

A Biological Spectrum of the Flora of the Great Smoky Mountains National Park

Stanley A. Cain

Follow this and additional works at: <http://digitalcommons.butler.edu/botanical>

The Butler University Botanical Studies journal was published by the Botany Department of Butler University, Indianapolis, Indiana, from 1929 to 1964. The scientific journal featured original papers primarily on plant ecology, taxonomy, and microbiology.

Recommended Citation

Cain, Stanley A. (1945) "A Biological Spectrum of the Flora of the Great Smoky Mountains National Park," *Butler University Botanical Studies*: Vol. 7, Article 3.

Available at: <http://digitalcommons.butler.edu/botanical/vol7/iss1/3>

Butler University
Botanical Studies
(1929-1964)

Edited by

Ray C. Friesner

The *Butler University Botanical Studies* journal was published by the Botany Department of Butler University, Indianapolis, Indiana, from 1929 to 1964. The scientific journal featured original papers primarily on plant ecology, taxonomy, and microbiology. The papers contain valuable historical studies, especially floristic surveys that document Indiana's vegetation in past decades. Authors were Butler faculty, current and former master's degree students and undergraduates, and other Indiana botanists. The journal was started by Stanley Cain, noted conservation biologist, and edited through most of its years of production by Ray C. Friesner, Butler's first botanist and founder of the department in 1919. The journal was distributed to learned societies and libraries through exchange.

During the years of the journal's publication, the Butler University Botany Department had an active program of research and student training. 201 bachelor's degrees and 75 master's degrees in Botany were conferred during this period. Thirty-five of these graduates went on to earn doctorates at other institutions.

The Botany Department attracted many notable faculty members and students. Distinguished faculty, in addition to Cain and Friesner, included John E. Potzger, a forest ecologist and palynologist, Willard Nelson Clute, co-founder of the American Fern Society, Marion T. Hall, former director of the Morton Arboretum, C. Mervin Palmer, Rex Webster, and John Pelton. Some of the former undergraduate and master's students who made active contributions to the fields of botany and ecology include Dwight W. Billings, Fay Kenoyer Daily, William A. Daily, Rexford Daudenmire, Francis Hueber, Frank McCormick, Scott McCoy, Robert Petty, Potzger, Helene Starcs, and Theodore Sperry. Cain, Daudenmire, Potzger, and Billings served as Presidents of the Ecological Society of America.

Requests for use of materials, especially figures and tables for use in ecology text books, from the *Butler University Botanical Studies* continue to be granted. For more information, visit www.butler.edu/herbarium.

A BIOLOGICAL SPECTRUM OF THE FLORA OF THE GREAT SMOKY MOUNTAINS NATIONAL PARK*

By STANLEY A. CAIN
The University of Tennessee

The present study of life-forms of the Great Smoky Mountains flora is based on the system of Raunkiaer (1934). Realizing the difficulties involved in correlation of meteorological and climatological data with the natural occurrences of plants, Raunkiaer designed his life-form system as a means of defining what he called phytoclimates. The theoretical basis was a familiar one in plant geography (Cain, 1944) and may be expressed as follows: (1) Plants are limited in their capacity to endure different environmental complexes. (2) There is usually a correlation between the morphology (growth-form, life-form) of an organism and its environment, *i. e.*, there is a morphological basis for adaptation in many if not all cases. (3) A plant, in its successful existence, represents what may be called an automatic physiological integration of all the factors of its environment. It follows, if these are general truths, that the life-forms of the plants of an area are a measure of the environmental conditions, especially climate. It remains only to find the key to the plant-climate interrelations.

Raunkiaer decided that the significant relationship was to be looked for in the seasonal climates. (and all climates but that of the constantly warm-humid tropical rainforest do have a seasonal rhythm in precipitation, temperature, or both). When growth is slowed or dormancy forced upon a plant by cold or drought the most critical tissues are the meristematic. Therefore, the amount of protection provided embryonic growing tissues and their success in enduring the unfavorable period represent a critical adaptation. It is for this reason that Raunkiaer selected the protection afforded the perennating buds as the principal basis for his life-form system.

