OAK-HICKORY COMPONENTS OF UPLAND FORESTS OF THE ALABAMA PIEDMONT

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ABSTRACT

Leading dominants analysis (LDA) and reciprocal averaging were used to construct species and stand ordinations from oak and hickory species data from 40 upland forest stands on the Alabama Piedmont. Results from the two techniques are substantially alike and highly correlated. Species ranking of the LDA ordination is (in order of increasingly dry site relationships): *Quercus nigra* L., *Quercus rubra* L., *Quercus alba* L., *Carya ovalis* (Wangenh.) Sarg., *Carya tomentosa* Nutt., *Quercus falcata* Michx., *Quercus coccinea* Muenchh., *Quercus velutina* Lam., *Quercus stellata* Wangenh., *Quercus glabra* (Mill.) Sweet, *Quercus prinus* L., *Carya pallida* (Ashe) Engl. & Grabn., and *Quercus marilandica* Muenchh. Soil parent material type and topographic position are directly related to the stand ordination. The ordinations appear to be related to a complex gradient, with available soil moisture a major factor.

INTRODUCTION

Before white settlement and land clearing, the uplands of the lower Piedmont were heavily forested with mixed stands of hardwoods and pines, with the hardwoods generally predominating (Nelson 1957). The most important species of the original upland forests were probably *Quercus alba* L., *Q. velutina* Lam., *Q. falcata* Michx., *Q. rubra* L., *Q. coccinea* Muenchh., *Q. stellata* Wangenh., *Carya* spp., *Pinus taeda* L., and *P. echinata* Mill. (Bartram 1791, Smith 1882, Loughridge 1883, Nelson 1957). The upland forest climax is generally considered to be predominantly a mixture of *Quercus* and *Carya* species (Braun 1950).

Nearly all of the original forests have been cut and most of the area has been cleared and cultivated at some time (Mohr 1901). Until recently little soil conservation was practiced and much of the fertile topsoil has eroded away. This resulted in widespread abandonment of formerly cultivated land and much of the area reseeded or has been planted to pines.

The present upland forests are dominated primarily by *P. taeda*, *P. echinata* and mixed hardwoods, although a substantial acreage of *Pinus palustris* Mill. occurs in Randolph County. Silvicultural practices are

generally designed to maximize pine stocking and reduce hardwood competition. However, the high-grading approach frequently applied on small land holdings has often led to very irregular stands of mixed pines and hardwoods.

The major objective of this study was to examine the oak-hickory components of these upland forests, particularly in regard to species interrelationships and species-site relationships. Since all the stands sampled were intermediate in successional stage, it was desired that the analyses have predictive value for estimating composition of the stands if they remain undisturbed until an equilibrium (climax) stage is reached.

STUDY AREA

The upland forest stands sampled are in Chambers and Randolph counties, in the Piedmont Province (Fenneman 1938) of east-central Alabama.

The climate is warm and humid, with long hot summers and short mild winters. The area has an average frost-free season of 229 days, usually from about March 26 to November 10. Annual precipitation averages about 137 cm (54 inches), nearly all as rainfall (USDA 1941).

The landscape is gently rolling to hilly except in the northwestern half of Randolph County, where it is strongly hilly to mountainous. Most of the surface ranges from 180 to 365 m (590 to 1,200 ft.) above mean sea level, with elevations generally increasing northward. The area is highly dissected by many small streams flowing between generally smooth ridges of various widths. The slopes range from gentle to very steep. Most of the river and stream flood plains are narrow and discontinuous.

Except for stream bottoms, the soils are residual, weathered from Pre-Cambrian igneous and metamorphic rocks, primarily granites, gneisses and schists. They are chiefly well-drained, strongly acid Ultisols. Soils are typically deep (commonly exceeding 2 m in depth), but lithosols occur in some areas, chiefly on ridges or steep slopes. Subsoil textures are commonly high in clay, generally ranging from sandy clay loam to clay. Common upland soil series are Cecil, Davidson, Appling, Madison, Louisa and Tallapoosa (Carter and Perry 1959, Parker *et al*. 1967).

METHODS

Data Collection

General Land Office subdivisions (1-mile-square Sections) were selected by a random procedure and in each Section the first stand meeting predetermined criteria was sampled. Each stand occupied a minimum of 0.2 ha (0.5 acre) and had sufficient oak and hickory to achieve a minimum cover frequency of 25% in a systematic sample of 4 m^2 (0.001 acre)

quadrats. In determining "cover frequency" as used here, a tree species was recorded as present if any above-ground part of the tree, exclusive of leaves, occurred in a vertical projection of the quadrat. Each stand was also required to be free to recent cutting, fire and grazing and to have relatively homogeneous soil and topography. Forty upland stands meeting these criteria were located and sampled. No stands were located on terrace or stream bottom sites.

