Vegetation of the Great Smoky Mountains

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INTRODUCTION

NATURE OF THE STUDY

The Great Smoky Mountains of Tennessee and North Carolina support vegetation which is particularly rich in species and varied in community types. In the summer of 1947 field work was carried out

for a study of this vegetation. The work was originally intended to provide information on the vegetation for the sake of its own interest and as a basis for studies in animal ecology (Whittaker 1952). A major purpose of both this and the preceding study, however, was use of the complex pattern of natural communities in the Great Smoky Mountains for research into the theory of community units or associations. For this purpose, the approach to vegetation was based on sampling without regard to apparent associations and analysis of the samples in

relation to environmental gradients. It was felt that relative validity of vegetation types should emerge from data impartially obtained, and that the relations of types to one another should be revealed in the study of their populations in relation to environmental gradients. The work thus departs from the traditional approach of studying intuitively recognized types or associations; it is an experiment in population analysis of a whole vegetation pattern.

The first part of the monograph describes results of the analysis in terms of relations of species populations to one another and environmental gradients, and trends in community composition and structure along environmental gradients. The second part interprets the vegetation as a complex pattern, within which vegetation types may be understood through the distributional relations of species populations. The third part presents a more conventional description of vegetation types and considers the relations of these to topography. The study as a whole thus seeks to analyze, interpret, and describe the complex vegetational mantle of the Great Smoky Mountains.

LITERATURE ON AREA

A series of studies by Cain deal with vegetation of the Smokies—the heath balds (1930b), subalpine forests (1935), and cove hardwoods (1943), floristic affinities (1930a), soil reaction (1931), Raunkiaer life-forms (1945), and bryophyte unions (Cain & Sharp 1938). A number of vegetation types were described by Cain *et al.* (1937). The grassy balds were reported on by Camp (1931, 1936) and Wells (1936a, 1936b, 1937); the subalpine forests were recently described by Oosting & Billings (1951) and the beech gaps by Russell (1953). These papers and the description in Braun (1950) are the extent of the literature dealing specifically with the vegetation of the Smokies. Other studies include descriptions of Southern Appalachian vegetation types, among them Harshberger's report (1903) and book (1911), Wells (1924) and the forestry reports of the *Message from the President* (Ayres & Ashe 1902), Reed (1905), Holmes (1911), Ashe (1922), and Frothingham *et al.* (1926). Of studies in nearby areas Braun's papers on the Cumberland Mountains—Pine Mountain (1935b), Black Mountain (1940a), and the Cumberlands (1942, 1940b)—and material in the book on the eastern forests (1950) were most valuable for the related vegetation of the Smokies. Other Appalachian and eastern studies—Harshberger (1905) and Heimburger (1934) on the Adirondacks, Core (1929) on Spruce Mountain, Davis (1930) on the Black Mountains, Conard (1935) on Long Island, Raup (1938) on the Black Rock Forest, Oosting & Billings (1939) on Ravenel's Woods, Oosting (1942) on the Piedmont, and, particularly, Brown (1941) on Roan Mountain—contributed comparative information. A bibliography of other papers dealing with the Smokies is given by Mason & Avery (1931). Taxonomic references for the area are Small (1933), Shanks & Sharp (1947), Gleason (1952), and Fernald (1950).

GEOLOGY AND CLIMATE

The Great Smoky Mountains are part of the Blue Ridge Province, a system of mountains of great antiquity. This part of the Southern Appalachians comprises two major ranges, the Blue Ridge proper and the Unaka Mountains, along with their connecting cross-ranges (Fenneman 1938). The two main ranges lie parallel, from northeast to southwest, with the Unakas, of which the Smokies are part, to the north. The drainage, north from the divide of the Blue Ridge, is northwest into the Great Valley of the Tennessee River; and rivers flowing from the Blue Ridge to the Great Valley through the Unakas cut the latter into a series of segments divided by deep gorges. The Great Smoky Mountains are the largest and highest of these segments, between the Little Tennessee and Big Pigeon Rivers.

The crest of the Great Smoky Mountains forms the state border of Tennessee and North Carolina, 25-50 miles southwest of the city of Knoxville in the Great Valley. The range has the appearance of a long, sinuous ridge connecting irregularly spaced domes, with secondary ridges and hills spreading on each side (Fig. 1). The mountains are stream-eroded to physiographic maturity; in form they are subdued (Fenneman 1938) though rugged. Many of the summits and ridges are rounded, and almost all the mountain surface is covered by a mantle of soil and vegetation. The resistant rocks have maintained high relief in spite of age. Sixteen peaks have elevations above 6000 ft (1830 m); and the highest summits rise more than 5000 ft above the valleys a few miles to the north. Valleys are cut deep into the mountain mass, with steep slopes and narrow flats. The slopes form most of the area of the mountains; it has been estimated that less than 10% of the surface has less than 10 degrees of slope (Message from the President 1902).
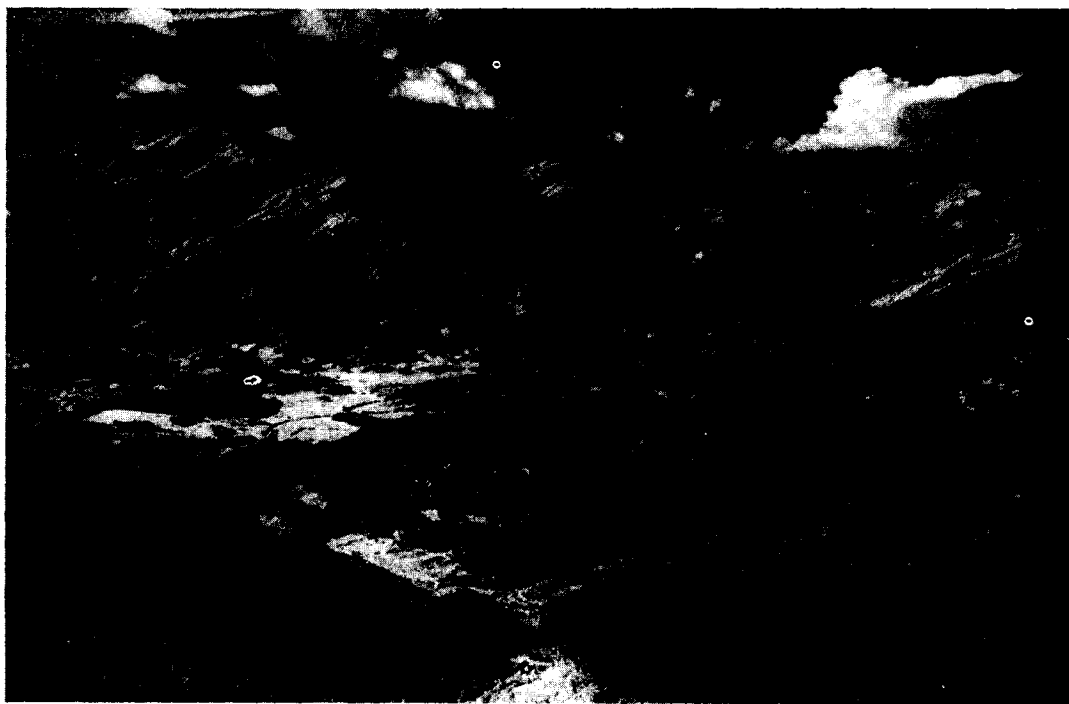
FIG. 1. Mature, forest-covered topography of the Great Smoky Mountains, a view of the southeast slope from Frye Mountain near Bryson City, North Carolina. Reproduced by permission of W. M. Cline Co., Chattanooga, Tenn.

Most of the rocks of the mountains belong to the Ocoee series (Safford 1869, Stose & Stose 1944, 1949, King 1949) of complexly folded, metamorphic sedimentary rocks which are resistant to erosion and fairly uniform in their reaction to it. Deposited in Cambrian or late pre-Cambrian time (Keith 1902, Stose & Stose 1949, King 1949), they were first folded into mountains in the Appalachian Revolution of the late Paleozoic. The mountains were raised further in the Cretaceous and have since that time been through three cycles of erosion, the Schooley, Harrisburg, and present (Wright 1931). While some higher ridges of the Smokies may remain from the Schooley cycle of the earlier Tertiary (Willis 1889, King & Stupka 1950), it is probable that throughout this the area was one of hills or low mountains (Fenneman 1938, Wright 1942, Braun 1950). After a second elevation, probably in the Miocene, the mountains persisted through the shorter Harrisburg cycle, the peneplane of which may be suggested by some of the lower ridges (King & Stupka 1950). The mountains were again raised at the end of the Tertiary. During the Pleistocene the Smokies were well south of the ice sheets and possessed no glaciers; but there are indications that climatic cooling produced a timberline on the higher summits (King & Stupka 1950), displacing forest vegetation toward lower elevations. It is believed, from distributional evidence discussed later (Part III) that high-elevation forests were displaced upward 1000 to 1300 ft above present levels during the warm dry period following glaciation.

The southern mountains have played a great part in the vegetational history of the East (Braun 1938, 1941, 1950). While other areas have been glaciated, submerged, and exposed to great climatic change (Fernald 1931), the Southern Appalachians have offered a sanctuary for many species of plants and animals. The Blue Ridge System has been continuously occupied by plants and animals for perhaps 200 million years (Cain et al. 1937). During the early Tertiary the higher elevations of the Smokies and Blue Ridge probably supported temperate forests ancestral to those now in the area while subtropical floras prevailed at sea level (Cain 1943). It is in the Blue Ridge Province and other areas where the Schooley peneplane was never perfected that most typical mixed mesophytic forests, most closely related to the Arctotertiary forests, have survived (Braun 1950:505). During the climatic changes to which eastern vegetation was subjected, the topography of the Southern Appalachians offered varied conditions of moisture and elevation in which species of diverse climatic adaptations might survive while sometimes destroyed elsewhere.

It might be expected that age and maturity of the mountains would be reflected in maturity of their plant cover, as well as in antiquity of some of the flora. Primary succession is nearly completed in the Smokies; it is perhaps in progress on a few peaks and ridges, but almost all the vegetation is either topographic climax or secondary. One of the major forest trees, the chestnut (*Castanea dentata*), was

infected by the blight in the period from 1925 to 1930; and most trees were killed by the early 1940's. Death of the chestnuts altered many forest stands by opening canopies and permitting increased reproduction of other species. Areas of second-growth due to human disturbance are extensive. Many valleys and lower slopes were cleared or cut in the course of settlement, and undisturbed valley stands at low elevations are rare. Some of the higher slopes have been logged. Fires, set by man and by lightning, have swept many of the drier slopes at all elevations. A large area of mountain vegetation which is virgin or but little disturbed, however, is protected by the Great Smoky Mountains National Park.

The complexity of the climax forests is a further expression of the the physiography and history of the mountains. Because of age and diversity of habitats, the flora is rich and contains a high proportion of endemic species for an eastern flora. Approximately 1300 species of flowering plants, including 130 species of native trees, have been found in the Smokies (King & Stupka 1950); and Cain *et al.* (1937) estimated that 3.1% of the flora is endemic to the Unaka Range, an additional 8.5% to the Southern Appalachian Mountains. The variety of habitats, ranging from most mesic valleys to dry slopes and ridges in moisture conditions and from austral to subalpine in temperature, causes the appearance of many vegetation types in different sites. Since, however, the rocks of the mountains themselves are relatively homogeneous (predominantly quartzites and slates), the vegetation is not further complicated by great differences in soil parent-material. Only in some of the northwestern coves, where fensters or windows through the overthrust rocks expose limestones (Fenneman 1938), do calciphile communities occur. Geologically and biologically these coves are inliers from the Great Valley; and they are considered outside the scope of this study. Aside from these coves, the soils of the Smokies are acid, with acidities generally increasing toward higher elevations and more exposed sites (Cain 1931).

From the high relief of the Smokies both marked variation in local climates and a humid general climate result. Mean temperatures decrease with elevation at an average rate of 2.23° F per 1000 ft, so that high elevations average 10-15° cooler than the base of the mountains during the growing season (Shanks 1954). Sea-level climates most nearly equivalent to those of high elevations in the Smokies may occur about 1000 mi. to the northeast, in northeastern Maine or adjacent New Brunswick (Shanks 1954). By the Thornthwaite (1931, 1941, 1948) climatic classifications, low elevations of the range are humid mesothermal, and high elevations perhumid microthermal; intermediate elevations are differently classified by the two systems (Shanks 1954).

Annual precipitation values range from 50 to 60 in. (127-152 cm) in the lower valleys (Gatlinburg, Elkmont, and Maryville records) to more than 80 in. (203 cm) at high elevations, the highest in the

United States outside the Northwest Coast. Series of summer thunderstorms advancing along the ridge and banks of cloud in the canyons are familiar sights in the mountains. The Smokies share with surrounding areas the distinctive Southern Appalachian precipitation regime, with two maxima, one in winter or early spring and the other in late summer (Henry 1902, Ward 1925, Kendrew 1937). Monthly precipitation data for low and high elevations have been previously published (Whittaker 1952:2, Shanks 1954). To the humid climate may be related also the haze which, most of the time, lies over the mountain landscape and which gave the Great Smoky Mountains their name.

METHODS

In Part I data on the vegetation of the Great Smoky Mountains will be discussed in relation to three groups of questions: (1) How are species populations distributed in relation to environmental gradients and one another? (2) What trends in community composition and structure along environmental gradients may be observed? (3) How are community-units to be understood in terms of the relations of stands and of species populations to one another? The third of these, and the objective of studying the nature of community-units, required the use of means of sampling unprejudiced by assumptions about community-units. The two methods of sampling used were *field transects*, with samples taken at fixed intervals along environmental gradients, and *site-samples* taken at random, so far as possible, through the whole vegetation pattern.

FIELD TRANSECTS AND TREE CLASSES

Almost any valley of the Smokies contains a series of vegetation types from the stream-side to the open slope or ridge above. The basic sequence of types below 4500 ft (1370 m) includes: (1) cove forest (mixed mesophytic association) in most mesic sites of valley bottoms and lower slopes, (2) oak-chestnut forest on less mesic sites, (3) oak-chestnut heath in still drier or more xeric sites, and (4) pine forests and pine heaths on the driest south- and southwest-facing slopes. At elevations above 2500 ft (760 m) stands dominated by hemlock (*Tsuga canadensis*) usually appear between the deciduous cove forests and the oak-chestnut forests, and below 2500 ft oak-hickory forests often occur between cove forest and oak-chestnut forest. Analysis of this sequence of plant populations and vegetation types along the "moisture gradient" was a major problem of the study. The *field transects* were used as a first step in this analysis, on which the more detailed *composite transects* described below are dependent.

In field transects, vegetation samples were taken at uniform intervals of distance or elevation from the valley bottom to the ridge above it. At each sampling point the site was described by topographic position, elevation, direction of exposure, and degree of slope. Trees were tallied, with diameters at breast height from 1 in. up recorded for each species; about 100

stems were the usual sample for each of 7 to 10 stations. Along with the tree count the undergrowth was recorded by a coverage estimate for each stratum and a list of major and minor species. An example, one of six such transects made, will show the method and its relation to the composite transects.

On the Bullhead Trail to Mt. Le Conte, seven sample counts were made at intervals of 25 m from the valley bottom to the southwest-facing slope, all at elevations of 3100 ft. In the tables an additional sample from a deep valley forest was added to the beginning of the series, since the small valley of the transect did not represent the extreme of mesic conditions. Percentages of stand for the trees and occurrences of shrubs and herbs were arranged for the 8 stations as in Table 1. In analyzing transects with relatively small samples, simple tallying of numbers of stems for each species was preferred to basal-area computation. Canopy dominance was determined separately from larger samples.

Individual species of trees are well scattered along the gradient, but certain loose groupings of species may be suggested. Some species have their maximum abundance in the deep-valley cove forest, station K of the transect, or are abundant there and have their

TABLE 1. Bullhead field transect of moisture gradient. Along trail from Cherokee Orchard to Mt. Le Conte, in a small dry valley at 3100 ft and out onto adjacent southwest slope. Trees by percentages of stand from 1-in. class up.

Tree species	K*	I	II	III	IV	V	VI	VII
Tsuga canadensis	11	2	4	3	..	..	.	..
Halesia monticola	29	24	25	24	1	..	..	..
Aesculus octandra	9	3	9	..	..	..	..	..
Acer saccharum	9	14	33	25	..	..	..	..
Tilia heterophylla	16	27	13	13	..	..	..	..
Fagus grandifolia	10	..	..	..	..	..	..	..
Betula alleghaniensis	9	..	..	..	..	..	..	..
Liriodendron tulipifera	1	..	..	..	..	..	..	..
Magnolia acuminata	x	..	..	..	..	..	..	..
Ilex opaca	x	..	..	...	..	..	..	..
Carya cordiformis	x	1	2	..	..	..	..	..
Fraxinus americana	1	..	1	..	..	..	..	..
Cladrastis lutea	x	11	3	1	..	..	..	..
Magnolia f. aseri	1	x	..	..	6	..	..	..
Acer rubrum	4	..	x	x	21	54	20	x
Quercus borealis v. maxima	..	1	1	..	..	..	..	..
Carya glabra	.	1	2	..	..	..	..	..
Ostrya virginiana	..	1	1	4	..	..	..	..
Acer pensylvanicum	..	14	1	11	6	..	..	..
Betula lenta	..	1	4	7	8	10	..	..
Hamamelis virginiana	..	..	3	8	28	..	..	..
Clethra acuminata	..	..	..	..	9	4	..	..
Amelanchier arborea	..	..	..	..	..	2	..	..
Robinia pseudoacacia	..	..	1	x	..	4	2	x
Castanea dentata (dead)	..	..	..	3	9	10	2	1
Quercus prinus	..	..	..	..	6	8	38	4
Oxydendrum arboreum	..	..	..	..	4	10	5	1
Nyssa sylvatica	..	..	..	..	1	x	16	2
Sassafras albidum	..	..	..	..	..	..	5	1
Quercus coccinea	.	..	..	..	..	..	x	2
Pinus pungens	..	..	..	..	..	..	11	12
Pinus rigida	..	..	..	..	..	..	2	77
Total stems	642	205	205	91	90	52	55	122

x, present at less than .5%.
*Kalanu Flats, a cove forest 6 mi. east of transect area, elevation 2800 ft.

maxima in the second or third stations. At the other extreme are species which have their maxima in the most xeric site, station VII, and do not extend to sites less xeric than station VI. Between these extreme groups there are a number of species with their maximum populations in stations III to VI. These might be grouped together; but they may also be separated into two groups, one having maxima in stations III and IV, extending on the mesic side to station I or II but not beyond V on the xeric side, and the other having maxima in stations V and VI and extending to the xeric extreme, but not beyond IV on the mesic side. The four groups are used as *classes* of trees along the moisture gradient. They may be characterized as follows:

1. Mesics—Species with maxima in or near the most mesic sites and with limited extent into more xeric situations, occurring rarely in the part of the gradient represented by oak-chestnut heath. These species predominate in the cove forests.

2. Submesics—Species which have their maxima in fairly mesic sites, but are uncommon or absent in most mesic sites and do not extend to most xeric sites. These species predominate in oak-hickory forests at lower elevations and in red oak-chestnut forests at higher elevations.

3. Subxerics—Species which have their maxima in more xeric sites, but occur in most xeric sites only as minor species and are absent from most mesic sites. These species predominate in oak-chestnut heaths and at higher elevations in white oak-chestnut forests.

4. Xerics—Species which have their maxima in most xeric sites and have limited extent into less xeric sites, extending into the range of dominance of the previous group and no further. These species predominate in pine forests and pine heaths.

The same "classes" are recognized for shrub and herb populations. Lists of species for each are given in the "Summary of Distributional Groupings."

The moisture gradient is one of great complexity; along the gradient from stream-side to south-facing slope and ridge many factors of soil moisture and atmospheric humidity vary, along with exposure to wind and insolation, and factors of temperature affected by insolation and by patterns of air movement. In relation to the "primary" gradients of environmental factors a sequence of vegetation types and a catena of soils develop; and the composition and physiognomy of vegetation and properties of soils form other "secondary" gradients of environmental factors affecting plants. The primary factors are so modified by the presence of plant communities that "primary" and "secondary" factors are not really to be distinguished in their effects on plants. At any point along the gradient the plant lives in relation to an environmental complex of interrelated factors of physical environment, soil, vegetation, and animal communities; along the "moisture gradient" factors of each of these change. The gradient is thus a complex of factor gradients, or a gradient of environmental complexes, which, in distinc-

tion from a factor gradient, may be termed a *complex-gradient* (Whittaker 1954b). The "elevation gradient" is likewise a complex-gradient, involving many factors of physical environment, soils, and natural communities other than temperatures and growing seasons.

The complex-gradient from valley bottoms to dry slopes will be called the "moisture gradient," but with no assumption that moisture factors directly control the distribution of any plant population along it. Measurements of all factors of environment and determination of which may be most significant for populations of different plant species are far beyond the scope of the present work. For the present study it may suffice that a complex-gradient exists, in relation to which the distributions of plant populations may be studied.

Such study is dependent on the definition of relative positions along the gradient. Since these could not be determined, for hundreds of site-samples, by direct environmental measurement, approaches through the vegetation itself were sought. Along the gradient the four moisture classes of trees rise and fall in sequence, forming a set of curves flowing continuously into one another (Figs. 2, 3, 4). If, as is shown by the transects, there is progressive shift in proportions of trees of different tolerances along the gradient, then it is not unreasonable to turn from this fact to its converse and regard the same proportions as expressions of position along the gradient. In the following discussion, stands and sites will be termed *mesic, submesic, subxeric,* and *xeric* according to which of the moisture classes predominate in stem numbers.

SITE-SAMPLES AND COMPOSITE TRANSECTS

The main reliance in solving the vegetation pattern was on the site-samples and their manipulation. A *site-sample* was a vegetation sample from a restricted site of uniform physical habitat—the floor of a valley, a single hillside slope of the same direction and inclination, or the crest of a ridge. In order to obtain an approximately random coverage of the whole vegetation pattern, samples were taken from the many trails at all elevations in the mountains. The method was to move along a trail recording a sample from each new slope exposure, inside or out of a valley, of sufficient extent to give a homogeneous sample. The site-samples were in no case selected to represent either apparent vegetation types or the transitions between them. The bulk of the site-samples were obtained from the mountains surrounding Greenbrier, Sugarland, and Cades Coves in the National Park on the Tennessee or northwest side of the range.

At each site the same data were recorded as in the transect stations. Sample size varied with the number of trees thought necessary to indicate stand composition: fifty were sufficient in some stands with one or two dominants, but most counts included about 100, while 200 or 300 were tallied for some mixed types. The dense small stems of Rhododendron

thickets were not counted in forests where they occurred. The 25,000 stems recorded in 300 site-samples were the total sample analyzed for the vegetation pattern.

Exacting phytosociological analysis of the undergrowth was not an objective. Information on shrubs is largely limited to presence and stratal dominance, that on herbs to visible presence at the time of sampling. Stratal coverages are estimates, intended only to permit comparisons between different stands in the Smokies. At 15 sample stations for another study (Whittaker 1952) location and coverage of individual plants were mapped in quadrats 10m square.

The site-samples were manipulated in several ways. By comparing series of them from north and south slopes or other exposures, the alterne effect on vegetation could be determined, a method found particularly effective at high elevations where alterne effects are more conspicuous in undergrowth than canopy. Groups of samples from sites with similar moisture conditions within limited ranges of elevations were compiled into composite stand counts. These counts, usually for about 1000 stems, compensated for the small size of the site-sample counts and were used for the characterization of vegetation types (Part III). Data from the site-samples were arranged in mosaic form on a chart with elevation and topographic sites as axes, to show distributions of species and vegetation types in relation to elevation and topography (Part III).

The site-samples were, finally, arranged in *composite transects* in terms of elevation, or of topographic site, or of moisture conditions as indicated by the vegetation itself. For the elevation transects some means of comparing stands of equivalent moisture conditions at different elevations was needed. The site-samples were consequently classified into four groups, according to which of the moisture classes of trees was predominant in a given sample. Within each of the four classes of stands, the site-samples were grouped by 200- and 300-ft intervals. Four composite transects were thus arranged to cover the whole of the vegetation pattern, showing the change in levels of plant populations from low elevations to high in each of the four classes of stands and sites recognized.

A more sensitive indication of relative positions along the moisture gradient is possible through the use of *weighted averages* as indicator values (cf. Ellenberg 1948, 1950, 1952, Curtis & McIntosh 1951, Whittaker 1954b). In a given stand the number of stems in each moisture class is multiplied by a weight (0 for mesics, 1 for submesics, 2 for subxerics, 3 for xerics), and the total of weighted stem numbers is divided by the total number of stems. Within elevation belts (1500-2500, 2500-3500, and 3500-4500 ft) the site-samples were arranged in sequence from most mesic to most xeric by these weighted averages, and were then grouped for tabulation into 12 or 13 steps along the gradient. This method of arranging the transects involves an evi-

dent circularity; distribution of tree species is studied in terms of previously determined distributional classes of these same tree species. The approach is based, however, on the objective data of the field transects; and the patterns of species distributions are essentially the same in the field transects and composite transects.

Other composite transects were made for elevations above 4500 ft in subalpine or spruce-fir forests, and in high-elevation deciduous forests outside the range of spruce and fir. In these the samples were grouped by topographic position rather than by weighted averages. The various composite transects were de-signed to form a grid covering the whole of the vegetation pattern of the Great Smoky Mountains. The following sections will discuss distributions of plant populations and trends in community composition shown by these transects. The whole body of tables cannot be published here. Two tables have already been published (Whittaker 1951), and the other tables for tree populations are presented here (with extension of elevation intervals from 200 to 400 ft in tables 5 and 6). The full set of tables for tree populations and undergrowth species are available to those desiring them (see Note on Supplementary Publication).

TABLE 2. Composite transect of moisture gradient between 2500 ft and 3500 ft, distribution of trees along gradient. Transect along the moisture gradient from mesic valley sites (Sta. 1) to xeric southwest slope sites (Sta. 13), based on 67 site counts including 6122 stems from elevations between 2500 and 3500 ft. All figures are percentages of total stems in station from 1-in. diameter class up.

Tree species	STATION NUMBER												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Acer spicatum	4	..	x	..	..	..	..	..	..	..	..	..	..
Fraxinus americana	2	1	2	1	1	..	..	..	..	..	..	..	..
Tilia heterophylla	17	..	14	16	1	..	..	..	..	..	..	..	..
Aesculus octandra	7	1	4	2	x	..	..	..	..	..	..	..	..
Fagus grandifolia	1	2	1	x	1	..	..	..	..	..	..	..	..
Acer saccharum	6	3	14	9	1	x	..	..	..	..	..	..	..
Magnolia acuminata	x	..	1	x	1	..	..	..	..	..	..	..	..
Ilex opaca	..	3	x	..	1	..	..	..	..	..	..	..	..
Prunus serotina	..	1	x	x	x	..	..	..	..	..	..	..	..
Tsuga canadensis	25	49	6	8	9	..	1	..	..	..	..	..	..
Betula alleghaniensis	26	10	13	3	5	..	x	..	..	..	..	..	..
Liriodendron tulipifera	2	2	1	3	10	1	1	x	..	..	..	..	..
Halesia monticola	5	19	28	17	3	7	1	2	1	..	..	..	..
Magnolia fraseri	2	5	1	2	4	4	1	1	2	..	..	..	..
Acer pensylvanicum	1	..	2	7	1	3	1	1	..	..	..	..	..
Betula lenta	2	2	5	4	5	2	2	1	1	..	..	..	..
Acer rubrum	x	1	2	9	27	37	35	24	16	16	7	5	3
Ilex montana	..	x	1	x	x	..	x	..	..	..	..	..	..
Quercus borealis v. maxima	..	1	1	1	2	1	4	2	2	..	..	..	..
Cornus florida	..	..	x	1	3	x	2	..	..	..	..	..	..
Hamamelis virginiana	..	..	1	15	6	17	9	3	..	..	..	..	..
Ostrya virginiana	..	..	x	1	..	..	..	..	..	..	..	..	..
Carya glabra	..	..	1	x	1	..	2	8	1	..	..	..	..
Clethra acuminata	..	..	..	..	x	4	2	..	1	..	..	..	..
Aralia spinosa	..	..	..	..	..	x	x	..	1	..	..	..	..
Carya tomentosa	..	..	x	..	..	..	..	3	..	..	..	..	..
Pyrularia pubera	..	..	..	..	..	..	x	..	..	..	..	..	..
Amelanchier arborea	..	..	..	..	x	..	x	..	..	..	..	..	..
Castanea dentata (dead*)	..	..	2	1	1	5	10	10	15	7	5	1	..
Robinia pseudoacacia	..	..	..	x	2	1	2	9	6	1	..	1	..
Oxydendrum arboreum	..	..	..	x	8	9	11	8	16	9	3	1	..
Quercus prinus	..	..	..	x	5	5	13	15	23	18	9	5	2
Sassafras albidum	..	..	..	..	x	1	1	2	2	2	x	1	1
Nyssa sylvatica	..	..	..	..	1	3	x	x	3	2	2	3	3
Quercus velutina	..	..	..	..	..	..	1	4	..	x	1	..	..
Quercus alba	..	..	..	..	..	..	..	x	1	1	x	..	..
Quercus coccinea	..	..	..	..	..	..	1	3	1	25	15	8	10
Pinus rigida	..	..	..	..	..	..	..	2	2	16	20	15	40
Pinus pungens	..	..	..	..	..	..	..	1	5	3	38	60	41
Percents by classes													
Mesic	97	96	84	61	37	12	4	3	3	..	..	..	..
Submesic	3	4	13	38	45	64	57	42	22	16	7	5	3
Subxeric	..	..	2	1	17	24	38	48	66	40	20	12	6
Xeric	..	..	..	..	..	..	1	6	8	44	73	83	91
Trees in stations	335	480	592	675	418	516	620	357	300	425	438	412	554
Site-samples used	5	3	6	6	5	6	5	6	5	4	5	6	5

x, Present below .5%.
*Dead chestnut trees were counted in all stands. Since the smaller stems had ceased to be identifiable as such in 1947, the number of chestnuts in the tables is smaller than the number of living stems would have been (see size distributions in Appendix C).

DISTRIBUTIONS OF SPECIES ALONG THE MOISTURE GRADIENT

Distributions of tree populations along the moisture gradient are shown in the three tables for different elevation belts (1500-2500 ft, Whittaker 1951, table 1; 2500-3500 and 3500-4500 ft, present work, tables 2 and 3). Almost all species show a rounded or bell-shaped curve of population distribution along the gradient (see Figs. 2, 3, 4). Population curves for different species, including many of those in different moisture classes, overlap broadly. Population centers for species and limits of their distributions are well scattered along the gradient. The basic se-quence of species populations along the moisture gradient is similar at all elevations below 4500 ft, but differs in detail because of the varied relations of species populations to elevation. From mesic sites to xeric, major tree species have their population maxima in the sequence: *Aesculus octandra**, *Tilia heterophylla*, *Betula allegheniensis* Britt., *Halesia monticola* (Rehd.) Sarg., *Acer saccharum*, *Liriodendron tulipifera*, *Tsuga canadensis*, *Quercus borealis* v. *maxima* (Marsh.) Ashe, *Carya glabra*, *Acer rubrum*, *Carya tomentosa*, *Castanea dentata*, *Quercus prinus*,

* Nomenclature follows that of Fernald (1950) except where authorities are given.

TABLE 3. Composite transect of moisture gradient between 3500 and 4500 ft, distribution of trees along gradient. Transect along the moisture gradient from mesic valley sites (Sta. 1) to xeric southwest slope sites (Sta. 12), based on 46 site counts including 4906 stems from elevations between 3500 ft and 4500 ft. All figures are percentages of total stems in station from 1-in. diameter class up.

Tree species	STATION NUMBER											
	1	2	3	4	5	6	7	8	9	10	11	12
Fagus grandifolia	10	5	1	1	1	..	..	..	..	..	..	..
Ilex opaca	..	1	..	x	..	..	..	..	..	..	..	..
Picea rubens	..	x	..	x	x	..	..	..	..	..	..	..
Cornus alternifolia	1	1	..	x	x	..	..	..	..	..	..	..
Aesculus octandra	8	9	4	2	6	1	..	..	..	..	..	..
Tilia heterophylla	29	11	9	1	14	3	..	..	..	..	..	..
Acer spicatum	..	16	11	..	17	1	..	..	..	..	..	..
Acer saccharum	17	7	1	1	5	1	..	..	..	..	..	..
Prunus serotina	2	1	..	1	x	2	..	..	..	..	..	..
Fraxinus americana	1	1	..	1	1	x	..	..	..	..	..	..
Betula allegheniensis	5	17	10	15	4	1	x	..	..	..	..	..
Magnolia acuminata	..	x	..	..	x	..	1	..	..	..	..	..
Magnolia fraseri	..	..	20	4	1	..	1	..	..	..	..	..
Tsuga canadensis	20	22	34	62	18	x	x	1	..	..	..	..
Halesia monticola	5	8	4	1	9	13	3	1	1	..	..	..
Ilex montana	1	x	..	1	1	1	2	..	..	..	..	..
Acer pensylvanicum	1	x	1	3	8	3	x	1	..	..	..	..
Amelanchier laevis	..	x	..	x	x	..	..	..	..	..	..	..
Quercus borealis	..	1	..	..	2	40	10	4	15	11	2	1
Acer rubrum	..	1	..	..	1	6	37	21	13	10	8	1
Prunus pensylvanica	..	..	2	..	..	..	1	..	..	..	..	..
Betula lenta	..	..	1	4	4	1	2	2	..	..	..	..
Clethra acuminata	..	..	..	1	x	..	..	..	..	..	..	..
Hamamelis virginiana	..	..	..	..	2	5	17	7	1	..	2	..
Cornus florida	..	..	..	..	1	..	x	4	..	..	..	..
Liriodendron tulipifera	..	..	..	..	2	..	..	1	..	x	..	..
Rhododendron calendulaceum	..	..	..	..	..	1	..	1	4	..	..	..
Carya glabra	..	..	..	..	..	4	x	2	6	5	..	..
Carya tomentosa	..	..	..	..	..	..	..	2	..	..	..	..
Carya ovalis	..	..	..	..	..	..	-	x	..	..	..	..
Nyssa sylvatica	..	1	..	..	..	2	4	1	2	7	..	..
Oxydendrum arboreum	..	x	1	..	1	3	8	14	16	1	1	..
Castanea dentata (dead)	..	..	..	2	5	7	9	10	12	1	..	..
Sassafras albidum	..	..	..	..	1	1	1	1	4	x	..	..
Quercus alba	..	..	..	..	2	1	8	24	10	x	..	..
Robinia pseudoacacia	..	..	..	..	4	5	1	3	8	3	x	..
Quercus prinus	..	..	..	..	3	4	15	4	16	11	1	..
Quercus velutina	..	..	..	..	..	x	x	1	1	..	..	..
Quercus coccinea	..	..	..	..	..	1	..	..	..	..	1	..
Pinus rigida	..	..	..	..	..	..	..	7	1	1	11	46
Pinus pungens	..	..	..	..	..	..	..	1	4	54	49	
Percents by classes												
Mesic	98	98	95	90	78	22	5	3	1	..	..	..
Submesic	2	2	4	9	19	62	70	44	39	26	12	2
Subxeric	..	..	1	1	2	16	23	46	58	69	23	2
Xeric	..	..	..	..	..	..	1	7	2	5	65	96
Trees in stations	377	597	520	232	449	594	472	266	369	378	297	355
Site-samples used	1	7	4	3	4	4	4	4	4	4	3	4

x, Present below .5%.

FIG. 2. Transect of the moisture gradient, 1500-2500 ft. Top—curves for tree classes: a, mesic; b, submesic; c, subxeric; d, xeric. Middle—curves for tree species: a, *Betula alleghaniensis*; b, *Cornus florida*; c, *Quercus prinus*; d, *Pinus virginiana*. Bottom—curves for undergrowth coverages: a, herbs; b, shrubs.
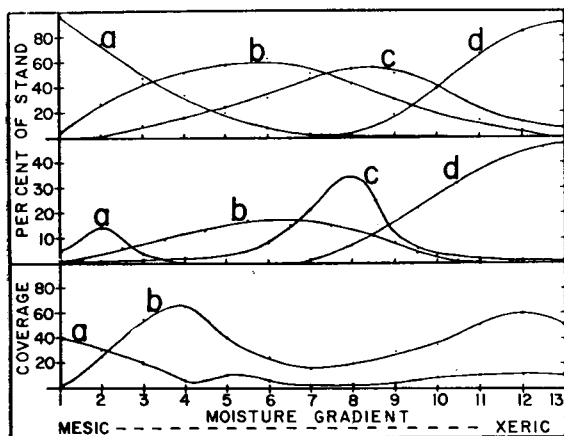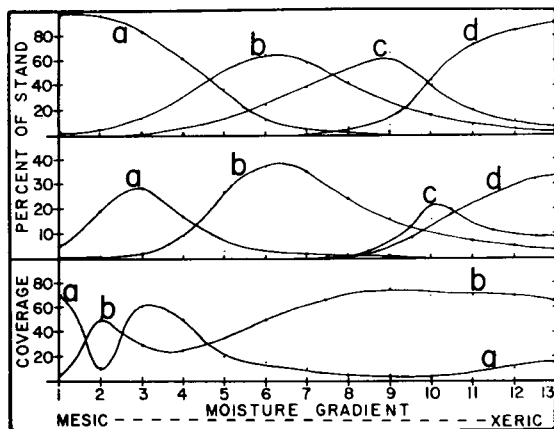

FIG. 3. Transect of the moisture gradient, 2500-3500 ft. Top—curves for tree classes: a, mesic; b, submesic; c, subxeric; d, xeric. Middle—curves for tree species: a, *Halesia monticola*; b, *Acer rubrum*; c, *Quercus coccinea*; d, *Pinus rigida*. Bottom—curves for undergrowth coverages: a, herbs; b, shrubs.

Quercus alba, Q. velutina, Q. coccinea, and *Pinus virginiana, P. pungens,* and *P. rigida.*

Comparable data on population levels are not available for shrubs and herbs, but these appear to be distributed in the same manner as the trees. Species populations overlap widely along the gradient, and centers and limits of distribution are scattered along the whole of the gradient.

Among the shrubs *Rhododendron maximum* is the most important species in mesic sites, but it is a major species in submesic sites also and occurs in subxeric and some xeric ones. *Hydrangea arborescens* is the only other shrub species very widely distributed through mesic and submesic forests. *Leucothoë editorum* occurs only locally in mesic forests; other mesic shrub species are restricted to low elevations or high ones. In submesic sites a number of deciduous species make up the shrub stratum along with the evergreen ericads *Rhododendron maximum* and *Kalmia latifolia.* Among the major species of submesic shrubs some (*Viburnum acerifolium, Calycanthus fertilis, Pyrularia pubera*) extend more widely into mesic sites, but these and others (*Gaylussacia ursina* (M. A. Curtis) T. & G., *Clethra acuminata, Rhododendron calendulaceum, Smilax rotundifolia*) extend varying distances into subxeric and xeric sites. In subxeric sites and some xeric ones, *Kalmia latifolia* is the principal shrub species. *Lyonia ligustrina, Smilax glauca,* and the widespread species *Vaccinium constablaei* A. Gray may best be grouped with it in a subxeric class. Several shrub species (*Vaccinium vacillans, V. hirsutum* Buckl., *V. stamineum, Gaylussacia baccata, Pieris floribunda, Ilex montana* v. *beadlei* (Ashe) Fern.) are centered in xeric sites and extend varying distances into subxeric and submesic ones.