Raunkiaer's life-form system met with ready acceptance and has been applied widely, if sporadically, over the world. This is because

*A contribution (Botanical Laboratories, The University of Tennessee, N. Ser. No. 75) in recognition of the 25th Anniversary of the Botany Department of Butler University.

the system is homogeneous, the life-forms are relatively few and easily determined, and the results can be employed statistically in the comparison of floras and climates. When the flora of an area is analyzed and it is found that a certain life-form percentage exceeds the proportion which that life-form is of the normal spectrum¹ the phytoclimate is designated by that superabundant or predominating life-form. Thus Raunkiaer spoke of the phanerophytic climate of the tropics, the hemicryptophytic climate of the humid temperate zone, the chamaephytic climate of arctic and alpine regions, and the therophytic climate of deserts.

After forty years there are still insufficient data for a close delineation of the major world climates, but certain general correlations originally pointed out by Raunkiaer have been confirmed, at least for certain regions.

In following Raunkiaer's system in making a biological spectrum of the Great Smoky Mountains flora, I used the preliminary catalogue of the flowering plants of the Great Smoky Mountains National Park, a checklist in preparation for several years under the supervision of Mr. Arthur Stupka, Park Naturalist. The principal field and herbarium work was carried on by the late Professor H. M. Jennison and more recently by Professor Aaron J Sharp. I have not employed the list completely in its present form, having omitted from consideration all varieties and forms except in cases where a species is represented in the area only by a variety. Also, numerous escapes from agriculture and gardens have been omitted where there is any uncertainty as to their establishment. The plant list and my assignment of life-forms to the individual species are not here published because the incomplete nature of the catalogue prevents its release at this time by the Park Naturalist.

In cases where I am not familiar with a species, its assignment to a certain life-form often has been on a basis of previously published classification, usually by Ennis (1928) or McDonald (1937). Cases of questionable life-form status for the Smoky Mountains area and cases of disagreement between authors have been settled by reference to herbarium material and the literature. I am aware of the probability of incorrect assignment of certain species to life-form classes and

¹ The normal spectrum, based on 1,000 carefully selected species, is no more than a yardstick, a statistical approximation of the life-form percentage composition of the flowering-plant flora of the world as a whole.

hope that the whole flora eventually may be studied in the field from this point of view. Most of the doubtful cases fall on the boundary between geophyte and hemicryptophyte and between hemicryptophyte and chamaephyte. Another need for further field work is in connection with subclasses, particularly among hemicryptophytes and chamaephytes. Finally, life-form studies of the flora of the Smoky Mountains can not be refined greatly without more knowledge concerning the altitudinal occurrences of the species and more complete information concerning the floristic composition of the major plant communities. Since such a thorough-going study may not be possible for years to come, I have assumed that the present preliminary analysis is worth doing for its immediate value.

The five principal classes of the life-form system of Raunkiaer (based, as we have said, on the protection afforded the perennating buds during the unfavorable season) are arranged according to increasing protection: phanerophytes (trees and shrubs), chamaephytes (low perennials with buds close to the ground surface), hemicryptophytes (buds at the soil surface), cryptophytes (buds beneath the soil or under water), and therophytes (annuals, buds within the seeds). These classes are subject to subdivision. The chamaephytes are so few in number that no breakdown was made. My information concerning the hemicryptophytes is inadequate for the detailed treatment of subclasses. The geophytes (the major group of cryptophytes) were classified according to whether the subterranean organs bearing the perennating buds are rhizomes, bulbs, stem tubers, root tubers, or roots, but the various groups seem to have little significance for present purposes. The phanerophytes, however, were easily treated according to four subclasses based on height. Megaphanerophytes exceed 30 meters; mesophanerophytes are between 8 and 30 meters; microphanerophytes are between 2 and 8 meters; and nanophytes are less tall than 2 meters and taller than chamaephytes (about 25 cm.).

