fires in 1803, 1811, and 1820. The fire in 1714 gave rise to the oldest red pine stands now in the park, about 240 to 250 years old. However, single trees or groups of trees can be found considerably older. Frissell (1969) aged by cross-dating a red pine tree 350 years old. Closed, pure white pine stands are rare. Areas burned in the two large fires in 1865 and 1886 were mainly regenerated to aspen and jack pine. There have been few large fires reported after 1886 in the park area. Since complete fire protection was introduced, the successional trend has been towards hardwoods.

Subsequent chapters will deal with the methods, present upland forest conditions, and the place of pine reproduction in relation to new growth of other species and site conditions in the park.

3. METHODS

3.1 General

Methods of vegetation analysis may be considered in four main groups: physiognomic, floristic, physiographic, and integrated. Physiognomy of vegetation deals with the outward, more or less superficial appearance of vegetation. Floristic approach prescribes the identification of taxa and determination of the role of individual taxa in the community. The two approaches are complementary, both being based on the characteristics of the vegetation itself. Physiographic approach emphasizes the importance of environmental factors. In fact, all three methods deal with ecosystems but with different emphases on the individual constituents. In application these three methods are often combined.

The floristic approach has been central in the method of Braun-Blanquet's school which deals with characteristic species combinations as they reflect environmental conditions. Characteristic species combinations are closely related to the concepts of ecological groups. Some of the methods developed by the Wisconsin school under the leadership of Curtis are more purely floristic than is the method of Braun-Blanquet. These methods by the Wisconsin school deal only with taxonomic similarity of communities independently of environmental considerations. Ellenberg (1956) defined ecological groups of species according to their similarity in relation to individual environmental factors or combinations of some environmental factors. If environmental factors are considered simultaneously, ecological groups are frequently called sociological groups. Janssen

(1967) analyzed the vegetation in Itasca Park and vicinity by means of sociological groups consisting of species which show comparable sociological amplitudes, i.e. the combined effect of all ecological factors. The concept of sociological groups considers the plants in a group to be similarly related to the whole environment. The method of synecological coordinates (Bakuzis, 1959) used in this study is a floristic approach to vegetation analysis. It belongs to the method of ecological groups, but it is also closely related to continuum and gradient methods. The method of synecological coordinates deals with plants which are similar in relation to one of the environmental factor complexes but not necessarily to others. It is a more formalized method than the method of sociological groups. The Wisconsin ecological school focuses attention on construction of multidimensional space based on vegetation similarity indices (Curtis, 1959). In contrast the synecological coordinate method of Minnesota does not attempt to construct a multidimensional vegetation space from similarity indices of species composition directly, but from the beginning total similarity is partitioned into similarity of occurrence along individual gradients of moisture, nutrients, heat, and light. These four factor complexes provide the major synecological axes.

Whittaker (1956) developed an environmental gradient approach which somewhat resembles the vegetational continuum by the Wisconsin school. Hills (1952, 1960) selected and combined physiographic characteristics significant for the vegetation to construct moisture, nutrient, and local climate axes. Loucks (1962) developed more exact moisture, nutrient, and local climate gradients and observed distribution of forest vegetation along these gradients as measured by importance values according to the Wisconsin school. Grigal (1968) related plant communities to environmental gradients in northeastern Minnesota, using numerical taxonomy methods. Jones (1967) constructed moisture and temperature ordinates and evaluated them in relationship to height-growth rate of aspen in the southern Rocky Mountains. Waring and Major (1964) developed moisture, nutrient, heat, and light coordinates calibrating species from field measurements of environmental factors. Coordinate methods represent further formalization of continuum and gradient ideas.

Environmental and synecological coordinates both belong to the wider group of ecosystem coordinates.

3.2 Synecological Coordinates

The method of synecological coordinates (Bakuzis, 1959) is based upon the knowledge of species behavior in nature under conditions of competition with respect to moisture, nutrient, heat, and light factor complexes. The term "synecological" is used to emphasize the point that all observations concerning the occurrence of individual species was made under conditions of competition with other species. Relative values from 1 to 5 are assigned to individual forest species according to their prevailing occurrence at different intensities of moisture, nutrient, heat, and light factors. Those species occurring predominantly at the lowest intensity of an environmental complex received the lowest coordinate value of 1; the highest intensities are graded as 5, and intermediate coordinates are 2, 3, and 4 depending on their relative position of occurrence along the gradient. This procedure is repeated independently for each of the four factor complexes. Thus in synecological coordinates, a species is assigned four values corresponding to its relative position with all other species in its requirements for moisture, nutrients, heat, and light.

Community coordinate values are computed as averages of the coordinate values of all species present in the community. The individual species is evaluated with respect to microsites; communities are interpreted in terms of macrosites.

A provisional assessment of coordinate values for individual species in Minnesota was obtained from earlier studies and observations adjusting them according to the species occurrence in different forest communities within the region.

Synecological coordinates provide a means of evaluating the intensity of the biotically effective part of the essential environmental factor complexes, moisture, nutrients, heat, and light. They provide models which can be used to present and investigate characteristics and relationships of the different constituents of biological systems, for comprehension of complexity, and for information storage. They can also be used to obtain additional information from data accumulated under the rules of many other methods, to demonstrate known laws and rules, and to indicate the existence of others.

In this study the method of synecological coordinates will be used to aid in defining forest types; to investigate the plant cover interrelationships; to analyze and compare the presence, density, and dynamics of conifer and hardwood reproduction; and to study its relationships to environmental factors. Appendix Table 5 presents the list of plants and their synecological coordinates.

3.3 Field Methods

Stand descriptions and plant lists were prepared for 130 forest communities in a reconnaissance survey of the park in 1963 and 1964. An attempt was made to cover the full range of upland site conditions of the general study area. Homogeneity of environmental conditions was sought, but stand variability of transient character was included. In 1964, 36 forest stands were selected for further study. Selection of forest stands was mainly based on their synecological coordinate values, tree species composition, stand age, and also geographical distribution. The minimum size of stand area was about two acres (8,000 m^2).

Eight circular two-milacre (8 m^2) plots for reproduction study were randomly located and permanently established in each stand. The number of seedlings, sprouts and shrubs, their age and height, was determined for individual species. The age of reproduction and shrubs was estimated by counting the whorls or annual node scars. Plant lists were prepared for each two-milacre plot separately and supplemented by species occurring outside the plots throughout the whole stand. Ground vegetation, shrub, and reproduction layers were estimated as cover percentages of the total area in reference to two-milacre plots. Tree canopy was estimated as cover percentage in reference to 1/10 or 1/20 acre circles.

Two soil pits (3 ft. x 6 ft. x 6 ft.) were dug in each stand and soil profiles were described. The organic and mineral horizons were sampled for mechanical and chemical soil analyses.

A permanent reproduction study area ("T" in Fig. 1) in red pine-balsam fir forest of variable stand density was established by E. V. Bakuzis in 1953 and plots were remeasured in 1959 and 1964. Forty circular 10 m^2 (2.5 milacre) plots, 20 m apart, for reproduction study were systematically located in two parallel lines, 40 m apart (Fig. 17b). All species were recorded according to their presence and cover estimates made for tree reproduction and layers of shrubs, herbs, mosses, litter, and slash. The number of seedlings, sprouts, and shrubs, their age and height was measured for individual species. Trees of one inch in diameter at breast height and larger were tallied on 100 m^2 (1/40 acre) plots having the same plot center as the 10 m^2 reproduction plots. Age and height measurements were made by diameter classes for red pine and balsam fir. Dead trees and stumps were also recorded. The study area was subdivided into five groups of plots based mainly on differences in density of balsam fir understory, forest undergrowth, and physiographic features. Four soil profiles were described in the area. In 1966, a 1,200 feet long and 16 feet wide transect was made over the area between the two parallel plot lines (Fig. 17a and 17b).

3.4 Laboratory Methods

Soil samples were air-dried, passed through a 2 mm sieve, and tests were performed on the less than 2 mm soil fractions.

Determination of soil texture and organic matter for the humus layer and A1 horizon was made in the laboratories of the School of Forestry. Determination of pH, organic matter, extractable phosphorus, exchangeable potassium, calcium, and magnesium was made by the Soil Testing Laboratories in the Department of Soil Science, University of Minnesota. The methods of analyses, except for calcium and magnesium, have been described by Grava (1962).

Textural analysis for percentage of sand fractions, silt, and clay for each mineral horizon was made using the modified hydrometer method (Day, 1965) and sieves. Readily available water capacity was computed according to procedures worked out by Franzmeier et al. (1960) for different soil texture classes. An assumption was made that under undisturbed forest soil conditions the bulk densities for the same soil texture classes are comparable.

Organic matter was determined by a colorimetric procedure using the Walkley-Black oxidation. In addition, organic matter of humus layers and A1 horizons was estimated by ignition at 550°C. Soil acidity was determined electrometrically with a Beckman Zeromatic pH Meter on a 1:1 soil to water suspension. Phosphorus was extracted using Bray's No. 1 solution and determined on a Coleman Junior Spectrophotometer. Exchangeable potassium, extracted with a 1N ammonium acetate solution buffered to pH 7, was determined on a Perkin-Elmer Flamephotometer. Exchangeable calcium and magnesium were leached from the soil by 1N ammonium acetate solution, buffered to pH 7, and the determination was made by Absorption Spectrophotometry, Perkin-Elmer Model 303.

4. CHARACTERISTICS OF FOREST ECOSYSTEMS

A "system" is usually defined as a set of elements together with their relationships. According to Tansley (1935), ecosystem is a particular category of physical systems, consisting of organisms and inorganic components in a relatively stable equilibrium, open, and of various kinds and sizes.

An ecosystem can be defined from different points of view. In forestry, attention is focused on trees as main components of the forest ecosystem and on their relationships to other ecosystem components. Lutz (1959) defined a forest as an ecosystem involving the total physical environment and the whole of living organisms.

An ecosystem can also be considered at different levels. The generally accepted level for forestry needs is based on delineation of ecosystems at a level of forest communities. In this study the forest community is conceived as the living part of an ecosystem with rather uniform species composition, physiognomy, and site conditions. The terms forest community, forest stand, forest cover, and site will be used along with the term ecosystem and considered as interrelated subsystems of the particular ecosystem.

Characteristics of forest ecosystems include general properties of ecosystem space and classification and description of local forest types.

4.1 General Properties of Ecosystem Space

Properties of ecosystem space will include the general extension and shape of the ecosystem space of upland forests, particularly the extention and shape of synecological fields. Further, the variability within the individual ecosystems will be considered with special emphasis on taxonomic variability, ecological variability, and site variability.

4.11 <u>Extention and shape of the ecosystem space of upland forests</u>

In this study, the upland forest ecosystem space is conceived as a distribution of individual ecosystems in moisture, nutrient, heat, and light coordinates, used as the principal coordinates. An ecosystem space can be imagined as a multidimensional space with many bivariate fields. This is a parameter space with an unlimited number of dimensions serving as a model for reference and understanding of ecosystem relationships. Since the method of synecological coordinates is the principal method used in this study, the terms synecological coordinates and synecological field are used as substitutes for ecosystem coordinates and ecosystem field. Synecological fields are areas of response of a phenomenon (e.g. individual ecosystems, their components and characteristics) as determined by two or more synecological coordinates. The main attention will be paid to the edaphic field (moisture-nutrient coordinates), although the four synecological coordinates allow for six bivariate combinations.

Locations of the investigated ecosystems in geographic or "real" space were shown in Figure 1. Figure 3 shows the distribution pattern of 36 studied forest ecosystems and six ecosystem types in edaphic (moisture-nutirent coordinates) and climatic (heat-light coordinates) fields.

The first two diagrams in Figure 3-1 show the extent and shape of three different edaphic and climatic fields of upland forests. The shaded fields indicate the pattern of ecosystem distribution when the presence of all species in a community is considered in assessment of community coordinate values. The medium sized field of ecosystem distribution is obtained from the averages of eight subplot coordinate values. Average coordinate values include plants of higher frequencies several times. This is to some degree an expression of dominance in community coordinate values as compared to those based purely on species presence. The largest of the fields refer to distribution of individual two-milacre subplots. Individual subplot coordinate values reflect the microsite conditions while community coordinate values, based on species presence, are an expression of macrosite conditions.

The other two diagrams in Figure 3-1 show functionally similar ecosystems with respect to moisture-nutrients and heat-light, grouped into six ecosystem types (forest types). The relationships of functionally similar communities in one ecosystem type are homomorphic (one-many relations), allowing for substitution of those species with similar synecological behavior. The distribution of ecosystem types is shown in edaphic and climatic fields. The individual ecosystems remain in the same types in both synecological fields. This is largely the case in the four remaining bivariate combinations of synecological fields not shown here.

The locations of ecosystem types (shaded) are based on total assessment of species present in each community while those with interrupted lines are based on average coordinate values of eight subplots. Similar to the first two diagrams where undivided total upland forest complex is shown, they reflect the macrosite and average microsite conditions, respectively. The arrows join the corresponding pairs of macro- and microsites. They also indicate the central tendency or contraction of edaphic and climatic fields when community coordinate values are determined on basis of species presence as compared to those determined based on species partial dominance.

The positions of ecosystem types (shaded) numbered from 1 to 5, based on species presence, are higher in relative moisture-nutrient values than those based on average subplot coordinate values (dominance effect) in the edaphic field. This indicates that in these five types species with higher moisture-nutrient requirements are distributed with low frequency. The same five types in the climatic field, based on species presence, are lower in light values but higher in heat values than those based on species dominance. This indicates that in these types species with higher light requirements are well distributed but species with high heat requirements are found with low frequencies. The reverse is true for the type 6 in both synecological fields.

At present, the forest types numbered from 1 to 5 are largely represented by the seral stages of upland forests with dominating tree covers of intolerant tree species. Forest type 6 is represented by communities of advanced northern hardwood development. A more detailed discussion about the delineation of the ecosystem types (forest types) will be given in the Section 4.2.

4.12 Variability within individual forest ecosystems

As previously pointed out, forest ecosystems were delineated at the level of forest communities to consider the practical aspects of silviculture and forest management. This reflects some variation

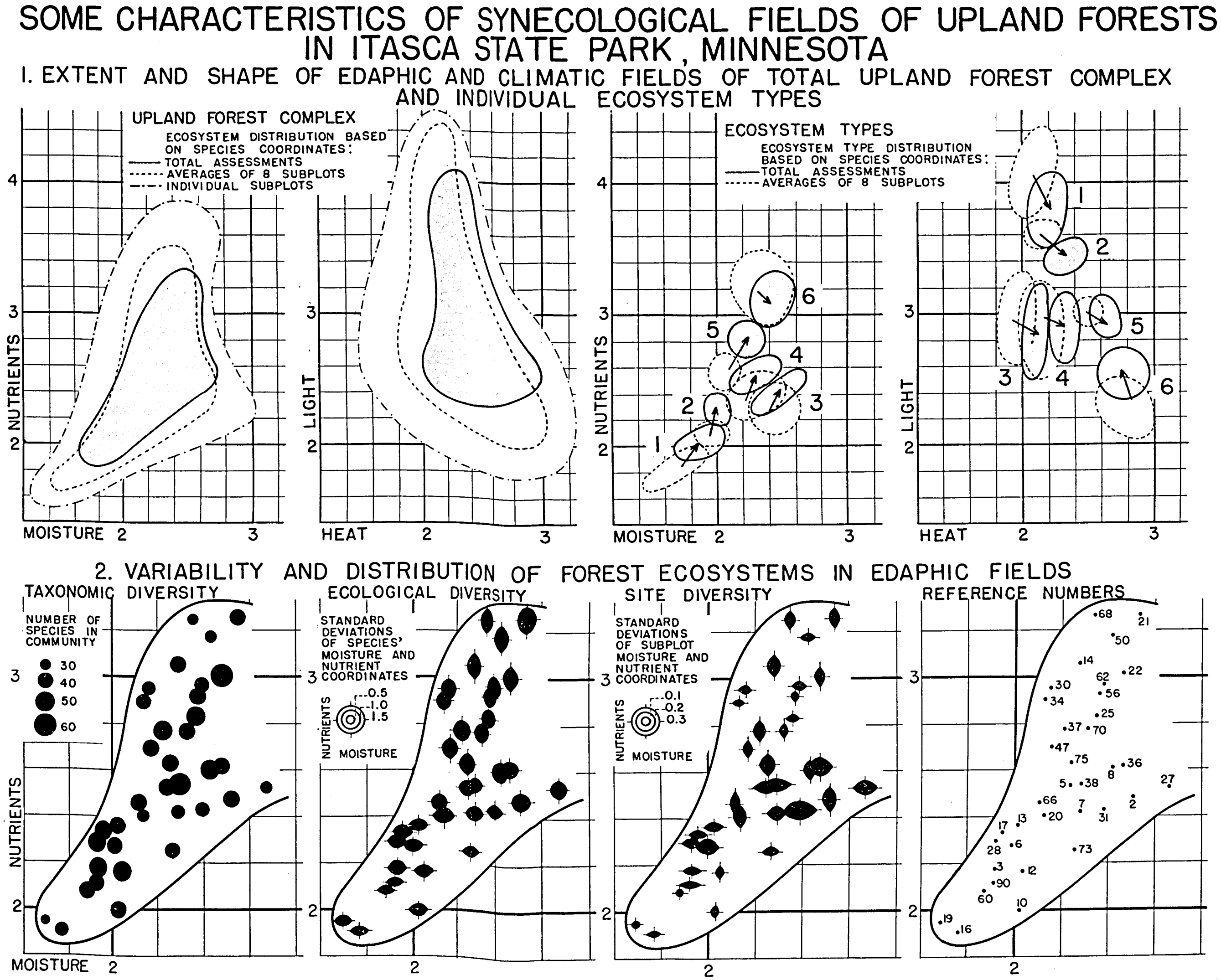


Figure 3. (1) Upland forest complex and ecosystem types (forest types) in edaphic and climatic fields (moisture-nutrient and heat-light coordinates), and (2) variability, distribution, and location of ecosystems studied in the edaphic field of upland forests in Itasca State Park, Minnesota.

in vegetation pattern and site conditions. In many cases only microsites assure homogneeous locality conditions. Microsite variability may influence vegetation patterns and affect forest reproduction both in terms of quality and quantity.

Figure 3-2 shows the locations of the studied individual forest ecosystems in the edaphic fields (moisture-nutrient coordinates). Each ecosystem location reflects the total plant response to moisture-nutrient conditions relative to positions of other ecosystems.

Figure 3-2 also demonstrates the variability of ecosystems in terms of number of species present in a community (taxonomic diversity), representation of different ecological groups in a community (ecological diversity), and variation of site from place to place in a community (site diversity). According to Bakuzis (1967), ecological diversity can be calculated as the standard deviation of species' synecological coordinates in a community and site diversity -- as the standard deviation of synecological coordinates from different subplots in a community.

The maximum taxonomic diversity occurs in communities of intermediate nutrient conditions and tends to be intensified in transitional areas along the boundaries of ecosystem types (Fig. 3-2). These areas in the edaphic field largely coincide with the distribution of communities with less dense forest cover of intolerant tree species. Forest communities on dry, nutrient-poor sites (lower part of the edaphic field) have rather open tree cover, but only less demanding species can persist here. Species in communities on mesic, nutrient-rich sites (upper part of the edaphic field) undergo severe competition and only a limited number of species can survive. There is no correlation between taxonomic diversity and moisture-nutrient coordinates (Table 1).

The terms "poor", "intermediate", and "rich" referring to nutrients, and "dry" and "mesic" referring to moisture, are used in a comparative sense, contrasting the site conditions of upland forests in this area. Site fertility refers to a number of soil characteristics and processes occurring within soils which are important to plant growth and includes climatic conditions. Synecological coordinates integrate the entire range of these characteristics, processes, and conditions, but can disagree with intensity levels of individual nutrients. They will be discussed in Section 4.21.

The maximum ecological diversity occurs in mesic, nutrient-rich forest ecosystems. The second diagram in Figure 3-2 shows ecological diversity of ecosystems in terms of moisture and nutrients. Ecological diversity in nutrients is highly correlated with nutrient coordinates (Table 1), while the diversity in moisture has no correlation with moisture coordinates. Species with low nutrient requirements are present in more or less large numbers in all communities while species with high nutrient requirements are limited to rich sites. Upland forests represent almost a full range of nutrient conditions while they cover only a half of the total moisture range of forest adaptation. Plants of high moisture requirements (coordinate 5) seldom occur in upland forests, even those with coordinate 4 are poorly represented, therefore the

Table 1. Correlation coefficients of community taxonomic diversity, ecological diversity, and site diversity with synecological coordinates in upland forests of Itasca State Park, Minnesota[1]

Diversity	Coordinates: Moisture (M)	Nutrients (N)	Moisture and nutrients (MN)
Taxonomic diversity	0.045	-0.025	-0.003
Ecological diversity (M)	0.079		
(N)		0.947**	
(MN)	0.756**	0.899**	0.908**
Site diversity (M)	0.222		
(N)		0.341*	
(MN)	0.430**	0.095	0.240

1/ Based on species presence in eight 2-milacre subplots per community.

* Significant at 5% level.

** Significant at 1% level.

variability in moisture is less well expressed. Combination of both kinds of diversities shows a high correlation with nutrient coordinates, combination of moisture and nutrient coordinates (based on Euclid's distance formula), and also a high correlation with moisture coordinates. There is a moisture-nutrient interaction and it seems that increase in nutrients make moisture more effective. A question could be raised as to what can be done with fertilizers for better utilization of moisture. Ehwald (1953) pointed out that physiological factors such as moisture and nutrients can be substituted only in the sense that better nutrition can increase the ability of a plant to take up more moisture.

The third diagram in Figure 3-2 shows site diversity of ecosystems in terms of moisture and nutrients. The magnitude of standard deviations of coordinates from different subplots reflects the microsite variation within a larger ecosystem. The maximum site diversity occurs near the center of the edaphic field. Relief and other characteristics of site variability have rather strong influence on the homogeneity and distribution pattern of the ground vegetation and is expressed in frequent occurrence of two-storied tree canopies in these ecosystems. The correlations between site diversity and synecological coordinates are not pronounced, both in terms of moisture and nutrients and combination of the two (Table 1).

The last diagram in Figure 3-2 shows the identification numbers of the ecosystems studied. In most of the following figures the identity of individual ecosystems will be shown. This will help to make comparisons between different measurements and characteristics of ecosystems.

4.2 Local Forest Types

Forest type is a descriptive term used to group stands of similar character as regards composition and development due to certain ecological factors by which they may be differentiated from other groups of stands. The term suggests repetition of the same character under similar conditions. A type is temporary if its character is due to passing influences such as logging or fire, permanent if no appreciable change is expected and the character is due to ecological factors alone (Soc. Amer. For., 1950).

Forest types, as used in this study, are units of the local ecosystem space and resemble forest types as recognized by

Pogrebnyak (1930). However, the type boundaries are adjusted to the distribution pattern of local ecological conditions and not drawn mechanically as in the universal type system by Pogrebnyak. According to Pogrebnyak, forest type includes forest lots occupied by one primary stand type and other characteristic associations with similar site conditions. This concept is also the essence of Cajander's approach to forest types which in English translation are known as forest site types.

In this study, synecological coordinates were used as an aid in interpreting different interrelationships among the elements of ecosystems and also as an aid in classifying ecosystem types (forest types). For this reason it is of particular importance to analyze soil and vegetation characteristics in relationship to synecological coordinates. Special attention will be given to forest cover types as recognized by the Society of American Foresters. Descriptions and comparisons of individual ecological forest types will follow.

4.21 Soil characteristics

The most commonly occurring soils on upland in Itasca Park were discussed in Chapter 2. Figure 4 shows the distribution of different soil characteristics of investigated forest ecosystems in the edaphic field. Soil characteristics were expressed in two ways, based on 6-inch top soil and 36-inch soil profile (including the organic layer), representing weighted average values of corresponding soil horizons on volume basis. Soil pH was given for the organic layer, 6-inch upper mineral soil, and soil parent material. The data show average values of two soil profiles per sample area.

While synecological coordinates provide a means of evaluating the intensity of the biotically effective part of the essential environmental factor complexes such as moisture, nutrients, heat, and light, they do not evaluate the intensities of individual soil factors. On the other hand, there is no single soil factor available which would fully define the vegetation's moisture and nutrient regimes. Conventional soil sampling and analysis provide only physiographic indication of the operational environment. According to Pallmann et al. (1949), relationships between plant communities and soils depend on the physiological conditions in terms of moisture, nutrients, aeration, and heat balance.

Certain soil chemical and physical characteristics were related to moisture and nutrient coordinates to explore the best possible relationships between the vegetational indication of the site conditions and individual soil factors. The diagrams in Figure 4 demonstrate these relationships graphically. Correlation coefficients are helpful in understanding and elaborating diagrams, especially when they are reviewed in sets. On the other hand, diagrams themselves show multidimensional relationships.

According to soil analysis data, the amount of extractable phosphorus ranged from 25 to 105 pp2m in the 6-inch top soil and from 25 to 80 pp2m in the integrated 36-inch soil profile (Fig. 4). Even the lowest amounts of extractable phosphorus can be rated as medium, but most of the soils can be categorized as high in

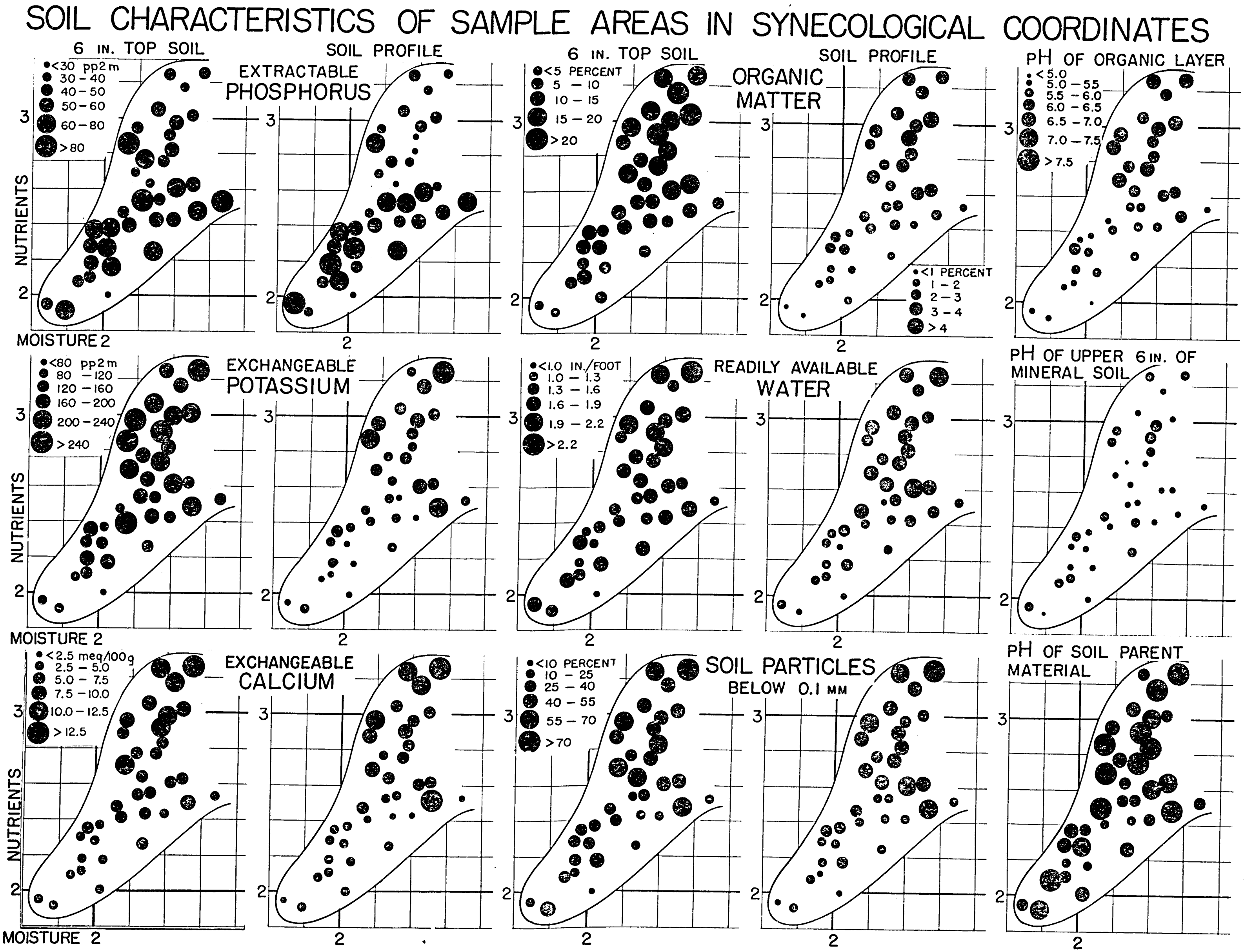


Figure 4. Some chemical and physical soil properties of 6-inch top soil and 36-inch profile in the edaphic field (moisture-nutrient coordinates) of upland forests in Itasca State Park, Minnesota.

phosphorus according to evaluation scales used by Farnham (1956) and Rust et al. (1958) for Minnesota soils.

In Figure 4 the first two diagrams show extractable phosphorus distribution in the edaphic field. It shows the most complicated relationship to nutrient coordinates of all soil characteristics presented. There is no simple linear correlation between phosphorus and nutrient coordinates. The correlation coefficients for the top soil and soil profile are - 0.108 and - 0.424, respectively (Table 2). If ecosystems were subdivided into two groups based on silt and clay content in soils, the correlation coefficient for the range of finer material soils (upper part of the edaphic field, primarily represented by Nebish-Rockwood soils) was - 0.196 as compared to + 0.532 for the range of coarser material soils (lower part of the edaphic field, primarily represented by Menahga-Marquette soils) in the top soil. Similar relationships exist between phosphorus and calcium ($r = -0.204$; $r = +0.354$) and between phosphorus and organic matter content ($r = -0.388$; $r = +0.251$), if ecosystems of finer and coarser material soils were considered separately. A weak positive correlation between phosphorus and nutrient coordinates was reached using the amount of phosphorus in the organic layer ($r = +0.394$). The relationships of phosphorus to other soil factors are similar to those to nutrient coordinates (Table 3).

The lack of direct relationships between soil phosphorus and forest productivity has long been known. Valmari (1921) pointed out that the available amount of phosphorus cannot be directly related to the yield capacity of forest soil, although there seems to be a negative correlation. Pluth and Arneman (1965) also found no significant or negative relationships between phosphorus in individual soil horizons or horizon combinations and nutrient coordinates. They stated that probably the determination procedure for phosphorus does not evaluate the phosphorus important to a plant's nutrition or that phosphorus is not a limiting factor affecting species' distribution in their Minnesota studies. Woodwell (1958) pointed out that Pinus serotina and certain other plants can take up phosphorus sufficiently from phosphates which are hard soluble. Baldovinos and Thomas (1967) indicated that clay content is a prime factor in phosphorus availability. It was found that good growth of plants occurs in clay soils where phosphorus extractable with a solution of 0.5 N NH4F is low comparable to that found in fertilized sandy soils. They claim that these observations should be helpful in devising an appropriate calibration of soil test values based on the percentage of clay in the soil.

There is a gradual increase in the amount of exchangeable potassium from the lower part of the edaphic field upwards with some tapering off at the highest nutrient level as indicated by nutrient coordinates. Potassium content varied from 60 to 310 pp2m in the top soil and 30 to 260 pp2m in soil profile. The absolute range of variation based on soil samples of individual horizons was from 20 to 600 pp2m. There are some ecosystems in the lower part of the edaphic field with soils which could be rated as very low in exchangeable potassium. However, the majority of soils are medium to high in potassium as rated by Farnham (1956) and Rust et al. (1958) for Minnesota soils.

The correlation coefficients between the amount of exchangeable potassium and nutrient coordinates are + 0.655 and + 0.672 in the top soil and soil profile, respectively. Similar relationship (r = + 0.674) between potassium of A2 + B2 + C horizons and nutrient coordinates was found in Minnesota studies by Pluth and Arneman (1965).

Exchangeable calcium shows the highest intensities in the upper part of the edaphic field. These are Nebish-Rockwood soils known to be adequately supplied with bases, especially calcium. According to soil analysis data, the exchangeable calcium ranged from 2.5 to 13.4 meq/100 g in the top soil and from 1.8 to 17.0 meq/100 g in the soil profile. The range of exchangeable magnesium (not shown in Figure 4), was from 0.7 to 2.7 meq/100 g and 0.5 to 4.3 meq/100 g in the top soil and soil profile, respectively. About 2.5 meq/100 g calcium and 1.0 meq/100 g magnesium are considered moderate levels of soil fertility, sufficient amounts for the majority of conifers by Wilde and Voigt (1955), provided other growth determining factors are satisfactory. Most of the areas studied fulfil these requirements, many of them would qualify for high level soil fertility in terms of calcium and magnesium exceeding 5.0 and 2.0 meq/100 g calcium and magnesium, respectively.

Exchangeable calcium shows a high correlation with nutrient coordinates in the top soil (r = + 0.839) and soil profile (r = + 0.632). Similar relationships exist between magnesium and nutrient coordinates (Table 2). In California, Waring and Major (1964) selected calcium

Table 2. Linear correlations between the community synecological coordinates and some soil physical and chemical characteristics for the organic layer, 6-inch top soil, and 36-inch soil profile in Itasca State Park, Minnesota.

Soil characteristics	Organic layer	Top soil	Soil profile	Organic layer	Top soil	Soil profile
	Correlation with:					
	Moisture coordinates			Nutrient coordinates		
Soil particles below 0.1 mm		0.452**	0.562**		0.713**	0.765**
Readily available water		0.411*	0.528**			
pH	0.540**			0.835**		
Organic matter		0.639**	0.654**	-0.652**	0.857**	0.856**
Extractable phosphorus				0.394*	-0.108	-0.424*
Exchangeable potassium				0.496**	0.655**	0.672**
Exchangeable calcium				0.815**	0.839**	0.632**
Exchangeable magnesium				0.554**	0.701**	0.660**

* Significant at 5% level.

** Significant at 1% level.

as a variable best related to soil fertility because, according to them, it more ably separated the nutritional aspects of the soil from other environmental effects. Computation of Grigal's (1968) data showed a linear correlation of + 0.777 between calcium levels and the environmental nutrient coordinates, and + 0.716 -- between calcium and the synecological nutrient coordinates in the 6-inch top soil in northeastern Minnesota. Relatively strong correlation between calcium and soil fertility was also emphasized by Aaltonen (1948) and other authors. Ehwald (1957) pointed out the special importance of calcium for forest crops indicating that considerably less mineral nutrients except calcium are required for production of one ton of dry matter forest crop than required for a ton of agricultural crop. In regard to conifer growth, especially to pine seedlings, the importance of Ca/K ratio in soils is stressed. Laatsch (1967) showed that on soils shallow to medium in depth and high in lime, young pine plantations often suffer from potassium deficiency. The richer the soil in calcium the more difficult for the conifers to obtain larger amounts of potassium. High lime content makes not only the uptake of potassium difficult, but also the uptake of boron, manganese, and iron. Potassium fertilization, together with silvicultural measures, may improve growth conditions of pine seedlings, especially their competitive ability for better moisture utilization, in some areas in the park.

Organic matter content varied from 3 to 28 percent in the top soil and from 1 to 5 percent in the soil profile. Organic matter content in the top soil shows the highest correlation with nutrient coordinate values ($r = + 0.857$) and also in the soil profile (Table 2). This is an indication that total nitrogen in the soil would also be highly correlated with nutrient coordinates. Organic matter content has a considerably better correlation with moisture coordinates than the percent of mineral soil particles below 0.1 mm and the amount of readily available water. The relationships of organic matter with other soil characteristics are shown in Table 3 and Figure 4.

The percent of soil mineral particles below 0.1 mm of the total soil ranged from 10 to 86 percent in the top soil and from 9 to 81 percent in the soil profile. The amount of readily available water varied from 0.9 to 2.5 inches per foot in the top soil and from 0.9 to 2.1 inches per foot in the soil profile. The percent of soil mineral particles below 0.1 mm shows better correlation with nutrient coordinates ($r = + 0.765$) than with moisture coordinates ($r = + 0.562$) in the soil profile. Similar correlation is found between the amount of readily available water and moisture coordinates ($r = + 0.528$). The relationship between the percent of soil mineral particles below 0.1 mm and the amount of readily available water is + 0.867 and + 0.752 in the soil profile and top soil, respectively.

The interpretation of soil moisture regime is complicated, especially in the Marquette profiles where the presence of thin, often interrupted bands of fine soil material in coarse textured soils may be more effective in moisture supply to plants than the soil analysis indicates. This fact may partially explain the relatively weaker correlations of soil physical properties with moisture coordinates than nutrient coordinates.

The pH values of the organic layers of Nebish-Rockwood soils (upper part of the edaphic field) ranged from 6.1 to 6.9 while those of Menahga-Marquette soils varied from 4.8 to 6.2 (Fig. 4). The distribution of pH values of the upper 6-inch mineral soil is rather uniform over the total upland forest complex. The pH values ranged from 4.7 to 6.1. The distribution of pH values of soil parent material is quite erratic ranging from 5.5 to 8.0.

Table 3. Linear correlations between some soil characteristics for 6-inch top soil and 36-inch soil profile of upland forests in Itasca State Park, Minnesota.

Soil characteristics	Organic matter	P	K	Ca	Mg
Organic matter					
Top soil		-0.230	0.578**	0.766**	
Soil profile		-0.446**	0.562**	0.501**	
pH (organic layer)					
Top soil	0.763**	-0.104	0.747**	0.846**	0.741**
Extractable phosphorus					
Top soil			0.122	-0.275	
Soil profile			-0.226	-0.450**	
Exchangeable potassium					
Top soil				0.678**	
Soil profile				0.808**	
Exchangeable calcium					
Top soil					0.853**
Soil profile					0.870**

* Significant at 5% level

** Significant at 1% level

The pH values of the organic layer are strongly related to nutrient coordinates (r = + 0.835). They also show strong relationship to moisture coordinates (Table 2). The relationships with organic matter and soil nutrients are strong, except phosphorus (Table 3).

Although some soil properties such as calcium, soil reaction, and organic matter content show strong relationships with nutrient coordinates, and some soil factors at least significant relationships with moisture coordinates, better correlation between vegetation indication and soil fertility may be expected if instead of individual soil factors an integrated factor complex could be used or a quantitative expression of soil physiological conditions could be worked out.

Most of the soils have adequate supplies of nutrients for plant growth, such as phosphorus, potassium, calcium, and magnesium except for some communities located in the lower part of the edaphic field. Moisture supply seems to be more critical. Levels of available soil moisture in upland forests are largely controlled by the precipitation pattern in the park area. With one exception, groundwater level was not reached in any of the six feet deep soil pits. Drought periods are common during the growing season affecting most the forest communities associated with sandy soils. These are forests where pine reproduction, red pine and jack pine especially, still has the chance to become established under favorable conditions because of the least competition from other plants.

4.22 Forest cover types

A cover type is a forest type now occupying the ground, no implication being made as to whether it is temporary or permanent (Soc. Amer. For., 1950). According to a survey conducted in 1952 by the School of Forestry, University of Minnesota in cooperation with the State Conservation Department, the major cover type in Itasca Park is aspen varying in composition from pure stands to those containing admixtures of paper birch, oaks, red maple, and other species to various degrees. This type occurs over 13,000 acres and is by far the largest forest cover type in the park. The total acreage of the three pine cover types ranks next with about 8,500 acres. Red pine occupies about 5,700 acres, jack pine about 1,800 acres, and white pine about 800 acres. An additional 1,600 acres are classified as spruce-fir type and contain white spruce, balsam fir, aspen, paper birch, and other species in different combinations. Northern hardwoods occupy about 1,500 acres with sugar maple, American basswood, red maple, oaks, and American elm as the most common species (Hansen and Duncan, 1954). More recent estimates of the distribution and extent of different forest cover types can be made from the vegetation map of Itasca State Park (Meyer, 1966).