A number of herb species are centered in mesic forests and dominate the herb stratum there; major

species include *Dryopteris spinulosa* v. *intermedia, Athyrium thelypterioides, Caulophyllum thalictroides, Cimicifuga racemosa, Eupatorium rugosum, Laportea canadensis, Impatiens pallida,* and *Aster divaricatus.* These extend varying distances into submesic forests. Other species which are important in mesic sites (*Smilacina racemosa, Polygonatum* spp., *Desmodium nudiflorum, Polystichum acrostichoides*) are major herb species also in submesic sites. The latter have been grouped with those more clearly centered in submesic sites (*Aureolaria laevigata* (Raf.) Raf., *Prenanthes trifoliolata, Medeola virginiana, Dryopteris noveboracensis, Veratrum parviflorum* Michx.) into a submesic class. A number of these species extend widely into subxeric sites, where they are joined by others (*Campanula divaricata, Chimaphila maculata*) of more limited extent into submesic sites. *Galax aphylla,* the most important subxeric herb species, is widely distributed from submesic sites to most xeric ones. Other herb species are centered in xeric sites; most of these (*Pteridium aquilinum* v. *latiusculum, Tephrosia virginiana, Baptisia tinctoria, Gaultheria procumbens*) extend widely into subxeric sites, and some of them (*Epigaea repens, Panicum* sp., *Coreopsis major, Andropogon scoparius*) extend into submesic sites, in part of their elevation range, at least. More complete lists of herb and shrub species assigned to moisture classes are given in the "Summary of Distributional Groupings."

There is no point along the gradient at which either floristic composition or dominance changes abruptly in any stratum. Rather than this, the rounded and tapered distributions of species populations, the scattering of their distributional centers and limits along the gradient, and their broad overlap with one another imply gradual and progressive change in relative importance of species and in total floristic composition from one extreme of the gradient to the other.
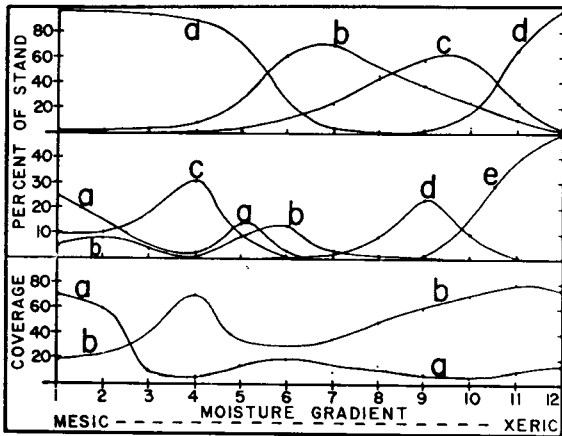
FIG. 4. Transect of the moisture gradient, 3500-4500 ft. Top—curves for tree classes; a, mesic; b, submesic; c, subxeric; d, xeric. Note expansion of mesic stands, compared with Figs. 2 and 3. Middle—curves for tree species: a, *Tilia heterophylla*; b, *Halesia monticola* (both the preceding are bimodal, with populations on each side of the mode of Tsuga); c, *Tsuga canadensis*; d, *Quercus alba*; e, *Pinus pungens*. Bottom—curves for undergrowth coverages: a, herbs; b, shrubs.

TRENDS IN RELATION TO THE MOISTURE GRADIENT

Various *trends* in community composition and structure can be followed from one extreme of the moisture gradient to the other. These trends, comparable to those already studied in foliage insect communities (Whittaker 1952), are in most cases continuous through whatever community-types or associations may be recognized.

GROWTH-FORMS

Four growth-forms of trees are recognized in the Smokies (see Part III): pines, abietines (*Tsuga canadensis*), oaks, and other deciduous trees. A continuous shift in proportions of these appears along the moisture gradient (Whittaker 1953:49). Deciduous trees other than oaks predominate in mesic sites, oaks in intermediate sites, and pines in xeric sites. Toward higher elevations a belt in which *Tsuga canadensis* is dominant is interposed between the first two of these. The pattern of growth-form composition, and the predominance of the semi-sclerophyllous, deciduous oak grouping in intermediate sites, is the same whether or not *Castanea dentata*, *Fagus grandifolia*, and the ericaceous tree *Oxydendrum arboreum* are grouped with the oaks. Among the shrubs a comparable shift in growth-form composition appears, involving deciduous and evergreen, ericaceous and non-ericaceous species. Deciduous non-ericaceous species predominate in mesic sites, with some exceptions; but deciduous species decline in importance along the gradient as evergreen ericads increase to become strongly predominant in subxeric sites. Toward the xeric extreme, evergreen ericads decline and deciduous ericads (Vaccinioideae or Vacciniaceae) increase to dominate the shrub stratum in most xeric pine heaths.

Herb species are less easily classified, but trends in importance may be observed among the more numerous growth-forms which might be recognized. Ferns with delicate foliage (Dryopteris and Athyrium) are centered in mesic sites and decline in importance through submesic into subxeric ones. A group of herbs of moderate stature with broad, thin leaves and a characteristic spreading or umbrella-shaped growth-form (Caulophyllum, Cimicifuga, Actaea, Impatiens, Trillium, Laportea, Osmorhiza, Thalictrum, *Eupatorium rugosum*, *Aster divaricatus*) prevail along with ferns in mesic sites and are of decreasing importance toward more xeric ones. Other herb forms —rosette plants (*Goodyera pubescens*, *Veratrum parviflorum*, *Viola hastata*) and those with leaves spaced along the stem (Aureolaria, Solidago, Smilacina, Uvularia, Melampyrum, Coreopsis)—are more important in submesic and subxeric sites; and foliage of herbs in these sites is, on the whole, tougher than that of the delicate-leaved mesic herbs. Species of these groups occur also in xeric sites, but a variety of other herb types prevail there: grasses (Andropogon, Panicum), ground heaths (Gaultheria, Epigaea), legumes (Baptisia, Tephrosia), a tough-leaved fern (Pteridium), and a club-moss (*Lycopodium obscurum*). Of these the grasses are the major herb growth-form in xeric sites at lower elevations; and the ground heaths are the major herb growth-form in subxeric sites and in xeric ones at higher elevations.

COVERAGES

In general, tree coverage and density of the canopy decrease along the moisture gradient from cove forests into pine forests; light penetration to lower strata consequently increases along the gradient (Whittaker 1952). Estimated tree coverages increase, however, from subxeric sites (oak-chestnut heath) into xeric ones; the very low canopy coverage in oak-chestnut heath is in part a consequence of death of the chestnuts. Shrub coverage in general increases along the gradient toward more xeric sites (Figs. 2, 3, 4). This trend is modified, however, by the presence of a secondary maximum of shrub coverage in hemlock forests in mesic sites, and by a final decrease of shrub coverage in most xeric sites. Herb coverage in general decreases along the gradient from mesic to xeric sites. This trend also is modified in two respects—by very low coverages in hemlock stands, and by a final increase of herb coverage from subxeric sites into xeric ones. Maximum herb coverages occur in mesic deciduous forests, where moisture conditions are most favorable, and in xeric pine forests, where light penetration to the herb level is greatest. Herb and shrub coverages show a clear inverse relation within the set of transects for elevations below 4500 ft in the Great Smoky Mountains (Figs. 2, 3, 4).

DIVERSITIES

Diversity of the tree stratum can best be approached through the *alpha* values of Fisher (Fisher et al. 1943; Williams 1947, 1950; Whittaker 1952).

These values provide a measurement of richness in species which is, within limits, independent of sample size. In Fig. 5 alpha values for composite stand counts are plotted on the vegetation pattern for the Smokies developed in Part III. At all elevations highest diversity values are in intermediate sites—in the cove forest transition below 3000 ft and oak-chestnut forests above 3000 ft. The hemlock stands, which provide exceptions to all the trends discussed, are less diverse than the more and less mesic stands on each side of them. In general, however, species diversity of the tree stratum rises along the gradient from one minimum in most mesic sites to a maximum in submesic sites and declines to a second minimum in xeric sites.
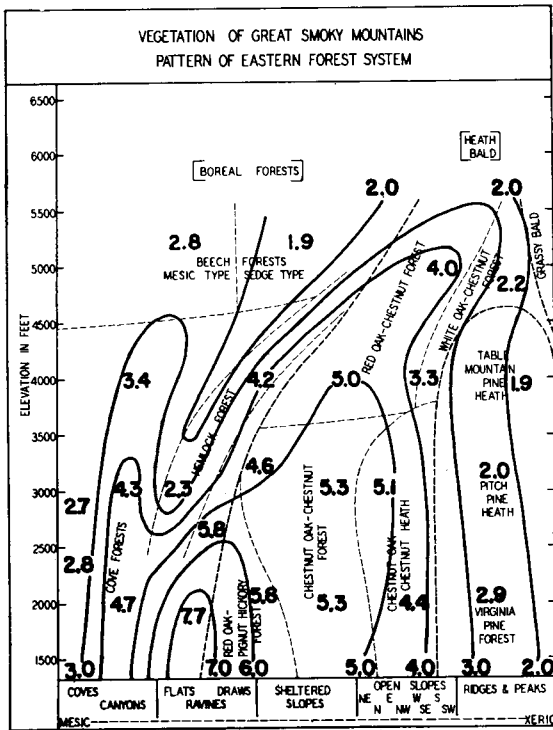

FIG. 5. Pattern of tree species diversities (*alpha* diversity values, for all tree stems in the composite stand counts of Appendix C).

Alpha values cannot be computed for the undergrowth data available. Analysis of the transects through average numbers of species listed per sample provides a more limited indication of diversity trends in the herb and shrub strata. For shrubs the average numbers of species recorded in mesic, submesic, subxeric, and xeric stands are: 5.2, 7.6, 6.2, 6.6. A submesic maximum corresponding to that for trees is thus suggested; but the shrub stratum in xeric sites may be more diverse than that in subxeric ones, often strongly dominated by *Kalmia latifolia*. Corresponding average numbers of herb species are: 19.1, 10.6, 7.1, 8.6. The herb stratum is thus richest in species, as well as of highest coverage, in mesic sites and

shows a secondary maximum of both diversity and coverage in xeric sites.

SIZES AND NUMBERS OF STEMS OF TREES

Stature and stem diameter of canopy trees in general decrease along the moisture gradient. In mesic sites canopy trees are more than 100 ft high and 3-4 ft or more in diameter; in xeric sites they are mostly 50-75 ft high and 1.0 to 1.5 ft in diameter. The number of tree stems per unit area in general increases along the gradient (cf. Ilvessalo 1921, Lutz 1932), in inverse relation to tree stature. The cove forests have mostly between 750 and 1000 stems per hectare from the 1-in. class up (except in stands of higher elevations where there are many small stems of *Acer spicatum*); the more xeric stands have mostly 2000 to 2500 stems per hectare. In part the increase in stem numbers toward xeric sites reflects the smaller stature and denser growth of canopy trees; but the numerous small stems in more xeric sites are predominantly made up of small-tree species. These small-tree species (*Carpinus caroliniana, Magnolia tripetala, Ostrya virginiana, Ilex opaca; Cornus florida, Betula lenta, Acer rubrum, Hamamelis virginiana, Clethra acuminata, Acer pensylvanicum; Robinia pseudoacacia, Oxydendrum arboreum, Sassafras albidum; Quercus marilandica*) are relatively unimportant in most mesic sites (as low as 1-2% of stems in some cove forests) and most xeric sites (10-15%). In submesic and subxeric stands of lower and middle elevations, however, the small-tree species comprise around 50% of stem numbers.

Trends in stand composition have been much affected by death of the chestnuts (*Castanea dentata*). In many submesic and subxeric stands chestnut formed 30-60% of the canopy stems, and death of the chestnuts both removed many of the largest stems from the stand and permitted heavy reproduction of other species. Effects of death of the chestnuts are most evident in chestnut oak-chestnut forests, in which maximum numbers of tree stems per unit area now occur, and in which 70% of the stems in some stands are now of the small-tree species.

Trends in tree sizes are illustrated in a family of curves (Fig. 6), in which steepness of slope reflects normal survival of small trees into larger size classes. The more xeric the site, the steeper the curve and the smaller the proportion of growth and survival into larger size classes. The oak-chestnut curve is altered by death of the chestnuts and increased reproduction of other species; the dotted curve is an interpolation of what might be expected otherwise. The hemlock forests are exceptional, for large sizes are even more heavily represented than in cove hardwoods forests. Fig. 7 indicates the effect of the same gradient on growth and survival in the populations of red maples (*Acer rubrum*).

SELF-MAINTENANCE OF STANDS

Curves such as those illustrated in Figs. 6 and 7 are expressions of the dynamics of stands, the manner in which the tree population is maintaining it-
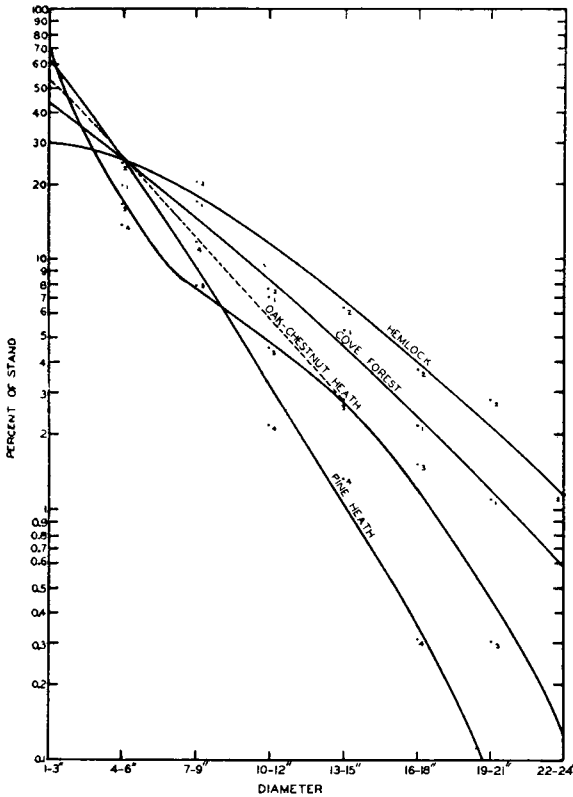
FIG. 6. Stem number-diameter curves for tree stands at middle elevations.
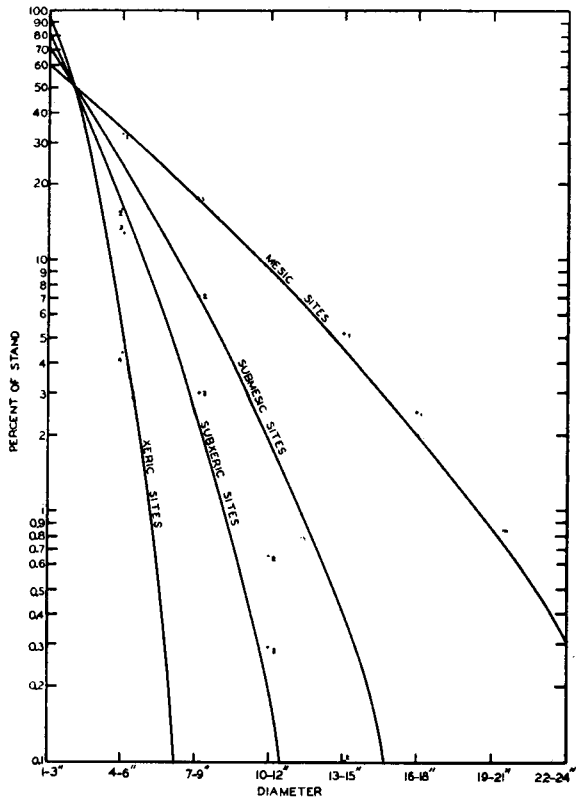
FIG. 7. Stem number-diameter curves for *Acer rubrum* in different sites.

self or failing to do so (Paczoski 1928, Meyer & Stevenson 1943). Meyer & Stevenson (1943) have indicated a relatively simple relation of diameter and stem number, which plots as a straight line on a log and linear graph like those of Figs. 6 & 7. Such a plot implies that growth rate and survival rate are largely constant with age; variation of growth rate with age introduces into log-linear plots the curvature to be observed in Figs. 6 & 7. A curve following the stand data more closely has been developed. Assuming $x = ar^w$ to be a fit for the stem number-age relation, and $w = (y + d)^c$ a reasonable approximation for the age-diameter relation, then the stem number-diameter relation becomes $x = ar^{(y + d)^c}$. In this x is the number of stems in a diameter class, a is the number of stems in the initial class, r is the survival ratio between successive classes, y is the middle diameter of the class, and d and c are constants relating diameter to age. (An alternative, purely empirical form which is less difficult to apply is the series a, ar, ar(r—b), ar(r—b)(r—2b) . . . , in which b is arbitrarily introduced to help the curve fit.)

The value of such curves is in the possibility of recognizing the self-maintaining, climax condition they describe. Many all-age and probably climax stands which have been analyzed show the basic form illustrated. It is also true that the continuous repro-

duction and replacement which these curves imply is by no means the only way climax stands can maintain themselves (Jones 1945, Whittaker 1953). Cyclic reproduction seems to occur in the Smokies pine stands (Part III). Other coniferous stands are "stagnant" in the sense that stems are concentrated in larger size-classes, with inadequate numbers of smaller stems to replace them if a constant survival ratio is assumed. Some of the stands more strongly dominated by *Tsuga canadensis* are of this form (cf. Meyer & Stevenson 1943), as are some of those of the spruce-fir forests, especially the high-elevation stands of *Abies fraseri*. It seems likely that reproduction in these stands is periodic, partial or complete destruction of the canopy permitting its replacement at irregular intervals, rather than continuously. If such limitations are kept in mind, however, analysis of all-age stand composition may contribute to the difficult problems of climax identification.

The basic similarity of the curves for different parts of the gradient may be observed in Fig. 6. Curves for individual tree species differ widely in slope from those for whole stands, but Fig. 7 (and the stand data for other species, Appendix C) indicate the same basic similarity. Apart from certain distortions of the curves clearly produced by death of the chestnuts, there is no evidence that any of

these undisturbed stands are changing toward other types. All, from cove forest to pine forest, have the self-maintaining properties of climax stands, so far as can be determined. Evidence of convergence toward a single climatic climax type is thus lacking.

HIGH-ELEVATION DECIDUOUS FORESTS

In the southwestern Smokies, outside the range of spruce-fir forests, deciduous forest types extend to the highest peaks (around 5500 ft or 1680 m). In order to study the distributions of plants in these deciduous forests above 4500 ft, a transect by site was arranged for 37 site-samples. The most mesic sites available at these elevations are gaps and concave slopes of north and northeast exposure, where forests of *Fagus grandifolia* mixed with other mesic trees occur. The south, southwest, and west exposures

TABLE 4. High-elevation deciduous forests, transect of exposure gradient by topographic sites for Eastern Forest System types above 4500 ft. Distributions of trees by percentages of stems in stand. Steps in gradient: 1, beech-mixed forests in sheltered north slopes; 2, gray beech forests in sheltered south slopes; 3, red oak-chestnut forests, open slopes; 4, white oak-chestnut forests, open south slopes; 5, grassy balds on exposed peaks.

Tree species	STATION				
	1	2	3	4	5
Acer spicatum	14	1	..	..	..
Aesculus octandra	11	2	x	..	—
Betula alleghenensis	10	3	x	..	—
Acer pensylvanicum	1	1	x	..	..
Acer saccharum	1	..	x	..	.
Tilia heterophylla	x	..	..	..	..
Sorbus americana	x	..	..	..	..
Cornus alternifolia	x	..	..	..	..
Fraxinus americana	x	..	..	..	..
Amelanchier laevis	4	1	1	x	—
Fagus grandifolia	50	81	7	..	—
Ilex montana	..	1	4	..	..
Prunus serotina	..	x	x	..	..
Halesia monticola	2	8	11	3	—
Quercus borealis	2	1	33	30	—
Tsuga canadensis	1	..	2	x	—
Acer rubrum	2	1	11	4	—
Hamamelis virginiana	..	..	10	..	..
Betula lenta	..	..	4	..	—
Vaccinium constablaei	..	..	1	..	..
Rhododendron calendulaceum	..	..	1	..	..
Magnolia fraseri	..	..	x	..	..
Magnolia acuminata	..	..	x	..	..
Oxydendrum arboreum	..	..	x	..	—
Castanea dentata (dead)	1	..	11	28	..
Sassafras albidum	..	..	x	1	—
Quercus alba	..	..	1	27	—
Robinia pseudoacacia	..	..	1	3	..
Nyssa sylvatica	..	..	..	2	..
Quercus velutina	..	..	..	1	..
Prunus pensylvanica	..	..	..	..	—
Pinus pungens	..	..	..	..	—
Pinus rigida	..	..	..	..	—
Pinus strobus	..	..	..	..	—
Liriodendron tulipifera	..	..	..	..	—
Total stems	823	643	1211	349	..
Site-samples used	11	8	9	4	6

x, present below 0.5%.   —, seedlings recorded.

are more xeric; and these may be grouped into three stages: sheltered south slopes and south-facing sides of gaps, supporting beech forests; more xeric open slopes supporting red oak-chestnut forests, and most xeric open south- and southwest-facing slopes, supporting red and white oak-chestnut or white oak-chestnut. Some most exposed summits of peaks, finally, are covered by grassy balds. Distributions of tree species may be observed along this five-stage transect (Table 4); distributions of shrub and herb species are not published here (see Note on Supplementary Publication).

Relations of tree species to the moisture gradient are in general the same at high elevations as at low ones. *Halesia monticola*, however, which is a highly mesic canopy tree at lower elevations is a submesic small-tree species at these highest elevations; this species comprises two population-types with separate distributional centers (see Part II and Appendix A). *Viburnum alnifolium*, *Cornus alternifolia*, and *Hydrangea arborescens* are major shrub species at the mesic extreme, *Vaccinium constablaei* and *Rhododendron calendulaceum* in the oak-chestnut forests. *Vaccinium constablaei* spans the whole of the gradient from north-slope beech stands to grassy balds, as do the less frequent species *Ribes rotundifolium* and *Rhododendron catawbiense*. Those shrub species (*Kalmia latifolia*, *Lyonia ligustrina*, *Gaylussacia baccata*, *Vaccinium vacillans*, *V. hirsutum*) which are most abundant in the forest-heath types at lower elevations are limited to the oak-chestnut forests and grassy balds in the transect. *Aronia melanocarpa* (Michx.) Ell. and *Viburnum cassinoides*, species which occur in the heath balds, were recorded in the transect only from the grassy balds.

At the mesic extreme, species of the mesic and high-elevation mesic herb groupings dominate the herb stratum; some of these species extend into south-slope beech stands and red oak-chestnut stands. *Carex aestivalis* is strongly dominant in south-slope beech stands and extends into both more mesic north-slope beech stands and less mesic red oak-chestnut forests. *Athyrium filix-femina* v. *asplenioides* is a major herb species of these high-elevation forests and extends along the gradient from north-slope beech stands to white oak-chestnut, as does *Medeola virginiana*. *Epigaea repens*, *Galax aphylla*, *Pedicularis canadensis*, *Pteridium aquilinum* v. *latiusculum*, and *Campanula divaricata*, species of more xeric forest types at lower elevations, are limited to the oak-chestnut stands in the high-elevation transect. Ecotypic populations of some forest herb species (*Angelica triquinata*, *Stellaria pubera*, *Rudbeckia laciniata*, *Prenanthes altissima*, *Houstonia serpyllifolia*, *Gentiana decora*) occur in the grassy balds with a variety of other species (see Part III). *Carex aestivalis* and other species centered in the south-slope beech stands and red oak-chestnut forests above 4500 ft have been grouped in a high-elevation submesic herb union.

Stratal trends are less clear-cut in these forests than in those of lower elevations. Tree-stratum di-

versity decreases from north-slope beech stands into south-slope ones, increases from these to a maximum in red oak-chestnut forests, and decreases again into white oak-chestnut. Coverage of the shrub stratum decreases from north-slope into south-slope beech stands, increases through red oak-chestnut to white oak-chestnut stands and the forest-edge of grassy balds, and is low in the grassy balds. Herb coverage increases from the north-slope to the south-slope beech stands, is lower in the oak-chestnut forests, and is near 100% in the grassy balds. As in forests of lower elevations, herb and shrub coverages are inversely related. Deciduous trees other than oaks decrease from mesic sites into submesic and subxeric ones, where oaks predominate; evergreen tree species are almost absent from these forests. In the shrub stratum non-ericaceous, deciduous shrubs prevail in mesic sites; but deciduous ericads (*Rhododendron calendulaceum* and *Vaccinium constablaei*) prevail in the oak-chestnut forests.

DISTRIBUTIONS OF SPECIES IN RELATION TO ELEVATION
MESIC SITES

Progressive change in composition of cove forests is indicated in the elevation transect of mesic sites (Table 5, Fig. 8). Species distributions show a rounded or bell-shaped form in most cases, overlap broadly, and have their centers and limits scattered along the gradient. Most major tree species occur throughout the elevations represented in the transect, but the sequence of their population centers from low elevations to high is: *Fagus grandifolia* ("white" population see Part II), *Liriodendron tulipifera*,

TABLE 5. Composite elevation transect in mesic sites, distribution of trees. All figures are percentages of total stems in station from 1-in. diameter class up.

Station	1*	2	3	4	5	6	7	8	9	10	11
Elevation, hundred feet	16	20	24	28	32	36	40	44	48	52	56
Tree species											
Fagus grandifolia	6	x	..	x	1	2	6	16	44	71	80
Tsuga canadensis	12	27	14	23	10	8	8	5	1	..	..
Halesia monticola	3	1	12	13	18	30	4	1	3	14	..
Fraxinus americana	x	1	2	2	1	6	1	1	..	..	..
Tilia heterophylla	6	3	3	15	15	20	22	4	x	..	..
Liriodendron tulipifera	1	8	2	4	1	x	x	..	..	..	..
Aesculus octandra	4	..	4	2	5	4	11	14	12	1	2
Betula alleghaniensis	1	4	5	16	11	8	8	10	10	2	1
Acer saccharum	4	2	4	2	12	5	12	4	1	3	x
Magnolia fraseri	2	5	3	5	2	x	..	x	x	.	..
Magnolia tripetala	1	..	1	..	..	..	..	..	..	.	..
Magnolia acuminata	..	2	1	..	x	1	1	..	..	.	..
Carpinus caroliniana	10	1	..	..	..	..	..	..	..	.	..
Ilex opaca	1	x	x	3	..	..	..	..	..	.	..
Carya cordiformis	2	x	..	..	1	x	x	..	..	.	..
Cladrastis lutea	..	1	..	..	4	..	..	..	..	.	..
Acer spicatum	..	..	..	x	1	4	17	30	7	2	13
Prunus serotina	..	..	..	..	..	x	1	1	..	1	..
Amelanchier laevis	..	.	..	..	..	..	..	1	3	2	3
Cornus alternifolia	..	.	..	..	..	..	..	1	x	.	..
Cornus florida	14	6	13	2	..	..	x	..	..	.	..
Quercus borealis & v. maxima	3	2	3	2	1	1	2	5	4	2	..
Amelanchier arborea	x	x	1	x	1	..	.	..	..	.	..
Betula lenta	8	10	2	3	5	2	x	2	1	.	..
Acer pensylvanicum	1	x	6	2	6	2	1	2	2	2	x
Acer rubrum	12	15	10	3	2	1	2	1	4	x	.
Ilex montana	x	1	..	x	x	2	..	x	6	1	.
Carya glabra	2	x	5	1	1	..	..	..	..	.	..
Carya tomentosa	..	..	x	..	..	..	..	..	..	.	..
Carya ovalis	x	..	.	..	..	..	..	..	..	.	..
Quercus prinus	2	1	3	1	1	..	x	..	..	.	..
Nyssa sylvatica	1	2	..	x	..	..	..	..	..	.	..
Castanea dentata (dead)	1	x	2	..	1	3	1	1	..	.	..
Quercus alba	1	2	..	..	..	..	..	..	..	.	..
Oxydendrum arboreum	2	4	4	1	x	..	x	..	..	.	..
Pinus strobus	x	2	x	..	..	..	..	..	..	.	..
Sassafras albidum	x	x	..	..	..	..	..	..	..	.	..
Robinia pseudoacacia	..	x	1	x	x	..	..	..	x	.	..
Sorbus americana	..	..	.	..	..	..	..	..	..	.	1
Total stems	600	841	518	639	793	429	358	468	646	360	406
Site-samples used	2	5	6	6	8	5	5	6	9	5	2

*Stations grouped at 400-ft. intervals (1450-1800 ft., 1850-2200 ft., etc.)
x, Present below 0.5%.
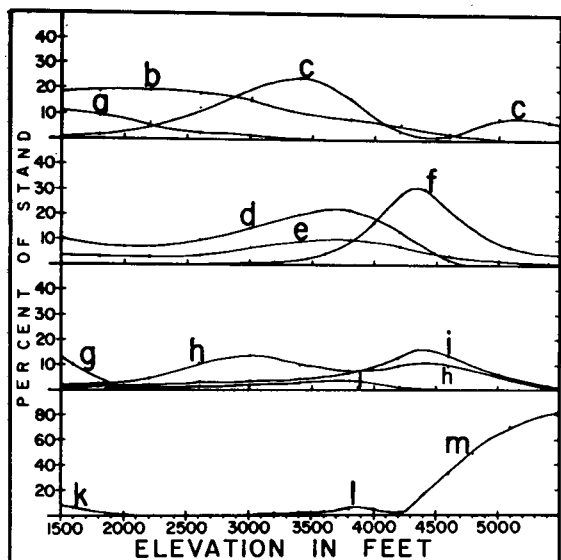
FIG. 8. Elevation transect in mesic sites, smoothed curves for tree species: a, *Liriodendron tulipifera*; b, *Tsuga canadensis*; c. *Halesia monticola*; d, *Tilia heterophylla*; e, *Acer saccharum*; f, *Acer spicatum*; g, *Carpinus caroliniana*; h, *Betula alleghaniensis*; i, *Aesculus octandra*; j, *Fraxinus americana*; k, white, l, red, and m, gray populations of *Fagus grandifolia* (based on data for 200-foot intervals).

Betula alleghaniensis, Halesia monticola, Acer saccharum, Tilia heterophylla, Aesculus octandra, and *Fagus grandifolia* ("red" and "gray" populations). The decline toward higher elevations of *Tsuga canadensis* and *Magnolia fraseri* does not reflect their true distributions (cf. Appendix A), for toward higher elevations these species are increasingly segregated into hemlock stands which were not included in the transect. The most significant change in composition of stands occurs at 4500 ft; at this elevation there is a relatively abrupt shift of dominance from other cove-forest species to gray beech (*Fagus grandifolia*). Some small-tree populations (*Acer spicatum* and *Amelanchier laevis*) are centered near 4500 ft along with *Aesculus octandra* and one population of yellow birches (*Betula alleghaniensis* or *B. lutea*). Trees and shrubs centered in the transition from cove forests to gray beech and spruce-fir forests

form the "ecotonal-mesic union" listed in the Summary of Distributional Groupings.

Among the mesic shrubs two species (*Euonymus americanus* and *Lindera benzoin*) are restricted to lowest elevations; certain others (*Cornus alternifolia* and *Viburnum alnifolium*) are centered around 4500 ft and form part of the "ecotonal-mesic" grouping. *Rhododendron maximum* and *Leucothoë editorum* occur at all elevations up to about 4500 ft; *Hydrangea arborescens* occurs from some of the lowest elevations to the highest recorded in mesic deciduous forests (5500 ft). No relatively abrupt change in the shrub stratum at 4500 ft is indicated in the transect.

Most of the mesic herb species occur over a wide range of elevations. Many of these species are centered in the more extensive mesic stands of higher elevations; and these species are of varied extents toward lower elevations. Among the major species some (*Dryopteris spinulosa* v. *intermedia, Trillium erectum* v. *albiflorum, Aster divaricatus*) occur at the lowest elevations sampled (1500 ft). *Caulophyllum thalictroides, Cimicifuga racemosa,* and *Laportea canadensis* extend downward to elevations around 2000 ft, *Oxalis montana* and *Impatiens pallida* to about 2500 ft, *Aster acuminatus* and *Monarda didyma* to about 3000 ft, *Streptopus roseus* and *Senecio rugelia* A. Gray to about 4000 ft, *Clintonia borealis* to about 4500 ft. (A species may occur locally outside the normal range of the population shown in the transects.) The last five species and others largely restricted to higher elevations form the "high-elevation mesic" union listed in the Summary of Distributional Groupings. In some sites a relatively abrupt change in composition of the herb stratum occurs at 4500 ft; *Carex aestivalis* becomes dominant in the gray beech stands of south-facing concave slopes at this elevation, and other species (*Angelica triquinata, Prenanthes altissima,* and *Carex* sp.) occur with it which are absent below 4500 ft.

SUBMESIC SITES

Distributions of some submesic tree species (Whittaker 1951; table 2) are indicated in Fig. 9. *Carya tomentosa* is largely restricted to elevations below 2500 ft, *Cornus florida* and the low-elevation population of *Carya glabra* (see Appendix A) to elevations below 3000 ft. The most significant change in the tree stratum occurs in the elevations between 3500 and 4000 ft, as *Quercus borealis* Michx. f. increases to become the major submesic tree at higher elevations. Some of the major shrubs of submesic sites (*Rhododendron maximum, Clethra acuminata, Gaylussacia ursina, Pyrularia pubera, Viburnum acerifolium, Calycanthus fertilis*) have their upper limits of distribution at elevations of 3500-4500 ft. *Rhododendron calendulaceum* and *Vaccinium constablaei* extend to elevations above 5000 ft. *Polystichum acrostichoides, Aureolaria laevigata,* and other major submesic herb species are confined to lower and middle elevations, but some (*Smilacina*
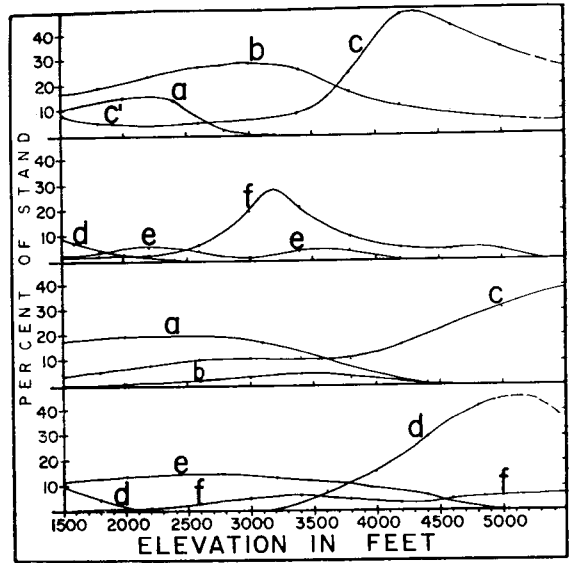
FIG. 9. Elevation transects in submesic and subxeric sites, smoothed curves for tree species. Above—submesic sites: a, *Cornus florida*; b, *Acer rubrum*; c and c', *Quercus borealis* and var. *maxima*; d, *Carya tomentosa*; e, *Carya glabra*; f, *Hamamelis virginiana*. Below—subxeric sites: a, *Quercus prinus*; b, *Sassafras albidum*; c, *Castanea dentata*; d, *Quercus alba*; e, *Oxydendrum arboreum*; f, *Robinia pseudoacacia*.

racemosa, Medeola virginiana, Pedicularis canadensis) extend to high elevations.

SUBXERIC SITES

One population of *Quercus alba* is largely restricted to elevations below 2500 ft, the other to elevations above 3500 ft (Table 6, Fig. 9). *Quercus prinus* is centered at lower elevations and has its normal upper limit below 4500 ft. *Castanea dentata* extends throughout the elevation range of the transect. At elevations below 3500-4000 ft *Quercus prinus* and *Castanea dentata* are dominant subxeric trees; above these elevations *Castanea dentata* shares dominance with the high-elevation populations of *Quercus alba* and *Q. borealis*.

Kalmia latifolia is the dominant shrub in the oak-chestnut heaths from lowest elevations to about 3500 ft; *Rhododendron maximum* and *Gaylussacia ursina* also occur. At elevations above 2500 ft *Rhododendron calendulaceum* and *Vaccinium constablaei* are important shrubs; at elevations above 3500 ft *Kalmia latifolia* shares dominance with these until Kalmia becomes a minor species in forests above 4000 ft. *Galax aphylla* is the most important subxeric herb at all elevations. *Chimaphila maculata, Campanula divaricata,* the submesic *Aureolaria laevigata,* and xeric *Epigaea repens* are major herb species in subxeric sites; and all extend through most of the elevations represented in the transect (1500-5000 ft).

XERIC SITES

Pinus virginiana is centered at low elevations and is scarce above 2500 ft; *Pinus pungens* is centered at

high elevations and is scarce below 2500 ft (Table 7, Fig. 10). *Pinus rigida* extends from lowest elevations to about 4500 ft, but is centered between 2500 and 3000 ft. *Quercus coccinea* is centered around 2500 ft and is important in middle- and lower-elevation xeric and subxeric sites; *Quercus marilandica* occurs only below 2500 ft. Some principal shrub species of xeric sites (*Vaccinium vacillans, Vaccinium stamineum, Kalmia latifolia*) extend throughout the elevation range of the transect (1500-4800 ft). *Gaylussacia baccata* and *Vaccinium hirsutum* are largely limited to elevations above 2000 ft, *Lyonia ligustrina* to elevations above 2500 ft, and *Pieris floribunda* to elevations above 4000 ft.

Some major herb species of xeric sites (*Pteridium aquilinum* v. *latiusculum, Epigaea repens, Gaultheria procumbens,* and *Galax aphylla*) occur at all elevations; but of these only *Pteridium* is important at low elevations. *Sericocarpus asteroides* is largely restricted to elevations below 2500 ft, *Baptisia tinctoria, Tephrosia virginiana,* and *Panicum* sp. to those below 3000-3500 ft, and *Andropogon scoparius* and *Coreopsis major* to those below 4000 ft. Shifts in dominance are gradual and changes in composition continuous from low elevations to high; and no well-defined sequence corresponding to that for xeric trees (*P. virginiana* and *Q. marilandica, P. rigida* and *Q. coccinea, P. pungens*) was recognized in the lower strata.
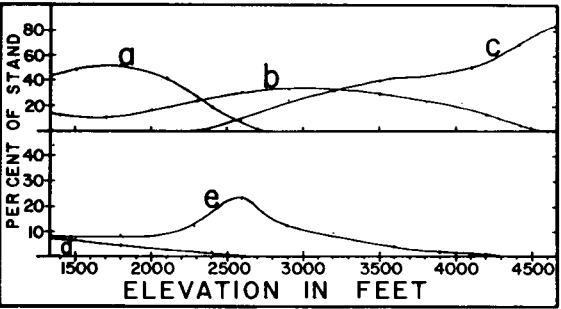

FIG. 10. Elevation transect in xeric sites, smoothed curves for tree species; a, *Pinus virginiana*; b, *Pinus rigida*; c, *Pinus pungens*; d, *Quercus marilandica*; e, *Quercus coccinea*.

TRENDS IN RELATION TO ELEVATION
GROWTH-FORMS

No trends in growth-form composition of communities as striking as those along the moisture gradient appear along the elevation gradient. Viewing the vegetation pattern as a whole, three growth-forms—abietine trees, ericaceous shrubs, and ground heaths—are of increasing importance toward higher elevations. Among the abietine trees, *Tsuga canadensis* is of increasing importance from low elevations to about 4500 ft; and *Picea rubens* and *Abies fraseri* dominate most forest stands above that elevation in the northeast half of the range. The great development of ericaceous shrub communities is one of the most characteristic features of the vegetation

of the Southern Appalachians, and heath strata occur in most vegetation types of open south-facing slopes and ridges. Viewing the ericaceous shrub complex as a whole; these shrubs are of increasing importance toward xeric sites and toward higher elevations, and have their maximum coverage and richness in species in the heath balds of steep, exposed slopes and ridges of high elevations in the area of spruce-fir forests. The stands with high development of a heath stratum have acid soils (Cain 1931), both in the more xeric sites and in the more mesic ones with Tsuga-Rhododendron stands. The ground heaths or evergreen ericaceous herbs (Epigaea, Gaultheria, and Chimaphila, with which the diapensiaceous Galax may conveniently be grouped) in general parallel the ericaceous shrubs in their greater importance toward more xeric sites and higher elevations. The ground heaths characteristically form the majority of herb coverage in the sparse herb strata under dense ericaceous shrub layers (except in the Tsuga-Rhododendron stands).