The analysis of the flora is found in table I where the total flora, including well-established adventives, is compared with species known to occupy the highest altitudinal belt, essentially from 4,500 feet to the tops of the mountains at slightly more than 6,500 feet. This belt corresponds in general with the altitudinal range of the spruce-fir subalpine forest. It is penetrated, however, by northern hardwoods in the valleys and lower gaps, and is interrupted in many places by heath balds (Cain, 1931). In the southwestern portion of the Park

below the southern limits of spruce-fir, the northern hardwoods go to the tops of the mountains and are interrupted by grassy balds. Raunkiaer's normal spectrum is added to table I for comparison.

The flora of the Great Smoky Mountains is conspicuously represented by hemicryptophytes and cryptophytes and is of a type generally referred to the hemicryptophytic climate. It is perhaps more accurate to say that the type of biological spectrum (life-form percentage distribution) here revealed is characteristic of a series of closely related climates of the humid temperate regions with a definite to pronounced winter and continuously favorable growing season. This can be illustrated by placing the spectrum for the Great Smoky Mountains in a series of spectra for eastern North America, table II.

TABLE I

Life-form statistics for the total flora and for the flora of the highest belt in the Great Smoky Mountains National Park.

Life-form	No.	Total flora		High altitude species		Raunkiaer's Normal Spectrum	
		spp.	Per cent	No.	spp.	Per cent	Per cent
Phanerophytes		223	19.5	64		21.2	46.0
(Mega-")	29		2.5	2		0.6	
(Meso-")	73		6.4	18		6.0	
(Micro-")	70		6.1	22		7.3	
(Nano-")	51		4.5	22		7.3	
Chamaephytes		20	1.7	7		2.3	9.0
Hemicryptophytes		595	52.1	170		56.5	26.0
Cryptophytes		173	15.1	52		17.2	6.0
Therophytes		131	11.5	8		2.6	13.0
Totals		1142	99.9	301		99.8	

TABLE II

Some life-form spectra for eastern North America representing areas of humid mesothermal and microthermal climates characterized as hemicryptophytic.

Flora and author Number of species	Phanero- phytes	Chamae- phytes	Hemi- crypto- phytes	Crypto- phytes	Thero- phytes
Alabama, Ennis, 1928 2,012 species	17.0	3.1	47.8	17.1	14.4
Mississippi, Ennis, 1928 1,724 species	17.7	3.1	49.4	16.2	12.8

TABLE II—(Continued)

Some life-form spectra for eastern North America representing areas of humid mesothermal and microthermal climates characterized as hemicryptophytic.

Flora and author Number of species	Phanero- phytes	Chamae- phytes	Hemi- crypto- phytes	Crypto- phytes	Thero- phytes
Great Smoky Mountains 1,142 species	19.5	1.7	52.1	15.1	11.5
Bull Run, Virginia, Allard, 1944 980 species	18.2	1.4	51.7	11.3	17.0
Connecticut, Ennis, 1928 1,453 species	15.0	1.9	49.4	21.7	11.7
Cape Breton, Ennis, 1928 637 species	14.1	1.8	51.3	25.6	6.7
Indiana, McDonald, 1937 2,109 species	14.3	1.9	49.0	18.0	16.7
Iowa, Ennis, 1928 1,320 species	14.8	1.0	48.6	20.9	14.2
Normal spectrum 1,000 species	46.0	9.0	26.0	6.0	13.0

Referring again to table I, it is seen that the hemicryptophytic portion of the total flora of the Smokies is 52 per cent, just double that of the normal spectrum. Cryptophytes, with 15 per cent, are two and one-half times the normal. These excesses over the corresponding percentages of the normal spectrum are primarily at the expense of phanerophytes, which are less than half the normal for the world.