In the central portion of each stand, 20 to 50 4 m^2 quadrats were placed systematically at least 6 m apart along parallel compass lines. In these quadrats, cover frequency of all size classes was determined and density of understory stems (less than 10 cm dbh) was tallied for each tree species. Density and basal area of overstory stems (10 cm or larger dbh) were measured by the method of random pairs (Cottam and Curtis 1949).

In the recording of cover frequency, a distinction was made for the climax Quercus and Carya as to whether any individual was in a dominant position. A tree was considered dominant if it was not overtopped by any other tree of the climax group.

Theoretically, a climax overstory tree species should ultimately replace any presently overtopping trees of an intermediate successional nature. It follows that, in a stand at an intermediate successional stage, individuals of a climax species presently dominant relative to all other direct competition have the highest probability of becoming part of the overstory of the climax stand.

Relative importance values were computed as the sums of relative density, relative cover frequency and relative dominant frequency. Only the values for Quercus and Carya species were used for these computations, so the values reflect each species' importance only among the oak-hickory group and other species are disregarded.

The soil profile was examined at each stand to a maximum depth of 122 cm (48 inches). The thickness and consistence (Coile and Schumacher 1953) of each soil horizon were determined and soil texture was estimated by the "feel" method (Soil Survey Staff 1951). Topographic position (cove, slope or ridge), slope angle and slope azimuth were also recorded for each site.

RESULTS

Leading Dominant Analysis

Thirty-one tree species were encountered in the stands sampled. Of these, thirteen were of the Quercus-Carya group. To explore the species interrelationships and soil-site relationships, a leading dominant analysis (Curtis and McIntosh 1951) was undertaken. Each stand was classified

according to its leading climax dominant, i.e., the Quercus or Carya species with the highest importance value. Eight species were leading dominants in two or more stands. Within each group of two or more stands with the same leading dominant, the mean importance value for each species was computed. By trial and error, average species importance values were arranged in a table so that they approached nearly smooth curves.

The 13 climax species were than ranked in a reasonable phytosociological order based primarily on the leading dominants table (Table 1). This resulted in a species ordination with Quercus nigra L. and Q. marilandica Muenchh., the end-point species. Theoretically, this ordination should roughly reflect the ability of the different species to compete across some environmental or successional gradient. In their Wisconsin studies, Curtis and McIntosh (1951) and Brown and Curtis (1952) concluded that the vegetation gradient was successional and assigned each species a "climax adaption number" according to its ranking in the leading dominant analysis. In small stream bottoms in the Lower Coastal Plain of Alabama, Gemborys and Hodgkins (1971) found the species ordination from a leading dominant analysis to be closely related to moisture regime.

Table 1. Average importance values of climax species (calculated excluding non-climax species) in stands with given climax species as leading dominants. Values were calculated for those species that were leading dominants in two or more stands.

Number of stands	Leading dominant	Quercus alba	Carya ovalis	Carya tomentosa	Quercus velutina	Quercus stellata	Quercus falcata	Quercus coccinea	Quercus marilandica
4	Quercus alba	96	33	30	21	20	58	22	--
4	Carya ovalis	45	86	30	51	11	8	35	--
5	Carya tomentosa	7	30	113	35	40	32	11	7
6	Quercus velutina	19	36	29	73	31	33	34	13
2	Quercus stellata	14	39	33	48	81	42	20	8
8	Quercus falcata	15	10	34	44	42	94	29	16
4	Quercus coccinea	18	15	48	29	44	41	73	2
4	Quercus marilandica	3	1	8	28	40	18	18	137

A "continuum number" ranging from one to ten was arbitrarily assigned to each of the 13 species (Table 2) on the basis of the order in the leading dominants table. Species which occurred together frequently and therefore appeared to have similar environmental tolerances were assigned identical or nearly identical numbers. Four less common species not included in the table, Q. nigra, Q. rubra, Q. prinus L. and Carya pallida (Ashe) Engl. & Grabn., were assigned numbers on the basis of observation and their occurrence with other species in the table.

As a basis for a stand ordination, a weighted "continuum index" was computed for each of the 40 stands. This index is the sum of products of each species' continuum number and importance value in the stand. Continuum indices had a potential range from 300 to 3,000, but actual stand indices ranged from 886 to 2,647. The two end-point stands had as leading dominants Q. nigra (lowest continuum index) and Q. marilandica (highest continuum index).

Table 2. Species ordinations by leading dominant analysis (LDA) and reciprocal averaging (RA).

Species	LDA continuum number	RA scaled value
Quercus nigra[1/]	1	0.0
Quercus rubra[1/]	1	22.2
Quercus alba	3	27.5
Carya ovalis	3	31.4
Carya tomentosa	4	34.5
Quercus velutina	5	42.8
Quercus falcata	5	36.8
Quercus coccinea	5	41.2
Quercus stellata[2/]	6	48.8
Carya glabra	7	48.0
Quercus prinus[1/]	8	25.6
Carya pallida[1/]	8	91.8
Quercus marilandica	10	100.00

[1/]Continuum numbers for these species are tentative only, due to their low occurrence.