TABLE 6. Composite elevation transect in subxeric sites, distribution of trees. All figures are percentages of total stems in station from 1-in. diameter class up.

Station	1*	2	3	4	5	6	7	8	9	10
Elevation, hundred feet	16	20	24	28	32	36	40	44	48	52
Tree species										
Tsuga canadensis	1	1	1	x	..	x	..	..	1	..
Liriodendron tulipifera	1	..	2	1	x	x	..	x	..	..
Halesia monticola	..	x	2	x	2	x	2	..	1	10
Magnolia fraseri	..	x	3	1	2	x	..	..	..	..
Acer saccharum	..	x	..	..	..	..	..	..	..	..
Magnolia acuminata	..	..	x	x	..	..	..	..	..	..
Ilex opaca	..	..	x	..	..	..	..	..	..	..
Betula alleghaniensis	..	..	..	x	..	..	..	..	..	..
Amelanchier laevis	..	..	..	..	x	x	..	..	..	I
Acer rubrum	20	25	31	26	27	13	13	10	7	3
Acer pensylvanicum	..	x	1	1	..	..	..	..	..	..
Cornus florida	5	9	2	2	..	..	..	..	..	..
Amelanchier arborea	x	..	..	x	..	..	..	x	..	..
Betula lenta	x	..	2	1	1	..	..	..	..	..
Carya glabra	4	2	.	2	5	4	..	6	..	..
Carya tomentosa	3	1	..	x	1	..	..	..	..	..
Carya ovalis	..	1	..	..	..	..	..	..	..	..
Quercus borealis & v. maxima	1	3	3	3	2	13	15	23	20	31
Hamamelis virginiana	3	..	3	8	2	..	..	5	..	..
Pyrularia pubera	..	x	..	x	..	x	..	..	..	..
Clethra acuminata	..	.	..	1	1	..	..	..	..	..
Ilex montana	..	.	..	x	..	..	..	..	..	..
Aralia spinosa	..	.	..	x	x	..	..	..	..	..
Nyssa sylvatica	1	2	2	3	3	2	..	..	10	..
Oxydendrum arboreum	15	10	18	9	14	16	15	3	..	..
Quercus prinus	24	18	14	18	17	15	19	..	..	..
Quercus velutina	4	1	x	2	2	1	1	..	4	..
Quercus alba	5	4	..	..	x	9	14	30	42	..
Quercus stellata	.	..	.	..	x	..	..	..	..	..
Sassafras albidum	1	x	2	1	4	4	1	1	..	..
Robinia pseudoacacia	1	x	3	3	5	7	6	..	4	7
Castanea dentata (dead)	5	6	10	12	10	12	0	23	12	47
Pinus strobus	..	10	..	..	..	..	..	..	..	..
Quercus coccinea	4	3	1	2	1	1	..	..	..	..
Pinus virginiana	2	3	..	..	..	..	..	..	..	..
Pinus rigida	..	x	1	2	x	1	1	..	..	..
Pinus pungens	..	..	..	1	..	x	4	..	..	..
Total stems	290	620	690	689	559	606	139	346	84	89
Site-samples used	5	5	5	7	8	8	2	3	2	1

*Stations grouped at 400-ft. intervals (1450-1800 ft., 1850-2200 ft., etc.)
x, Present below 0.5%.

TABLE 7. Composite elevation transect in xeric sites, distribution of trees. All figures are percentages of total stems in station from 1-in. diameter class up.

| Station.... | 1* | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
Elevation, hundred feet....	14	17	20	23	26	29	32	35	38	41	44	47
Tree species												
Tsuga canadensis			1									
Liriodendron tulipifera	2											
Liquidambar styraciflua	x											
Amelanchier laevis												7
Cornus florida	x	x										
Quercus borealis										1	3	
Carya glabra	x											
Carya tomentosa	1	x	x									
Carya ovalis				x								
Hamamelis virginiana									1	2		3
Acer rubrum	6	7	6	5	14	7	10	2	9	3	14	1
Quercus falcata	1											
Stewartia ovata	x											
Pinus strobus			10	2							1	
Robinia pseudoacacia				x				x	1	2		1
Sassafras albidum	1						1	2	x			
Nyssa sylvatica	4		2	4		3	3	2	3	4	3	1
Oxydendrum arboreum	8	5	9	6		2	4	1	2	2	2	
Castanea dentata (dead)	5	1		x	1	1	3	2	1	1		
Quercus velutina		2	x	2								
Quercus alba	1	3										
Quercus prinus	x	x	2	2	14	3	7	6	11	7	11	
Quercus marilandica	7		8	2								
Quercus coccinea	10	12	2	8	26	14	9	2	5	1	2	
Pinus virginiana	40	56	48	38	1	1						
Pinus rigida	13	12	10	30	34	28	36	16	39	16	10	
Pinus pungens					10	41	28	65	27	62	55	87
Total stems	301	217	212	366	88	572	378	410	246	362	122	90
Site-samples used	2	4	2	5	2	5	3	5	3	3	2	1

*Stations grouped at 300 ft intervals (1250-1500 ft , 1550-1800 ft., etc.)
x, Present below 0.5%.

TREE STATURES AND STRATAL COVERAGES

The transect data do not show the relatively slight decrease in tree statures and coverages toward higher elevations which may occur below 4500 ft. Tree sizes in stands above this elevation are distinctly smaller than in the deciduous and hemlock forests below it. Importance of the small-tree species decreases toward higher elevations, except in mesic stands. In submesic and subxeric stands below 3500 ft the small-tree species make up 45-70% of stem numbers, between 3500 and 4500 ft 30-50%, and above 4500 ft in deciduous stands 10-45%. Shrub coverages (Fig. 11) in mesic deciduous forests are lower above 3000 feet than below, except as the ecotonal-mesic shrub grouping forms a secondary maximum at elevations around 4500 ft. Maximum shrub coverages in submesic and subxeric stands occur at middle elevations (around 3000 ft); but in xeric stands the heath stratum increases in coverage from low elevations to high. In all four transects herb coverages increase toward higher elevations. Although the inverse relation of shrub and herb coverage is suggested in three of the transects (Fig. 11), the parallel trends of the two strata in xeric sites provide an exception to this relation.

Community structure changes profoundly along the moisture gradient through three or four physiognomic types; but major physiognomic types recog-
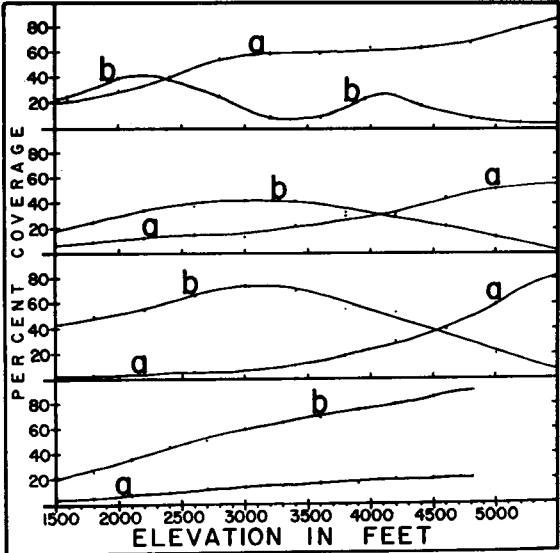

FIG. 11. Elevation transects, curves for undergrowth coverages: a, herbs; b, shrubs. From top to bottom, in mesic, submesic, subxeric, and xeric sites.

nized here (mesic deciduous forests, abietine forests, oak forests, and pine heaths and forests) extend from the lowest elevations to 4500 ft and above. Floristic

change also is more conspicuous along the moisture gradient than the elevation gradient. No species spans completely the moisture gradient, but many extend from lowest elevations to 4500 ft and above. Within the limits of the transects so far described and excluding the spruce fir forests, community composition and structure change more radically along the moisture gradient within a single elevation belt than with a change of elevation from 1500 to 4500 or 5500 ft.

DIVERSITY AND ENVIRONMENTAL FAVORABLENESS

Species diversity of the tree stratum decreases from low elevations to high (Fig. 5); the trend is most apparent within a single moisture-class of stands. Tree-species diversity is maximal in the cove forest transition of low elevations and mesic-sub-mesic sites, and decreases with any departure from these stands toward more or less mesic conditions or higher elevations. It is in the cove forest transition that species of the cove-forest or mesic grouping and the oak-forest or intermediate grouping are most highly mixed; in the interpretation of Braun (1950) the cove forest transition forms part of the Mixed Mesophytic Association, from which some other, less diverse stand types may be said to "segregate." The more limited data on undergrowth diversities are based on averaging the numbers of species recorded per sample in transects of different elevation belts. Herb strata show some evidence of increasing diversity toward higher elevations; average numbers of species for the elevation belts 1500-2500, 2500-3500, 3500-4500, 4500-5500 ft (the last for deciduous stands only) are 12.8, 15.5, 16.8, and 18.8. Corresponding values for the shrub strata (6.1, 7.9, 7.7, 7.0) suggest only that shrub strata may be less rich in species, on the average, at lower elevations than at middle and higher ones.

Two properties of natural communities, diversity and productivity, may be thought in general correlated with "favorableness" of environment. Thus Finnish authors have found parallel trends of decreasing productivity and decreasing numbers of plant species along ecological series of site-types (Cajander 1909; Ilvessalo 1921, 1922; Linkola 1924). Data from the Smokies indicate how much more complex than this the relations of these community properties to one another, and presumptive favorableness of environment, may be.

Major trends in the Smokies are consistent with the general tendency toward increasing stature and differentiation into strata of communities with increasingly favorable conditions of moisture, temperature, and nutrients (Dansereau 1951; Whittaker 1953, 1954a). Stature and coverage of canopy trees in general decrease, while the development of undergrowth strata increases, toward most xeric sites and highest elevations. Relative development of herb, shrub, and moss strata are complexly related to one another as well as to the tree stratum and environmental "favorableness," however. Diversity trends in different strata do not parallel one another; and, with

the possible exception of the herb stratum, maximum diversities occur not in the "most favorable" conditions of the cove forests but in the intermediate ones of cove forest transition or oak-chestnut forest. Within a given stratum or community-fraction diversity and productivity (or coverage) may not run parallel (Whittaker 1952), although they often appear partially correlated.

It was suggested in the previous study (Whittaker 1952) that interpretations based on favorableness of environment may have little meaning unless the community property or group of organisms for which environments are to be favorable is specified. Data of the present study may further indicate that "favorableness" of environment is relative to the group of organisms under consideration, and that for a given group diversity and productivity may define different centers of maximum "favorableness."

SPRUCE-FIR FORESTS

In studying subalpine forests of the Smokies, site-samples from three elevation belts (spruce forests from 4500 to 5400 ft, spruce-fir forests from 5500 to 6100 ft, and fir forests from 6200 ft up) were arranged in topographic transects similar to the one for high-elevation deciduous forests. Sites were grouped along the moisture gradient in five stages—moist valley sites, north slopes and flats, intermediate east and west slopes, xeric south and southwest slopes, and exposed ridges. Table 8 is so arranged as to form a grid of transects covering the spruce-fir forest pattern; distributional relations to the topographic gradient within an elevation belt and to elevation within a given type of site may be observed in the table. Data on species distributions have been compressed for presentation into stratal unions as follows:

1. Mesic herb union (*Solidago glomerata* Michx., *Senecio rugelia*, *Chelone lyoni* Pursh, *Diphylleia cymosa*, *Aster acuminatus*, *Trillium erectum*, *Streptopus roseus*, *Rudbeckia laciniata*, etc.). Some species of the low-elevation mesic herb union (*Eupatorium rugosum*, *Impatiens pallida*, *Cimicifuga racemosa*, *Aster divaricatus*) are of wide extent in subalpine forests and have been grouped here with the high-elevation union.

2. Deciduous trees other than *Sorbus americana* Marsh. (*Betula lutea*, *Amelanchier laevis*, *Acer spicatum* and *A. pensylvanicum*, and trees of the cove forest grouping).

3. Ground moss unions, described in more detail by Cain & Sharp (1938).

4. Low-herb layer—*Oxalis montana* with *Clintonia borealis*.

5. Mesic fern union, with *Dryopteris spinulosa* v. *americana* most important.

6. Low shrub union—*Vaccinium erythrocarpum* with *Menziesia pilosa*.

7. Deciduous high shrubs (ecotonal-mesic union) —*Viburnum alnifolium*, with *Cornus alternifolia* and *Sambucus pubens*.

8. High heath union—*Rhododendron catawbiense*

TABLE 8. Transect data for subalpine forests. Percentages of coverage or stems for stratal groupings in different sites along the moisture gradient in five steps: 1, most mesic valley and sheltered-slope sites; 2, open north-facing slopes; 3, east and west slopes; 4, south-facing slopes; and 5, ridges. Figures are based on averages from several site-samples of stem numbers and estimated coverages.

Elevation belt....	RED SPRUCE FORESTS 4500-5500 ft.					SPRUCE-FIR FORESTS 5600-6200 ft.					FRASER FIR FORESTS above 6200 ft.				
Site.............	1	2	3	4	5	1	2	3	4	5	1*	2	3	4	5
Plant species or union—Mosses (*Hylocomium splendens* etc.), coverage %.................	5	24	17	8	0	30	55	48	13	2	..	90	85	50	5
Low herb (*Oxalis montana*).....................	2	55	29	23	0	25	54	25	5	0	..	47	8	3	0
Fern (*Dryopteris spinulosa* v. *americana*)........	30	45	22	8	0	20	39	12	5	0	..	37	1	1	0
Low shrub (*Vaccinium erythrocarpum*)...........	2	8	5	4	0	5	14	4	5	0	..	5	2	2	0
High shrub (*Viburnum alnifolium*)..............	20	18	7	4	0	20	13	9	1	0	..	2	1	0	0
Total, "five-story undergrowth"..............	59	150	80	47	0	100	175	98	29	2	..	181	97	56	5
Mesic herb grouping.........................	50	5	1	1	0	40	3	1	1	0	..	2	1	1	0
High heath (*Rhododendron catawbiense* and R. *carolinianum*)........................	0	0	5	40	84	0	0	10	30	70	..	0	0	37	88
Picea rubens, % of conifers.....................	40	33	48	79	100	10	12	7	40	55	..	1	2	4	12
Deciduous trees (except *Sorbus americana*), % of stems........................	30	8	13	7	14	15	13	11	4	5	..	2	1	0	2
Sorbus americana, % of stems.................	0	0	0	0	0	1	1	3	0	0	..	8	8	3	2

*Not observed.

and *R. carolinianum* Rehd., with *Kalmia latifolia, Vaccinium constablaei,* and other species of the heath balds.

9. Mountain ash (*Sorbus americana*), a mesic small tree of highest elevations.

STRATAL DISTRIBUTIONS

In the tree stratum composition of subalpine forests changes more conspicuously with elevation than along the moisture gradient. At 5000 ft on south-facing slopes 100% of the conifers may be spruce (*Picea rubens*); above 6300 ft 100% may be fir (*Abies fraseri*), while intermediate sites have mixed stands. Spruce and fir cross in numbers of stems at around 5600 ft if exposure differences are averaged out. The change in canopy dominance occurs higher, near 6000 ft, because of the greater size of spruce. Elevation alone, however, does not determine proportions in the mixture of these two dominants; at any elevation fir increases relative to spruce toward more mesic sites (Table 8).

Sorbus americana is confined to high elevations and is centered in the more mesic forest stands above 6200 ft. *Fagus grandifola* ("gray" population) dominates stands in the concave slopes of "gaps" in the area of spruce-fir forests, and it occurs also to a limited extent in stands dominated by spruce and fir. All other deciduous tree species which occur in the spruce-fir forests are at least equally important in deciduous stands below 4500 ft. The high-elevation population of yellow birch (*Betula lutea*) is centered in the transition from cove forests to spruce forests at 4500 ft, but is of wide extent at higher elevations as the major deciduous tree species of spruce-fir forests. Yellow birch and other "ecotonal-mesic" species (*Acer spicatum, Amelanchier laevis, Cornus alternifolia*) decrease in importance with departure from their centers in mesic stands near 4500 ft to-

ward higher elevations and less mesic sites. The cove-forest tree species which occur in subalpine forests (*Aesculus octandra, Tilia heterophylla, Halesia monticola, Acer saccharum, Fraxinus americana,* and the submesic *Acer pensylvanicum*) are similarly related to the gradients; their numbers decrease toward higher elevations and more xeric sites.

Three shrub unions with different distributional relations have been distinguished in the spruce-fir forests. The distributional relation of the deciduous high shrubs of the ecotonal-mesic union is the same as that of *Betula lutea* and *Acer spicatum*; their importance declines with departure from mesic stands near 4500 ft. The shrub species of the group differ in extent and importance in the spruce-fir forest pattern; *Viburnum alnifolium* is the most wide-spread and much the most important of them. The low-shrub union dominated by *Vaccinium erythrocarpum* is centered in middle elevations of the spruce-fir forests, rather than lower ones, and in mesic sites (north-facing slopes and flats) other than the valley sites where the ecotonal-mesic species are most important. The high heath union is most important on ridges, but the heath species also occur with lower coverage in south-slope stands and on some intermediate slopes. Of these shrub species *Vaccinium constablaei* occurs more widely in spruce-fir forests than the heath dominants *Rhododendron catawbiense* and *R. carolinianum.*

In valley sites the mesic herbs strongly dominate the herb stratum. Most of the herb species listed are of wide extent in spruce-fir forests (other than those of most xeric sites), but their coverage is low outside valleys. The moss stratum, the low-herb stratum, and the fern stratum are, in contrast, centered in stands of north slopes and flats. These three unions also are of wide extent through the spruce-

fir pattern and decrease in importance along the
moisture gradient from north slopes and flats to south
slopes and ridges.

Layered structure seems especially evident in some
vegetation of high elevations and the far north; the
same strata are to be distinguished elsewhere but
are more obvious and give a greater impression of
distinctness in such vegetation as the spruce-fir pat-
tern in the Great Smoky Mountains. Analysis shows
that the various stratal unions, and the species which
make up a given union, are differently distributed.
Among the undergrowth unions recognized, however,
several are of wide extent in the spruce-fir pattern
and are of decreasing importance from more mesic
sites toward more xeric ones. Five unions dominate
the undergrowth of north-, east-, and west-facing
slopes and flats, each of the unions being strongly
dominated by a single species. Together they form
a five-story undergrowth complex (moss, *Hyloco-
mium splendens;* low herb, *Oxalis montana;* fern,
Dryopteris spinulosa v. *americana;* low shrub, *Vac-
cinium erythrocarpum;* high shrub, *Viburnum alni-
folium*) which is most characteristic of the spruce-
fir forests of the Smokies, although other under-
growth unions predominate in most mesic and in
more xeric sites.

TRENDS

Major structural features of the spruce-fir pattern
along the moisture gradient are shown in Fig. 12,

in contrast with the pattern of forests at lower ele-
vations. Deciduous trees decrease in importance from
valleys toward xeric sites; ericaceous shrubs increase
in importance from intermediate sites to ridges.
Herb coverage and species diversity decrease along
the moisture gradient. There is thus a trend of de-
creasing importance of non-evergreen elements in all
three strata toward more xeric sites. Valley spruce-
fir forests resemble high-elevation cove forests in
most respects, even though the canopy is dominated
by conifers. At the xeric extreme, however, ever-
green elements are strongly dominant both in canopy
and in the dense ericaceous shrub stratum, and ground
heaths predominate in the sparse herb stratum.

Along the elevation gradient within the spruce-fir
forests, moss coverage increases strongly from lower
elevations toward higher ones (Table 8). Coverage
of shrubs other than the heath is in general lower at
highest elevations, but undergrowth coverage trends
with elevation are not otherwise conspicuous. Repre-
sentation of deciduous trees other than *Sorbus amer-
icana* decreases toward higher elevations, and (since
Sorbus is a small-tree species) the fraction of decidu-
ous trees in the canopy decreases toward higher ele-
vations. Species diversity of the tree stratum de-
creases toward higher elevations, and the same is
probably true of other strata of vascular plants.

The most conspicuous change in canopy of sub-
alpine forests is the increase of fir and decrease of
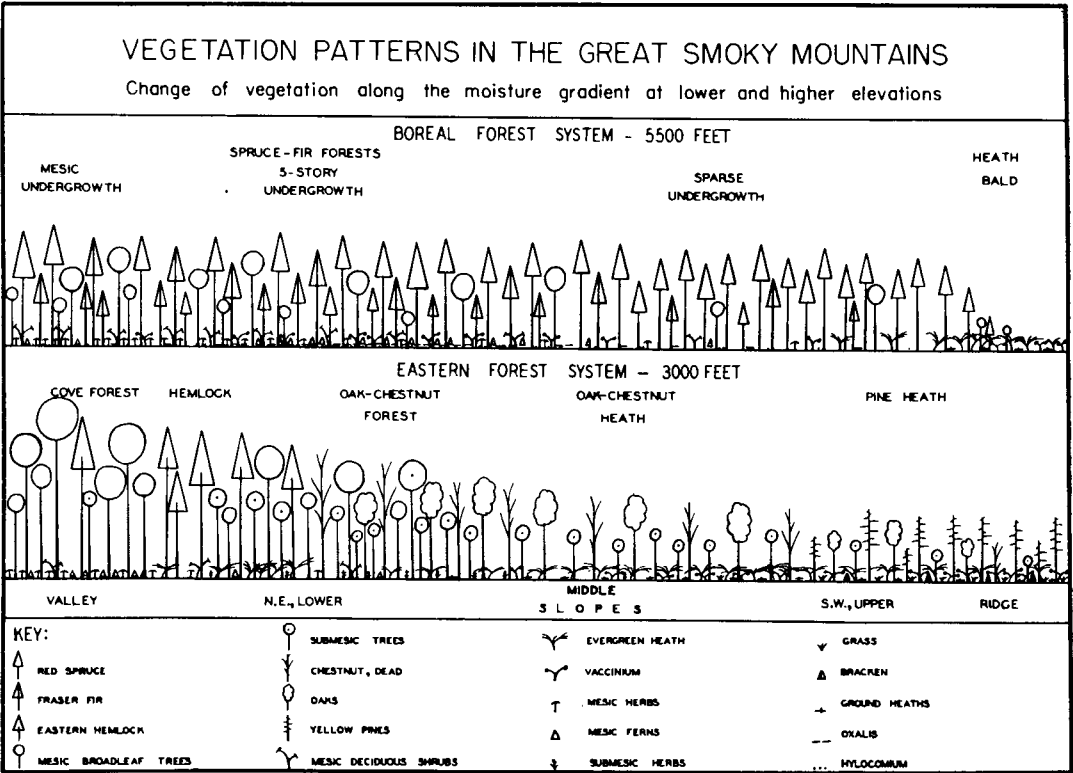spruce toward higher elevations, but the most con-

FIG. 12. Vegetation patterns along the moisture gradient.

spicuous change in the undergrowth is that along the moisture gradient. The canopy and understrata thus seem at cross purposes, as it were, in the patterning of these forests. Extensive patterning, or change in community composition and structure in relation to environmental gradients, appears in these subalpine forests, as in the deciduous, pine, and hemlock forests of lower elevations. Differences in site along the moisture gradient at low elevations are reflected as much in species and growth-form composition of the canopy as of the undergrowth. In the spruce-fir forests, however, as in other subalpine and boreal forests, canopy trees are broadly tolerant of differences in sites; and site differences are reflected primarily in undergrowth.

RELATIONS OF SPECIES TO UNIONS AND ASSOCIATIONS

A final group of questions to be considered relate to the nature of community-units. The transects offer evidence bearing on three aspects of the community problem: continuity and discontinuity of stands and community-types, naturalness or arbitrariness of species groups, and relation of dominant species to minor species and undergrowth.

CONTINUITY OF VEGETATION TYPES

Three relative discontinuities affect the vegetation pattern described—those between cove forests and beech-gap stands of south-facing slopes, between grassy balds and the forests surrounding them, and between heath balds and spruce-fir forests. Apart from these, community-types are continuous with one another. The transect data thus suggest that some vegetation types are relatively discontinuous with one another along continuous gradients of "primary" environment, but that many vegetation types exist within a continuum of populations (cf. Whittaker 1951, 1952; Curtis & McIntosh 1951; Brown & Curtis 1952). Problems of continuity and discontinuity will be further discussed in terms of "gradation" and "zonation."

NATURE OF SPECIES GROUPINGS

An alternative approach to the recognition of vegetation types is through groups of species which are similarly distributed and have their boundaries together, presumably at the boundaries of vegetation types. Inspection of the transect data reveals no such groupings of species with closely similar distributions, with the possible, partial exception of the discontinuous types already mentioned. In general, no two species have quite the same distribution in a set of transects for elevation, or for the moisture gradient. Dissimilarity of distributions is even more evident when species are followed through both sets of transects or compared in the population charts of Appendix A. Even such familiar pairs of "associates" as *Tilia heterophylla* and *Aesculus octandra*, *Quercus prinus* and *Castanea dentata*, *Quercus alba* and *Carya glabra* are distributed quite differently, especially in relation to the elevation gradient. Other pairs of species (*Tsuga canadensis* and *Magnolia fraseri, Pinus rigida* and *Quercus coccinea, Abies*

fraseri and *Sorbus americana*) show varying degrees of distributional similarity. It was not found possible to define vegetation types through groups of tree species having closely similar distributions in the transects and nomograms. All species groupings used in the present work are considered to be primarily *arbitrary* groupings of species with different distributions.

The moisture classes are species groupings which correspond in part to traditional associations in the American sense—mixed mesophytic, oak-hickory, oak-chestnut, and pine-oak (cf. Braun 1950). Species of the oak-hickory and oak-chestnut associations do not fall naturally into submesic and subxeric classes, however. *Quercus borealis* v. *maxima* and three hickory species may be regarded as "submesic"; but other major oak species of the oak-hickory forests (*Q. alba* and *Q. velutina*) are slightly more xeric than *Castanea dentata* and *Quercus prinus* and must be classed with these as "subxeric." Although *Castanea dentata* and *Quercus prinus* are subxeric, the third dominant of oak-chestnut forests (*Quercus borealis*) is distinctly less xeric and must be classed as "submesic." One of the major species of the pine forests (*Quercus coccinea*) is intermediate in its relation to the xeric pine and the subxeric oak-chestnut groupings. Species of the Mixed Mesophytic Association of Braun (1950) are widely scattered along the moisture gradient and have been classed with the mesic, submesic, and subxeric groups. There is thus no clear and simple relation between the moisture classes (and other groupings attempted by the author) and the regional vegetation types or "associations" in the sense of American authors.

The essential problem may be whether the groupings of species used by ecologists are "arbitrary" or "natural," and some definition of these expressions is necessary. Any classification of stands or of species is a product of interaction (or of "transaction" in the sense of Dewey & Bentley 1949) between vegetation and ecologist through observations and sample data. A classification is, like human knowledge in general (Carmichael 1930: 182-200, 223), a joint product of the observer and the observed. Distributional relations of species in the field set limits on the groupings which an ecologist will attempt; some combinations of species which rarely occur together are obviously "unnatural." On the other hand, a combination of species which do occur together, although "natural" in the sense that it does not violate obvious distributional relations, may be "arbitrary" in the sense that this combination is only one which the ecologist has chosen to recognize from the many which are equally justified by distributional relations of species.

If groups of species which have closely similar distributions occur, clearly separated from other such groups of species, then the ecologist's choice of distributional groupings is narrowly restricted by distributional relations of species in his data. The distributional groupings which he recognizes should be

"natural" in the sense that they are clearly determined by the data in his possession. If species are quite variously distributed, forming no well-defined groups distinctly separate from other groups, the groupings recognized are free or "arbitrary." They are not clearly determined by the data, but represent one among a series of groupings which might be recognized without violating the more evident distributional relations of species in the data. Relative arbitrariness and naturalness of species groupings may thus depend on the degree to which the ecologist is clearly guided and limited in his choice of groupings by actual distributional relations of species in the field and in adequately representative sample data.

The basis of groupings in the present study is the location of centers of maximum population level for species along gradients, and the problem of naturalness *vs.* arbitrariness of groupings may be further defined on this basis. Various manners in which species population centers might be related to one another may be conceived in terms of degrees of clustering along a hypothetical gradient from 0 to 10: (1) Species populations are absolutely clustered, so that species of one group are centered at 2.0 and those of another at 8.0, and none are centered between these points. (2) Species populations are relatively clustered along the gradient, so that in the sequence of their centers along the gradient (1.3, 1.6, 2.0, 2.3, 3.5, 6.0, 7.2, 7.5, 8.1, 9.0) groupings may be recognized, even though the centers are somewhat scattered and some species are intermediate. (3) Species are distributed irregularly along the gradient (0.9, 1.4, 2.1, 3.5, 4.2, 5.5, 6.0, 7.3, 8.1, 9.0), and the spacing of their centers approaches randomness. (4) Distribution of centers along the gradient is less irregular than randomness would require, and the centers are approximately equidistant from one another (1.0, 2.0, 3.0, 4.0....).

The problem of relative "naturalness" of species groupings may thus be approached through degrees of clustering suggestive of the degrees of "contagion" or clustering of individuals in a stand. Condition (1) would imply that associations of species are "natural" groupings (though community-types might still be continuous with one another). Condition (2) would define varying degrees of relative "naturalness" *vs.* relative "arbitrariness" of groupings which would not necessarily represent either obligate associations of species or discrete community-types. Groupings of species distributed according to conditions (3) and (4) would be primarily arbitrary. The transect data and nomograms (Appendix A) apparently exclude conditions (1) and (4) for the distributions of species in the Smokies. The data show no evidence of high degree of clustering according to condition (2). No sensitive statistical tests are available at present to distinguish condition (3) from low degrees of clustering in condition (2) and slight departure from randomness toward the regularity of condition (4). The impres-

sion given by the transect data is one of approximate randomness, when the distributions of many species are being compared (see Whittaker 1951, Fig. 1).

The moisture classes of trees are consequently regarded as arbitrary groupings, justified by their usefulness rather than by any correspondence to distinct clusters of species existing in the field. The locations of population modes along the moisture gradient provide a basic sequence of species which should not be violated in forming the groupings; but within these limits various ways of grouping species seem equally reasonable. When major species only are considered, these sometimes appear to have a low degree of clustering in the moisture-gradient transects. Thus in the transect for elevations between 2500 and 3500 ft (Table 2), six major species (*Acer saccharum, Tilia heterophylla, Aesculus octandra, Betula alleghaniensis, Halesia monticola,* and *Tsuga canadensis*) have their centers in steps 1 to 3 of the transect. Four major species (*Quercus borealis, Acer rubrum, Castanea dentata,* and *Quercus prinus*) are centered in steps 6 to 9, while the two pines (*P. rigida* and *P. pungens*) are centered in step 12. It is thus possible to regard these as three "natural" groups along the gradient if the intermediate positions of other, minor species and one major one (*Quercus coccinea*) are not considered. Such groupings of dominants are, at best, weak or of low degree among the trees of the Smokies. It may also be observed that the more attention is limited to a few major species, the more the irregularity inherent in approximate randomness may give an appearance of clustering which is not supported by the distributional relations of other species.

Distributions of some species affected by vegetational discontinuity suggest a degree of natural clustering. The ecotonal-mesic group of shrubs and trees are centered in mesic sites near 4500 ft. Although no two of the species are otherwise alike in distribution (see Table 5 and Fig. 13), the group may form a "natural" cluster. Other transitional groupings will be discussed below in relation to ecotones (Part II). Some species of other discontinuous types, notably the grassy balds, may form natural clusters in relation to the rest of the vegetation pattern of the Smokies. The data for the Smokies thus suggest: (1) Natural clustering of species is probably absent or of low degree in most of the vegetation pattern. (2) Recognized types and associations are for the most part definable by single dominant species or by distributional overlaps of two or more dominant species, but not by natural clusters. (3) A tendency toward natural clustering may exist among some of the species of some communities, at least if the distributions of species concerned are considered only within the limits of the Great Smoky Mountains. Such relative clustering as may occur in these cases involves the relatively discontinuous communities of more "extreme" environments and the transitions between these and other communities.

DOMINANCE IN RELATION TO COMMUNITY COMPOSITION

The tradition of regarding dominants as the keys to natural communities is well established in American ecology. The American association was defined by Nichols (1923) as essentially constant in floristic composition, at least with regard to dominant species; and associations of American authors are in general defined by dominant species or genera. It was considered by Clements that dominant species determined the conditions of life for other species, characterized the community-type, and indicated the habitat of the community (Clements 1928:236, 253; Weaver & Clements 1938:91, 478; Clements & Shelford 1939:238-239); dominants were the master-keys to the understanding of communities. If such is the case, the effects of dominant species on conditions of life for other species should be clearly shown in the distributions of undergrowth and minor canopy species. Boundaries of other species might be expected in general to coincide with the distributional limits of dominants and the boundaries of the community-types they define. The transect data provide means of evaluating the hypotheses that (1) Dominant species through effects on conditions of life determine the distributions of other species, and (2) dominant species characterize community-types which are relatively homogeneous in floristic composition.

One of the significant findings of the transect analysis is the manner in which floristic composition of communities changes continuously through and between many of the vegetation types defined by dominance. In the elevation transects of submesic and subxeric sites, the dominant species of oaks change at around 3700 ft, but the limits of minor canopy species and undergrowth species are scattered through the whole of the transect rather than concentrated around 3700 ft. In the elevation transect of xeric sites, dominant pine species change at elevations around 2300 and 3300 ft; but limits of other species are again scattered along the gradient rather than concentrated at these elevations. In the deciduous cove forests, various combinations of dominant species occur which are not, so far as could be determined, reflected in corresponding combinations of major undergrowth species or ·in total undergrowth composition. In the gray beech forests and hemlock forests, two quite different, but continuously intergrading types of undergrowths occur under canopies dominated by the same species. In spruce-fir forests, rates of change of canopy and undergrowth along gradients, and directions of most conspicuous change are different; and a variety of undergrowth subtypes or site-types occur under canopies dominated by the same species. Quite different undergrowths can occur under similar canopies and closely similar undergrowths under quite different cinioideae.

Distributions of undergrowth species do not appear closely related to those of dominant species. Association of dominant species with other green plant species is not obligate, and almost all undergrowth species occur in several types of stands, dominated by different canopy species. One exception to the apparent independence of strata is in the close correspondence of the range of gray beech dominance in the canopy with that of *Carex aestivalis* in the herb stratum in south-slope beech gaps. In other cases in which there is difference in dominant growth-form between stands, this difference is reflected in undergrowth composition. Stands strongly dominated by hemlock differ in undergrowth composition from those dominated by mesic deciduous trees, and stands of drier sites dominated by spruce and fir differ in undergrowth from stands of comparable elevations and sites dominated by deciduous trees outside the range of spruce and fir. In other cases, however, quite similar undergrowths appear under canopies dominated by different growth-forms. In the elevations around 4500 ft, similar shrub and herb strata occur in valley spruce forests, deciduous cove forests, and north-slope beech forests. Similar shrub and herb strata occur in oak-chestnut heaths and pine heaths of the same elevation, when the shrub layers of the latter are not dominated by Vaccinioideae.

These evidences of partial independence of strata may give some support to the synusial approach of Gams (1918, 1927) and others (Bolleter 1921; Lippmaa 1933, 1935, 1939; Du Rietz 1930, 1932, 1936). Distributions of canopy and undergrowth species cannot be unrelated when both occur along the same complex-gradients, and distributions of undergrowth species can scarcely be unaffected by factors of light and soil conditions influenced by growth-forms of dominants. The approach to communities through stratal associations or unions has been criticized (Beger 1922-3, Cain 1936, Gleason 1936), especially on the basis that canopy and undergrowth species are parts of each others' environments, at least during some stages of life-histories. On the other hand, there is no close and exact correspondence of undergrowth composition and community dominance. Probably no single, simple key to composition of the whole community exists; certainly community dominance often fails to provide such a key. Both "interdependence" and "independence" of strata are relative; distributionally they are expressed in partial correlations of varying degrees in different situations, rather than in full correlation or the absence of correlation. Because these correlations are only partial, the author has chosen to follow the synusial tradition in seeking distributional groupings within strata as part of the present study.

The transect data suggest these conclusions on the theory of community-units: (1) Many vegetation types are fully continuous with one another, though others are relatively discontinuous. (2) Species populations are distributed variously or "individualistically" (Gleason 1926), no two alike. (3) "Natural" clustering of species is probably of limited and special, rather than general, significance. (4) Dominant species do not, in many cases, define clearly delim-

ited and homogeneous community-units. These statements may imply (5) that, in general, community-units are more "arbitrary" products of classification than "natural" units clearly defined in the field. This possibility must be further considered in relation to other problems of ecological theory and logic in following sections (Part II).

SUMMARY OF DISTRIBUTIONAL GROUPINGS

Distributional groupings of plant species will be listed to summarize some results of the gradient analysis and reduce repetition of species lists in type descriptions (Part III). The conception on which the groupings are based is that of the "commodium" (see Part II). Species are grouped together whose modes or distributional centers are relatively close together in relation to environmental gradients. Species thus grouped tend to occur together in many stands; but they will also occur separately in other stands, since no two have the same distributions. For reasons already indicated, the groupings are considered primarily arbitrary in the sense that the number recognized, their limits and relations to the gradients, are determined by subjective choice and convenience. The groupings will be termed *unions* and will in most cases be named for environmental relations rather than major species. Herb-layer groupings may be considered also groups of unions, since species are not separated according to life-forms.

I. Tree strata

1. Mesic tree class or union, centered in cove forests below 4500 ft: *Tilia heterophylla* (including var. *michauxii* and *T. truncata* Spach.), *Aesculus octandra, Halesia monticola, Betula allegheniensis, Tsuga canadensis, Acer saccharum, Liriodendron tulipifera, Fagus grandifolia* ("white" and "red" populations), *Fraxinus americana* and v. *biltmoreana, Magnolia acuminata, M. fraseri, M. tripetala, Cladrastis lutea, Prunus serotina, Carya cordiformis, Ilex opaca, Carpinus caroliniana, Ostrya virginiana.*

2. Submesic tree class or union, centered in oak-hickory and oak-chestnut forests: *Quercus borealis* and v. *maxima, Carya glabra, C. tomentosa, C. ovalis, Acer rubrum, Betula lenta, Acer pensylvanicum, Cornus florida, Hamamelis virginiana, Amelanchier arborea, Ilex montana, Clethra acuminata.*

3. Subxeric tree class or union, centered in oak-chestnut heath and drier oak-chestnut forests: *Castanea dentata, Quercus prinus (Q. montana* Willd.), *Q. alba, Q. velutina, Nyssa sylvatica, Oxydendrum arboreum, Pinus strobus, Robinia pseudoacacia, Sassafras albidum.*

4. Xeric tree class or union, centered in pine forests and pine heaths: *Pinus virginiana, P. rigida, P. pungens, Quercus coccinea, Q. marilandica.*

5. *Fagus grandifolia* ("gray" population) in mesic deciduous stands above 4500 ft.

6. Ecotonal-mesic union, centered in mesic sites at elevations around 4500 ft: *Betula lutea, Acer spicatum, Amelanchier laevis, Cornus alternifolia.*

7. *Picea rubens,* dominating subalpine forests between 4500 and 6000 ft.

8. *Abies fraseri* and *Sorbus americana,* centered in subalpine forests of highest elevations.

II. Shrub strata

1. Low-elevation mesic shrub union: *Euonymus americanus* and *Lindera benzoin.*

2. Mesic heath union: *Rhododendron maximum* and *Leucothoë editorum.*

3. *Hydrangea arborescens,* widespread in mesic and submesic sites.