That this spectrum is typical of the spectra for the humid temperate climates is seen from the data in table II. These spectra are all of the same pattern and vary only in small ways. The position of the Smokies in the latitudinal series from Alabama and Mississippi to Cape Breton is somewhat misleading because we are here dealing with a mountainous area in which much of the vegetation and the higher climates are characteristic of higher latitudes. Thus the Smoky Mountains spectrum exceeds in hemicryptophytes even that of Cape Breton, and the spectrum for high altitudes in the Smokies (table I) accentuates certain characteristics of the flora as a whole. All the other classes of life-forms are increased at the expense of therophytes. The high position of phanerophytes in the Smoky spectrum (within the series, of course) is an expression of the southern position of the area together with the variation of conditions resulting from the alti-

tudinal range. Its low position for cryptophytes is due entirely to the absence in the mountains of marshes, ponds, and lakes and the consequently very small number of helophytes and hydrophytes.

It is not within the purposes of this paper to discuss life-form spectra in general, especially how the spectra for the hemicryptophytic climate differ from those of steppe, desert, tropical and other climates, but the similarities of the spectra in table II indicate the close similarity in climate of the areas of the deciduous, summer-green forest regions of eastern United States. They do not differ as to the fundamental type of climate, but only in details of length and coldness of winter, etc.

The type of life-form statistics employed in the preceding section depends on the use of total floras of whole areas. In such an analysis one species counts as much as another irrespective of its role in the structure of the vegetation of the area. The other use of life-forms is their employment in the description of vegetation types including communities of all sociological rank. The description of vegetation partly at least in terms of life-form and especially the life-forms of the dominants is an ancient practice in plant geography, as witnessed by such terms as woodland, bushland, steppe, etc. In complex communities the whole phytocoenosis may be referred to in terms of the life-form of the dominating layer. Lippmaa (1933) has developed a system of vegetation description which depends upon the separate analysis of each synusia of the phytocoenosis, the synusiae being single-layered communities each composed of plants of one or of two closely related life-forms. Raunkiaer, however, introduced the most useful, graphically descriptive employment of life-forms in community analysis. I say this because his method uses simultaneously the complete life-form data for the community and statistical information on the quantitative roles of the species. That is to say, he developed life-form spectra for plant communities in which the percentages for each life-form are based on their total frequency points resulting from quadrat analysis. For the Smokies it is possible for me to apply this method only to the cove hardwood forest complex for which some quantitative data recently have been published (Cain, 1943a).

The cove hardwood forest complex is frequently considered to be a unit, especially by foresters, and is sometimes designated as undifferentiated or mixed mesophytic forest by ecologists. Even in the limited Greenbrier area of the Smokies it is, however, recogniz-

able with close study as consisting of seven minor forest types in two alliances, as follows: Aesculion, including the buckeye-basswood, sugar maple-silver-bell, yellow birch, and beech segregates; and the Tsugion, including the hemlock-beech, hemlock tuliptree, and hemlock segregates. I have statistical data for 31 stands of this complex forest, each sampled by a plot of about one acre area. Sample plot data for the shrub and field layers were obtained from 10 of these stations under spring conditions, and from nine other stations under summer conditions. At each station the vernal flora was sampled by 10 quadrats of one sq. m. area, whereas the aestival flora was sampled by 10 quadrats of six sq. m. area.¹ The cove hardwoods paper cited above contains the results of the quadrat study and presents the results for all the species by constancy and frequency percentages. These long tables will not be repeated here, but they provide the data for the subsequent life-form spectra.

The constancy percentage of a species for a community type is the relationship between the total number of stations studied and the number of stations in which the species occurred in the sample areas. Frequency is the same sort of concept, but it is based on the individual quadrats, rather than on the data for stations.

The following lists of species present the flora of the cove hardwoods as determined by the above procedure, and arranged by life-form. The nomenclature follows Small's Manual and the arrangement in each group is one approximately according to constancy percentages. The resulting life-form statistics compose Table III.