The first two diagrams in Figure 5 show the forest cover types and stand volumes of the ecosystems studied. Figure 5 was placed in Chapter 5 to focus attention on the relationships between advance reproduction and different characteristics of upland forests. The cover types were determined according to predominance of a species or group of species. The predominance was estimated on the basis of volume in cubic feet. The volume estimates included trees of four inches and larger in diameter at breast height. In the case of open overstory of old growth pine only those stands were named white pine or red pine cover types which showed at least 10 trees per acre. Mixed pine stands were named after the pine which occupies the largest volume in that particular stand. The volume estimates in cubic feet (including bark) were made based on the composite volume tables for timber in Lake States, prepared by Gevorkiantz and Olsen (1955).

Stands of red pine cover type show the largest volume on the average. Jack pine occupied areas are relatively low in volume, as well as aspen and paper birch stands with well developed shrub layers. The stands on the mesic, nutrient-rich sites with different stages of northern hardwood development and more or less open overstories of old aspen and pine, are intermediate in volume.

4.23 <u>Descriptions of forest types</u>

An attempt was made to work out a local forest type classification of upland forests in the Itasca Park area. Synecological coordinates were used as an aid in the establishment of forest classification units. In discussing characteristics of forest ecosystems (Fig. 3-1) it was shown how functionally similar ecosystems with respect to moisture-nutrients and heat-light were grouped in six ecosystem types (forest types). In separating these six types individual species distribution in the edaphic field, interrelationships between trees, reproduction, and shrubs, as well as soil characteristics were taken into account (Fig. 5).

Janssen (1967) stated that the vegetation in Itasca Park and vicinity is essentially a continuum in which delineation of plant communities can only be arbitrary; however, a clustering of species' occurrence is noticeable. Species' distribution in the edaphic field showed similar features in this study, creating difficulties in drawing type boundaries based on species' distribution. However, a forest type should not only be a type of the present vegetation, but also a forest development (succession) type (Aichinger, 1960). Thus, the data about reproduction development, shrub development, and soil characteristics were consulted in drawing the final type boundaries. But even so the boundaries in nature are not distinct, they gradually grade into each other between most of the established forest types.

Most of the upland forests in Itasca Park can be considered as temporary expressions or successional stages, mainly due to extensive fires in the past. They are still in a process of post-fire stabilization. Most of the types represent ecological types in an unstable stage. Just how many units are to be recognized depends on practical considerations. Some of the types in the central part of the edaphic field (Fig. 5) could be subdivided to achieve better uniformity in tree composition and thus more uniform response to silvicultural treatment.

Figure 5 shows the six local forest types in the edaphic field. The names of these types indicate some of the dominant and/or associated tree species. The names of ground cover and shrub species were added which were characteristic of a particular type, or to differentiate a type from the neighboring types. These ground cover and shrub species do not necessarily show high frequencies of occurrence. The type names give some characteristics of the forest types but they do not define them in detail. Brief forest type descriptions will follow.

General information about forest type characteristics in terms of synecological coordinates, vegetation, and soils is given in Tables 4, 5, 6, and 7. More detailed information about individual forest ecosystems can be obtained from Appendix Tables 2, 3, and 4.

(1). Pinus banksiana-Arctostaphylos type (Pb-T). This type includes mainly jack pine forests with some red pine. White pine, paper birch, and quaking aspen are scattered. Soils are somewhat excessively to well drained, medium to coarse textured sands and loamy sands. Relief is level to rolling.

Pine reproduction, mainly white pine, is present in considerable numbers in some areas and exhibits satisfactory early growth. Red pine seedlings are only scattered. Jack pine seedlings are common but most of them are heavily dee-browsed. In some specific areas balsam fir may be present. There are a few hardwood seedlings, mainly paper birch and quaking aspen. Shrub development is weak to medium as indicated by their abundance and height. Corylus cornuta, Amelanchier spp., Rosa spp., Symphoricarpos albus, and Diervilla lonicera are the prevalent shrub species. The last three species plus some others, grouped as low shrubs, constitute almost 50 percent of the total number of shrubs. Ground cover is characterized by halfshrubs such as Vaccinium angustifolium, Gaultheria procumbens, Arctostaphylos uva-ursi, Rubus idaeus var. strigosus, and herbs: Maianthemum canadense, Galium boreale, Lathyrus venosus. Mosses such as Pleurozium schreberi and Dicranum spp. show considerable frequencies; however, their cover percentage is rather low. Arctostaphylos uva-ursi, used in the type name, is largely restricted to this type. Classifying jack pine sites, Hansen (1946) found that Arctostaphylos uva-ursi had the highest indicator value for indicating poor site conditions.

(2). Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica type (PbPr-T). This type comprises mainly jack pine forests with various degrees of red pine admixture. White pine, quaking aspen, paper birch, bigtooth aspen, bur oak, and red maple are the minor tree species. Soils represent a range from loamy coarse sands to gravelly sandy loams. They are somewhat excessively to well drained. Cobbles are common to abundant. Relief is nearly level to rolling.

White pine reproduction is scattered, only a few seedlings have reached one foot height. Red pine and jack pine seedlings are practically absent. Red maple and red oak are the most prevalent of hardwood reproduction, but their presence is rather scattered. Shrubs are abundant. Corylus cornuta accounts for almost 50 percent of the total number of shrubs. The percentage of low shrubs such as Diervilla lonicera, Symphoricarpos albus, and Rosa spp. (39 percent of the total) is almost as high as in the preceding forest type (Pb-T). Ground cover is characterized by such halfshrubs as Vaccinium angustifolium, Rubus spp., and Gaultheria procumbens. Maianthemum canadense, Pteridium aquilinum, and Aster macrophyllus show the highest frequencies of herbs and ferns. Gaultheria procumbens and Hepatica americana are used in the type name to emphasize the differences of this type from the neighboring types. The distribution of Gaultheria procumbens extends further into drier, nutrient-poorer site conditions while Hepatica americana extends towards more mesic, nutrient-richer site conditions.

(3). Pinus-Abies-Picea-Lycopodium type (PAP-T). This type includes pine-spruce-fir forests with red pine plus some white pine and paper birch as the overstory species. Balsam fir and white spruce are present to various degrees of density and composition in the understory. Paper birch is the most important hardwood species. Soils show a rather wide range of textural differences. They vary from sands to coarse sandy loams and loams. They are usually well drained with varying amounts of pebbles and cobbles. Relief is undulating to hilly.

Red pine and white pine seedlings are only of occasional occurrence. Balsam fir reproduction generally shows thrifty growth. Its distribution pattern is characterized by clustering. Hardwood reproduction is weakly developed of which red maple and black ash are the main representatives. The shrub layer is weakly developed. *Corylus cornuta*, *Amelanchier spp.*, and *Prunus virginiana* are the major species of the tall shrub group. Low shrubs such as *Diervilla lonicera* and *Lonicera spp.*, plus some others account for 56 percent of the total number of shrubs. Ground cover is represented by *Rubus idaeus* var. *strigosus* and *Vaccinium angustifolium* of the half-shrubs. *Maianthemum canadense*, *Aster macrophyllus*, *Galium triflorum*, and *Linnaea borealis* show the highest frequencies of herbs, and ferns and allies. *Lycopodium spp.*, used in the type name, are restricted to this upland forest type. However, their distribution is rather sporadic. This type and the next discussed (Pr-T) have some common features. The intensity of shrub development and the performance of balsam fir reproduction were used for establishing the final boundary.

(4). Pinus resinosa-Dryopteris-Osmorhiza type (Pr-T). Red pine forests are characteristic of this type. Quaking aspen and paper birch are the major hardwood representatives. Occurrence of oaks and red maple is scattered. White spruce and balsam fir are present in some communities. Balsam fir shows signs of decadence. Soils are well drained, loamy coarse sands to gravelly sandy loams and loams. Cobbles are common to abundant. Boulders are present. Relief is undulating to rolling.

White pine reproduction is scattered and shows poor growth performance. The same is true for balsam fir seedlings, although in some communities quite a few one-year old seedlings can be found. Red maple is the most aggressive of the hardwood reproduction followed by quaking aspen and red oak. Red maple seedlings constitute about 50 percent of the total hardwood reproduction. The shrub layer is moderately to well developed. Corylus cornuta accounts for about 75 percent of the total number of shrubs. The proportion of low shrubs has decreased considerably as compared to the previous types. In ground cover Rubus pubescens, Vaccinium angustifolium, and Rubus idaeus var. strigosus are the most prominent halfshrub species. Ubiquitous species such as Aster macrophyllus, Maianthemum canadense, and Pteridium aquilinum show the highest frequencies of herbs and ferns, followed by Galium triflorum and Thalictrum dioicum. Dryopteris spinulosa and Osmorhiza claytoni are used in the type name to emphasize the differences of this type from its neighboring types. Dryopteris spinulosa extends its distribution towards nutrient-poorer site conditions on uplands and Osmorhiza claytoni is distributed towards nutrient-richer site conditions. Being located in the central portion of the edaphic field, this type is related to PbPr-T, PAP-T, and also with the next discussed type (QPB-T).

(5). Quercus-Populus-Betula-Viburnum-Amphicarpa type (QPB-T). This type includes mainly aspen and paper birch forests with red oak and bur oak admixture to a varying degree. Occasionally some white pines and red pines may be present. Soils are moderately well to well drained sandy loams to loams and sandy clay loams. Cobbles and boulders are occasional to common. Relief is undulating.

Conifer reproduction is almost non-existent. Red oak, red maple and quaking aspen reproduction is prevalent followed by black ash, sugar maple, and American basswood. Shrubs are abundant. Corylus cornuta, Diervilla lonicera, Prunus virginiana, Viburnum rafinesquianum, Cornus rugosa, and Amelanchier spp. are the most conspicuous. Corylus cornuta accounts for over 50 percent of the total number of shrubs. Ground cover is characterized by Rubus spp. halfshrubs, and herbs and ferns are mainly represented by Aster macrophyllus, Aralia nudicaulis, Uvularia grandiflora, Thalictrum dioicum, Uvularia sessilifolia, and Pteridium aquilinum. Viburnum rafinesquianum and Amphicarpa bracteata, used in the type name, show high intensities of occurrence in this type, extending farther into nutrient-richer sites. This type shows some transitional features towards the next discussed type (AT-T).

(6). Acer-Tilia-Pinus strobus-Dirca type (AT-T). This type includes forests with rather advanced northern hardwood development. Sugar maple, red oak, and American basswood are the most prevalent northern hardwood species. More or less open overstories usually consist of old growth aspen, white pine, and bur oak. Soils are moderately well to well drained sandy loams to loams and silt loams. Cobbles and boulders are common. Relief is nearly level to rolling.

Sugar maple is by far the most abundantly reproducing species followed by red oak, red maple, ironwood, black ash, and American basswood. White pine seedlings are present in considerable numbers, but survival and growth is poor. The shrub layer is weakly developed with *Corylus cornuta*, *Prunus virginiana*, *Viburnum rafinesquianum*, and *Acer spicatum* being the most abundant species. Ground cover is represented mainly by *Uvularia grandiflora*, *Uvularia sessilifolia*, *Thalictrum dioicum*, *Aster macrophyllus*, and *Aralia nudicaulis*. *Dirca palustris*, used in the type name, is characteristic of this type.

4.24 Comparisons of forest types

In this section, forest types will be compared with each other in terms of their vegetation and soil characteristics, and relative to their location in the edaphic field. Variation in some of these characteristics will be indicated.

Section 4.12 dealt with taxonomic, ecological, and site diversities of individual ecosystems. Analogous diversities can also be computed for forest types which were established by grouping together functionally similar forest ecosystems. Taxonomic diversity, expressed as a number of species, varies in individual ecosystems from 29 to 63 species as compared to from 78 to 91 species in individual forest types. Forest types have larger number of species because they reflect the pooled number of species of related ecosystems. Forest types are represented by characteristic ecoystems and ecosystems of transitional nature (ecotones). The latter, as stated before, show maximum taxonomic diversity. This explains the narrower range of variation in species' number in forest types as compared to that in individual ecosystems. The characteristics of forest types refer to a set of different successional stages which might lead to more uniform permanent types. This is another explanation of the rather great variability of characteristics of forest types.

Ecological diversity, expressed as the standard deviation of species' synecological coordinates for moisture ranged from 0.80 to 1.13 in individual ecosystems and from 0.95 to 1.01 in forest types. Ecological diversity in terms of nutrients varied from 0.54 to 1.46 in individual ecosystems and from 0.69 to 1.25 in forest types. Similarly to taxonomic diversity, ecological diversities on forest type basis show narrower range of variation as compared to individual ecosystems. The reasons are the same; an additional contributing factor being the central tendency of sample averages in general.

Site diversity, expressed as the standard deviation of synecological coordinates of different subplots in individual ecosystems (microsite variation), ranged from 0.05 to 0.44 and from 0.05 to 0.28 in terms of moisture and nutrients, respectively. Site diversity, expressed as the standard deviation of synecological coordinates of different ecosystems in forest types (macrosite variation), ranged from 0.05 to 0.17 and from 0.07 to 0.14 in terms of moisture and nutrients, respectively (Table 4). The pattern of variation of site diversity in forest types as compared to individual ecosystems is similar to that of taxonomic and ecological diversities.

Table 4 presents the synecological coordinates of the forest types and their variations within the types. Pinus banksiana-

Arctostaphylos (Pb-T) type is characterized by the lowest moisture and nutrient coordinates and the highest light coordinates. Pinus-Abies-Picea-Lycopodium (PAP-T) type has the highest moisture coordinates and the lowest heat coordinates. Light coordinates show the largest variation in this type. Acer-Tilia-Pinus strobus-Dirca (AT-T) type is characterized by the highest nutrient and heat coordinates and the lowest light coordinates. Synecological coordinates of individual forest ecosystems are shown in Appendix Table 2.

Tables 5 and 6 give some information about the soil physical and chemical characteristics of the forest types and their variation within the types. There is a gradual increase in the amount of soil mineral particles below 0.1 mm, readily available water capacity, organic matter, exchangeable potassium, calcium, and magnesium in the top soil and soil profile from Pinus banksiana-Arctostaphylos (Pb-T) type to Acer-Tilia-Pinus strobus-Dirca (AT-T) type. Extractable phosphorus shows some increase up to Pinus-Abies-Picea-Lycopodium (PAP-T) type and then it decreases towards Acer-Tilia-Pinus strobus-Dirca (AT-T) type (Table 6).

There is a gradual increase in the thickness of organic layer and pH values of the organic layer from Pinus banksiana-Arctostaphylos (Pb-T) type to Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) and Acer-Tilia-Pinus strobus-Dirca (AT-T) types. Soil pH values of the A2 horizon show little change over the entire upland forest range and pH values of parent material show only higher values in the Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) and Acer-Tilia-Pinus strobus-Dirca (AT-T) types as compared to the other four types

Table 4. Synecological coordinate values and their standard deviations of upland forest types in Itasca State Park, Minnesota.

Forest types*	Number of stands**	Synecological coordinates: Moisture	Nutrients	Heat	Light
Pb-T	6	1.86 / 0.12***	2.04 / 0.10	2.21 / 0.04	3.78 / 0.21
PbPr-T	5	1.99 / 0.05	2.29 / 0.07	2.34 / 0.09	3.44 / 0.08
PAP-T	4	2.46 / 0.17	2.43 / 0.11	2.13 / 0.07	2.85 / 0.31
Pr-T	8	2.28 / 0.12	2.53 / 0.09	2.30 / 0.07	2.92 / 0.16
QPB-T	6	2.23 / 0.09	2.82 / 0.09	2.62 / 0.07	2.91 / 0.11
AT-T	7	2.41 / 0.08	3.09 / 0.14	2.77 / 0.13	2.53 / 0.10

* For type full names see type descriptions in Section 4.23 or Appendix Tables 2 to 4.

** Eight 2-milacre subplots per stand.

*** Standard deviations.

Table 5. Soil pH and organic layer thickness and their standard deviations of forest types in Itasca State Park, Minnesota.

Forest types*	Number of stands**	Soil pH: organic layer	A_2 horizon	parent material	Organic layer thickness (inches)
Pb-T	6	5.2 / 0.3***	5.4 / 0.4	6.6 / 0.8	0.95 / 0.25
PbPr-T	5	5.6 / 0.4	5.5 / 0.3	6.5 / 0.7	1.60 / 0.70
PAP-T	4	5.6 / 0.4	5.3 / 0.3	6.6 / 0.7	1.95 / 0.36
Pr-T	8	5.8 / 0.5	5.3 / 0.3	6.6 / 0.7	2.65 / 0.89
QPB-T	6	6.5 / 0.1	5.3 / 0.5	7.5 / 0.7	2.75 / 0.77
AT-T	7	6.5 / 0.2	5.7 / 0.5	7.0 / 0.7	2.70 / 0.27

* For type full names see type descriptions in Section 4.23 or Appendix Tables 2 to 4.

** Eight 2-milacre subplots per stand.

*** Standard deviations.

Table 6. Averages and standard deviations of some soil physical and chemical properties of the 6-inch top soil and 36-inch soil profile by forest types in Itasca State Park, Minnesota.

Forest types*	** Number of stands	Soil particles 0.1 mm (%)	Readily available water (inches)	Organic matter (%)	P (pp2m)	K (pp2m)	Ca (meq/100 g)	Mg (meq/100 g)
			Top Soil					
Pb-T	6	26	1.38	6.8	48	120	3.6	0.9
		13	0.28***	3.0	13	47	0.8	0.2
PbPr-T	5	32	1.47	10.2	68	148	4.1	1.0
		7	0.22	2.7	6	41	0.9	0.2
PAP-T	4	33	1.58	8.9	75	152	5.0	1.2
		19	0.20	1.2	22	35	2.6	0.4
Pr-T	8	36	1.60	14.6	57	176	6.1	1.3
		13	0.13	1.8	19	57	1.0	0.2
QPB-T	6	53	1.83	14.8	59	224	7.2	1.5
		13	0.23	1.8	23	52	2.0	0.4
AT-T	7	57	1.88	20.3	47	230	10.7	1.7
		15	0.37	3.8	7	42	1.8	0.5
			Soil Profile					
Pb-T	6	15	1.09	1.3	58	64	3.3	0.8
		6	0.13***	0.4	25	22	1.0	0.3
PbPr-T	5	23	1.29	2.1	63	87	3.4	1.0
		8	0.24	0.5	16	23	0.5	0.2
PAP-T	4	30	1.38	1.9	62	120	6.1	1.5
		22	0.21	0.4	11	75	7.3	1.5
Pr-T	8	32	1.42	2.7	47	109	4.6	1.5
		17	0.40	0.6	17	33	2.2	0.8
QPB-T	6	49	1.61	3.1	40	155	6.9	2.6
		10	0.12	0.3	20	51	2.8	1.1
AT-T	7	51	1.64	3.8	36	158	9.4	2.5
		15	0.22	0.7	8	51	3.8	1.1

* For type full names see type descriptions in Section 4.23 or Appendix Tables 2 to 4.

** Eight 2-milacre subplots per stand.

*** Standard deviations

mainly associated with Menahga-Marquette soils (Table 5).

In general, soil characteristics change from type to type along the moisture-nutrient gradient; however, the variation within the types is often large. Forest types are not discrete units which can be separated, but boundaries are set depending on the purpose they should serve and the overlapping of characteristics in the forest types are recognized.

Some brief vegetation characteristics of the forest types are shown in Table 7. Pinus resinosa-Dryopteris-Osmorhiza (Pr-T) and Pinus-Abies-Picea-Lycopodium (PAP-T) types show the highest basal areas and volumes per acre followed by Acer-Tilia-Pinus strobus-Dirca (AT-T) type mainly due to the presence of old growth pine and aspen in the overstory. Jack pine, red pine, and aspen are the predominant tree species in the six forest types. Only Pinus banksiana-Arctostaphylos (Pb-T) type shows somewhat satisfactory pine reproduction, although these figures include one-year old seedlings and also those of doubtful survival ability. In all other types the number of pine seedlings per acre is low. Spruce-fir reproduction has significant appearance in the Pinus-Abies-Picea-Lycopodium (PAP-T) type. Hardwood reproduction increases gradually with improving moisture-nutrient conditions from Pinus banksiana-Arctostaphylos (Pb-T) type to Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) type reaching its peak in the Acer-Tilia-Pinus strobus-Dirca (AT-T) type. The extremely high count of hardwood seedlings per acre is due to the abundance of one-year old sugar maple seedlings in 1965. Shrubs show high densities in Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T), Pinus resinosa-Dryopteris-Osmorhiza (Pr-T), and Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) types. Stand summary data by individual ecosystems and forest types are shown in Appendix Table 3.

Table 7. Some vegetation characteristics of upland forest types in Itasca State Park, Minnesota.

Forest types*	Number of stands	** Dominant species. Average ht.(ft) dbh(in.)	Stand basal area ft^2/ acre	Stand volume ft^3/ acre	Reproduction: Pine	Reproduction: Spruce-fir	Reproduction: Hard-woods	Shrubs
					Number per acre			
Pb-T	6	Jack pine 60/ 8	116	3330	2460 (2450)	790 (780)	490 (250)	15300 (9500)***
PbPr-T	5	Jack pine 66/10	149	4660	250 (240)	120 (40)	1060 (700)	44400 (26600)
PAP-T	4	Red pine 76/16	176	5690	90 (90)	6850 (6100)	2590 (1980)	6100 (4400)
Pr-T	8	Red pine 80/15	172	5980	220 (110)	1630 (510)	4100 (2610)	32100 (23200)
QPB-T	6	Aspen 59/ 8	117	3230	10 (0)	40 (40)	5180 (3310)	34200 (23700)
AT-T	7	Aspen 80/14	153	4890	840 (360)	290 (240)	68800 (41400)	7800 (6700)

* For full type names see type descriptions in Section 4.23 or Appendix Tables 2, 3, and 4.

** Eight 2-milacre subplots per stand.

*** Stems over two years old.

5. ABUNDANCE AND COVER OF REPRODUCTION IN GENERAL STUDY AREA

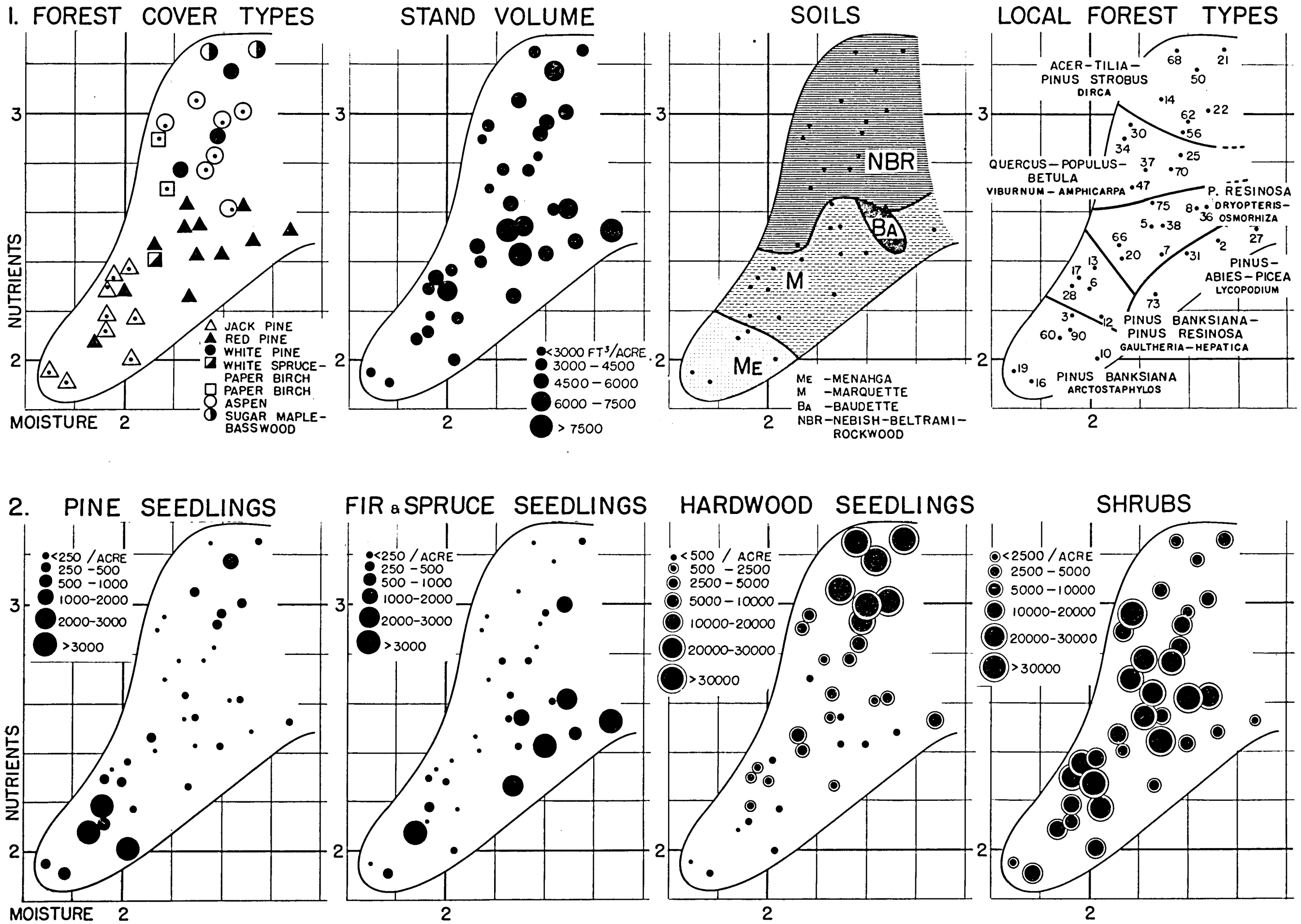
In this chapter, the abundance of tree reproduction will be discussed in relationship to forest types and the abundance of total shrubs and individual shrub species. The discussion will also include the reproduction cover in relationship to tree cover, shrub cover, and ground cover, and the interrelationships of forest covers.

5.1 Abundance of Reproduction in Relationship to Shrubs

The diagrams in Figure 5 link the discussion about forest types in the preceding chapter with the following discussion about the tree reproduction. Figure 5 illustrates, in general, the conditions of tree reproduction in upland forests by species' groups such as pines, spruce-fir, and hardwoods. The reproduction pattern and abundance are shown in relationship to moisture-nutrient gradients and to each other. Further, reproduction is shown in relationship to forest types, stand volumes, soils, and shrubs. The number of reproduction per acre includes all seedlings over two-years old.

There are three main areas of reproduction concentration in the edaphic field (Fig. 5-2). Pine reproduction, mainly white pine, appears on dry, nutrient-poor sites in the Pinus banksiana-Arctostaphylos (Pb-T) type and to some extent on mesic, nutrient-rich sites in Acer-Tilia-Pinus strobus-Dirca (AT-T) type with low to medium shrub densities. Spruce-fir reproduction, mainly balsam fir, occupies the mesic, nutrient-poor to intermediate nutrient sites in Pinus-Abies-Picea-Lycopodium (PAP-T) type with low shrub density.

ADVANCE REPRODUCTION IN RELATIONSHIP TO FOREST TYPES, SOILS, AND SHRUBS IN EDAPHIC FIELDS OF UPLAND FORESTS



Seedlings >2 yrs old

Figure 5. (1) Distribution of forest cover types, stand volumes, soils, local forest types, and (2) tree reproduction and shrubs in the edaphic field (moisture-nutrient coordinates) of upland forest in Itasca State Park, Minnesota.

Hardwood reproduction, mainly sugar maple, is concentrated on mesic, nutrient-rich sites in Acer-Tilia-Pinus strobus-Dirca (AT-T) type with low shrub density. Shrubs show the largest abundance in the central part of the edaphic field, occupying a large portion of the dry to mesic, intermediate nutrient sites. The individual concentration areas of these four forest undergrowth groups supplement each other in such a way that a combination of all four undergrowth groups in one edaphic field would result in a more uniform density distribution of the total undergrowth. This indicates a rather strong competition between these groups, especially the shrub effect on the tree reproduction. Ellenberg (1956) stated that the natural occurrence of plants is seldom directly determined by environmental factors, but more often by the absence or presence of competitors. The environmental factors as such change only the competitive ability of plants, and therefore they influence only indirectly the distribution of plants.

In Itasca Park, the abundance of shrubs plays an important role in the establishment and later growth of tree seedlings. Lee in 1924 pointed out that shrubs have a tremendeous influence on the existence and development of tree seedlings, particularly on reproduction of pines. In discussing the various reasons for the lack of young pines in the park area, Hansen and Duncan (1954) emphasized the significance of the extremely heavy canopy of shrubs in the establishment of pine seedlings.

Figure 6 illustrates the distribution and abundance of different shrub species. Corylus cornuta, Corylus americana, Prunus virginiana,

Forest types in Itasca State Park: 1. Pinus banksiana-Arctostaphylos (Pb-T). 2. Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T). 3. Pinus-Abies-Picea-Lycopodium (PAP-T). 4. Pinus resinosa-Dryopteris-Osmorhiza (Pr-T). 5. Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T). 6. Acer-Tilia-Pinus strobus-Dirca (AT-T).

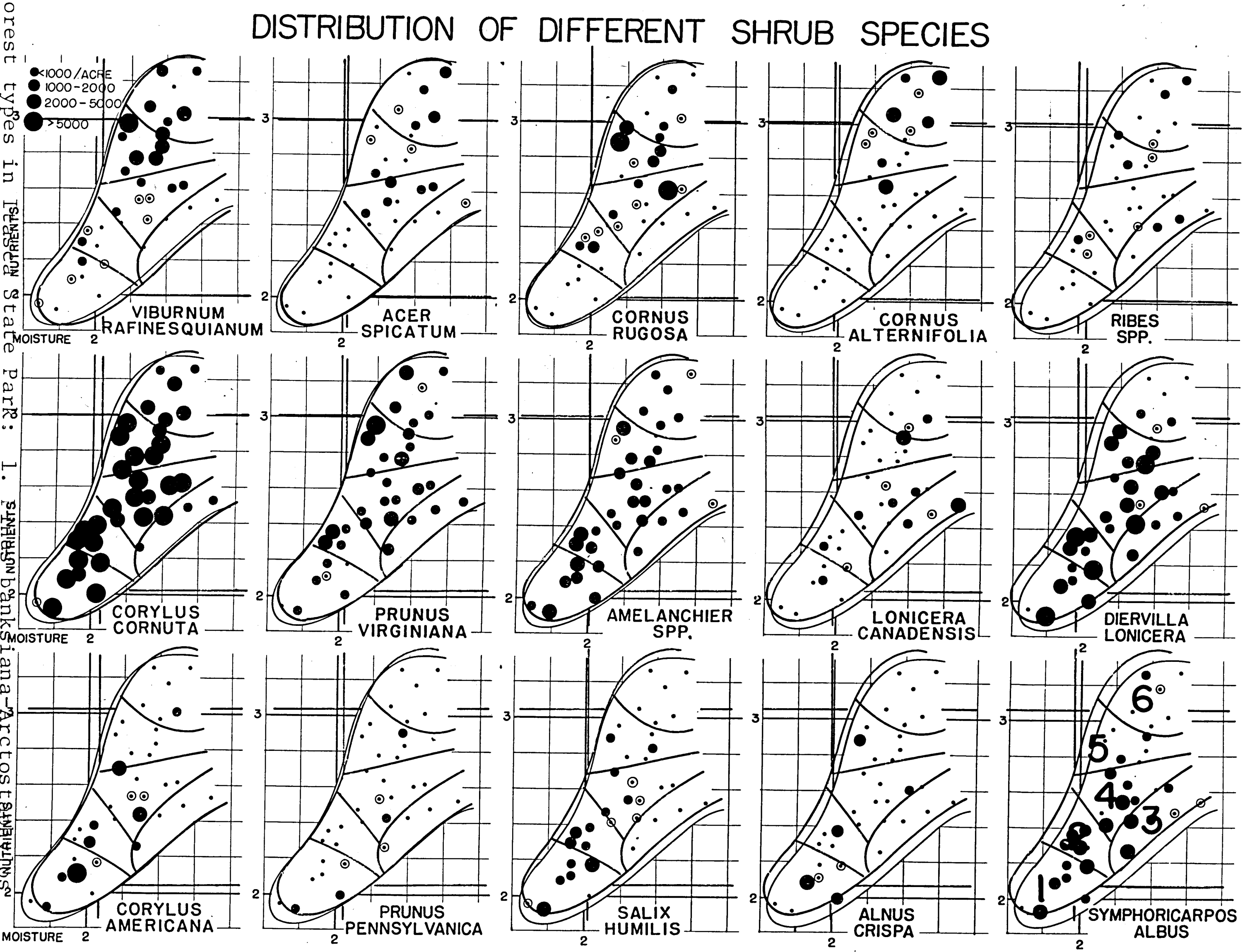
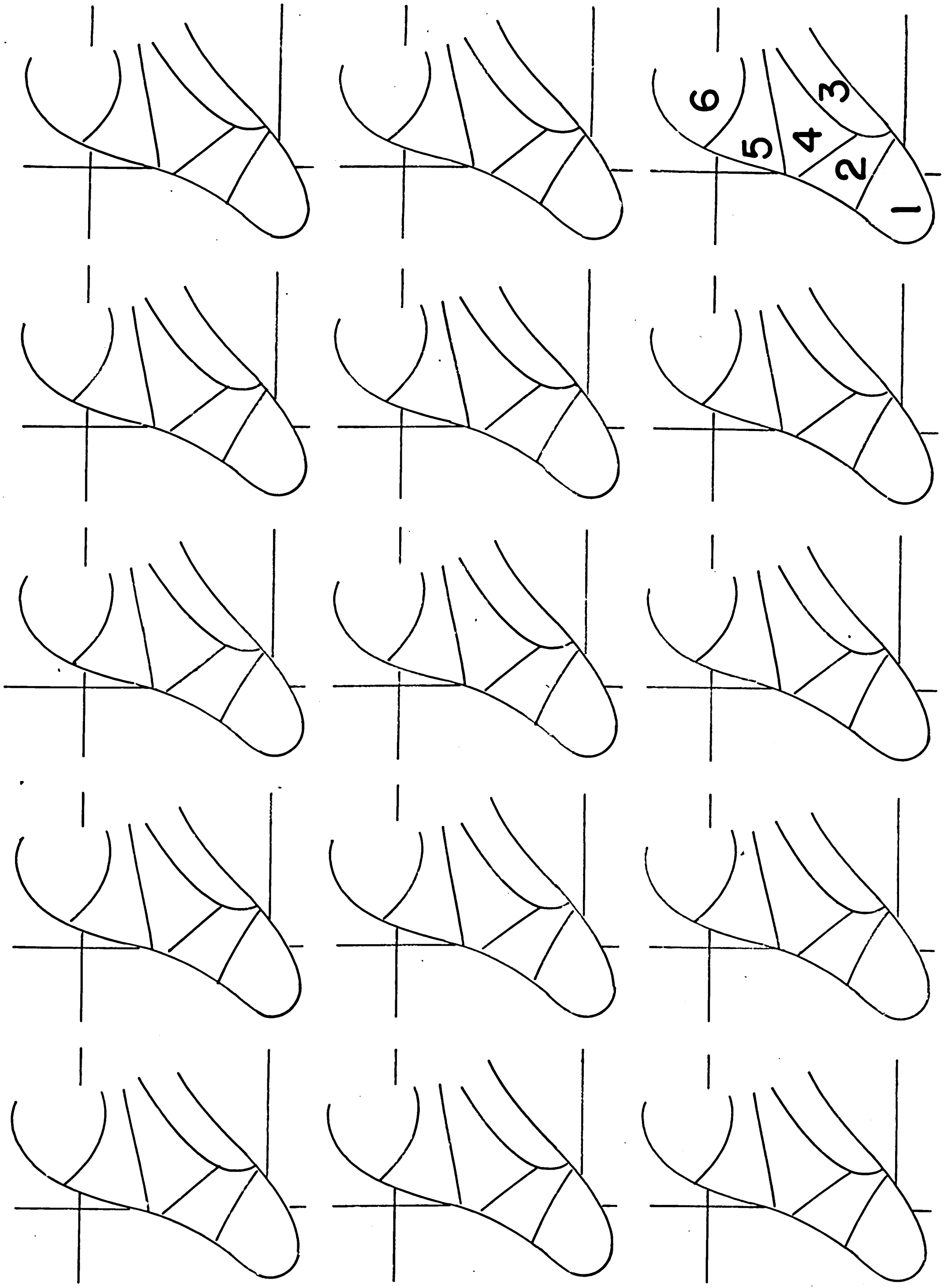


Figure 6. Distribution of shrub species in the edaphic field of upland forests in Itasca Park, Minnesota. Circled dots indicate the presence of shrub species in stands outside the sample plots.



Forest types in Itasca State Park: 1. Pinus banksiana-Arctostaphylos (Pb-T). 2. Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T). 3. Pinus-Abies-Picea-Lycopodium (PAP-T). 4. Pinus resinosa-Dryopteris-Osmorhiza (Pr-T). 5. Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T). 6. Acer-Tilia-Pinus strobus-Dirca (AT-T).

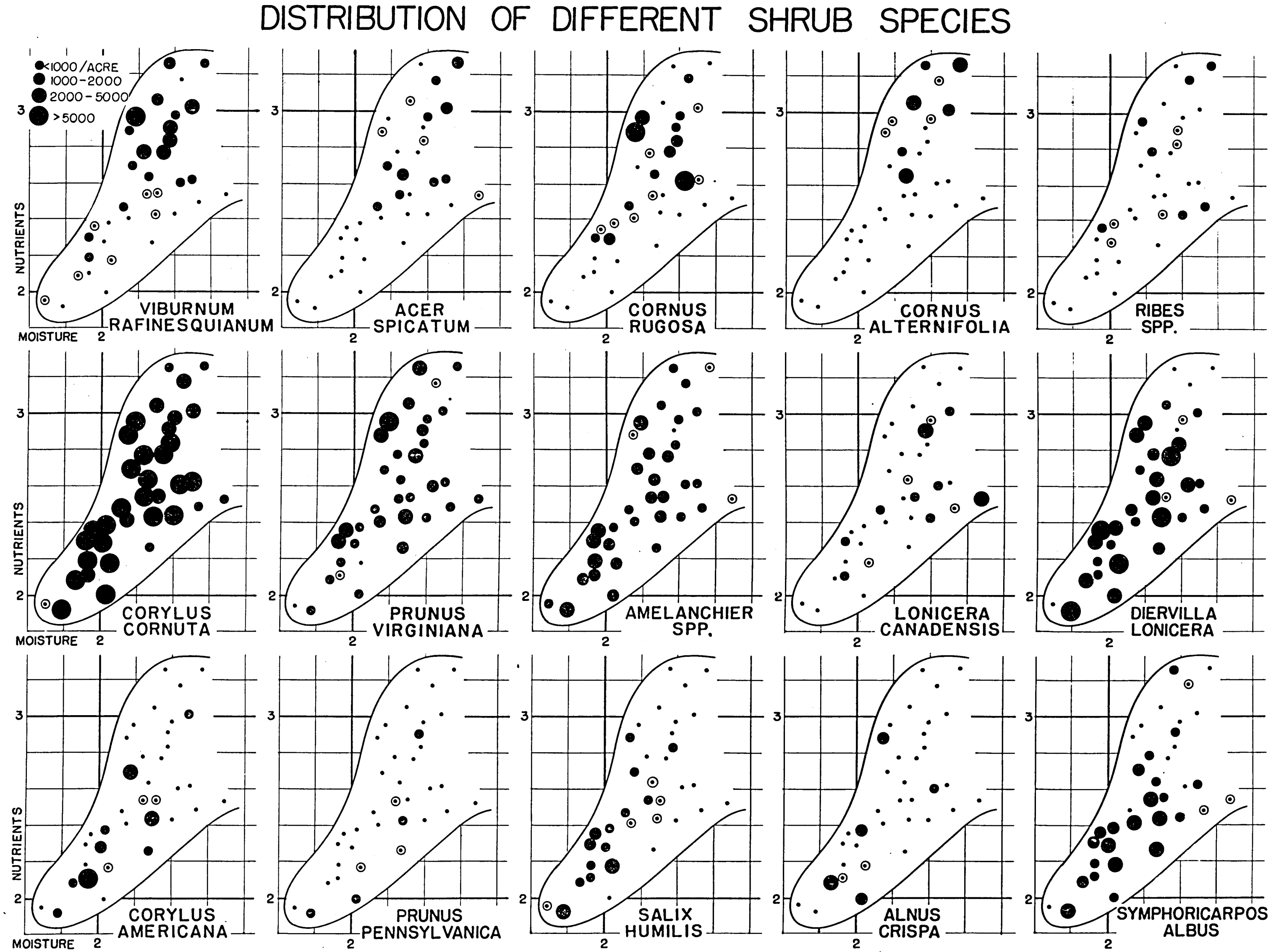


Figure 6. Distribution of shrub species in the edaphic field of upland forests in Itasca Park, Minnesota. Circled dots indicate the presence of shrub species in stands outside the sample plots.

