

**Zeitschrift:** Veröffentlichungen des Geobotanischen Institutes der Eidg. Tech. Hochschule, Stiftung Rübel, in Zürich

**Herausgeber:** Geobotanisches Institut, Stiftung Rübel (Zürich)

**Band:** 69 (1980)

**Artikel:** Preliminary analysis of vegetation in the Thompson River Watershed, North and South Carolina

**Autor:** Wentworth, Thomas R.

**DOI:** <https://doi.org/10.5169/seals-308600>

### **Nutzungsbedingungen**

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

### **Conditions d'utilisation**

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

### **Terms of use**

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

**Download PDF:** 26.08.2025

**ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>**

Preliminary Analysis of Vegetation in the Thompson River Watershed,  
North and South Carolina<sup>1</sup>

by

Thomas R. WENTWORTH

Contents

1. Introduction	145
2. Study area	146
3. Methods and materials	149
4. Results	153
5. Discussion	157
Summary - Zusammenfassung	158
References	159

1. Introduction

Pronounced relief, variation in topographic features, and a generally mild climate with unusually high precipitation create a wide diversity of favorable habitats for plant growth in the southeastern escarpment region of the Blue Ridge Mountains. Evolution and migration of floristic elements through the Tertiary and Quaternary Periods have endowed the region with a diverse flora.

---

<sup>1</sup> Paper No. 6163 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh, North Carolina.

Affinities exist, therefore, to various floristic provinces of the Old and New Worlds. Because of the interesting ecology and systematics of its flora and fauna, the escarpment region has been the object of a recently renewed interest.

Information presently available provides an excellent background for an intensive, quantitative study of the vegetation in the escarpment region. The Thompson River watershed was selected for further research, with four research needs and objectives identified from previous work in the area: (1) the investigation of vegetation-environment relationships, (2) comparative community-type description, (3) analysis of species diversity, and (4) analysis of geographic floristic affinities. In the present paper I address the first two objectives, based on preliminary analyses of distributional data for 47 arborescent species.

### Acknowledgements

Financial support of this project from the North Carolina Agricultural Research Service and Highlands Biological Station is gratefully acknowledged. I am indebted to John DeLapp, Dan Lazar, and Stephen Hight for their enthusiastic and dedicated assistance during the months of field sampling in rugged and sometimes inhospitable terrain.

## 2. Study area

### 2.1. *Physiography and geology*

The Thompson River is centrally located among six major streams (Chattooga, Whitewater, Thompson, Horsepasture, Toxaway, and Eastatoe) which drain the southeastern escarpment region of the Blue Ridge Mountains. In this region, located between Hendersonville, N.C., and Highlands, N.C., the Blue Ridge divide has an east-west orientation, departing from its general northeast-southwest trend. The Blue Ridge escarpment is diffuse here and located to the south of the divide, creating an embayed area. Elevational differences are in excess of 1000 m, ranging in the Thompson River watershed from the upper piedmont of South Carolina (approximately 335 m) to the higher peaks in North Carolina (1340 m). With the exception of the Chattooga River, the streams of

the escarpment region drain southward with steep gradients; spectacular waterfalls and precipitous gorge walls are common (COOPER and HARDIN 1970). Bedrock in the region consists of Precambrian or lower Paleozoic igneous and metamorphic rocks (STUCKEY 1965).

## 2.2. *Climate*

One of the most interesting and unusual features of the southeastern escarpment region is the high annual precipitation, especially at the heads of the major gorges. Mean annual values from reports of stations along the escarpment rim are in the vicinity of 200 cm (COOPER 1963). No permanent weather stations are located in the gorges proper, but fragmentary records from the Whitewater, Thompson, and Horsepasture gorges indicate that annual precipitation at the gorge heads is approximately 230 - 250 cm (BILLINGS and ANDERSON 1966, MOWBRAY and OOSTING 1968). Similarly high precipitation within continental United States occurs on the western slope of the Cascade Mountains in Oregon and Washington. Possible causal factors for this high annual precipitation are discussed by BILLINGS and ANDERSON (1966).

Temperature data for the escarpment region are less readily available (COOPER and HARDIN 1970), but data from Highlands, N.C., give a general regional overview. According to COOPER and HARDIN (1970), mean annual temperature in Highlands is  $11.4^{\circ}\text{C}$  with a low monthly mean in January ( $2.9^{\circ}\text{C}$ ) and a high monthly mean in July ( $20.2^{\circ}\text{C}$ ). The record high temperature was  $30.6^{\circ}\text{C}$  and the record low temperature was  $-30.0^{\circ}\text{C}$ . Highlands has 157 frost-free days (May 3 - October 7). In summary, then, "... the climate of the gorges is characterized by high rainfall, moderate, reliable temperatures, and lack of extremes of heat and drought." (COOPER and HARDIN 1970).