PHANEROPHYTES. Megaphanerophytes: *Tsuga canadensis*, *Aesculus octandra*, *Betula allegheniensis*, *Saccharodendron barbatum*, *Fagus grandifolia*, *Fraxinus americana*, *Liriodendron tulipifera*, *Padus virginiana*, *Castanea dentata*, *Picea rubens*, *Rufacer rubrum*, *Tulipastrum acuminatum*, *Quercus maxima*, *Quercus montana*.— Mesophanerophytes: *Halesia monticola*, *Tilia neglecta*, *Magnolia Fraseri*, *Acer pennsylvanicum*, *Hicoria cordiformis*, *Amelanchier laevis*, *Ilex opaca*, *Betula lenta*, *Wallia cinceae*, *Cynoxylon floridum*, *Cladrastis lutea*, *Oxydendrum arboreum*, *Robinia pseudoacacia*, *Parthenocissus quinquefolia* (liana), *Aristolochia macrophylla* (liana).— Microphanerophytes: *Acer spicatum*, *Sida alternifolia*, *Hamamelis virginiana*, *Ilex monticola*, *Aralia spinosa*, *Viburnum lantanoides*,

¹ A brief note on the sampling problem is appended at the end of this paper.

Euonymus americanus, *Sambucus pubens*.—Nanophanerophytes: *Euonymus obovatus*, *Hydrangea arborescens*, *Pyrularia pubera*, *Grossularia Cynosbati*.

CHAMAEPHYTES. *Alsine tennesseensis*, *Mitchella repens*, *Phlox stolonifera*, *Sedum ternatum*, *Cymophyllus Fraseri*.

HEMICRYPTOPHYTES. *Tiarella cordifolia*, *Aster acuminatus*, *Viola sororia*, *Viola blanda*, *Solidago Curtisii*, *Eupatorium urticaefolium*, *Nabalus* sp., *Viola hastata*, *Oxalis montana*, *Ranunculus recurvatus*, *Monarda didyma*, *Poa cuspidata*, *Osmorrhiza Claytoni*, *Viola canadensis*, *Viola rostrata*, *Galium triflorum*, *Carex flexuosa*, *Carex plantaginea*, *Rudbeckia laciniata*, *Hepatica acuta*, *Carex austro-caroliniana*, *Viola rotundifolia*, *Cryptotaenia canadensis*, *Viola eriocarpa*, *Campanulastrum americanum*, *Geum canadense*, *Peranium ophioides*, *Viola pallens*, *Viola cucullata*, *Mitella diphylla*, *Geranium maculatum*, *Zizia Bebbii*, *Juncoides bulbosum*, *Carex prasina*, *Ranunculus fascicularis*, *Micranthes micranthidifolia*, *Juncoides saltuense*, *Ranunculus abortivus*, *Heuchera americana*, *Senecio Rugelii*, *Taenidia integerrima*, *Blephilia hirsuta*, *Solidago axillaris*, *Hystrix Hystrix*, *Houstonia purpurea*, *Meibomia nudiflora*, *Juncus tenuis*, *Thalictrum dioicum*, *Panicum* sp? *Carex stellata*, *Asclepias exaltata*, *Lysimachia quadrifolia*.

CRYPTOPHYTES (all geophytes). *Erythronium americanum*, *Dentaria diphylla*, *Anemone quinquefolia*, *Urticastrum divaricatum*, *Bicuculla canadensis*, *Panax trifolium*, *Caulophyllum thalictroides*, *Claytonia virginica*, *Trillium erectum* var. *album*, *Cimicifuga americana*. *Polygonatum biflorum*, *Disporum languginosum*, *Tovara virginiana*, *Hydrophyllum canadense*, *Medcola virginiana*, *Validallium tricoccum*, *Veratrum viride*, *Arisaema quinatum*, *Podophyllum peltatum*. *Xeniatrum umbellulatum*, *Arisaema triphyllum*, *Chrosperma muscaetavicum*, *Syndesmon thalictroides*, *Vagnera racemosa*, *Lilium superbum*. *Trillium grandiflorum*, *Actea alba*, *Diphylleia cymosa*, *Collinsonia canadensis*, *Circaea latifolia*, *Bicuculla cucullaria*, *Clintonia borealis*, *Glycine Apios*, *Monotropa uniflora*, *Carex pennsylvanica*.

THEROPHYTES. *Impatiens pallida*, *Galium circaezans*, *Cuscuta* sp., *Adicea pumila*, *Phacelia fimbriata*, *Galium aparine*.