Prunus pennsylvanica, *Amelanchier spp.*, *Salix humilis*, *Alnus crispa*, *Viburnum rafinesquianum*, *Acer spicatum*, *Cornus rugosa*, and *Cornus alternifolia* were included in the tall shrub group. *Corylus cornuta* is by far the most abundant shrub species in upland forests of Itasca Park. The percentage of *Corylus cornuta* in the total number of shrubs and the group of tall shrubs is large (Table 8). Only in the Acer-Tilia-Pinus strobus-Dirca (AT-T) type, does *Corylus cornuta* constitute less than half of the total of tall shrubs. *Amelanchier spp.* and *Prunus virginiana* are numerous, but their distribution is more scattered. *Viburnum rafinesquianum* and *Cornus rugosa* occur in larger numbers on better sites.

Diervilla lonicera and *Symphoricarpos albus* are the most prominent species in the low shrub group (Fig. 6). The proportion of total low shrubs such as *Diervilla lonicera*, *Symphoricarpos albus*, *Rosa spp.*, *Ribes spp.*, *Lonicera canadensis*, and *Lonicera hirsuta* decreases in forest types of higher moisture-nutrient intensities (Table 8). On dry, nutrient-poor sites, except on the most extreme sites, the low shrubs supplement the moderately dense occurrence of tall shrubs in such a way that these sites also become unavailable for pine reproduction.

All of the shrub species are more or less well represented in the central portion of the edaphic field forming a rather solid shrub layer which effectively competes with the tree reproduction in general, and practically eliminates any chance for the establishment of pine reproduction.

Table 8. Composition of shrubs by selected species, species groups, and upland forest types in Itasca State Park, Minnesota.

Forest types*	** Number of stands	Shrubs in percent: Corylus cornuta	Viburnum rafinesq.	Cornus rugosa	Amel. spp.	High shrubs	Low shrubs	Total number of shrubs
Pb-T	6	33	0.2	0	8	58	42	1559
PbPr-T	5	49	0.2	1	4	61	39	3554
PAP-T	4	25	0	0	6	44	56	390
Pr-T	8	72	0.5	3	3	88	12	4089
QPB-T	6	57	8	7	4	87	13	3311
AT-T	7	30	19	1	2	87	13	878

* For type full names see type descriptions in Section 4.23 or Appendix Tables 2, 3, and 4.

** Eight 2-milacre subplots per stand.

5.2 Reproduction Cover in Relationship to Tree Cover, Shrub Cover, and Ground Cover

Natural reproduction largely depends on the state of the whole forest in which the tree cover, shrub cover, ground cover, and upper layer of the soil play an important role. These forest covers strongly affect the success or failure of reproduction because the degree of cover closure influences the amount of available light, heat, and moisture.

In the preceding section the relationships between tree reproduction and shrubs were discussed based on stem counts per unit area in different forest types. Figure 7-1 illustrates the distribution patterns of different forest covers in the edaphic field based on their degree of closure. Figure 7-2 shows the changing cover interrelationships depending on the position of each forest type in the edaphic field.

Tree cover is rather open on dry, nutrient-poor to intermediate nutrient sites, mainly jack pine and red pine forests. The closure of tree cover increases towards more mesic site conditions in pine-spruce-fir and aspen-birch-oak forests, and is greatest on mesic, nutrient-rich sites in maple-basswood forests.

Reproduction cover shows three peaks in the edaphic field, similar to those discussed in Figure 5. Pine reproduction occurs on dry, nutrient-poor sites, spruce-fir reproduction on mesic, nutrient-poor to intermediate nutrient sites, and hardwood reproduction on mesic, nutrient-rich sites. The peaks of hardwood and spruce-fir reproduction cover coincide with the distribution pattern of dense tree cover while the peak of pine reproduction cover on dry, nutrient-poor sites is associated with rather open tree cover.

Shrub cover reaches its peak on dry to mesic, intermediate nutrient sites showing the least closure on mesic, nutrient-poor and mesic, nutrient-rich sites. The effect of dense tree cover on shrub cover is rather striking. Also the impact of the shrub cover on tree reproduction is distinct. Shrubs and tree reproduction do co-exist to some extent on dry, nutrient-poor sites under rather open tree cover.

Ground cover has its greatest closure on dry, nutrient-poor to intermediate nutrient sites showing the least closure on sites with dense tree cover and reproduction cover. On dry, nutrient-poor sites under open tree cover there is a co-existence between ground cover and reproduction, and on mesic, nutrient-rich and intermediate nutrient sites under dense tree cover they co-exist to some extent.

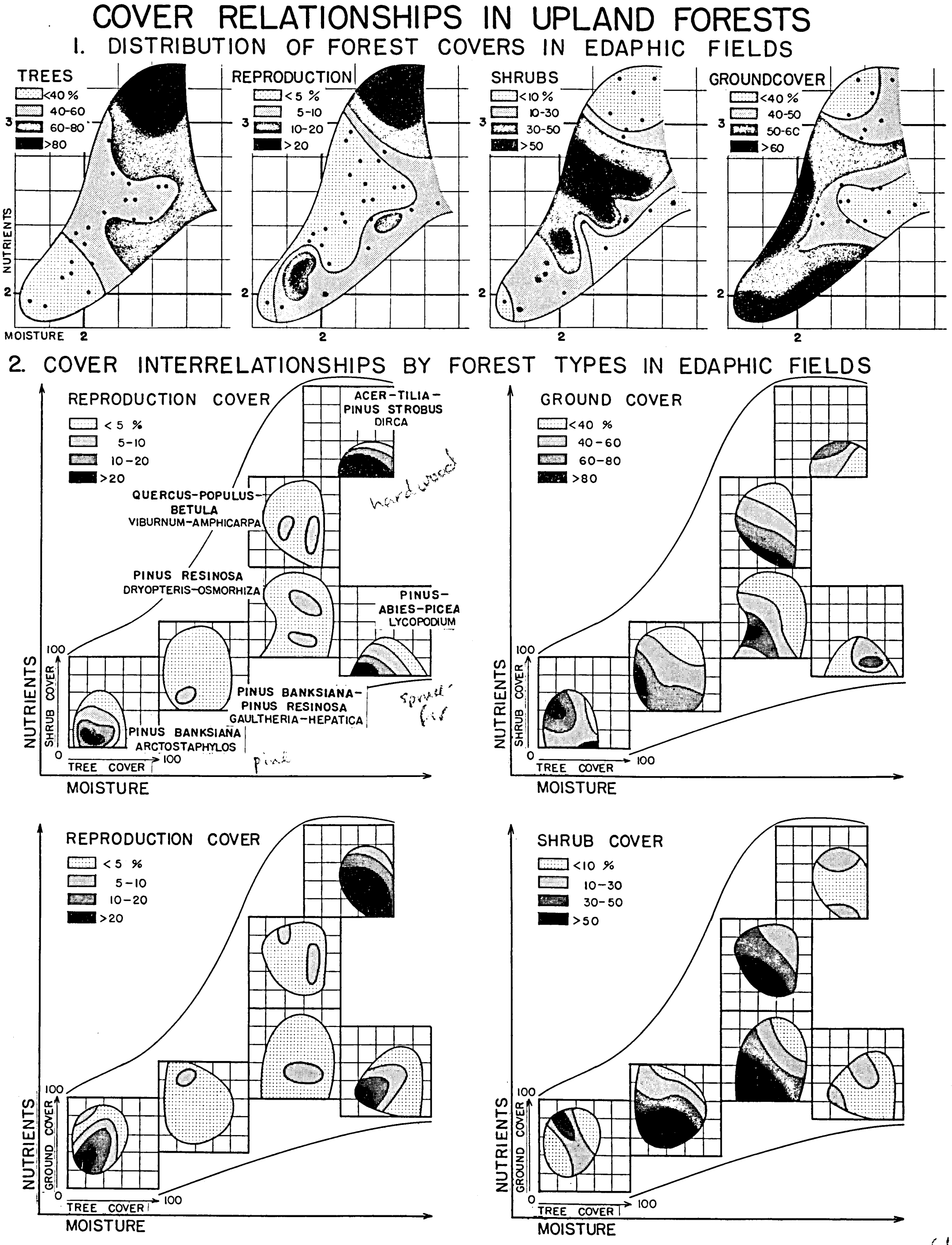


Figure 7. (1) Distribution of tree cover, reproduction cover, shrub cover, and ground cover in edaphic fields, and (2) cover interrelationships by forest types of upland forests in Itasca State Park, Minnesota.

On dry to mesic, intermediate nutrient sites under rather open tree cover, ground cover co-exists with shrub cover largely because of discontinuous distribution pattern of both covers.

Figure 7-2 shows interrelationships of forest covers by forest types in the edaphic field. The contour lines are drawn based on cover estimates of individual subplots. Reproduction cover is shown related to tree-shrub covers and to tree-ground covers. In Pinus banksiana-Arctostaphylos (Pb-T) type the maximum reproduction cover is related to open shrub and ground covers, and to open to intermediate tree cover. On these sites there is some co-existence between the reproduction cover, shrub cover, and ground cover due to the patchy distribution pattern of these three forest covers. Similar relationships exist between reproduction cover and tree-shrub covers as well as tree-ground covers in Pinus-Abies-Picea-Lycopodium (PAP-T) type. The maximum of reproduction cover occurs at tree cover closure less than 40 percent and under rather open shrub cover and ground cover. The dense tree cover has less impact on the reproduction cover in Acer-Tilia-Pinus strobus-Dirca (AT-T) type.

Reproduction cover decreases with increased shrub and ground covers. Reproduction cover in the three centrally located forest types (PbPr-T, Pr-T, and QPB-T) does not show any distinct relationship with tree cover, shrub cover, and ground cover. The reproduction in these three types, if present, is of young age or stunted growth resulting in low cover percentages.

Ground cover shows a certain degree of independence from tree and shrub covers in Pinus banksiana-Arctostaphylos (Pb-T) type and also in Pinus-Abies-Picea-Lycopodium (PAP-T) type. In the latter, ground cover shows a slight peak at intermediate tree and shrub cover closures. In the Acer-Tilia-Pinus strobus-Dirca (AT-T) type the ground cover increases with the decrease in tree cover. The peak of ground cover is associated with relatively dense shrub cover under these conditions. The product of tree and shrub covers is rather constant in relationship to ground cover in the three centrally located types (PbPr-T, Pr-T, and QPB-T). With increased tree and shrub covers the ground cover decreases. Pinus resinosa-Dryopteris-Osmorhiza (Pr-T) type shows some irregularities from the above stated at low tree and shrub cover levels.

Shrub cover does not show a distinct relationship with tree and ground covers in Pinus banksiana-Arctostaphylos (Pb-T) type. Shrub cover seems to co-exist more with ground cover than with reproduction cover. Shrub cover is rather open in Pinus-Abies-Picea-Lycopodium (PAP-T) type and Acer-Tilia-Pinus strobus-Dirca (AT-T) type, and the relationships with tree and ground covers are weak. Shrub cover relationships with tree and ground covers in the three centrally located forest types (PbPr-T, Pr-T, and QPB-T) are similar to the ground cover relationships with tree and shrub covers in the diagram above (Fig. 7-2). With increased tree and ground covers the shrub cover decreases.

Figure 7 focused attention on reproduction cover in relationship to tree cover, shrub cover, and ground cover, and in relationship to moisture-nutrient gradients. The knowledge of characteristics of each forest type provides additional information. Each of the four diagrams in Figure 7-2 shows five dimensional relationships.

6. DYNAMICS OF TREE REPRODUCTION IN THE GENERAL STUDY AREA

The preceding chapter dealt with static relationships between tree reproduction and associated vegetation, forest types, and moisture-nutrient gradients. This chapter will consider these relationships from a dynamic viewpoint. The changes in reproduction composition, abundance, and distribution pattern with increased age will be analyzed. The age and height relationships of tree reproduction in different forest types will be discussed.

6.1 Changes in Conifer, Hardwood, and Shrub Composition

Species' composition reflects the interrelationships between individuals of different species and forest reproduction conditions. Composition of conifer reproduction, hardwood reproduction, and shrubs, based on total stem counts and analyzed by age groups in triangular coordinates (the first five diagrams in Figure 8), shows that with increased age there are no forest communities where these three undergrowth components are well mixed. Somewhat uniform mixtures of these three components are still expressed in the one to two-year-age group in some communities. However, considerable fluctuations are possible from year to year in the amount of one-year old seedlings present; depending on seed year or even on time of sampling. In the six to 10-year-age group there are communities with different degrees of hardwood-shrub and conifer-shrub mixtures. Combinations of well mixed all three undergrowth components or mixtures of conifers and hardwoods are non-existent. Conifers, hardwoods, and shrubs over 10 years old show further separation.

DYNAMICS OF UNDERGROWTH COMPOSITION IN TRIANGULAR AND SYNECOLOGICAL COORDINATES

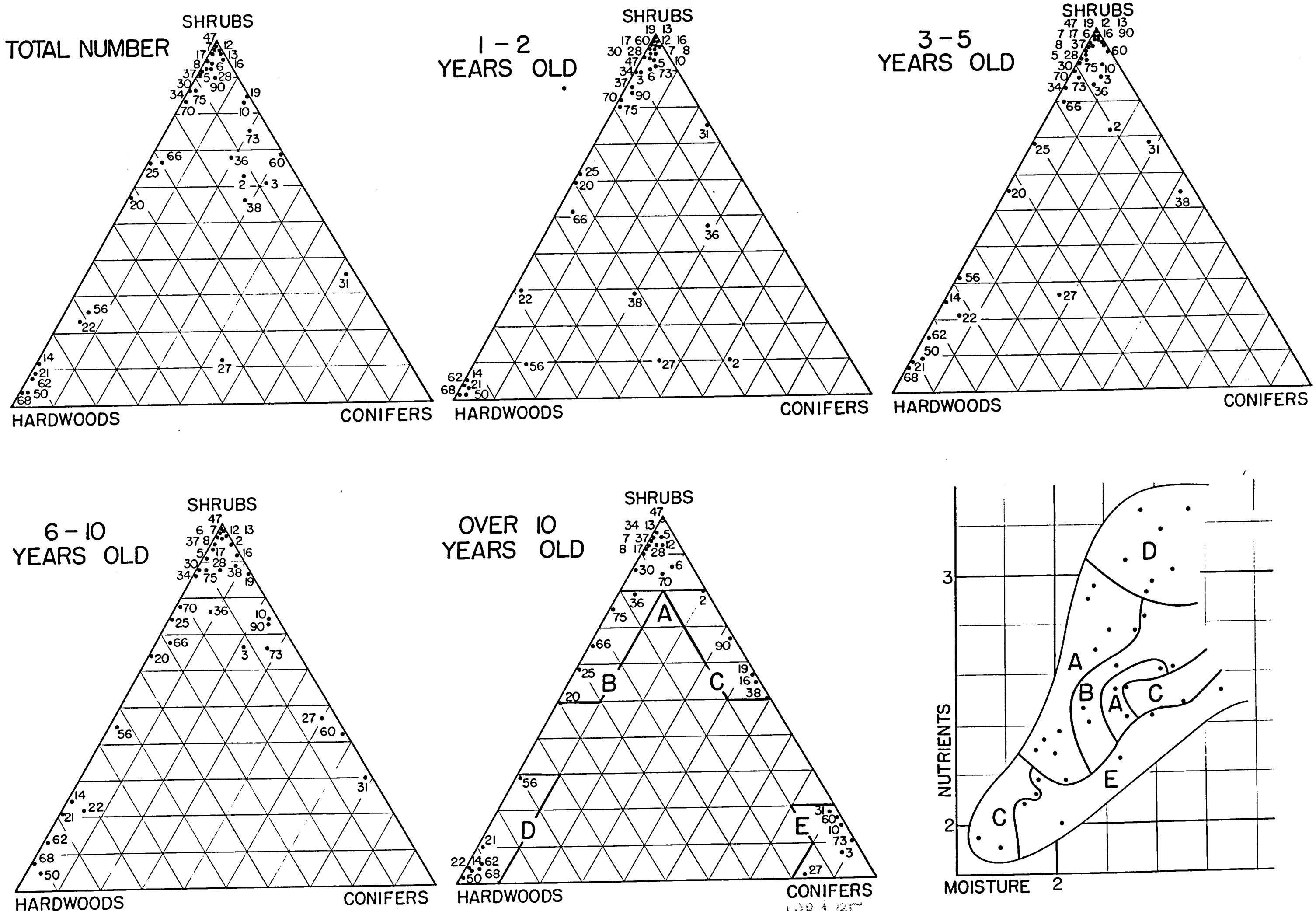


Figure 8. Composition of conifers, hardwoods, and shrubs, by age groups and individual sample areas in triangular coordinates. Distribution of undergrowth composition classes over 10 years old (from A to E) is also shown in the edaphic field of upland forests in Itasca Park, Minnesota.

Five composition classes of forest undergrowth (A, B, C, D, and E) can be recognized in the last triangular diagram in Figure 8. The distribution of stands belonging to these individual undergrowth composition classes is also shown in moisture-nutrient coordinates in the last diagram in Figure 8. Stands in class "A" show over 80 percent shrubs of the total number of undergrowth over 10 years old, in class "B" shrubs are from 50 to 80 percent, associated with hardwoods, in class "C" shrubs are from 50 to 80 percent, associated with conifers, and in class "D" hardwoods and in class "E" conifers are over 70 percent of the total number of undergrowth over 10 years old.

Class "E", shown in triangular and moisture-nutrient coordinates, includes stands with a relatively large proportion of conifer seedlings, mainly white pine and balsam fir. This is an indication that these stands will have at least some conifer admixture in the future. However, the locations of these stands in triangular coordinates of younger age groups indicate that proportionally the number of shrubs exceeds by far the number of conifers. Stand classes "E" and "C" largely belong to Pinus banksiana-Arctostaphylos (Pb-T) and Pinus-Abies-Picea-Lycopodium (PAP-T) types, classes "A" and "B" to Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T), Pinus resinosa-Dryopteris-Osmorhiza (Pr-T), and Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) types, while class "D" coincides with the boundaries of Acer-Tilia-Pinus strobus-Dirca (AT-T) type.

The composition of undergrowth is more characteristic in the marginal forest types (Pb-T, PAP-T, and AT-T) than it is in the types centrally located in the edaphic field. The Acer-Tilia-Pinus strobus-Dirca (AT-T) type represented by stands of class "D" shows rather stable hardwood proportions in all age groups and it can be considered as a permanent type, while Pinus banksiana-Arctostaphylos (Pb-T) and Pinus-Abies-Picea-Lycopodium (PAP-T) types are subjected to certain changes based on the undergrowth characteristics.

Table 9 indicates the total undergrowth composition by forest types. Conifers, mainly balsam fir, show the strongest appearance proportionally in Pinus-Abies-Picea-Lycopodium (PAP-T) type followed by Pinus banksiana-Arctostaphylos (Pb-T) type with predominant white pine reproduction. The relatively weakest occurrence of shrubs is in Pinus-Abies-Picea-Lycopodium (PAP-T) and particularly in Acer-Tilia-Pinus strobus-Dirca (AT-T) types. The latter is dominated by hardwood reproduction, mainly sugar maple.

Table 9. Composition of forest undergrowth by upland forest types in Itasca State Park, Minnesota.

Forest types*	Number of stands**	Undergrowth in percent			Total number of undergrowth
		Conifers	Hardwoods	Shrubs	
Pb-T	6	17	2	81	1937
PbPr-T	5	1	2	97	3670
PAP-T	4	44	16	40	1001
Pr-T	8	5	12	83	4895
QPB-T	6	0.1	13	87	3815
AT-T	7	1	88	11	8721

* For type full names see type descriptions in Section 4.23 or Appendix Tables 2, 3, and 4.

** Eight 2-milacre subplots per stand.

6.2 Change in Abundance and Distribution Pattern of Individual Tree Species

This section will discuss tree reproduction in upland forests by individual species in relationship to motherstands and forest types which are primarily the reflections of moisture-nutrient gradients. The change in abundance and distribution patterns of reproduction will be analyzed by age groups. The age and height relationships of reproduction will be compared in different forest types. Emphasis will be placed on pine reproduction because of the management problems related to securing pine continuity in the park area. Some ecological implications regarding pine reproduction in natural forests will be discussed.

Success or failure of tree reproduction in natural forests depends on a complexity of factors. Ecological processes are multi-conditioned, and it is difficult to point to a single factor as responsible for the establishment and performance of seedlings. According to Rowe (1955), combined effects of seed production and distribution, seedbed quality, and favorable climatic and biotic factors are important.

6.21 Pine reproduction

The three Minnesota pines, jack pine, red pine, and white pine are characterized as very intolerant, intolerant, and moderately tolerant tree species, respectively (Baker, 1949). They are primarily "fire species" in that their silvicultural characteristics are adapted to conditions best effected by forest fires, especially in the case of jack pine and red pine. Environmental conditions may not be directly responsible for natural pine distribution, except indirectly through fire history (Horton and Bedell, 1960). Schenck (1924) pointed out that after a fire, the mass-dying of motherstands connected with soil surface fires gave pine the chance to reproduce in large numbers. Forests in Itasca Park, on the contrary, are in the process of post-fire stabilization with a strong development of hardwoods and shrubs leaving little chance for pine reproduction.

Seedling studies in natural forests have shown that the prerequisite for pine to become established is largely due to the coincidence of seed years with favorable light, moisture, and biotic conditions. Pine seedlings often become established along the margins of forests but rarely within the forest stands. The importance of light in root development of seedlings and consequently the increased ability of seedlings to compete for soil moisture has been stressed by Shirley 1945, Oosting and Kramer 1946, Kozlowski 1949, and Fernell 1953, among others. Strothmann (1967) showed that planted red pine seedlings under dense Corylus cover responded better to the removal of competition for light than moisture. Maximum response occurred only when both types of competition were eliminated or greatly reduced. According to Shirley (1932) about 35 percent of full sunlight is needed for satisfactory establishment of red pine seedlings. After the establishment period survival and growth of white pine seedlings become critical at below 20 percent of full sunlight (Shirley, 1945). Wittich (1955) stated that pine seedlings tolerate considerable shade only under specific site conditions, e.g., shallow infertile sand over loam which slows the water movement.

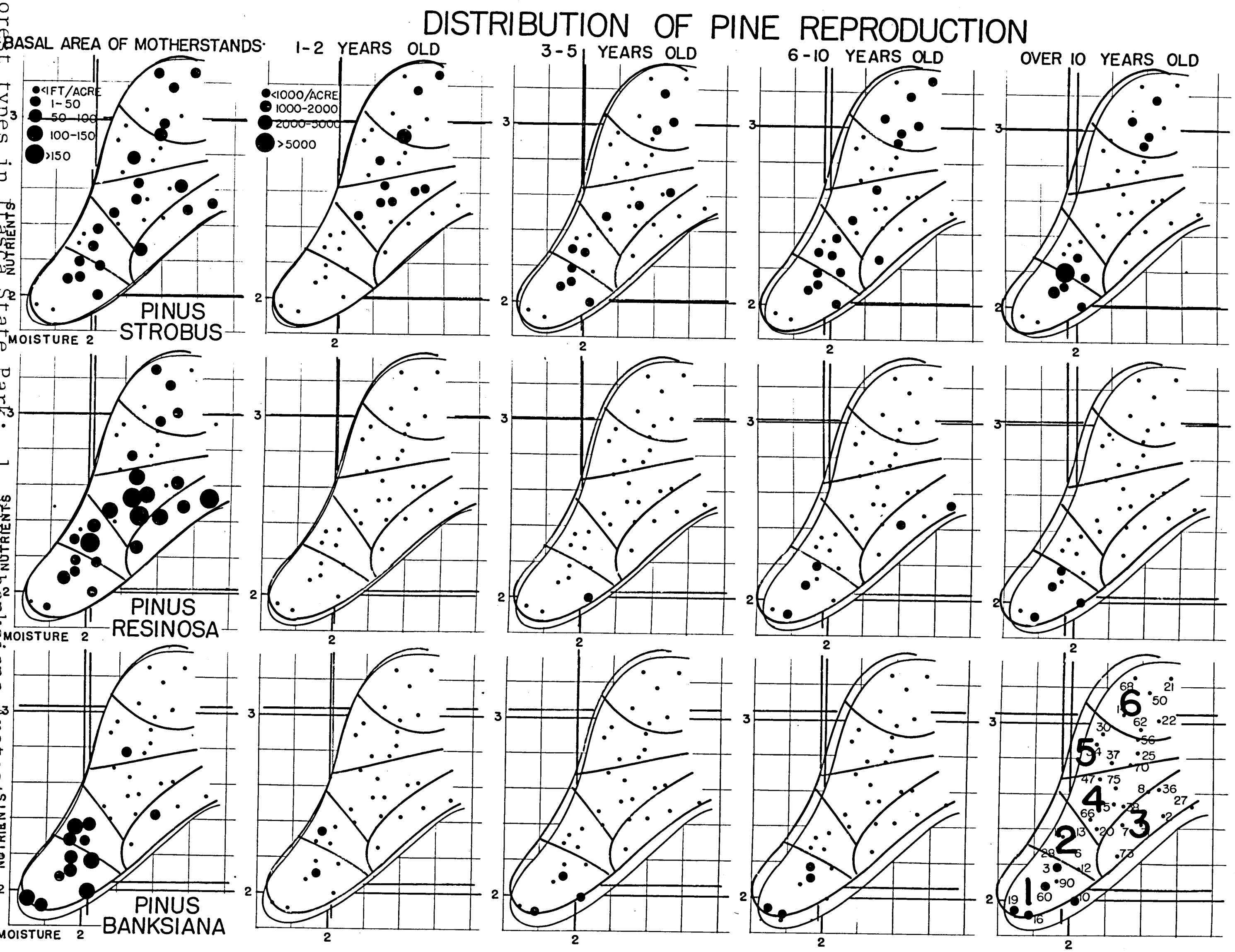
If root competition is removed, pine seedlings may become established on deep sands.

The importance of seedbed condition is emphasized in numerous studies. In general, mineral soil is considered a better seedbed than the humus layer for germination and development of pine seedlings. Five times as many red pine seedlings were established on mineral soil as on undisturbed surface in northern Minnesota (Shirley, 1933). It is also well recognized that white pine reproduction depends on some degree of protection for germination and survival more than does red pine. Under full exposure to sunlight, Polytrichum moss or a shortgrass cover of light density are favorable seedbeds for white pine seedlings (Smith, 1951). In natural forests, best germination conditions for pines consist of partial shade, sparse vegetation, and a thin litter layer with some mineral soil exposed. These conditions are usually created after fire or local disturbances such as windfall or erosion. Through these disturbances microsite variations affect reproduction both in terms of quantity and quality. Pine reproduction does not succeed on thick litter, sod, or in the heavy ashes of recent burns (Smith, 1940; Cheyney, 1942). Soil surface cover of dead leaves and needles is not only unfavorable as a seedbed (Schenck, 1924; Vanselow, 1949) but accumulation of leaves also mechanically smoothers young seedlings. Moss covered soil surfaces, especially Hypnum moss without a tendency of grass invasion, protect the mineral soil from rapid evaporation and are considered favorable for pine reproduction, by helping the seedlings to overcome drought periods (Wiedemann, 1948; Wittich, 1947). Forest soils support a growth of mosses and lichens only if the soils are not too rich in nutrients. Upland forests in Itasca Park, even on relatively poor sites show only scattered moss clusters, mainly Pleurozium schreberi and Dicranum spp., which are not considered to have the drought-protective qualities of Hypnum moss.

The impact of ground vegetation and shrubs on tree reproduction in different forest types in Itasca Park has been discussed in preceding chapters. Investigating the light effect on pine seedling establishment and growth, Shirley (1932) stated that the whole study pointed to the importance of the forest undergrowth in determining conifer establishment in natural forests. The increase in abundance and vigor of the competing vegetation, controlled mainly by the site conditions and stand history, results in exclusion of pine reproduction. The interference of neighboring plants increases the susceptibility of seedlings to the drought injury. This is largely a consequence of poor root development due to insufficient light. According to Sarvas (1950), ground vegetation in connection with summer drought are considered as the most important factors in pine reproduction. White pine seedlings may persist under a rather dense shade of competing vegetation on some sites for a considerable time, but jack pine and red pine reproduction rarely become established under these conditions. Advance pine reproduction is largely restricted to dry, nutrient-poor sites due to the strong competition of shrubs, tolerant hardwoods, and ground cover species on better sites. Horton and Bedell (1960) emphasized that all features which reduce competition encourage pine reproduction and vice versa.

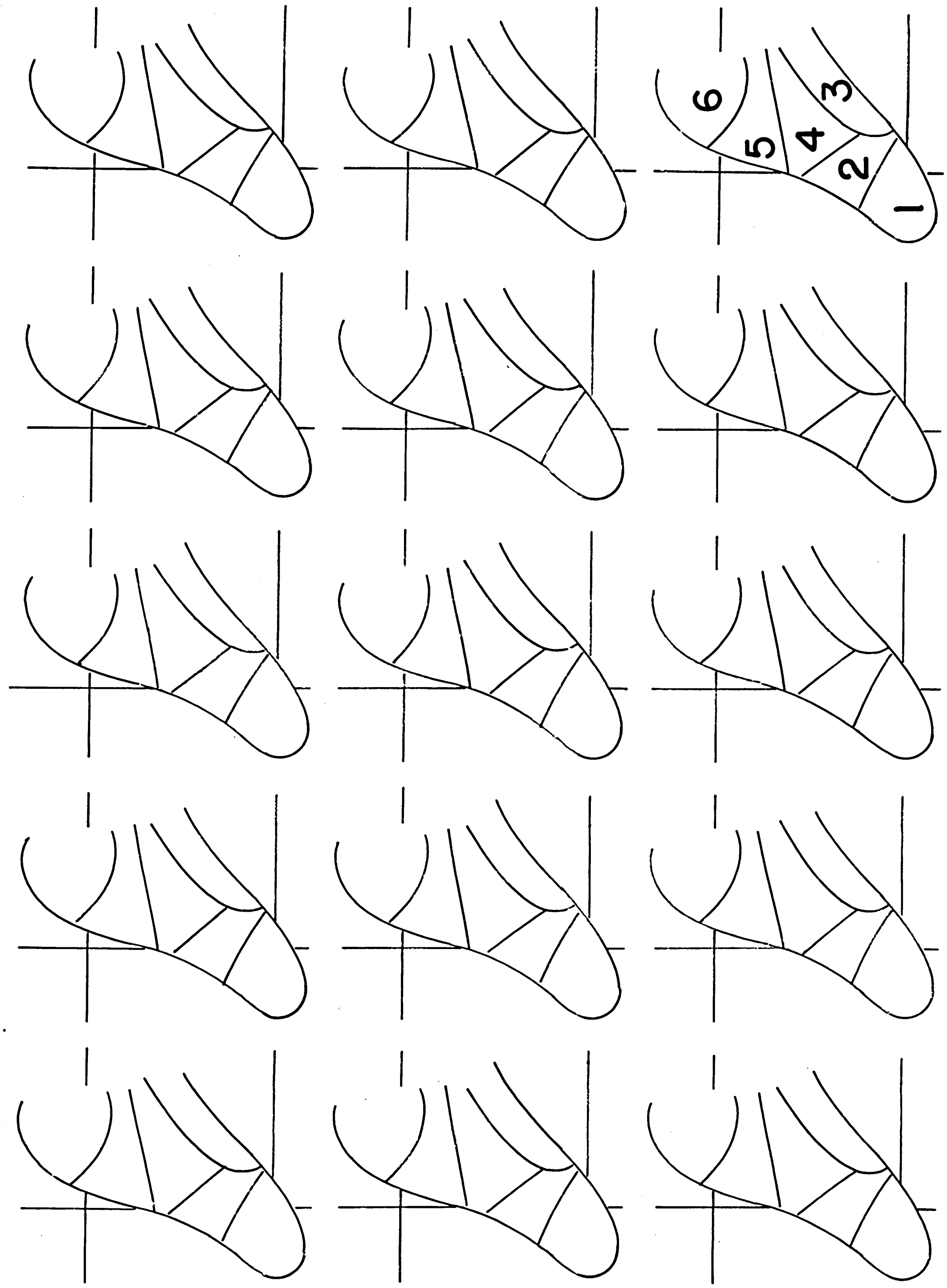
Figure 9 illustrates a comparison of the three Minnesota pines. It shows pine reproduction by age groups in relationship to motherstands, forest types, and moisture-nutrient gradients. The basal area of mature trees representing age groups from approximately 70 to 80, 140 to 160, and 200 to 250 years for red pine and white pine, and 70 to 90 years for jack pine (Appendix Table 3). The diagrams in Figure 9 clearly reflect the jack pine concentration on dry, nutrient-poor sites and red pine on dry to mesic, intermediate nutrient sites. White pine is more evenly distributed over the upland forest complex, mainly as an admixture species in a variety of forest stands.

Seedlings of the first year were considered one year old. One to two years old seedlings mean the first and second year seedlings. The maximum limit for reproduction was set at one inch in diameter at breast height. Saplings of the three pines from one to four inches in diameter were rare in the areas studied, mainly limited to Pinus banksiana-Arctostaphylos (Pb-T) type. The scale in the figures, for number of seedlings per acre, was selected to serve tree reproduction of all species. It does not reflect too well the scarcity of pine reproduction. The actual numbers per acre are shown by age groups in Figure 10 and Appendix Tables 3. It was intended to group seedlings in five-year classes but the large fluctuations in numbers, especially in the first year, was the reason for establishing of one to two and three to five-year-age groups. For comparative purposes these two age groups should be counted together. The absence of mortality data of seedlings poses another difficulty in evaluating the changes in reproduction pattern and abundance. Stands 3, 10, and 16 were specially selected and added to the general study to contrast stand and site conditions under



Forest types in Itasca State Park: 1. Pinus banksiana-Arctostaphylos (Pb-T). 2. Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T). 3. Pinus-Abies-Picea-Lycopodium (PAP-T). 4. Pinus resinosa-Dryopteris-Osmorhiza (Pr-T). 5. Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T). 6. Acer-Tilia-Pinus strobus-Dirca (AT-T).

Figure 9. Distribution of basal areas of white pine, red pine, and jack pine and their reproduction (<1" DBH) by age groups in the edaphic field of upland forests in Itasca State Park, Minnesota.



Forest types in Itasca State Park: 1. Pinus banksiana-Arctostaphylos (Pb-T). 2. Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T). 3. Pinus-Abies-Picea-Lycopodium (PAP-T). 4. Pinus resinosa-Dryopteris-Osmorhiza (Pr-T). 5. Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T). 6. Acer-Tilia-Pinus strobus-Dirca (AT-T).

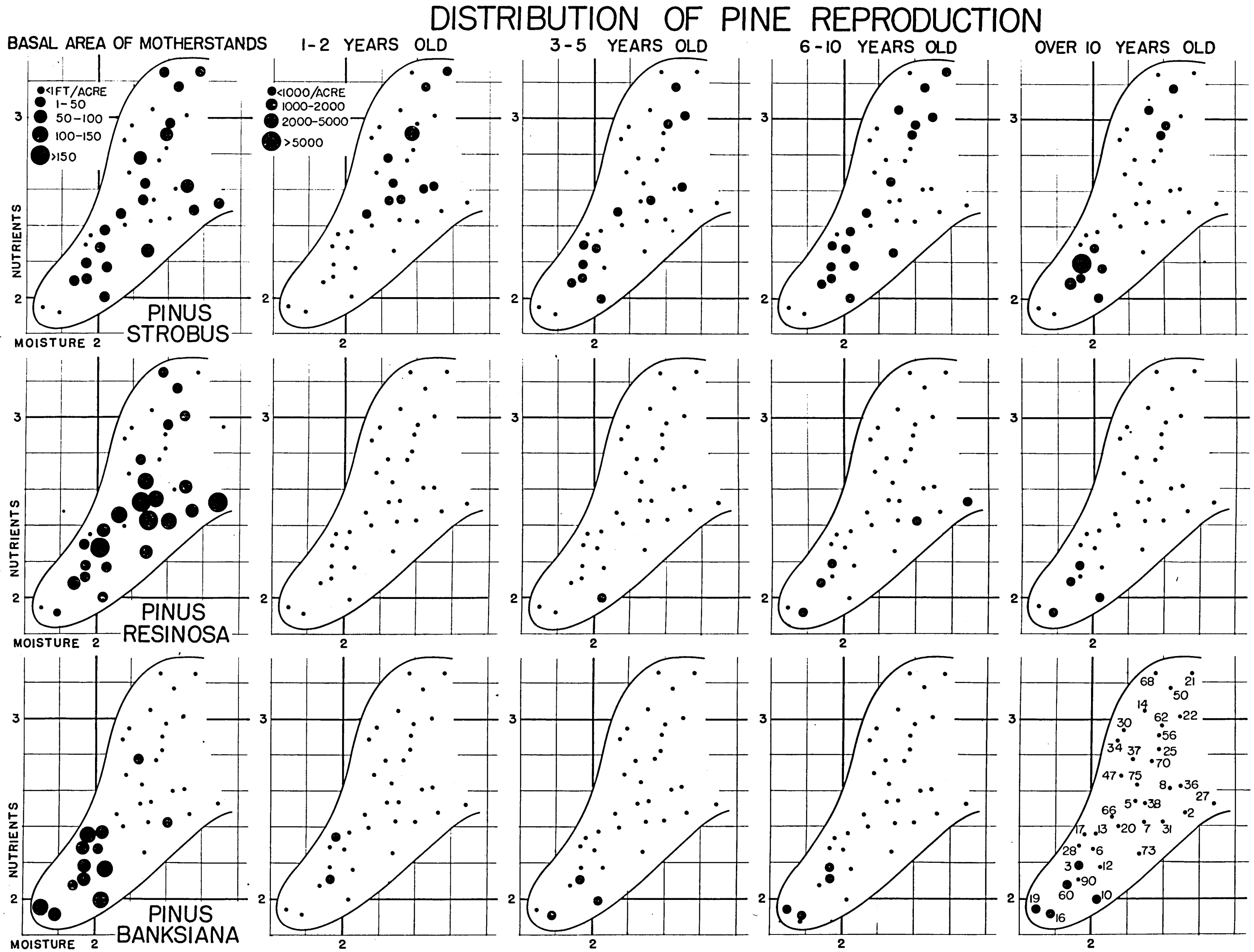


Figure 9. Distribution of basal areas of white pine, red pine, and jack pine and their reproduction by age groups in the edaphic field of upland forests in Itasca State Park, Minnesota.

which some pine reproduction still occurs with the overall upland forest conditions.