4. Submesic shrub union, identical with submesic tree union listed above but also including shrubs: *Pyrularia pubera, Rhododendron calendulaceum, Gaylussacia ursina, Viburnum acerifolium, Calycanthus fertilis* and f. *nanus, Ceanothus americanus, Aralia spinosa,* and *Smilax rotundifolia.*

5. Subxeric heath union: *Kalmia latifolia* with *Lyonia ligustrina, Vaccinium constablaei,* and *Smilax glauca.*

6. Xeric shrub union, with low Vaccinioideae dominant: *Vaccinium vacillans* (including *V. pallidum), V. hirsutum, V. stamineum* (including *V. candicans* (C. Mohr) Sleumer and *V. melanocarpum), Gaylussacia baccata, Pieris floribunda, Ilex montana* v. *beadlei.*

7. Ecotonal-mesic shrub union, identical with ecotonal-mesic union listed above but also including shrubs: *Viburnum alnifolium, Sambucus pubens, Ribes cynosbati.*

8. Low-shrub union of subalpine forests: *Vaccinium erythrocarpum, Menziesia pilosa, Diervilla sessilifolia.*

9. Lower-elevation heath bald shrub union: *Kalmia latifolia, Viburnum cassinoides, Aronia melanocarpa.*

10. High-elevation heath bald shrub union: *Rhododendron catawbiense, R. carolinianum, Leiophyllum lyoni* Sweet.

III. Herb strata

1. Mesic herb union: *Dryopteris spinulosa* v. *intermedia, Athyrium thelypterioides, Eupatorium rugosum, Cimicifuga racemosa, Impatiens pallida, Caulophyllum thalictroides, Laportea canadensis, Trillium erectum* f. *albiflorum, Aster divaricatus, Adiantum pedatum, Actaea pachypoda, Thalictrum dioicum, Hepatica acutiloba, Viola rotundifolia* and spp., *Stellaria pubera, Tiarella cordifolia, Mitella diphylla, Euonymus obovatus, Galium triflorum, Mitchella repens, Osmorhiza longistylis.*

2. Mesic high-elevation herb union: *Rudbeckia laciniata, Circaea alpina, Dryopteris spinulosa* v. *americana, Allium tricoccum, Solidago glomerata, Chelone lyoni, Clintonia borealis, Diphylleia cymosa, Lilium superbum, Oxalis montana, Senecio rugelia, Monarda didyma, Aster acuminatus, Streptopus roseus, Trillium erectum.*

3. Submesic herb union: *Polystichum acrostichoides, Smilacina racemosa, Viola hastata, Aureo-*

laria laevigata, Solidago sp., *Prenanthes trifoliolata, Uvularia pudica* and *U. sessilifolia, Pedicularis canadensis, Desmodium nudiflorum, Medeola virginiana, Veratrum parviflorum, Goodyera pubescens, Galium latifolium, Dryopteris noveboracensis, Thaspium trifoliatum, Parthenocissus quinquefolia, Polygonatum* spp.

4. Submesic high-elevation herb union: *Carex aestivalis, Carex* sp., *Prenanthes altissima, Solidago* sp., *Arisaema quinatum* (Nutt.) Schott., *Houstonia serpyllifolia, Smilax herbacea, Athyrium filix-femina* v. *asplenioides, Angelica triquinata, Thalictrum polygamum.*

5. Subxeric herb union: *Galax aphylla, Chimaphila maculata, Campanula divaricata.*

6. Xeric herb union: *Coreopsis major, Andropogon scoparius, A. virginicus, Tephrosia virginiana, Baptisia tinctoria, Pteridium aquilinum* v. *latiusculum, Sericocarpus asteroides, S. linifolius, Aster* sp., *Antennaria* sp., *Panicum* sp., *Gaultheria procumbens, Epigaea repens.*

7. Heath bald herb union: *Trillium undulatum, Melampyrum lineare, Lycopodium obscurum.*

8. Grassy bald herb union: *Danthonia compressa, Potentilla canadensis* v. *caroliniana* Poir., *Stachys clingmanii,* and introduced species (*Agrostis alba, Phleum pratense, Hieracium scabrum, Rumex acetosella, Prunella vulgaris*).

II. DISCUSSION: AN INTERPRETATION OF VEGETATION PATTERNING

DISTRIBUTIONS OF SPECIES AND THE STUDY OF GENECOLOGY

In Part I a number of curves for distributions of plant populations along environmental gradients were illustrated. Such curves are doubtless of fundamental significance in ecology, clarifying as they do the relations of species populations to one another, to habitats, and to community-types. Real understanding of phenomena of population dynamics which underlie these curves must await future research. Present knowledge of the genetics of species populations may, however, permit at least partial interpretation of some distributions observed in the Great Smoky Mountains. For much of the genetic information used in this discussion the author is indebted to W. H. Camp, who has given the author the benefit of his experience with plant populations in the Smokies through personal communication as well as published work (Camp 1945, 1951; Camp & Gilly 1943).

An ideal situation may first be imagined: an unbroken complex-gradient of environment along which a population consisting of a single biotype is distributed and is maintaining itself. A maximum population level should occur at that point of the gradient which represents optimum conditions for the biotype, and the number of individuals should decrease with increasing departure from the optimum in either direction. The curve of distribution for this population would be essentially a curve of probability of survival against factors of environment which prevent germination or kill increasing proportions of the population with increasing departure from the optimum. It seems likely that the curve of population level along the gradient would be of the classical bell-shaped binomial, or Gaussian, form. It has been suggested by Gause (1930, 1931) and others (Whittaker 1951, 1952; Brown & Curtis 1952) that the distributions of species approximate this form. The majority of the curves indicated by transect data in the present work are of this form, if one allows for occurrence of very wide dispersions and sometimes of more than one peak or mode.

It is suggested that curves approaching the binomial form are the most general pattern in the distribution of species populations along environmental gradients. Various departures from the ideal form may be expected as conditions depart in various ways from the ideal situation considered above. In the Smokies data four conditions (which are interrelated and may differ only in degree) affecting population curves may be recognized: genetic diversity of a relatively homogeneous species population, genetic complexity in a relatively heterogeneous species population, effects of interspecific competition, and direct environmental limitation of the population.

Seldom does a population in the field consist of a single biotype (i. e. of individuals which are genetically identical), though such populations can be produced through apomixis. Usually the population contains some range of variation, and genotypically different individuals encounter different environments in the range of conditions occupied by the species. Probability of survival of different genotypes differs at different points along a gradient, and progressive change in genotypic composition of the population along a gradient is consequently to be expected. Since genotypic differentiation within the population permits different individuals to occur in different environmental conditions, the range of environments occupied by the species is in part a reflection of its range of genotype diversity. In relation to dispersions or amplitudes of species distributions along gradients we may distinguish: a) the range of tolerance and corresponding environmental dispersion of a single biotype of the species, and b) the additional range of tolerance and dispersion resulting from diversity of biotypes.

Among the distributions of species along the elevation gradient (Figs. 8, 9, 10; tables 5, 6, 7; Whittaker 1951, table 2), three intergrading types of curves may be observed: a) sharply peaked binomial curves, e.g. *Acer spicatum, Quercus coccinea,* b) widely dispersed binomial curves, occupying much of the gradient, e.g. *Acer saccharum, Acer rubrum, Pinus rigida,* and c) curves extending along the whole of the gradient studied, with population levels changing gradually from one extreme to the other, e.g. *Tsuga canadensis, Castanea dentata.* The species of the first group appear in the field to be relatively homogeneous, so far as may be judged from

their morphologies. In most species of the second and third groups there is some morphological evidence of genetic heterogeneity.

A genetic trend in a population along an environmental gradient may be termed a *cline* (Huxley 1938, 1940, 1943; Gregor 1939, 1946). Since its introduction by Huxley, the term *cline* has been used in two senses which are related but should be distinguished. Probably the majority of authors using it have applied the term to continuous change in an individual character in populations observed along an environmental gradient. Some authors have rejected the cline concept as an approach to ecotypic variation because of the irregular or zig-zag variation in some morphological characters (e.g. Clausen 1951: 26-28). Irregularity in some morphological traits should not obscure the trends in more fundamental physiological characters of populations along gradients, such as are illustrated in the studies of Clausen, Keck, and Hiesey (1940, 1948) and Clausen (1951). Because genes are interrelated, it is probably seldom the case that a single character of a plant population changes quite independently of others in relation to environment. Changes in many genes, affecting in different but related ways the physiological pattern of the whole plant, may be expected along environmental gradients. It is the trends in genotypic composition of populations along environmental gradients which are of real ecological significance, and in the present work the term *cline* will be applied in the second sense, to these trends.

Even without experiments, the morphologies and distributions of tree species in the Great Smoky Mountains provide limited evidence that wide range of environmental tolerance of a continuous species population may be based on a wide range of clinal variation in that population. Some indications of this effect are provided by the nomograms of Appendix A, as well as by the transects. The nomograms outline with population contour lines the distributions of species in relation to the two major complex-gradients studied in the Great Smoky Mountains, elevation and moisture-balance. In each species one (at least) environmental optimum for the population may be recognized in the peak of the population figure; and as one departs from this optimum in any direction the population levels decline with the tapering slope of a binomial curve. The area of the diagram covered by the whole population represents its range of tolerances of combinations of elevation and moisture-balance, and hence its full ecological amplitudes in relation to these complex-gradients.

In an essay on evolution Wright (1932) has described a symbolic landscape of adaptation, in which a given favorable combination of genes forms an "adaptive peak" for the species, surrounded by "valleys" of less favorable genetic combinations. The diagrams of Appendix A may be compared with Wright's landscape of adaptation, with the restriction that the population figures represent only the

one or more adaptive peaks which a given species population has succeeded in occupying within the limits of the Great Smoky Mountains. As the great diversity of possible gene combinations is reduced to a representation on two dimensions by Wright, so the whole range of environmental gradients encountered by a species is reduced in the nomograms to two complex-gradients within the limits of one mountain range. In the nomograms "adaptive peaks" are represented by maximum population levels reached by the biotypes occurring in an environmental optimum, and these peaks are surrounded by slopes and valleys of lower populations and absence.

Many species with particularly wide distributions in the Smokies are complexes of population-types, races, or ecotypes. It may be thought a general principle that species occupying a wide range of environmental conditions are able to do so because they have evolved series of physiologically distinct races (Clausen 1951:29). The red maples (*Acer rubrum*), which have probably a wider ecological range in the Smokies than any other "species," form an array of high-polyploid races. Genetic differentiation in the sugar maples (*Acer saccharum*), which occupy a wide range of elevation in the Smokies, has been described by Desmarais (1952). *Quercus falcata*, which extends widely along the moisture gradient from cove forest transition to pine forest as a scarce species of lowest elevations in the Smokies, is well known as a member of a complex. The white basswoods, here designated *Tilia heterophylla*, form a complex in which *T. heterophylla* v. *michauxii* and *T. truncata* have also been named. The squaw-huckleberries are likewise a complex in which *Vaccinium candicans* and *V. melanocarpum* have been named, as well as *V. stamineum*, the name here applied to the whole complex. Two species which are familiar as part of the forests of the northeastern states appear in the Smokies with contrasting distributions. *Pinus strobus* is confined to low elevations, but *Tsuga canadensis* extends from lowest elevations to high ones. Presumably the high-elevation populations of *Tsuga canadensis* are ecotypic variants related to the northern ones, and equivalent ecotypic variants are lacking in the population of *P. strobus* in the Smokies. It is of interest to observe that *Tsuga canadensis* is confined to low elevations in the nearby Cumberland Mountains (Braun 1950), as *Pinus strobus* is in the Smokies.

In other species partial or complete division of the populations into two or more population peaks appears. The two birches of the Smokies are both high-polyploid complexes showing evidence of differentiation along the elevation gradient. The yellow birches are designated *Betula alleghaniensis*, and one mode or point of highest population density in relation to elevation is around 3,000 ft. At higher elevations the yellow birches extend into spruce-fir forests from a second mode near 4,500 ft, and these high-elevation yellow birches are probably to be compared with the northern *B. lutea*. The sweet or

black birches (*B. lenta*) have a wide range through community-types, with a principal population center at lowest elevations and a secondary mode at high elevations. The birches of the yellow complex, and probably those of the sweet or black, are facultatively apomictic. Establishment of apomictic races with characters segregated from the polyploid complexes is a probable means of their occupation of wide ranges of environments in the Smokies. Apomixis does not create new genotypes, but can fix and maintain favorable ones already achieved which permit the occupation of an environment, especially one becoming newly available. Both the birch complexes are important trees of fire successions, as well as of climax forests, in the Smokies.

In Appendix A the bimodal populations of *Quercus borealis, Carya glabra, Halesia monticola,* and *Hamamelis virginiana* may be observed. In these four cases the populations are continuous along the elevation gradient and appear to gradate into one another morphologically (morphological differentiation in *C. glabra* and *H. virginiana* was not observed). In the first three of these, at least, the high-elevation ecotype appears relatively less mesic than the one of low elevations (so far as can be inferred from their relations to the whole vegetation pattern). The two modes in each case represent different, favorable genetic combinations and adaptive peaks within a species poplation, which also occupies the valley between them at lower population levels.

The white oaks (*Quercus alba*) in the Great Smoky Mountains consist of two fully discontinuous population-types, separated by an elevation gap of 1000 ft or more. In the Cumberlands the high-elevation white oaks are lacking, and the upper altitudinal limit for white oak is about 2000 ft (Braun 1950). Low- and high-elevation ecotypes may be recognized also in the red oaks, although these are not separated by a comparable hiatus. The low-elevation population of northern red oaks may be identified as *Quercus borealis* v. *maxima;* in the high-elevation population characters of *Quercus borealis* v. *borealis* predominate, though somewhat mixed with those of var. *maxima.* From lowest elevations to highest the characteristics of populations change from those of var. *maxima* toward those of var. *borealis,* although a range of variation in these characters occurs in each population observed. An extended cline thus connects *Quercus borealis* and var. *maxima* along the elevation gradient (and the moisture gradient, var. *maxima* being relatively more and var. *borealis* less mesic). It is believed that this cline is one formed through introgressive hybridization (Anderson 1949, 1953) between two ancestral oak population-types, though it is not assumed that the red oaks of lowest and highest elevations in the Smokies are representative of these ancestral types.

A gap of about 1000 ft also exists in the distribution of beeches (*Fagus grandifolia*), among which three population-types and modes are to be distinguished (Camp 1951). At lowest elevations in cove forests and cove forest transition the "white" beech, of primarily southern distribution, may be recognized. About 1000 ft above the upper limit of the white beech, other, "red" beeches appear in the upper cove forests (3500-4500 ft). The third beech type, the "gray," appears in the beech gap forests of still higher elevations, above 4500 ft. The red and gray beeches in the northeast half of the Smokies are distinctive population-types, each with its own habitat and population mode; but they are only partially discontinuous. Where the two types come in contact they are connected by clines leading through intermediate types, and genes have apparently crossed between them extensively. To a more limited extent genes may also have crossed in both directions the gap separating the white from the red and gray beeches. At high elevations outside the range of the spruce-fir forests, in the southwestern part of the Great Smoky Mountains, the habitat distinction between "gaps" (cols of the high ridges and the steep concave slopes extending down from them) and "coves" (bottoms of V-shaped valleys with flowing streams) breaks down. In this area, slopes of the mountains above 4500 ft occupied by beeches correspond to the habitat of neither red nor gray beech; and correspondingly the partial discontinuity between them appears to break down. The beech populations of the southwestern Smokies appear to be formed by thorough mixture of characters of the gray and red, variously segregating into different individuals and stands.

Several patterns of response have been observed among species of wide extent along the elevation gradient in the Great Smoky Mountains. Some extend from low elevations to high with a continuous population embodying clinal variation. Others show partial discontinuity, with the appearance of two or more modes along the gradient within the population. In two species population-types which are fully discontinuous may be recognized; but one of these, the beeches, forms a complex combination of continuity and discontinuity involving three or four major population-types. It may thus be apparent that there are all degrees of continuity and discontinuity in the relations of natural populations to environmental gradients. There are all degrees of segmentation of a clinal population into partially or wholly discontinuous population-types or ecotypes.

The term *ecotype* has been variously interpreted since its introduction by Turesson (1922a, 1922b) for the genotypic response of the plant species to habitat. If the ecotypic variation of a species is in the form of a fully continuous cline, then any ecotypes which may be recognized are arbitrarily distinguished parts of the cline (Gregor 1944). The term *ecotype* may also be restricted to those population-types which are wholly or partially discontinuous and are differentiated in relation to habitat, within a species population. In the terminology used here, *cline* is a general term for genetic trends through populations, trends which may extend as "intergroup clines"

(Huxley 1938, 1940, 1943) through series of partially or wholly discontinuous populations. *Cline* is customarily applied to the populations through which a genetic trend exists as well as to the trend itself. Along a segmented cline *ecotypes* may be recognized as relatively discontinuous population-types, marked by a distinct population mode, at least. The term *ecotypic population* is conveniently applied to a population-type which is recognized as distinctive in its adaptation to habitat, when it is not known whether this is a *clinal population* continuous with other populations along a cline, or an *ecotype* relatively discontinuous with other ecotypes.

Because of the separation of populations into local habitats not arranged along gradients, and because of the possibility of genetic drift within local populations, these will not always form clines. In some species there may be much ecotypic variation which cannot be reduced to clines and related to environmental gradients. It may further be observed that ecotypes occur within ecotypes (e.g., edaphic within climatic ecotypes, Zherebina 1931, Kruckeberg 1951, 1954), that ecotypes occur along clines and clines within ecotypes, that clines may cross one another in various ways, and that minor clines may occur within segments of major ones. Ecotypes and clines, as defined here, occur in all possible combinations. Clines and ecotypes are thus alternative and complementary means of abstracting from the ecotypic variation of species, emphasizing relative continuity and relative discontinuity, respectively, applicable according to the particular combination of continuity and discontinuity existing in a given species population (cf. Stebbins 1950, Whittaker 1954b).

Both clines and ecotypes may be thought fundamentally physiological (in a broad sense) in meaning though sometimes recognizable also in morphology. The ecotype may be thought to represent a relatively favorable genetic combination within the species, an adaptive peak in relation to environment which has actually been attained. It seems likely that such favorable genetic combinations are usually expressed in local maxima of population density, in population peaks such as are illustrated in Appendix A. The occurrence of clines and the ridge-like shape of some of the population figures in Appendix A (granting that the relative lengths of the ordinate and abscissa are wholly arbitrary) suggest that adaptive "peaks" may take the form of "ridges" in relation to combinations of gradients. The genetic pattern and the more abstract adaptive landscape of a complex species, or of a genus or comparium, may be visualized as a complex topography of hills, peaks, and ridges of different heights and extents, variously related to one another and variously separated by cols, ravines, and level valley bottoms of different depths and widths.

The role of introgressive hybridization in modifying the genetic pattern of species has been referred to. An introgressive cline suggestive of that in the northern red oaks appears among the blueberries,

for the low-bush blueberries which occur in pine forests at all elevations from 1500 to 4500 ft form a cline gradating upward from populations approaching *Vaccinium vacillans* to those approaching *V. pallidum* (Camp 1945). The population of black oaks (*Quercus velutina*) has a ridge extending upward in subxeric sites from the main population center toward the high-elevation population of *Q. borealis* (Appendix A). It is believed that this ridge results from the introgression of genes from *Q. borealis*, permitting an extension of the *Q. velutina* population toward higher elevations. Introgression may thus permit extension of range of a population, as in the more conspicuous example of *Helianthus bolanderi*, a serpentine endemic turned weedy (Heiser 1949; Anderson 1949:76). By hybridization also, essentially new population types may be produced from the genetic materials of old. Thus the high-elevation beeches of the southwestern Smokies may be interpreted as a new ecotype produced from the genetic materials of the other basic beech types. The importance of introgressive hybridization has been emphasized especially in relation to the new habitats produced by man (Anderson 1948, 1949). The few examples given from the Smokies may suggest the importance of hybridizations among woody plants in this pattern of climax vegetation (cf. Muller 1952).

Certain distributional patterns are affected by polyploidy. Among the maples the diploid mountain maple (*Acer spicatum*), with a restricted distribution and sharply peaked binomial curve, may be compared (see Appendix A) with the widely ranging polyploid red maples (*Acer rubrum*). Among the magnolias the relatively sharply peaked and restricted diploids *Magnolia fraseri* and *M. tripetala* may be compared with the tetraploid *M. acuminata*. The high-bush blueberries of the Smokies are a hexaploid complex (*Vaccinium constablaei*) derived by allopolyploidy from *V. altomontanum* and *V. simulatum* (Camp 1945). *V. constablaei* occupies a particularly wide range of habitats, ranging from lower elevations to high ones, from oak-chestnut forests to pine heaths along the moisture gradient, and into types as physiognomically different as deciduous forest and pine heath, subalpine forest, grassy bald, and heath bald. The genetic characters derived from its parents segregate into individuals resembling the parent species, as well as in other combinations. *V. constablaei* has been regarded by Camp (1945) as a typical *alloploidion* (Camp & Gilly 1943) because of this utilization in different habitats of genetic materials derived from two ancestral species.

There is no reason why a diploid species with extensive ecotypic variation should not have a wider range than a polyploid derived from it. The Fagaceae of the Great Smoky Mountains form an instructive series on the diploid level: from *Quercus prinus*, *Q. coccinea*, *Q. marilandica*, and *Q. stellata*, which are relatively homogeneous and of restricted ecological amplitude (within this study area), through *Q. velutina* with a limited extension of its range by intro-

gression and *Castanea dentata* with an extended cline of unknown derivation, *Q. alba* and *Q. borealis* with two distinct ecotypes, discontinuous or connected by introgression, to the complex pattern of *Fagus grandifolia*. Allopolyploidy, however, combines the genetic stock of two species from which characters may be segregated in relation to environment and is a means by which, in some cases, species of wide ecological amplitudes may be produced.

Genetic knowledge of the plants of the Great Smoky Mountains is very limited. It may nevertheless be evident from the preceding how closely interrelated are the genetic pattern and distributional pattern of a species. Although these develop together in relation to environmental possibilities, the distributional pattern may to some extent be regarded as an expression of the genetic pattern. In terms of Wright's topographic analogy, the population center or centers occupied by the species are expressions of the one or more favorable adaptive combinations in relation to environment possible for that species which have actually been occupied. Selection, restricting the diversity of biotypes, may tend to confine or reduce the area of these population peaks; but differential selection in different environments may tend also to produce clines and to cause the differentiation of ecotypes. Mutation, cross-fertilization, and introgression may tend to maintain or increase the area of population peaks by maintaining or increasing the diversity of biotypes. Other reproductive patterns which limit the recombination of characters (self-fertilization, apomixis, structural hybridity) may increase the range of environments effectively occupied by quite different means, facilitating the maintenance of favorable genetic combinations which have already been achieved. Hybridization, involving either introgression or polyploidy, may permit the formation of new favorable genetic combinations and hence the occupation of different habitats and the development of new population peaks.

Effects of environmental limitation and the presence of other plants on these distributional patterns have not yet been discussed. For those effects of plants which reduce growth of individual plants and the populations of species, the conveniently vague term "competition" exists. The forests of the Smokies are (excluding disturbed stands and allowing for effects of death of the chestnuts) mature and self-maintaining forest communities, fully occupied by plants. The population patterns described are population patterns maintained against a background of relatively rigorous competition.

One of the tree species in the Smokies may be thought a particularly effective "competitor." Eastern hemlock (*Tsuga canadensis*) forms stands strongly dominated by itself in sites which are relatively mesic, though less so than those of cove hardwoods forests. The hemlock thus divides the deciduous forests along the moisture gradient by a belt of coniferous forests which approach single-species dominance and offer

quite different edaphic conditions (see Part III). A series of deciduous tree species show evidence in the nomograms (see also Fig. 4) of partial division of their populations by hemlock. The partially separated populations may well be ecotypes or incipient ecotypes; some genetic differentiation may be expected to accompany partial separation of populations into different habitats. Because of effects of "competition" on populations, the physiological optimum for a species or ecotype, as it may be determined in the laboratory or experimental garden, and the population mode in relation to environments occupied by other plants, should be clearly distinguished. The necessity of the distinction may be illustrated with special effectiveness by serpentine plants which are largely confined to serpentine soils by intolerance of competition on other soils, on which they may show better growth in the absence of other plants than on serpentine (Kruckeberg 1954).

Most of the mature forests of the Smokies are mixed stands of several or many species, whose populations are in competition for resources of environment. Since the space, water, and nutrients of a habitat are limited, and since several species grow together there in competitive balance, none of these species can reach the abundance which its reproduction, growth, and survival might permit if it were alone in the site. When several species of rather broad amplitudes are distributed together along a gradient as the subxeric trees are (Fig. 9), they are competing with one another at or near their optima; and the peaks of their distributions must consequently be mutually depressed. Such depressed distributions may be contrasted with those of the pines illustrated in Fig. 10, in which the modes of a series of dominant species are spaced along the gradient at different elevations. Two effects may thus be distinguished in producing distributional curves which appear "depressed" in contrast with the ideal, sharply peaked binomial—biotype diversity which increases dispersion, and competitive limitation of the height of the curve.

When environmental resources more directly limit a single species, an even more distinctly flattened curve may result. If a species has such competitive advantage that it approaches single-species dominance along part of a gradient, height of the curve may be limited by the maximum density of that species possible in the environment. The distribution may then be vertically truncated, flattened under a ceiling in the form of a plateau, with fairly constant abundance along part of the gradient. A distribution of this type is shown for a field transect from cove forest into gray beech forest (Fig. 13). Implications of such "plateau" distributions will be discussed further below. "Competition" may thus affect distributional patterns in various ways: formation of a plateau with competition occurring within the species, depression of population levels through competition with other species, competitive splitting of the dis-

tribution, and displacement of the environmental mode from the physiological optimum.

It is sometimes said that distributions of species are ultimately to be understood through their physiologies, and that autecology becomes in the end applied physiology. It should be clear that there is far more to the distributions of species than is to be learned from physiological experiments with small numbers of individuals. The ecological amplitude of a population is in large part also the genetic amplitude of that population, and not only the physiological tolerance of a few individuals. The population mode is the environmental optimum for the species, but this is an optimum in relation to competition, etc., in natural communities and not simply a physiological optimum. Species populations in the Smokies did not in general have sharp boundaries at particular physiological limits, but tapered gradually to scarcity and absence with decreasing probability of survival of individuals. Outlines of distributions were rounded, as the population levels were affected by different combinations of interrelated moisture and temperature factors, rather than by particular limits for one factor or another.

Distributions of species are to be understood not from limits of tolerance of experimental individuals alone, but from various types of information, which may include history, physiology, ecological life history, population dynamics, genetics, etc. To be adequate for distributional interpretation of complex species, knowledge of physiology and life histories should include differences in these among ecotypic populations. Population dynamics of plants is a major area of neglect in ecology, and could be given little discussion here except in terms of "competition." Ecological genetics and population genetics have not been brought extensively into autecological interpretation, but their importance should be clear. The implications of genetic understanding in synecology may be less direct, but scarcely less significant, than those in autecology. The vegetation pattern of the Smokies would, for example, be scarcely intelligible if population complexities of the red and white oaks and beeches were not recognized.

A particular type of genetic knowledge, relating the genetics of populations to habitats and distributional patterns, has been emphasized here, an area of study termed *genecology* by Turesson (1923), its pioneer. In spite of Turesson's name, genecological or ecogenetic knowledge has developed primarily in the fields of systematics and the study of evolution, and not in ecology. Genecology may appear as a scientific crossroads relating the four major fields of genetics, ecology, systematics, and the study of evolution. As an essential part of understanding both in ecology and in the systematics on which the ecologist is dependent, genecology may well be a major concern of ecologists (cf. Constance 1953, Whittaker 1954b)

THE ASSOCIATION-UNIT THEORY AND INDIVIDUALISTIC HYPOTHESIS

One of the most nearly universal ideas among different schools of ecology is that of vegetation units, which have most commonly been termed *associations*. Some representative statements on associations from different schools are the following: Flahault & Schröter (1910:152, Pavillard 1935), "An association is a plant community of definite floristic composition, presenting a uniform physiognomy, and growing in uniform habitat conditions. The association is the fundamental unit of synecology." Braun-Blanquet (1921), "The association is a plant community, characterized by certain floristic and sociological marks, which reveals a certain independence through the presence of character-species." Nichols (1923), "Viewed in the abstract, an association may be described as a vegetation-unit characterized by its essentially constant physiognomy and ecological structure and by its essentially constant floristic composition, at least with regard to dominant species." Conard (1939), "The association of individuals and species is much more than a chance meeting. It is part of the order of nature. . . . Associations of plants on land are definable entities, susceptible of naming and classifying." Du Rietz (1929), ". . . the association is a concrete part of actual vegetation, though mostly split up into a large number of isolated parts. I am quite unable to regard each of these isolated parts as a fundamental unit of vegetation analogous to the individuals, the real fundamental unit being the sum of all the parts showing essentially the same composition." Tansley (1920), "But if we admit, as everyone who has worked at the subject does admit, that vegetation forms natural units which have an individuality of their own, and that these units owe their existence to the interaction of individual plants of different species with their environment, then it becomes clear that a mere study of the distribution of species as species cannot form the basis of the science of vegetation. We have instead to focus our attention on the vegetational units themselves."

The central idea of these conceptions of vegetation may be termed the *association-unit theory,* the belief that vegetation consists of distinct, natural units called associations. With the association, so far as basic philosophy is concerned, may be grouped such other units as the formation or biome, sociation, union and socion, site-type, life-zone, etc. We may regard the association-unit theory as a form of a broader community-unit theory, which assumes that natural communities are made up of units and that these units are themselves the proper objects of study. Like the cell theory and the molecular theory, the community-unit theory is a conception of the structure and organization of the phenomena with which the scientist deals. Whatever the present status of the community-unit theory, for its role in the development of ecology and for its influence

within and beyond the field, it may be recognized as one of the major theories of science.

An alternative conception, the "individualistic hypothesis," has been held by some authors. The principle of species individuality was advanced in Russia by Ramensky (1924) and within a few years independently recognized in this country by Gleason (1926) and in France by Lenoble (1926, 1928) and Fournier (1927). In the American literature it has been supported by Gleason (1926, 1929, 1939), Cain (1947), Mason (1947), Egler (1947), Whittaker (1951, 1952), Curtis & McIntosh (1951), and Brown & Curtis (1952), and has been criticized by Clements et al. (1929:315), Nichols (1929), and Cain (1934). By this conception the species of plants are regarded as "individualistic," each responding to environmental factors according to its own characteristics, and hence no two alike; and stands are regarded as essentially individual phenomena, varying combinations of species populations which may only arbitrarily and artificially be grouped into associations. The significance of biotic factors may be granted, but species populations respond individualistically to biotic, as well as physical, factors; and interaction among species is not, in general, of the obligate character necessary to accomplish the organization of complex communities into distinct units. The essential propositions are two: (1) Species are distributed individualistically, each according to its own physiology and biotic relations; and (2) communities, formed by the overlap of species distributions, are not organized into discrete units or associations.

The controversy has centered on the question of whether or not associations are "real," "natural," "valid," or "fundamental" units. The association is an abstract type or class of communities; and the statement that such an abstract class is, or is not, a real, natural, valid, and fundamental unit conveys little that is not subject to varied interpretation. The discussion of such a problem is likely to be a semantic skirmish unless the issue is so defined that research can be done and evidence brought to bear upon it. For effective discussion it seems necessary to formulate the question in terms of properties of stands in relation to one another and distributions of species in relation to one another which may satisfy one hypothesis or the other.

Relations between stands which would make the association an ideal, "natural" unit are simply defined: the association should be homogeneous internally, its stands being very much like one another, and discontinuously externally, its stands being quite different from those of other associations. Transitions between associations should be, if not absent, of very limited extent compared with that of the homogeneous associations themselves. Homogeneity of an association, in the sense of close similarity of its stands, implies that its species are similarly distributed, having similar population levels in the different stands. Discontinuity of associations implies abrupt change in species populations wherever a stand of one association meets a stand of another association; it may further imply that many, if not all, species populations will have their limits in the boundaries of their associations. Any interpretation of associations may poorly represent the views of some authors, but a formulation of the association-unit theory based on distributional relations of species may be attempted (cf. Du Rietz et al. 1920, Du Rietz 1921).

A few essential ideas are implicit or explicit in the statements quoted and in most ecological thinking on associations. The first is that vegetation is made up of units, the associations, which are "fundamental" and not subjective in nature. Second is the belief that the unity of associations is intrinsic and dynamic, that species are organized into associations by common response to environment and by necessary relations among them. Third is the conception that species are distributed in terms of these units. If the units are fundamental and the organization of species into units real, the reality of the units should appear in the distributions of species. Interdependent species cannot very well be independently distributed. The third proposition is a consequence of the second and an explanation of the first; and we may formulate the association-unit theory as a logical triangle of three interrelated propositions: (1) Vegetation is made up of units, the associations, which are real because (2) their unity is intrinsic and dynamic, based upon necessary relations among species, with the result that (3) species are distributed in terms of the units, so that similarity of distributions of associated species and correspondence of their distributional limits with the boundaries of associations may justify statement (1).

In all three points such a formulation is in contrast with the individualistic hypothesis. The point which is most directly subject to controlled research is the third. Choice between the two conceptions may rest primarily on the decision as to whether or not analysis of natural communities reveals them to be units of species having closely similar distributions. The individualistic hypothesis may be rejected if organization of groups of species into bounded units appears generally in their distributions. Evidence may also be considered for the first point: whether or not vegetation samples taken by unprejudiced means fall into clearly defined units which are homogeneous within themselves. For the second point, it may be unnecessary to argue whether or not the web-of-life *should* imply dynamic organization of species into units when research can reveal whether or not it actually does so.

It has not proved possible to establish the existence of associations as natural units by statistical means (Clapham 1936, Ashby 1948, Curtis & McIntosh 1950, Goodall 1952, 1954a). The present research was undertaken with the assumption that existence of "real" or "natural" vegetation units could be established in two ways: First, by gradient analysis which revealed the natural distributional groups of species,

second, by study of random samples which should fall into relatively homogeneous and discontinuous groups. Results are recounted in Part I: Species are not organized into distributional units, and stands and vegetation types are for the most part continuous with one another. Although limited clustering of species and limited vegetational discontinuity are suggested, the degree of approach toward these conditions of natural units is slight. The Smokies sample is a limited one; but stand tables compiled by Braun (1950: 53, 62, and 64; 83, 95, 97, 139, 167, 191, 219, 221, 311) suggest that the phenomena of species individuality and stand continuity may be generally valid in the eastern forests. Especially the concurrent, independent studies of Curtis and his associates in the widely different conditions of Wisconsin forests (Curtis & McIntosh 1951, Brown & Curtis 1952) indicate that these phenomena are not peculiar to the Great Smoky Mountains.

A conception of vegetation quite different from that of a mosaic of natural units may be suggested. Vegetation forms a *complex population pattern* in relation to environment. In this pattern species (of green plants, at least) distribute themselves "individualistically"; they occur together wherever their distributions overlap, and associate and dissociate freely in space and in evolutionary time (Mason 1947). Neither in time nor in space does a species occur in terms of associations, but where it may—where at a given time some combination of genetic and environmental possibility for that species is realized in one of its populations. In relation to the population pattern of vegetation, outlines of species distributions are most varied and centers are well scattered. Most population distributions take the form of tapered curves, and the pattern is largely continuous. Because of environmental interruptions and some relative discontinuities inherent in vegetation itself, the pattern may also be considered a complex mixture of continuity and relative discontinuity. In this it is important to recognize that continuity which does exist, rather than overlooking it in an emphasis of "natural" units. It is not infrequently the case that approaches based on the study of continuity and relation are more productive of understanding than those which treat an object of study in terms of units, assuming discontinuity or self-sufficiency of these.

THE DISTRIBUTIONAL BASIS OF COMMUNITY-TYPES
GRADATION AND THE GROUPING OF SPECIES

When population curves of species are drawn together along a gradient (Whittaker 1951, Fig. 1; 1954b, Fig. 3), the resulting picture is not one of a series of associations marked off from one another, but of a pattern of curves flowing into one another, a continuum of populations. This vegetational characteristic of continuous change in proportions of populations along an environmental gradient may be thought a fundamental and general condition, and termed *gradation*. The forests of the Smokies form

a complex, gradating pattern of populations, within which a number of vegetation types may be recognized. According to the conception developed here, the types recognized are "arbitrary" rather than "real" or "fundamental" units. Nevertheless, a major problem in the interpretation of community-types remains: How are these types to be understood in terms of the distributions of species populations?

Certain vegetation types (see Part III) are defined by a single dominant species—*Tsuga canadensis, Fagus grandifolia, Pinus virginiana, P. rigida, P. pungens, Abies fraseri, Picea rubens*. These are easily recognized and defined as types, and they appear essentially constant in floristic composition with regard to dominant species according to the association definition of Nichols (1923). They may consequently appear at first glance to be truly distinct and homogeneous community-types (*consociations* in American usage). It has been shown, however, that these types are heterogeneous in undergrowth composition and intergrade continuously with other types. Other vegetation types are defined by a pair of dominant species. Thus *Castanea dentata* shares dominance with *Quercus prinus* in some low-elevation stands, but with *Q. borealis* or *Q. alba* in other, high-elevation stands. Castanea and the three oaks are quite differently distributed in the vegetation pattern; and they define vegetation types not by a high degree of "association," but simply by distributional overlap in relation to environmental gradients.

Within gradating vegetation the area of dominance of a single species, or the area of overlap of two dominant species, may be used to characterize part of the vegetation pattern and define a community-type. Gradation within the types thus defined and between them and other types implies that these community-types are neither truly homogeneous nor discrete. It should be understood that definition of community-types by one or two dominant species represents an ecologist's *choice* of a single criterion of vegetation by which stands otherwise relatively heterogeneous can be grouped.

A more general problem in the interpretation of community-types is the grouping of several or many species which are to be considered "associated." The wide ranges and genetic complexities of some species, discussed in the preceding section, render such grouping difficult. Widely distributed species normally consist of diverse ecotypic populations, and often of some numbers of ecotypes partially discontinuous with one another. Such species, when they occur in different habitats with different sets of associates, may presumably be grouped with each of their sets of associates (e. g. *Castanea dentata* with the three oak species). A species may in this sense "belong" to two or more associations or other community-types in which its ecotypic populations occur.

The traditional means of grouping species is by the limits of their distributions (Transeau 1905, Hultén 1937, Böcher 1938, Meusel 1939, Raup 1947). Useful as limits of distribution may be for some

kinds of ecological analysis, they cannot easily be determined for binomial curves which taper continuously from scarcity to absence. While arbitrary limits can be defined in the tails of the curves, these limits may still not effectively indicate the relations of species to one another. Populations with similar distributional outlines may be important in different parts of their common area; along the gradients their distributions may be differently skewed.

If maximum populations of two species appear in the same habitats, however, these species appear associated even if their distributional limits differ. Since these species usually occur together when they are sufficiently abundant to characterize stands, their "association" (in this sense of distributional relation) is the basis of our subjective recognition of an "association" (an abstract stand-type). Association of population-types (species, ecotypes, etc.) may be defined for some purposes by coincidence of population centers in relation to environment. Such association is, clearly, relative. There are all degrees of association and non-association, from species with quite similar distributions (*Tsuga canadensis* and *Magnolia fraseri*), through those with distributions related along one gradient but different along another gradient (*Castanea dentata* and *Quercus prinus*), and those with distributions overlapping only toward their limits, to those which do not occur together.

The appropriate measure for locating distributional centers of populations is the mode. The mean may also be used to express the average environmental adaptation of a relatively homogeneous population. But the mean may be difficult or impossible to determine for skewed or bimodal distributions and those which are cut short by absence of more extreme habitats into which they might extend in an area. If the mode is the datum to be used, associated populations are those with their modes near the same location along the gradients of environment. Species (ecotypes, etc.) having their modes close together may be described as *commodal*, and a group of species (etc.) related by the approximation of their modes in relation to environment may be designated a *commodium*.*

The commodium is proposed as a conception of distributional association and as a term which may be applied to any grouping of plants or animals in natural communities by the location of their population centers. The groupings of species in the present work may illustrate the concept. The "classes" of trees are groupings in relation to the moisture gradient of species with quite different distributions in relation to the elevation gradient. The grouping was accomplished by (1) grouping together species of narrower amplitudes whose population centers occurred in the same span of the moisture gradient, (2) use of the location along the moisture gradient of maximum population levels of widespread species

* Latin *con*, together, plus *modus*, in the sense in which it has entered statistics.