Lines 1-3 of table III present life-form spectra for the cove hardwoods in which the species as such form the basis of the statistics. The total flora spectrum, line 1, differs strongly from that for the Park as a whole, table I. Phanerophytes increase from 19.5 to 36.3 per cent, a change that would seem to be due to the fact that this is a

very rich forest community (14 mega-, 15 meso-, 8 micro-, and 4 nanophanerophytes) in primeval condition with rather uniform microclimatic and soil conditions under the arborescent dominance. The second conspicuous change from the spectrum for the whole Park is from 15.1 to 25.8 per cent cryptophytes. Chamaephytes likewise are increased, from 1.7 to 4.4 per cent, but these figures are too small to be of much consequence. The increases are at the expense of the hemicryptophytes, which drop from 52.1 to 30.1 per cent, and therophytes, from 11.5 to 3.4 per cent.

TABLE III

Life-form spectra for the primeval cove hardwoods of the Smokies.

	Ph	Ch	H	Cr	Th	
Spectra based on species						Species
1. Total flora	36.3	4.4	30.1	25.8	3.4	113
2. Field layer, vernal aspect	7.0	47.2	40.3	5.5	72
3. Field layer, aestival aspect	6.6	61.3	29.3	2.6	75
Spectra based on constancy						Points
4. Total flora	31.1	5.9	33.1	26.9	3.0	4,052
5. Field layer, vernal aspect	9.0	48.0	39.0	4.0	2,790
6. Field layer, aestival aspect	8.1	58.1	31.1	2.7	2,877
Spectra based on frequency						Points
7. Field layer, vernal aspect	11.0	43.3	41.9	3.8	1,309
8. Field layer, aestival aspect	14.2	58.6	23.9	3.3	1,258

When the phanerophytes are left out of consideration and the herbaceous synusia is considered alone there naturally are percentage changes, so comparison will be made only between the vernal and aestival aspects of this layer. The most striking result is the pronounced representation of cryptophytes in the vernal flora (40.3 per cent, and all geophytes) and the preponderance of the more slowly developing but ultimately rank-growing hemicryptophytes in the aestival flora (61.3 per cent). The contrast between six per cent cryptophytes for the normal spectrum, 15 per cent for the whole Smoky Mountains flora, and 40 per cent of geophytes alone for the vernal flora of the cove hardwoods is a very striking phenomenon.

Seven geophytes in the vernal flora which were absent in the aestival aspect, apparently because of having rapidly completed their life-cycle and retreated again to their subterranean organs, are *Erythronium americanum*, *Bicuculla canadensis*, *Bicuculla cucullaria*, *Panax*

trifolium, *Claytonia virginica*, *Trillium grandiflorum*, and *Actea alba*. The seven other geophytes unsampled in the aestival flora are the longer enduring *Veratrum viride*, *Podophyllum peltatum*, *Lilium superbum*, *Diphylleia cymosa*, *Collinsonia canadensis*, *Circaea latifolia*, and *Clintonia borealis*. The six geophytes sampled in the aestival flora and not in the vernal flora are *Tovara virginiana*, *Chrosperma muscaetoxicum*, *Syndesmon thalictroides*, *Glycine Apios*, *Monotropa uniflora*, and *Carex pennsylvanica*. Although the differences in geophyte listing for the vernal and aestival aspects of the field layer are partly due to sampling and partly due to normal variability in composition of such a rich community, it still seems that the first group of species listed immediately above represents a distinct excess of geophytes in the vernal flora. Furthermore, that the cryptophyte-hemicryptophyte relationship in the vernal and aestival societies is a true one is substantiated by the constancy and frequency studies (lines 4-8, table III) where very similar ratios reoccur.