## 2.3. *Soils*

LEE (1955) indicates that soils of the Porters-Ashe, Halewood-Hayseville, and Talladega-Ramsey associations dominate the region. These soils would be classified primarily as hapludults and dystrochrepts (NELSON and ZILLGITT 1969) in modern terminology. Detailed information on the soils is limited, but one intensive study by LOSCHE (1967, summarized in COOPER and HARDIN 1970) has provided valuable data. Contrary to expectations, the soils in this region of

rugged topography show evidence of advanced weathering. In some cases the solum supplies only limited amounts of nutrients for plant growth; under such conditions the bulk of the nutrient cycling and regeneration must involve the regolith and organic horizons (COOPER and HARDIN 1970). The integrity of the vegetation-soil-climate complex of the region has been shown by MOWBRAY and OOSTING (1968), who found that the clay/silt ratio (B horizon) of soils was the best predictor of vegetation composition. This result apparently reflects the combined effects of topography, vegetation, and climate on soil genesis.

#### 2.4. *Flora*

Interest in the origins and floristic affinities of vegetation in the southern Appalachian region dates from the botanical explorations of the eighteenth century. GRAY (1846), and later, FERNALD (1929) investigated the floristic affinities of eastern North America and eastern Asia, focusing attention on distribution patterns relevant to the Southern Appalachian flora. Other researchers, such as CHANEY (1947), considered the Tertiary origin of the region's mixed mesophytic floristic component as an integral part of the Arcto Tertiary Flora concept. More recent analysis of fossil evidence (WOLFE 1969) suggests that the mixed mesophytic forest has a complex lineage, with both tropical and temperate ancestries.

Much effort has also been devoted to study of Pleistocene distributions of the regional flora and vegetation (DEEVEY 1949, BRAUN 1955, WHITEHEAD 1963, 1964, 1967). Recent analyses of the fossil record (WHITEHEAD 1965, 1967) support the theory of DEEVEY (1946) and others that major changes occurred in vegetation and climate in the southern Appalachian region during full-glacial times. This topic is discussed further in Vol. 1 of the 16th IPE report by DELCOURT and DELCOURT (1979). In addition, numerous investigations have documented the region's relationships to floras of eastern Asia (LI 1952, HARA 1962), western North America (CLEMENTS 1936, McVAUGH 1943, SHARP 1951, WOOD 1970), Mexico (MIRANDA and SHARP 1950, SHARP 1953, DRESSLER 1954), and the New World tropics (RAVEN 1963, BILLINGS and ANDERSON 1966, FARRAR 1967).

#### 2.5. *Vegetation*

Forest vegetation patterns in the escarpment region have been described

by COOPER and HARDIN (1970). In general, the vegetation types and vegetation-environment relationships are representative of those described for the Southern Appalachian portion of the eastern deciduous forest complex (e.g. BRAUN 1950, WHITTAKER 1956). Yet several unique aspects of gorge vegetation have attracted the interests of numerous investigators. For example, the gorges harbor a number of Southern Appalachian endemics, including *Shortia galacifolia*, the famous "lost plant" of Asa Gray. The gorges are also notable for the absence or rarity of several important species (*Acer saccharum*, *Betula allegheniensis*, *Magnolia acuminata*) which characterize areas of similar habitat elsewhere in the Southern Appalachians (COOPER and HARDIN 1970). Finally, the discovery of several fern (FARRAR 1967) and bryophyte (BILLINGS and ANDERSON 1966) species of tropical affinity in the Blue Ridge escarpment gorges has resulted in considerable interest in the floristic relationships of the regional vegetation.

## 2.6. Previous research in the Thompson River watershed

A major research effort by numerous workers in the 1960's produced valuable information concerning the flora in the escarpment region. This research, summarized by COOPER and HARDIN (1970), consisted of both inventory and descriptive work, as well as analytical and experimental research. Several of these studies concentrated on the Thompson River watershed. WARE (1973) compiled a list of vascular plant species with some observations on the distribution of major vegetation-types. Other studies include a localized but intensive investigation of vegetation and microclimate (MOWBRAY and OOSTING 1968), and studies of pine forests of the area (RACINE 1966, 1969).

## 3. Methods and materials

### 3.1. Site selection

Sample sites were chosen by means of a stratified-random procedure. An initial population of potential sample sites was obtained by overlaying topographic maps of the Thompson River watershed with a 0.25 x 0.25 km gridwork. This procedure established approximately 700 points regularly spaced over the

Table 1. Elevation, aspect, and topographic position classes used in classification of an initial population of sample sites prior to sampling by a stratified-random procedure.

*Elevation classes*

- (1) High : 1005 - 1340 m
- (2) Medium: 670 - 1005 m
- (3) Low : 335 - 670 m

*Aspect classes*

- (1) Northerly (N, NNW, NNE, NE)
- (2) Northerly - intermediate (NW, WNW, ENE, E)
- (3) Southerly - intermediate (W, WSW, ESE, SE)
- (4) Southerly (SW, SSW, SSE, S)

*Topographic position classes*

- (1) Protected (ravines, coves, concave lower slopes)
- (2) Protected-intermediate (open lower to middle slopes, gaps, upper ravine and cove sides, wide bottomlands)
- (3) Exposed-intermediate (open middle to upper slopes, wide upland areas)
- (4) Exposed (peaks, ridges, upper convex slopes)

35 km<sup>2</sup> watershed. As far as possible, all sites were then classified according to a simple system incorporating elevation, topographic position, and aspect (Table 1). Two sample sites were selected at random from each of the 48 possible combinations of the various classes. Additional sites were also chosen to represent topographic situations not readily fitting into the classification scheme of Table 1. Each site thus selected was located in the field by means of compass and altimeter and then sampled unless found to be recently disturbed. When a given site could not be sampled because of disturbance, its replacement was selected at random from the remaining members of its class. Approximately 100 sites were sampled in this fashion. Other sites were chosen in the field to supplement the sample set based on the stratified-random procedure, resulting in a total of 150 sites sampled during the summer months of 1976, 1977, and 1978.