(e. g. *Acer rubrum*) to group these with species of narrower amplitudes, and (3) grouping of bimodal populations (e. g. *Halesia monticola*) by their major population centers only. As distribution groupings arbitrarily defined in relation to a single gradient, these classes correspond to the *ecological groups* of Ellenberg (1950, 1952, cf. the *biological plant types* of Iversen 1936).

Plant associations, when defined by several species, are best conceived as commodia of character-species, or of dominants. The association in the sense of the school of Zürich-Montpellier (Braun-Blanquet 1921, 1951) is normally defined by a group of *character-species*, which have narrow ecological amplitudes and are largely restricted to, or at least centered in, a given association. Since the species of high *Treuegrad*, or degree of fidelity, to the association are those having their modes within the association, the character-species form a commodal grouping. The "characteristic species composition" of an association in the sense of Braun-Blanquet (1951:108) comprises these character-species, plus other species of wider amplitudes (companions or *Begleiter*) which have ecotypic populations reaching constancy levels of 60% or more in the stands chosen to represent the association. It is probably not necessary for success of the method that the character-species groupings represent natural clusters. The distributional individuality of species and the scattering of their modes should imply considerable freedom in the recognition of character-species groupings and in the corresponding definition and delimitation of associations.

The associations of American authors (Clements 1928, Weaver & Clements 1929, Oosting 1948, Braun 1950) are in general based on very broad groupings of dominant species. In some cases (*Quercus-Carya, Quercus-Pinus* Associations) the species grouped together are so widely different in ecological relations and geographic distributions that some dominants of the association may not occur together in the same stands. It is in general impossible to define the American associations quantitatively through their species composition (Braun 1950:11). They may be interpreted, however, as very loose commodal groupings of dominant species, at least some of which are sufficiently related distributionally to be important in the same stands.

The distributional groupings used in the present paper are considered primarily "arbitrary"; it is believed that they are not, for the most part, based on natural clusters of species which are clearly separated from one another in the field. The same may be said for the grouping of character-species or dominants into associations in general; such grouping is possible without any assumption of discontinuity between species-groups or vegetation types. It has also been suggested that a degree of natural clustering of species in natural communities may sometimes exist. In relation to the theory of community-types it should be observed that such relative clustering is in no way inconsistent with either the individualistic hy-

pothesis or the frequent continuity of types with one
another. Whether some associations already recog-
nized are supported by natural clustering would seem
a matter for research, rather than assumption. For
the present, the "commodal" conception provides a
means of grouping species in vegetation analysis and
the definition of community-types without assuming
natural clustering which cannot now be demonstrated.

ZONATION

Most of the vegetation pattern of the Great Smoky
Mountains is one of continuous gradation; but cer-
tain relative discontinuities in the pattern are also to
be recognized. Some of these, as the edges of burns
and old fields, are products of disturbance. Others
appear as interruptions or telescopings of the gra-
dation where there are environmental discontinuities,
as along sharp ridges. A few vegetation types of the
Smokies, however, are separated from the rest of the
pattern by more abrupt transitions not produced by
environmental discontinuity.

Some characteristics of these relatively discon-
tinuous types may suggest their meaning. It may
first be observed that they are types strongly domi-
nated by one (or two) species. The beech gap forests,
which are relatively discontinuous with the cove for-
ests below them, are dominated by *Fagus grandi-
folia*. The grassy balds, separated from surrounding
forests by a shrubby forest-edge, are dominated by
mountain oat grass (*Danthonia compressa*). The
subalpine forests, which may be interpreted as a
zone above the deciduous forests, are dominated by
Picea rubens and, at higher elevations, *Abies fraseri*.
In the heath balds, which may be abruptly separated
from the subalpine forests, one or two of several
major shrub species dominate a given stand.

Transect data are available for the distributions of
species in two of these relatively discontinuous types.
The distribution of gray beech (*Fagus grandifolia*)
in relation to elevation (Fig. 13) shows a "plateau"
distribution, in which the species strongly dominates
some stands above 4600 ft, but is rather sharply
limited between 4600 and 4400 ft. In the coniferous
zone of high elevations, *Picea rubens* and *Abies
fraseri* appear to have ordinary, tapered curves in re-
lation to elevation; no tendency toward plateau dis-
tribution has been established for these two species.
The relative discontinuity is in this case between
growth-forms; grouping all deciduous and all conifer-
ous species together, the subalpine forests form a
coniferous zone which is relatively discontinuous with
the deciduous cove forests (but not with the hemlock
forests) below them. These "zones" are thus char-
acterized by plateau distributions of a species popula-
tion or a growth-form along one gradient which has
been studied.

The discontinuous types of the Smokies are mostly
characterized by dominant growth-forms differing
from the predominantly deciduous forests. The rela-
tively discontinuous types include grassland com-
munities (grassy balds), evergreen shrub communi-
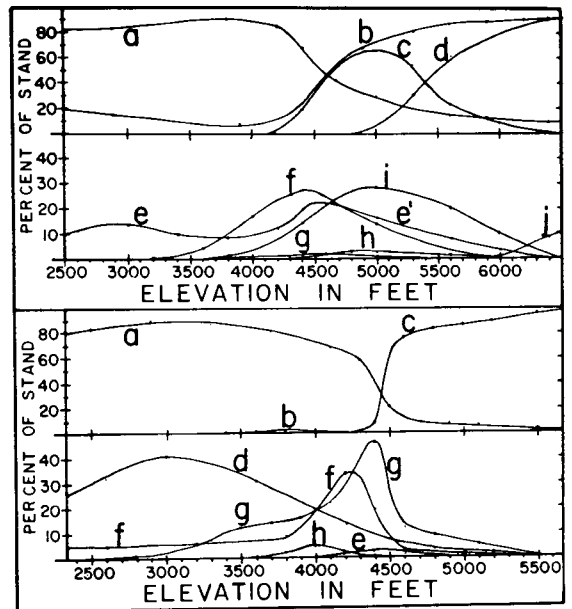
FIG. 13. Distributions of plant populations in rela-
tion to "zones." Above—the transition from cove for-
ests below 4500 ft to mesic spruce-fir forests above,
based on composite transect data. Zoned distribution of
evergreen and deciduous growth-forms relative to one
another: a, all deciduous, broad-leaved trees; b, all ever-
green, needle-leaved trees (*Picea rubens, Abies fraseri,*
and, below 4700 feet, *Tsuga canadensis*); c, *Picea ru-
bens*; d, *Abies fraseri*. Distribution of other species in
relation to the transition and spruce-fir forests: e and e',
Betula alleghaniensis and *B. lutea*; f, *Acer spicatum*;
g, *Cornus alternifolia*; h, *Amelanchier laevis*; i, *Vi-
burnum alnifolium* (estimated coverage percents); j,
Sorbus americana. Below—the transition from cove
forests below 4500 ft to gray beech forests above, based
on a field transect iu Trillium Gap. Zoned distribution
of gray beech relative to other tree species: a, major
mesic tree species (*Halesia monticola, Betula allegheni-
ensis, Aesculus octandra, Tsuga canadensis, Acer sac-
charum, Tilia heterophylla, Fraxinus americana, Lirio-
dendron tulipifera*); b, red, and c, gray populations of
beech (*Fagus grandifolia*). Distribution of other spe-
cies in relation to the transition: d, *Betula allegheni-
ensis*; e, *Cornus alternifolia*; f, *Aesculus octandra*; g,
Acer spicatum; h, *Prunus serotina*.

ties (heath balds), and coniferous forests (spruce-fir
zone). The gray beech is a deciduous tree, but differs
from many of the cove forest trees in its small stature
and manner of reproduction. At a contact between
different dominant growth-forms, such as that of the
grassy balds and forests, environmental conditions
related to dominance of one growth-form may largely
prevent individuals of the other from establishing
themselves. The two dominant growth-forms may
thus, in some cases, replace one another abruptly
rather than forming mixed stands along a wide span
of the gradient. Because stands of mixed dominance
are limited, the two growth-forms appear, in human
interpretation, relatively "incompatible."

The relation of the relatively discontinuous types
to the gradients is of interest. All are types of high
elevations; and the two which are most clearly dis-

continuous, the heath bald and grassy bald, are types both of high elevations and of most exposed situations. To these observations may be added geographic ones. In eastern North America, well-defined zones seem more characteristic of the Far North than of more temperate climates; and in the West, zones are more apparent in some more arid regions than in the mesophytic coastal forests. Zones, we may think, are more characteristic of those conditions interpreted by ecologists as "extreme." A converse interpretation must be rejected; it is by no means generally true that community-types of more extreme environments are discontinuous with one another. The data of Mølholm Hansen (Hansen 1930) for the vegetation of Iceland offer some of the most impressive evidence of vegetational continuity available (see also Ostenfeld 1908, Cooper 1942).

The term *zone* has been variously applied to vegetation, but often with the implication that relatively discontinuous belts of vegetation could be recognized along a gradient. For present purposes a *zone* will be defined as a vegetation type dominated by a species (or growth-form) possessing a plateau distribution, and consequently relatively discontinuous in at least one observed contact with another vegetation-type along a presumably continuous gradient of "primary." environmental factors. The condition of *zonation,* or partial discontinuity of types, may thus be distinguished from the continuous *gradation* already discussed. Evidence discussed above suggests these interpretations of the condition of zonation:

1. Under some conditions plant communities are "simpler" or of limited species-diversity; this is true especially of some successional communities and those of some environments interpreted by ecologists as "extreme" or "unfavorable." In contrast to the mixed dominance of many communities in "favorable" environments, these communities are often dominated strongly by one or two species; and the dominants of adjacent community-types are more often of different growth-forms.

2. Populations of dominants of these communities *may* have "plateau" distributions in relation to a given environmental gradient, and the communities may consequently appear relatively discontinuous with other communities.

3. Contrast of dominant growth-forms between communities may steepen and render more obvious the relative discontinuity between them. "Zones" which are not definable by discontinuity of species populations may sometimes be defined by relatively abrupt change in dominant growth-forms.

4. Zonation is not a general characteristic of vegetation; it is a special and local condition which sometimes results from the manner in which a species is distributed, or from a contrast in dominant growth-forms, or both. Neither single-species dominance, nor contrast in dominant growth-forms, nor occurrence in "extreme" environments, nor any combination of these necessarily implies vegetational discontinuity—

as is illustrated by the continuity of the xeric, pine forests of the Smokies with one another and with deciduous forests.

Since zones are relatively discontinuous, they conform better to traditional ideas of distinct community-units than do the types recognized in continuously gradating vegetation. Evidence on the nature of zones as vegetation units may be considered in terms of four types of questions: (1) How significant is the boundary as a population discontinuity, what part of the species populations of the zone are limited by it? (2) To what extent are species of a zone restricted to that zone, not occurring elsewhere with different associates? (3) To what extent is the zone homogeneous, or to what extent does gradation occur within it? (4) To what extent does the zone intergrade with other communities along gradients other than the one on which discontinuity has been observed—is the zone bounded in all directions, or only in one observed direction?

When we examine the zones in the Smokies in terms of (1), we find the ericaceous dominants of the heath balds ranging extensively into forest types, and most forest species ranging through the boundary between cove forests and other types below, and beech and spruce-fir forests above, 4500 ft. The forest-edge of the grassy balds seems more effective as a discontinuity and limits some of the species, but by no means all of them. Very few species are restricted to a zone as asked in (2). Gray beech and spruce and fir are (since the zones are defined by their distributions); and some undergrowth species are restricted to the high elevations of these forests. No species is restricted to the heath balds (Cain 1930b), and apparently all species of the grassy balds except the introduced weeds occur also in forests. Zones are not homogeneous, but show the gradation of (3) within themselves. A marked elevation gradation appears in the heath balds (Cain 1930b and below); the grassy balds are not homogeneous and appear to intergrade with sedge balds (Wells 1937). Gradation within the gray beech and spruce-fir forests is described elsewhere (Parts I & III).

Finally, according to (4), it may be observed that zones defined by their boundaries in one direction gradate into other vegetation in other directions. Continuity of the gray beech forests along the moisture gradient with high-elevation oak-chestnut forests, which in turn are continuous with the rest of the pattern of deciduous and pine forests, has been indicated. The gray beech zone is discontinuous with other deciduous forests in one contact only. The heath balds appear to gradate into oak-chestnut heath at lower elevations, although no transect data are available on this transition. The spruce-fir forests of the Appalachians gradate northward into the different spruce-fir forests of Canada (Oosting & Billings 1951).

"Zones" should not be taken for granted as ideal vegetation units, nor should their existence be interpreted as evidence that vegetation in general consists

of well-defined units. As the plateau distributions by which zones are here defined may be regarded as modifications of the more general binomial form, so zonation may be regarded as a modification of the general condition of vegetational gradation. Gradation occurs within the zones but is steepened between them; and apparent zones are to varying degrees definable by plateau distributions—some not at all, while others have poorly defined or well-defined plateau distributions. Zonation may be interpreted, not as a state apart from gradation, but as a tendency, more or less developed under some circumstances, toward partial or apparent segmentation of the fundamental vegetational continuum.

ECOTONES

Transitions between vegetation types have usually been called "ecotones" by English-speaking ecologists. Like the term "zone," "ecotone" has been widely and loosely used, with little attention to what distributional phenomena were involved. In gradating vegetation, an ecotone is any part of the pattern which an ecologist chooses to regard as transitional between other parts. For the purposes of the present paper, transitions between types recognized in gradating vegetation will be termed simply "transitions"; and the term "ecotone" will be applied only to the relative discontinuities bounding zones.

If the boundaries of zones are relative discontinuities, they should be demonstrable as such by suitable quantitative methods. The data for the gray beech zone offer a test of this possibility. Percentage difference (Odum 1950, Whittaker 1952) may be used as an approach to rate of change of plant populations between stands sampled at fixed intervals along the elevation gradient. Comparing successive stand counts taken at 200-ft intervals in a field transect from cove forest up into a beech gap (Whittaker 1948, Appendix B, table 6) yields percentage differences for 2600 and 2800 ft, 2800 and 3000 ft, etc., of 34, 19, 35, 33, 6, 41, 17, 29, 33, 77, 7, 2, 6. The difference of 77% is for the interval 4400-4600 ft and expresses the change of dominance between gray beech and the cove forest species in these elevations. The apparent discontinuity in this transect may be sharpened, however, by an environmental change from V-shaped ravine to concave "gap" in the same elevations. Applying the measurement to the composite transect (Table 5) and grouping samples for 400-ft intervals gives values for 1800 and 2200, 2200 and 2600 ft, etc., of 40, 42, 46, 28, 40, 50, 62, 30, 23. The difference of 62% is for the interval 4200-4600 ft and may be contrasted with the less rapid change of populations indicated by the values for higher elevations, within the gray beech zone.

These percentage differences are strongly influenced by irregularity in the distributions of populations (cf. Whittaker 1952). Because of the wide fluctuation of these values in other transects for which they have been computed, it is believed that such measurements do not yet provide a reliable and objective means of defining ecotones. As a supplement to the demonstration of a plateau distribution of gray beech, however, the percentage differences may support the interpretation that there is a relatively steeper rate of change in those populations to which the measurement has been applied in the elevation interval on each side of 4500 ft. Considered together with the fact that most populations occurring on either side of the ecotone extend through it, the percentage differences may further emphasize that this is a *relative* discontinuity only.

Competition has often been assigned the major role in producing discontinuities between natural communities (Cajander 1909, 1925; Elton 1947; Allee *et al.* 1949: 476-8), and these discontinuities have been regarded as "tension zones" between competing communities. A few cases of mutual exclusion have been observed among animal species, when pairs of species which are ecological equivalents come in contact (Beauchamp & Ullyott 1932, Hairston 1951). It seems clear from the transect data of the present study that the change from one vegetation type to another is not in general a matter of mutual exclusion of species. Only in the case of the grassy balds is there evidence that one dominant growth-form occupies the environment to the near exclusion of the other. Competition among plants occurs as much in the stands on each side of the ecotone as in the ecotone itself, and it seems difficult to conceive of a fundamental difference in the character of competitions among plants in stands which are interpreted as ecotonal or transitional and in those which are not.

Neither should the ecotone be interpreted as a boundary between two communities and a line or tension zone along which the two are in competition as communities. Natural communities do not form units of many species bound together by obligate relations, integrated wholes which can meet and compete as wholes. Examination of species distributions in transects is revealing in this respect. Species populations show in relation to the ecotone between cove forest and gray beech forest the same individuality of distribution which is demonstrated throughout the vegetation pattern. Species also respond variously to the forest-edge of the grassy balds. In this case the abrupt change of physiognomy implies a strong telescoping of gradients of light, evaporative conditions, etc. Plant populations which extend into or through the ecotone respond individualistically to the very steep gradient of environments-within-communities in the forest-edge. Some extend different distances into or through the ecotone; others have population modes within the ecotone.

Phytosociologists recognizing the extent of gradual transition between community-types have tended also to regard the transitions as community mixtures. There seems to be no sense in which the ecotones are mixtures in which the communities on each side of them are not also mixtures. Ecotones are not simply intermediate between the stands on each side of them (cf. Odum 1953:207 on "edge effect"). A union or

commodium of species centered in or near the ecotone is illustrated for the transition from cove forest to mesic spruce forests (Fig. 13); and a related commodium appears between cove forest and gray beech forest. Several woody species appear in the forest-edge between deciduous forests and grassy balds. No such grouping appears between subalpine forest and heath bald, although *Sorbus americana* may have an ecotonal mode there. These ecotones are characterized by smaller woody species; and another grouping of shrubs and small trees appears in the Smokies, the submesic commodium between cove forests and oak-chestnut forests. Species of the three transitional commodia which are best developed are:

and of a distinct biotic community with its own physiognomy and characteristic bird species. Kendeigh (1948, 1954) has shown that a characteristic assemblage of bird and mammal species occurs in the forest-edge, and considered this as in part a stabilized biotic community-type (biociation). Many ecotones may be regarded as community-types in their own rights by any of the traditional criteria—character-species, dominant species, total species composition, physiognomy, and stratal structure and stratal dominance.

In the occurrence of gradation within them and, so far as is known, in the manner in which "competition" operates within them, communities desig-

Ecotonal-mesic union	Grassy bald edge	Submesic union
Betula lutea	*Betula lenta*	*Betula lenta*
Acer spicatum		*Acer pensylvanicum*
	Acer rubrum	*Acer rubrum*
Amelanchier laevis	*Amelanchier laevis*	*Amelanchier arborea*
Viburnum alnifolium		*Viburnum acerifolium*
Cornus alternifolia		*Cornus florida*
	Rhododendron calendulaceum	*Rhododendron calendulaceum*
	Vaccinium constablaei	*Vaccinium constablaei*
	Lyonia ligustrina	
	Crataegus macrosperma v. *roanensis*	
	Rubus canadensis	
	Salix spp.	*Pyrularia pubera*
		Ilex montana
		Calycanthus fertilis
		Ceanothus americanus

Some of the species of each group are centered in the transition, so far as occurrence within the Smokies is concerned; the transitions thus have their own *character-species*. Other species appear to link these transitional groupings, in the sense that they have populations centered in more than one of them. Certain genera of shrubs and smaller trees are especially characteristic of the ecotones in the Smokies, and apparently elsewhere also. The transitional groupings also share species with seral communities; *Betula lenta* and *B. lutea, Acer rubrum, Amelanchier laevis,* and *Rubus canadensis* are major successional species in the Smokies, and some others listed occur in seral stands. All the species listed, except some of those of the grassy-bald edge, occur also as undergrowth species in climax forests beyond the influence of the ecotones. The ecotones are thus populated in part by "versatile" species which have ecotypic populations (or apomictic races) in a wide variety of habitats.

It was observed by Gleason (1926) that some species tend to colonize transition zones more freely than either contiguous association so that, measured by component species, such a transition zone is almost an independent association. In studying the deciduous chaparral of the Wasatch Mountains, Hayward (1948) observed that this has properties both of an ecotone between desert scrub and montane forest.

nated as ecotonal do not differ fundamentally from communities not designated as ecotonal. "Transition," "boundary," "tension zone," and "mixture" represent human attitudes or interpretations imposed on vegetation. It is suggested that ecotones and transitions are not phenomena distinct and different from communities, and that no "ecotonal principle" of the general occurrence of distinct boundaries between communities (Allee *et al.* 1949:476) is actually known to ecologists. In the sense of the present paper, "ecotones" are communities and parts of the whole vegetation pattern in which the gradation occurring throughout the pattern is relatively steeper at the limits of a few of the recognized community-types, those interpreted as "zones."

CLIMAX PATTERNS AND THEIR COMPARISON

It has been indicated that undisturbed vegetation in the Smokies is in a self-maintaining or climax condition at all points along the moisture gradient (Part I). Recent death of the chestnuts has unbalanced many stands and set in motion changes in their composition, but there is no evidence that vegetation of these mountains is converging toward a climatic climax (Whittaker 1951). According to the climax theory as stated by Clements (1916, 1928, 1936; Phillips 1934-5, Cain 1939, Braun 1950), the cove forests and pine forests of most mesic and xeric sites in the

Smokies might be regarded as postclimax and preclimax, respectively. Oak-chestnut forests, occupying many of the lower slopes of the mountains, might then be interpreted as climatic climax. Alternatively, by the polyclimax theory (Nichols 1917, 1923; Tansley 1935), the five types distinguished along the moisture gradient at low elevations are so many polyclimaxes. Of these oak-chestnut forest would presumably be designated climatic climax and the remainder physiographic or topographic climaxes.

In the present study these five types are regarded not as discrete associations but as parts of a single vegetation continuum. If stands at all points along the gradient are accepted as self-maintaining, and therefore climax in this sense, the continuum itself should be regarded as the climax. Rather than a single climatic climax or set of polyclimaxes, climax vegetation in the Smokies comprises a whole vegetation pattern ranging from cove forest to pine forest along the moisture gradient and from these low-elevation types to spruce and fir forests in one part of the range and to other deciduous types in the other part of the range at high elevations.

In such conditions as those of the Smokies, the pattern of vegetation along the moisture gradient provides a reasonable description of climax vegetation in a given elevation belt. Through the moisture-gradient patterns (and the transect data representing them), composition of vegetation at different elevations may be compared. Population levels of species can be compared from one elevation to another; thus the changing role and importance of hemlock at different elevations may be revealed (Fig. 15). Within the climax pattern for a given elevation, relative importance and relative position along the moisture gradient of species may be compared. When different climax patterns are compared, statements may be made about the relative importance of a given species population or community fraction in different patterns, relative importance of growth-forms or life-forms in different patterns, relative variety of species or of dominants in different patterns, relative extent of change in composition from most mesic to most xeric sites in different patterns, etc. Some of these possibilities may be illustrated in the following statements on climax composition in the Great Smoky Mountains:

1. The climate of low elevations (1500-2500 ft) is a deciduous forest climate, as expressed in composition of climax stands. Deciduous trees form 73%, hemlock 14%, and pine species 13% of total canopy stems in the low-elevation moisture-gradient transect (Whittaker 1951, table 3).

2. The climate of high elevations (4500-5500 ft) in the northeastern half of the range is a coniferous (taiga) climate. Two abietine dominants, *Picea rubens* and *Abies fraseri*, make up 87% of canopy stems in the sample, deciduous trees only 13%. Toward still higher elevations the deciduous trees decline to 7 per cent (5600-6100 ft) and 1% (6200-6600 ft) of canopy stems. In the southwestern half of the

range, however, a pattern in which deciduous broad-leaved trees form 100% of canopy stems occurs at elevations between 4500 and 5500 ft.

3. Major climax tree species at low elevations are, in order of over-all importance with percentages of canopy stems for the whole transect (Whittaker 1951, table 3): *Quercus prinus* 14, *Tsuga canadensis* 14, *Castanea dentata* 13, *Quercus borealis* v. *maxima* 6, *Pinus virginiana* 6, *Acer saccharum* 4, *A. rubrum* 4, *Tilia heterophylla* 4, *Pinus rigida* 4, *Liriodendron tulipifera* 4, *Pinus strobus* 3, *Aesculus octandra* 3, *Quercus alba* 3, *Carya glabra* 3, *Halesia monticola* 2, *Betula alleghaniensis* 2, *Quercus coccinea* 2, *Carya tomentosa* 2. No other species is represented by more than 1 per cent of canopy stems.

4. In contrast to these diverse stands of low elevations, composition of canopy trees at highest elevations, above 6100 ft, is simple: *Abies fraseri* 90, *Picea rubens* 9, and *Betula lutea* 1% of canopy stems. Undergrowths of these stands are varied, but in the canopy there is profound simplification in composition from lowest elevations to highest.

5. If a criterion is chosen for the oak-forest grouping (all stands in which oaks plus other submesic and subxeric species make up at least 50% of stems), then 57% of the climax stands sampled at low elevations are oak forests, as defined. Among the same samples only 28% are oak-chestnut forests, if these are defined as all stands in which *Castanea dentata* and *Quercus prinus* form at least 50% of canopy stems.

6. The relative importance of oak stands in the climax pattern decreases somewhat with elevation. For the elevation belts 1500-2500, 2500-3500, 3500-4500, and 4500-5500 ft outside the range of spruce, percentages of stands classified as oak forests were —57, 46, 44, and 41. The relative importance of mesophytic stands correspondingly increased—11, 28, 41, 59—while that of pine stands decreased—32, 25, 15, 1.

7. Stand composition at the mid point of the moisture gradient may be determined—by the middle station of the transect, by a "median" stand so chosen that half the samples have more highly mesic and half more highly xeric moisture-class formulas, or by percentage-similarity comparison with stands representative of the extremes of the gradient. More complicated means of finding an "elective mean" in a multi-dimensional pattern are described by Ramensky (1930). The three techniques mentioned give equivalent results in the Smokies. Using the first as the simplest, intermediate stands at different elevations are: stands dominated by *Quercus prinus* at 1500-2500 feet, stands in which *Q. prinus* and *Castanea dentata* share dominance at 2500-3500 ft, and stands in which *C. dentata* and *Quercus borealis* share dominance at 3500-4500 ft. More limited data for high elevations give stands in which *C. dentata* and *Q. borealis* share dominance (45 and 40% of canopy stems), with *Acer rubrum*, *Halesia monticola*, and *Fagus grandifolia* as major subordinate species.

Moisture-class formulas (Mesics: Submesics: Subxerics: Xerics) change in a manner which indicates increasingly mesic conditions for these intermediate stands toward higher elevations—2:50:46:2, 4:57: 38:1, 5:70:23:1, 15:73:12:0.

Three quantitative approaches to the "climatic climax" may be recognized in the above statements. Numbers 1 and 2 define the over-all character of climax vegetation in terms of dominant growth-forms. Numbers 3 and 4 may also express the over-all, climatic character of the vegetation in terms of "average climax composition" for different elevations. Number 5 determines the stand type to which the largest proportion of climax stands at a given elevation belong; number 6 describes the differing relative importance of types at different elevations. It is suggested that the type to which the majority of climax stands in an area belong be termed the "prevailing climax type" as an approximation to the climatic climax, but with no implication that types other than the prevailing are not also climax. The fact that recognition of a prevailing climax type is contingent on the subjective delimitation of types should be evident. At high elevations in the northeastern Smokies a prevailing climax type is easily recognized in the spruce-fir forests; at low elevations, it seems of much more limited meaning to describe the oak-chestnut forest as a prevailing type. Finally, number 7 defines an "intermediate climax stand" to which other stands are presumably more or less postclimax or preclimax in Clementsian nomenclature.

Complications in the definition of *average climax composition, prevailing climax type,* and *intermediate climax stand* in other areas may be evident. Their recognition in the Smokies was much simplified by the mature and stream-eroded topography, absence of hydric sites and near-absence of primary succession, lack of contrast in parent materials, and existence of extensive undisturbed stands. Where it is possible to use them, they offer quantitative, definable abstractions from the climax pattern in place of the more subjective "climatic climax." They permit quantitative comparisons of climax patterns which are scarcely possible on the basis of the climatic climax. As comparison between patterns of different elevations was possible in the Smokies, so comparisons between different soil parent-materials, different climates, etc. should be possible elsewhere. Their use will be further illustrated below in drawing comparisons between the Smokies and the related vegetation pattern of the Cumberlands.

A further measurable property of climax patterns is that of *diversity,* in two senses—diversity or richness in species of stands and the pattern as a whole (see also Part I), and diversity or variety of stand types occurring along the moisture gradient in the pattern. Measurement of species-diversity of patterns is possible through application of the *alpha* index of Fisher *et al.* (1943) to the whole sample of tree stems included in the composite transect for a given elevation. Values derived are 7.4, 5.6, and 6.1

for the elevation belts 1500-2500, 2500-3500, and 3500-4500 ft, and 4.6 for deciduous forests above 4500 ft. The tree stratum of the spruce-fir forests is much less rich in species, and the diversity values are 2.2, 1.3, and 0.7 for 4500-5500, 5600-6100, and 6200-6600 ft.

One approach to measurement of type diversity of a vegetation pattern is through percentage similarity. These values give some indication, necessarily subject to sampling error, of "ecological distance" (Whittaker 1952), the extent to which community populations differ in response to separation along environmental gradients. When cove forests and pine forests as extremes of the moisture gradient are compared, the percentage similarity is zero. An alternative means of comparing "ecological distances" along gradients is the determination of "half-changes." If percentage similarities are measured between an extreme and successive points along a gradient, a point is reached at which the value is 50%. If this point is then used as a standard and further points along the gradient compared with it, a second point of 50% change may be determined. The number of these "half-changes" occurring along a gradient may thus indicate the extent of change in species populations along the gradient, for the particular stratum or group of organisms to which the measurement has been applied. Half-change, like half-life, may serve as a useful measurement along a curve without a sharp lower limit. From the nature of the data, the values obtained here must be very approximate. Indicated numbers of half-changes along the moisture gradient are—7, 6.5, and 9 for 1500-2500, 2500-3500, and 3500-4500 ft. Computed in terms of moisture-balance classes rather than species composition, the values become 4, 4, and 5.

Published data of Braun (1950) permit more limited application of these approaches to climax characteristics. Extremes of the pattern in the Cumberlands are taken to be the sugar maple-basswood-buckeye forest (Braun 1950, table 2), and the oak-chestnut subclimax (Braun 1950, table 7) occurring on some of the driest slopes and ridges. Pine stands in the Cumberlands (Braun 1950, table 8) occur only in special situations of rocky summits and sandstone outcrops. The following comparisons are possible:

1. Average climax composition in the Cumberlands is approximated by the tabulation for Mixed Mesophytic on all sites (Braun 1940a:237), although the sample is biased for this particular purpose by the exclusion of hemlock segregates. Average climax composition given above for low elevations in the Smokies was a mélange of species, some of which do not occur together. That for the Cumberlands is, in contrast, recognizable as a type, the Mixed Mesophytic forest, though more highly mixed than individual stands.

2. Mixed mesophytic may also be regarded as the prevailing climax type in the Cumberlands, in contrast to the prevalence of oak forests of various types at low elevations in the Smokies.

3. Percentage similarity comparisons with the extremes suggest a stand of the chestnut-sugar maple-tuliptree segregate (Braun 1950, table 5) or corresponding drier mixed mesophytic (Braun 1950, table 1B) as intermediate climax stand in the Cumberlands, in contrast to the oak-chestnut intermediate climax of the Smokies.

4. In composition and diversity the all-deciduous mixed mesophytic forest (Braun 1940a:237) is closely similar to the most highly diverse stands in the Smokies, those described as cove forest transition. Diversity conditions of stands in the two ranges appear to be similar, although the samples are not strictly comparable. The sum of a set of tables which approximate a moisture-gradient pattern (Braun 1950, tables 2, 1A, 5, 7, 8) gives a diversity value (5.5) scarcely different from the 5.8 obtained for canopy stems at low elevations in the Smokies (Whittaker 1951, table 3).

5. Indicated half-changes along the moisture gradient in this same set of tables are slightly more than 2 in terms of species and approximately 2 in terms of moisture classes, if the pine stands of special sites are excluded.

Comparing the vegetation pattern of the Cumberlands with that of the Smokies, it may be said that the former is more clearly mesophytic in character and of comparable species diversity, but less diverse in terms of stand types along the moisture gradient. The Cumberlands pattern largely corresponds to the mesic half of the Smokies pattern (cove forest, cove forest transition, and oak-chestnut forest), while the more xeric types of the Smokies (oak-chestnut heath and pine forest) are reduced in the Cumberlands to stands of special edaphic situations. The two climax patterns are thus related through a shift of relative emphasis of the mesophytic grouping and the oak-forest grouping.

Such shift in relative importance of parts of climax patterns is further illustrated in Braun's treatment of vegetation of the Southern Appalachians, the Ozarks, and the area between. Three regions are recognized from the Cumberlands west: a region of mixed mesophytic climax in and around the Cumberlands, a region of oak-hickory climax in the Ozarks and west and north from them, and between these the Western Mesophytic Region, regarded as ecotonal, and forming "a mosaic of like and unlike climaxes" (Braun 1947). Of this last region Braun (1950:123) writes, "In its eastern part, mixed mesophytic forests are of frequent occurrence; westward they become more and more limited in extent and more closely dependent on very favorable habitat conditions.... Because of the many mixed forest communities, and of the gradual change from east to west in extent of mixed mesophytic communities and in composition of forests, and of the increasing frequency of communities in which oaks are dominant, this is considered a transition region."

The description seems most expressive of gradation on a grand scale, along a major climatic gradi-

ent. Oak-hickory stands are of limited extent in the Southern Appalachians, where mixed mesophytic prevails; mixed mesophytic stands are very limited in the Ozarks, where oak-hickory prevails; between the Southern Appalachians and the Ozarks there is continuous shift of emphasis between the populations of these groupings. It may have little meaning to say that one association is the climax here and another association the climax there, with an ecotone between them. Fundamentally, the difference in climaxes is one of relative importance of populations at different points along gradients. Along the moisture gradient at a given elevation in the Smokies, the stand populations shift progressively as species and groups of species decrease and drop out while others enter and increase. Along the elevation gradient the whole moisture-gradient pattern changes in character as species populations and vegetation types change in relative importance from lower elevations to higher. Along the climatic gradient west from the Cumberlands species populations, vegetation types, and whole groups of species, or associations, drop out and enter, decrease and increase, or replace one another in relative importance. The gradient west from the Cumberlands provides an especially favorable opportunity to observe how the climax pattern of one area may be gradually transformed along a climatic gradient to that of another area.

CONSIDERATIONS OF LOGIC AND METHOD

In the phenomena with which the student of vegetation deals, at least three major levels may be recognized. The first of these is that of environment, formulated here as a pattern of gradients. A second is that of populations of individual organisms, distributed in relation to these gradients. A third is that of community phenomena as such—community composition, diversity, productivity, metabolic and energetic function, etc. The level of the individual organism itself is hardly to be omitted from consideration between the first and second; but the present study relates distributions of populations to environmental gradients.

It is generally thought that interpretation in science should proceed from lower to higher levels, as from the chemical to the biological, the individual to the social. Because of the mutual interrelations of levels, study and interpretation must sometimes proceed in the opposite direction; thus the individuality of the person is scarcely to be understood except in relation to a social milieu, and the individuality of distribution of a species population is to be understood in relation to a pattern of communities. Some of the methods of synecology may well be considered, however, in relation to the ideal of proceeding from lower levels to higher.

When a vegetation study proceeds from community-types to a consideration of species distributions, it is proceeding from the third to the second level. In relation to species distributions, community-types are secondary or derivative phenomena; for it

is the distributional relations of species which cause ecologists to recognize community-types. The approach to species distributions through community-types thus involves a methodological inversion, proceeding from a higher to a lower level and from secondary phenomena to the distributional relations which underlie them. If, on the other hand, problems of the validity and meaning of associations are approached by way of the associations themselves, other difficulties of method appear. Samples are taken from the vegetation, and it is difficult to take such samples without preference for those which conform to subjective ideas of associations and some exclusion of those which do not. If, now, the samples are used to study validity of associations, a clear circularity is introduced into the procedure; associations are being studied in terms of samples taken in terms of associations. The student is thus caught in a circle of studying secondary phenomena and his own abstractions from them in terms of themselves, in place of the more reasonable procedure from lower levels to higher. The contrary viewpoints of Du Rietz (1921:215) and Tansley (1920) may be noted.

It has been indicated that the approach to species distributions along the moisture gradient (but not along the elevation gradient) used in this paper also involves a circularity. It is further clear that the approach to the moisture gradient proceeds from the higher level of the community gradient to the lower one of the assumed gradient of physical environment —the approach is inferential. The point is not that such procedures are excluded from ecological methods; it is that they should be understood, allowed for, and made explicit. The author has sought to state such limitations in his own methods and feels that certain limitations of other methods which may be advanced as alternatives should also be observed.

The relation of abstract types to the stands from which they are abstracted involves further difficulties. In preliminary field work a type or association is recognized, and a number of samples conforming to it are taken. The samples are relatively uniform and as a group distinct from those taken to represent other associations; the further sampling thus reinforces the conception of the association. This, now, is likely to be seen as a "good," "real," or "valid" unit, verified by the sampling. The abstract conception is likely to be projected back into nature and regarded as a real unit of structure of that which has been sampled; the unit in the ecologist's mind is reified or hypostatized (cf. Tansley 1929). The initial choice of a "climatic climax" may similarly be reinforced by observations of successions and used as a basis for further interpretation, until the "climatic climax" seems an established and necessary fact. It is all too easy to move from the view that such abstractions have real usefulness to the view that they are part of, or must correspond to, reality.

The reification of the community-type is often apparent in the manner in which quantitative data on communities are interpreted. In sampling, an ecologist must usually choose certain stands as "typical" or "representative" while other stands are passed by as atypical, transitional or mixed, or disturbed. When a number of stand samples are presented in a compiled table for a community-type, the table and the properties of the community-type indicated by it represent not merely "the community," but an ecologist's *conception* of the community as this influences his choice of samples. A constancy value of 100% for species A may sometimes mean little more than that an ecologist regards as typical only stands containing species A. Consistent difference and apparent discontinuity between compiled tables for two community-types may imply only that intermediate stands were not sampled. Statement that a community-type is homogeneous or heterogeneous may reflect the narrowness or broadness of the ecologist's conception, as this directs his sampling. The author would emphasize both the value of such compiled tables and the fact that sample choice, and therefore statements about the community-type and constancy and fidelity of species, can seldom be wholly independent of a given ecologist's conception of the community-type. In practice compiled tables are often presented and inferences drawn from them as if the table represented "the community" in nature, wholly independently of the ecologist's interpretation of it.

Two very general difficulties appear here, in the failure to allow for the ecologist's interpretation of vegetation as guiding choice of data on which further interpretation is based, and the confusion of levels involved in the word "community." At least three levels of phenomena may be recognized among the applications of this term (cf. Dice 1952:426): (1) *communities* or *stands* which are essentially homogeneous over some area of the earth's surface and comprise all organisms above and below the soil surface in this area, (2) *community-fractions* and *micro-communities*, comprising some organisms of the community or stand which are for some reason grouped together, as in a stratal community of plants or animals, a community of animals of a particular taxonomic category, or the community of a special micro-environment, and (3) *community-complexes*, comprising a number of distinguishable communities or stands arranged in a mosaic or pattern in space, such as landscapes, biotic provinces, the complexes of bogs and frost-determined landforms, topographic patterns, etc. On each level abstract *types* of communities may be recognized, such as: (1) formations, associations, sociations, dominance-types, site-types, (2) unions, socions, micro-associations, (3) landscape-types, bog types, climax-complexes, the generalized topographic patterns of the present work. The ambiguity of the term *community* results not from the accepted convention that it may apply on any level of community-size from the inhabitants of a termite's gut to those of an ocean basin, but from its application on at least two levels of abstraction: the con-

ception of a particular "concrete" stand, and that of an abstract type derived from several more or less similar stands.