It often happens that the use of quantitative data for species in the development of life-form spectra produces strikingly different results from spectra based solely on species with each species having the same weight. In this case, however, the various field spectra are all of the same pattern, as shown by lines 2, 5, and 7 for the vernal aspect and lines 3, 6, and 8 for the aestival aspect. This result would seem to be due to the fact that the cove hardwoods flora is a very rich one in which no small number of species is clearly predominant. This situation is in strong contrast to the more impoverished but comparable field layers of the mesophytic deciduous forests of Europe (Lippmaa, 1938, and Raunkiaer, 1934). The most interesting new feature of the compared spectra (obtained from species alone, constancy points, and frequency points) is the steady increase of chamaephytic percentages from 7.0 to 9.0 to 11.0 for the vernal aspect and from 6.6 to 8.1 to 14.2 for the aestival aspect.

Theoretically the most significant spectra for the microphytoclimate of the field layer of the cove hardwoods are those based on frequency points because they provide better data on the roles of the species in the community. Raunkiaer showed that frequency points approach density values when numerous small quadrats are used. The best way of preparing statistical life-form data for spectra would probably be by the use of dominance data because of the biological significance of dominance in a community, but such information is

not at hand for the cove hardwoods. At any rate, the spectra based on frequency points are more revealing as to the role played by the various life-forms than are the spectra based on species composition alone.

In table IV are spectra on certain American forest associations the data for which I believe to be comparable. The two spectra for mixed mesophytic climax are strikingly similar. The communities would appear to be wholly comparable ecologically and probably are climatically, the higher altitude of the Tennessee stands compensating for the higher latitude of the Ohio stands. The Long Island oak "association segregate" has a conspicuous increase in chamaephytes which is maintained by the Laurentian maple "association segregate" and to which is added a striking increase in hemicryptophytes. These trends at the expense of phanerophytes and cryptophytes, and within the deciduous forest climax formation, are in accord with expectation according to Raunkiaer's theory of phytoclimates and experience with regional spectra. The two studies on *Populus* associations also produce similar spectra. Although the data are fragmentary, there is a suggestion that association spectra may be used better to distinguish climatic differences and delimit types than areal and regional spectra. Specifically, spectra based upon floras as large as those of states, or even areas like Cape Breton and the Great Smoky Mountains, include too much variability of microclimate and habitat for any but the most general comparisons.

One technical point concerning the quadrat technique may be added here as a sort of appendix, and that concerns the use of different sizes of quadrats in the sampling of the vernal and aestival aspects of the field layer. I have discussed this problem elsewhere (Cain, 1932, 1938, 1943b), but these data offer a new approach. Notice in table III that the constancy points for the vernal aspect are 2,790 and for the aestival aspect 2,877 although the sampled area in the latter was about six times that of the former. The same relationship holds for the frequency points where the numbers are 1,309 and 1,258, respectively. No such close approximations could have resulted had constant-size quadrats been used in the sampling of both aspects. The larger size for the aestival aspect was necessitated by the larger stature and area of the summer plants.

TABLE IV

Life-form spectra of certain American deciduous forest associations.

	No. Species	Ph	Ch	H	Cr	Th
Cove hardwoods mixed mesophytic climax, Great Smoky Mountains	113	36.3	4.4	30.1	25.8	3.4
Mixed mesophytic climax, Cincinnati area. Withrow, 1932	127	33.6	3.9	34.4	23.4	3.9
Quercetum montanae, Long Island, New York, Cain, 1936	92	34.8	10.9	32.6	20.6*	1.1
Aceretum saccharophori, Laurentian region. Dansereau, 1943	346	17.0	10.0	56.0	15.0	2.0
Aspen association, Northern Lower Michigan. Gates, 1930	310	22.9	3.9	47.1	16.1	10.3
Poplar association, Central Alberta. Moss, 1932	170	25.8	1.8	48.2	17.1	7.0

* Including 2.1% Monotropaceae.

SUMMARY

1. The life-form spectrum for 1,142 species of the Great Smoky Mountains National Park is entirely similar in pattern to other spectra for humid mesothermal and microthermal climates and the eastern American deciduous summergreen forest region. Hemicryptophytes predominate, being the life-form of 52 per cent of the total flora.