### 3.2. Sampling procedures

A tenth-hectare (20 x 50 m) quadrat was located at each sampling site, extending 10 m to either side of a 50 m tape that was oriented to minimize

vegetational and environmental heterogeneity within the quadrat. Information recorded for each quadrat included elevation, slope, aspect, topographic position, exposure, and the nature and degree of disturbances. A composite soil sample of the A horizon was also collected in each quadrat.

The number of individual plants of all tree species, and all shrub species with a mature height of greater than 1 m, were recorded in a stand count of the full tenth-hectare quadrat. Tree counts were recorded in 2.54 cm dbh (diameter breast height, the diameter at 1.3 m above ground) classes; individuals less than 1 m tall were classed as seedlings while individuals greater than 1 m tall, but less than 1.27 cm dbh, were classed as saplings.

Twenty-five meter-square subquadrats were arranged at 1 m intervals and on alternate sides of the 50 m tape. In each subquadrat, percentage cover for all shrub and herb species were recorded along with percentage cover and density of tree seedlings. In addition, percentage cover for miscellaneous categories, including bedrock, loose rock, litter, wood, water, moss, lichen, and liverwort, were determined in the meter-square subquadrats.

Nomenclature for all species follows RADFORD et al. (1968).

### 3.3. Analyses

The preliminary analyses described in this paper were based on the quadrat data for tree species only. Within each quadrat, the density of tree stems greater than 6.35 cm dbh was determined for each species and expressed on a relative basis as the percentage of total density for all species. The data on diameter distributions were used to calculate basal area for all species in a quadrat, and this measure was also expressed as a relative percentage of total quadrat basal area. Averaging of the relative density and relative basal area measures provided a synthetic importance value for each species in each quadrat. The synthetic importance values were used in all further data analyses.

The importance value matrix was subjected to a variety of indirect ordination techniques, including Wisconsin polar ordination (BRAY and CURTIS 1957), reciprocal averaging or correspondence analysis (HILL 1973, 1974), and principal components analysis (PIELOU 1969, ORLOCI 1973, 1975). All ordinations were performed using program ORDIFLEX (GAUCH 1977). The Wisconsin polar ordination was constructed from a percentage distance matrix with end point selection by



the method of BRAY and CURTIS (1957). The principal components analysis was computed from centralized and standardized (unit variance) species importance values.

An environmental scalar was constructed to provide a direct gradient analysis based on temperature and moisture conditions. As illustrated in Table 2, the scalar is an average of relative indices for stand elevation, topographic position, and annual potential direct beam solar irradiation. The latter data were obtained by interpolation from tables in FRANK and LEE (1966). The three indices were arranged such that the scalar would take on low values for cool, mesic sites (high elevation, protected topographic position, low annual potential direct beam solar irradiation) and high values for warm, xeric sites (low elevation, exposed topographic position, high annual potential direct beam solar irradiation).

Table 2. Computation of a simple moisture/temperature scalar. Three indices were assigned to each stand and these were averaged to obtain the scalar value. The elevation and solar irradiation indices range continuously from 0.00 to 100.00, while the topographic position index has four discrete values over the same range.

	Site characteristic	Index value
Elevation Index (EI)	1340 m (max.)	0.00
	to	to
	335 m (min.)	100.00
Topographic Position Index (TPI)	Protected	0.00
	Protected-intermediate	33.33
	Exposed-intermediate	66.67
	Exposed	100.00
Solar Irridation Index (SII)	North aspect, 45 <sup>o</sup> slope (min.)	0.00
	to South aspect, 32 <sup>o</sup> slope (max).	100.00
Environmental Scalar (ES) = $\frac{EI + TPI + SII}{3.0}$		

Stand classification was accomplished by means of a computer program, TWINSPAN (GAUCH 1973), developed for indicator species analysis as described by HILL et al. (1975). The program essentially performs the steps used in the traditional European methods for ordering species-by-stand phytosociological tables (see MUELLER-DOMBOIS and ELLENBERG 1974, Chapter 9).