Figure 9 should be evaluated in comparison with Figures 13, 14, 15, and 16, and in addition to all figures giving information on soils, climate, and vegetation, and particularly to Figure 5 which shows the general stand and site conditions of upland forests. For further details, forest type descriptions and Appendix tables should be consulted.

The distribution pattern of advance white pine reproduction shows that white pine possesses the best competitive ability of all three pines (Fig. 9). Young white pine seedlings are able to withstand competition for some time even in Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica, Pinus resinosa-Dryopteris-Osmorhiza, and Quercus-Populus-Betula-Viburnum-Amphicarpa types with high shrub densities (Fig. 5, 6, and 7). However, the endurance of white pine seedlings is limited. Seedlings over 10 years old show a bi-modal distribution with seedlings present only on dry, nutrient-poor sites, mainly in the Pinus banksiana-Arctostaphylos (Pb-T) type, and on mesic, nutrient-rich sites in the Acer-Tilia-Pinus strobus-Dirca (AT-T) type. In pine forests with a rather dense understory of spruce-fir (Pinus-Abies-Picea-Lycopodium type) white pine seedlings are largely absent. White pine reproduction reaches its peak in the Pinus banksiana-Arctostaphylos (Pb-T) type with about 1,500 seedlings per acre followed by the Acer-Tilia-Pinus strobus-Dirca (AT-T) type with about 800 seedlings per acre. The stocking percentage in both cases is about 50 (based on 2-milacre plots) considering all sizes of seedlings. In general, white pine is an invading species becoming initially established over a wide range of stand and site conditions. However, it does not survive under strong shrub competition.

Herbicide applications to release suppressed white pine seedlings have been effective in encouraging white pine growth and development in Itasca Park. Hansen (1956a) showed that eight years after 2,4-D application and the suppression of shrubs, mainly hazel, the number of white pine seedlings over six inches tall and over five years old had increased from about 375 to 4,875 per acre on the sprayed plots. During the same period the number of such seedlings had increased from about 290 to 1,430 per acre on the control plots. There was a 13 fold increase on the sprayed plots as compared to a five fold increase on the control plots.

The distribution patterns of red pine and jack pine seedlings in the edaphic field differ considerably from the distribution pattern of white pine seedlings (Fig. 9). The distribution range of red pine and jack pine seedlings is narrower than the distribution range of mature mothertrees. Scattered red pine and jack pine seedlings in all age groups are largely confined to dry, nutrient-poor sites, mainly to the Pinus banksiana-Arctostaphylos (Pb-T) type, characteristics of which were discussed in preceding chapters. Even in this type, ground cover species, mainly halfshrubs, grasses, and invading shrubs, become serious competitors for soil moisture to pine seedlings. In addition, repeated summer drought periods limit the chance for these two species to become established. Furthermore, forest communities of the Pinus banksiana-Arctostaphylos type constitute only a small fraction of the total area of upland forests in Itasca Park. Without disturbance, even this forest type renders itself unsuitable for new pine establishment. The absence of one to two-year old red pine seedlings and the lack of white pine seedlings of this age group on dry, nutrient-poor sites (Fig. 9) is probably a result of drought in July 1965 (Fig. 2), connected with inadequate seed supply. The total number of red pine and jack pine seedlings per acre has some significance only in the Pinus banksiana-Arctostaphylos (Pb-T) type. There are about 300 red pine seedlings per acre with 25 percent stocking. The occurrence of jack pine seedlings is more frequent than red pine; however, survival of most jack pine seedlings is questionable.

Table 10 shows stocking percentages and average height of pine, spruce-fir, and hardwood reproduction in major forest cover types in Itasca Park based on an extensive survey in 1956, carried out by the School of Forestry, University of Minnesota. The low stocking percentages indicate the inadequacy of pine reproduction in the entire upland forest complex. According to Candy (1951), stocking percentages below 20 can be considered as reproduction failures. The average height of pine reproduction does not exceed one foot in any of the major forest cover types.

In assessing reproduction, the number of seedlings per acre and stocking percentages are very important. In addition, especially in natural forests with advance tree reproduction, knowledge of juvenile height growth rates and the distribtuion of size classes present is important. Figure 10 shows the actual age-height relationships of tree seedlings under conditions of competition with associated

Table 10. Stocking percentages and average height of pine, spruce-fir, and hardwood reproduction in major forest cover types in Itasca State Park, Minnesota.

Forest cover type	Stocking percentages and average height of tree reproduction:*						Number of milacre plots
	Pine		Spruce-fir		Hardwoods		
	(%)	(feet)	(%)	(feet)	(%)	(feet)	
Red pine-white pine	17	1	13	1	24	2	1149
Jack pine	14	1	1	2	5	4	590
Spruce-fir	5	1	72**	1	21	3	511
Aspen	4	1	0	4	55	3	766

* Includes all trees up to 2 inches in diameter at breast height.

** Predominantly balsam fir.

Source: after Hansen, 1956b

vegetation in different forest types. The growth performance of Corylus cornuta is shown for comparison. The potential height growth rates of these seedlings grown without competition may be quite different; therefore, it is not possible to substitute height for age in reproduction studies. Figure 10 also illustrates the number of conifer seedlings per acre by age groups in different forest types in comparison with the abundance of hardwoods and shrubs.

Age-height relationships of pines clearly indicate that white pine and red pine seedlings show a satisfactory height growth only in Pinus banksiana-Arctostaphylos (Pb-T) type. At age 15 to 20 they have reached at least the height of the Corylus cornuta canopy in this type (Fig. 10). Poor growth performance of jack pine seedlings is partly due to heavy deer browse. In Acer-Tilia-Pinus strobus-Dirca (AT-T) type with dense tree cover and strong competition of hardwood reproduction, white pine seedlings, although relatively numerous (Fig. 9 and 10) and showing quite adequate stocking percentages

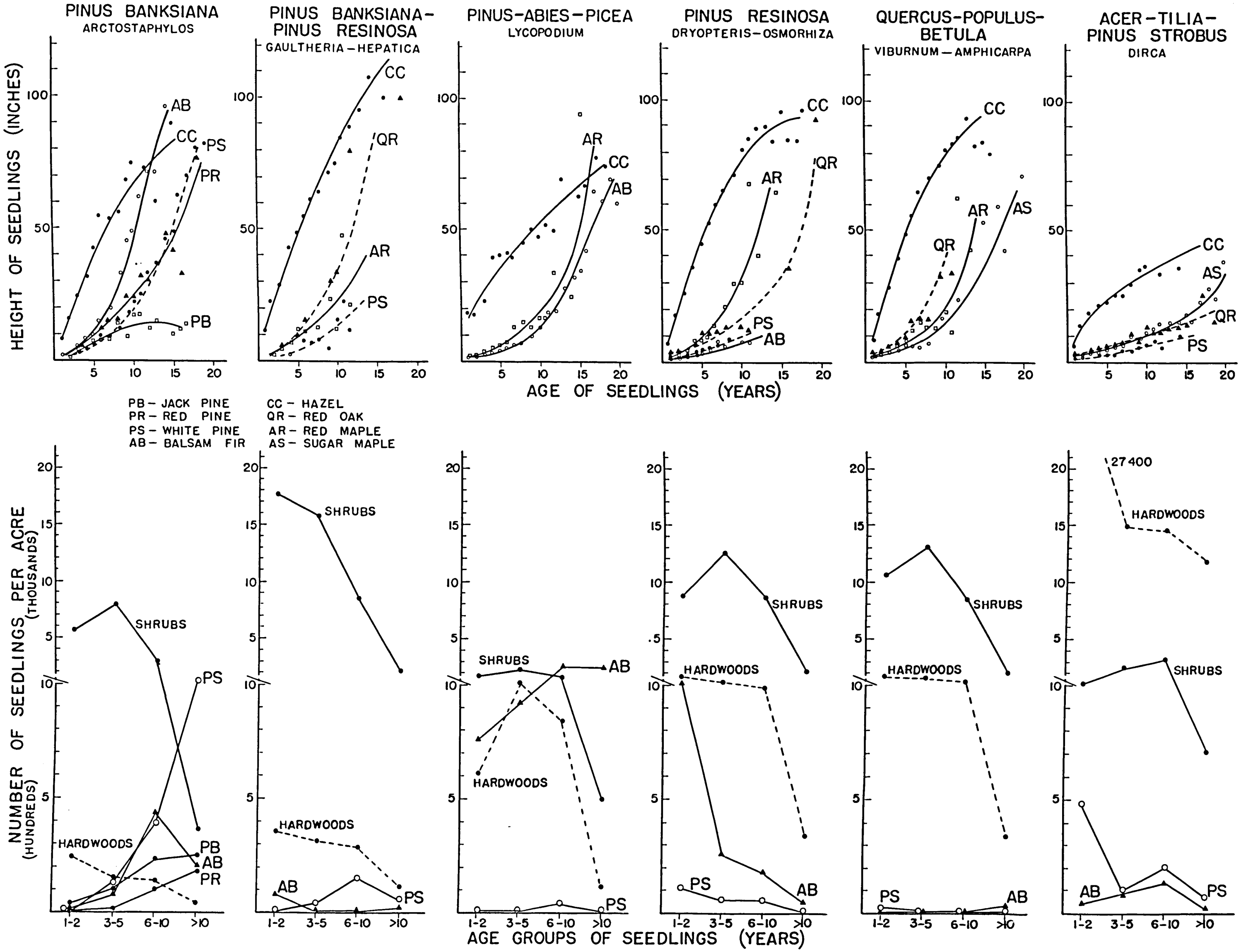


Figure 10. Agè and height relationships of reproduction and shrubs; number of seedlings and shrubs by age groups and local forest types in Itasca State Park, Minnesota.

(Table 11), have not reached a foot of height at the age of 15 years. Table 11 shows the stocking percentages of the total number of seedlings and by height classes. The lack of pine seedlings in height class over one foot in most of the forest types, except in Pinus banksiana-Arctostaphylos (Pb-T) type, is striking especially in comparison with hardwood reproduction. This indicates that although the first establishment of pine seedlings is important, their future development is a critical problem, particularly in the case of white pines. Rowe (1955) pointed out that the problem of reproduction is not so much of germination as of survival.

Shrubs, particularly <u>Corylus spp.</u>, not only retard the growth of pine reproduction but also keep it at size susceptible to animal browse. Orke (1966) reported that 95 percent of white and jack pine seedling were browsed in jack pine cover types and 73 percent of white pine seedlings in red pine-white pine cover types. The intensity of browsing was light for most of the white pine seedlings, but it appeared to be causing severe mortality of jack pine seedlings. From the small red pine sample about 2/3 of seedlings were not browsed, and the others were only lightly browsed, mainly by hare. White pine appears to be more browsed than red pine, but less than jack pine. However, white pine is considered more resistant to overbrowsing than red pine due to its ability to produce new shoots sooner than red pine (Krefting and Stoeckeler, 1953; Marshall et al., 1955).

The Mary Lake deer and hare exclosure was erected in red pine-white pine cover type in 1937 to study the browsing effects on forest undergrowth, especially pine seedlings. A comparison of the number of pine seedlings inside and outside the exclosure revealed that

Table 11. Stocking percentages of conifer and hardwood reproduction by height classes and local forest types in Itasca Park, Minnesota.1/

Species	Height classes (feet)	Local forest types*					
		Pb-T	PbPr-T	PAP-T	Pr-T	QPB-T	AT-T
		Percent of plots stocked with:					
Jack pine	any	35	2	0	0	0	0
	over 1	25	0	0	0	0	0
	over 3	0	0	0	0	0	0
Red pine	any	25	0	6	0	0	0
	over 1	23	0	0	0	0	0
	over 3	14	0	0	0	0	0
White pine	any	56	30	9	25	2	48
	over 1	50	10	0	0	0	0
	over 3	23	0	0	0	0	0
All pines	any	77	32	16	25	2	48
	over 1	62	10	0	0	0	0
	over 3	33	0	0	0	0	0
White spruce	any	6	7	6	3	4	0
	over 1	4	0	6	0	2	0
	over 3	4	0	3	0	2	0
Balsam fir	any	21	5	81	30	2	20
	over 1	17	2	37	4	0	3
	over 3	14	0	34	0	0	0
Spruce-fir	any	23	10	81	30	4	20
	over 1	19	2	41	4	2	3
	over 3	17	0	37	0	2	0
Hard-woods	any	37	55	66	84	90	100
	over 1	19	40	44	72	83	100
	over 3	17	27	16	41	40	71
Number of 2-milacre plots		48	40	32	64	48	56

* For type full names see type descriptions in Section 4.23 or Appendix Tables 2, 3, and 4.

1/ Includes all tree reproduction up to one inch in diameter at breast height.

heavy deer browsing prevented pine reproduction. There were no pine seedlings present outside the exclosure in 1946 (the park was first opened to deer hunting in 1945) as compared to 580 white pine and 19 red pine seedlings per acre inside the exclosure. In 1952 there were 375 white pine seedlings per acre outside the exclosure but red pine and jack pine seedlings were still absent (Hansen, 1953). After the park was opened to hunting, Hansen and Brown (1950) also observed that pine seedlings were becoming established along roads and other areas where mineral soil was exposed. During the time of high deer population pine seedlings were almost non-existent.

Similar observations can be made at the present time. Road sides, gravel pits, and some places along trails are sites where red pine and jack pine seedlings can be found. However, the area occupied by red pine and jack pine seedlings as compared to the acreage of mature red pine and jack pine stands is minute.

Table 12 shows the composition of conifer reproduction by species and forest types. The absence of jack pine and red pine seedlings can be seen in all types, except in the Pinus banksiana-Arctostaphylos (Pb-T) type. White pine seedlings constitute a large proportion of the total conifers in Pinus banksiana-Arctostaphylos (Pb-T) and Acer-Tilia-Pinus strobus-Dirca (AT-T) types. In Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T) and Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) types the total number of conifer reproduction counted is very small and, therefore, the composition percentages have a limited importance.

Table 12. Composition of conifer reproduction by species and upland forest types in Itasca State Park, Minnesota.

Forest types*	Number of stands**	Conifer reproduction in percent: Jack pine	Red pine	White pine	Balsam fir	White spruce	Total number of conifers
Pb-T	6	17	9	51	21	2	331
PbPr-T	5	3	0	63	23	10	30
PAP-T	4	0	0.3	0.7	98	1	445
Pr-T	8	0	0	12	86	2	237
QPB-T	6	0	0	20	40	40	5
AT-T	7	0	0	75	25	0	126

* For type full names see type descriptions in Section 4.23 or Appendix Tables 2, 3, and 4.

** Eight 2-milacre subplots per stand.

There are some specific areas in the park where the establishment of most of the pine seedlings can be traced back to the period from 1946 to 1951. A jack pine stand on LaSalle Trail is one of such areas (stand 3 in Figure 9), the reproduction study of which was initiated in 1947 by Dr. H. L. Hansen, School of Forestry, University of Minnesota. Figure 11 shows the course of white pine and jack pine reproduction over a 20-year period. The data are based on 60 temporary milacre plots from 1947 to 1953 and on 72 permanent milacre plots from 1954 to 1966.

This jack pine stand was characterized as almost shrub-free in 1947, the weather data (Fig. 2) indicate that there were no serious summer drought periods from 1945 to 1955, and the overpopulation of deer was removed by opening the park to hunting in 1945. In addition to these favorable conditions, good seed crops were probably available. Figure 12 shows the average estimates of seed crops for red pine, white pine, balsam fir, and white spruce in northern Minnesota (Rudolf, 1950-1963). The good white pine seed years of 1950 and also 1954 probably induced the peak seedling years of 1951 and 1955 respectively, in the LaSalle Trail jack pine stand (Fig. 11). White pine usually produced a good seed crop at intervals of three to five years and red pine at intervals of three to seven years, both with light crops in most intervening years. Balsam fir produces a good seed crop every two to four years and white spruce every two to six years (Fowells, ed., 1965).

Severe drought periods occurred in Itasca Park area in August 1955, June 1956, and July 1958 (Fig. 2). They are reflected in the decrease of white pine and jack pine seedlings during this time period (Fig. 11). A series of dry or wet seasons can have an influence on the germination and development of seedlings and further, on the composition of the forest for the entire generation. At present, in this LaSalle Trail reproduction study area there are about 3,000 white pine seedlings per acre over one year old. The number of jack pine seedlings has declined to about 100 per acre. Red pine seedlings are about as abundant as jack pine seedlings. The data on browse in 1963 indicate that 28 percent of white pine seedlings, 85 percent of jack pine seedlings, and 11 percent of red pine seedlings were browsed by deer. Six percent of white pine seedlings and 35 percent of jack pine seedlings were browsed by hare. Four percent of white pine seedlings showed blister rust (caused by Cronartium ribicola Fisher) infection and three percent of white pine seedlings were apparently rust killed. Orke (1966) reported that 10 percent of white pine seedlings taller than six inches in height had symptoms of blister rust in his browse study in Itasca Park. Along with the

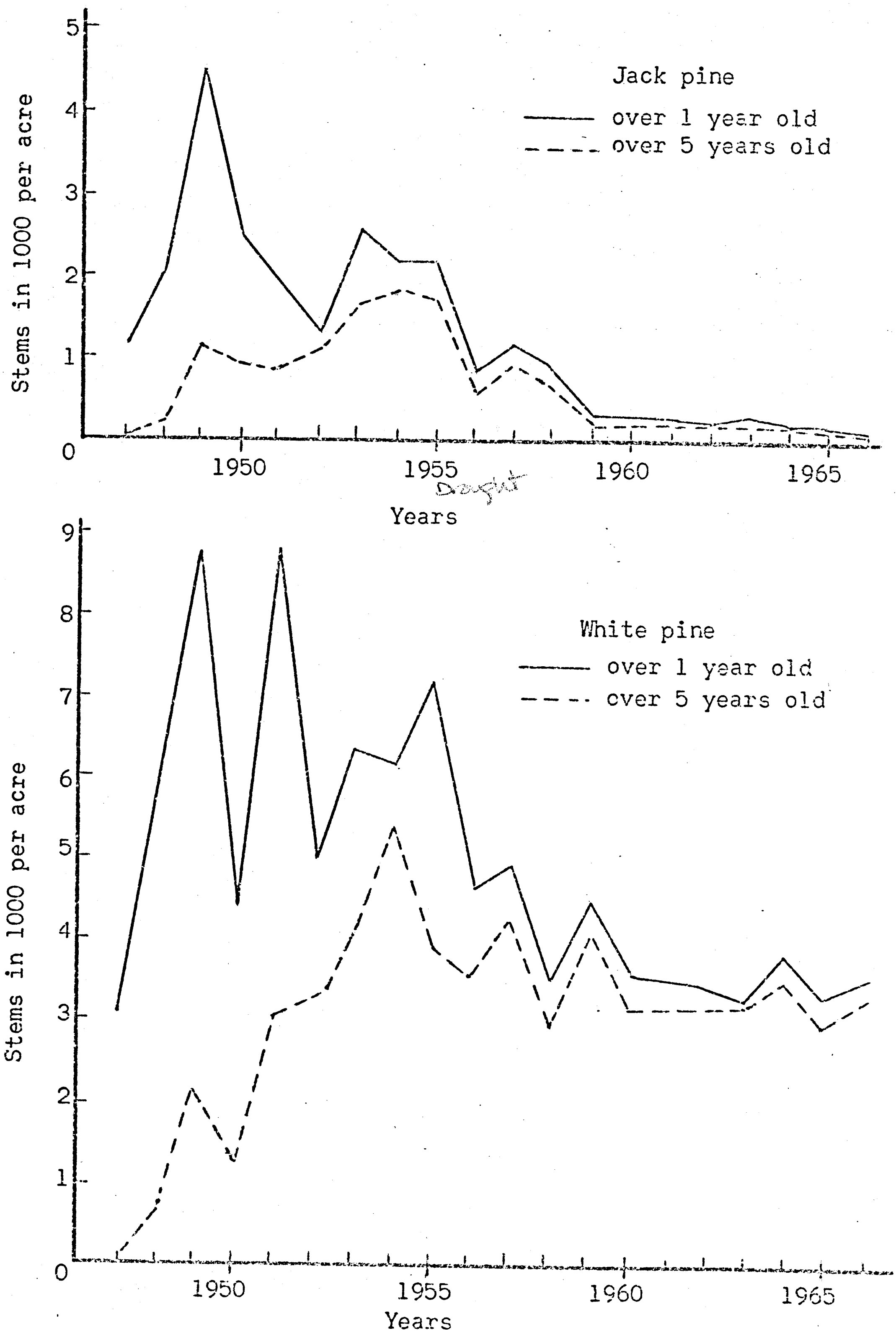
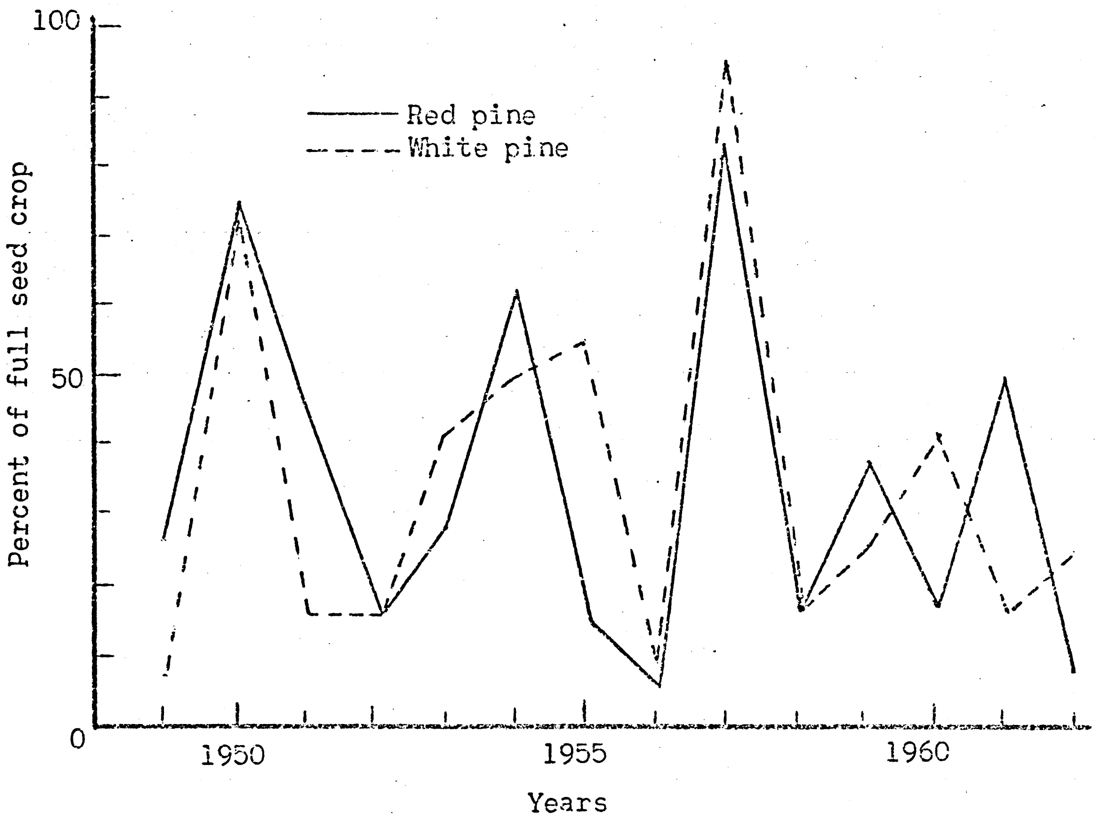


Figure 11. Change in white pine and jack pine reproduction over a 20-year period in a jack pine stand in Itasca State Park, Minnesota (after Hansen, 1967).

Stand 3, on LaSalle Trail



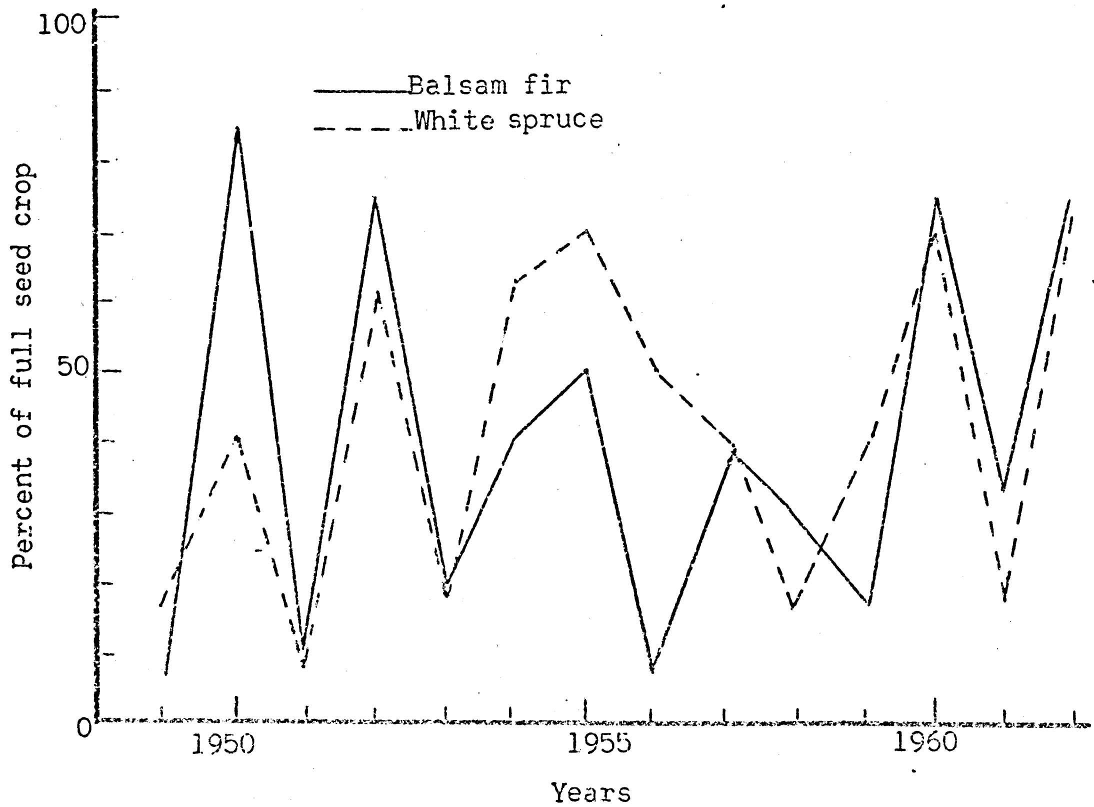


Figure 12. Estimated average percentage of a full seed crop for red pine, white pine, balsam fir, and white spruce in northern Minnesota from 1949 to 1962 (after Rudolf, 1950-1963).
Annual Report, Tech Notes Lake St. For. Exp. Sta.

development of white pine reproduction in the LaSalle Trail study area, shrubs have increased in size and abundance, reaching about 24,000 stems per acre in 1966. Shrubs and hardwoods have doubled in number in the last 10 years. However, they are not serious competitors for pines because most of the young white pines have outgrown the shrubs in height. Old jack pine overstory was removed from the larger part of the study area in 1957 and 1958. Young white pines show thrifty growth and many of the young trees have reached the sapling stage.

In general, most of the upland forest types in Itasca Park occur on soils which are well supplied with nutrients. These soils and sufficient light available under pine and aspen canopies favor the growth of herbs, shrubs, and hardwoods which are strongly moisture demanding and develop dense undergrowth layers in the absence of fire. There are very few red pine and jack pine seedlings under these conditions. The growth of white pine seedlings is largely restricted by the strong competition of dense associated vegetation, resulting in a prolonged period of exposure to animal damage. Occurrence of summer drought is critical for the initial establishment.

The comparison of areas occupied by mature pines and pine seedlings in the edaphic field (Fig. 9) clearly indicates that without major disturbances or silvicultural measures the present acreage of pine dominated stands will continue to decline. Normally this is a gradual process in which the old and disease-weakened pine trees are wind thrown. This results in a complete disappearance of pines from the areas where they are only scattered at present time, and in opening up the still solid old growth stands.

On dry, nutrient-poor sites, Pinus banksiana-Arctostaphylos

(Pb-T) type, pine seedlings become established to some degree; however, their height growth is rather slow due to existing competition from associated vegetation for light and moisture. This type occupies only a small portion of the total upland forest complex in the park. White pine is the major reproducing species in this type. Red pine is better suited to these site conditions than white pine which shows signs of decay at younger ages in this type than in types with higher nutrient levels.

On mesic, nutrient-poor sites, Pinus-Abies-Picea-Lycopodium (PAP-T) type, balsam fir prevents shrub invasion. Observations indicate that after windthrow of the poorly rooted and decayed balsam fir, pine reproduction may become established.

On dry to mesic, intermediate nutrient sites, Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T), Pinus resinosa-Dryopteris-Osmorhiza (Pr-T), and Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) types, with dense shrub layers and herbaceous ground cover, pine reproduction is prevented from germinating or, if established, is largely suppressed.

On mesic, nutrient-rich sites, Acer-Tilia-Pinus strobus-Dirca (AT-T) type, white pine seedlings are quite numerous; however, their height growth development is poor. Uprooting of old trees, resulting in large size openings and exposure of mineral soil, might stimulate some white pine establishment and development on these favorable microsites. Continuity of some white pine admixture can be expected even under a very limited chance for the seedlings to become established and grow because of the longevity of white pine.

6.22 Spruce-fir reproduction

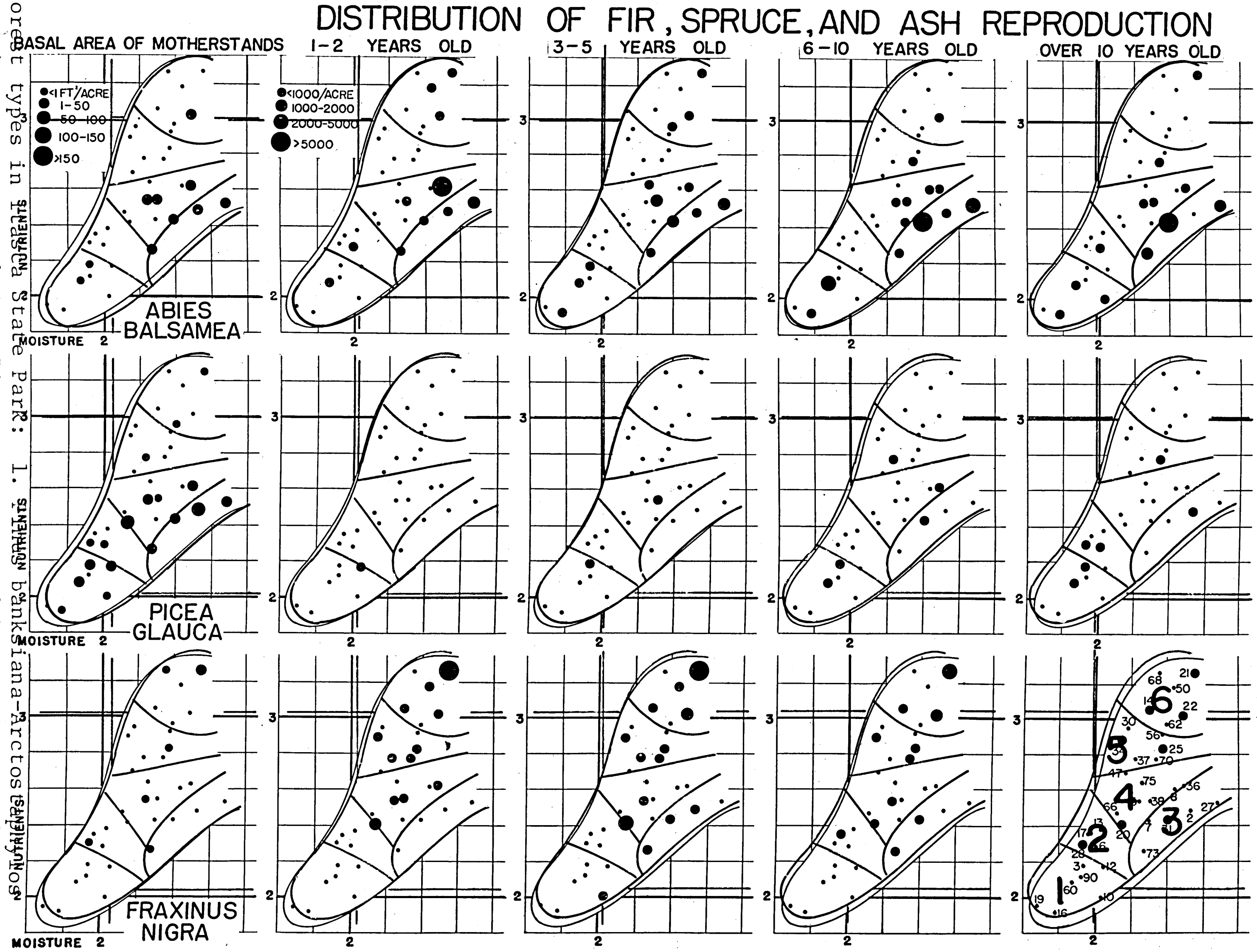
Balsam fir and white spruce, being boreal species, are on the southwestern edge of their natural distribution in the Itasca Park area. Away from the Boreal Region, balsam fir retains its boreal character as expressed in its tendency to occupy moist and cool sites, e.g., swamp borders, lake shores, north facing slopes, and shaded understories of pine and hardwood stands.

Figure 13 shows the distribution and abundance of balsam fir, white spruce, and black ash reproduction by age groups in relationship to motherstands, forest types, and moisture-nutrient gradients. Black ash, a minor species on uplands, is shown for comparison. In the edaphic field of upland forests, balsam fir trees occupy mesic, nutrient-poor to intermediate nutrient sites. They are represented mainly in Pinus-Abies-Picea-Lycopodium (PAP-T) type, and also occur in Pinus resinosa-Dryopteris-Osmorhiza (Pr-T) type. The location of Pinus-Abies-Picea Lycopodium (PAP-T) type in heat-light coordinates (climatic field) was shown as No. 3 in Figure 3. The average heat value for this type is 2.13, the lowest of all forest types (Table 4). This indicates the specific site conditions which contribute to maintain balsam fir and ecologically related species in areas bordering the southern limits of balsam fir natural distribution. White spruce trees occupy sites similar to those of balsam fir extending more towards drier site conditions.

Balsam fir and white spruce seedlings differ considerably in abundance and distribution pattern in upland forests (Fig. 13). Balsam fir, as white pine, is an invading species in its early years of life while white spruce reproduction can be called retreating as compared to the distribution of mothertrees. After initial success on wide range of site conditiond, balsam fir seedlings decrease in numbers and area occupied with increasing age. Buell (1956) pointed out that temporary favorable weather conditions are partly responsible for establishment of balsam fir seedlings outside suitable habitats. In this study, this trend is not well expressed because of the poor germination conditions due to drought and probably insufficient seed supply prior to the data collection. Almost complete lack of white spruce seedlings in younger age groups reflects these conditions. In general, the occurrence of white spruce seedlings throughout the upland forests is very scattered. Balsam fir usually produces a good seed crop every two to four years and white spruce every two to six years. The average estimates of seed crops for balsam fir and white spruce in northern Minnesota are shown in Figure 12.

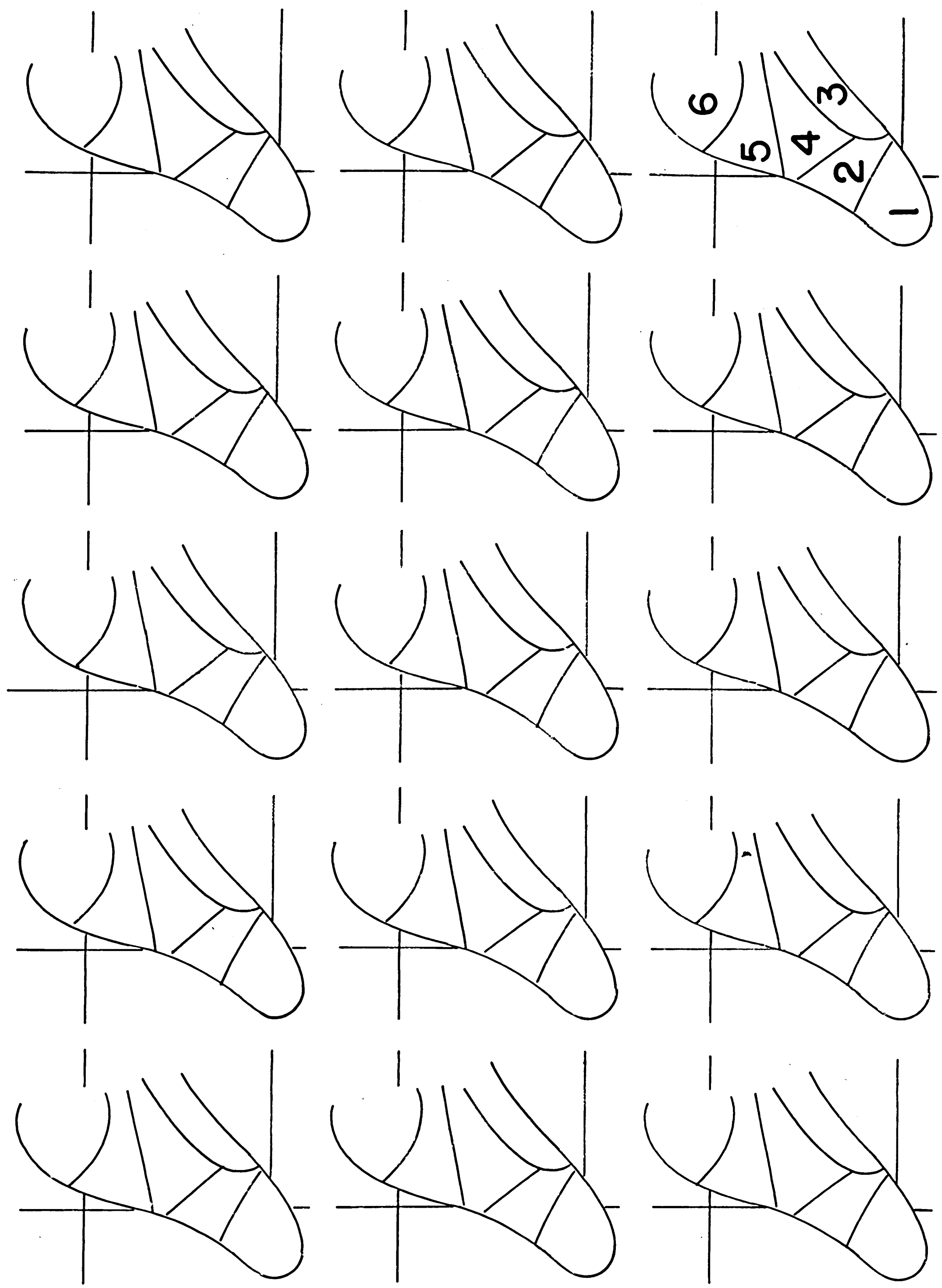
The total number of balsam fir seedlings reaches its peak on mesic, nutrient-poor to intermediate nutrient sites, mainly in Pinus-Abies-Picea-Lycopodium (PAP-T) type, with about 6,800 seedlings per acre and 80 percent frequency followed by Pinus resinosa-Dryopteris-Osmorhiza (Pr-T) type with about 1,600 seedlings per acre and 30 percent frequency. White spruce reproduction ranges from 20 to 70 seedlings per acre in upland forest types and frequency does not exceed 10 percent (Appendix Tables 3 and 4).