Other fields are not similarly affected by use of the same term for such different concepts as, say, organism and taxon, individual and social class, personality and character-type. An association is not a community; it is a type of community. Various authors have interpreted the association as a "concrete" unit (Du Rietz 1921:15, 1928, 1929, Alechin 1925, Clements 1928:128); many others have recognized associations as abstract units (Nordhagen 1922, 1928, Wangerin 1925, Kylin 1926, Lüdi 1928, Wendelberger 1951, 1952, Dice 1952:425). Abstract character of the association has in general been emphasized in the school of Zürich-Montpellier, and the stand has often been termed the association-individual (Pavillard 1912, 1935, Braun-Blanquet & Pavillard 1922, Braun-Blanquet 1921, 1951). Nevertheless, the confusion of levels in the term *community* exists as an encouragement to ambiguity and the uncritical transfer of information and inferences about communities in one sense to communities in the other sense. In the author's opinion, this usage is a major factor of confusion, misunderstanding, and ineffectiveness in discussions of the nature of communities and types of communities. It is suggested that clarity of discussion is greatly enhanced by a simple and fundamental distinction of terms: *Community* should be applied only to the concrete community or stand, and any abstract type or class of communities may be termed a *community-type*.

The general conception most appropriate to the theory of community-types is that of *class* (Langer 1953). A stand is an individual member of that class which is an association or other community-type; in this relation it need be assumed neither that the stand is discontinuous with other stands nor that the class is discontinuous with other classes. The membership of the class forms its extensional or denotative definition; those criteria by which it may be decided whether a given stand is, or is not, a member of the class constitute its intensional or connotative definition. (E. g. Members of association A shall contain at least 4 of the following character-species . . . *or,* Members of association B shall have canopies containing at least 50% *Fagus grandifolia* and *Acer saccharum*).

Intensional and extensional definitions are coupled and normally develop in relation to one another in the interaction or transaction between ecologists and vegetation. The relation of members to the class is not, however, one of parts to the whole; for the community-class is not a unified, functional whole of which stands are the interacting or interrelated parts. The class, in extension, is the collection of stands or stand-samples to which a class-concept (the intensional definition) applies. The class is thus a *conceptual* entity; and membership in the class is the relation of falling under, or corresponding to, a concept. An association or other community-type is the product of an ecologist's study of natural communities and formulation of a class-concept.

In a complex pattern such as that formed by natural communities, the creation of class-concepts is in general "free" or "arbitrary" (see also Part I). No properties of vegetation force an ecologist to choose a single manner of defining community-types. Emphasis of different properties of vegetation will lead to different class-concepts of vegetation types; these class-concepts in extension will have differing memberships, variously related to one another. The different definitions of community-types in different schools, the nature of the data presented in this study, and the recent research of Goodall (1953) may show how variously stands may be grouped and class-concepts derived from them. The concept of the "complex continuum" may be modified in two respects—granting that a degree of discontinuity exists in vegetation and that a degree of species clustering may also occur—without altering this understanding that ecologists enjoy considerable freedom in the creation of their class-concepts for associations and other units.

A further means of clarifying relations of communities and community-types is through the emphasis of non-identification in general semantics (Korzybski 1933, Johnson 1946, Vogt 1948, Rapoport 1952). A manner of thinking based upon classification and limited by that classification, tending to identify classes with the phenomena from which they are abstractions, to accept the classes as inherent in these phenomena and to approach the phenomena only through the classes, may be termed "Aristotelian" in the sense of the general semanticists. Fundamental to the classificatory approach and to ways of thinking related to it are three "Aristotelian laws."

1. The law of identity: A is A, beech-maple is beech-maple, beech-maple stands A_1, A_2, A_3, . . . A_n belong to or *are* Beech-Maple Association A.

2. The law of the excluded middle: Anything either is or is not A; each of a set of stands A_1, A_2, A_3, . . . A_n either is or is not a stand of Beech-Maple Association A.

3. The law of non-contradiction: Something cannot be both A and not-A; stands A_1, A_2, A_3, . . . A_n cannot both belong and not belong to Association A.

The limitations of these laws may be observed in relation to the diversity and intergradation of stand types. A is not A; beech-maple stand A_1 is not beech-maple stand A_2; the Beech-Maple Association is not beech-maple stands A_1, A_2, A_3, . . . A_n; the Beech-Maple Association is not beech-maple vegetation; the beech-maple concept of one ecologist is not the beech-maple concept of another ecologist; beech-maple, in general, is not beech-maple. Something can just as well be both A and not-A; a stand can be both the Beech-Maple Association of one ecologist and not the Beech-Maple Association of another ecologist, to whom it may be the Maple-Basswood Association. If the class-concept is so stated as to provide a sharp limit (50% Fagus plus Acer), then

a stand either is, or is not, a member; but the limit is arbitrary. If (as is more generally the case) the class-concept is that of an ideal stand approached by actual stands (full dominance of Fagus plus Acer, *or*, possession of all or most of the following character-species . . .), then stands are not simply beech-maple or not-beech-maple; they may be 90, 65, 40, 15, 5% beech-maple by the chosen criterion of beech-mapleness.

The justification of the classificatory approach is not that classes are inherent in, or necessarily appropriate to, the phenomena being studied, but that they serve the needs of investigation and scientific communication. In the latter part of this work the author will venture to classify stands of the Great Smoky Mountains. Up to the present, however, a different and non-classificatory conception has been developed. This interpretation which is, like the association-unit theory, a conceptual construction permitting the relation to one another of data on environments, organisms, and communities, may be briefly formulated. Physical environment forms a complex pattern of gradients. At each point in this pattern, communities develop through succession; and as community and soil develop and physical environment is modified, a successional gradient of community composition corresponds to a successional complex-gradient of environments. At the culmination of successions, a complex climax vegetation pattern corresponds to the complex pattern of environmental gradients. In this pattern species populations distribute themselves individualistically, each maintaining itself where it can in relation to gradients which are, now, complex-gradients of environments in communities. Species distributions mostly take the form of tapered curves; and the vegetation itself forms a complex continuum of populations, in which local steepenings and interruptions of gradation occur.

One approach to this pattern is through classification of its parts. An effective alternative is through study of gradients of species populations and of community characteristics in relation to gradients of environment (Whittaker 1951, 1952, 1954a, 1954b). These two approaches, emphasizing relative discontinuity *vs.* relative continuity, may be regarded as mutually complementary and as serving different needs, rather than antagonistic. It is the latter approach, of relating gradients to gradients, which has been explored in the preceding parts of this paper. With varied details of technique the basic method may be recognized also in work of Ramensky (1924, 1930) and other Russian authors studying ecological series, in Finnish work with ecological series of site-types, and in studies by Mølholm Hansen (Hansen 1930, 1932),Tuomikoski (1942), Ellenberg (1948, 1950, 1952), Curtis & McIntosh (1951), Brown & Curtis (1952), and Hale (1955), Major (1951), Goodall (1954a, 1954b), and Beard (1955). It is suggested that this approach of relating gradients to gradients be termed *gradient analysis*.

CONCLUSION

The thesis of this discussion, developed through the five preceding sections, is that (1) species populations are variously distributed, each according to its own physiology and genetic pattern, so that (2) community-types are not organized units of many species, but (3) can be interpreted and defined in terms of population distributions along gradients and (4) understood as part of the complex population patterns of climax vegetation, to which (5) the method of gradient analysis is appropriate. In simile, vegetation may be compared with a pattern of colored lights cast upon a screen, a pattern formed by innumerable overlapping individual beams of light, some bright, some faint, some broad, some thin, some of simple and some of complex form, but most having a brighter center and dimming gradually away from this, all somewhat mobile, changing position and intensity through time, moving somewhat independently and thus changing their relations to one another, composing all together a blended, intricate, and fluid pattern. Parts of the pattern may be classified; but an essential complement to the classificatory approach is one treating vegetation patterns as wholes, regarding vegetation units not as objects in themselves but as fragments abstracted from the design within and in relation to which they exist and have their meaning.

III. VEGETATION TYPES AND THEIR DISTRIBUTIONAL RELATIONS

BASES OF RECOGNIZING AND DESCRIBING TYPES

Vegetation of the Great Smoky Mountains has been interpreted (Parts I and II) as a complex population pattern, but it is difficult to describe as such. For the descriptions to follow, the author has resorted to a system of vegetation types. The different schools of ecology offer a variety of vegetation units from which to choose according to the purposes of a particular study. The most widely used system, that of Braun-Blanquet (1921, 1932, 1951), is not well suited to the present study because data on herbs, bryophytes, and lichens are incomplete. Rather than follow this or any other established system, the author has sought to let vegetational conditions of the Smokies and the kind of data available determine the choice of units. In the recognition of types physiognomy and dominance are emphasized, following the traditions of English-language ecologists.

Two vegetation patterns or complexes are first to be distinguished. At elevations over 4500 ft (1370 m) in the northeastern half of the Smokies, forests of spruce and fir prevail. These may be regarded as the subalpine forests of this range, and as the local representation of the taiga or boreal forests of high latitudes and altitudes. At elevations below 4500 ft (and above 4500 ft outside the range of spruce), forests are predominantly of deciduous trees, as are the forests of the eastern United States south of the spruce-fir belt. Each of these patterns includes

more than one physiognomic type; they are conse-
quently not formations. The word "system" has been
used for them here, with no intention of establishing
this as a new vegetation unit. These two major parts
of the vegetation pattern are named, for their geo-
graphic relations, the "Eastern Forest System" and
the "Boreal Forest System."

Physiognomic types within each system are a logi-
cal basis of further division. Vegetation of the
Smokies includes types dominated by four major
growth-forms—needle-leaved evergreen or coniferous
trees, deciduous broad-leaved trees, evergreen-sclero-
phyllous shrubs, and grasses. It is useful for the
present study to divide the tree growth-forms
further. The pines of the Smokies, forming open,
xeric, lower-elevation stands are conveniently distin-
guished as a growth-form from the abietine trees
(Picea, Abies, Tsuga) forming denser and less xeric
stands, predominantly of higher elevations. Oaks
affect lower strata through late leafing and type of
leaf-litter differently from many other deciduous trees
(Braun 1935b, Kucera 1952) and may be distin-
guished as a growth-form. Along the moisture gradi-
ent in the "eastern" forest pattern, non-quercine trees
predominate in mesic sites, oaks in intermediate ones,
and pines in xeric ones (see Part I). Ericaceous
shrubs are a major growth-form in the Smokies,
dominating heath balds and sharing dominance with
an open tree stratum in forest-heaths. The heath
strata are predominantly evergreen but contain, and
are in some types dominated by, deciduous Vac-
cinioideae. Physiognomic types recognized in the
Smokies are thus: abietine forest, non-quercine de-
ciduous forest, oak forest, pine forest, forest-heaths
(pine heaths and oak-chestnut heath), heath bald,
and grassy bald.

Vegetation types are further distinguished accord-
ing to their dominant species. All but two of the
vegetation types described below are defined by domi-
nance of one species or a pair of species. The two
exceptions (cove forest and heath bald) are domi-
nated by several important species, the proportions
of which vary from one stand to another. These types
are consequently defined by distributional groupings
or commodia (Part II) of species.

Since the vegetation units are not defined primarily
by character-species, according to the system of
Braun-Blanquet (1951), they are not necessarily as-
sociations in the sense of that term which most nearly
has international acceptance. They consequently will
be designated only as "types" and will not be given
formal, latinized names. In deference to phytosocio-
logical practice, however, character-species have been
designated for these types as far as possible. To in-
dicate these without repetition, names of character-
species are marked with asterisks (*) in the descrip-
tion of the type to which they apply. In view of the
distributional data already discussed, it need hardly
be emphasized that these character-species are of low
degree (mostly preferential or holde). Very few spe-
cies of the Smokies can be considered exclusive or

treue for vegetation types, unless these are defined
more broadly than in the present work. In certain
cases species have been designated character-species
for two vegetation types in which their varieties or
distinguishable population-types are centered. No
effort has been made to distinguish local and regional
character species, and character-species indicated can-
not be assumed to have more than local usefulness.

The units used differ also from the very broad
dominance-types, characterizing extensive regions as
prevailing climaxes, which are termed associations by
many American authors (Clements 1928, Weaver &
Clements 1929, Oosting 1948, Braun 1950). What-
ever their value for geographic treatment of vegeta-
tion, the American associations are considered too
broad and ill-defined to be suitable as units in the
Great Smoky Mountains. In dealing with the vegeta-
tion of this range it is surely a question not of "oak-
hickory," "oak-chestnut," and "oak-pine," but of
particular types dominated by certain species from
these genera.

The fifteen types listed below are by no means the
only ones which might be recognized. In a vegetation
pattern as complex as that of the Smokies, a large
number of dominance-types may be distinguished in
variations in stand composition. The author has
subjectively chosen those types which seem most sig-
nificant in the vegetation pattern. The types recog-
nized are those which occur most frequently in the
pattern and occupy largest areas of the mountain
surface. They are those types which seem to be
combinations of dominants usually appearing in a
particular range of environmental conditions, rather
than occasional variations in stand composition. Only
those types considered "climax" in the sense of ap-
parent stability in their present sites will be de-
scribed. Major successional types which may be men-
tioned include Prunus pensylvanica, Betula lutea, and
Amelanchier laevis forest types at high elevations,
Betula lenta and Acer rubrum forests in intermediate
sites of most elevations, stands of Pinus spp. in drier
sites of middle elevations and many sites of lower
ones, and Liriodendron tulipifera in more mesic sites
of lower elevations. A type list for the Smokies, in-
cluding some successional types, is given by Cain
et al. (1937).

The use of vegetation units is in contrast to the
approach developed in parts I and II. The funda-
mentally different approach through units has been
chosen for Part III strictly as a matter of conveni-
ence in describing parts of the vegetation pattern and
relating the pattern to topography. It should be
emphasized that the classification developed is only
one of many, equally valid, ways of classifying vege-
tation of the Smokies. It should not be supposed that
the units to be described are "real" units, already
marked out in the vegetation, which the author has
recognized by studying it. Classifications of vege-
tation are human creations, resulting from the study
of vegetation for certain purposes, emphasizing cer-
tain properties of vegetation which become criteria

of classification. Continuity of most vegetation types has been previously discussed and may well be kept in mind; but, for brevity's sake, most transitions between types will not be described.

The descriptions are based on data compiled in the composite stand tables (Appendix C). For these, the 300 site-samples were classified into types according to dominant species. Within each vegetation type the site-samples were further divided by 1000-ft elevation belts and, in some cases, by relative importance of moisture classes of trees. By this classification, the site-samples were grouped into 27 composite tables for vegetation types and their subdivisions, each table including about 1000 tree stems and 100 canopy stems. The tables cannot be published here, but are otherwise made available (see Note on Supplementary Publication). Numbers of tables in Appendix C on which descriptions are based are indicated after the names of types.

The classification of climax vegetation types in the Great Smoky Mountains is as follows:

I. Eastern Forest System

  A. Mesic, non-quercine forests
    1. Cove hardwoods forest (1-7)
    2. Eastern hemlock forest (8, 9)
    3. Gray beech forest (10, 11)

  B. Intermediate, oak forests
    4. Red oak-pignut hickory forest (12)
    5. Chestnut oak-chestnut forest (13-15)
    6. Chestnut oak-chestnut heath (16, 17)
    7. Red oak-chestnut forest (18, 19)
    8. White oak-chestnut forest (20, 21)

  C. Xeric, pine forests
    9. Virginia pine forest (22)
    10. Pitch pine heath (23)
    11. Table mountain pine heath (24)

  D. Extreme exposure type
    12. Grassy bald

II. Boreal Forest System

  A. Subalpine forests
    13. Red spruce forest (25, 26)
    14. Fraser fir forest (27)

  B. Extreme exposure type
    15. Heath bald

VEGETATION TYPES OF THE GREAT SMOKY MOUNTAINS

1. COVE HARDWOODS FOREST

The cove forests of the Southern Appalachians are doubtless among the most beautiful deciduous forests in the world. Trunks of the canopy trees, 3 and 4 ft or more in diameter, rise to bear crowns 75 and 100 ft from the forest floor. Tops of the trees reach 100 to 150 ft with occasional great tulip trees (*Liriodendron tulipifera*), 6 and 7 ft in diameter, approaching 200 ft. Below the canopy smaller trees form a broad, but not dense, foliage layer. In summer a verdant growth of mesophytic ferns and other herbs nearly covers the forest floor. Small tree species and shrubs are almost absent from many stands,
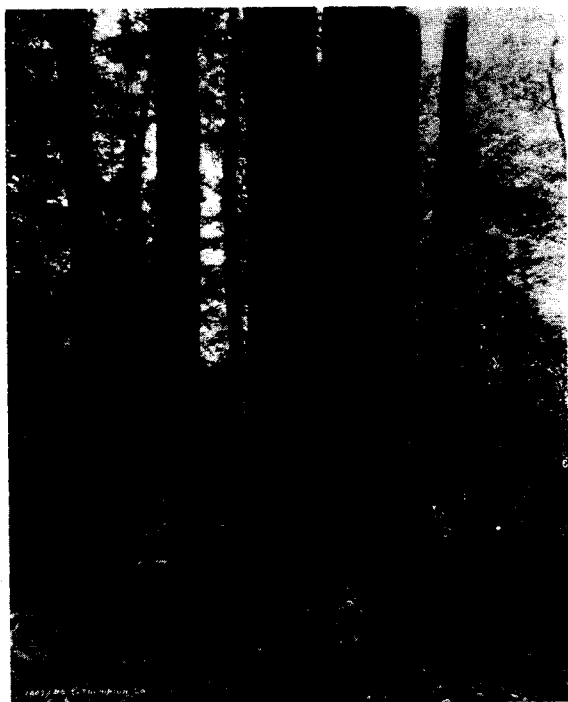
FIG. 14. Cove hardwoods forest, Porter Creek Flats. Reproduced by permission of Thompsons, Inc., Knoxville, Tenn.

and the small stems of the reproducing trees are not dense. The forest has an open and spacious appearance, with a high deciduous canopy borne above a rich herbaceous carpet and little intervening woody undergrowth.

Six tree species share dominance in most of the cove forests—*Tsuga canadensis, Halesia monticola*, Aesculus octandra*, Tilia heterophylla*, Acer saccharum*,* and *Betula alleghaniensis**—, while *Liriodendron tulipifera* and *Fagus grandifolia* are important in some stands. Each of these forms 10 or 20% of the canopy in some stands and is locally more important. Together these 8 species make up 80 or 90% of the canopy of cove forests, dominating stands in different combinations. With them occur a number of other species. *Fraxinus americana* and v. *biltmoreana, F. pennsylvanica* v. *subintegerrima, Quercus borealis* v. *maxima, Magnolia acuminata, Carya cordiformis*,* and the large mesic population of *Acer rubrum* are widely distributed canopy species which are seldom numerous. *Prunus serotina** is locally important between 3500 and 5500 ft. Species of small and medium stature include *Magnolia tripetala** and *Carpinus caroliniana** at low elevations, *Magnolia fraseri, Cladrastis lutea*, Ilex opaca,* and *Ostrya virginiana* at most elevations, and *Acer spicatum* and *Amelanchier laevis* at high elevations. *Castanea dentata* and other subxeric species are absent from the most mesic stands of deep valley flats (see tables 2 & 3; Appendix C, tables 3 & 4; Whittaker 1951, tables 1 & 3).

The shrub stratum is poorly developed or absent in stands of valley flats at middle elevations. *Euonymus americanus** and *Lindera benzoin** occur in low-elevation stands, *Cornus alternifolia, Viburnum alnifolium,* and *Ribes cynosbati* in high-elevation ones. *Hydrangea arborescens* occurs locally at all elevations; *Rhododendron maximum* occurs along streams and (often with *Leucothoë editorum*) in some other sites, particularly under hemlocks. There is, however, no shrub grouping characteristic of the cove forests as a whole.

The herb stratum is the richest in the mountains. Cain (1943) lists over a hundred species for the spring and summer aspects, and Braun gives comparable lists in her papers (1935b, 1940a, 1942). Summer herb coverage is as high as 80 percent in some sites, with a luxuriant growth of mesic ferns and herbs of spreading or umbrella-shaped foliage form. Most species of the mesic herb union are centered in the cove forests and may be regarded as character-species for them. The most abundant species of the union in summer are *Eupatorium rugosum**, *Cimicifuga racemosa**, *Caulophyllum thalictroides**, *Impatiens pallida**, *Laportea canadensis**, *Trillium erectum* v. *albiflorum**, *Aster divaricatus**, and the ferns *Dryopteris spinulosa* v. *intermedia**, and *Athyrium thelypterioides**. Beneath them grow smaller species—*Viola* spp., *Stellaria pubera, Tiarella cordifolia**, Galium triflorum,* and *Euonymus obovatus.* The beautifully developed herb community is stratified as the forest is, with a canopy of tall spreading herbs and ferns and an undergrowth of lower and prostate plants. Some species of the submesic herb union occur, and toward higher elevations species of the mesic high-elevation union form a conspicuous part of the stratum.

The relation of cove forest and mixed mesophytic to the Arctotertiary forests has been indicated by Braun (1935a, 1947, 1950). Cain (1943) studied the Tertiary character of the cove forests in the Smokies, using fossil records of genera and distributions, particularly the frequent eastern Asia-eastern North America disjuncts. Cain considered that all genera of ferns and shrubs and most genera of trees and herbs were of Tertiary history. His figures for trees and flowering herbs were 86 and 75% of genera with known or indicated Tertiary history, including the minor species in his lists. On the basis of his constancy-class V or the most abundant species of the low-elevation mesic herb union listed here, all principal herb species are of Tertiary history. The union is related, and linked by its predominant growth-form, to Lippmaa's (1939) *Galeobdolon-Asperula-Asarum* Union of herbs surviving from Eurasian Arctotertiary forests. Of the trees listed by Cain, if Tulipastrum is grouped with Magnolia, and if *Robinia pseudoacacia* and *Oxydendrum arboreum,* which are extraneous to the cove forests, are set aside, all are of Tertiary history. The Tertiary history of the genera certainly does not imply that extensive changes have not occurred. However, as Cain suggests, a naturalist wandering, unknown to him, into some Tertiary forests might see no very conspicuous difference except the presence of Ginkgo and Sequoia (or Metasequoia).

Various combinations of dominants appear locally in the cove forests: *Acer saccharum-Halesia monticola, A. saccharum-Tilia heterophylla, Tsuga canadensis-T. heterophylla, Aesculus octandra-T. heterophylla, A. octandra-Betula alleghaniensis, T. canadensis-Liriodendron tulipifera, T. canadensis-Fagus grandifolia, T. canadensis-B. alleghaniensis, A. saccharum-F. grandifolia.* None of these (cf. Cain 1943) represents a well-defined and extensive type. The most significant change in the cove forests, other than the transition to oak types, is the gradual rise of *Aesculus octandra, Tilia heterophylla,* and *Betula alleghaniensis* toward their different modes at higher elevations, where they form the so-called northern hardwoods dominated by these three southern tree species (cf. Braun 1950:207). The upper cove forests may be regarded as a sub-type of the cove forests with the same dominants in different proportions, but with Liriodendron and Tsuga often absent, and with *Acer spicatum, Amelanchier laevis, Viburnum alnifolium,* and *Cornus alternifolia* dominating the stratum of shrubs and low trees. *Monarda didyma, Rudbeckia laciniata, Oxalis montana,* and other species of the high-elevation mesic union appear in the herb stratum.

An additional subtype may be recognized in the cove forest transition between the mesic forest and oak forest groupings. As less mesic sites are approached from the cove forests, increasing percentages of submesic species occur in the stands. Subxeric species (*Castanea dentata, Oxydendrum arboreum, Quercus alba* and *Q. prinus, Nyssa sylvatica*) also appear in significant numbers. In the cove forest transition 25 or more tree species, representing all classes but the xeric, may be encountered among 200 or 300 stems. In the shrub stratum *Rhododendron maximum* is most important, and many of the shrub species of oak-chestnut forests appear. With their heavier growth of small trees and greater shrub coverage (20-50%), these stands are less open and spacious in appearance than the cove forests themselves. Herb coverages in cove forest transition vary widely (5-50%), the extremes of this range corresponding to the low coverages in oak-chestnut forests and the high ones in cove forests.

Mixed Mesophytic in the Smokies and Cumberlands

The cove forests of the Smokies are closely related to the mixed mesophytic forests of the Cumberland Mountains (Braun 1935b, 1940a, 1942, 1950), but the mesophytic communities of the two ranges differ in some respects (see also Part II). With the greater area occupied by mixed mesophytic in the Cumberlands, there is a greater differentiation of the association into segregates; some of the combinations mentioned by Braun were not observed in the Smokies. Notable among these are the beech (*Fagus grandifolia*) ravine communities, *Quercus alba-F.*

grandifolia, F. grandifolia-Castanea dentata, Tsuga canadensis-F. grandifolia, and *T. canadensis-Q. alba* forests. In the Smokies the low-elevation (white) beech is a minor tree, and the low-elevation population of *Quercus alba* is important only in oak-hickory stands which are limited in area. In the somewhat lower elevations of the Cumberlands these two low-elevation populations are major tree species and dominants of types.

In general composition mixed mesophytic of the Cumberlands may best be compared with cove forest transition as recognized in the Smokies. Thus the average composition of mixed mesophytic on Black Mountain, based on 2,000 stems (Braun 1940a: 237) shows a striking correspondence with cove forest transition below 2500 ft (Appendix C, table 6) in the Smokies. Principal differences are in the occurrence of *Tsuga canadensis* as a major species in the Smokies, and the appearance of *Halesia monticola* and *Pinus strobus* in the Smokies stands. The formulas for composition in terms of moisture-classes (Part I) permit further comparison of forests in the two areas. These formulas (Mesics: Submesics: Subxerics: Xerics) are, for Braun's table of mixed mesophytic, 67:12:20:0, and for the cove forest transition in the Smokies, 65:14:21:0. Table 1 of Braun (1950:53) indicates the differences in composition of all-deciduous mixed mesophytic forests of the Cumberland Mountains according to slope. The stands of mesic slopes (81:9:10:0 to 70:12:18:0) correspond to more mesic cove forest transition stands in the Smokies, while in stands of south slopes in the Cumberlands the mesics are slightly in the minority (49·15:35:0, 42:20:39:0).

Cove forests themselves in the Smokies are more distinctly mesophytic in composition. For three composite stand counts from different elevations (Appendix C, tables 1, 2, 5) canopy composition was— 88:10:2:0, 89:8:3:0, and 94:6:0:0. The cove forest stands of Porter Creek and Kalanu Prong gave formulas of 98:2:0:0 and 96:4:0:0, respectively. These cove forests are most nearly comparable with one of the segregates of the mixed mesophytic, the sugar maple-basswood-buckeye forest (*Acer saccharum-Tilia heterophylla-Aesculus octandra*), except for the absence of *Halesia monticola* from the latter (see Braun 1950:56). In this segregate mesics may form more than 90 percent of the stand; composition in examples given (Braun 1950:58) ranges from 93:6:1:0 to 78:15:7:0. In some examples of beech ravine communities also the mesics comprise more than 90 percent of the stand (Braun 1950:60). For comparison between the two ranges, the cove forest transition is best identified with the all-deciduous mixed mesophytic (and equivalents with some *Tsuga canadensis*), the cove forests themselves with the sugar maple-basswood-buckeye mesic segregate.

In Braun's scheme of interpretation, the cove forest transition should perhaps be given primary emphasis and the cove forests and oak forests adjacent to it regarded as segregates. Certain features of these mesophytic forests in the Smokies have discouraged the author from following this course:

1. *Tilia heterophylla* and *Aesculus octandra* are indicated by Braun (1950:43) to be characteristic species of Mixed Mesophytic. In the Smokies, at least, other character-species may be added to these, notably *Halesia monticola, Betula alleghreniensis, Cladrastis lutea,* and the local population of *Acer saccharum.* The populations of these character-species are centered not in the cove forest transition but in cove forests proper.

2. The optimum development of mesophytic forests, with the richest mesophytic herb stratum as well as strongest dominance by five of the character-species above, is in the cove forests of deep valleys, not in the cove forest transition.

3. *Castanea dentata* and other tree species characteristic of the oak forests are almost absent from the cove forests proper and extend into cove forest transition only with the tails of their distributions. It is difficult to interpret these species as belonging to the cove forests and segregating into oak forests. Rather than this, their distributions appear simply to overlap in part with those of cove forest species.

4. Applied to the Smokies, the Mixed Mesophytic in Braun's sense seems less a definable vegetation type than a range of stand conditions from cove forests to more mesophytic oak forests. Mixed Mesophytic seems too broad and heterogeneous a grouping, bringing together into one association species whose relations to the moisture gradient are too widely different.

In the Cumberlands, stands of mesic species mixed with oak-forest species form the prevailing climax type. It is consequently reasonable to emphasize these highly mixed stands and to regard the mesic and xeric extremes as secondary to them. The diverse stand types of the Cumberlands may then be given unity in terms of the monoclimax theory, very broad definition of associations, and the conception of association-segregates. In the Smokies it seems preferable to identify the mesophytic association in question with the cove forests and to regard stands highly mixed with oaks and *Castanea dentata* as transitional. Applied to the Cumberlands, the author's interpretation would suggest that the Mixed Mesophytic comprises: (1) truly mesophytic forests (sugar maple-basswood-buckeye), (2) a wide range of highly mixed transitional stands between these and oak forest types, and (3) various segregate types dominated by species which are represented also in stands of the preceding.

There are no signposts in nature to tell us whether we should see mixture occurring in one direction or segregation in the other, where in a vegetational continuum we should locate our associations and where our transitions. The interpretations of Braun and the author are different, possible patterns of abstraction from the vegetation of the Southern Appa-

lachians. It is not asserted that the interpretation of Braun (1950:195-215) is in any way erroneous when applied to the Smokies. For the present study, however, "cove forest," and "cove forest transition" have been preferred to the broader conception of "Mixed Mesophytic" for locally recognized, quantitatively distinguished types.

2. EASTERN HEMLOCK FOREST

Toward higher elevations hemlock (*Tsuga canadensis**) has an increasingly high population peak in mesic sites (Fig. 15). The heavily hemlock-dominated stands of upper slopes and ridges have been called the hemlock ridge forest and suspected of being segregated by thin soils (Cain *et al.* 1937).
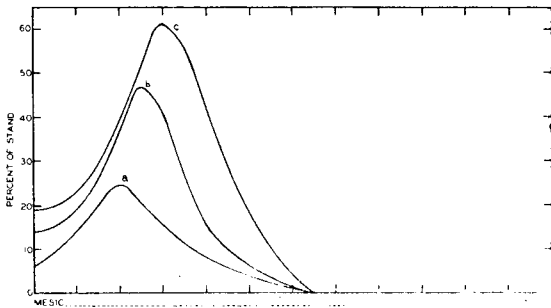
Fig. 15. Rise of *Tsuga canadensis* toward higher elevations, distribution in moisture-gradient transects: a, 1500-2500 ft; b, 2500-3500 ft; c, 3500-4500 ft.

Some broadleaf cove forests occur on equally steep slopes, however, and some hemlock stands occur on valley flats. Hemlock stands appear in sites which are somewhat less mesic than those of the cove forests themselves, whether on open valley flats at middle elevations, or slopes above the valleys at high elevations.

Hemlock stands are so different from deciduous cove forests as to appear almost unrelated. The stands have the dense, dark appearance of some abietine forests; the herb layer may be almost absent and the shrub layer a tangle of Rhododendron. The forests have a somber aspect, unrelieved by the verdant green of deciduous forests, with no colors but the brown floor and tree trunks and dark evergreen tree and shrub foliage, except for flower clusters of Rhododendron shining white and purple where they may be caught by sunlight down the slopes. The trees are as large as those of broadleaf cove forests; stems 3 and 4 ft in diameter bear the canopy crowns, reaching heights above 100 ft. The large stems are more closely spaced than in the cove forests, and small tree stems are fewer.

Hemlock may form more than 70 or 80% of the canopy at higher elevations, but stands may include most other mesics and some other tree species. Because of the large size of hemlock, stands in which it comprises only 20 or 30% of the stems may be dominated by it. The most important associates of hemlock are *Halesia monticola*, *Betula alleghaniensis*,

*Magnolia fraseri**, and sometimes *Liriodendron tulipifera* or *Fagus grandifolia*. A low-tree layer of *Ilex opaca**, *Betula lenta*, *Acer pensylvanicum*, and most other small-tree species of the submesic and ecotonal-mesic unions, is well developed in some stands but relatively unimportant in others in which Rhododendron dominates the undergrowth.

On steep slopes the shrub layer may be strongly developed as a high heath. At higher elevations heath coverage may be 60 to 80% with *Rhododendron maximum* or *R. catawbiense* dominant. The *Tsuga-Rhododendron* combination resembles the type described by Oosting & Billings (1939), but the combination with Vaccinium (Polycodium) was not encountered in the Smokies. *Leucothoë editorum* is frequent in these forests, *Hydrangea arborescens*, *Kalmia latifolia*, and others are occasional. Some stands on lower flats, more mixed with hardwoods, have little shrub undergrowth.

The herb stratum may be nonexistent in dense stands with heavy heath undergrowth. The effect of hemlock needles and the superficial root system is to produce a surface soil much more acid than that of hardwoods stands and to reduce water penetration to lower levels, drying the soil (Daubenmire 1930, 1931). Although hemlock stands occur in mesic sites, they are relatively xeric and acid for undergrowth plants. A dense Rhododendron heath may develop under these conditions, and the forest floor may be a sterile surface of hemlock and Rhododendron leaves. In stands with less heath an herb stratum of low coverage may appear. *Dryopteris spinulosa* v. *intermedia*, *Mitchella repens**, with *Goodyera repens* v. *ophioides** often growing among its stems, and *Tiarella cordifolia* are the most successful herbs. *Polypodium virginianum* is frequent on exposed rocks and roots. Herb coverage varies from zero up, related to the proportion of hardwoods and development of heath.

The hemlock forest type is most distinctive, with heaviest hemlock dominance, densest heath growth, and most impoverished herb stratum on steep slopes at higher elevations. At lower elevations stands are more mixed with hardwoods, with less heath and more herbs. Below 2500 ft the hemlock forest gradually merges with the cove forests; and hemlock becomes only one of the dominants, though the most important one, of lower-elevation cove forests.

3. GRAY BEECH FOREST

Above 4500 ft the high-elevation or "gray" population of beech (*Fagus grandifolia**) is the most important tree of mesic deciduous forests (see also Russell 1953). Gray beech forms small-tree forests. The beech itself seldom exceeds 15 in. diameter; and the bulk of canopy stems may be in the 8- to 12-in. classes, though cove-forest hardwoods occurring with it may reach fair size. In two quadrat studies canopy stems (8-10 inches) were only 25 to 40 ft high, with crowns 12 to 20 ft from the ground. Small stems may be numerous, but frequently the undergrowth is slight, with few seedlings and few or

no shrubs above a floor of sedges, ferns, and other herbs. The small, low trees with rounded crowns and the grass-like floor of sedges, open and free of woody undergrowth, led the natives to call these woods "beech orchards," a fair description of them. Trunks of the trees are mottled gray from the lichens which cover them and are so lichen-coated that barks as distinctive as those of beech and buckeye cannot be distinguished. Compared with the superb cove forests, the trees have a stunted appearance; and other species share with beech the "orchard" growth-form. In form, flora, and single-species dominance the beech woods suggest a vegetation of extreme conditions, a deciduous type in a limiting and stunting subalpine environment.

The gray beech forests of north and south slopes are so different they may best be described separately. Stands of north-facing slopes, occurring on north and northeast sides of gaps within the range of spruce and on many open slopes of the same orientations in the southwest half of the mountains, are a continuation and modification of the upper cove forests. Although beech is most numerous in stems, two trees of the upper cove forests, *Betula alleghaniensis* (or *B. lutea*) and *Aesculus octandra* are equally important in the canopy and dominate some stands. The low-tree stratum usually includes numerous small stems of *Acer spicatum*, *A. pensylvanicum*, and *Amelanchier laevis*. *Viburnum alnifolium*, *Cornus alternifolia*, *Hydrangea arborescens* and, infrequently, *Ribes rotundifolium* occur in the shrub stratum. Shrub coverage is quite low, usually 2 to 10%. The herb stratum is essentially like that of upper cove forests, but with sedges nearly always present in small coverage and with greater representation of herbs of the high-elevation mesic union—*Senecio rugelia*, *Rudbeckia laciniata*, *Streptopus roseus*, and others. Herb coverage is 40 to 60%, of the same order as that in cove forests. The north-slope beech forests are in all strata a distinctly mesic type, closely related to upper cove forests and to be distinguished as a type only by larger numbers of beech stems, limitation of tree size, and more subalpine cast of the flora.

When one crosses a gap from the north to the south side, one enters quite different beech forests, transitions to which occur in the intermediate southeast and west exposures. The south-facing, sedge-floored beech woods are among the most limited forest types in the Smokies, largely restricted to gaps and concave slopes within the range of spruce. These stands differ significantly in canopy composition from north-slope ones—in smaller number of species, greater preponderance of beech, and occurrence of *Halesia monticola* as second most important species. The ecotonal small trees are absent or unimportant; the shrub stratum is insignificant or absent, with only *Hydrangea arborescens* appearing occasionally. It is in the herb stratum that the south-slope beech forests are most distinctive, however. Sedges (*Carex aestivalis** and sp.) dominate the herb stratum with coverage up to 80 and 90%. With the sedges occur scat-

tered plants of most of the herb species of north slopes and upper cove forests except Cimicifuga. With the mesics occur a few submesics, notably *Medeola virginiana*, and members of the submesic high-elevation union, including *Prenanthes altissima**, *Arisaema quinatum**, *Angelica triquinata**, and *Solidago* sp. The abundant fern, as on north slopes, is *Athyrium filix-femina* v. *asplenioides**. The south-slope beech stands are in many respects intermediate to north-slope beech-mixed stands and high-elevation red oak-chestnut forests.

4. RED OAK-PIGNUT HICKORY FOREST

At lower elevations, usually below 2500-3000 ft, oak-hickory forests occupy the next position toward xeric sites beyond cove forest transition. In many places they are poorly developed or absent as a type, their place being taken by forests of mixed oaks and chestnut with some hickories. In their best development oak-hickory forests are dominated by combinations of northern red oak (*Quercus borealis* v. *maxima**), pignut hickory (*Carya glabra**), white oak (*Q. alba**), and mockernut hickory (*C. tomentosa**). Stands usually include *Q. velutina* and *C. ovalis**, *Q. prinus*, *Castanea dentata*, *Nyssa sylvatica*, and *Liriodendron tulipifera*. *Acer rubrum*, *Cornus florida*, and *Oxydendrum arboreum* are important small trees.

The lower strata of oak-hickory forests in the Smokies may be much like those of oak-chestnut forests. Where oak-hickory stands occur on limestone soils on the northwest edge of the range, they are quite unlike those of the mountains themselves. *Juglans nigra*, *Carya ovata*, and *Cercis canadensis* occur, and on limestone outcrops *Juniperus virginiana*, *Rhamnus caroliniana*, and *Viburnum rufidulum*, with conspicuously different lower strata of a middle-western aspect. On acid soils of the mountains, however, shrubs of the oak-chestnut forest appear, with variable coverage (5 to 50%). The ericads *Gaylussacia ursina* and *Kalmia latifolia* are usually most important, with *Rhododendron maximum*, *R. calendulaceum*, *Pyrularia pubera*, and most other shrubs of the submesic union sometimes present. Most herb species are shared with oak-chestnut forests: *Polystichum acrostichoides*, *Solidago* sp., *Aureolaria laevigata*, and *Galax aphylla* are most frequent; *Viola hastata*, *Chimaphila maculata*, *Desmodium nudiflorum*, *Goodyera pubescens*, *Prenanthes trifoliolata*, *Smilacina racemosa*, and *Uvularia pudica* all occur, along with a few mesics (*Cimicifuga racemosa*, *Aster divaricatus*, *Actaea pachypoda*). Herb coverage is generally low, in the range of 1 to 10%.