#### 4. Results

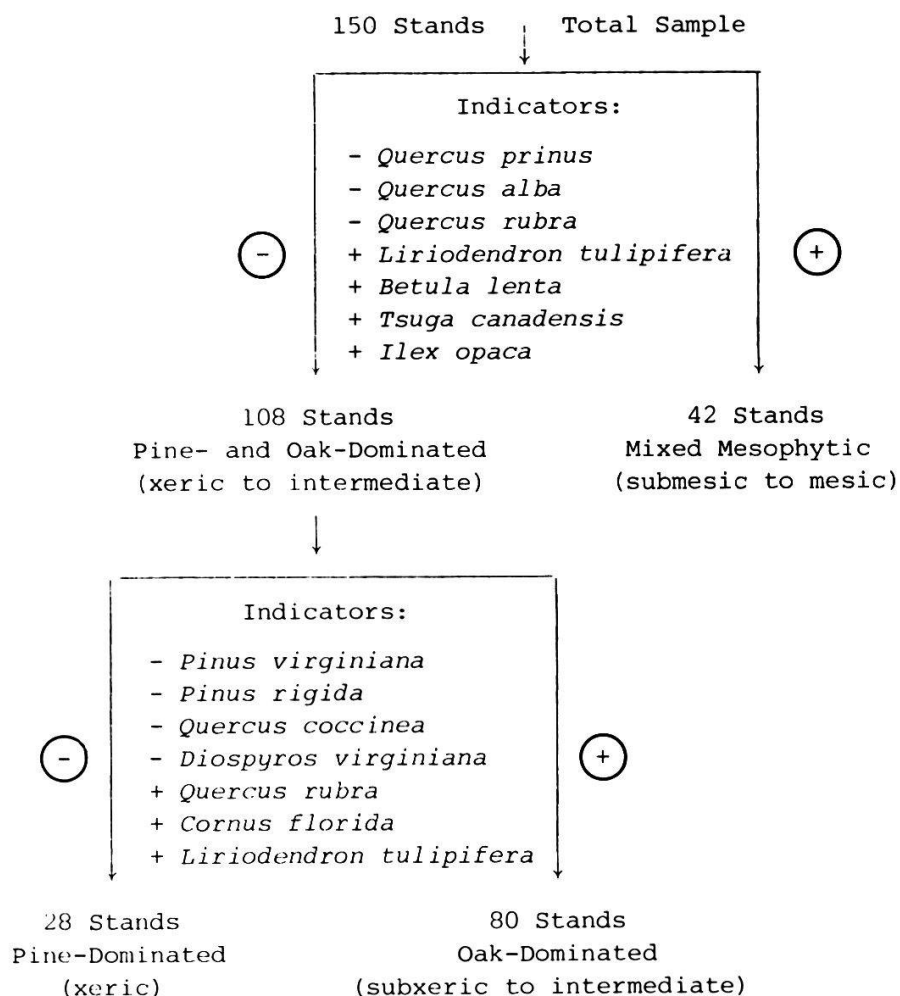
The first-axis stand vectors derived from Wisconsin polar, principal components, and reciprocal averaging ordinations are compared with one another and with the environmental scalar in Table 3. The Spearman rank correlation coefficients used to measure vector similarity showed moderate to strong, highly significant correlations among the four stand arrangements. Agreement among the three indirect ordination techniques suggests that each technique arranged the stands with respect to similar compositional trends. I interpret such trends as a response to the predominant moisture and temperature environmental gradients found in the Thompson River watershed. This interpretation is supported by the moderate similarity between each of the indirect ordinations and the environmental scalar.

Table 3. Spearman rank correlation coefficients among four ordination vectors. ES is the environmental scalar, while WP1, PC1, and RA1 are the first axis indirect ordination vectors from Wisconsin polar, principal components (centered and standardized), and reciprocal averaging, respectively.

	ES	WP1	PC1	RA1
ES	-	0.45	0.63	0.65
WP1		-	0.56	0.76
PC1			-	0.81
RA1				-
All P < 0.0001				

The first two dichotomies of indicator species analysis resulted in three stand groupings whose environmental relationships were readily interpretable (Table 4). The first dichotomy divided the 150 stands into two groups which might be best characterized in terms of moisture/temperature relationships as xeric to intermediate (the "negative" group) and mesic (the "positive" group). Indicator (or differential) species for the negative group were the oaks, *Quercus prinus*, *Q. alba*, and *Q. rubra*. Positive group indicators were *Liriodendron tulipifera*, *Betula lenta*, *Tsuga canadensis*, and *Ilex opaca*. The larger negative group resulting from the first dichotomy was subsequently divided into a negative group of xeric stands whose indicators are *Pinus*

Table 4. Outline of stand classification by indicator species analysis. Two dichotomy levels are illustrated with the positive and negative indicator or differential species used in each dichotomy listed.



*rigida*, *P. virginiana*, *Quercus coccinea*, and *Diospyros virginiana*, and a positive group of subxeric to intermediate stands whose indicators are *Quercus rubra*, *Cornus florida*, and *Liriodendron tulipifera*. The smaller posi-

Table 5 (see opposite site). Species list and summary of compositional data for trees in the Thompson River watershed. Data are presented for the total sample set as well as for each of the tree major forest types recognized by indicator species analysis. Two values are given for each species in each group; the first is its average relative importance value and the second (in parentheses) is its percentage constancy. The species are listed according to their position on the first axis of the reciprocal averaging ordination. Species at the top of the list are typically found in xeric sites, those at the bottom in mesic sites.