Seedbed requirements of both species are similar but usually less rigid for balsam fir because of more rapid initial growth and



Forest types in Itasca State Park: 1. Pinus banksiana-Arctostaphylos (Pb-T). 2. Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T). 3. Pinus-Abies-Picea-Lycopodium (PAP-T). 4. Pinus resinosa-Dryopteris-Osmorhiza (Pr-T). 5. Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T). 6. Acer-Tilia-Pinus strobus-Dirca (AT-T).

Figure 13. Distribution of basal areas of balsam fir, white spruce, and black ash and their reproduction by age groups in the edaphic field of upland forests in Itasca Park, Minnesota.



Forest types in Itasca State Park: 1. Pinus banksiana-Arctostaphylos (Pb-T). 2. Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T). 3. Pinus-Abies-Picea-Lycopodium (PAP-T). 4. Pinus resinosa-Dryopteris-Osmorhiza (Pr-T). 5. Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T). 6. Acer-Tilia-Pinus strobus-Dirca (AT-T).

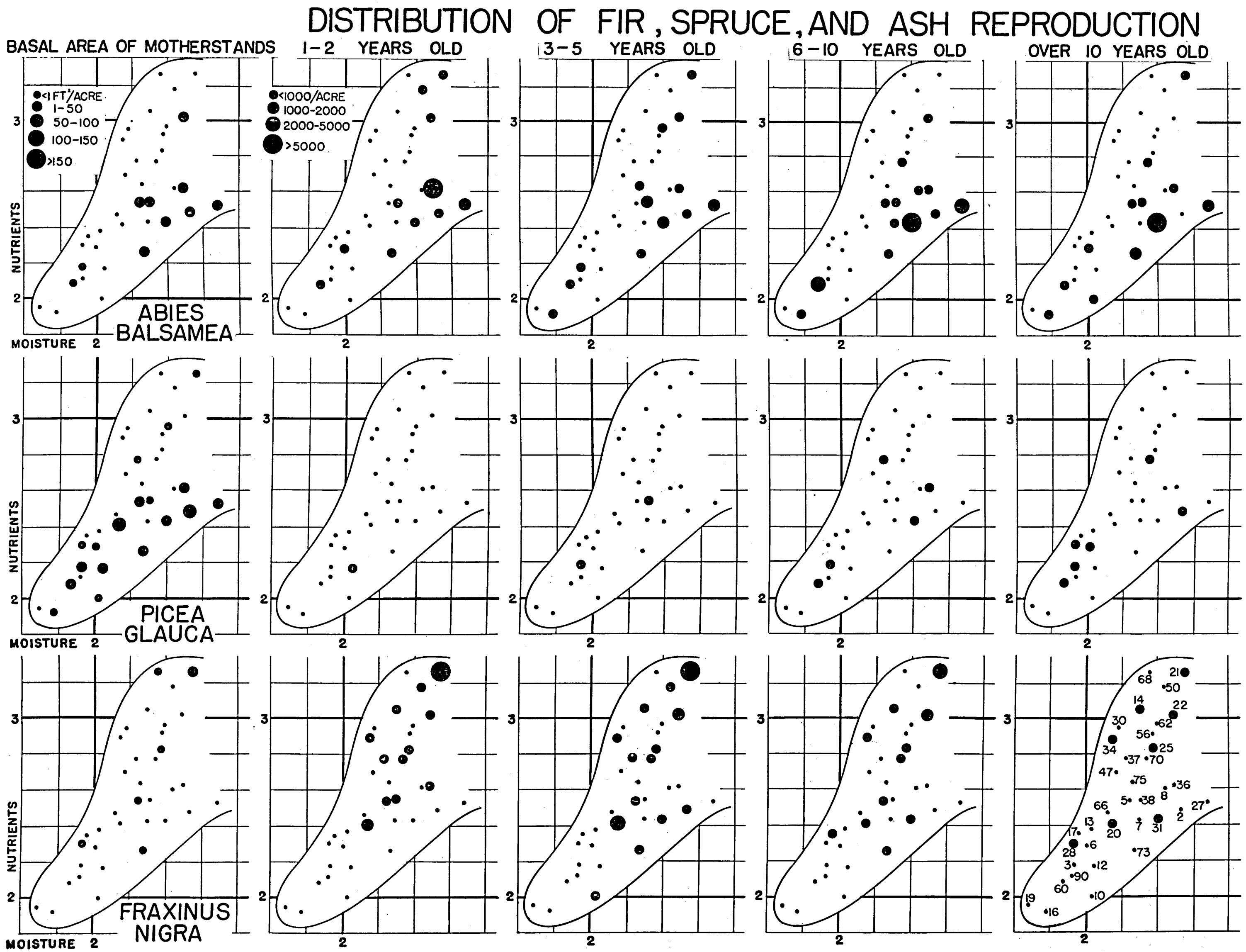


Figure 13. Distribution of basal areas of balsam fir, white spruce, and black ash and their reproduction by age groups in the edaphic field of upland forests in Itasca Park, Minnesota.

generally greater robustness (Place, 1955). Balsam fir seedlings have longer taproots than white spruce seedlings. This partly explains the better survival of balsam fir in the initial establishment, especially under upland forest conditions in Itasca Park where drought periods are common during the growing season. Place (1955) pointed out that seedbeds such as humus, litter, and moss which easily dry out to a depth of two to three inches or more, are detrimental to white spruce during the first season. In natural forests the majority of seedlings are found on decayed wood; this is also very often the case with balsam fir seedlings (Hosie, 1947). The advantage of exposed mineral soil in seedling establishment is emphasized by LeBarron (1945) in his studies in northern Minnesota. White spruce seedlings are rather common on trails in Itasca Park where they can establish an early contact with mineral soil. Balsam fir seedlings are often found close to red pine trunks. Favorable seedbed and less root competition from mature red pine trees at the base of the trees are largely responsible for this kind of establishment pattern.

White spruce seldom reproduces on better sites even if they are moist unless decayed wood is present or the humus layer is disturbed. The chief unfavorable factor appears to be severe competition, mechanical and nutritional, from the dense growth of broad-leaved herbs (Rowe, 1955). Aspen and maple leaves are particularly detrimental to young seedlings, aspen being one of the worst offenders (Place, 1955). Balsam fir invasion is also handicapped by hardwoods and shrubs on sites with higher nutrient intensities (Fig. 13). Bowman (1944) reported from Michigan that 73 percent stocking of spruce-fir reproduction at zero to 50 percent groundcover density decreased gradually to 24 percent stocking at 90 to 100 percent groundcover density.

Once balsam fir seedlings have become established their early growth is determined largely by the amount and character of overhead competition. Shrubs are particularly serious competitors in prairie border areas such as Itasca Park, and where competition for moisture is severe. The differences in height growth of balsam fir seedlings are distinct between Pinus-Abies-Picea-Lycopodium (PAP-T) and Pinus resinosa-Dryopteris-Osmorhiza (Pr-T) types (Fig. 10), the latter having rather strong shrub development in terms of abundance and height growth. In Pinus resinosa-Dryopteris-Osmorhiza (Pr-T) type the presence of balsam fir seedlings in mature pine stands does not assure that pines will be succeeded by spruce-fir, or even that an understory of balsam fir will be formed. Under conditions of effective shrub and ground-cover competition balsam fir seedlings disappear with time or do not make any significant height growth for many years. Stocking percentages of balsam fir seedlings by height classes indicate that only a few seedlings have surpassed a foot in height in this type as compared to their larger size in the Pinus-Abies-Picea-Lycopodium (PAP-T) type (Table 11).

Balsam fir shows ability to become established in Pinus banksiana-Arctostaphylos (Pb-T) type on sandy Menahga soils under specific conditions. In this case, north-facing slopes aided by the cooling effect of ponds, creeks, and lakes are favorable factors in the survival of spruce-fir seedlings. Lee (1924) reported that spruce-fir reproduction in Itasca Park is less abundant in areas remote from lakes and that the percentage of reproduction increases in almost inverse proportions to the distance from the lake shore.

The composition of conifer reproduction by species and upland forest types was shown in Table 12. The proportion of white spruce reproduction in the total number of conifers is small, but scattered white spruce seedlings can be found in most of the forest types. Balsam fir or white pine seedlings, depending on the forest type, have proportionally the largest occurrence of all conifers.

Balsam fir can hold its position in upland forests on sites which are most suitable to its boreal character (Pinus-Abies-Picea-Lycopodium type). It is declining on sites where invading shrubs and hardwoods can compete for soil moisture better than can balsam fir seedlings (Pinus resinosa-Dryopteris-Osmorhiza type). There will be an occasional occurrence of balsam fir seedlings in other types provided favorable microsite conditions are available for initial establishment and growth. White spruce is a more continental species than balsam fir and can compete better with shrubs and hardwoods on more droughty site conditions. The scattered occurrence of white spruce reproduction in upland forests in Itasca Park is mainly due to the inability of white spruce seedlings to become established on undisturbed, often droughty soil surfaces.

The positive contribution of balsam fir is its ability to compete with shrubs on moist, cool sites. Balsam fir understories can keep out shrubs and improve the seedbed for pine reproduction. However, silvicultural measures may be necessary to assist pine reproduction. Balsam fir is susceptible to rot diseases and is a rather short-lived tree; it will have only a secondary role in the composition of upland forests. In comparison to balsam fir, white spruce is a healthy long-lived tree and, in general, better adapted to upland site conditions than balsam fir. White spruce can play a primary role in upland forest composition and structure.

Figure 13 also illustrates the abundance and distribution pattern of black ash reproduction in upland forests as related to moisture-nutrient gradients and mothertrees. Black ash is a lowland species and is most commonly found growing in peat soils or on mineral soils with a high water table. Black ash trees, even in the sapling stage, are infrequent on upland sites in Itasca Park (Fig. 13). However, the occurrence of seedlings is rather common in upland forests due to the intermingling of upland and lowland features on a small area. The seed supply from mature black ash trees on lowlands is usually close to the uplands and as a result black ash seedlings occur over a wide range of the edaphic field, except for dry, nutrient-poor sites. The total number of black ash reproduction ranges from 10 seedlings per acre in Pinus banksiana-Arctostaphylos (Pb-T) type, gradually increasing to about 3,300 seedlings per acre in Acer-Tilia-Pinus strobus-Dirca (AT-T) type. The range of frequency is from about two to 40 percent (Appendix Tables 3 and 4).

In early years of establishment black ash can be characterized as an aggressive species; however, with increased age it is unable to compete with other species on upland sites. Seedlings over 10 years old are represented in fewer forest stands than are the younger age groups, and their abundance has decreased. Black ash has a limited importance in upland forest composition.

6.23 Aspen-birch reproduction

Paper birch, quaking aspen, and bigtooth aspen are characteristic pioneer species reproducing vigorously after disturbances. They usually are not successful in reproducing themselves under the shade of mature stands. In the natural succession they are replaced by more tolerant species. Paper birch is rated as an intolerant tree species and quaking aspen as very intolerant. Bigtooth aspen is considered as one of the most intolerant deciduous forest trees (Baker, 1949).

Figure 14 shows the distribution and abundance of aspen-birch reproduction by age groups in relationship to motherstands, forest types, and moisture-nutrient gradients. Paper birch and quaking aspen trees occur over a wide range of upland site conditions reflecting widespread disturbances in the past. Paper birch is largely an admixture species in most of the forest types while quaking aspen more often forms relatively pure stands. Bigtooth aspen is usually associated with quaking aspen and occurs as scattered trees or groups of trees in quaking aspen stands.

Paper birch reproduction in younger age groups is scattered over the upland forest range (Fig. 14). It is present as small seedlings on patches of exposed mineral soil or decayed logs, and as sprouts arising from the bases of standing trees. The limited occurrence of young paper birches in age group over 10 years old indicates that most of the seedlings and sprouts disappear before reaching this age because of severe competition from trees and shrubs. Paper birch needs an adequate supply of light for successful growth and development. There are no older seedlings or sprouts in Pinus-Abies-Picea-Lycopodium (PAP-T) and Acer-Tilia-Pinus strobus-Dirca (AT-T) types with dense tree canopies nor on dry, sandy soils in the Pinus banksiana-Arctostaphylos (Pb-T) type. The total number of paper birch reproduction fluctuates from about 100 to 350 stems per acre in all forest types except Pinus-Abies-Picea-Lycopodium (PAP-T) type where there are 30 stems per acre. Low frequences from five to 16 percent indicate the clustering pattern of young seedlings and sprouts (Appendix Tables 3 and 4).

The distribution pattern of quaking aspen reproduction by age groups is similar to that of paper birch (Fig. 14). There are numerous stems present in younger age groups, mainly as root suckers. However, almost all of them disappear in later years. Studying forest succession in Itasca Park, Kell (1938) pointed out that most of the aspen root suckers die before reaching a meter in height. In this study, aspen suckers were found dead after they had reached six to eight feet in height under aspen motherstands. Zehngraff (1949) indicated that for vigorous sucker development strong light must reach the forest floor. This is usually not the case in forests with well developed tree canopies and dense shrub layers. Observations, however, indicate that in some areas in the park after wind damage, resulting in adequately large openings in crown cover, aspen root suckers can succeed; securing at least some aspen for the future. The total number of young quaking aspen reproduction ranges from about 100 to 200 stems per acre on nutrient-poor sites, predominantly with pine cover, and from about 700 to 800 stems per acre on nutrient-rich sites, mainly with aspen and northern hardwood cover (Appendix Table 3).

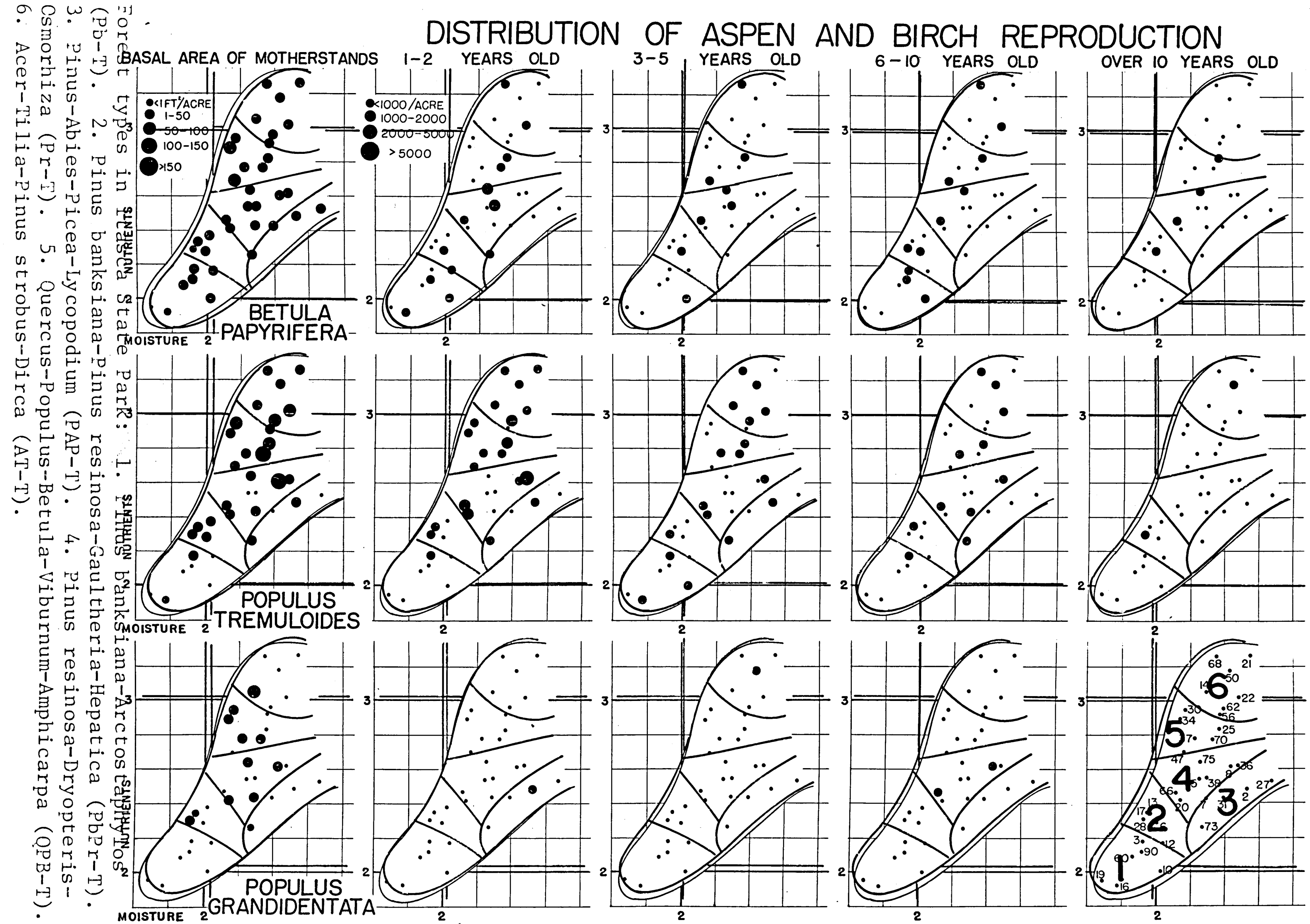
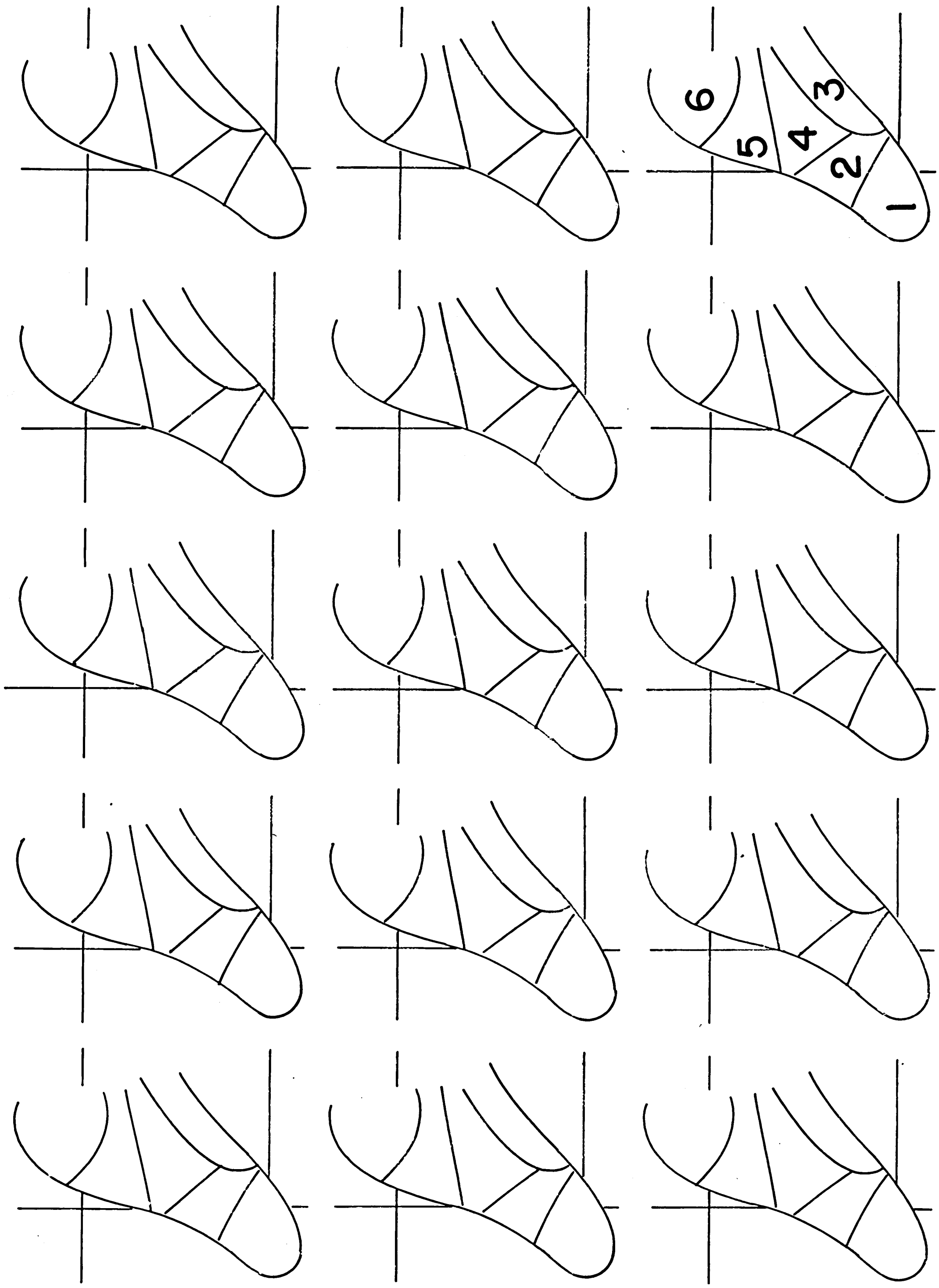


Figure 14. Distribution of basal areas of paper birch, quaking aspen, and bigtooth aspen and their reproduction by age groups in the edaphic field of upland forests in Itasca State Park, Minnesota.



Forest types in Itasca State Park: 1. Pinus banksiana-Arctostaphylos (Pb-T). 2. Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T). 3. Pinus-Abies-Picea-Lycopodium (PAP-T). 4. Pinus resinosa-Dryopteris-Osmorhiza (Pr-T). 5. Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T). 6. Acer-Tilia-Pinus strobus-Dirca (AT-T).

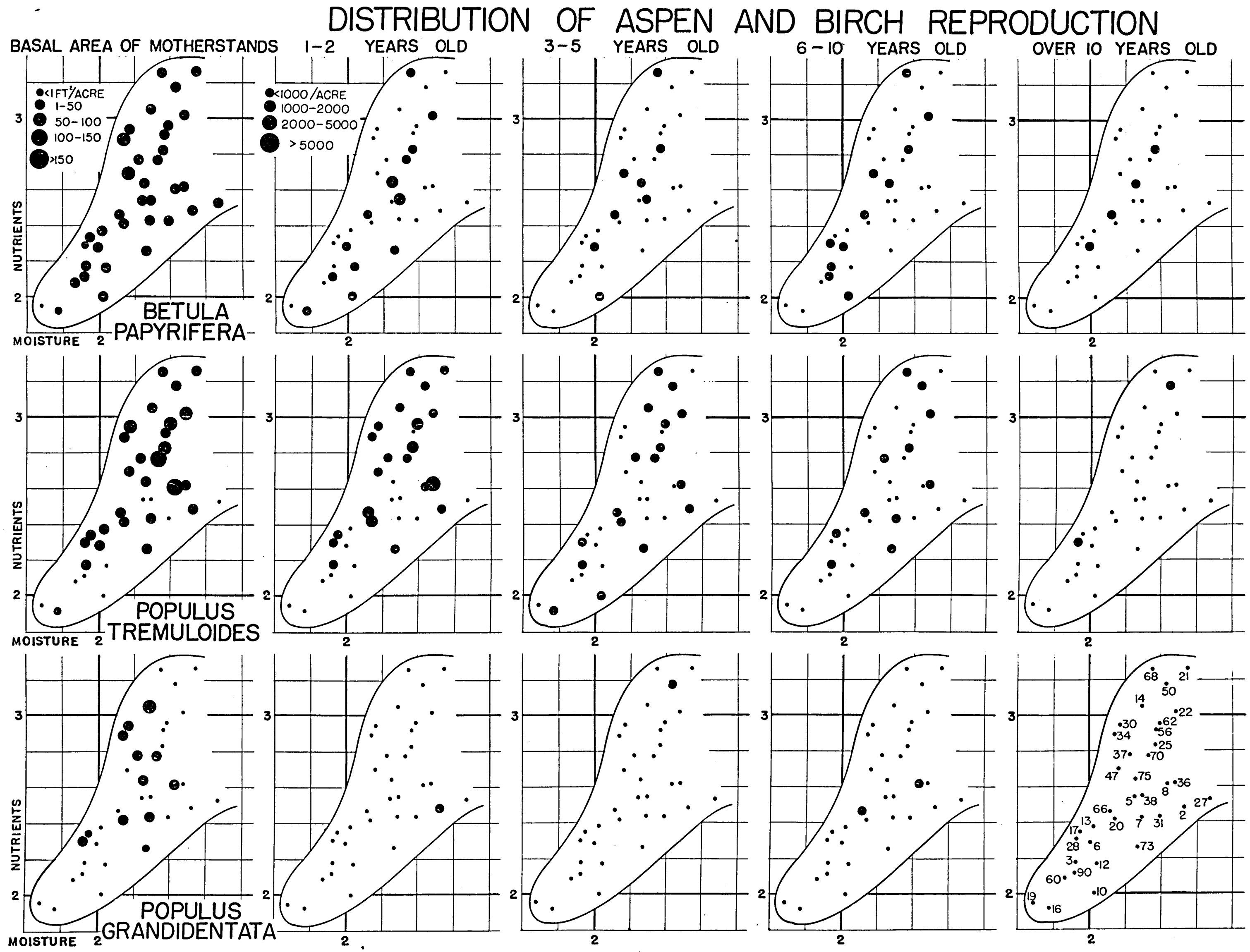


Figure 14. Distribution of basal areas of paper birch, quaking aspen, and bigtooth aspen and their reproduction by age groups in the edaphic field of upland forests in Itasca State Park, Minnesota.

Table 13 shows the composition of hardwood reproduction by species and forest types. Paper birch and aspen reproduction are proportionally the commonest of hardwood species in Pinus banksiana-Arctostaphylos (Pb-T) and Pinus banksiana-Pinus resinosa-Gaultheria Hepatica (PbPr-T) types, although most of the aspen-birch seedlings and sprouts are in the youngest age groups.

Bigtooth aspen reproduction, being somewhat more sensitive to inadequate light supply than quaking aspen and paper birch, does not even become established in forest stands. Bigtooth aspen reproduction in all age groups is almost non-existent (Fig. 14). Studies by Stoeckeler and Mason (1956) showed that even a light residual stand of aspen or associated species greatly inhibits suckering. The shade of shrubs and ground cover species is also detrimental to sucker development and seedling establishment. The undisturbed soil surface covered by leaf litter is usually unfavorable seedbed because seedling roots are unable to penetrate this layer.

Table 13. Composition of hardwood reproduction by species and upland forest types in Itasca State Park, Minnesota.

Forest types*	Number of stands**	Hardwood reproduction in percent								Total number of hardwoods
		Aspen	Paper birch	Bur oak	Red oak	Red maple	Sugar maple	Bass-wood	Others	
Pb-T	6	34	45	11	2	6	0	0	2	47
PbPr-T	5	20	32	1	12	28	0	1	6	86
PAP-T	4	8	1	1	2	82	0.6	0	5	166
Pr-T	8	17	8	1	9	48	0	0	17	569
QPB-T	6	14	4	1	21	27	13	5	15	499
AT-T	7	1	0.1	0.3	3	10	75	1	9	7717

* For type full names see type descriptions in Section 4.23 or Appendix Tables 2, 3, and 4.

** Eight 2-milacre subplots per stand.

The reproduction analyses of paper birch, quaking aspen, and bigtooth aspen indicate that the mortality of young aspen and paper birch is large under tree canopies. Only a few young stems have surpassed 10 years. Bigtooth aspen reproduction seldon becomes established. Clusters of young aspen in sapling stage can only be found in areas where wind damage has resulted in sufficiently large openings in the tree cover. At present, the aspen cover type is the largest in the park. In the absence of disturbances the acreage of aspen will decline as indicated by the reproduction situation.

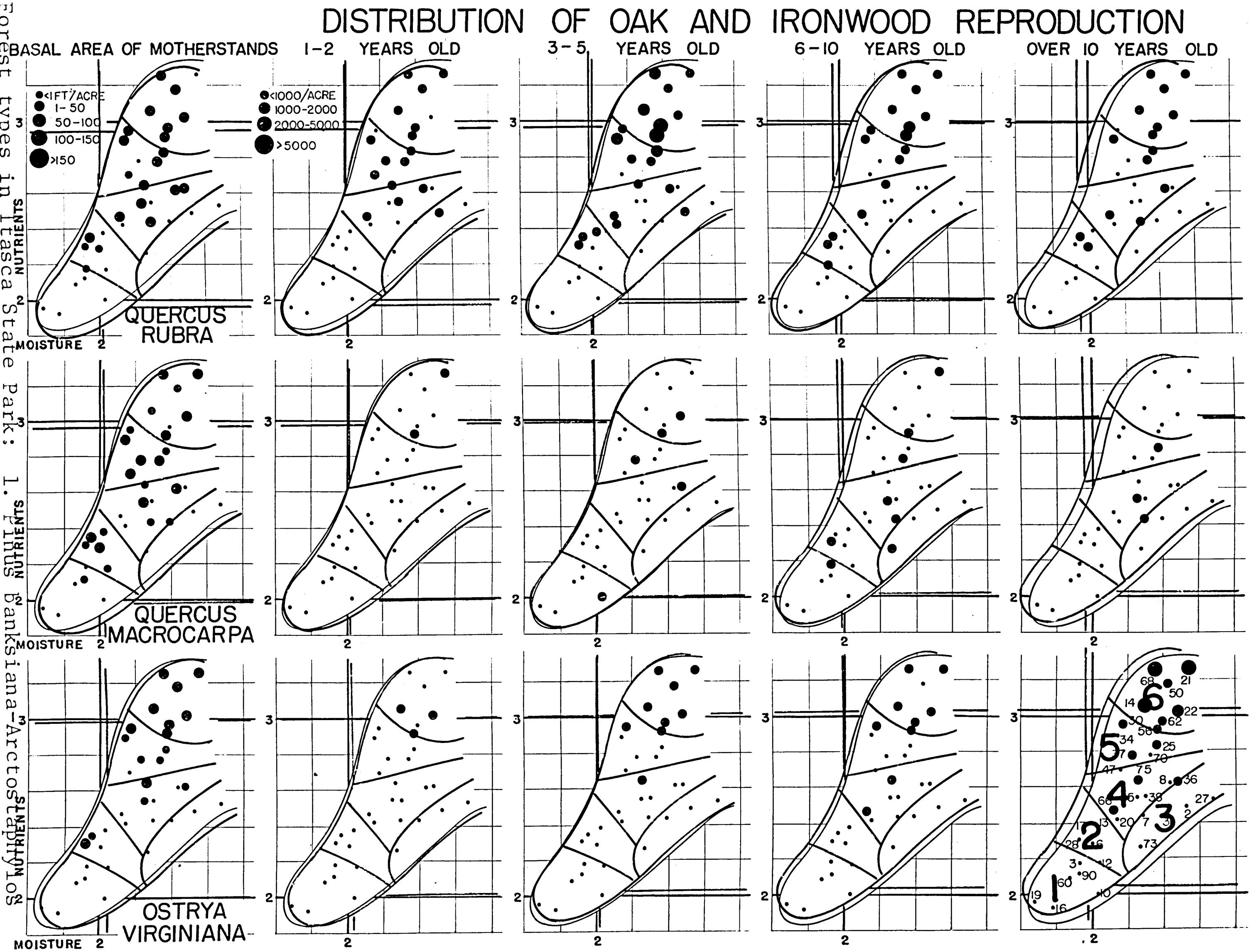
6.24 Oak reproduction

Red oak and bur oak are intermediate in tolerance and they are able to adjust to a wide range of moisture and nutrient conditions. In Itasca Park they are found in association with a variety of other tree species. Ironwood, considered here for the purpose of comparison, is a minor species and seldom exceeds five inches in diameter at breast height in the park. It is shade tolerant and is usually found in forest understories on better sites.

Figure 15 shows the distribution and abundance of oak and ironwood reproduction in upland forests by age groups in relationship to mothertrees, forest types, and moisture-nutrient gradients. Red oak and bur oak trees are common stand components on dry to mesic, intermediate nutrient to nutrient-rich sites occurring in most of the forest types. They are less frequent in Pinus banksiana-Arctostaphylos (Pb-T) and Pinus-Abies-Picea-Lycopodium (PAP-T) types. Ironwood follows a similar distribution pattern; however, it is more concentrated in Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) and

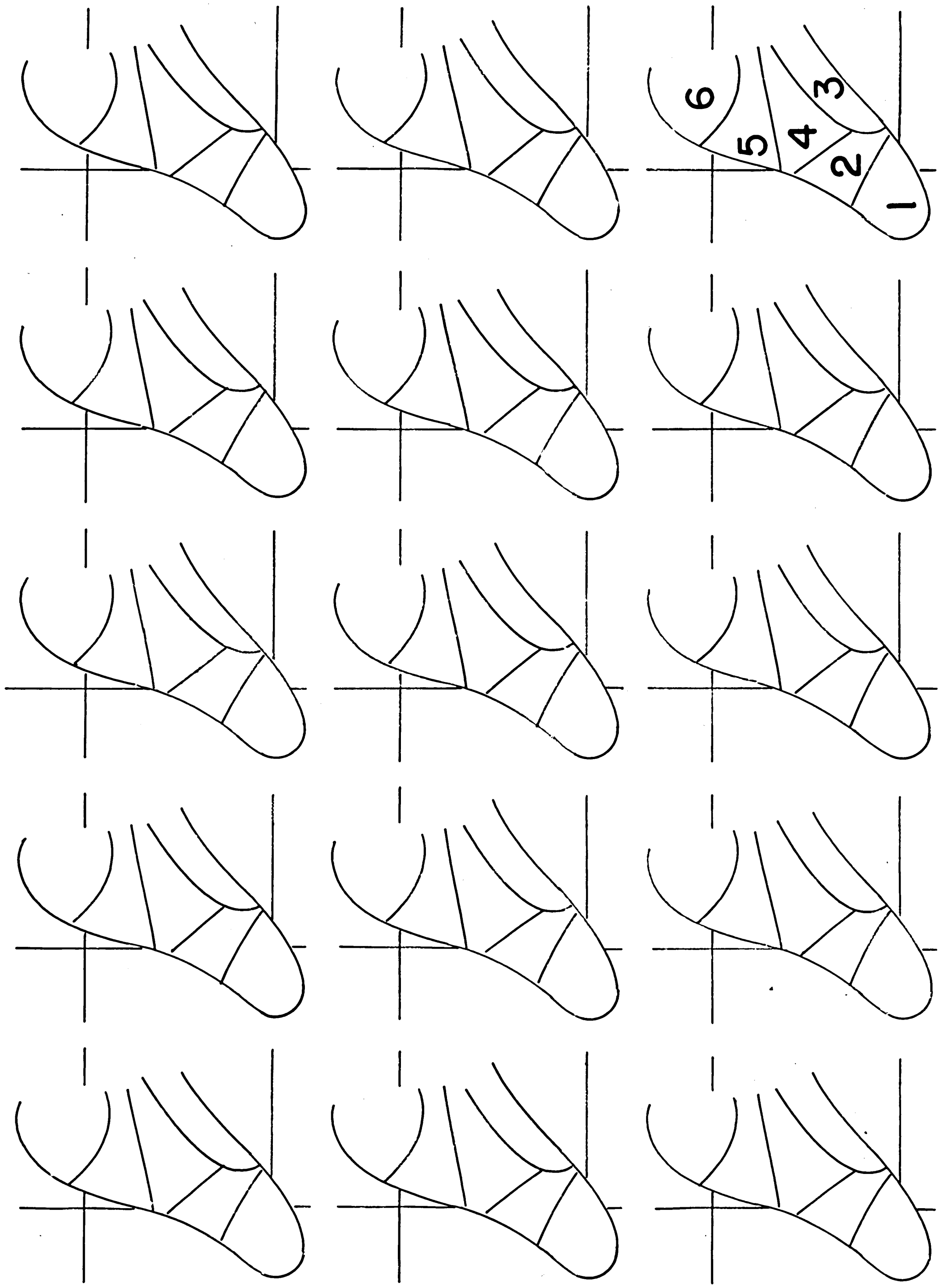
Acer-Tilia-Pinus strobus-Dirca (AT-T) types.

The distribution pattern and abundance of red oak reproduction is rather constant in all age groups (Fig. 15). The area covered by the reproduction in the edaphic field coincides approximately with the area covered by mothertress. Red oak reproduction is relatively well represented in the three centrally located forest types (Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica, Pinus resinosa-Dryopteris-Osmorhiza, and Quercus-Populus-Betula-Viburnum-Amphicarpa) with dense shrub canopies indicating its ability to compete with associated forest undergrowth species. This competitive ability is well expressed in age-height relationships of red oak reproduction in these three forest types (Fig. 10). Its height growth is not quite as good in the Acer-Tilia-Pinus strobus-Dirca (AT-T) type under a dense tree canopy and in competition with other species of hardwood reproduction; however, all of the reproducing species including shrubs are characterized by slow height growth rate in this type (Fig. 10). The total number of red oak reproduction is about 2,400 stems per acre in Acer-Tilia-Pinus strobus-Dirca (AT-T) type followed by Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) type with about 1,100 stems per acre. The corresponding frequencies for these types are 87 and 62 percent, respectively. Pinus banksiana-Arctostaphylos (Pb-T) type shows only 10 young red oak stems per acre (Appendix Tables 3 and 4). The composition of hardwood reproduction by species and forest types was shown in Table 13. Red oak reproduction is proportionally the strongest in Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) type. Together with red maple reproduction



Forest types in Itasca State Park: 1. Pinus banksiana-Arctostaphylos (Pb-T). 2. Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T). 3. Pinus-Abies-Picea-Lycopodium (PAP-T). 4. Pinus resinosa-Dryopteris-Osmorhiza (Pr-T). 5. Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T). 6. Acer-Tilia-Pinus strobus-Dirca (AT-T).

Figure 15. Distribution of basal areas of red oak, bur oak, and ironwood and their reproduction by age groups in the edaphic field of upland forests in Itasca State Park, Minnesota.



Forest types in Itasca State Park: 1. Pinus banksiana-Arctostaphylos (Pb-T). 2. Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T). 3. Pinus-Abies-Picea-Lycopodium (PAP-T). 4. Pinus resinosa-Dryopteris-Osmorhiza (Pr-T). 5. Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T). 6. Acer-Tilia-Pinus strobus-Dirca (AT-T).