5. CHESTNUT OAK-CHESTNUT FOREST

The most extensive forests of middle and lower elevations in the Smokies are those dominated by chestnut oak (*Quercus prinus*) and chestnut (*Castanea dentata*). Oak-chestnut heaths and forests occur on almost all slopes except those facing south and southwest, and are marked unmistakably now by the gray striae of dead chestnut trunks and branches. From accounts of old-residents and from trends in

secondary forests, it seems that forests of great chestnut trees once covered most of the lower coves and broad open valleys away from stream-banks. The slope oak-chestnut stands which have survived settlement and the blight are not impressive forests. Only a few of the surviving trees, mostly chestnut oak, exceed 2 ft in diameter, although chestnuts with diameters of 4-5 ft and more are still standing in places (1947). The death of the chestnuts, by opening the stands, permitted heavy reproduction of other trees formerly limited by competition and shading, and has to date strongly favored small-tree species (cf. Keever 1953). The forests now have dense stands of small stems of *Acer rubrum*, *Oxydendrum arboreum*, *Cornus florida*, and others. One who crosses a flat or slope in the oak-chestnut forest finds his vision limited and progress retarded by the heavy undergrowth of small trees and shrubs and the spines of the catbriers (*Smilax rotundifolia*), particularly abundant here.

Chestnut was formerly dominant in the forests, with probably 30 to 70% of canopy stems. Chestnut oak was the second dominant, and with chestnut dead is now the first. There is no other very important canopy species; these two made up 75% or more of the canopy, with the rest divided among *Quercus borealis* v. *maxima*, *Q. alba*, *Q. velutina*, *Nyssa sylvatica*, *Acer rubrum*, *Liriodendron tulipifera*, and small percentages of hickories and mesics. The dominant chestnut oaks are mostly in the 1.5- to 3.0-ft diameter classes, with heights of 50 to 75 ft—distinctly smaller and lower than the cove forest trees, and with the stockier growth-form which is still more marked in the open growth of oak-chestnut heath.

Shrub coverage is much higher than in mesic forests; 50 to 80% is general at middle elevations, declining to 20 to 50% below 2500 ft. *Kalmia latifolia*, *Rhododendron calendulaceum*, *R. maximum*, and *Gaylussacia ursina* are the most important shrub species. *Pyrularia pubera**, *Clethra acuminata*, *Calycanthus fertilis**, and *Vaccinium constablaei* are usually present, the last seldom below 2500 ft; *Viburnum acerifolium**, *Lyonia ligustrina* and *Hydrangea arborescens* are occasional.

The herb flora is similar to that of oak-hickory, but other species occur. Species of the submesic union (*Aureolaria laevigata**, *Prenanthes trifoliolata**, *Pedicularis canadensis*, *Desmodium nudiflorum**, *Goodyera pubescens**, *Veratrum parviflorum**, etc.) dominate the stratum, along with the subxeric *Galax aphylla* and occasional xerics (*Epigaea repens* and *Panicum* sp.) and mesics (*Aster divaricatus* and *Eupatorium rugosum*). Herb coverage is low, but variable, grading from 1 to 5% at low elevations to 5 to 30% at higher elevations and in more mesic sites.

6. CHESTNUT OAK-CHESTNUT HEATH

Stands in which chestnut oak (*Quercus prinus**) and chestnut (*Castanea dentata*) are dominant are customarily designated oak-chestnut forest regardless of their structure. Not all that is dominated by oak and chestnut is forest, however; and no one who has mapped quadrats or traveled cross-country through oak-chestnut heath and forest would wish to overlook the distinction. The two types are distinguished by Conard (1935) in his study on Long Island as the *Quercetum kalmietosum* and *Quercetum prini*. Submesic stands in the Smokies are unquestionably forests, with closed canopies; but in the oak-chestnut heath total tree coverage, including small trees, may fall below 40 or 50%. Large chestnut oaks and chestnuts are widely scattered, and under the open tree stratum the shrub layer is closed; the mountain slopes are covered by a continuous evergreen heath of Kalmia and other species. Travel through the oak-chestnut heath is difficult; effort and the force of either exertion or gravity are necessary to push one's way through the heath, and only the pressure of the shrubs supports one and prevents frequent tripping among the dense stems.

Chestnut and chestnut oak make up 80% or more of the "canopy" of tall trees. The chestnuts are now dead; and the coverage of large chestnut oaks, while difficult to measure, is probably no more than 20 to 30% in many cases. The trees are fairly small; only occasional ones exceed 2 ft in diameter, and few are more than 40 to 60 ft high. Other species which enter the canopy in small percentages are *Nyssa sylvatica*, *Acer rubrum*, *Quercus alba*, *Q. coccinea*, *Q. velutina*, and locally *Pinus strobus*. *Acer rubrum* and *Oxydendrum arboreum* are the most important small trees, and *Robinia pseudoacacia* and *Sassafras albidum* are generally present at middle and higher elevations.

The shrub layer is strongly dominated by *Kalmia latifolia*, with *Clethra acuminata*, *Lyonia ligustrina**, *Rhododendron maximum*, *Pyrularia pubera*, and, above 2500 ft, *Vaccinium constablaei* also in the shrub canopy. *Gaylussacia ursina* usually forms a low shrub layer underneath. Most of the submesic shrubs occur occasionally, and *Vaccinium vacillans* may appear where the heath is less dense. Shrub coverage is in many places not noticeably below 100% and is usually 80 to 100% where the type is well developed. With the scattered trees, many stands could as well be regarded as heath communities with a tree overgrowth. Fires and death of the chestnuts have influenced this structure; although reduction of tree cover would permit abundant tree reproduction in oak-chestnut forest, it might favor the shrubs in oak-chestnut heath. Stand counts indicate, however, that tree reproduction has increased since the death of the chestnuts in spite of such increase as may have occurred in the shrub stratum. Proportions of chestnut oak and chestnut in the counts indicate that the canopy was open—perhaps 40 to 70%—before the death of the chestnuts.

*Galax aphylla** is the most important herb-layer plant. A variety of herb species listed for the submesic and xeric unions range into the type. None reach any appreciable coverage, although the ground

heaths *Gaultheria procumbens* and *Epigaea repens*, *Panicum* sp., *Campanula divaricata**, and *Aureolaria laevigata* are fairly frequent. Herb coverage is quite low, 1 to 5%, with herbs other than Galax and the ground heaths well below 1%.

7. RED OAK-CHESTNUT FOREST

The red oak-chestnut combination is submesic in composition of both tree canopy and lower strata, and is the high-altitude equivalent of chestnut oak-chestnut forest. Northern red oak (*Quercus borealis**) and chestnut (*Castanea dentata*) form 70 or 80% of the canopy, with the former usually more important. Although most of the chestnuts are dead, many large chestnut trees in these and other high-elevation forests had at least a few branches living in 1947. No canopy associate reaches any substantial percentage in most stands; of other species *Acer rubrum* is most important. The lower-elevation stands may have a fair percentage of mesics—*Tilia heterophylla, Prunus serotina, Betula allegheniensis, Aesculus octandra, Fraxinus americana*—, but few mesic trees except *Fagus grandifolia* enter the canopy of stands above 4500 ft. The submesic small trees, with *Halesia monticola* joining them here, form 30 to 50% of the stems, having taken advantage of the death of the chestnuts along with northern red oak. The chestnuts were less numerous in submesic stands of higher elevations, however, and reproduction and appearance have not been altered as much by their death as in the chestnut oak-chestnut forests.

Shrub coverage above 4500 ft is low, with *Rhododendron calendulaceum* and *Vaccinium constablaei* the principal species. *Vaccinium pallidum* and *V. hirsutum* occur in some stands, especially on ridges, and *Vaccinium erythrocarpum* and *Viburnum alnifolium* are occasional. In forests below 4500 ft *Rhododendron calendulaceum* is most important; but most other submesic shrubs appear in some stands, and *Hydrangea arborescens* is occasional. *Kalmia latifolia* is almost absent from submesic stands above 3800 ft. Shrub coverage varies from 20 to 50% below 4500 ft to only 0 to 20% above.

The herb layer above 4500 ft often resembles closely that of south-slope beech stands, but with lower coverage. Sedges (*Carex* spp.) and ferns (mostly *Athyrium filix-femina* v. *asplenioides*) are abundant. A few mesic species, notably *Eupatorim rugosum, Laportea canadensis,* and *Aster divaricatus,* appear along with the submesic and high-elevation submesic unions and *Potentilla canadensis* v. *caroliniana*. Below 4500 ft the herb flora is much the same as in chestnut oak-chestnut forests, with only the subalpine species *Trillium undulatum, Solidago glomerata,* and *Diphylleia cymosa* distinguishing the list from that of the lower type. Herb coverage is 10 to 40% in the lower stands, 20 to 60% above 4500 ft.

8. WHITE OAK-CHESTNUT FOREST

Below 4500 ft white-oak chestnut forests are seldom clearly distinguishable from red oak-chestnut. Above 4500 ft, however, white oak (*Quercus alba**)

becomes strongly dominant on some exposed southwest ridges, with a rather open growth of small trees and a fairly rich herb layer with grasses often conspicuous. In structure and appearance these forests suggest the white oak woods of hills far west of the Smokies, though very different in their floristics. In some stands chestnut (*Castanea dentata*) is dominant (cf. Cain 1931). *Quercus borealis* is almost always present; and *Carya glabra* and *Quercus prinus* occur in the canopy at lower elevations. Of the small trees *Acer rubrum* is most important; *Oxydendrum arboreum* and *Robinia pseudoacacia* are fairly numerous toward lower elevations.

The shrub layer is predominantly ericaceous, with *Rhododendron calendulaceum* and *Vaccinium constablaei* most important. *Kalmia latifolia* is frequent at lower elevations and is often the most important shrub species there. Shrub coverage is fairly high—generally 30 to 60% below and 20 to 50% above 4500 ft. The herb stratum is a mixture of ferns (*Dryopteris noveboracensis, Athyrium filix-femina* v. *asplenioides*) with other herbs of the submesic, subxeric, and high-elevation submesic unions. Grasses, *Pteridium aquilinum* v. *latiusculum,* and other xeric species also are prominent. Herb coverage is 10 to 50% below and 20 to 50% above 4500 ft.

Pine Stands and Their Maintenance

Most steep, open south- and southwest-facing slopes on the Tennessee side of the mountains are occupied by pine forest and pine heath. Usually the population of a single pine stand shows a bimodal size distribution; often other modes are represented by a few old trees of earlier generations (Fig. 16). In these dry sites occasional severe fires destroy the forests, and following the fires dense stands of young pines develop. As these trees mature, age, and die, the canopy is opened; and a new generation of pines establish themselves. When these in turn mature, a third generation of seedlings appears, while some scattered stems of the first are still present. The effects of fires in permitting the establishment of initial single-age stands thus introduces into the maintenance of the pine stands a rhythm of generations which may persist for some time. The composite stand counts from mature stands smooth out the double-age composition of individual stands, and the composite curves then take on the characteristic form of self-maintaining forests (Fig. 6). The dense small-tree stands on disturbed and recently burned sites were not included in these counts; but reproduction appears adequate to replace the stands indefinitely.

Since chance may determine the species of pine seeds available to restock a stand after a fire, chance, as Cain et al. (1937) noted, may determine which of the pines available at a given elevation first dominates the stand. Once dominant, the species tends to maintain its dominance through several generations while other pines and oaks may gradually increase to approach a balanced stand for that elevation and site. Most immature pine stands in the Smokies are
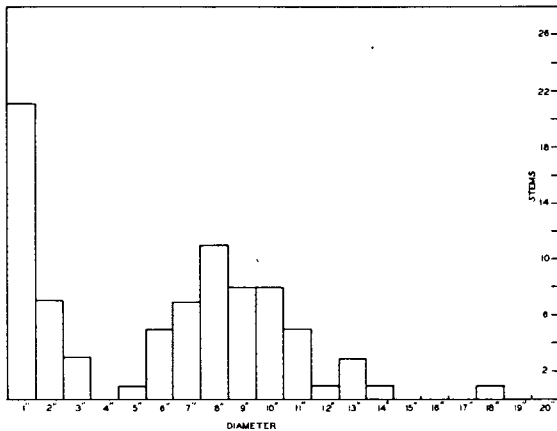
FIG. 16. Stand chart for *Pinus pungens* in a pine heath at 4150 ft on Greenbrier Pinnacle, showing periodic reproduction of stand.

single-species stands; most mature ones are mixed.

In the mature stands the oaks, also, are reproducing well; but it is by no means certain that the oaks and their associates are capable of taking dominance from the pines on these sites. It seems likely that the mature pine stands are in balance, the pines, with a small population of oaks, being all that the dry sites will support. The near-absence of oak-chestnut forests from open south and southwest slopes below 4500 ft on the Tennessee side of the Smokies is one indication that such may be the case. Only on sheltered slopes and those of small inclination are oaks and chestnuts dominant, or apparently replacing the pines as dominants. Even in many of the stands in which oaks share dominance with pines, the latter are reproducing well. But whether or not the oaks might ultimately succeed pines in most sites, the time necessary to effect the change exceeds the normal expectation of fire on dry mountain slopes in an area of summer thunderstorms.

The fires which have swept the drier slopes of the mountains have certainly favored the pines in some sites where pines form stands seral to oak-chestnut. The same fires that may favor pines in most xeric sites, however, favor the shrubs of oak-chestnut heath in other sites; fire alone is not an explanation of the pine stands. Fires are part of the environmental complexes in which the pine stands and oak-chestnut heaths exist, and the stands are scarcely the same as those hypothetical stands which might exist in their sites in the absence of fire. Both types are, however, self-maintaining in their xeric and subxeric sites under present conditions; they are not seral. Pine stands have often been relegated to subclimax status in the eastern forests, but there are good reasons for accepting the Appalachian pine stands as topographic or edaphic climaxes of their dry and exposed sites (cf. Braun 1935b, Cain *et al.* 1937).

9. VIRGINIA PINE FOREST

In low-elevation pine stands Virginia or scrub pine (*Pinus virginiana**) is usually dominant, both

in climax stands of south-facing slopes and in the many seral stands of old fields on other sites. *Pinus rigida* ordinarily occurs in the mature climax stands. *Quercus coccinea* is most important, next to the pines. *Quercus prinus* and *Castanea dentata* are usually present; and *Pinus strobus, Nyssa sylvatica, Quercus velutina,* and *Q. alba* occur and may enter the canopy. *Oxydendrum arboreum, Acer rubrum,* and *Quercus marilandica** are the only important small-tree species. The trees of these forests are not large; stems over 18 in. diameter are rare, and the dominants in most stands are only 12 to 15 in. Canopy heights in a sample were 50 to 75 ft. The forest is open, with tree coverage about 70% and much light admitted through the open canopy to lower layers. With their southwest exposures, open structure, and partly bare soil, these forests have in the afternoon a bright, hot, and arid climate which is in palpable contrast with that of forests in nearby valleys.

Shrub coverage is variable with 10 to 40% the usual range, but pine-heath stands with shrub coverage over 50% occur even at low elevations. The shrub stratum is strongly dominated by ericads. *Kalmia latifolia* is the usual shrub dominant, but *Vaccinium vacillans* is almost always present and in places is dominant. *Vaccinium stamineum* is frequent, and *Gaylussacia baccata* is occasional above 2000 ft. The only non-ericads are *Ilex montana* v. *beadlei* and the catbriers, *Smilax glauca* and *S. rotundifolia.*

The herb layer is low in coverage, with 2 to 10% the usual range. Herb species include *Andropogon scoparius*, A. virginicus, Panicum* sp., *Pteridium aquilinum* v. *latiusculum, Tephrosia virginiana*, Baptisia tinctoria*, Coreopsis major, Sericocarpus asteroides** and *S. linifolius*, Aster* sp., *Solidago* sp., *Antennaria* sp., *Epigaea repens,* and *Galax aphylla.* Of these *Andropogon scoparius* leads in coverage.

10. PITCH PINE HEATH

Between elevations of 2200 and 3200 ft pitch pine (*Pinus rigida**) most frequently dominates pine stands. *Quercus coccinea** sometimes shares dominance with the pine and is almost always present along with *Quercus prinus, Castanea dentata,* and one or both of the other pine species. *Nyssa sylvatica* occurs in small numbers, and *Acer rubrum* and *Oxydendrum arboreum* are important small trees. In tree coverage and stature the pitch pine stands differ little from the Virginia pine forests; but shrub coverage is higher at middle elevations. Shrub coverage is 40 to 70% and is in most cases over 50%; the type is consequently termed a pine heath. *Kalmia latifolia* and *Vaccinium vacillans* or *V. hirsutum** share dominance in different proportions in different stands; and *V. stamineum, Gaylussacia baccata,* and *Lyonia ligustrina* are also important shrubs. Species of the xeric union (*Andropogon scoparius, Pteridium aquilinum* v. *latisculum, Epigaea repens, Gaultheria procumbens*) dominate the herb stratum; but legumes

and composites, except *Coreopsis major,* are less common than in Virginia pine forests. Herb coverage is usually 5 to 20%.

11. TABLE MOUNTAIN PINE HEATH

Toward higher elevations table mountain pine (*Pinus pungens*) is more and more frequently dominant; at the upper limit of the pine heaths it is strongly dominant, and other trees occur only in small percentages. The stands are small, low, and open. Canopy stems are usually only 10 to 15 in. in diameter, canopy tree height in a sample was only 40 to 50 ft, and tree coverage is usually 70 or 80%. *Pinus rigida* is the second most important species, but is often absent at higher elevations. *Quercus coccinea, Q. prinus, Castanea dentata,* and *Nyssa sylvatica* usually occur in small numbers, with *Acer rubrum, Oxydendrum arboreum, Robinia pseudoacacia,* and *Sassafras albidum* as small trees.

The shrub stratum is dominated by *Kalmia latifolia* or by Vaccinioideae—*Vaccinium pallidum, V. hirsutum,* or *Gaylussacia baccata. Vaccinium stamineum* and *Lyonia ligustrina* are usually present, and *Vaccinium constablaei* and *Rhododendron catawbiense* occur in some stands. *Pieris floribunda** occurs toward higher elevations and is occasionally dominant. Shrub coverage is high, 60 to 90%; and most stands have an open pine canopy above a dense, low heath. Herb coverage is usually 5 to 20%. *Andropogon scoparius* is important; but *Galax aphylla, Epigaea repens** and *Gaultheria procumbens** lead in coverage, and species of the heath bald herb union occur.

12. GRASSY BALD

The most limited vegetation type of the Smokies is one of the most distinctive and celebrated. In an area where forests continuously clothe the valleys and ridges and most of the peaks, a few of the latter bear patches of grassland on their summits. In reaching the balds one may climb 3000 or 4000 ft through forests, to emerge at last in an open meadow with full view of the mountains in all directions. The change from forest to bald is abrupt; except that tree stature may decrease up the slopes and along the ridges toward the balds. The trees do not thin out gradually into the bald, however, but end in a forest-edge where ericads (*Vaccinium constablaei, Rhododendron calendulaceum, Lyonia ligustrina, Vaccinium pallidum* and *V. hirsutum*) are mixed with other shrubs and small trees (*Betula lenta, Amelanchier laevis, Crataegus macrosperma* v. *roanensis, Salix* sp., *Rubus canadensis,* and dwarfed trees of the surrounding beech and oak-chestnut forests).

Beyond the forest-edge the balds are meadows where mountain oat grass (*Danthonia compressa**) is strongly dominant. Grasses introduced when the balds were used for pasture (*Agrostis alba* and *Phleum pratense*) may also occur. Sedges have been reported as dominant in balds in other areas (Wells 1937) in contact with spruce-fir forests, and are important in Andrews Bald, in contact with both deciduous and spruce-fir forests, in the Smokies. Various herbs are scattered through the grass, *Potentilla canadensis* v. *caroliniana** being much the most widespread and abundant. *Stachys clingmanii*, *Solidago* sp., *Prenanthes altissima, Smilax herbacea,* and *Houstonia serpyllifolia,* which occur in the high-elevation deciduous forests, are frequent; and some mesic herb species (*Rudbeckia laciniata, Gentiana decora,* and *Stellaria pubera*) occur here. With these are many introduced weeds—the grasses mentioned, *Hieracium scabrum, Rumex acetosella, Prunella vulgaris,* etc.

Although the balds are primarily herb-layer communities, shrubs occur at low coverage over most of their surfaces. *Rhododendron calendulaceum, Vaccinium constablaei,* and *Rubus canadensis* are the most important species. Tree seedlings are almost always present (see Part I, table 4). The scattered seedlings do not necessarily imply that the balds are becoming forest; their successional status will be discussed below.

The Southern Appalachian Subalpine Forest Center

In the northeastern half of the Great Smoky Mountains, forests of spruce and fir cover nearly all slopes and valleys down to 4500 ft. In structure and composition these forests resemble those of Canada; but they are floristically quite different. Of the dominants, *Abies fraseri* is a southern endemic, while *Picea rubens,* though it ranges far to the north, is primarily Appalachian rather than Canadian and occurs mainly in the mountains above 1000 ft throughout its range (Harlow & Harrar 1941). The southern population of *Picea rubens* has been distinguished as *P. australis* Small. A large proportion of the plants are southern species or distinctive southern populations; in addition to *Abies fraseri* these include the important shrubs *Vaccinium erythrocarpum* and *Menziesia pilosa* and the herbs *Solidago glomerata, Senecio rugelia, Geum radiatum* Michx. *Parnassia asarifolia,* and *Chelone lyoni.* Others (*Viburnum alnifolium, Clintonia borealis*) are species of the eastern United States and Canada, while a few (*Oxalis montana, Sambucus pubens, Sorbus americana*) are widespread boreal species whose Southern Appalachian populations have not been distinguished. Cain *et al.* (1937) considered that 25% of the woody species are endemic, while 60% extend into the Northeast, although many of these are primarily Appalachian.

It consequently seems inappropriate to refer to these forests as either boreal or Canadian. The term boreal is used in this paper, but only in the loose sense in which it may be applied to coniferous forests or *taiga* of both high latitudes and high altitudes. Although they gradate into the Canadian forests through the Northeast, the Southern Appalachian spruce-fir forests seem distinct. Far from being merely a southern fragment derived from the Canadian forests, they may well be a center from which some species have spread into the latter. They should,

in any case, be regarded as an additional cordilleran member of the boreal and subalpine forests of North America, with status equivalent to those of western ranges (Whittaker 1948, Oosting & Billings 1951). The Southern Appalachian subalpine forests are of small extent—originally perhaps 1,000,000 acres, now much reduced (Korstian 1937)—but admirable virgin stands are preserved in the Smokies.

13. RED SPRUCE FOREST

In their lower elevations the subalpine forests of the Smokies are dominated by red spruce (*Picea rubens**). Fraser fir occurs in most stands except those of dry lower slopes, but is a much smaller species than spruce and scarcely enters the canopy. The only important canopy associate of spruce is high-elevation yellow birch (*Betula lutea*), with 10 to 15% of canopy stems. Along with birch the small trees *Acer spicatum*, *A. pensylvanicum*, and *Amelanchier laevis* are important, increasingly so toward lower elevations and more mesic sites. *Aesculus octandra*, *Fagus grandifolia*, *Halesia monticola*, and other cove forest species also occur in some spruce forests of lower elevations and more mesic sites. Canopy trees are of only medium size, 18 to 30 in. diameter for the most part, and of medium height, 50 to 80 ft in two samples.

Spruce and fir forests of the Smokies have been described also by Cain (1935, Cain et al. 1937) and Oosting & Billings (1951), and these studies contain useful data for stands representing only part of the spruce-fir pattern. The more extensive coverage of the present work (51 samples) is intended to provide limited information on the striking variations with site in these forests. Trends in forest composition along environmental gradients have been described in Part I. Canopy composition is relatively uniform, compared with the forests of lower elevations, but undergrowths vary greatly in structure and floristic composition. Five "subtypes" will be distinguished in the undergrowth as it changes continuously along the moisture gradient. Undergrowth variations are comparable to those which occur in other boreal and subalpine forests and have been recognized in the *site-types* of Finnish and other forest ecologists (Cajander 1909, 1926, 1949; Linkola 1924; Ilvessalo 1929; Heimburger 1934; Arnborg 1940, 1953), *sociations* of Scandinavian phytosociologists (Du Rietz 1932), and *associations* of Russian phytocenologists (Katz 1930, 1933; Sukatschew 1928, 1932; Sokolowa 1935, 1936). The "subtypes" of the author differ in manner of definition from these, however, and do not include all the sociations which might be recognized (see also Cain 1935).

Although undergrowth is variable in any topographically defined type of site, average undergrowth coverage and composition are correlated with site in the series of topographic subtypes: valleys, north slopes, intermediate slopes, south slopes, and ridges. In the valley subtype, coverages of moss, Oxalis, and low shrubs are generally below 5%. The

high herb and high shrub strata are of moderate coverage (around 30 and 20%), and various species of the mesic and high-elevation mesic unions occur in the former. The subtype of north slopes and flats has high coverages of moss and Oxalis (25-55%) and moderate ones (5-20%) for low and high shrubs. The high herb stratum is strongly dominated by a fern (*Dryopteris spinulosa* v. *americana**); other herbs are *Clintonia borealis**, *Aster acuminatus*, *Senecio rugelia**, *Trillium erectum**, and *Streptopus roseus**. These stands show a characteristic layering (see Part I), with a five-story structure of ground moss (*Hylocomium splendens*), low herb layer (*Oxalis montana*), fern (*Dryopteris spinulosa* v. *americana*), low shrub (*Vaccinium erythrocarpum**) and high shrub (*Viburnum alnifolium*). *Acer spicatum* forms a low tree stratum.

Coverages for all these strata are less in the intermediate subtype of east- and west-facing slopes; moss, Oxalis, and fern coverages in this are usually between 15 and 30%, low and high shrub coverages between 5 and 10%. In the south-slope subtype, coverages for all five strata are usually below 10% (Oxalis may be higher). Species occurring on south slopes, which are rare in more mesic subtypes, include *Medeola virginiana*, *Lycopodium lucidulum*, and *Monotropa uniflora*, *Vaccinium constablaei*, *Ilex montana*, and *Rhododendron catawbiense*. In the fifth subtype of ridges and steep upper south slopes, the Rhododendron heath approaches full coverage. Under the heath, coverages for species of the five-story undergrowth approach zero, and there are few herbs (*Trillium undulatum*, *Gaultheria procumbens*, *Epigaea repens*). Floristically the undergrowths of such stands are related to the heath balds. On some ridges the canopy of spruce is open, forming a physiognomically distinctive spruce-heath transitional to the heath balds. In most cases, however, the boundary between spruce forest and heath bald is relatively abrupt.

14. FRASER FIR FOREST

Most subalpine forests of the Smokies are mixtures of red spruce with southern balsam or Fraser fir (*Abies fraseri**); but above 6200 ft (1890 m), on the upper slopes of the highest peaks, forests are dominated by fir alone. Tree composition of these forests of extreme elevations is the simplest in the Smokies; there is one dominant, the fir, and one deciduous tree, mountain ash (*Sorbus americana**). These are the only tree species at the extreme development of the type; but many stands have red spruce, and some have yellow birch and other deciduous species in small numbers.

Undergrowth varies as strikingly as in the spruce forests. Valley sites were not observed at these elevations. The subtype of north-facing slopes has very high coverages of moss and Oxalis (around 90 and 50%). The Dryopteris stratum is of high coverage (40%); and other herbs include *Aster acuminatus*, *Clintonia borealis*, *Solidago glomerata*, *Senecio ru-*

gelia, Chelone lyoni, and *Geum radiatum.* In the intermediate subtype moss coverage is high (80-90%); but coverages of the other strata are low, usually less than 10%. Undergrowth of mesic and intermediate forests of highest elevations consists largely of the lowest strata of the five-story undergrowth—moss, Oxalis, and fern. Shrubs may be almost absent from these stands, although *Viburnum alnifolium, Sambucus pubens, Vaccinium erythrocarpum, Menziesia pilosa,* and *Diervilla sessilifolia* occur.

In the subtype of south facing slopes, moss coverage is 60% or less, and heath coverage is usually substantial (40-60%). In the ridge subtype the heath (*Rhododendron catawbiense* and *R. carolinianum*) approaches full coverage; and other undergrowth is limited to moss coverage of a few percent and scattered herbs of the heath bald herb union.

In appearance the fir forests are like no others; they are even unlike the spruce forests. The trees are quite small—the bulk of canopy stems may be 7, 8 and 9 in. in diameter with correspondingly low height (30 to 40 ft). Stems as large as 12 in. are rare. Many of the forests are stagnant pole stands, with seedlings and smaller stems numerous, but mostly dead. Undergrowth may be sparse; and the forests, with their small and rather open canopy, have an impoverished and stunted appearance. Mosses and lichens, however, flourish. They may carpet the floor; and trunks and branches of trees and fallen poles are coated, crusted, and tufted with them, giving the forests a gray-green, hoary aspect. From this, and from the small trees and dead seedlings, the forest appears appropriate to the subalpine extremity in the Appalachians, a dwarf conifer forest which on a fair day has a charm of its own but at other times, with the summits involved in cloud and a raw wind whipping fog through the firs, assumes the bleakness of the climate in which it lives.

15. HEATH BALD

The heath balds are one of the most attractive vegetation features of the Smokies, becoming when Rhododendrons and Kalmia are in bloom the celebrated floral epaulets on the shoulders of these mountains. In the northeastern part of the range, in the area of subalpine forests, many of the ridges and steep faces bear these shrub communities, which were studied by Cain (1930b). They are dominated by evergreen ericaceous shrubs which approach not only full coverage but complete impenetrability in their dense thickets of tough stems. The shrub canopy may be 10 ft high, but on ridges and summits is more frequently 3 or 4 ft. On sharp crests of ridges or peaks the heath may be open, with scattered cushions of *Leiophyllum lyoni.*

The balds occur throughout the elevations of the subalpine forests and down to 4000 ft and show considerable difference in composition with altitude. *Kalmia latifolia* is most important at lower elevations, with *Rhododendron maximum* and *R. catawbiense, Aronia melanocarpa*, Clethra acuminata, Vaccinium constablaei, Ilex montana, Viburnum cassinoides*,* and *Smilax rotundifolia,* and with *Gaylussacia baccata* in more open parts. *Rhododendron maximum* is absent above the lower balds, Kalmia and most of the other species listed are absent above 6000 ft. The high-elevation balds are somewhat lower in canopy height and more open. *Rhododendron catawbiense* and *R. carolinianum** are dominant, with *Vaccinium constablaei.* The low shrubs *Vaccinium erythrocarpum, Menziesia pilosa,* and *Leiophyllum lyoni** occur in the more open parts; *and Sorbus americana* appears along the edges. The balds may well be divided into two intergrading types, the lower dominated by *Kalmia latifolia* and *Rhododendron maximum* and related to the oak-chestnut heath, the

FIG. 17. Fraser fir forest, near summit of Mt. LeConte. Reproduced by permission of Thompsons, Inc., Knoxville, Tenn.

upper dominated by heaths of the subalpine forests
and related to them.

The herb stratum of the balds is limited, with cov-
erage below 5% and in denser stands approaching
zero. *Gaultheria procumbens* is the leading species,
with *Galax aphylla, Melampyrum lineare*, Medeola
virginiana,* and *Trillium undulatum**. A few other
species occur along trails. Tree seedlings are com-
monly present—*Abies fraseri, Picea rubens, Sorbus
americana,* and *Prunus pensylvanica* at higher eleva-
tions, *Betula lenta, Acer rubrum, Castanea dentata,
Oxydendrum arboreum, Sassafras albidum, Pinus
pungens, Robinia pseudoacacia,* and *Hamamelis vir-
giniana* at lower. As Cain indicates, there is no rea-
son to think that the deciduous trees could take
dominance from the heath, though the conifers may
be successfully invading some balds.

The Balds as Topographic Climaxes?

Much discussion has centered on the various bald
types of the Southern Appalachians and the reasons
for their existence. In relation to the climatic climax
theory it has been tempting to apply logic to them:
Forests are climax in the region; the balds are not
forests; therefore they are not climaxes. Some evi-
dence may be considered on whether they are neces-
sarily seral types, or whether the balds may cap the
climax forest patterns of the Appalachians with non-
forest climax types.

The problem of the heath balds in the Smokies has
been considered by Cain (1930b). In general inter-
pretation Cain considered them secondary replace-
ments of forests, in which the trees were destroyed by
fire, windfall, or landslide, permitting the heath al-
ready beneath them in these sites to close in and
largely exclude tree reproduction by density of cover
and effects on soil. Since they are fairly stable shrub
communities, the balds were interpreted as, in this
sense, postclimax. Dead spruces and firs can be seen
in some balds, suggesting in some cases retrogression
from forest to heath.

It seems likely that some of the balds represent
primary succession. The high balds of Mt. Le Conte
and its spurs have bare rocks along the ridges, with
lichens, mosses, and tufts of grass invading them.
Scattered cushions of *Leiophyllum lyoni* surround the
bare area. Farther from the crest of the ridge these
have closed in; still farther they are over-topped by
the higher heath species, which form a continuous
shrub canopy and exclude Leiophyllum from the dense
heath of the slopes. The soil grades from absent
or a thin crust on the ridges to a thick peat below.
It seems unlikely that a soil which once supported a
spruce-heath was secondarily lost from under the
shrubs. The soil and vegetation structure of the
balds seem better explained by assuming that pri-
mary succession is still in progress on some of these
high ridges. Once the heath is established, the highly
acid, podsolized soil described by Cain and the dense
shrub canopy should retard forest invasion and tend
to maintain the heath. Spruce and fir appear to be

FIG. 18. Heath bald and succession, on a spur of Mt.
Le Conte. Reproduced by permission of Thompsons, Inc.,
Knoxville, Tenn.

invading the edges of some of the balds. In most
of the balds, however, such invasion is proceeding
very slowly at best; and in many of the balds there
is no convincing evidence that the conifers are, or
are capable of, occupying the site.

The balds are thus probably successional, in part.
Some represent primary successions and others re-
sult from destruction of the forest canopy; some of
these will probably develop, or will return, to forest.
Many of the balds, however, are relatively stable
communities; they seem clearly to be self-maintaining
stands under present conditions, and therefore cli-
max in this sense. In relation to Clementsian theory
they may be considered long-arrested seral types—
i.e. serclimaxes. The author would prefer to regard
them as topographic climaxes in accordance with the
polyclimax theory or, in the pattern interpretation
of this paper, simply as parts of a complex climax
pattern.

The heath balds are characteristically communities of exposed summits and ridges, especially ridges with steeper slopes and those with axes sloping toward the south or west. Although heath balds occur on slopes of all orientations below peaks and ridges, their greatest extent is on slopes of south and west exposure. This pattern of occurrence suggests that effects of exposure are critical. Precipitation is high at the elevations of the balds; but on these summits and ridges much of the water from summer thunder-showers is lost by surface run-off and much of the rest by sub-surface drainage down the slopes. The balds are fully exposed to drying effects of winds. It seems likely that these edaphic and climatic consequences of their exposed positions are responsible for the existence of the heath balds.

A number of naturalists—Harshberger (1903), Davis (1930), Camp (1931, 1936), Fink (1931), Cain (1931), Wells (1936a, 1936b, 1937, 1946), and Brown (1941, 1953)—have reported on the grassy balds and speculated on their history. Clements (1936) held the unshared opinion that they were produced and maintained by fire; Gates (1941) suggested killing of oaks by gall-flies at high elevations as their cause; Wells considered them man-made, cleared as camp-sites and lookouts by the Cherokee Indians. Other authors have considered them natural; Camp suggested that exposure to drying westerly winds during the late-summer dry season was critical. Clearing by Indians has been doubted by Fink because of the labor involved for stone-age men and by Brown (1941) because of the lowland habits of the Indians. Cain observed that the grassland soil is rich and deep, too deep for the balds to have been formed in recent history, and that the eccentric growth rings of trees on their margins indicate that these trees have been in their present positions in relation to the forest-edge for nearly a century. Brown (1953) found conifers capable of growing in a grassy bald on Roan Mountain, and suspected that failure of seeds to germinate or of seedlings to survive in the balds may inhibit their invasion by forest.

Camp has suggested that the grassy balds were originally meadows with ericaceous islands and overgrowth, the ericads and grasses sharing dominance. A number of introduced Eurasian plants appear in the balds now; and, whether or not they are "climax," the balds are not the same natural communities they were before they were grazed. Close similarity of the vegetation of the balds with the cleared fields of the Smokies (Spence and Russell Fields) might suggest that the grassy balds also were cleared by man at some time in the past. This same similarity may only imply that similar grassland communities are able to exist at high elevations in these mountains in the absence of trees, whether the trees are naturally excluded or artificially removed. Tree invasion is evident in the cleared fields, but is proceeding slowly, if at all, in the grassy balds and probably in response to recent climatic amelioration (Brown 1941). The positions of the balds, their forest-edges, and rela-

tion to adjacent forests suggest natural causes. They are suggestive of the balds and false timberlines on isolated ranges of the West (Rydberg 1913, Daubenmire & Slipp 1943, Merkle 1951), where the tree line is depressed below its normal elevation for the latitude. Grassy mountain summits above a pattern of deciduous (beech) and pine forests are reported also from the Crimea (Poplawskaja 1933).

All grassy balds of the Smokies are at fairly high elevations, on peaks or points, in contact with high-elevation deciduous forests. Usually the balds cap the peaks; but, in six of them which were paced off and mapped, the longer axis or greater extent down the slope was always toward the south, southwest, or west. This orientation, together with the fact that the most stunted and open oak-chestnut forests occur on southwest ridges below some of them and the fact that in the cleared fields tree invasion is more evident along north and east edges and in draws than along south and west edges, suggest that climatic factors connected with south and west exposure are critical. Even more than the heath balds these communities of most exposed summits are affected by water loss through run-off and exposure to the full force of winds, with no obstruction to the west. It seems likely that resulting conditions of unfavorable moisture-balance have excluded trees from the grassy balds. To this may be added the fact that the deciduous forests involved are high-elevation members of their group, of reduced stature, and perhaps well beyond favorable conditions of temperature and growing season.

Relations of the grassy balds to deciduous forest in the southwest half of the range and of the heath balds to spruce-fir forest in the northeast half of the range are similar. The heath balds, however, are much more extensive and contact deciduous forest types as well as spruce-fir forests. Without drawing too close a parallel between the two bald types, both may be thought climax vegetation types of the two "systems" developing in related conditions of extreme exposure.

DISTRIBUTIONAL RELATIONS

THE MOSAIC CHART

As a final step in the analysis, disposition of the types described upon the topography of the Smokies may be studied. The pattern, with the complexity of sites and variety of types, cannot be a simple one but may be based upon the two major gradients of elevation and site. Reduction of environment to two complex-gradients requires various assumptions and simplifications; but, for the special conditions within the Smokies, these seem within reason.

The method of developing the pattern may be described as the *mosaic chart*. The two major gradients were used as axes, with elevation from 1500 to 6600 ft (460-2010 m) on the ordinate, moisture-balance as indicated by site on the abscissa. The sites in the Smokies were arranged along the gradient in five steps by topographic and climatic considerations:

(1) deep coves and valley flats, deep canyons; (2) open shallow valleys and flats, smaller ravines and draws; (3) lower sheltered slopes of valleys; (4) open slopes; and (5) ridges, summits, and peaks. Open slopes were further subdivided by orientation from the mesic northeast to xeric southwest. The overlap of the site groups, due to complexity of topography, different sizes and forms of valleys, different degrees of exposure of slopes and ridges, etc., is evident. But on the whole, these steps form a series with roughly graded conditions of exposure and moisture-balance, a topographic gradient along which distribution of vegetation types can be studied.