Species	Total Sample (n=150)	Major forest types		
		Pine- dominated (n=28)	Oak- dominated (n=80)	Mixed Mesophytic (n=42)
<i>Quercus marilandica</i> Muenchh.	0.25( 5)	1.34( 25)	0.01( 1)	-
<i>Pinus virginiana</i> Miller	1.15( 12)	5.58( 39)	0.14( 8)	0.09( 2)
<i>P. rigida</i> Miller	3.25( 24)	15.88( 89)	0.37( 13)	0.27( 2)
<i>Castanea pumila</i> (L.) Miller	0.01( 8)	0.01( 14)	0.01( 10)	-
<i>Pinus echinata</i> Miller	0.79( 7)	3.56( 21)	0.23( 6)	-
<i>Carya ovalis</i> (Wang.) Sargent	0.10( 2)	0.17( 7)	0.13( 1)	-
<i>Quercus coccinea</i> Muenchh.	4.11( 38)	14.49( 93)	2.43( 33)	0.36( 12)
<i>Q. stellata</i> Wang.	0.03( 2)	0.00( 7)	0.05( 1)	-
<i>Q. falcata</i> Michaux	0.03( 1)	-	0.05( 3)	-
<i>Q. velutina</i> Lam.	1.72( 43)	3.40( 64)	1.79( 48)	0.46( 21)
<i>Nyssa sylvatica</i> Marshall	3.56( 90)	6.41(100)	3.25( 96)	2.25( 71)
<i>Diospyros virginiana</i> L.	0.05( 11)	0.13( 36)	0.04( 6)	0.00( 2)
<i>Castanea dentata</i> (Marshall) Borkh.	0.11( 41)	0.13( 29)	0.16( 58)	0.01( 17)
<i>Oxydendrum arboreum</i> (L.) DC.	7.54( 93)	9.16(100)	8.58( 98)	4.49( 79)
<i>Quercus prinus</i> L.	9.95( 77)	8.71( 86)	13.02( 91)	4.95( 43)
<i>Q. alba</i> L.	7.40( 67)	5.11( 61)	10.40( 81)	3.22( 45)
<i>Q. rubra</i> L.	9.22( 77)	4.22( 68)	14.40( 84)	2.70( 71)
<i>Betula nigra</i> L.	0.00( 1)	-	0.00( 1)	-
<i>Pinus strobus</i> L.	4.30( 71)	4.99( 82)	4.22( 78)	3.99( 52)
<i>Carya ovata</i> (Miller) K. Koch	0.04( 1)	-	0.07( 1)	-
<i>Acer rubrum</i> L.	13.56(100)	9.37(100)	15.83(100)	12.05(100)
<i>Carya glabra</i> (Miller) Sweet	5.64( 80)	3.28( 75)	6.66( 90)	5.25( 64)
<i>Robinia pseudo-acacia</i> L.	2.97( 75)	1.52( 82)	3.22( 81)	3.47( 60)
<i>Carya tomentosa</i> (Poiret) Nuttall	2.01( 32)	0.65( 46)	2.42( 31)	2.14( 24)
<i>Cornus florida</i> L.	4.97( 83)	1.55( 61)	6.09( 90)	5.13( 86)
<i>Sassafras albidum</i> (Nuttall) Nees	0.65( 42)	0.05( 39)	0.78( 53)	0.81( 24)
<i>Aralia spinosa</i> L.	0.01( 4)	-	0.01( 4)	0.02( 7)
<i>Acer pensylvanicum</i> L.	0.01( 1)	-	0.01( 3)	-
<i>Amelanchier arborea</i> (Michaux f.) Fern.	0.16( 19)	0.01( 14)	0.12( 21)	0.34( 17)
<i>Magnolia fraseri</i> Walter	0.78( 29)	0.02( 7)	0.49( 25)	1.84( 52)
<i>Prunus serotina</i> Ehrhart	0.04( 5)	-	0.01( 5)	0.11( 10)
<i>Morus rubra</i> L.	0.00( 2)	-	-	0.00( 7)
<i>Liriodendron tulipifera</i> L.	7.35( 65)	0.18( 21)	3.24( 64)	19.93( 98)
<i>Halesia carolina</i> L.	1.15( 22)	0.00( 4)	0.32( 15)	3.50( 48)
<i>Hamamelis virginiana</i>	0.46( 22)	0.02( 4)	0.09( 19)	1.46( 40)
<i>Tsuga canadensis</i> (L.) Carr.	2.61( 43)	0.03( 18)	0.48( 35)	8.37( 74)
<i>Ilex ambigua</i> (Michaux) Torrey	0.12( 11)	0.00( 4)	0.02( 11)	0.38( 17)
<i>I. opaca</i> Aiton	0.32( 18)	0.00( 4)	0.07( 9)	1.00( 45)
<i>Betula lenta</i> L.	1.94( 32)	-	0.42( 20)	6.11( 76)
<i>Fagus grandifolia</i> Ehrhart	0.35( 11)	-	0.07( 5)	1.13( 29)
<i>Liquidambar styraciflua</i> L.	0.55( 9)	-	0.09( 8)	1.77( 19)
<i>Fraxinus americana</i> L.	0.32( 10)	-	0.12( 6)	0.91( 24)
<i>Juglans cinerea</i> L.	0.01( 1)	-	-	0.04( 5)
<i>Asimina triloba</i> (L.) Dunal	0.00( 1)	-	-	0.01( 5)
<i>Tilia heterophylla</i> Vent.	0.28( 5)	-	-	0.98( 19)
<i>Carpinus caroliniana</i> Walter	0.05( 3)	-	-	0.20( 12)
<i>Carya cordiformis</i> (Wang.) K. Koch	0.07( 1)	-	-	0.25( 2)

tive group resulting from the first dichotomy was also divided, but the resulting groups were rather narrowly defined and are not considered further in this paper.