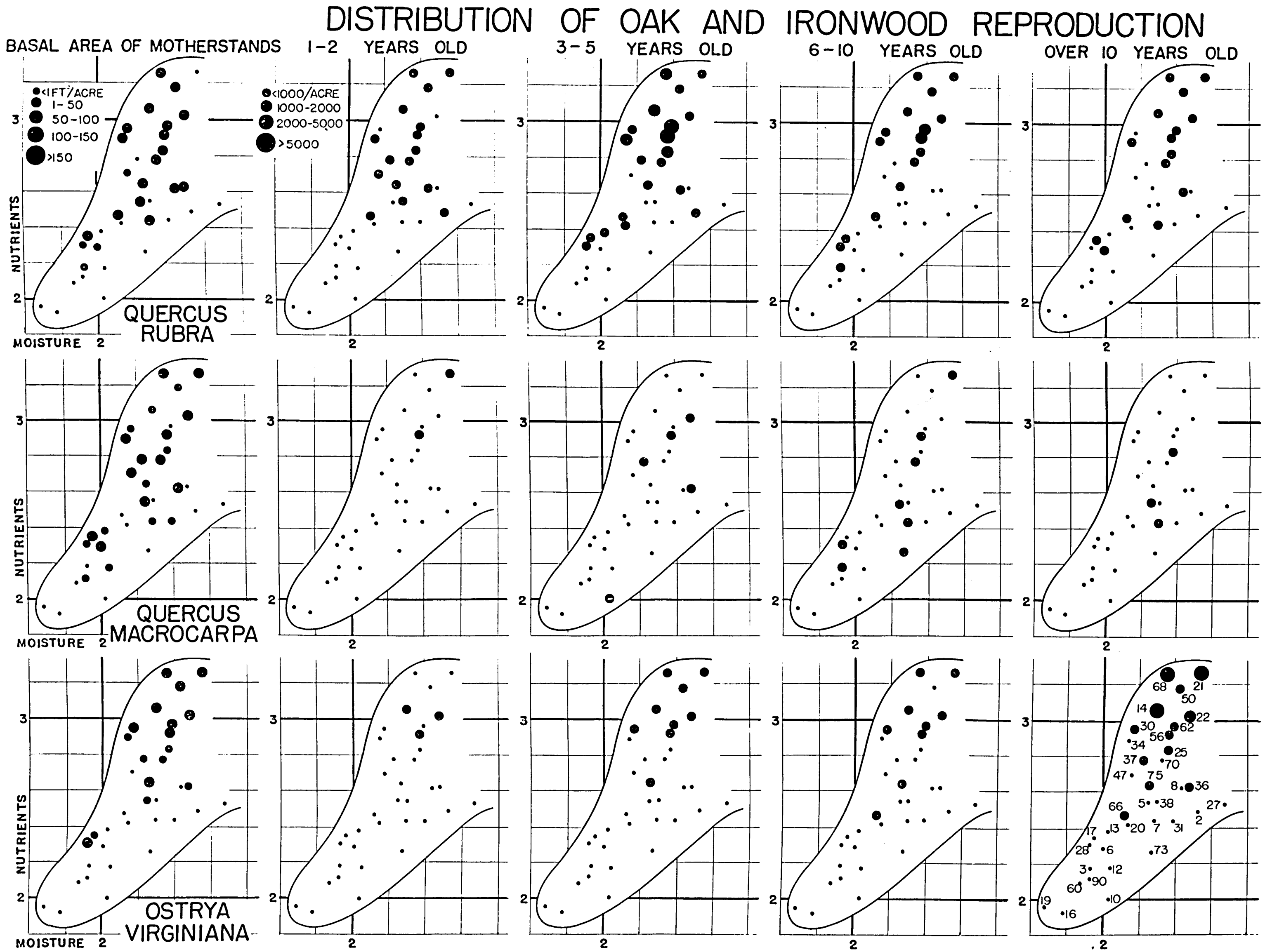


Figure 15. Distribution of basal areas of red oak, bur oak, and ironwood and their reproduction by age groups in the edaphic field of upland forests in Itasca State Park, Minnesota.

they compose almost 50 percent of the total number of hardwood reproduction in this type.

The bur oak reproduction is more scattered than red oak reproduction in upland forests (Fig. 15). Although bur oak is known as a species which can successfully compete with shrubs and grasses, it does not do well in the Itasca Park area. Buell and Cantlon (1951) reported that in old growth white pine and bur oak stands in forest prairie transition areas bur oak reaches only sapling size before dying from suppression and is replaced by sugar maple and basswood. Similar observations were made in this study in Acer-Tilia-Pinus strobus-Dirca (AT-T) type. Bur oak reproduction reaches its peak in this forest type with about 200 stems per acre. Pinus banksiana-Arctostaphylos (Pb-T) type averages about 50 young bur oak stems per acre. In this type, however, bur oak reproduction is higher proportionally than in all other types of the total number of hardwoods (Table 13).

Red oak seedlings are well adapted to competition. The root growth of first-year seedlings is rapid and the taproots penetrate deeply into the soil enabling the seedlings to compete efficiently for soil moisture. There is practically no competition for nutrients in the first year, and still in second year seedlings may profit from nutrient supply of the seed. After disturbances such as cutting and fire, red oak and bur oak possess the ability to reproduce by sprouts.

Ironwood reproduction is largely limited to mesic, nutrient-rich sites and shows its main concentration in Acer-Tilia-Pinus strobus-Dirca (AT-T) type reaching on the average about 2,500 stems per acre as compared to Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) type with about 150 stems per acre.

Red oak reproduction shows its peak on mesic, nutrient-rich sites, mainly in Acer-Tilia-Pinus strobus-Dirca (AT-T) type. It shows also a good competitive ability on dry to mesic, intermediate nutrient sites with high shrub densities. Red oak reproduction is rather well represented in all age groups. Bur oak reproduction shows only a scattered occurrence over the total upland forest complex. The number of bur oak seedlings per acre exceeds red oak reproduction only in Pinus banksiana-Arctostaphylos (Pb-T) type. In general, oak reproduction is capable to maintain its position in mixed forest stands with different composition. Oak seedlings are never present in such numbers that they would be serious competitors for pine reproduction. Ironwood, a minor tree species in the park, is most abundant in Acer-Tilia-Pinus strobus-Dirca (AT-T) type.

6.25 Maple-basswood reproduction

Red maple is considered a subclimax species, and it functions as an intermediate in many forest stands. It is most commonly found in forest understories. Sugar maple and American basswood are both climax species and selective in their site requirements. They occur mainly on moist, fertile, and well drained soils. According to Baker (1949), sugar maple and American basswood are classified as very tolerant and tolerant species, respectively.

Figure 16 shows the distribution and abundance of red maple, sugar maple, and American basswood reproduction by age groups in relationship to mothertrees, forest types, and moisture-nutrient gradients. Red maple is an admixture species in a variety of upland forest stands in the park with a more common occurrence on intermediate nutrient to nutrient-rich sites. Mature sugar maple and basswood are largely restricted to mesic, nutrient-rich sites, mainly to Acer-Tilia-Pinus strobus-Dirca (AT-T) type with some occurrence in Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) type.

Red maple reproduction is well represented in all age groups and its distribution range in the edaphic field is similar to that of mothertrees (Fig. 16). There are only scattered seedlings present on dry, nutrient-poor sites. On mesic, nutrient-rich sites red maple reproduction decreases or even disappears in typical northern hardwood communities (stands 21 and 68). The ratio of sugar maple and red maple reproduction may indicate the development stage of a particular community.

Characteristics of red maple reproduction are such that red maple does not require much light to germinate, and it can become established on rather unfavorable seedbeds through rapid root development. Red maple can also reproduce by sprouts. These qualities enable red maple to compete successfully with shrub and ground cover species. Its growth rate under conditions of strong shrub competition is similar to that of red oak (Fig. 10). Red maple reproduction also does relatively well in the Pinus-Abies-Picea-Lycopodium (PAP-T) type with a rather dense tree canopy where it constitutes about 80 percent of the total hardwood reproduction (Table 13). The total number of red maple reproduction in forest types with well developed

Forest types in Itasca State Park: 1. Pinus banksiana-Arctostaphylos (Pb-T). 2. Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T). 3. Pinus-Abies-Picea-Lycopodium (PAP-T). 4. Pinus resinosa-Dryopteris-Osmorhiza (Pr-E). 5. Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T). 6. Acer-Tilia-Pinus strobus-Dirca (AT-T).

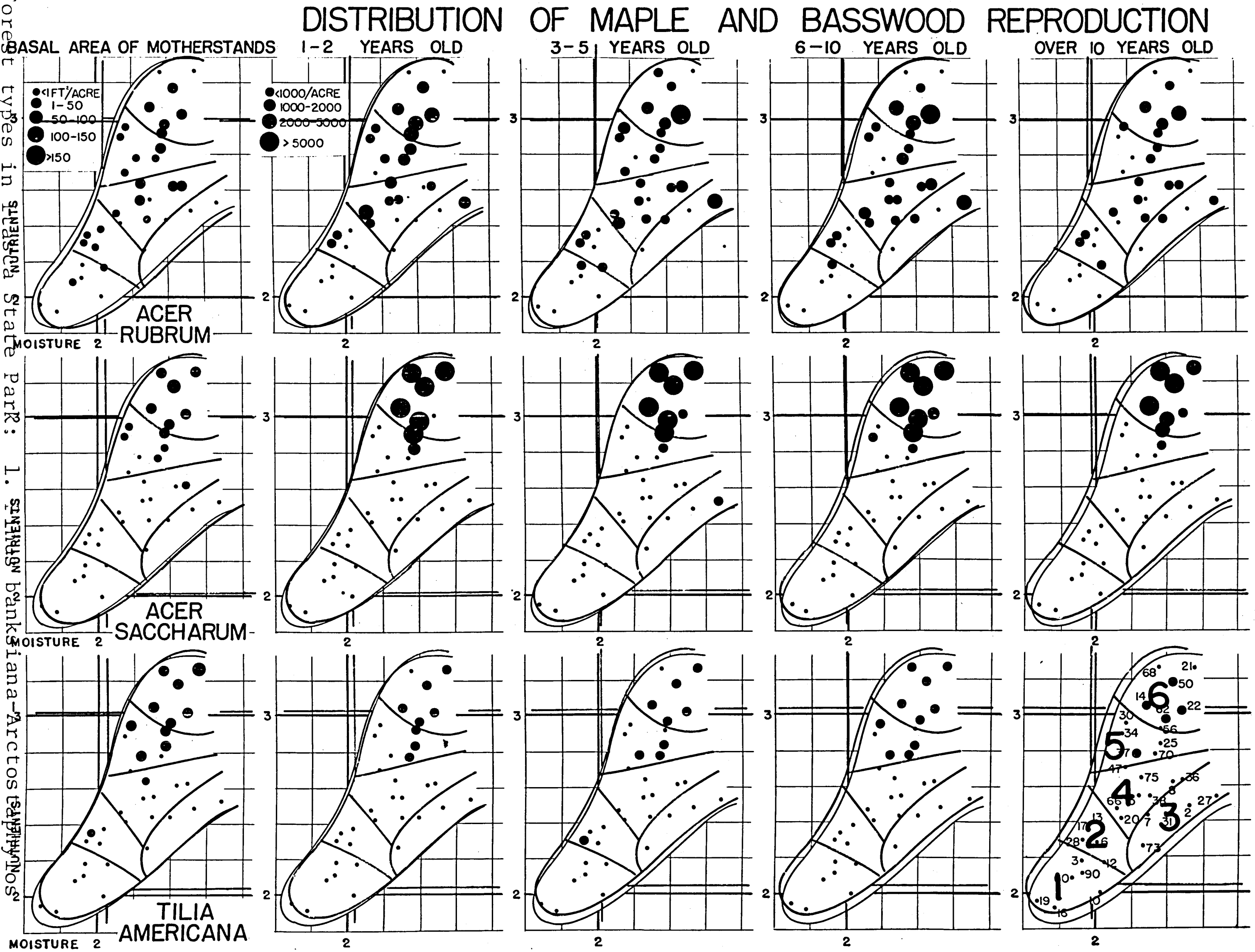
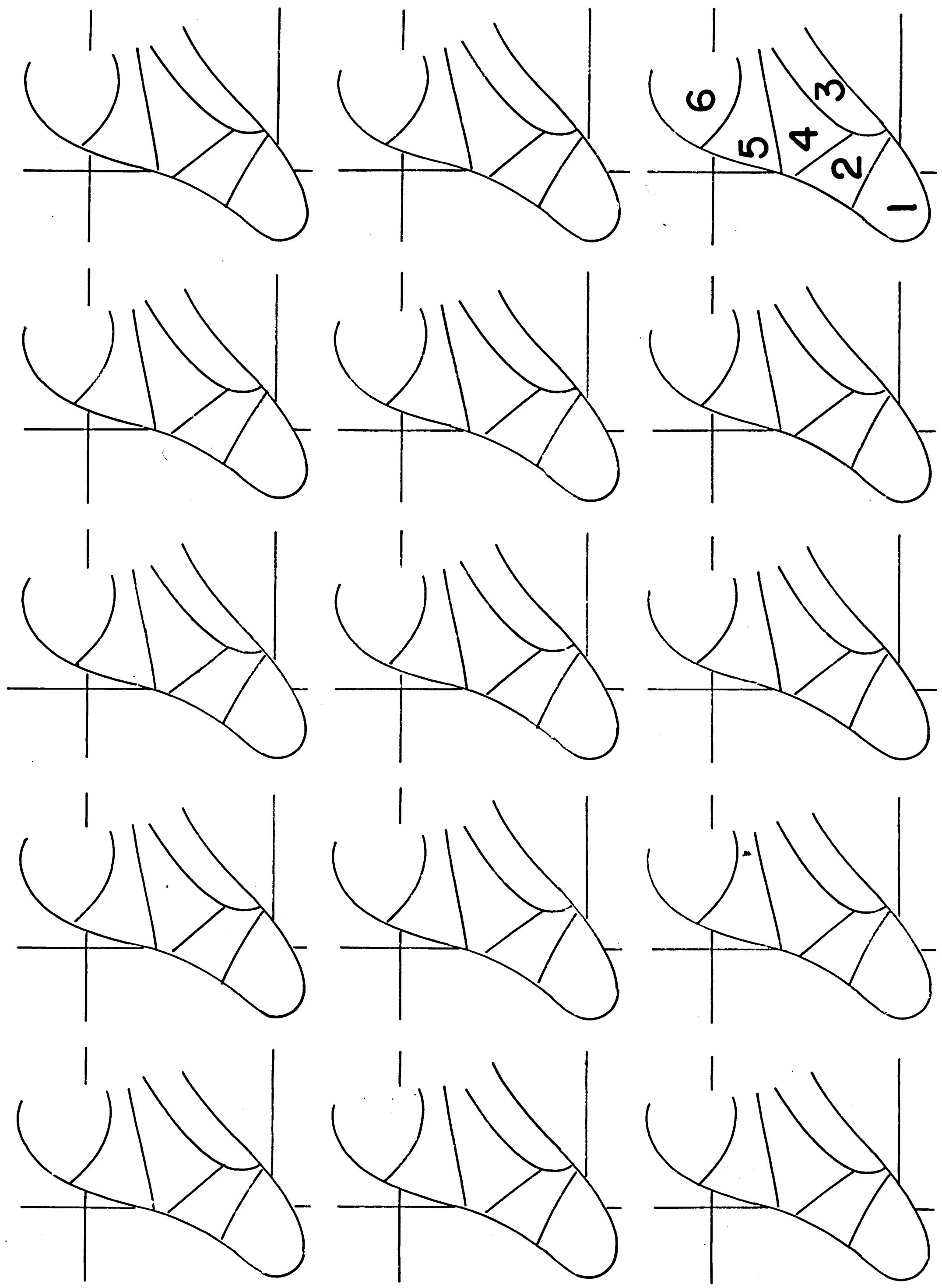


Figure 16. Distribution of basal areas of red maple, sugar maple, and American basswood and their reproduction by age groups in the edaphic field of upland forests in Itasca Park, Minnesota.



Forest types in Itasca State Park: 1. Pinus banksiana-Arctostaphylos (Pb-T). 2. Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T). 3. Pinus-Abies-Picea-Lycopodium (PAP-T). 4. Pinus resinosa-Dryopteris-Osmorhiza (Pr-T). 5. Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T). 6. Acer-Tilia-Pinus strobus-Dirca (AT-T).

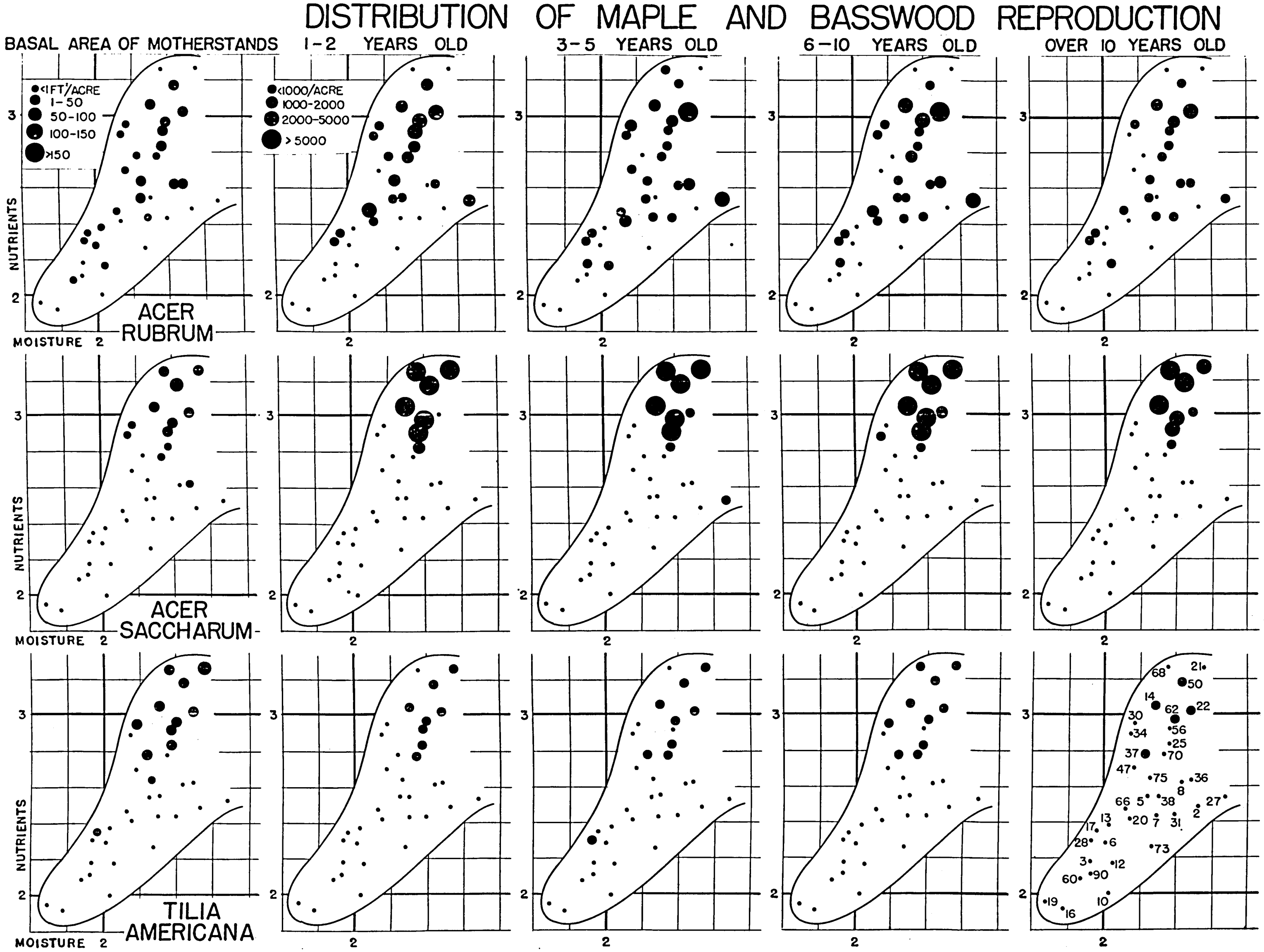


Figure 16. Distribution of basal areas of red maple, sugar maple, and American basswood and their reproduction by age groups in the edaphic field of upland forests in Itasca Park, Minnesota.

shrub layers ranges from about 300 to 2,100 stems per acre with frequencies from 22 to 66 percent (Appendix Tables 3 and 4).

Sugar maple reproduction is limited to mesic, nutrient-rich sites, mainly in Acer-Tilia-Pinus strobus-Dirca (AT-T) type (Fig. 16) where it composes 75 percent of all hardwood reproduction (Table 13). In some communities sugar maple even exceeds 90 percent of the total number of hardwoods. This is partly due to the extremely high number of first year seedlings in 1965. The total number of sugar maple reproduction is, on the average, about 50,000 stems per acre in the Acer-Tilia-Pinus strobus-Dirca (AT-T) type with 98 percent frequency. In age groups from three to five and from six to 10 years old, there are about 10,000 stems per acre in each. Quercus-Populus-Betula-Viburnum-Amphicarpa (APB-T) type shows only about 600 stems per acre with 18 percent frequency, mainly because sugar maple reproduction is not present in all communities in this type (Appendix Tables 3 and 4). The abundance of sugar maple reproduction connected with dense tree canopy in typical maple-basswood communities may be responsible for the relatively small number of other species (taxonomic diversity) as shown in Figure 3.

The height growth rate of sugar maple reproduction is slow under dense tree cover reaching about two to three feet on the average in 15 to 20 years (Fig. 10). In places where old pines are windthrown and openings are created in the tree canopy sugar maple responds rapidly. Conover and Ralston (1959) pointed out that sugar maple reproduction is able to withstand complete suppression for several years and still show a strong response to release.

The distribution pattern of American basswood reproduction is similar to that of sugar maple, occupying mesic, nutrient-rich sites. However, basswood reproduction is far less abundant (Fig. 16). American basswood reproduces with ease by sprouts arising from the bases of standing trees. Few seedlings were found in the forest communities studied with mature basswood trees present. The total basswood reproduction is about 500 stems per acre in Acer-Tilia-Pinus strobus-Dirca (AT-T) type and about 250 stems per acre in Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) type. The corresponding frequencies are 50 and 16 percent, respectively (Appendix Tables 3 and 4).

Red maple reproduction occurs on a wide range of stand and site conditions. Its ability to compete with shrubs is characteristic, particularly in pine and aspen forests with dense shrub layers. Sugar maple is the most vigorously reproducing species on better sites. It is an exceptional species because its reproduction secures the continuity of sugar maple. Sugar maple and American basswood are restricted to mesic, nutrient-rich sites, mainly Acer-Tilia-Pinus strobus-Dirca (AT-T) type. The dense tree canopy effectively excludes most shrubs. Further expansion of sugar maple and American basswood reproduction can be expected into Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) type.

7. DYNAMICS OF TREE REPRODUCTION IN THE PERMANENT STUDY AREA

There are only a few permanent plot studies carried out in Itasca Park concerning initial establishment and development of tree reproduction. The change in abundance of white pine and jack pine reproduction in a jack pine forest over a 20-year period was discussed in the preceding chapter. In this chapter, change in abundance, composition, age, and height, and evaluation of survival of pine reproduction and associated undergrowth species in a red pine-balsam fir forest will be analyzed in relationship to stand and site characteristics based on data of permanent plots initiated in 1953 (Bakuzis, 1954). Plot layout and the procedure of data collection were described in Chapter 3 discussing field methods.

7.1 Characteristics of the Permanent Study Area

The study area is located on both sides of the main park drive west of Elk Lake (southeast corner of Section 16, Township 143 N, Range 36 W), and its location is designated by "T" on the Itasca Park map (Fig. 1). Structure and composition of the stand in the study area are characterized from a transect through the red pine-balsam fir forest established in 1966 (Fig. 17a and 17b). Stand profiles and vertical projections are frequently used as illustrations of specific situations featuring reproduction conditions, competition conditions, effects of thinning, windthrow etc. Figure 17b also shows a schematic profile of the total transect, plot layout, and five subdivisions of the study area based mainly on variations in understory density and forest undergrowth.

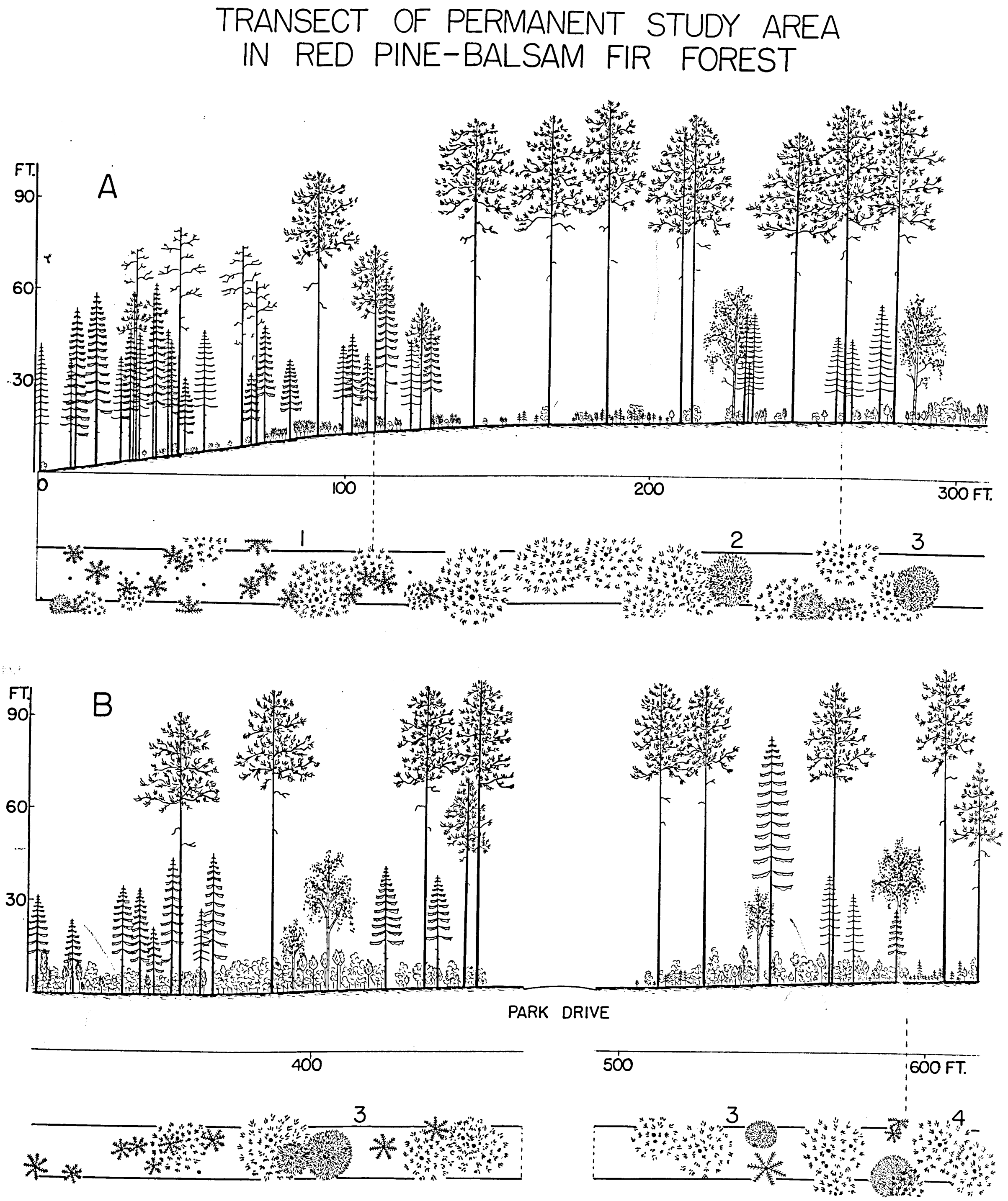


Figure 17a. Profile (sections A and B) and horizontal projections of red pine - balsam fir forest in Itasca State Park, Minnesota. See Figure 17b for continuation and for schematic plot layout.

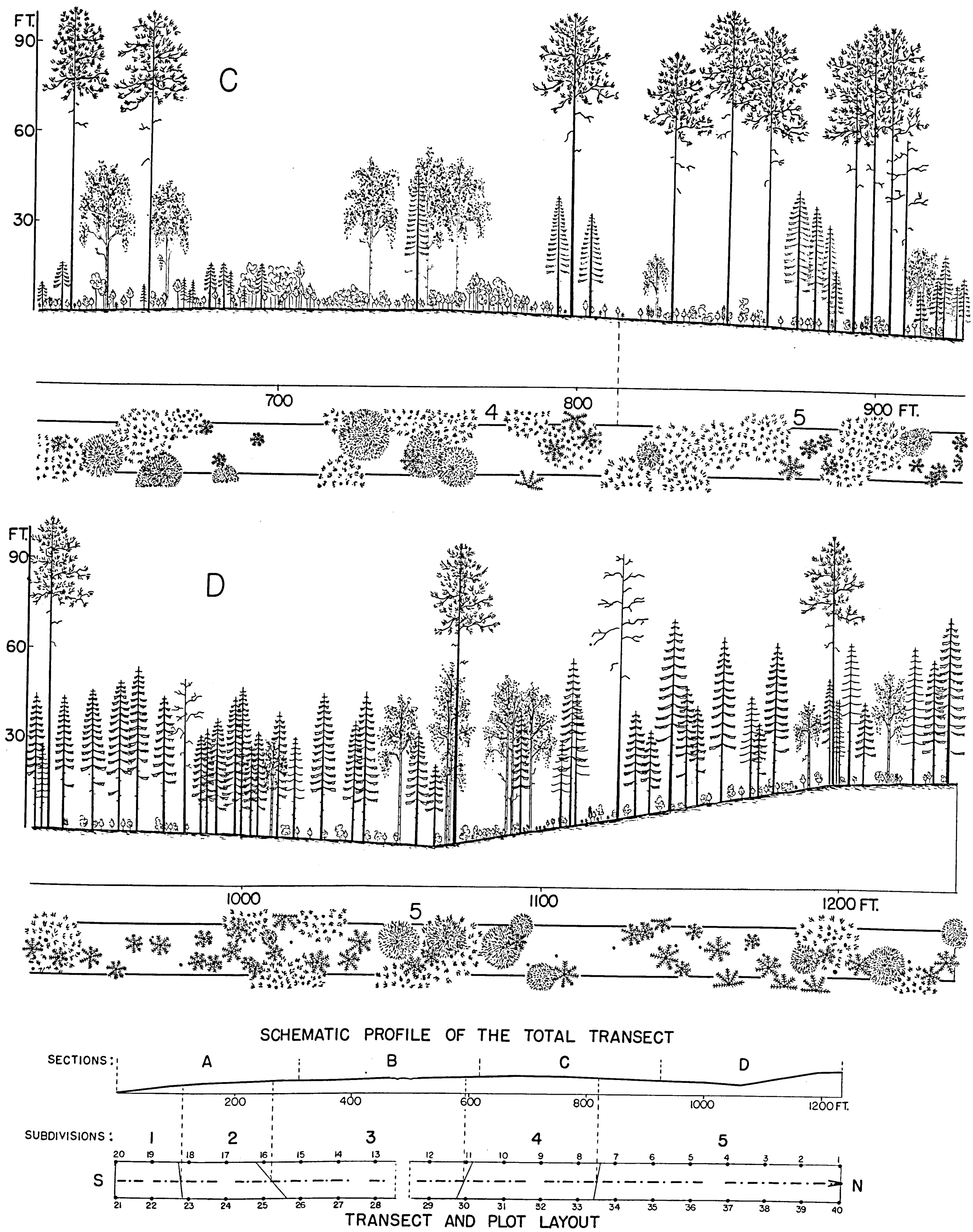


Figure 17b. Continuation of the profile (sections C and D) and horizontal projection of red pine - balsam fir forest in Itasca State Park, Minnesota. Schematic plot layout (1 to 40) and ecological subdivisions (1, 2, 3, 4, and 5) of the permanent study area.

The red pine-balsam fir stand which was investigated belongs to the Pinus-Abies-Picea-Lycopodium (PAP-T) type as it can be judged from the locations of its five subdivisions in the edaphic field (Fig. 18). It has the typical stand characteristics of this forest type. In addition to red pine there are scattered white pines in the overstory. The dead standing red pines (Fig. 17a and 17b), particularly in subdivision 1, are the result of porcupine (Erithizon dorsatum (Linnaeus)) damage. In more recent years, porcupines have done considerable damage by girdling old red pine in subdivisions 4 and 5. Balsam fir is the main tree species in forest understory. Paper birch and white spruce have occasional occurrence.

Soils are Marquette loamy sands and are somewhat excessively drained. They range in texture from loamy coarse sands to coarse sandy loams in the upper 10 to 18 inches overlaying sand and gravel in the subsoil. Boulders are common. Average pH values vary from 6.0 in A2 horizon to 6.6 in C horizon.

Balsam fir understory was largely removed in subdivisions 2 and 4 after the windthrow in 1936, and partly windthrown at the southern edge of subdivision 5 in 1952. Balsam fir understory is rather dense in subdivisions 1 and 5, and it has a medium density in subdivision 3 (Fig. 17a and 17b). In 1953, the age of balsam fir was about 65 years in the subdivision 1 and on the average from 45 to 50 years in subdivisions 3 and 5. The oldest red pines, particularly in subdivisions 2, 3, and 4 can be traced back to the fire in 1714, and red pines on the southern edge of the study area, adjacent to the spruce-fir-black ash swamp, can be related to the 1803 fire.

According to Bakuzis (1954) subdivision 5 showed the greatest age diversity in red pine and even assuming that all the fires mentioned by Spurr (1954) swept over the area, fires alone could not account for all red pine reproduction. Scattered individuals are found in the area which could be hardly attributed to the fires. Balsam fir understory may have played a considerable role in the age diversity of red pine in the area. The adjacent spruce-fir-black ash swamp provides a seed source which enables balsam fir to repeatedly invade the pine forest. Balsam fir understory can keep out shrubs and ground vegetation. Being itself a short-lived species and often subjected to windthrow, balsam fir may provide occasionally suitable conditions for pine establishment. The next sections in this chapter will deal with such an example where after balsam fir windthrow in 1936, red pine became established in the study area.

7.2 Change in Number and Ratio of Reproduction and Shrubs

Most of the pine reproduction in this area became established from 1946 to 1951 after the balsam fir understory was windthrown and removed in subdivisions 2 and 4 in 1936. This time period coincides with the establishment of pine reproduction in the jack pine forest and in a few other places in the park, discussed in the preceding chapter.

Weather conditions were studied and analyzed for the last 30 years from the data of U.S. Weather Station located about five miles northeast from the study area (Fig. 2). Table 14 illustrates the average temperature and precipitation from May to August and their

Table 14. Average temperature and precipitation from May to August and their deviations from the normal from 1936 to 1965 in Itasca State Park, Minnesota.

Years	Temperature degrees F°	Deviation	Precipitation inches	Deviation
1936 - 1940	62.8	+ 1.2	3.01	- 0.77
1941 - 1945	61.0	- 0.6	4.11	+ 0.33
1946 - 1950	60.6	- 1.0	4.09	+ 0.31
1951 - 1955	61.5	- 0.1	3.66	- 0.12
1956 - 1960	61.6	0.0	3.90	+ 0.12
1961 - 1965	62.1	+ 0.5	3.91	+ 0.13

Source: after U.S. Weathear Bureau (1936-1965)

deviations from the normal by five-year periods. The deviations from the 30-year average temperature and precipitation show that the periods from 1941 to 1945 and 1946 to 1950 are characterized by lower temperature and higher precipitation that the normal. The increase in moisture and decrease in temperature during the growing season may have played a significant role in the initial establishment of pine seedlings in this area and in some other places having suitalbe site and biotic conditions. Pine reproduction was not initiated immediately after the windthrow of balsam fir in 1936, mainly because of combined effects of severe drought in late 1930's and deer overpopulation until 1945 when the park was opened to hunting.

Short term fluctuations in weather conditions affect species' dominance and frequency more than species' presence in an area. Therefore, trends in synecological coordinates, weighted by the species' frequency, seem to reflect the short term weather and climatic changes modified by the long range stand development. Table 15 shows the trends in moisture, nutrient, heat, and light

Table 15. Trends in synecological coordinates of red pine-balsam fir stand from 1953 to 1968 in Itasca State Park, Minnesota.

Year	Synecological coordinates*			
	Moisture	Nutrients	Heat	Light
1953	2.49	2.10	1.87	2.79
1959	2.34	2.19	2.03	2.96
1964	2.40	2.20	2.08	2.89
1968	2.46	2.21	2.01	2.87

* Average of 40 individual subplot coordinates.

Source: Henry (1968).

coordinates from 1953 to 1968 in the permanent study area. The highest moisture coordinate in 1953 reflects the favorable moisture conditions in 1940's and early 1950's (Table 14 and Figure 2) when most of the red pine reproduction was established. The lowest moisture coordinate in 1959 reflects the years of severe drought conditions: 1955, 1956, and 1958 when most of the red pine seedlings disappeared. Gradual increase in nutrient coordinate and also heat coordinate, at least up to 1964 (Table 15), may be related to general successional trend towards increasing hardwoods in the park area. The highest light coordinate in 1959 is related to the drought conditions and to the decline in pine overstory from 1953 to 1959 (Fig. 18). After 1959 the light coordinate decreases, probably due to an increase in size and numbers of tree saplings, mainly hardwoods, and due to the improvement of moisture conditions.

Figure 18 shows the distribution of total tree reproduction by individual species over the study area from south to north by subdivisions 1 to 5, and the change in number of stems per acre from 1953 to 1964. It also illustrates the forest understory and overstory densities during the time interval and gives the estimates of tree cover, shrub cover, ground cover, and reproduction cover in 1964. The ecological locations of five subdivisions in the edaphic field are shown in the last diagram of Figure 18.

Red pine reproduction reached its peak in subdivision 4 in 1953, having the lowest understory basal area (Fig. 18). The number of red pine seedlings per acre in other subdivisions is also closely related to the density of balsam fir understory. It has no relationship with total basal area or basal area of overstory. White pine reproduction follows a similar distribution pattern in 1953. There is a decrease in red pine and white pine reproduction from 1953 to 1964. Balsam fir reproduction shows just the reverse distribution pattern with greater abundance of seedlings under canopy of mother-trees than without it. Subdivision 4, with the least balsam fir seedlings present, has the driest site conditions as indicated by moisture-nutrient coordinates. The amount of balsam fir reproduction from 1953 to 1964 varies, mainly due to fluctuations in one-year old seedlings.

Distribution pattern of red maple and black ash seedlings over the study area definitely reflects the distance from the seed source (Fig. 18). Mature red maple trees are located just north and north-east of subdivision 5 spreading seed southward, while the adjacent spruce-fir-black ash swamp south of subdivision 1 provides black ash seed for the area. The number of black ash seedlings per acre decreases rapidly in a northerly direction towards subdivision 5. The number of red maple and black ash seedlings present in each sub-

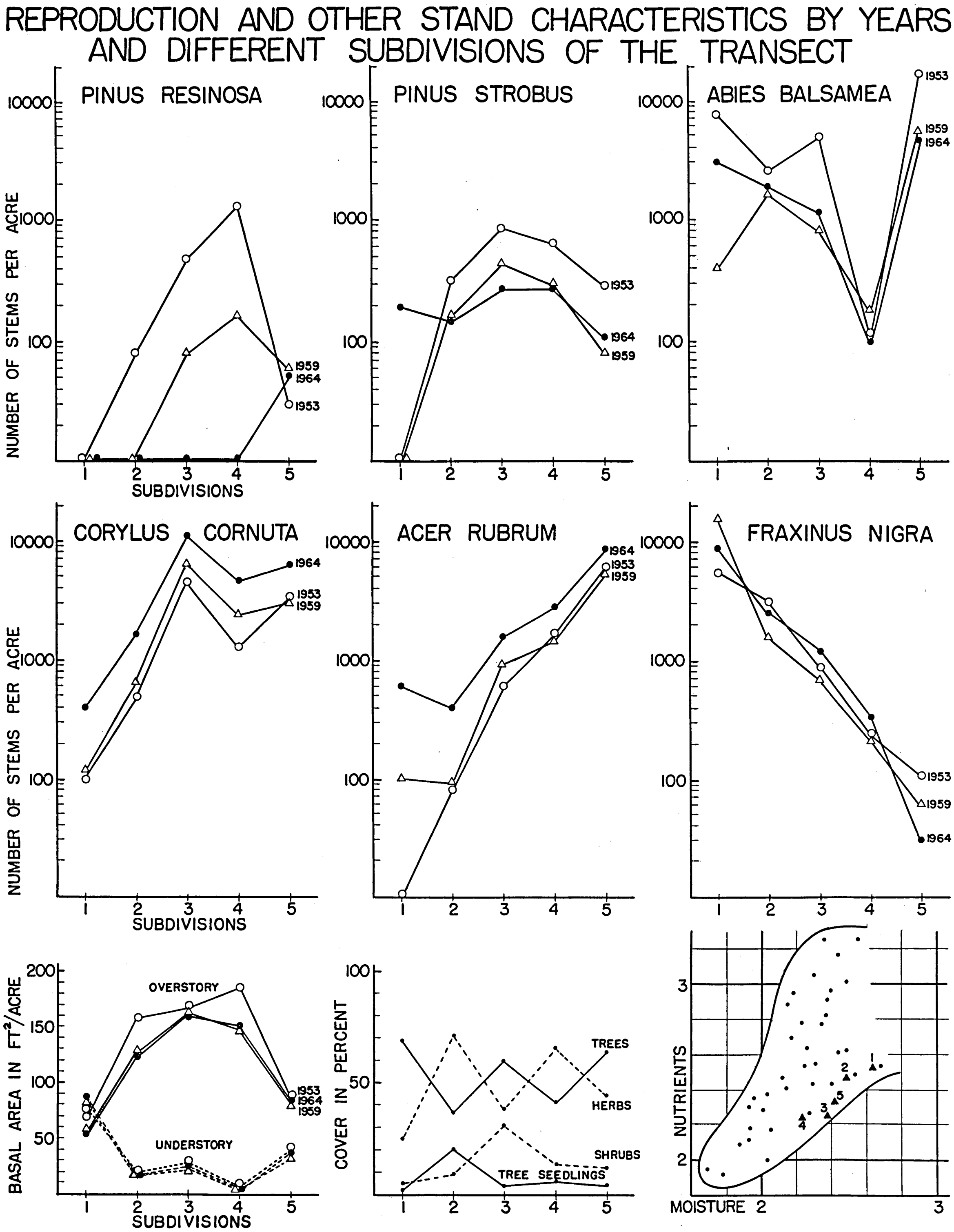


Figure 18. Distribution of main conifer, hardwood, and shrub species by ecological subdivisions of the permanent study area in different years. Basal area of trees in different years and cover of stand components by subdivisions in 1964. Location of subdivisions in the edaphic field of upland forests in Itasca State Park, Minnesota.

division is not related to the variations in stand density. The number of black ash seedlings fluctuates during the years in different subdivisions while red maple seedlings show an increase in numbers from 1953 to 1964. Corylus cornuta reaches the peak in subdivision 3. This subdivision had the lowest understory basal area before balsam fir was windthrown and removed in subdivisions 2 and 4 which enabled Corylus cornuta and other shrub species to invade this area first.