[2/]Quercus stellata was assigned a continuum number higher than the red oaks, due to its close relationship to Q. marilandica.

Reciprocal Averaging Ordinations

Reciprocal averaging is an eigenvector ordination technique described by Hill (1973). It results in unique one-dimensional ordinations of both species and stands simultaneously. The method has been tested on simulated coenoclines (community gradients) and is highly recommended by Gauch *et. al.* (1975).

Both species and stand ordinations were achieved by the reciprocal averaging (RA) technique with species importance values as input. The primary purpose was to compare the ordinations of the leading dominant analysis (LDA) with ordinations derived from a different approach.

The species ordination by RA resembled the LDA ordination (Table 2), and their correlation coefficient was 0.81. The species values were placed on a scale of 0-100 in the RA ordination, which simplifies comparisons with the LDA ordination. The end-point species were the same, *Quercus nigra* and *Q. marilandica*. The species order was quite close, with the obvious exception of *Q. prinus*, which was assigned a value of 8 in the LDA but scaled 25.6 in the RA ordination. The placement of *Q. prinus* in the LDA is quite arbitrary and is based primarily on limited observation. This species was present in only four stands and had an importance value greater than 25 in only one stand.

The stand ordination of LDA and RA were compared by simple product-moment correlation and are highly correlated (r=0.92). The two end-point stands were the same in both ordinations.

Species Relationships

Importance values of the nine major species were plotted against the LDA continuum indices of the stands (Figures 1-3). Though typically broad, the curves show fairly definite trends toward each end of the ordination axis. The curves of *Q. alba* and *Carya ovalis* (Wangenh.) Sarg. have similar curves, with highest importance values at the left end of the axis. It can readily be observed that *Q. falcata*, *Q. velutina*, *Q. coccinea*, *Q. stellata* and *C. tomentosa* Nutt. have rather broad flat curves which are similar in shape and position. They generally peak in the middle of the continuum index range. The curve for *Q. marilandica* appears to approach a peak at the upper end of the ordination. The three groups represent, respectively, a low, medium and high range along the axis of continuum indices. *Carya glabra* (Mill.) Sweet also exhibits a fairly broad curve but has a moderate peak in the upper mid-range of the ordination.

Carya glabra and *C. ovalis* are sometimes not distinguished as separate species in taxonomic works (Bloomquist and Oosting 1949, Little 1953) or in silvical descriptions (Fowells 1965). The species ordinations separate the two species somewhat, with values of seven and three in the LDA, 48.0 and 31.4 in the RA (Table 2). The importance value curves for

the two species (Figure 3) overlap somewhat, but are different in shape and general position. One or the other of these two hickories is present in 37 of the 40 stands and they occur jointly in 24 stands. However, C. ovalis is almost always more important in stands with continuum indices below 1470.