Table 5 summarizes average compositional data for the full 150 stand sample set and for the three stand groups resulting from the second dichotomy of the indicator species analysis. Capsule descriptions of each of these major vegetation groupings are provided in the following paragraphs:

*Pine-dominated type* (28 stands)

Stands representative of this type are usually found at low to middle elevations below 1000 m. Southerly aspects and generally exposed topographic positions are typical of many stands in the group, resulting in generally xeric conditions. As a group the stands are codominated by *Pinus rigida* and *Quercus coccinea*, with *Acer rubrum*, *Oxydendrum arboreum*, *Quercus prinus*, and *Nyssa sylvatica* of secondary importance. The pine-dominated type is often subdivided into xeric pine and subxeric pine-oak dominated types by other authors (see COOPER and HARDIN 1970).

*Oak-dominated type* (80 stands)

This large group of stands is representative of sites throughout the elevational range of the study area, although sites above 1000 m are somewhat better represented than sites of middle and low elevations. Topographic locations are of intermediate exposure. Sites of extreme exposure or extreme protection are poorly represented. Aspects vary considerably among the sites, but a slight tendency toward south exists. The ubiquitous *Acer rubrum* shares dominance with two oaks, *Quercus rubra* and *Q. prinus*, while *Q. alba*, *Oxydendrum arboreum*, *Carya glabra*, and *Cornus florida* are also important. Prior to the onset of the chestnut blight in this century, *Castanea dentata* was a major component of many of the sites included in this type. Because of the wide range of environmental conditions and considerable land area covered by forests of the oak-dominated type, we may consider it representative of the dominant and characteristic forests of the Thompson River watershed and adjacent region. COOPER and HARDIN (1970) recognized chestnut oak (*Quercus prinus*) and mixed oak-hickory (*Quercus-Carya* spp.) segregates within this rather broad vegetation type.

#### *Mixed mesophytic type* (42 stands)

Stands in the mixed mesophytic type are typically from low to middle elevations (to 1000 m) although a few occur at higher elevations. Most are located in protected sites (cove or ravine bottoms), although some moderately protected sites are represented. Aspects in the group are generally northerly, with southerly aspects also represented; aspect appears to play a secondary role to topographic features in determining moisture and temperature regimes of these mesic, protected sites. *Liriodendron tulipifera* is a strong dominant in stands of this type, with *Acer rubrum*, *Tsuga canadensis*, *Betula lenta*, *Carya glabra*, and *Cornus florida* as important secondary species. COOPER and HARDIN (1970) have emphasized that mixed mesophytic forests of the escarpment region have a somewhat attenuated flora, differing from their counterparts to the north in the absence or rarity of such species as *Betula lutea*, *Acer saccharum*, *A. pensylvanicum*, *Aesculus octandra*, *Magnolia acuminata*, *M. tripetala*, *Cercis canadensis*, and *Ostrya virginiana*.

### 5. Discussion

There is a major compositional gradient in forest communities of the Thompson River watershed, the essential features of which are consistently retrieved by any of a variety of indirect ordination procedures. Environmental gradients of temperature and moisture conditions should be expected to account for much of the compositional variation in a mountainous region. Agreement between a stand arrangement based on a simple moisture/temperature environmental scalar and those obtained by indirect ordination of quantitative data support such an expectation for the Thompson River watershed. Assuming that the scalar is a reasonable approximation of a moisture/temperature complex-gradient, Spearman rank correlation coefficients suggest that the complex-gradient accounts for somewhere between 20 % and 40 % of the compositional variation expressed in the first-axis ordination vectors. Clearly much compositional variation remains unexplained. I expect that understanding of the vegetation pattern in the Thompson River watershed will be enhanced by refinement of the moisture/temperature environmental scalar, incorporation of information about soil properties into other environmental scalars, and

analysis of successional trends. The latter may be particularly important as nearly all sites in the region have been disturbed by logging (both selective and clear-cut) one or more times during the past 100 years (COOPER and HARDIN 1970).

The stand classification provided by indicator species analysis proved useful, as the environmental relationships of the types recognized could be readily interpreted. The types also correspond closely with various taxa of classificatory schemes available from other studies, both qualitative and quantitative, conducted in the region (see COOPER and HARDIN 1970). Interpretation of the indicator species analysis beyond the second dichotomy proved difficult, however; further work with both this and other classification methods using tree as well as shrub and herb distributional data will be necessary before a sufficiently detailed vegetation classification is realized.

The studies described in this paper provide a preliminary understanding of the vegetation in the Thompson River watershed. A predominant compositional gradient and three broad vegetation classes have been defined, and these have been related to major environmental gradients. When refined by further analysis, the vegetation pattern will serve as a background for the study of geographic floristic affinities, community diversity and organization, and population biology in the southeastern escarpment region of the Blue Ridge Mountains.