The change in number of reproduction per acre is also shown in Figure 19 emphasizing the time period from 1953 to 1964 instead of subdivisions and geographical gradient of the study area as it was done in Figure 18. The diagrams of Figure 19 consider only reproduction over two years old to avoid the influence of very young seedlings which may fluctuate strongly in numbers from year to year. Figure 19 also shows the change in ratio of conifer reproduction, hardwood reproduction, and shrubs from 1953 to 1964.

Main attention will be paid to the change in number of red pine seedlings, most of which were about three to six years old in 1953. Red pine reproduction shows a sharp decrease from 1953 to 1959 and it is almost absent in the area by 1964. White pine and balsam fir reproduction have also decreased in numbers while hardwoods and shrubs show a gradual increase in the area (Fig. 19).

Summer drought and deer browse were mentioned as the unfavorable factors contributing to the late start of pine reproduction in the area after balsam fir understory was removed in 1936. After 1945, favorable weather conditions, reduced deer population, and probably sufficient seed available were stimulating factors for the red pine

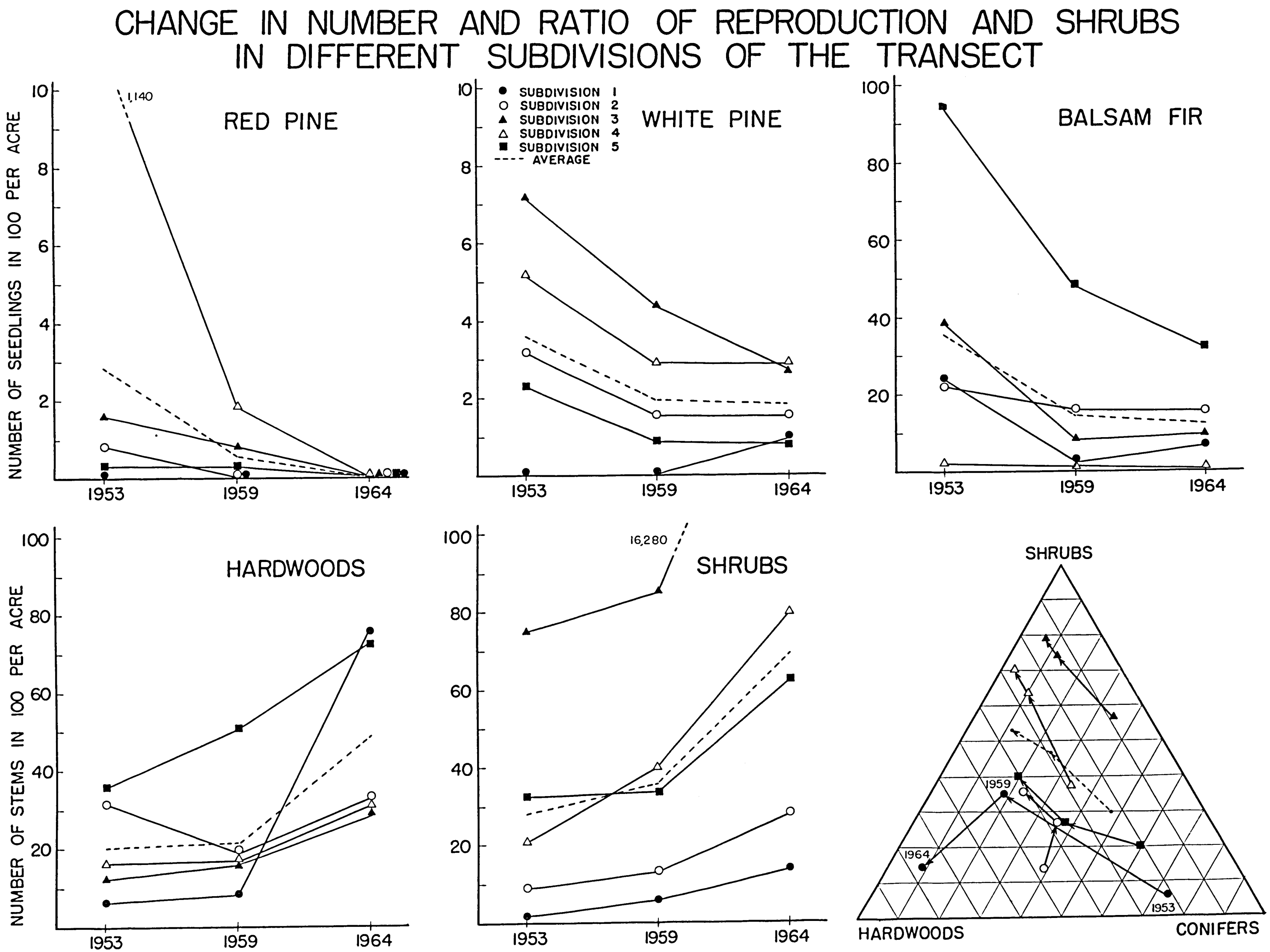


Figure 19. Number of conifer and hardwood seedlings and stems of shrubs over two years old by ecological subdivisions and different years in red pine-balsam fir forest. Changes in group composition of conifer and hardwood seedlings and shrubs in triangular coordinates from 1953-1964.

establishment, especially in subdivision 4, exceeding 1,000 stems per acre in 1953 (Fig. 19). At this time, probably the rather dense pine overstory with about 150 to 180 square feet basal area per acre, became the critical factor for red pine seedlings. The amount of light reaching the forest floor was not sufficient for seedlings to meet the gradually increasing competition of hardwoods, shrubs, and ground cover species for soil moisture. According to weather data, severe summer drought occurred in 1955, 1956, and 1958 (Fig. 2) which may be largely responsible for the very sharp decrease in red pine reproduction from 1953 to 1959. Reduction in the number of white pine and balsam fir seedlings is also greater from 1953 to 1959 than from 1959 to 1964 in most of the subdivisions. This drought effect is even reflected in the slower rate of increase in hardwoods and shrubs from 1953 to 1959 than from 1959 to 1964 (Fig. 19).

During the period from 1953 to 1964, red pine reproduction decreased from an average of 300 stems per acre to near zero, white pine -- from 400 to 200, balsam fir -- from 3,500 to 1,600. In the same time, hardwood reproduction increased from an average of 2,000 stems per acre to 5,000 stems per acre, and shrubs -- from 3,000 to 7,000 stems per acre.

The last diagram in Figure 19 shows the change in percentage of conifer reproduction, hardwood reproduction, and shrubs by individual subdivisions and for the whole study area. The average change in percentage (interrupted line in the last diagram of Figure 19) for the whole study area was:

year	conifers	hardwoods	shrubs
1953	48	22	30
1959	24	29	47
1964	11	36	53

The hardwood reproduction and shrubs almost doubled their proportions on expense of conifers.

7.3 Change in Average Age and Height of Reproduction and Shrubs

Changes in the average age and height of reproduction and their number provide an insight into the processes of natural reproduction. Figure 20 indicates the change in average age and height of tree reproduction and shrubs from 1953 to 1964 in the permanent study area.

Red pine reproduction suffered a heavy loss in the years after 1953. The increase in average age, about six years, from 1953 to 1959 in subdivisions 3 and 4 indicates that no new seedlings became established during this time period. The increase in height growth of those seedlings still living in 1959 had been slow during the six-year period. In 1964, only subdivision 5 showed a few young seedlings present; in other subdivisions they had disappeared.

As discussed in previous chapters, white pine seedlings are better able to compete with shrubs and hardwoods than red pine seedlings. However, here again, the average age and height comparisons indicate that white pine seedlings initially become established and later disappear. Even in subdivision 2 where the average age of white pine seedlings shows continuous increase there is no significant increase in average height growth. In subdivision 4 where the number of white pine seedlings has remained almost unchanged from 1959 to 1964 the average age and height of seedlings have decreased considerably indicating high mortality of older seedlings and initial establishment of new seedlings. In general, white pine re-

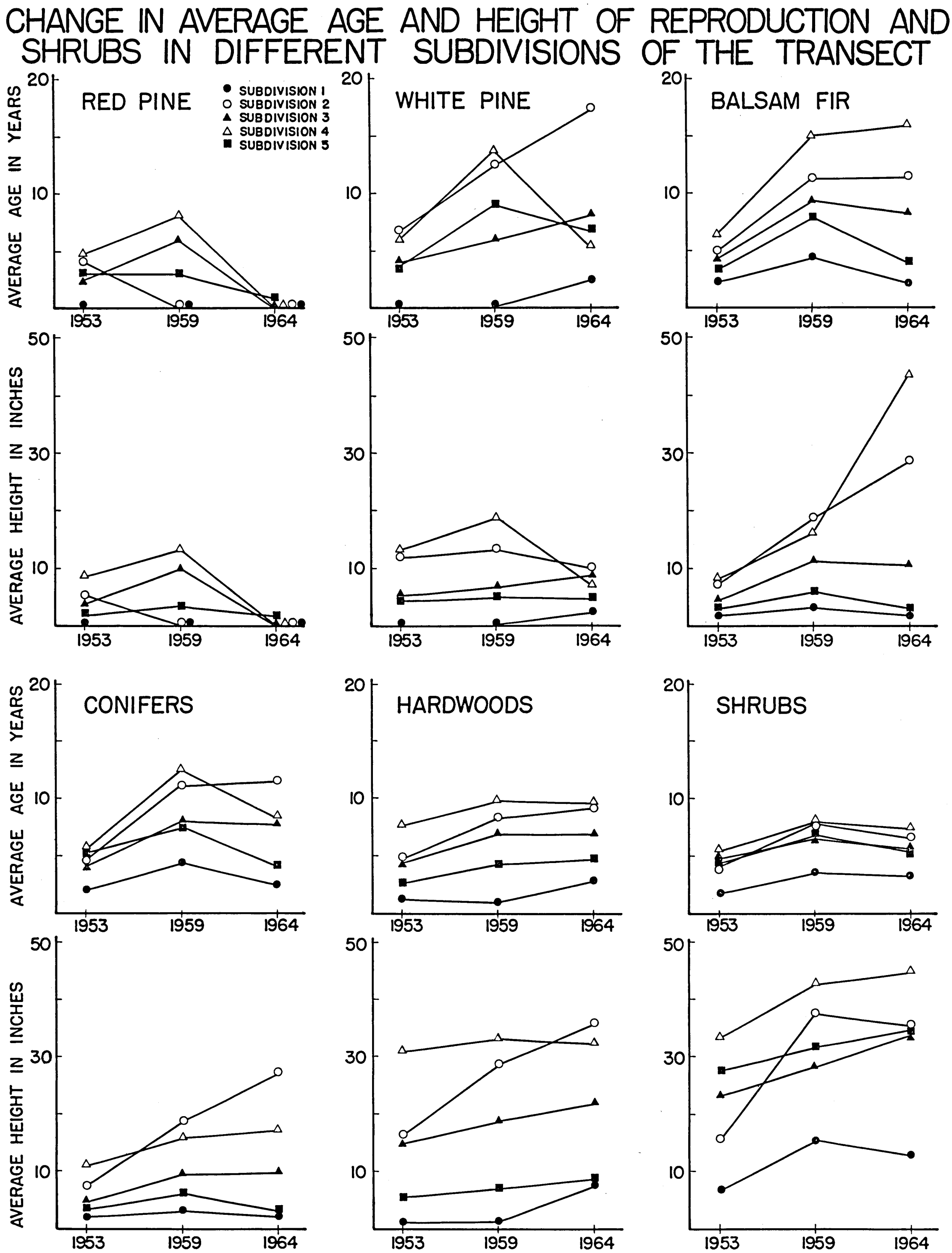


Figure 20. Change in average age and height of the total number of reproduction and shrubs from 1953 to 1964 by ecological subdivisions of the permanent study area in red pine-balsam fir forest in Itasca State Park, Minnesota.

production is stationary, site and biotic conditions have not been favorable for height growth development and survival.

Balsam fir reproduction shows an increase in average height growth in subdivisions 2 and 4 with the lowest understory basal area. In subdivisions 1 and 5 where the understory basal area is relatively high, balsam fir seedlings do not show an increase in average age and height. The number of seedlings fluctuates; seedlings become established and later disappear. Under dense shade of mothertrees the development of balsam fir seedlings is suppressed.

Change in average age and height of conifers reflect the integrated performance of red pine, white pine, and balsam fir seedlings. Conifer reproduction is most successful in subdivision 2, mainly due to the progress in height growth of balsam fir seedlings. Hardwood reproduction also shows the best performance in subdivision 2. Although the average age of hardwood reproduction is higher in subdivision 4 than in subdivision 2, the average height growth is slower. Subdivision 4 is the driest of all subdivisions and shrub competition is severe as indicated by the growth performance of shrubs in this subdivision in the last diagram of Figure 20.

7.4 Survival of Reproduction and Shrubs

An attempt was made to assess the survival of one to five years old conifer, hardwood, and shrub new growth which were recorded in 1953. These stems should have been seven to 11 years old in 1959 and 12 to 16 years old in 1964 (Fig. 21). Greater mortality occurred in the period from 1953 to 1959 in conifer and also hardwood reproduction as compared to the period from 1959 to 1964. Although higher mortality figures can be expected in the early stage of seedling development, the occurrence of severe drought periods in 1955, 1956, and 1958 was an important contributing factor.

In 1953, one to five years old red pine and white pine seedlings were relatively well represented in all subdivisions except subdivision one which had an extremely dense balsam fir understory. Red pine showed the most seedlings per acre in subdivision 4 with almost no balsam fir understory. White pine reproduction had its best representation in subdivision 3. Relatively dense pine overstory, increased competition from shrubs and ground vegetation, summer drought, and droughty soil can be considered the main reasons for the poor survival of pine reproduction. Survival of balsam fir is similar to that of white pine. The best survival of white pine and balsam fir seedlings occurred in subdivision 2. Hardwoods and shrubs also had low mortality in this subdivision. Ecologically this subdivision is characterized by greater moisture availability than subdivision 4, and in both subdivisions the balsam fir understory was largely removed.

The average change in percentage of surviving conifer and hardwood reproduction, and shrubs (interrupted line in the last diagram of Figure 21) for the whole study area was:

year	age	conifers	hardwoods	shrubs
1953	1-5	51	29	20
1959	7-11	30	27	43
1964	12-16	14	32	54

Hardwood seedlings have largely maintained their position from 1953 to 1964 while the mortality losses of conifer seedlings have been balanced by shrubs. It is interesting to note that the most drastic changes in proportions occurred in subdivisions 1 and 5 with

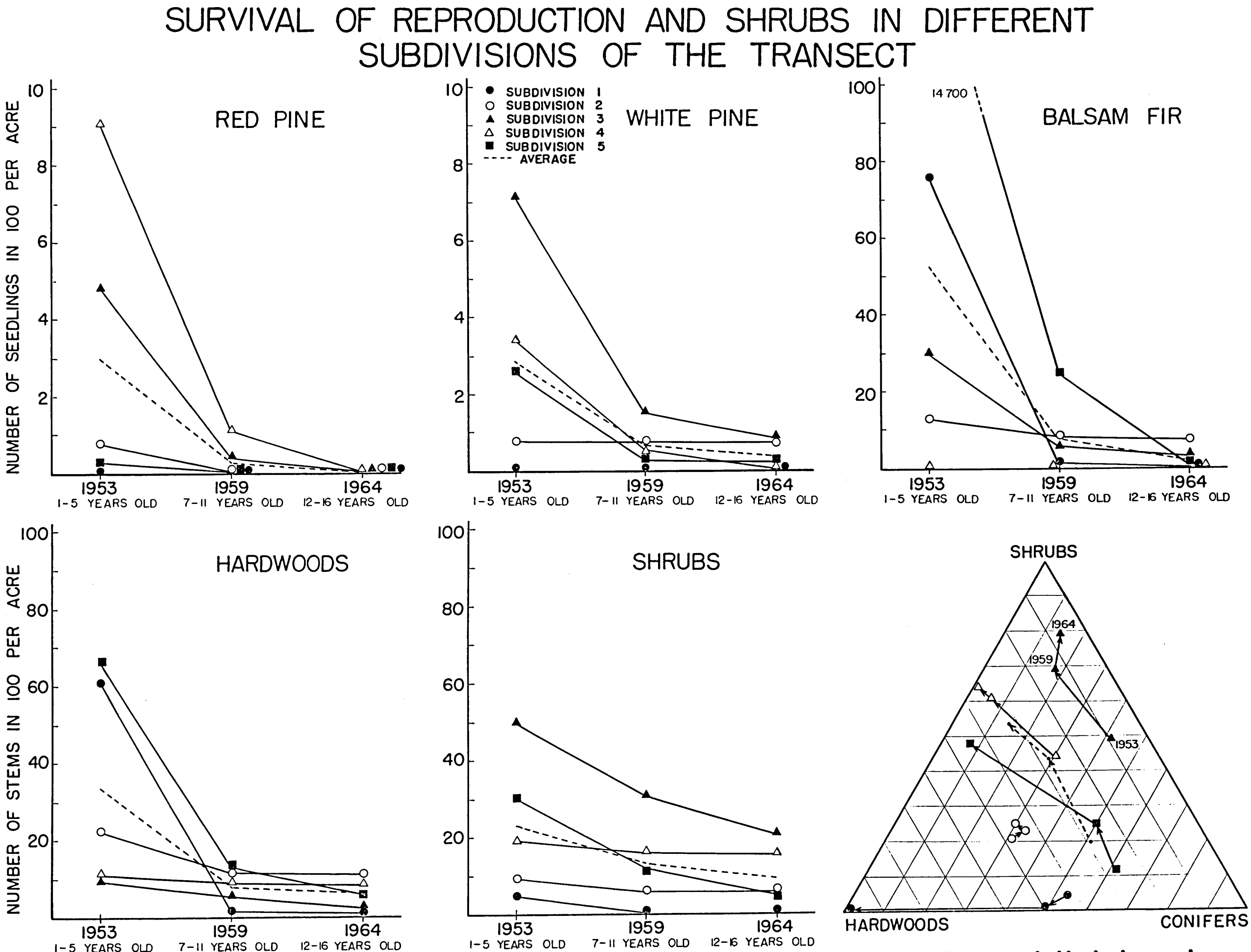


Figure 21. Survival of reproduction and shrubs from 1953 to 1964 by ecological subdivisions in red pine-balsam fir forest. Survival refers to seedlings which were 1 to 5 years old in 1953. Change in group composition of these seedlings and shrubs is shown in triangular coordinates.

dense balsam fir understories (Fig. 21). The dense balsam fir understory limits reproduction and shrubs and also hastens their mortality. In subdivision 1 hardwoods gained proportionally at the expense of conifers; however, hardwood mortality was also high. In subdivision 5 both hardwoods and shrubs gained proportionally from conifers. In subdivisions 3 and 4 shrubs showed the best survival. Subdivision 2 is characterized by almost equal survival of conifer reproduction, hardwood reproduction, and shrubs.

Pine reproduction in a pine stand is very difficult because seedlings are unable to compete for light and moisture with the usually vigorous forest undergrowth and mothertrees. Pine-spruce-fir stands have characteristic vertical structure which has a definite influence on natural reproduction. Balsam fir understory is an important factor in preventing the invasion of shrubs and ground vegetation. Shrub invasion is a rather slow process and a sufficiently dense understory can keep out shrubs; but once shrub invasion has occurred, the same understory density cannot eliminate them. In general, tree reproduction enters an area more rapidly than shrubs do; however, under unfavorable conditions it also disappears fast.

Data from the permanent study area indicate that under a combination of favorable conditions the natural reproduction of pines can occur in Pinus-Abies-Picea-Lycopodium type. Because of the longevity of red and white pines, failure of pine reproduction on several occasions does not exclude such possibility completely.

Balsam fir basal areas of about 80 to 100 square feet per acre completely exclude all new growth including shrubs. After the balsam fir becomes decadent and windthrown, the ground surface is prepared for pine seedling establishment.

Pine seedlings can become established at overstory basal areas up to 180 square feet per acre. If the overstory is reduced to about 60 square feet per acre, the reproduction may permanently establish.

SUMMARY AND CONCLUSIONS

Advance tree reproduction was studied in 36 upland forest communities in Itasca State Park, Minnesota in relationship to stand and site characteristics. The forest communities, all apparently undisturbed for at least 40 years, were selected from a reconnaissance survey of the area to cover the full range of upland moisture and nutrient conditions. Tree species composition, age, and geographical distribution were also considered in the community selection.

The method of synecological coordinates was used to analyze and compare the vegetation and soil characteristics, to aid in establishing ecological forest types, to investigate plant cover interrelationships, and to study the presence, abundance, and dynamics of conifer and hardwood reproduction.

Forest ecosystem was defined at a level of forest community, having homogeneous vegetation and environmental conditions. Forest community and site were considered as the two principal subsystems of forest ecosystems.

The extent and shape of the ecosystem space of upland forests were presented based on community coordinate values of moisture, nutrients, heat, and light. Coordinates were computed for the community as a whole, for individual subplots, and as averages of subplots within a community.

The variability of the forest ecosystems was defined and discussed in terms of taxonomic diversity, ecological diversity, and site diversity. The maximum taxonomic diversity occurred in communities of intermediate nutrient conditions and tended to be intensified in transitional areas along the boundaries of forest types. The maximum ecological diversity occurred in forest ecosystems on mesic, nutrient-rich sites. The maximum site diversity occurred in mesic, nutrient-poor ecosystems, influencing homogeneity and the distribution pattern of reproduction and ground vegetation and often resulting in two-storied tree canopies.

Soil properties of individual ecosystems were related to moisture and nutrient coordinates and to each other. The percent of soil mineral particles below 0.1 mm, organic matter content, pH, potassium, calcium, and magnesium were significantly related to nutrient coordinates. Calcium and pH of the organic layer, organic matter content and calcium of 6-inch top soils, and organic matter content and percent of soil mineral particles below 0.1 mm of 36-inch soil profile showed the highest correlations with nutrient coordinates. The relationships between phosphorus and nutrient coordinates were weak or negative. Organic matter content, the percent of soil mineral particles below 0.1 mm, and readily available water were significantly related to moisture coordinates; however, the relationships were weaker than those with nutrient coordinates.

Except for phosphorus, there were rather strong interrelationships between individual soil chemical properties. Most of the upland soils in Itasca Park can be rated as medium to high in phosphorus, potassium, calcium, and magnesium, except for some ecosystems located in the lower part of the edaphic field. Moisture supply is more critical. Drought periods are common during the growing season in this area.

Ecosystems functionally similar with respect to moisture-nutrients and heat-light were grouped into six ecosystem types (forest types), adjusting the type boundaries to individual species distribution in the edaphic field, soil characteristics, and interrelationships between trees, reproduction, and shrubs, and other specific characteristics. These types represent a unit of ecosystem space and come close to the concept of forest site types. Type boundaries in nature are not distinct, but the types grade into each other, especially those in the central part of the edaphic field. Brief forest type descriptions were given and comparisons between the types were made in terms of their synecological coordinates, vegetation, and soil characteristics.

The distribution pattern and abundance of pine, spruce-fir, and hardwood reproduction and shrubs were analyzed in relationship to moisture-nutrient gradients, forest types, and soils. Three main areas of reproduction concentration in the edaphic field were noted; pines appeared on dry, nutrient-poor sites (Pinus banksiana-Arctostaphylos type), spruce-fir -- on mesic, nutrient-poor sites (Pinus-Abies-Picea-Lycopodium type) and hardwoods -- on mesic, nutrient-rich sites (Acer-Tilia-Pinus strobus-Dirca type). Shrubs showed the largest abundance in the central part of the edaphic field, occupying a large portion of the dry to mesic, intermediate nutrient sites (Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica, Pinus resinosa-Dryopteris-Osmorhiza, and Quercus-Populus-Betula-Viburnum-Amphicarpa types). Shrub effects on the distribution and abundance of tree reproduction were strongly indicated. The distribution and abundance of individual shrub species and their importance in competition with tree reproduction were discussed. The change in interrelationships of forest covers, depending on the position of forest types in the edaphic field was analyzed.

Interrelationships of conifer reproduction, hardwood reproduction, and shrubs based on stem counts and analyzed by age groups showed that with increased age of new growth (over six years old) there were no forest communities where these three undergrowth components were well mixed.

The changes in presence, abundance, and distribution pattern of individual reproduction species were analyzed by age groups in relationship to motherstands and forest types. On dry, nutrient-poor sites (Pinus banksiana-Arctostaphylos type), white pine was the major reproducing species of all three pines. Red pine and jack pine seedlings were almost limited to this type, but their occurrence was only scattered as compared to white pine. In general, the height growth of white pine and red pine seedlings was slow. Jack pine seedlings suffered the most from animal browse. Pinus banksiana-Arctostaphylos type, in which some pine reproduction occurs, constitutes only a small fraction of the total area of upland forests in the park.

The change in abundance of white pine and jack pine reproduction was studied over a 20-year period in a jack pine stand (Pinus banksiana-Arctostaphylos type) in which pine reproduction had been abundant. Opening of the park to deer hunting in 1945, a series of years with adequate moisture in late 1940's, almost shrub-free forest stand, and thin humus layer were the main conditions favorable for the establishment and development of white pine reproduction. Shrubs and hardwoods have doubled their numbers in the last 10 years providing increased competition for light and moisture for the existing pine seedlings and largely preventing further seedling establishment.

On mesic, nutrient-poor sites (Pinus-Abies-Picea-Lycopodium type), studies indicated that a spruce-fir understory largely prevents shrub invasion and that after a windthrow of balsam fir, pine reproduction may become established.

The changes in abundance, composition, average age and height, and evaluation of survival of pine reproduction and associated conifer reproduction, hardwood reproduction, and shrubs were analyzed in relationship to stand and site characteristics in a red pine-balsam fir forest based on data from permanent plots. The establishment of pine reproduction in this area, after a windthrow of balsam fir understory, coincided with the establishment of pine reproduction in the permanent study area of the jack pine forest and a few other places in the park.

The change in number and ratio of conifer reproduction, hardwood reproduction, and shrubs indicated a substantial decrease in pine and also balsam fir reproduction and an increase in hardwood reproduction and shrubs from 1953 to 1964. Hardwood reproduction and shrubs almost doubled their proportions at the expense of conifers during this time period. Red pine seedlings, in spite of the good start in the late 1940's, almost disappeared during the time span of 11 years. White pine seedlings did not show any significant increase in average height growth over the years. Balsam fir seedling numbers fluctuated greatly and made progress in height growth only in a subdivision of the study area with sufficient moisture available and open forest understory. The highest mortality of pine seedlings occurred from 1953 to 1959, due to confounding effects of insufficient light, increased hardwood, shrub, and ground cover competition, and years with serious summer drought periods.

On dry to mesic, intermediate nutrient sites (Pinus banksiana-Osmorhiza, and Quercus-Populus-Betula-Viburnum-Amphicarpa types) with dense shrub layers and herbaceous ground cover, pine seedlings were largely absent.

On mesic, nutrient-rich sites (Acer-Tilia-Pinus strobus-Dirca type) white pine seedlings were quite numerous; however, their height growth development was poor. Seedlings at ages of 15 to 20 years had not reached one foot in height.

Balsam fir can hold its position in upland forests on sites which are most suitable to its boreal character (Pinus-Abies-Picea-Lycopodium type). It is declining on sites where invading shrubs and hardwoods can compete better for soil moisture. White spruce, being a more drought resistant species than balsam fir, can compete better with shrubs and hardwoods. The scattered occurrence of white spruce reproduction in upland forests is mainly due to inability to become established on undisturbed soil surfaces.

Loss of quaking aspen and paper birch reproduction was considerable under tree canopies. Only a few young stems had reached an age of 10 years and older. Bigtooth aspen reproduction seldom occurred. Clusters of young aspen in saplings stage could only be found in areas where wind disturbance had resulted in sufficiently large openings in tree cover.

Red oak reproduction reached the peak on mesic, nutrient-rich sites, mainly in Acer-Tilia-Pinus strobus-Dirca type. It also showed good competitive ability on dry to mesic, intermediate nutrient sites with high shrub densities. Red oak reproduction was rather well represented in all age groups. The occurrence of bur oak reproduction was scattered over the whole upland forest complex. Oak reproduction is capable of maintaining its position, or even improving it, in forest stands over a wide range of site conditions.

Red maple occurred over a wide range of stand and site conditions. Its ability to compete with shrubs is characteristic of the species. Sugar maple was the most vigorously reproducing species on the better sites. Sugar maple and American basswood were largely restricted to mesic, nutrient-rich sites. Their further expansion into the Quercus-Populus-Betula-Viburnum-Amphicarpa type can be expected as indicated by reproduction analysis.

Most of the upland forest stands in Itasca Park are still in a process of post-fire stabilization and can be considered as temporary expressions or successional stages. In the absence of fire the predominantly rich forest soils favor the growth of herbs, shrubs, and hardwoods under the open canopies of pine and aspen stands. There are very few red pine and jack pine seedlings under these conditions, and growth of white pine seedlings is severely restricted. In addition, the occurrence of summer drought is critical for the initial establishment and survival of pine seedlings.

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APPENDIX

Appendix Table 1. Locations of studied forest communities in Itasca State Park area, Minnesota.

Stand No.	Section	T - N*	R - W**
2	NW 1/4 sec. 22	143	36
3	SE 1/4 " 1	143	36
5	SW 1/4 " 9	143	36
6	SE 1/4 " 4	142	36
7	SW 1/4 " 4	142	36
8	NW 1/4 " 4	142	36
10	NE 1/4 " 6	143	35
12	NE 1/4 " 7	143	35
13	NE 1/4 " 19	143	35
14	SE 1/4 " 24	143	36
16	NE 1/4 " 3	143	36
17	SW 1/4 " 33	144	36
19	NE 1/4 " 8	143	34
20	SE 1/4 " 17	143	36
21	NE 1/4 " 22	143	36
22	SE 1/4 " 3	143	36
25	NW 1/4 " 18	143	36
27	NE 1/4 " 28	143	36
28	SE 1/4 " 34	143	36
30	NW 1/4 " 28	143	36
31	SW 1/4 " 15	143	36
34	NW 1/4 " 5	143	36
36	NE 1/4 " 2	142	36
37	NW 1/4 " 1	142	36
38	SW 1/4 " 3	143	36
47	SE 1/4 " 6	143	35
50	SW 1/4 " 10	143	36
56	NE 1/4 " 1	143	36
60	NE 1/4 " 6	143	35
62	SE 1/4 " 24	143	36
66	NE 1/4 " 36	143	36
68	SW 1/4 " 24	143	36
70	NW 1/4 " 26	143	36
73	NW 1/4 " 2	143	36
75	SW 1/4 " 35	143	36
90	NW 1/4 " 17	143	35

* Arkansas base line.

** 5th Principal meridian.

Appendix Table 2. List of synecological coordinates of upland forest communities by forest types in Itasca State Park area, Minnesota.

Stand No.	Synecological coordinates* Moisture	Nutrients	Heat	Light
Pinus banksiana-Arctostaphylos (Pb-T) type				
3	1.93	2.17	2.29	3.71
10	2.02	2.00	2.20	3.78
16	1.76	1.91	2.17	4.00
19	1.68	1.95	2.22	4.05
60	1.87	2.08	2.23	3.58
90	1.91	2.11	2.14	3.54
Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T) type				
6	2.00	2.28	2.30	3.47
12	2.04	2.17	2.18	3.43
13	2.02	2.37	2.37	3.47
17	1.95	2.33	2.40	3.33
28	1.93	2.30	2.43	3.52
Pinus-Abies-Picea-Lycopodium (PAP-T) type				
2	2.52	2.48	2.19	2.77
27	2.67	2.53	2.02	2.50
31	2.39	2.43	2.13	2.88
73	2.26	2.26	2.17	3.25
Pinus resinosa-Dryopteris-Osmorhiza (Pr-T) type				
5	2.27	2.54	2.37	3.00
7	2.29	2.43	2.27	3.02
8	2.45	2.61	2.33	2.77
20**	2.13	2.41	2.26	3.13
36	2.45	2.62	2.26	2.62
38	2.28	2.54	2.28	2.95
66	2.12	2.45	2.24	2.96
75	2.25	2.63	2.42	2.93
Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T) type				
25	2.36	2.83	2.60	2.83
30	2.16	2.94	2.73	2.86
34	2.14	2.89	2.71	2.86
37	2.22	2.77	2.56	2.93
47	2.17	2.69	2.56	3.11
70	2.33	2.77	2.58	2.85
Acer-Tilia-Pinus strobus-Dirca (AT-T) type				
14	2.29	3.05	2.82	2.63
21	2.54	3.26	2.86	2.38
22	2.48	3.01	2.62	2.51
50	2.43	3.17	2.83	2.49
56	2.38	2.93	2.67	2.70
62	2.39	2.95	2.61	2.47
68	2.35	3.25	2.95	2.50

* Based on species' presence in the community.

** plantation?

Appendix Table 3. Summary data of upland forest stands in Itasca State Park, Minnesota.

Stand No.	Composition and age of main tree species		Dominant Species. Average ht.(ft), dbh(in.)	Stand basal area ft²/ acre	Stand volume ft³/ acre	Reproduction: Pine	Reproduction: Spruce-fir	Reproduction: Hard-woods	Reproduction: Total	Shrubs
						Number per acre				
	Forest type: *Pinus banksiana-Arctostaphylos* (Pb-T)									
3	8 JP, 60-70, +95 + WS, + QA	2 RP, 60-70	JP 63/ 9	102	2890	6000* (6000)** WP***	310 (310) WS	1300 (940) QA	7610 (7250)	14300 (10900)
10	9 JP, 60-70, +95 + WP, + PB.	1 RP, 60-70, +140	JP 70/10	128	4260	3300 (3300) JP	130 (130) BF	560 (440) PB	3990 (3870)	19200 (12200)
16	10 JP, 75-85, +20		JP 55/ 8	100	2680	810 (810) JP	310 (310) BF	180 (60) PB	1300 (1180)	25000 (12700)
19	10 JP, 40-50, +80		JP 41/ 5	107	2100	310 (310) JP	0	0	310 (310)	1700 (1600)

* Total number.
** Over 2 years old.
*** Main species.