With the framework of the chart set up in terms of the major gradients, the 300 site-samples were plotted by topographic position and elevation. The samples had been classified into the 15 types and transitions between them. Subtypes distinguished by lower strata were plotted in the high-elevation forests; and degree of slope and percentages of key tree species and groups were entered for each sample. Isorithms for each of the moisture-balance classes of the eastern forests were drawn, and lines for certain important species were drawn in—hemlock and beech, spruce and fir. The percentage values were well scattered; but intermediate positions for the isorithms, reflecting average conditions of many sites, were sought. The two systems at high elevations were plotted separately because of their overlap along the gradients.

The result was a gratifying reduction to pattern of the complex vegetation; the final charts are presented as Figs. 19 and 20. About 40 of the 300 site-samples were outside the lines drawn for their types. A few limitations of the pattern may be noted. Gentle slopes often support vegetation a step less xeric than indicated on the pattern. Although sharp peaks are more xeric than slopes below them, rounded or level summits may support more mesic vegetation than their south slopes. The beech gaps in certain concave slopes in the subalpine forests are not indicated in the boreal forest pattern. The two bald types appear in similar topographic positions for the two systems, but are shown in contact with only one other type in each case. The contact indicated is the critical one of the most closely related type, normally adjoining the bald on the south slope. Other types meet the balds on other slopes through abrupt transitions, and the grassy balds thus contact red oak-chestnut and beech forests. The heath balds may come in contact with oak-chestnut and pine heaths and occasionally with oak-chestnut and hemlock forests. Wherever the environmental gradient is telescoped, as along a sharp ridge, two types whether adjacent ones or not may meet with a telescoped transition between them.

One noteworthy feature of the pattern is the expansion of mesic forests toward higher elevations. Vertical lines on the chart extend through topographically similar sites at different elevations, but not through sites of similar moisture-balance. Change of moisture conditions in topographically similar
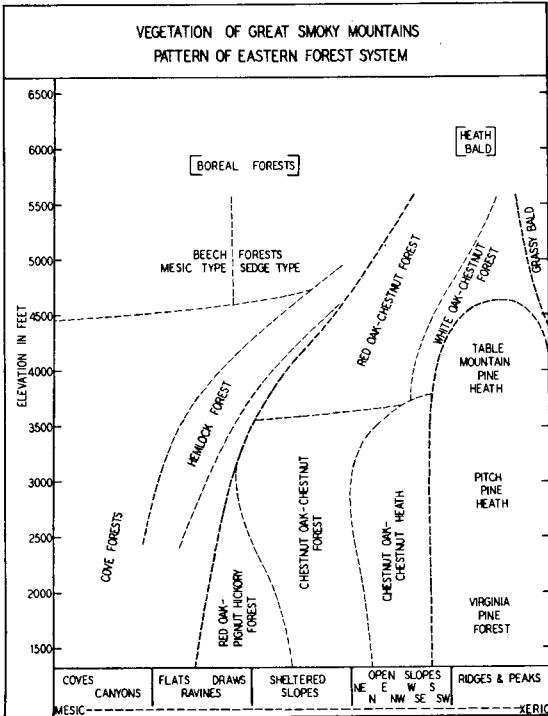
FIG. 19. (Vegetation of Great Smoky Mountains, pattern of Eastern Forest System.)
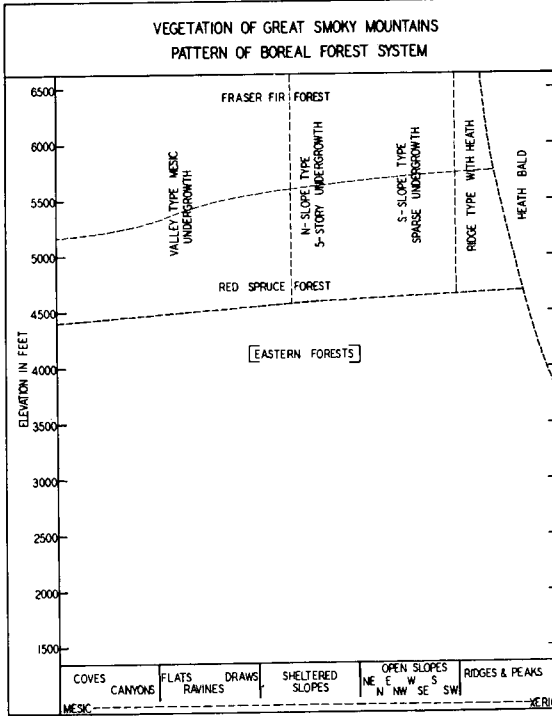
FIG. 20. (Vegetation of Great Smoky Mountains, pattern of Boreal Forest System.)

sites toward higher elevations is indicated by the curving boundary of the cove forest grouping. The boundary between spruce and fir dominance is oblique, and the lower boundary of the subalpine forests is slightly oblique. Since valleys may be somewhat cooler than open south-facing slopes at a given elevation, occurrence of spruce 2-300 ft lower in valleys would be expected. If the lower limit of spruce were largely dependent on moisture conditions, the boundary should be much more steeply oblique than is the case. Factors of temperature or growing season closely correlated with elevation appear to be of primary importance in determining the lower limits of spruce, rather than moisture conditions as suggested for subalpine forests in the Rockies (Daubenmire 1943).

DISTRIBUTIONS OF TYPES

Topographic distributions of types on the northwest slope of the Smokies may be summarized:

1. Cove hardwoods forest. At low elevations cove forests are restricted to valleys and lower slopes, with cove forest transition occupying smaller ravines and flats of shallow valleys. Toward higher elevations cove forests spread outward on sheltered and northerly slopes, occupying all valley sites except dry, open draws on south slopes. The upper limit is near 4500 ft, where either spruce or beech usually becomes dominant. The cove forest transition extends from its lower sites upward on the xeric side of hemlock, to become above 2500 ft a transition between hemlock and oak-chestnut forests.
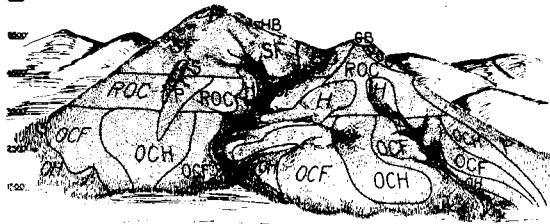
FIG. 21. Topographic disposition of vegetation types. View of idealized mountain and valley, looking east, with 6500-ft peak bearing subalpine forest on left, lower 5500-ft peak covered up to summit bald with deciduous forest on right. Vegetation types:

BG—Beech Gap
CF—Cove Forest
F—Fraser Fir Forest
GB—Grassy Bald
H—Hemlock Forest
HB—Heath Bald
OCF—Chestnut Oak-
    Chestnut Forest
OCH—Chestnut Oak-
    Chestnut Heath

OH—Oak-Hickory Forest
P—Pine Forest and Pine
    Heath
ROC—Red Oak-Chestnut
    Forest
S—Spruce Forest
SF—Spruce-Fir Forest
WOC—White Oak-Chestnut
    Forest

2. Eastern hemlock forest. At elevations below 3500 ft hemlock stands occupy valley flats which are elevated above or remote from the stream. Toward higher elevations, as cove forest occupies these sites, hemlock moves up on sheltered northerly slopes and, still higher, onto sheltered southerly slopes and ridges.

Throughout its range, as the cove forests expand toward higher elevations, hemlock moves ahead into sites which are one step less mesic.

3. Gray beech forest. The south-slope subtype with sedge floor occupies gaps, draws, and concave sheltered slopes facing southeast through south to west above 4500 ft. The north-slope subtype with beech or beech-mixed canopy and herbaceous floor occupies comparable sites of northerly orientation. Outside the range of spruce forests the north-slope subtype occupies open northerly slopes.

4. Red oak-pignut hickory forest. Oak-hickory forests in the Smokies are restricted to the lower slopes of the range, where they occur in draws and ravines, on sheltered northerly slopes, and on lower sheltered southeast and west slopes.

5. Chestnut oak-chestnut forest. Sheltered southerly and open northerly slopes are occupied by chestnut oak-chestnut forests at lower elevations, but toward middle elevations the oak-chestnut heath expands to replace them on most open slopes and some sheltered southerly ones. The oak-chestnut forests expand at the same time to take the place of oak-hickory on sheltered slopes and in draws, and to adjoin cove forest transition. At 3700 ft chestnut oak-chestnut forests occupy a wide range of sites from draws through sheltered slopes to open northerly slopes; above that elevation they are replaced by red oak-chestnut forests.

6. Chestnut oak-chestnut heath. At lower elevations the type occupies intermediate slopes. Toward middle elevations, above 2000 ft, it expands to occupy most open slopes except south and southwest ones. Toward higher elevations chestnut oak-chestnut forests occupy some of the open slopes, and above 3700 ft the oak-chestnut heaths drop out with expansion of oak-chestnut forest and replacement of chestnut oak by red and white oaks.

7. Red oak-chestnut forest. Red oak-chestnut forests occupy sheltered southerly slopes, more xeric than those occupied by hemlock, and open northerly slopes above 3700 ft. Toward higher elevations they occur on open slopes while hemlock occupies the sheltered ones; and above 4500 ft red oak-chestnut occupies open intermediate and southerly slopes as beech forests occupy open northerly slopes. Outside the range of spruce, high cols and ridges, except the most exposed ones, bear red oak-chestnut.

8. White oak-chestnut forest. Slopes more xeric than those covered by red oak-chestnut are occupied by red and white- or white oak-chestnut forests. Below 4500 feet white oak-chestnut occurs on some open southeast and west slopes. Above 4500 ft open south and southwest slopes and some exposed ridges and summits support white oak-chestnut.

9. Virginia pine forest. South- and southwest-facing slopes and summits of low hills bear Virginia pine forests, and successional stands are frequent on other sites. Virginia pine extends above 2300 ft but seldom dominates stands above that elevation.

10. Pitch pine heath. Open south and southwest

slopes and some ridges support pitch pine stands between 2200 and 3200 ft. Individual stands dominated by pitch pine may be found at any elevation, but are uncommon at higher and lower elevations.

11. Table mountain pine heath. Pine heaths above 3200 ft occupy open south and southwest slopes and some ridges, and are usually dominated by table mountain pine. Few pine stands occur above 4500 ft, but some appear on exposed slopes up to 4700-4800 ft.

12. Grassy bald. The grassy balds are restricted to the highest elevations and most exposed points outside the range of spruce, where they appear on summits and extend a short distance down the south and west slopes of peaks.

13. Red spruce forest. The spruce forests are restricted to the northeast half of the range and occur there above 4500 ft, occupying all sites except those of beech gaps and heath balds. Red spruce is dominant in subalpine forest stands at lower elevations—below 5500 to 6000 ft, depending on site. Undergrowth subtypes of red spruce and Fraser fir forests have been related to topography in the preceding descriptions.

14. Fraser fir forest. Above about 6000 ft fir is dominant; and all available sites except the extreme exposures of heath balds are occupied by it, with subtypes similar to those of red spruce forests.

15. Heath balds. Heath balds occur on sharp exposed ridges, peaks, and points above 4500 ft and locally down to 4000 ft. Ridges pointing south and west are especially likely to bear them, and they extend farther down south and west slopes on other ridges. They may occur, however, wherever slope is steep and exposure great.

DISTRIBUTION OF SUBALPINE FORESTS

One aspect, a most interesting one, of the distribution of types remains. In the northeast half of the range sites above 4500 ft, with some exceptions, are occupied by forests of spruce and fir. Southwest of the middle of the range, not far beyond Clingmans Dome, spruce-fir forests are absent from the high mountains even though considerable areas above 4500 ft exist there. In the southwestern Smokies the place of the subalpine forests is taken by high-elevation deciduous forests—beech-mixed and beech in mesic sites, red and white oak-chestnut in more xeric ones. The change between the two halves of the range is not one of gradual tapering away and dilution of the spruce-fir forests toward the south but of their presence, with full dominance, in one area and complete absence in the other. Climates in the two halves of the range cannot differ greatly, for vegetation patterns below 4500 ft are the same. Precipitation above 4500 ft may be less in the southwestern half of the range, but there is no reason to doubt that the high slopes of these mountains could support spruce-fir forests. The fact that they do not do so is a striking example of failure of physiognomic convergence of vegetation in similar climates (cf. Beadle 1951).

Of the historical interpretations which might be offered, one seems most adequate and is based on topography of the mountains. Observation of a map of the Smokies reveals a suggestive correlation: Clingmans Dome, southwest of which the last red spruce grow, is the high point of the range and the first of a series of peaks extending above 6000 ft along the ridge to near the northeast end of the range. The spruce-fir forests grow on these high peaks and on the adjacent ridges, slopes, and valley sites down to 4500 ft. The highest points south of Clingmans Dome are Thunderhead Mountain and Silers Bald, 5530 and 5620 ft, which support deciduous forests only and, on their peaks, grassy balds. The spruce-fir forests are limited to that part of the range where peaks above 5700 ft occur (Fig. 22).

FIG. 22. Profile of Great Smoky Mountains to illustrate hypothesis on southern limit of Appalachian spruce-fir forests. Distribution of spruce-fir forests on higher peaks in northeast half of the range is indicated by diagonal shading. Grassy balds are indicated by black caps on lower peaks of the southwest half of the range, otherwise covered by deciduous forest. Climatic warming during the xerothermic period sufficient to displace the lower limits of spruce-fir forests upward from 4500 ft to approximately 5700 ft would account for present distribution of these forests.

The survival of spruce-fir forests in the area of higher peaks may be thought to have been dependent on these peaks, where the forests could find sanctuary during the xerothermic period. If, in the warm period following the last glaciation, temperatures rose sufficiently to displace the spruce-fir forests upward by 1000 ft or a little more—implying a mean temperature rise of 2° or 3° F (Shanks 1954)—their absence south of Clingmans Dome would be accounted for. A somewhat greater warming, with a displacement upward of 1300 ft, would still permit spruce to survive on summits near 6000 ft and fir and mountain ash to exist with it on northeast slopes of the peaks only a few hundred feet higher.

Of the history of high-elevation vegetation in the Smokies, it may be suggested that the spruce-fir forests extended farther south during glaciation than at present—how much farther can scarcely be guessed. During the last xerothermic period they

were pushed upward to 5600-5800 ft elevation and were pushed off the tops of the lower peaks south of Clingmans Dome. As the climate cooled again, the forests advanced down the slopes from the higher northeastern peaks where they had had found sanctuary and reoccupied the land above 4500 ft. Southwest of Clingmans Dome absence of spruce forests would leave mountain surfaces above 4500 ft available for those species of the eastern forests best adapted to high-elevation conditions—gray beech, northern red and white oaks, and chestnut particularly—while other deciduous species were displaced downward by the cooling climate. The spruce forests should have been moving southwest along the ridge from Clingmans Dome in the 4000 years since the peak of the xerothermic period (Flint 1947), but are perhaps retarded or halted by the extensive beech forests of Double Spring Gap.

RELATION OF THE VEGETATION PATTERN TO THOSE OF
OTHER MOUNTAIN RANGES

Most of the site-samples were for the northwest or Tennessee side of the Smokies, and the pattern derived applies to that side. The vegetation pattern of the southeast side is closely similar; but mesic forests are more narrowly restricted to valleys, and pine stands are much more limited. The apparent inconsistency, with both mesic and xeric types reduced, should be due to effects of the mountains themselves on climate. Because of the rain-shadow effect, there is less precipitation to the southeast to support mesic valley types; but the open slopes and ridges are somewhat protected from the westerly winds which contribute to the dryness of pine sites on the northwest side. The result is an expansion of intermediate, oak-chestnut types at the expense of the extremes on the southeast, as compared with the northwest side of the range. Farther east of the Smokies in the Blue Ridge, the oak-chestnut grouping is further expanded as a prevailing climax, and mesophytic communities are very restricted.

West from the Smokies in the Cumberland Mountains, the mesophytic portion of the pattern expands to become prevailing climax, while oak-chestnut and pine types are much restricted (see also Part II). Seen from the Smokies the vegetation of the Cumberlands is a somewhat reduced, more highly mesophytic version of the Smokies pattern, to which are added low-elevation types not recognized in the Smokies. Seen from the Smokies the vegetation of the Blue Ridge is a comparable transformation by expansion of the oak-chestnut types and contraction of the mesophytic communities. Seen from the Cumberlands the pattern of the Smokies represents a reduction of the mesophytic part of the pattern and expansion of oak-chestnut, and a transition toward the oak-chestnut prevailing climax of the Blue Ridge and beyond.

Changes in vegetation patterns along climatic gradients and from one mountain range to another may be interpreted on the basis of changes in relative importance of species, groups of species, types, and parts of vegetation patterns (see also Part II). Semantic limitations of such interpretation may be evident. Expansion in one direction is, with equal justice, contraction in the other. The types and parts of vegetation patterns which expand and contract are subjectively chosen fractions of the whole patterns. A type or part of a pattern which is treated as the same in different mountain ranges is not really the same; and the further apart the two ranges are, the less meaningful it is to treat it as the same. Such interpretation offers an alternative to that based on climax regions and ecotones, however, and may do more justice to the complexities and relativities of vegetation patterning (cf. the mosaic interpretation of Krause 1952).

Five major forest groupings of the eastern United States meet in the Smokies and contribute to the variety of their vegetation pattern. Vegetations of other ranges north and south along the Appalachians are suggestive in part of reduced versions of the pattern of the Smokies (or of the Cumberlands or Blue Ridge). Thus Raup (1938) describes a pattern in the Black Rock Forest of New York which may be compared with that of the Smokies: mixed hardwoods and hemlock hardwoods in mesic sites (swamp types also occur), red oak and chestnut oak forests on slopes, white oak-pignut hickory on northerly faces of hill tops, and pitch pine-scrub oak (*Q. ilicifolia*) on southerly faces. Southern exposures of summits have small areas of natural meadow interspersed with scrub oak, suggestive of grassy balds. Because in the Smokies an Appalachian vegetation pattern of maximum diversity appears, intermediate to the mixed mesophytic and oak-chestnut prevailing climaxes of the Cumberlands and Blue Ridge, the author has regarded the vegetation of this range as "central" to that of other Appalachian Mountains not too distant.

The Southern Appalachians have long been recognized (Adams 1902; Harshberger 1903, 1911:198, 209-211) as a geographic center for the forests of the eastern United States. In the interpretation of Braun the Appalachian center has been given special prominence, and the Mixed Mesophytic Region in and around the Cumberland Mountains is regarded as the center. It is Braun's thesis (Braun 1950:39) that "The Mixed Mesophytic association, which characterizes this region, is the most complex and the oldest association of the Deciduous Forest Formation. It occupies a central position in the deciduous forest as a whole, and from it or its ancestral progenitor, the mixed Tertiary forest, all other climaxes of the deciduous forest have arisen." The choice of which of two ranges of the Southern Appalachians is to be designated as central is not a matter of great moment. With due respect for the case for the Cumberlands developed by Braun, certain other considerations related to the Smokies and the Unaka Mountains of which they are part, may be mentioned.

1. "Centers" are products of human interpretation

and, like such other concepts as "association" and "climatic climax," should not be taken for granted. Designation of a center may be thought meaningful only as the criterion or criteria (Adams 1902, Cain 1944) one chooses to define a center are stated.

2. There is no reason, *a priori*, for locating a center in an area possessing a well-defined prevailing or climatic climax. If, on the other hand, diversity is regarded as a primary criterion, then location of centers in areas like the Smokies with vegetation too varied to possess a well-defined prevailing climax is perhaps to be expected.

3. Designation of one area, the Smokies, as transitional between other areas which are non-transitional seems of little intrinsic meaning. Areas of great vegetational diversity are most conveniently regarded as transitional in a framework of thought which includes climatic climaxes and climax regions as major concepts. These concepts should not necessarily be applied to the biogeographic problems of "centers."

4. A traditional primary criterion of a center, though not the only possible one, is biotic diversity— richness in species in general, or in a particular group being studied. Some secondary criteria are features usually associated with areas of maximum biotic diversity—age of the area, wide range of habitats, and occurrence of narrow endemism among its species.

5. The greater ranges of elevation and moisture conditions of the Smokies imply greater floristic diversity, as well as greater variety of vegetation types. This fact, as well as the secondary criteria mentioned, may point to the Smokies rather than the Cumberlands as "central" for the Southern Appalachians. Both ranges are doubtless to be regarded as parts of the broader Southern Appalachian center. Within this area the different criteria of Braun and the author lead rather naturally to their different emphasis of the Cumberlands and the Smokies. A major concern of the present paper is with vegetation patterns in relation to environmental gradients, and it is thought that in the Smokies the eastern forests show their greatest diversity and differentiation into types within a limited area. The pattern is doubtless one of the most complex on the continent. Also in the Siskiyou Mountains and Klamath Region, somewhat comparable forest center of the West, an observer is at first overwhelmed by variety of vegetation types; but this variety is expressive of climatic gradients and variety of soil materials as well as of elevation and local moisture conditions. The author knows no pattern of climax vegetation, occurring within a limited area on relatively uniform soil materials, more varied than that of the Great Smoky Mountains.

SUMMARY

I. Gradient Analysis

1. Vegetation of a range of the Southern Appalachians, the Great Smoky Mountains of Tennessee, was analyzed. Field transects, with samples taken at fixed intervals along environmental gradients, and *site-samples* taken widely through the vegetation pattern as an approach toward randomization, were used as means of vegetation sampling unprejudiced by assumptions about associations.

2. Arbitrary classes or ecological groups of tree species and weighted averages based on these classes were used for indication of relative positions of stands along the moisture gradient. The site-samples were arranged into composite transects, showing the relation of plant populations to environmental gradients. Major environmental gradients, those of elevation and moisture conditions of site, are conceived as *complex-gradients* of many interrelated factors affecting plants.

3. The sequence of vegetation types from mesic sites to xeric at low elevations is: cove forest (mixed mesophytic), oak-hickory forest, oak-chestnut forest, oak-chestnut heath, and pine forest. Deciduous trees other than oaks predominate in mesic sites, oaks in intermediate sites, and pines in xeric sites; but relative proportions of these growth-forms change continuously along the moisture gradient through the various types. Along the same gradient, stature of trees and canopy coverage in general decrease; but the number of tree stems is greater in xeric sites than in mesic. At all points along the gradient, undisturbed forest stands are self-maintaining; and a curve relating stem numbers and diameters in these all-age, climax stands is suggested. Diversity, or richness in species, of the tree stratum is maximal in low-elevation stands transitional between cove forests and oak forests; and diversity values decrease with increasing departure from these stands toward more mesic or more xeric conditions and toward higher elevations.

4. Coverage of the shrub stratum in general increases along the moisture gradient toward xeric sites. Deciduous, non-ericaceous shrubs predominate in mesic sites, evergreen ericaceous shrubs in intermediate sites, and deciduous ericads (Vaccinioideae) in xeric sites. With increase of shrub coverages along the gradient, herb coverages decrease; coverages for the two strata are inversely related. Ferns and delicate, umbrella-shaped herbs prevail in mesic forests but decrease in coverage along the moisture gradient as other herb growth-forms (rosette plants, grasses, ground heaths, etc.) increase. Herb coverages in general increase toward higher elevations, but shrub coverages are more complexly related to elevation.

5. In subalpine forests *Picea rubens* is dominant from 4500 ft up through the lower part of the forests; *Abies fraseri* is dominant above 6000 ft. Subalpine forests show limited difference in canopy composition along the moisture gradient but striking difference in undergrowths. The same herbs and shrubs as those in mesic deciduous forests appear in valleys; a complex undergrowth of five strata (Hylocomium, Oxalis, Dryopteris, Vaccinium, and Viburnum) occurs on north and east slopes and decreases in coverage around to west and south slopes; and a dense

Rhododendron heath occurs in spruce-fir stands on ridges.

6. Species populations have for the most part rounded and tapered curves of population distribution along environmental gradients; these curves appear to be of binomial form. Both centers and limits of population curves for different species are well scattered along the gradients. Natural clustering of populations into groups of associated species is absent or weakly developed. Vegetation types are, with some exceptions, fully continuous with one another. Distributions of undergrowth species do not correspond to those of dominant species, and change in floristic composition of communities is continuous through vegetation types defined by dominant species.

II. Discussion: An Interpretation of Vegetation Patterning

7. The distributional pattern of a species to some extent expresses the genetic pattern of that species. Certain major species in the Great Smoky Mountains consist of two or more ecotypes; and distributions of species are significantly affected also by occurrence of clines, introgressive hybridization, polyploidy, and apomixis. "Competition" may affect distributional patterns in various ways: (1) formation of a plateau distribution with competition occurring within the species, (2) depression of population levels through competition with other species, (3) competitive splitting of a species distribution, and (4) displacement of the environmental mode from the physiological optimum.

8. Species are distributed not in terms of associations, but each according to its own physiology and genetic pattern, and hence no two alike. The assumption that species are organized into associations as real units, designated the *association-unit theory,* is rejected in favor of the individualistic hypothesis of Ramensky and Gleason. Vegetation may be interpreted as a complex and largely continuous *population pattern.*

9. The condition of continuous population change along continuous environmental gradients in natural communities is termed *gradation.* In gradating vegetation, some community-types are conveniently defined by one dominant species or the distributional overlap of two dominant species. Associations defined by several species may be conceived as groupings of character-species (or of dominant species) with their population modes close together in relation to environmental gradients. Species thus related may be termed *commodal,* and a group of such species may be termed a *commodium.*

10. Some vegetation types of more extreme environments are separated from the rest of the vegetation pattern by relative discontinuities. These discontinuous types or *zones* may be characterized by flattened or "plateau" distributions of dominant species or growth-forms. *Zonation* is distinguished from gradation as a tendency toward partial segmentation of the vegetation continuum. "Ecotones" are not in any very real sense boundaries between communities; they are communities themselves and may often be characterized by commodal groupings of smaller woody species.

11. Climax vegetation is interpreted as a whole continuum or *climax pattern,* rather than as a single climatic climax or set of polyclimaxes. The moisture-gradient pattern permits comparison of climax characteristics of different elevations or areas in terms of dominant growth-forms, species diversities, relative importance of species and species groups, etc. Three quantitative approaches to the "climatic climax" are suggested: *average climax composition, prevailing climax type,* and *intermediate climax stand.*

12. Associations are not communities; they are community-types or *classes* of communities, and hence conceptual units which should not be thought inherent in vegetation itself. A necessary complement to the classificatory approach is one considering vegetation patterns as wholes. The approach of relating gradients of plant populations and community characteristics to gradients of environment is termed *gradient analysis.*

III. Vegetation Types and Their Distributional Relations

13. Vegetation types of the Great Smoky Mountains are defined as units of recognized subjectivity by criteria of physiognomy and dominance. Character-species are designated for the types, so far as possible. Fifteen climax vegetation types are described. The relation of cove forests to mixed mesophytic forest in the Cumberland Mountains is considered; and types of driest and most exposed sites in the Smokies (pine stands, heath balds, and grassy balds) are interpreted as topographic climax.

14. The site-samples were plotted on a *mosaic chart* to show the relation of vegetation types to elevation and topography. The southwestern limit of the Appalachian spruce-fir forests is reached in the Smokies, in the northern half of the range where peaks of 6000 ft and above occur. It is believed that the spruce-fir forests found sanctuary on higher peaks during the xerothermic period, when a displacement upward of 1000-1300 ft destroyed these forests in lower parts of the range and farther south.

15. The vegetation of the Smokies is interpreted as an Appalachian pattern of maximum diversity and differentiation of types, intermediate in some respects to the patterns of the Cumberlands and Blue Ridge. Vegetation patterns of different mountain ranges are often related by the relative expansion and contraction of different, recognized parts of the patterns. Both the Smokies and Cumberlands are parts of the Southern Appalachian center of the eastern forests.

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Appendix A. Population Charts for Major Tree Species.

In the following population charts, stand percentages of tree species in composite stand counts (Appendix C) have been plotted on the vegetation pattern in relation to elevation and site (Fig 19). Isorithms for stand percentages have been drawn in, forming nomograms of tree population levels in relation to the two major gradients studied. The population figures thus outlined may be visualized in three dimensions as hills with their summits representing environmental optima for species, and with slopes of decreasing population density with increasing departure from the optima. Population charts are included for 44 major tree species; charts are available also for canopy populations and minor species (see Note on Supplementary Publication).

Note on Supplementary Publication of Appendixes B and C

The author regrets the impossibility of publishing the full body of tabulations on which the study is based. Tables which cannot be presented here are made available to those desiring them through the American Documentation Institute, Auxiliary Publications Project, Photoduplication Service, Library of Congress, Washington 25, D. C. Advance payment is required. Make checks or money orders payable to: Chief, Photoduplication Service, Library of Congress.

Appendix B comprises the full set of transect tables which were to accompany Part I. Transect tables show population levels (stand percentages) of trees, presence of shrubs, and presence of herbs along environmental gradients in the following sets of transects:

Tables 2-4, moisture gradient between 1500 and 2500 ft.

Tables 5-7, moisture gradient between 2500 and 3500 ft.

Tables 8-10, moisture gradient between 3500 and 4500 ft.

Tables 11-13, moisture gradient in deciduous forests above 4500 ft.

Tables 14-16, elevation gradient in mesic sites, 200-ft intervals.

Tables 17-19, elevation gradient in submesic sites, 200-ft intervals.

Tables 20-22, elevation gradient in subxeric sites, 200-ft intervals.

Tables 23-25, elevation gradient in xeric sites, 300-ft intervals.

Photostats of these tables (35 pages) may be purchased from the American Documentation Institute for $5.00, microfilms for $2.25, as Document No. 4722.

Appendix C comprises the composite stand counts on which the descriptions of Part III are based. Data on trees include numbers of stems for each species in 3-in. diameter classes, percentage of stand from the 1-in. diameter class up, and percentage of canopy stems, based in each case on approximately 1000 stems and 100 canopy stems. Presences of shrub and herb species are given. The 27 tables represent 13 climax forest types recognized in the Great Smoky Mountains; tables available for the various types are indicated in the classification of vegetation types at the beginning of Part III. Photostats of these tables (46 pages) may be purchased from the American Documentation Institute for $6.25, microfilms for $2.50, as Document No. 4723.

The full set of population nomograms for tree species (Appendix A) may also be obtained. Nomograms are for 54 species of trees and arborescent shrubs; of these the 32 marked with an asterisk (*) are represented by nomograms both for total stems and for canopy stems only. The charts thus permit study of the vegetation as a population pattern in terms of all tree populations, and of canopy stems alone. Photostats of these nomograms (22 pages) may be purchased from the American Documentation Institute for $3.75, microfilms for $2.00, as Document No. 4721. The set of charts includes: *Abies fraseri*, Acer pensylvanicum, A. rubrum*, A. saccharum*, A. spicatum, Aesculus octandra*, Amelanchier arborea, A. laevis, Aralia spinosa, Betula allegheniensis*, B. lenta*, Carpinus caroliniana, Carya cordiformis, C. glabra*, C. ovalis*, C. tomentosa*, Castanea dentata*, Cercis canadensis, Cladrastis lutea*, Clethra acuminata, Cornus alternifolia, C. florida, Fagus grandifolia*, Fraxinus americana*, Halesia monticola*, Hamamelis virginiana, Ilex montana, I. opaca, Juglans nigra, Liriodendron tulipifera*, Magnolia acuminata*, M. fraseri*, M. tripetala, Nyssa sylvatica*, Ostrya virginiana, Oxydendrum arboreum, Picea rubens*, Pinus pungens*, P. rigida*, P. strobus*, P. virginiana*, Prunus serotina*, Quercus alba*, Q. borealis* and var. *maxima*, Q. coccinea*, Q. marilandica, Q. montana** (Q. prinus), *Q. velutina*, Rhododendron calendulaceum, Robinia pseudoacacia*, Sassafras albidum, Sorbus americana, Tilia heterophylla*, Tsuga canadensis*.*

Abies fraseri stems

Acer pensylvanicum stems

Acer rubrum stems

Acer saccharum stems

Acer spicatum stems

Aesculus octandra stems

Betula allegheniensis stems

Betula lenta stems

Carya cordiformis stems

Carya glabra stems

Carya ovalis stems

Carya tomentosa stems

Castanea dentata, dead stems

Cladrastis lutea stems

Clethra acuminata stems

Cornus florida stems

Fagus grandifolia stems

Fraxinus americana and var. biltmoreana stems

Halesia monticola stems

Hamamelis virginiana stems

Magnolia tripetala stems

Nyssa sylvatica stems

Oxydendrum arboreum stems

Picea rubens stems

Pinus pungens stems

ELEVATION IN FEET

BOREAL FORESTS

HEATH BALD

BEECH FORESTS
MESIC TYPE | SEDGE TYPE

RED OAK-CHESTNUT FOREST

WHITE OAK-CHESTNUT FOREST

GRASSY BALD

HEMLOCK FOREST

COVE FORESTS

RED OAK-PIGNUT HICKORY FOREST

CHESTNUT OAK-CHESTNUT FOREST

CHESTNUT OAK-CHESTNUT HEATH

.8

.9

TABLE MOUNTAIN PINE HEATH 50.9

50

35.9 PITCH PINE HEATH

20

VIRGINIA PINE FOREST

2.0

1

| COVES | FLATS | DRAWS | SHELTERED | OPEN SLOPES | RIDGES & PEAKS |
| CANYONS | | RAVINES | SLOPES | NE E W S / N NW SE SW | |

MESIC — — — — — — — — — — — — — — XERIC

Pinus rigida stems

ELEVATION IN FEET

BOREAL FORESTS

HEATH BALD

BEECH FORESTS
MESIC TYPE | SEDGE TYPE

RED OAK-CHESTNUT FOREST

WHITE OAK-CHESTNUT FOREST

GRASSY BALD

HEMLOCK FOREST

COVE FORESTS

RED OAK-PIGNUT HICKORY FOREST

CHESTNUT OAK-CHESTNUT FOREST

CHESTNUT OAK-CHESTNUT HEATH

.7

1.5

.5

1.5

TABLE MOUNTAIN PINE 24.2 HEATH

10

20

28.7 PITCH PINE HEATH

30

40

30

25.8 VIRGINIA PINE FOREST

20

1 10

| COVES | FLATS | DRAWS | SHELTERED | OPEN SLOPES | RIDGES & PEAKS |
| CANYONS | | RAVINES | SLOPES | NE E W S / N NW SE SW | |

MESIC — — — — — — — — — — — — — — XERIC

Pinus strobus stems

ELEVATION IN FEET

BOREAL FORESTS

HEATH BALD

BEECH FORESTS
MESIC TYPE | SEDGE TYPE

RED OAK-CHESTNUT FOREST

WHITE OAK-CHESTNUT FOREST

GRASSY BALD

HEMLOCK FOREST

COVE FORESTS

RED OAK-PIGNUT HICKORY FOREST

CHESTNUT OAK-CHESTNUT FOREST

CHESTNUT OAK-CHESTNUT HEATH

TABLE MOUNTAIN PINE HEATH

PITCH PINE HEATH

.2

2

1.7

2.4

2.8

7.1

2.8 VIRGINIA PINE FOREST

1.0

5.0

5.0

1.0

| COVES | FLATS | DRAWS | SHELTERED | OPEN SLOPES | RIDGES & PEAKS |
| CANYONS | | RAVINES | SLOPES | NE E W S / N NW SE SW | |

MESIC — — — — — — — — — — — — — — XERIC

Pinus virginiana stems

ELEVATION IN FEET

BOREAL FORESTS

HEATH BALD

BEECH FORESTS
MESIC TYPE | SEDGE TYPE

RED OAK-CHESTNUT FOREST

WHITE OAK-CHESTNUT FOREST

GRASSY BALD

HEMLOCK FOREST

COVE FORESTS

RED OAK-PIGNUT HICKORY FOREST

CHESTNUT OAK-CHESTNUT FOREST

CHESTNUT OAK-CHESTNUT HEATH

TABLE MOUNTAIN PINE HEATH

1.0 PITCH PINE HEATH

1

20

.6

1.8

41.2 VIRGINIA PINE FOREST

50

50

20 50

| COVES | FLATS | DRAWS | SHELTERED | OPEN SLOPES | RIDGES & PEAKS |
| CANYONS | | RAVINES | SLOPES | NE E W S / N NW SE SW | |

MESIC — — — — — — — — — — — — — — XERIC

Prunus serotina stems

ELEVATION IN FEET

HEATH BALD

BOREAL FORESTS

BEECH FORESTS MESIC TYPE | SEDGE TYPE

.3

.1

RED OAK-CHESTNUT FOREST

WHITE OAK-CHESTNUT FOREST

GRASSY BALD

1.0

1.5   0   1.3   1.0

1.0

HEMLOCK FOREST

TABLE MOUNTAIN PINE HEATH

COVE FORESTS

RED OAK-PIGNUT HICKORY FOREST

CHESTNUT OAK-CHESTNUT FOREST

CHESTNUT OAK-CHESTNUT HEATH

PITCH PINE HEATH

VIRGINIA PINE FOREST

COVES CANYONS | FLATS DRAWS RAVINES | SHELTERED SLOPES | OPEN SLOPES NE E W S N NW SE SW | RIDGES & PEAKS

MESIC ————————————— XERIC

Quercus alba stems

ELEVATION IN FEET

HEATH BALD

BOREAL FORESTS

BEECH FORESTS MESIC TYPE | SEDGE TYPE

1   5   5   1

1.4   27.5

20

2.0   19.5

1.1

RED OAK-CHESTNUT FOREST

WHITE OAK-CHESTNUT FOREST

GRASSY BALD

HEMLOCK FOREST

TABLE MOUNTAIN PINE HEATH

0   .2   0

.1

PITCH PINE HEATH

COVE FORESTS

2.2   5.7   1.3   3.5

.5

RED OAK-PIGNUT HICKORY FOREST

CHESTNUT OAK-CHESTNUT FOREST

CHESTNUT OAK-CHESTNUT HEATH

VIRGINIA PINE FOREST

5

COVES CANYONS | FLATS DRAWS RAVINES | SHELTERED SLOPES | OPEN SLOPES NE E W S N NW SE SW | RIDGES & PEAKS

MESIC ————————————— XERIC

Quercus borealis and var. maxima stems

ELEVATION IN FEET

HEATH BALD

BOREAL FORESTS

BEECH FORESTS MESIC TYPE | SEDGE TYPE

1   5   10   30   10   5

1.8   .9   33.0

30.7

.9   34.6   16.6

.8   .3   3.2   5.0   3.0   2.2

RED OAK-CHESTNUT FOREST

WHITE OAK-CHESTNUT FOREST

GRASSY BALD

HEMLOCK FOREST

TABLE MOUNTAIN PINE .7 HEATH

PITCH PINE HEATH

1

COVE FORESTS

2.5   2.7   7.0   4.3   12.4

RED OAK-PIGNUT HICKORY FOREST

CHESTNUT OAK-CHESTNUT FOREST

CHESTNUT OAK-CHESTNUT HEATH

VIRGINIA PINE FOREST

5   5

COVES CANYONS | FLATS DRAWS RAVINES | SHELTERED SLOPES | OPEN SLOPES NE E W S N NW SE SW | RIDGES & PEAKS

MESIC ————————————— XERIC

Quercus coccinea stems

ELEVATION IN FEET

HEATH BALD

BOREAL FORESTS

BEECH FORESTS MESIC TYPE | SEDGE TYPE

RED OAK-CHESTNUT FOREST

WHITE OAK-CHESTNUT FOREST

GRASSY BALD

TABLE MOUNTAIN PINE 1.7 HEATH

12.7   20   25

HEMLOCK FOREST

.2   3.5

.1

.1   3.5

10

7.2

COVE FORESTS

RED OAK-PIGNUT HICKORY FOREST

CHESTNUT OAK-CHESTNUT FOREST

CHESTNUT OAK-CHESTNUT HEATH

PITCH PINE HEATH

VIRGINIA PINE FOREST

COVES CANYONS | FLATS DRAWS RAVINES | SHELTERED SLOPES | OPEN SLOPES NE E W S N NW SE SW | RIDGES & PEAKS

MESIC ————————————— XERIC

Quercus marilandica stems

Quercus prinus stems

Quercus velutina stems

Robinia pseudoacacia stems

Sassafras albidum stems

Sorbus americana stems

Tilia heterophylla, etc. stems

Tsuga canadensis stems