### Summary

The Thompson River watershed of the southeastern Blue Ridge escarpment covers approximately 35 km<sup>2</sup> and extends from a maximum elevation of 1340 m in North Carolina to 335 m at its base on Lake Jocassee in South Carolina. Quantitative data on the distribution and importance of over 300 vascular plant species were collected from 150 tenth-hectare quadrats located throughout the watershed. The data were analysed by Wisconsin polar, principal components, and reciprocal averaging ordination techniques, which demonstrated a predominant and consistently defined first axis of compositional variation. Construction of a simple environmental scalar supported the interpretation that a moisture/temperature complex-gradient is associated with the ordination pattern. Classification of the stands by indicator species analysis revealed three broad community-types: a xeric pine-dominated type, a subxeric to intermediate oak-dominated type, and a submesic to mesic mixed mesophytic type.



## Zusammenfassung

Das Einzugsgebiet des Flusses Thompson in den südöstlichen Blue Ridge-Bergen umfasst ungefähr 35 km<sup>2</sup> und erstreckt sich von der höchsten Erhebung auf 1340 m in North Carolina bis hinunter auf 335 m zur Einmündung in den Lake Jocassee in South Carolina. Es wurden über das ganze Gebiet verteilt in 150 0.1 ha grossen Quadraten quantitative Daten über die Verbreitung und die Bedeutung von über 300 Phanerogamen aufgenommen. Die Daten wurden nach folgenden Methoden analysiert: Wisconsin polar-Ordination, reciprocal averaging-Analyse, principal components-Analyse. Daraus ergab sich eine vorherrschende und eindeutig umschriebene erste Achse der zusammengesetzten (compositional) Variation. Mit der Verwendung einer einfachen Environmental-Skala konnte gezeigt werden, dass mit dem Ordinationsmuster ein komplexer Feuchtigkeits-Temperatur-Gradient verbunden ist. Eine Einteilung der verschiedenen Bestände nach Zeigerarten ergab drei weit gefasste Vegetationstypen: 1. Trockener Wald mit dominierender Föhre, 2. mässig trockener Wald mit dominierender Eiche, 3. mässig feuchter sommergrüner Laubmischwald.

## References

- BILLINGS, W.D., and ANDERSON, L.E., 1966: Some microclimate characteristics of habitats of endemic and disjunct bryophytes in the southern Blue Ridge. *The Bryologist* 69, 76-95.
- BRAUN, E.L., 1950: *Deciduous forests of eastern North America*. Blakiston Co., Philadelphia. 596 pp.
- 1955: The phytogeography of unglaciated eastern United States and its interpretation. *Bot. Rev.* 21, 297-375.
- BRAY, J.R., and CURTIS, J.T., 1957: An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27, 235-349.
- CHANEY, R.W., 1947: Tertiary centers and migration routes. *Ecol. Monogr.* 17, 141-148.
- CLEMENTS, F.E., 1936: The origin of the desert climax and climate. In: *Essays in geobotany in honor of William Albert Setchell*. Univ. California Press, Berkeley. 87-140.
- COOPER, A.W., 1963: A survey of the vegetation of the Toxaway River gorge with some remarks about early botanical exploration and an annotated list of the vascular plants of the gorge area. *J. Elisha Mitchell Sci. Soc.* 79, 1-22.
- and HARDIN, J.W., 1970: Floristics and vegetation of the gorges on the southern Blue Ridge escarpment. In: HOLT, P.C. (ed.), *The distributional history of the biota of the Southern Appalachians. Part II: Flora*. V.P.I. and S.U. Res. Div. Monogr. 2, 291-330.
- DEEVEY, E.S., Jr., 1949: Biogeography of the Pleistocene. *Bull. Geol. Soc. Amer.* 60, 1315-1416.
- DELCOURT, P.A., and DELCOURT, H.R., 1979: Late Pleistocene and Holocene distributional history of the deciduous forest in the southeastern United States. *Veröff. Geobot. Institut ETH, Stiftung Rübel, Zürich* 68, 79-108.