JP - Jack pine
RP - Red pine
WP - White pine
BF - Balsam fir
WS - White spruce

QA - Quaking aspen
BgtA - Bigtooth aspen
PB - Paper birch
BO - Bur oak
RO - Red oak

RM - Red maple
SM - Sugar maple
BW - Amer. basswood
AE - Amer. elm
BA - Black ash

GA - Green ash
BP - Balsam poplar
IW - Ironwood
BCh - Black cherry

Appendix Table 3, continued

Stand No.	Composition and age of main tree species	Dominant species. Average ht.(ft), dbh(in.)	Stand basal area ft^2/ acre	Stand volume ft^3/ acre	Reproduction: Pine	Reproduction: Spruce-fir	Reproduction: Hardwoods	Reproduction: Total	Shrubs
					Number per acre				
60	6 RP, 65-75, +150; 3 JP, 65-75; 1 WP, + WS, + PB.	RP 63/11	133	4250	3500 (3500) WP	4000 (3900) BF	0	7500 (7400)	16700 (10100)
90	7 JP, 70-80; 3 RP, 70-80; + WP, + PB.	JP 65/10	124	3810	870 (740) WP	0	870 (60) PB	1740 (800)	14700 (9800)
	Forest type: Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T)								
6	9 RP, 140-150; + JP, + WP, + PB, + QA, +BO, +RM	RP 79/15	170	6180	310 (310) WP	500 (120) BF	1700 (750) PR	2510 (1180)	52000 (38800)
12	8 JP, 65-75, +90; 2 RP, 65-75, +240; +WP, +WS, +PB.	JP 68/10	158	4490	190 (190) WP	60 (0) WS	190 (130) RM	440 (320)	42300 (25100)
13	6 JP, 70-80; 3 RP, 70-80; 1 WP, 70; +QA.	JP 66/10	145	4340	190 (190) WP	0	120 (120) RO	310 (310)	27300 (19900)
17	10 JP, 60-70; +PB, +QA, +BO, +RO.	JP 67/ 9	148	4590	60 (0) JP	0	1600 (1100) RM	1660 (1100)	67500 (26800)

Appendix Table 3, continued

Stand No.	Composition and age of main tree species	Dominant species. Average ht.(ft), dbh(in.)	Stand basal area ft^2/ acre	Stand volume ft^3/ acre	Reproduction: Pine	Reproduction: Spruce-fir	Reproduction: Hard-woods	Reproduction: Total	Shrubs
					Number per acre				
28	7 JP, 70-80; 2 QA, 70-80; +RP, +PB, +BgtA, +IW.	JP 65/ 9	124	3710	500 (500) WP	60 (60) WS	1800 (1400) QA	2360 (1960)	32800 (22400)
	Forest type: Pinus-Abies-Picea-Lycopodium (PAP-T)								
2	8 RP, 150-160; 1 WP, 1 PB, +QA, +BP / 9 WS, 40-60; 1 BF 40-80	RP 77/18	165	4820	0	1300 (500) BF	620 (250) QA	1920 (750)	3200 (3100)
27	9 RP, 240-250; 1 BF, 60-70; +WP, +WS, +PB.	RP 98/23	217	8560	60 (60) RP	8400 (6600) BF	8400 (6600) RM	16860 (13260)	2400 (2000)
31	8 RP, 140-160; 1 BF, 70-90; +WS, +WP, +PB.	RP 66/12	155	4800	60 (60) RP	15200 (14900) BF	500 (500) RM	15760 (15460)	8700 (7800)
73	5 RP, 80-90; 3 WP, 80-90; 1 PB, +WS, +BF, +QA, +BgtA.	RP 61/11	166	4570	250 (250) WP	2600 (2400) BF	880 (570) QA	3730 (3220)	10100 (4600)

Appendix Table 3, continued

Stand No.	Composition and age of main tree species	Dominant species. Average ht.(ft), dbh(in.)	Stand basal area ft²/ acre	Stand volume ft³/ acre	Reproduction: Pine	Reproduction: Spruce-fir	Reproduction: Hard-woods	Reproduction: Total	Shrubs
					Number per acre				
	Forest type: Pinus resinosa-Dryopteris-Osmorhiza (Pr-T)								
5	9 RP, 140-160; 1 WP, 140; +PB, +RO, +BO, +BF, +WS, +RM, +AE.	RP 87/14	191	7790	120 (0) WP	120 (120) BF	2700 (2200) RM	2940 (2320)	41000 (29500)
7	10 RP, 140-150; +PB, +QA, +BgtA, +RO.	RP 88/16	208	8540	0	60 (60) BF	500 (500) BO	560 (560)	55200 (39100)
8	8 QA, 50-60; 1 BgtA, 50-60; +PB, +RO, +BO, +RM.	QA 67/ 9	132	4060	120 (0) WP	60 (60) BF	1800 (1600) RM	1980 (1660)	47200 (35500)
20	5 WS, 35-45; 3 PB, 35-50; 1 QA, 40-50; 1 BgtA 40-50	WS 45/ 6	129	3230	0	0	7400 (4800) BA	7400 (4800)	10400 (6100)
36	4 RP, 140-150; 4WP, 140-150; 1 PB, 60-120; +QA, +BF, +WS, +RO, +RM, +IW	RP 83/21 WP 92/22	181	6850	250 (120) WP	10000 (2100) BF	6500 (3300) RM	16750 (5520)	34000 (23900)

Appendix Table 3, continued

Stand No.	Composition and age of main tree species	Dominant species. Average ht.(ft), dbh(in.)	Stand basal area ft^2/acre	Stand volume ft^3/acre	Reproduction: Pine	Reproduction: Spruce-fir	Reproduction: Hardwoods	Reproduction: Total	Shrubs
					Number per acre				
38	9 RP, 150-160; 1 BF, 60-70; +PB, +WS.	RP 85/15	176	6780	250 (120) WP	2600 (1700) BF	1700 (200) PB	4550 (2020)	6000 (5000)
66	7 RP, 65-75; 1 WP, 65-75; 1 PB, 65-75; +QA, +RO, +RM.	RP 55/ 8	196	5290	750 (440) WP	0	8800 (5200) RM	9550 (5640)	21000 (16300)
75	8 RP, 140-160; 1 PB, 50-55; +WP, +RO, +QA, +RM, +BgtA, +BW.	RP 80/18	160	5340	250 (190) WP	60 (60) BF	6100 (3100) RM	6410 (3350)	42100 (29900)
	Forest type: Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T)								
25	5 QA, 50-70; 2 PB, 40-70; 2 RO, 50-60; +BW, +SM, +RM, +BO, +AE.	QA 60/ 9	113	2900	0	0	13400 (7900) SM	13400 (7900)	27000 (18400)
30	7 QA, 50; 2 BgtA, 50; +RO, +PB, +BW, +RM, +BO, +IW.	QA 60/ 7	127	3650	0	0	4100 (3700) RM	4100 (3700)	46300 (33400)

Appendix Table 3, continued

Stand No.	Composition and age of main tree species	Dominant species. Average ht.(ft), dbh(in.)	Stand basal area ft²/ acre	Stand volume ft³/ acre	Reproduction: Pine	Reproduction: Spruce-fir	Reproduction: Hard-woods	Reproduction: Total	Shrubs
					Number per acre				
34	5 PB, 40-60; 2 QA, 40-60; 2 RO, 50-60; +BgtA, +BO, +GA, +SM, +BCH.	PB 49/ 6	96	2440	0	0	4800 (3400) RO	4800 (3400)	32100 (19200)
37	4 WP, 65-75; 2 PB, 50-70; 1 RP, 65-75; 1 QA, 1 BgtA.	WP 65/10	149	4330	60 (0) WP	60 (60) WS	2100 (800) QA	2220 (860)	29100 (20600)
47	8 PB, 50-70; 1 QA, 30-60; +BO, +RM.	PB 50/ 6	86	2210	0	0	560 (180) QA	560 (180)	38700 (28700)
70	8 QA, 50-60; 2 BgtA, 50-60; +PB, +RO, +BO, +RM, +AE.	QA 58/ 7	132	3850	0	190 (190) BF	6100 (3900) RM	6290 (4090)	32200 (21600)
	Forest type: Acer-Tilia-Pinus strobus-Dirca (AT-T)								
14	5 BgtA, 70-80; 2 QA, 70-90; 1 SM, 40-80; 1 RO, 60-80; +BW, +PB, +RM, +IW, +AE.	BgtA 84/13	143	4910	310 (310) WP	0	64000 (32100) SM	64310 (32410)	8600 (6900)

Appendix Table 3, continued

Stand No.	Composition and age of main tree species	Dominant species. Average ht.(ft), dbh(in.)	Stand basal area ft^2/ acre	Stand volume ft^3/ acre	Reproduction: Pine	Reproduction: Spruce-fir	Reproduction: Hard-woods	Reproduction: Total	Shrubs
					Number per acre				
21	4 BW, 70-130; 2 QA, 90; 1 WP, 160; 1 SM, 50-150; 1 PB, 90; +BA, +AE, +BO, +IW.	BW 48/ 8	141	4310	190 (60) WP	190 (130) BF	69000 (45700) SM	69380 (45890)	7200 (6600)
22	6 QA, 70-90; 3 BF, 60-80; +BO +BW, +PB, +RM, +GA, +BA, +AE, +RO.	QA 80/16	154	4700	440 (440) WP	1600 (1500) BF	37500 (33200) RM	39540 (35140)	9900 (8000)
50	3 WP, 180-200; 2 SM, 60-100; 2 QA, 70-100; 1 RP, 180-200; +BgtA, +PB, +BW, +RO, +BO, +RM.	WP 103/34	176	6040	1500 (1100) WP	120 (0) BF	96700 (57000) SM	98320 (58100)	3800 (3400)
56	5 WP, 130-170; 1 RO, 50-60; 1 BO, 50-60, +350; 1 SM, 40-60; 1 PB, 50-60; +QA, +BW, +RM, +GA, +IW, +AE.	WP 96/24	166	5420	3100 (310) WP	0	38200 (21400) SM	41300 (21710)	14500 (12700)

Appendix Table 3, continued

Stand No.	Composition and age of main tree species	Dominant species. Average ht.(ft), dbh(in.)	Stand basal area ft^2/ acre	Stand volume ft^3/ acre	Reproduction: Pine	Reproduction: Spruce-fir	Reproduction: Hard-woods	Reproduction: Total	Shrubs
					Number per acre				
62	4 QA, 70-80; 2 WP, 200; 1 RO, 70-80; 1 SM, 70-80; 1 PB, 60-80; +BW, +RP, +RM, +BO, +IW.	QA 77/13	160	5240	310 (310) WP	60 (60) BF	57400 (30500) SM	57770 (30870)	5100 (4000)
68	2 SM, 50-80; 2 QA, 70-80; 2 BW, 60-80; 1 PB, 70-80; 1 BO, 80; 1 RP, 240; 1 WP, 180; +RO, +BA, +IW, +AE.	SM 40/ 5 BW 50/ 7	134	3640	0	0	118800 (69800) SM	118800 (69800)	5500 (5000)

Appendix Table 4. Average basal area of major tree species; frequency and presence of reproduction, shrub, and ground-cover species; cover estimates of tree, reproduction, shrub, and ground cover layers by local forest types in Itasca State Park, Minnesota.*

Forest type: Pinus banksiana-Arctostaphylos (Pb-T).
Sample size: 6 stands.
Average cover: crown cover -- 35%, reproduction -- 12%, shrubs -- 15%, halfshrubs, vines, herbs, ferns and allies -- 60%, mosses and lichens -- 13%.

Trees

Species	basal area ft²/acre
Pinus banksiana	88
Pinus resinosa	24
Pinus strobus	2
Picea glauca	1
	115
Betula papyrifera	1
Populus tremuloides	-
	1
Total:	116

Reproduction

Species	Freq.	Pres.
Pinus strobus	56.2%	66%
Pinus banksiana	35.4	100
Pinus resinosa	25.0	66
Abies balsamea	21.0	66
Picea glauca	6.2	33
Betula papyrifera	16.6	66
Populus tremuloides	14.6	50
Quercus macrocarpa	4.2	33
Acer rubrum	4.2	17
Quercus rubra	2.1	17
Fraxinus nigra	2.1	17

Shrubs

Species	Freq.	Pres.
Corylus cornuta	75.0%	100%
Amelanchier spp.	64.6	100
Rosa spp.	60.4	83
Symphoricarpos albus	35.4	83
Diervilla lonicera	33.3	83
Salix humilis	25.0	83
Prunus virginiana	22.9	83

Shrubs, continued

Species	Freq.	Pres.
Corylus americana	18.7%	50%
Prunus pumila	12.5	33
Alnus crispa	8.3	50
Juniperus communis	4.2	33
Prunus pennsylvanica	2.1	17
Viburnum rafinesquianum	2.1	17
Lonicera canadensis	2.1	17
Lonicera hirsuta	2.1	17

Halfshrubs and vines

Species	Freq.	Pres.
Vaccinium angustifolium	97.9%	100%
Gaultheria procumbens	66.6	100
Rubus idaeus var. strig.	52.1	83
Arctostaphylos uva-ursi	45.8	100
Rhus radicans	12.5	33
Rubus pubescens	10.4	33
Chimaphila umbellata	6.2	33
Rubus alleghaniensis	6.2	33

Herbs, ferns and allies

Species	Freq.	Pres.
Maianthemum canadense	81.2%	100%
Lathyrus venosus	81.2	100
Galium boreale	79.2	100
Aster laevis	70.8	100
Fragaria virginiana	64.6	100
Antennaria canadensis	52.1	83
Anemone quinquefolia	52.1	100
Aster macrophyllus	45.8	83
Pteridium aquilinum	41.7	83
Linnaea borealis	39.6	83
Apocynum androsaemifolium	35.4	100
Thalictrum dioicum	33.3	100
Hieracium canadense	29.2	100

* Species presence is a percentage of occurrence of individual species in a number of stands each whole stand being considered as a separate sample unit. Species frequency is considered here as a percentage of occurrence of individual species in a number of stands based on measured eight two-milacre (8 m2) subplots per stand.

Appendix Table 4, continued

Herbs, ferns and allies

Species	Freq.	Pres.	Species	Freq.	Pres.
Agastache foeniculum	22.9%	50%	Clintonia borealis	4.2%	33%
Campanula rotundifolia	20.8	83	Uvularia sessilifolia	4.2	33
Vicia americana	20.8	83	Viola adunca	4.2	17
Aralia nudicaulis	20.8	66	Potentilla tridentata	4.2	17
Achillea lanulosa	18.7	66	Aquilegia canadensis	2.1	17
Melampyrum lineare	18.7	50	Cornus canadensis	2.1	17
Sanicula marilandica	16.6	50	Dryopteris spinulosa	2.1	17
Pedicularis canadensis	16.6	33	Hepatica americana	2.1	17
Solidago canadensis	14.6	66	Pyrola secunda	2.1	17
Viola pubescens	14.6	50	Pyrola virens	2.1	17
Solidago hispida	14.6	33	Botrychium virginianum	2.1	17
Galium triflorum	12.5	66			
Lathyrus ochroleucus	10.4	33			
Goodyera repens	8.3	50			
Lithospermum canescens	8.3	17			
Pyrola rotundifolia	6.2	50			
Senecio pauperculus	6.2	33			
Lactuca canadensis	6.2	17			

Mosses and lichens

Species	Freq.	Pres.
Pleurozium schreberi	60.4%	100%
Dicranum spp.	41.7	66
Polytrichum juniperinum	29.2	66
Cladonia rangiferina	10.4	33

Forest type: Pinus banksiana-Pinus resinosa-Gaultheria-Hepatica (PbPr-T).
Sample size: 5 stands.
Average: crown cover -- 40%, reproduction -- 1%, shrubs -- 40%, halfshrubs, vines, herbs, ferns and allies -- 60%, mosses and lichens -- 7%.

Trees

Species	basal area ft²/acre
Pinus banksiana	86
Pinus resinosa	49
Pinus strobus	4
Picea glauca	-
	139
Populus tremuloides	6
Betula papyrifera	3
Populus grandidentata	-
Quercus macrocarpa	-
Quercus rubra	-
Acer rubrum	-
	9
Total:	148

Reproduction

Species	Freq.	Pres.
Pinus strobus	30.0%	80%
Picea glauca	7.5	60

Reproduction, continued

Species	Freq.	Pres.
Abies balsamea	5.0%	20%
Pinus banksiana	2.5	20
Acer rubrum	22.5	60
Quercus rubra	17.5	80
Betula papyrifera	15.0	60
Populus tremuloides	12.5	40
Fraxinus nigra	7.5	40
Prunus serotina	5.0	40
Quercus macrocarpa	2.5	20
Tilia americana	2.5	20

Shrubs

Species	Freq.	Pres.
Corylus cornuta	97.5%	100%
Amelanchier spp.	67.5	100
Rosa spp.	65.0	100
Diervilla lonicera	57.5	100
Salix humilis	40.0	100
Symphoricarpos albus	37.5	100

Appendix Table 4, continued

Shrubs, continued

Species	Freq.	Pres.
Prunus virginiana	30.0%	80%
Corylus americana	10.0	60
Lonicera hirsuta	10.0	40
Cornus rugosa	5.0	40
Viburnum rafinesq.	5.0	40
Alnus crispa	2.5	20
Lonicera canadensis	2.5	20
Cornus stolonifera	2.5	20
Ribes cynosbati	2.5	20
Halfshrubs and vines		
Vaccinium angustif.	75.0%	100%
Rubus idaeus var. strigosus	65.0	100
Rubus pubescens	40.0	100
Rubus alleghaniensis	27.5	100
Gaultheria procumbens	25.0	100
Rhus radicans	17.5	80
Chimaphila umbellata	5.0	40
Vaccinium myrtilloides	5.0	20
Herbs, ferns and allies		
Maianthemum canadense	95.0%	100%
Pteridium aquilinum	85.0	100
Aster macrophyllus	77.5	100
Lathyrus venosus	70.0	100
Anemone quinquefolia	70.0	100
Thalictrum dioicum	55.0	80
Linnaea borealis	47.5	100
Fragaria virginiana	47.5	100
Galium boreale	47.5	80
Aralia nudicaulis	42.5	100
Galium triflorum	40.0	100
Hepatica americana	37.5	80
Apocynum androsaemif.	32.5	100
Clintonia borealis	30.0	100
Aster laevis	17.5	80

Species	Freq.	Pres.
Streptopus roseus	17.5%	80%
Antennaria canadensis	17.5	60
Cornus canadensis	15.0	80
Aster ciliolatus	15.0	20
Pyrola secunda	12.5	60
Vicia americana	12.5	60
Uvularia sessilifolia	12.5	60
Achillea lanulosa	12.5	40
Agastache foeniculum	10.0	80
Hieracium canadense	10.0	80
Sanicula mariiandica	10.0	60
Uvularia grandiflora	10.0	40
Campanula rotundifolia	7.5	20
Lathyrus ochroleucus	5.0	40
Lactuca canadensis	5.0	40
Pyrola virens	5.0	40
Solidago canadensis	5.0	40
Viola incognita	5.0	40
Dryopteris spinulosa	5.0	40
Anaphalis margaritacea	2.5	20
Viola pubescens	2.5	20
Amphicarpa bracteata	2.5	20
Aquilegia canadensis	2.5	20
Goodyera repens	2.5	20
Lithospermum canescens	2.5	20
Melampyrum lineare	2.5	20
Osmorhiza claytoni	2.5	20
Pyrola rotundifolia	2.5	20
Senecio pauperculus	2.5	20
Circaea alpina	2.5	20
Arisaema atrorubens	2.5	20
Mosses and lichens		
Pleurozium schreberi	30.0%=	40%
Polytrichum juniperinum	27.5	40
Dicranum spp.	15.0	40
Cladonia rangiferina	2.5	20

Appendix Table 4, continued

Forest type: Pinus-Abies-Picea-Lycopodium (PAP-T).
Sample size: 4 stands.
Average cover: crown cover -- 60%, reproduction -- 7%, shrubs -- 5%, halfshrubs, vines, herbs, ferns and allies -- 35%, mosses and lichens -- 1%.

Trees

Species	basal area ft^2/acre
Pinus resinosa	102
Picea glauca	23
Pinus strobus	18
Abies balsamea	16
Pinus banksiana	1
	160
Betula papyrifera	13
Populus tremuloides	1
Populus balsamifera	-
	14
Total:	174

Reproduction

Species	Freq.	Pres.
Abies balsamea	81.2%	100%
Pinus strobus	9.4	25
Picea glauca	6.2	50
Pinus resinosa	6.2	50
Acer rubrum	21.9	50
Fraxinus nigra	18.7	75
Populus tremuloides	18.7	50
Quercus rubra	9.4	25
Betula papyrifera	6.2	25
Quercus macrocarpa	3.1	25
Acer saccharum	3.1	25
Prunus serotina	3.1	25

Shrubs

Species	Freq.	Pres.
Amelanchier spp.	31.2%	100%
Corylus cornuta	28.1	100
Prunus virginiana	28.1	75
Diervilla lonicera	25.0	100
Lonicera hirsuta	25.0	100
Lonicera canadensis	15.6	75
Symphoricarpos albus	9.4	75
Rosa spp.	6.2	25
Corylus americana	3.1	25
Ribes americanum	3.1	25
Ribes cynosbati	3.1	25

Halfshrubs and vines

Species	Freq.	Pres.
Rubus idaeus var. strig.	46.9%	100%
Vaccinium angustifolium	28.1	100
Rubus pubescens	18.7	75
Rhus radicans	15.6	75
Chimaphila umbellata	9.4	50
Arctostaphylos uva-ursi	3.1	25
Gaultheria procumbens	3.1	25
Vaccinium myrtilloides	3.1	25

Herbs, ferns and allies

Species	Freq.	Pres.
Maianthemum canadense	81.2%	100%
Aster macrophyllus	75.0	100
Galium triflorum	62.5	100
Linnaea borealis	46.9	100
Aralia nudicaulis	40.6	100
Fragaria virginiana	40.6	100
Cornus canadensis	40.6	100
Lathyrus venosus	37.5	75
Thalictrum dioicum	34.3	50
Pteridium aquilinum	31.2	75
Anemone quinquefolia	28.1	100
Asarum canadense	28.1	100
Pyrola secunda	21.9	75
Hepatica americana	18.7	75
Pyrola virens	15.6	75
Lycopodium complanatum	15.6	75
Uvularia grandiflora	15.6	25
Aquilegia canadensis	12.5	75
Clintonia borealis	12.5	75
Uvularia sessilifolia	12.5	50
Viola renifolia	12.5	25
Aster ciliolatus	9.4	50
Viola pubescens	9.4	50
Lycopodium obscurum	6.2	50
Trientalis borealis	6.2	50
Streptopus roseus	6.2	50
Solidago hispida	6.2	50
Osmorhiza claytoni	6.2	50
Petasites palmatus	6.2	50
Dryopteris spinulosa	6.2	50

Appendix Table 4, continued

Herbs, ferns and allies

Species	Freq.	Pres.	Species	Freq.	Pres.
Sanicula marilandica	6.2%	25%	Viola conspersa	3.1%	25%
Antennaria canadensis	3.1	25	Viola incognita	3.1	25
Aster laevis	3.1	25			
Circaea alpina	3.1	25	Mosses and lichens		
Goodyera repens	3.1	25	Pleurozium schreberi	28.1%	100%
Lathyrus ochroleucus	3.1	25	Polytrichum juniperinum	21.9	50
Athyrium filix-femina	3.1	25	Dicranum spp.	6.2	50
Mitella nuda	3.1	25	Mnium spp.	6.2	50
Actea rubra	3.1	25			

Forest type: Pinus resinosa-Dryopteris-Osmorhiza (Pr-T).
Sample size: 8 stands.
Average cover: crown cover -- 55%, reproduction -- 2%, shrubs -- 40%
halfshrubs, vines, herbs, ferns and allies -- 40%,
Mosses and lichens -- -%.

Trees

Species	basal area ft^2/acre
Pinus resinosa	107
Pinus strobus	13
Picea glauca	9
Abies balsamea	5
	134
Populus tremuloides	16
Betula papyrifera	13
Populus grandidentata	4
Quercus rubra	3
Acer rubrum	1
Quercus macrocarpa	-
	37
Total:	171

Reproduction

Species	Freq.	Pres.
Abies balsamea	29.7%	75%
Pinus strobus	25.0	63
Picea glauca	3.1	25
Acer rubrum	65.6	100
Populus tremuloides	31.3	63
Quercus rubra	26.5	75
Fraxinus nigra	21.9	50
Betula papyrifera	14.1	38
Ostrya virginiana	7.8	38
Quercus macrocarpa	6.2	38
Populus grandidentata	3.1	25

Shrubs

Species	Freq.	Pres.
Corylus cornuta	93.8%	100%
Amelanchier spp.	48.4	100
Diervilla lonicera	48.4	100
Prunus virginiana	42.2	100
Symphoricarpos albus	25.0	75
Cornus rugosa	15.6	75
Rosa spp.	15.6	50
Viburnum rafinesquianum	10.9	88
Acer spicatum	10.9	63
Lonicera hirsuta	7.8	63
Lonicera canadensis	4.7	38
Salix humilis	3.1	25
Corylus americana	3.1	25
Alnus rugosa	3.1	25
Cornus alternifolia	3.1	13
Crataegus spp.	3.1	13
Alnus crispa	1.6	13
Prunus pennsylvanica	1.6	13

Halfshrubs and vines

Species	Freq.	Pres.
Rubus pubescens	53.1%	100%
Vaccinium angustifolium	46.9	88
Rubus idaeus var. strig.	42.2	100
Rhus radicans	17.2	88
Rubus alleghaniensis	7.8	63
Gaultheria procumbens	3.1	25
Chimaphila umbellata	1.6	13
Vaccinium myrtilloides	1.6	13

Appendix Table 4, continued

Herbs, ferns and allies

Species	Freq.	Pres.	Species	Freq.	Pres.
Maianthemum canadense	89.1%	100%	Goodyera repens	6.2%	25%
Aster macrophyllus	84.4	100	Polygonatum pubescens	4.7	38
Pteridium aquilinum	60.9	100	Actea rubra	4.7	38
Galium triflorum	56.2	100	Lactuca canadensis	4.7	38
Thalictrum dioicum	54.7	100	Pyrola asarifolia	4.7	38
Aralia nudicaulis	50.0	100	Antennaria canadensis	3.1	25
Fragaria virginiana	50.0	100	Aster laevis	3.1	25
Anemone quinquefolia	45.3	100	Prenanthes alba	3.1	25
Clintonia borealis	45.3	100	Pyrola virens	3.1	25
Hepatica americana	37.5	100	Viola pubescens	3.1	25
Uvularia sessilifolia	37.5	100	Lycopodium clavatum	3.1	25
Streptopus roseus	36.0	100	Amphicarpa bracteata	1.6	13
Cornus canadensis	34.4	88	Lathyrus ochroleucus	1.6	13
Uvularia grandiflora	34.4	88	Mentha arvensis	1.6	13
Lathyrus venosus	26.5	88	Mitella nuda	1.6	13
Osmorhiza claytoni	23.4	75	Osmunda claytoniana	1.6	13
Circaea alpina	21.9	75	Petasites palmatus	1.6	13
Linnaea borealis	15.6	63	Smilax herbacea	1.6	13
Apocynum androsaemif.	14.1	75	Solidago flexicaulis	1.6	13
Aster ciliolatus	14.1	38	Trientalis borealis	1.6	13
Dryopteris spinulosa	12.5	75	Trillium cernum	1.6	13
Pyrola secunda	12.5	50			
Sanicula marilandica	10.9	63	Mosses and lichens		
Galium boreale	9.4	50	Pleurozium schreberi	18.8%	75%
Smilacina racemosa	9.4	50	Polytrichum juniperinum	7.8	63
Viola incognita	7.8	63	Mnium spp.	6.2	25
Viola rugulosa	7.8	50	Dicranum spp.	3.1	25
Athyrium filix-femina	6.2	50			

Forest type: Quercus-Populus-Betula-Viburnum-Amphicarpa (QPB-T).
Sample size: 6 stands.
Average cover: crown cover -- 65%, reproduction -- 3%, shrubs -- 45%, halfshrubs, vines, herbs, ferns and allies -- 55%, mosses and lichens -- 0%.

Trees

Species	basal area ft^2/acre	Species	basal area ft^2/acre
Populus tremuloides	47	Ulmus americana	-
Betula papyrifera	32	Acer rubrum	-
Populus grandidentata	10		103
Quercus rubra	10	Pinus strobus	9
Quercus macrocarpa	2	Pinus resinosa	2
Tilia americana	2	Pinus banksiana	1
Acer saccharum	-	Picea glauca	-
			12
		Total:	115

Appendix Table 4, continued

Reproduction

Species	Freq.	Pres.
Quercus rubra	62.5%	100%
Acer rubrum	56.3	100
Populus tremuloides	47.9	100
Fraxinus nigra	31.3	66
Acer saccharum	18.7	33
Tilia americana	16.6	66
Betula papyrifera	12.5	50
Ostrya virginiana	8.3	50
Quercus macrocarpa	6.2	50
Prunus serotina	6.2	17
Ulmus americana	2.1	17
Picea glauca	4.2	33
Abies balsamea	2.1	17
Pinus strobus	2.1	17

Shrubs

Corylus cornuta	100.0%	100%
Diervilla lonicera	64.6	100
Prunus virginiana	58.3	100
Viburnum rafinesq.	52.1	100
Amelanchier spp.	39.6	100
Cornus rugosa	39.6	83
Rosa spp.	22.9	66
Lonicera hirsuta	12.5	83
Salix humilis	12.5	50
Corylus americana	8.3	17
Symphoricarpos albus	4.2	33
Ribes cynosbati	2.1	17
Acer spicatum	2.1	17
Alnus crispa	2.1	17
Alnus rugosa	2.1	17
Cornus alternifolia	2.1	17
Crataegus spp.	2.1	17

Halfshrubs and vines

Rubus idaeus var. strigosus	52.1%	100%
Rubus pubescens	43.8	100
Rubus alleghaniensis	20.8	66
Vaccinium angustif.	20.8	66
Rhus radicans	18.7	66
Celastrus scandens	10.4	33

Herbs, ferns and allies

Species	Freq.	Pres.
Aster macrophyllus	100.0%	100%
Aralia nudicaulis	93.7	100
Uvularia grandiflora	85.4	100
Thalictrum dioicum	81.2	100
Uvularia sessilifolia	79.2	100
Maianthemum canadense	79.2	100
Pteridium aquilinum	79.2	100
Fragaria virginiana	66.7	100
Anemone quinquefolia	62.5	100
Streptopus roseus	50.0	100
Galium triflorum	45.8	100
Sanicula marilandica	45.8	100
Lathyrus venosus	43.7	100
Apocynum androsaemif.	41.7	100
Amphicarpa bracteata	29.2	83
Hepatica americana	27.1	100
Osmorhiza claytoni	27.1	100
Solidago canadensis	20.8	66
Clintonia borealis	16.6	83
Viola rugulosa	12.5	66
Cornus canadensis	12.5	66
Aster laevis	12.5	50
Smilacina racemosa	8.3	66
Prenanthes alba	8.3	50
Trillium cernum	8.3	33
Botrychium virginianum	6.2	50
Petasites palmatus	6.2	50
Pyrola secunda	6.2	33
Actea rubra	4.2	33
Desmodium glutinosum	4.2	33
Hieracium canadense	4.2	33
Smilax herbacea	4.2	33
Viola conspersa	4.2	33
Viola incognita	4.2	33
Solidago flexicaulis	2.1	17
Pyrola rotundifolia	2.1	17
Lathyrus ochroleucus	2.1	17
Geum canadense	2.1	17
Asarum canadense	2.1	17
Aquilegia canadensis	2.1	17

Mosses and lichens

Polytrichum juniperinum	2.1%	17%

Appendix Table 4, continued

Forest type: Acer-Tilia-Pinus strobus-Dirca (AT-T).
Sample size: 7 stands.
Average cover: crown cover -- 85%, reproduction -- 30%, shrubs -- 5%, halfshrubs, vines, herbs, ferns and allies -- 35%, mosses and lichens -- 0%.

Trees

Species	basal area ft^2/acre
Populus tremuloides	35
Acer saccharum	28
Quercus rubra	21
Tilia americana	17
Betula papyrifera	12
Populus grandidentata	7
Quercus macrocarpa	5
Acer rubrum	2
Ostrya virginiana	2
Ulmus americana	2
Fraxinus nigra	-
Fraxinus pennsylvanica	-
	131
Pinus strobus	19
Abies balsamea	7
Pinus resinosa	5
	31
Total:	162

Reproduction

Species	Freq.	Pres.
Acer saccharum	98.2%	100%
Quercus rubra	87.5	100
Acer rubrum	71.4	86
Ostrya virginiana	69.6	100
Populus tremuloides	55.4	86
Tilia americana	50.0	100
Fraxinus nigra	42.8	57
Ulmus americana	19.6	57
Prunus serotina	12.5	57
Quercus macrocarpa	10.8	43
Betula papyrifera	5.4	29
Populus grandidentata	1.8	14
Pinus strobus	48.2	86
Abies balsamea	19.6	57

Shrubs

Species	Freq.	Pres.
Corylus cornuta	50.0%	100%
Prunus virginiana	46.4	100
Viburnum rafinesquianum	44.6%	86%
Acer spicatum	25.0	71
Amelanchier spp.	23.2	100
Cornus alternifolia	23.2	86
Dirca palustris	19.6	71
Lonicera hirsuta	12.5	71
Ribes cynosbati	7.2	57
Symphoricarpos albus	7.2	43
Cornus rugosa	5.4	43
Diervilla lonicera	5.4	43
Lonicera canadensis	5.4	43
Rosa spp.	5.4	29
Cornus stolonifera	3.6	14
Viburnum trilobum	3.6	14
Rhamnus alnifolia	3.6	14
Prunus pennsylvanica	1.8	14
Corylus americana	1.8	14

Halfshrubs and vines

Species	Freq.	Pres.
Rubus pubescens	34.0%	86%
Rhus radicans	10.8	57
Rubus idaeus var. strig.	7.2	29
Parthenocissus quinquef.	5.4	29
Vaccinium angustifolium	3.6	29
Rubus alleghaniensis	3.6	14
Celastrus scandens	1.8	14

Herbs, ferns and allies

Species	Freq.	Pres.
Uvularia grandiflora	98.2%	100%
Uvularia sessilifolia	91.1	100
Thalictrum dioicum	83.9	100
Aster macrophyllus	67.8	100
Aralia nudicaulis	53.6	100
Hepatica americana	53.6	100
Streptopus roseus	51.8	100
Galium triflorum	50.0	100
Anemone quinquefolia	41.0	100
Maianthemum canadense	35.8	86
Viola rugulosa	34.0	71
Amphicarpa bracteata	34.0	71

Appendix Table 4, continued

Herbs, ferns and allies

Species	Freq.	Pres.	Species	Freq.	Pres.
Osmorhiza claytoni	32.2%	100%	Cornus canadensis	3.6%	29%
Solidago flexicaulis	28.6	100	Cypripedium calceolus	3.6	29
Fragaria virginiana	25.0	71	Smilacina stellata	3.6	29
Lathyrus venosus	21.4	71	Viola incognita	3.6	29
Sanicula marilandica	19.6	86	Pyrola virens	3.6	14
Smilacina racemosa	19.6	86	Pyrola rotundifolia	3.6	14
Pteridium aquilinum	14.4	43	Prenanthes alba	3.6	14
Trillium cernum	14.4	43	Aster ciliolatus	3.6	14
Polygonatum pubescens	12.6	71	Apocynum androsaemif.	1.8	14
Viola pubescens	12.6	57	Circaea alpina	1.8	14
Actea rubra	10.8	71	Vicia americana	1.8	14
Pyrola secunda	10.8	43	Desmodium glutinosum	1.8	14
Asarum canadense	10.8	14	Galium boreale	1.8	14
Smilax herbacea	9.0	71	Lathyrus ochroleucus	1.8	14
Clintonia borealis	9.0	57	Petasites palmatus	1.8	14
Botrychium virginianum	7.2	57	Phryma leptostachy	1.8	14
Pyrola asarifolia	7.2	43			
Athyrium filix-femina	5.4	43	Mosses and lichens		
Trientalis borealis	5.4	43	Mnium spp.	3.6%	14%
Viola conspersa	5.4	29			

Appendix Table 5. Check list of plants and their synecological coordinates* of upland forest communities studied in Itasca State Park area, Minnesota.

Species	Coordinates M	N	H	L
TREES				
Abies balsamea	4	2	1	2
Acer rubrum	2	2	3	3
Acer saccharum	3	5	3	1
Betula papyrifera	3	2	2	5
Fraxinus nigra	4	3	3	2
Fraxinus pennsylvanica	3	5	4	4
Ostrya virginiana	2	5	4	1
Picea glauca	3	2	1	2
Pinus banksiana	1	1	2	5
Pinus resinosa	1	2	2	4
Pinus strobus	2	2	2	3
Populus balsamifera	4	3	2	3
Populus grandidentata	1	3	3	3
Populus tremuloides	2	2	2	4
Prunus serotina	2	3	4	3
Quercus macrocarpa	1	3	4	3
Quercus rubra	1	4	3	3
Tilia americana	2	5	4	1
Ulmus americana	3	5	4	2
SHRUBS				
Acer spicatum	3	2	2	1
Alnus crispa	2	1	1	4
Alnus rugosa	5	2	1	4
Amelanchier spp.	3	2	2	4
Cornus alternifolia	2	5	4	1
Cornus rugosa	2	3	3	2
Cornus stolonifera	4	2	2	3
Corylus americana	1	2	3	5
Corylus cornuta	2	1	2	3
Crataegus spp.	3	5	4	4
Diervilla lonicera	1	2	2	3
Dirca palustris	3	5	4	1
Juniperus communis var. depressa	1	1	2	5
Lonicera canadensis	3	2	2	1
Lonicera hirsuta	3	2	2	3
Prunus pensylvanica	1	2	3	5
Prunus virginiana	2	3	3	4
Rhamnus alnifolia	5	1	2	4
SHRUBS, continued				
Ribes americanum	3	5	3	2
Ribes cynosbati	3	4	4	2
Ribes triste	4	3	1	2
Rosa spp.	1	2	2	5
Salix humilis	1	2	3	4
Sambucus pubens	3	5	3	3
Symphoricarpos albus	1	2	3	5
Viburnum rafinesquianum	2	2	3	3
Viburnum trilobum	3	3	3	3
HALFSHRUBS AND VINES				
Arctostaphylos uva-ursi	1	1	2	5
Celastrus scandens	1	3	3	4
Chimaphila umbellata	1	1	2	4
Gaultheria procumbens	1	1	2	5
Parthenocissus quinquefolia	3	3	4	3
Rhus radicans	1	3	3	4
Rubus allegheniensis	3	2	2	5
Rubus idaeus var. strigosus	3	2	2	3
Rubus pubescens	4	2	1	1
Vaccinium angustifolium	1	1	1	5
Vaccinium myrtilloides	2	1	1	4
FERNS AND ALLIES				
Athyrium filix-femina	3	3	2	1
Botrychium virginianum	4	4	3	1
Dryopteris cristata	4	2	1	3
Dryopteris disjuncta	4	3	1	1
Dryopteris spinulosa	4	2	1	1
Equisetum hyemale	2	2	1	5
Equisetum silvaticum	3	2	1	3
Lycopodium annotinum	4	2	1	1
Lycopodium clavatum	3	1	2	1
Lycopodium obscurum	2	3	1	2
Osmunda claytoniana	2	5	5	2
Pteridium aquilinum	1	2	2	4

* M -- moisture, N -- nutrients, H -- heat, L -- light.

Source: coordinate values after Bakuzis (1959)

Appendix Table 5, continued

Species	Coordinates M	N	H	L
MOSSES AND LICHENS				
Cladonia rangiferina	1	1	1	5
Dicranum spp.	3	2	1	2
Mnium spp.	3	4	2	1
Pleurozium schreberi	2	2	1	2
Polytrichum juniperinum	2	2	1	3
HERBS				
Achillea lanulosa	1	1	3	2
Actea rubra	3	3	2	1
Agastache foeniculum	2	2	3	4
Amphicarpa bracteata	3	2	4	3
Anaphalis margaritacea	1	2	2	5
Anemone quinquefolia	4	3	3	4
Antennaria canadensis	1	1	2	5
Apocynum androsaemi-folium	1	2	3	4
Aquilegia canadensis	1	3	3	4
Aralia nudicaulis	3	5	4	1
Aralia racemosa	3	5	4	1
Arisaema atrorubens	3	5	4	1
Asarum canadense	4	5	3	1
Aster ciliolatus	2	2	2	4
Aster laevis	1	2	3	5
Aster macrophyllus	2	2	2	3
Campanula rotundifolia	2	2	3	4
Circaea alpina	4	3	2	1
Clintonia borealis	3	2	1	2
Convolvulus spithamaeus	1	2	3	4
Cornus canadensis	3	2	1	2
Cypripedium calceolus	3	3	3	3
Desmodium glutinosum	2	5	4	1
Epilobium angustifolium	3	2	2	5
Fragaria virginiana	2	2	2	4
Galium boreale	1	2	2	5
Galium triflorum	3	2	2	1
Geum canadense	3	4	3	2
Goodyera repens	3	2	2	3
Hepatica americana	1	3	3	2
Hieracium canadense	1	2	3	4
Impatiens capensis	4	5	4	1
Lactuca canadensis	2	3	3	4
Lathyrus ochroleucus	1	2	3	5
Lathyrus venosus	1	2	2	5

Species	Coordinates M	N	H	L
HERBS, continued				
Lilium philadelphicum	2	3	3	4
Linnaea borealis	3	2	1	3
Lithospermum canescens	1	2	4	5
Maianthemum canadense	1	2	2	4
Melampyrum lineare	1	1	3	5
Mentha arvensis	3	3	2	4
Mitella nuda	4	2	1	1
Osmorhiza claytoni	3	5	3	1
Pedicularis canadensis	1	1	3	5
Petasites palmatus	4	2	1	3
Phryma leptostachya	3	5	5	3
Polygonatum pubescens	3	5	4	2
Potentilla tridentata	2	2	1	5
Prenanthes alba	2	3	1	3
Pyrola asarifolia	3	4	2	2
Pyrola elliptica	2	2	3	3
Pyrola rotundifolia	2	2	2	3
Pyrola secunda	2	2	2	3
Pyrola virens	2	3	2	3
Sanicula marilandica	2	3	3	3
Senecio pauperculus	1	2	3	5
Smilacina racemosa	3	5	4	1
Smilacina stellata	2	5	4	3
Smilax herbacea	2	5	4	2
Solidago canadensis	2	2	2	5
Solidago flexicaulis	3	5	3	1
Solidago hispida	2	2	3	4
Streptopus roseus	2	3	3	1
Thalictrum dioicum	2	3	3	3
Trientalis borealis	4	2	1	1
Trillium cernum	3	5	3	1
Urtica dioica	4	5	5	1
Uvularia grandiflora	2	5	4	1
Uvularia sessilifolia	2	4	3	1
Vicia americana	3	3	4	3
Viola adunca	1	1	2	4
Viola conspersa	3	5	4	1
Viola incognita	3	2	2	3
Viola pubescens	2	2	2	3
Viola renifolia	3	3	2	2
Viola rugulosa	4	2	2	1