2. Species of the area known to exceed 4,500 feet elevation and grow in what is essentially the spruce-fir belt produce a similar spectrum to that of the Park as a whole, but with all classes slightly increased at the expense of therophytes which drop from 11.5 to 2.6 per cent.

3. Statistical data (on constancy and frequency) for the flora of the virgin cove hardwood forests of the Greenbrier region of the Park allowed a special analysis of life-forms in that community:

a. In comparison with the Park as a whole, the cove hardwoods show an exceptionally high percentage of geophytes (25.8%), and a high percentage of phanerophytes (36.3%) for the latitude.

b. Comparison of the vernal and aestival aspects of the herbaceous layer of the cove hardwoods showed the importance of geophytes in the vernal flora (40.3%) and of hemicryptophytes in the aestival flora (61.3%).

c. Spectra obtained from constancy and frequency points are entirely of the pattern of ones from species *per se*. This is due to the large number of species involved and the lack of preponderance in numbers and mass by one or a few species.

4. A comparison of certain forest-association spectra reveals close similarity between closely related associations, such as the Southern Ohio and Eastern Tennessee mixed mesophytic associations and the Alberta and Michigan *Populus* associations. The Laurentian *Acer* "association segregate" reveals the influence of more northern position in its relatively high Ch and H percentages better than does a regional spectrum in the case of Cape Breton.

LITERATURE CITED

- ALLARD, H. A. An analysis of the flora of the Bull Run Mountain region of Virginia using Raunkiaer's "life-form" method. Journ. Wash. Acad. Sci. 34 (4): 112-119. 1944.
- CAVIN, STANLEY A. Ecological studies of vegetation of the Great Smoky Mountains of North Carolina and Tennessee. I. Bot. Gaz. 91 (1): 22-41. 1931.
- . Concerning certain phytosociological concepts. Ecol. Monogr. 2: 475-508. 1932.
- . The composition and structure of an oak woods, Cold Spring Harbor, Long Island, with special attention to sampling methods. Amer. Midl. Nat. 17 (4): 725-740. 1936.
- . The species-area curve. Amer. Midl. Nat. 19 (3): 573-581. 1938.
- . The Tertiary character of the cove hardwood forests of the Great Smoky Mountains National Park. Bull. Torrey Bot. Club 70 (3): 213-235. 1943a.
- . Sample-plot technique applied to alpine vegetation in Wyoming. Amer. Jour. Bot. 30 (3): 240-247. 1943b.
- . *Foundations of Plant Geography*. xiv + 556. Harper & Bro., New York. 1944.
- DANSEREAU, PIERRE. L'Érablière Laurentienne. I. Valeur d'indice des espèces. Contr. Inst. Bot. Univ. Montréal No. 45: 66-93. 1943.
- ENNIS, B. The life forms of Connecticut plants and their significance in relation to climate. Conn. State Geol. Nat. Hist. Surv., Bull. 43. 1928.
- GATES, F. C. Aspen association in Northern Lower Michigan. Bot. Gaz. 90 (3): 233-259. 1930.
- LIPPMAN, T. La méthode des associations unistrates et la système écologique des associations. Acta Inst. et Horti Bot. Univ. Tartuensis 4 (1-2): 1-7. 1933.
- . Areal und Alterbestimmung einer Union sowie das Problem der Charakterarten und der Konstanten. Acta Inst. Horti Bot. Univ. Tartuensis 6 (2): 1-152. 1938.

- McDONALD, E. S. The life-forms of the flowering plants of Indiana. Amer. Midl. Nat. 18 (5): 687-773. 1937.
- MOSS, E. H. The vegetation of Alberta IV. The poplar association and related vegetation of Central Alberta. Jour. Ecol. 20: 380-415. 1932.
- RAUNKIAER, C. *The Life Forms of Plants and Plant Geography*. 632 pp. Oxford Press. 1934 (This book contains translated papers of Raunkiaer since 1903 on statistical plant geography, and is the source of all reference to Raunkiaer in this paper.)
- WITHROW, ALICE P. Life forms and leaf size classes of certain plant communities of the Cincinnati region. Ecology 8(1): 12-35. 1932.