- DRESSLER, R.L., 1954: Some floristic relationships between Mexico and the United States. *Rhodora* 56, 81-96.
- FARRAR, D.R., 1967: Gametophytes of four tropical fern genera reproducing independently of their sporophytes in the Southern Appalachians. *Science* 155, 1266-1267.
- FERNALD, M.L., 1929: Some relationships of the flora of the northern hemisphere. *Proc. Intern. Congr. Plant Sci. Ithaca* 2, 1487-1507.
- FRANK, E.C., and LEE, R., 1966: Potential solar beam irradiation on slopes: tables for 30° to 50° latitude. U.S.D.A. For. Serv., Rocky Mt. For. Range Exp. Sta. Res. Paper RM-18, 116 pp.
- GAUCH, H.G., Jr., 1973: The Cornell ecology programs series. *Bull. Ecol. Soc. Amer.* 54, 10-11.
- GRAY, A., 1846: Analogy between the flora of Japan and that of the United States. *Amer. J. Sci. Arts*, II. 2, 135-136.
- HARA, H., 1962: Racial differences in widespread species, with special references to those common to Japan and North America. *Amer. J. Bot.* 49, 647-652.
- HILL, M.O., 1973: Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.* 61, 237-249.
- 1974: Correspondence analysis: a neglected multivariate method. *J. Roy. Stat. Soc., Ser. C* 23, 340-354.
- BUNCE, R.G.H., and SHAW, M.W., 1975: Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. *J. Ecol.* 63, 597-613.
- LEE, W.D., 1955: The soils of North Carolina. North Carolina Agr. Expt. Sta. Tech. Bull. 115, 187 pp.
- LI, H.L., 1952: Floristic relationships between eastern Asia and eastern North America. *Trans. Amer. Phil. Soc.* 42, 371-429.
- LOSCHKE, C.K., 1967: Soil genesis and forest growth on steeply sloping landscapes of the Southern Appalachians. Ph.D. Thesis, North Carolina State Univ., Raleigh, N.C., 185 pp.
- McVAUGH, R., 1943: The vegetation of the granitic flat rocks of the southeastern United States. *Ecol. Monogr.* 13, 119-166.
- MIRANDA, F., and SHARP, A.J., 1950: Characteristics of the vegetation in certain temperate regions of eastern Mexico. *Ecology* 31, 313-333.
- MOWBRAY, T.B., and OOSTING, H.J., 1968: Vegetation gradients in relation to environment and phenology in a southern Blue Ridge gorge. *Ecol. Monogr.* 38, 309-344.
- MUELLER-DOMBOIS, D., and ELLENBERG, H., 1974: Aims and methods of vegetation ecology. J. Wiley and Sons, New York. 547 pp.
- NELSON, T.C., and ZILLGITT, W.M., 1969: A forest atlas of the south. Southern For. Expt. Sta., New Orleans, and Southeastern For. Expt. Sta., Asheville, 27 pp.
- ORLOCI, L., 1973: Ordination by resemblance matrices. In: WHITTAKER, R.H. (ed.), *Handbook of Vegetation Science*. Vol. 5. Ordination and classification of communities. Dr. W. Junk, The Hague. 249-286.
- 1975: Multivariate analysis in vegetation research. Dr. W. Junk, The Hague. 276 pp.
- PIELOU, E.C., 1969: An introduction to mathematical ecology. Wiley-Interscience, New York. 286 pp.
- RACINE, C.H., 1966: Pine communities and their site characteristics in the Blue Ridge escarpment. *J. Elisha Mitchell Sci. Soc.* 82, 172-181.

- 1969: Tree reproduction in relation to vegetational and environmental gradients on slopes in the southern Blue Ridge Mountains. Ph.D. Thesis, Duke Univ., Durham, N.C., 192 pp.
- RADFORD, A.E., AHLES, H.E., and BELL, C.R., 1968: Manual of the vascular flora of the Carolinas. Univ. of North Carolina Press, Chapel Hill. 1183 pp.
- RAVEN, P.H., 1963: Amphitropical relationships in the floras of North and South America. *Quart. Rev. Biol.* 38, 151-177.
- SHARP, A.J., 1951: Relationships between the floras of California and southeastern United States. *Contr. Dudley Herb.* 4, 59-61.
- 1953: Notes on the flora of Mexico: world distribution of the woody dicotyledonous families and the origin of the modern vegetation. *J. Ecol.* 41, 374-380.
- STUCKEY, J.L., 1965: North Carolina: its geology and mineral resources. North Carolina Department of Conservation and Development, Raleigh. 550 pp.
- WARE, D.M.E., 1973: Floristic survey of the Thompson River watershed. *Castanea* 38, 349-378.
- WHITEHEAD, D.R., 1963: Northern elements in the Pleistocene flora of the southeast. *Ecology* 44, 403-406.
- 1964: Fossil pine pollen and full-glacial vegetation in southeastern North Carolina. *Ecology* 45, 767-776.
- 1965: Palynology and Pleistocene phytogeography of unglaciated eastern North America. In: WRIGHT, H.E., Jr., and FREY, D.G. (eds.), *The Quaternary of the United States*. Princeton Univ. Press, Princeton, N.J. 417-432.
- 1967: Studies of full-glacial vegetation and climate in southeastern United States. In: CUSHING, E.J. and WRIGHT, H.E., Jr. (eds.), *Quaternary paleoecology*. Yale Univ. Press, New Haven, Conn. 237-248.
- WHITTAKER, R.H., 1956: Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26, 1-80.
- WOLFE, J.A., 1977: Paleogene floras from the Gulf of Alaska region. U.S. Geol. Surv. Prof. Paper 997, 108 pp.
- WOOD, C.E., Jr., 1970: Some floristic relationships between the southern Appalachians and western North America. In: HOLT, P.C. (ed.), *The distributional history of the biota of the southern Appalachians. Part II: Flora*. V.P.I. and S.U. Res. Div. Monogr. 2, 331-404.

Address of the author: Dr. Thomas R. WENTWORTH  
 Department of Botany  
 North Carolina State University  
 Raleigh, N.C. 27650, U.S.A.