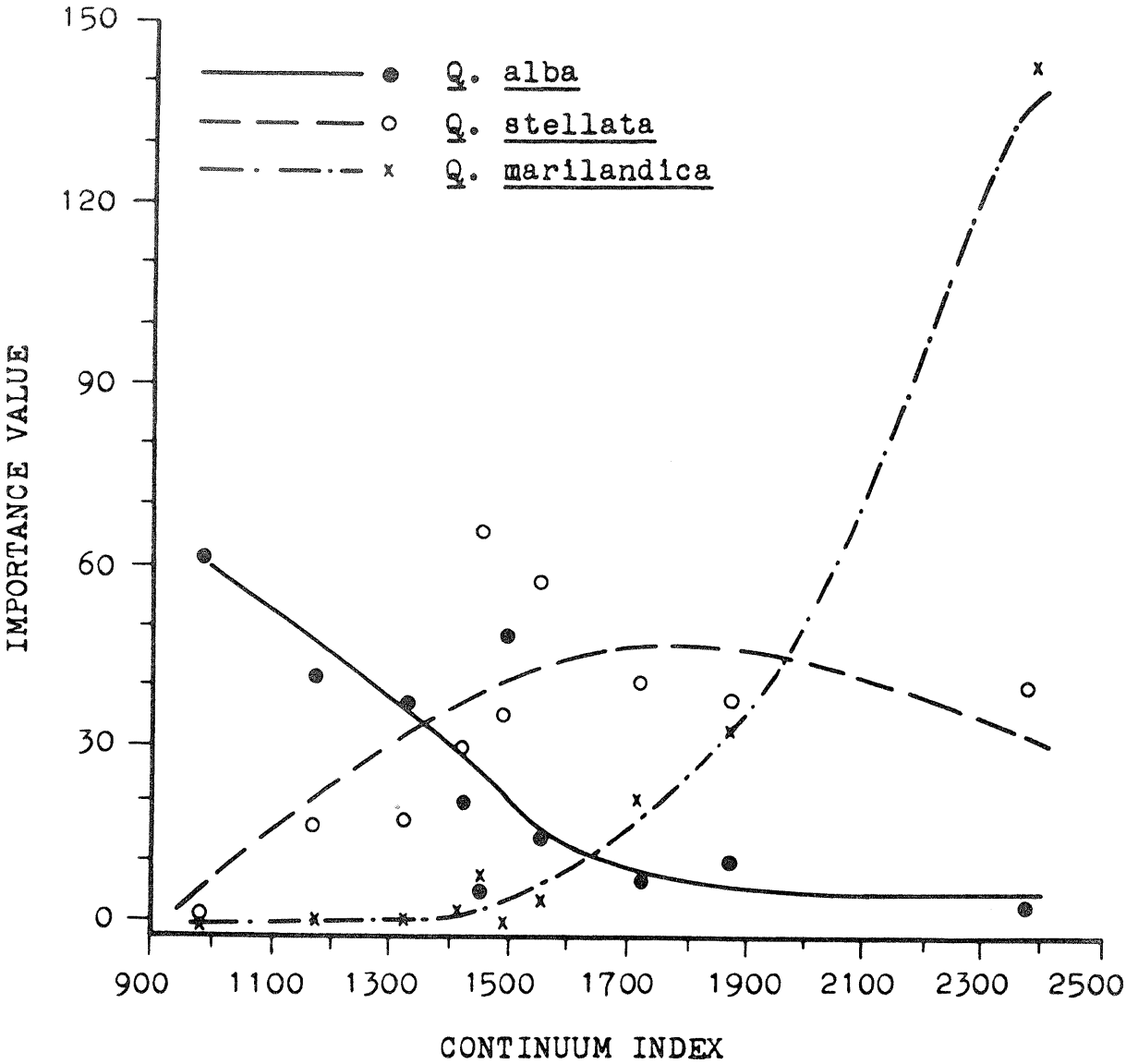

Figure 1. Importance value curves for three Quercus species. Each point is an average for four stands that are sequential in continuum indices. The smooth lines are free-hand curves through the points.

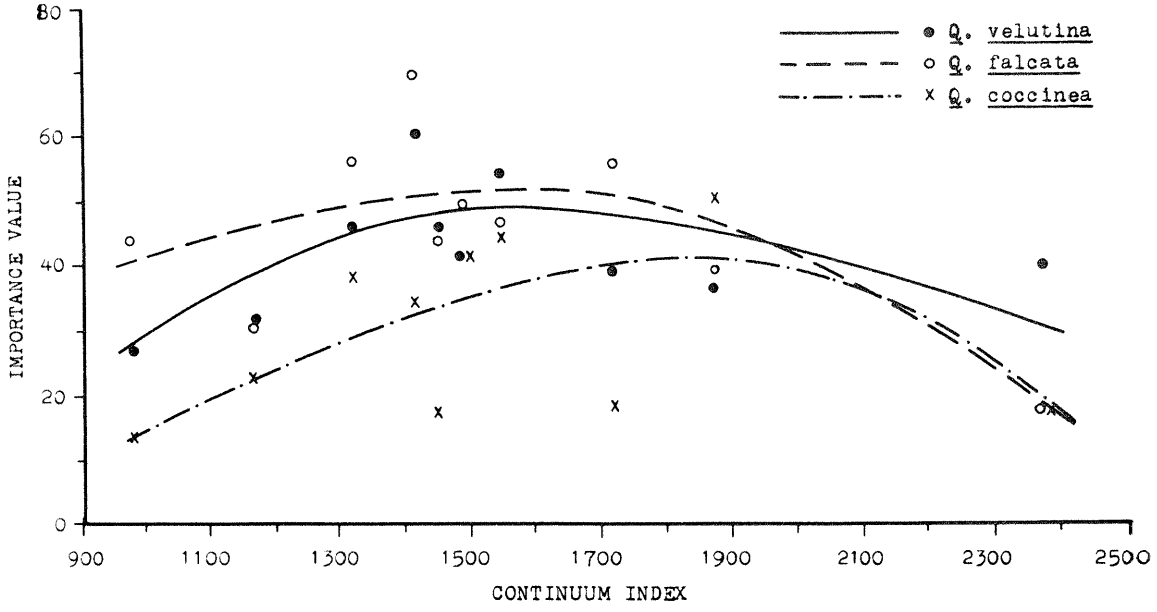

Figure 2. Importance value curves for three Quercus species. Each point is an average for four stands that are sequential in continuum indices. The smooth lines are free-hand curves through the points.

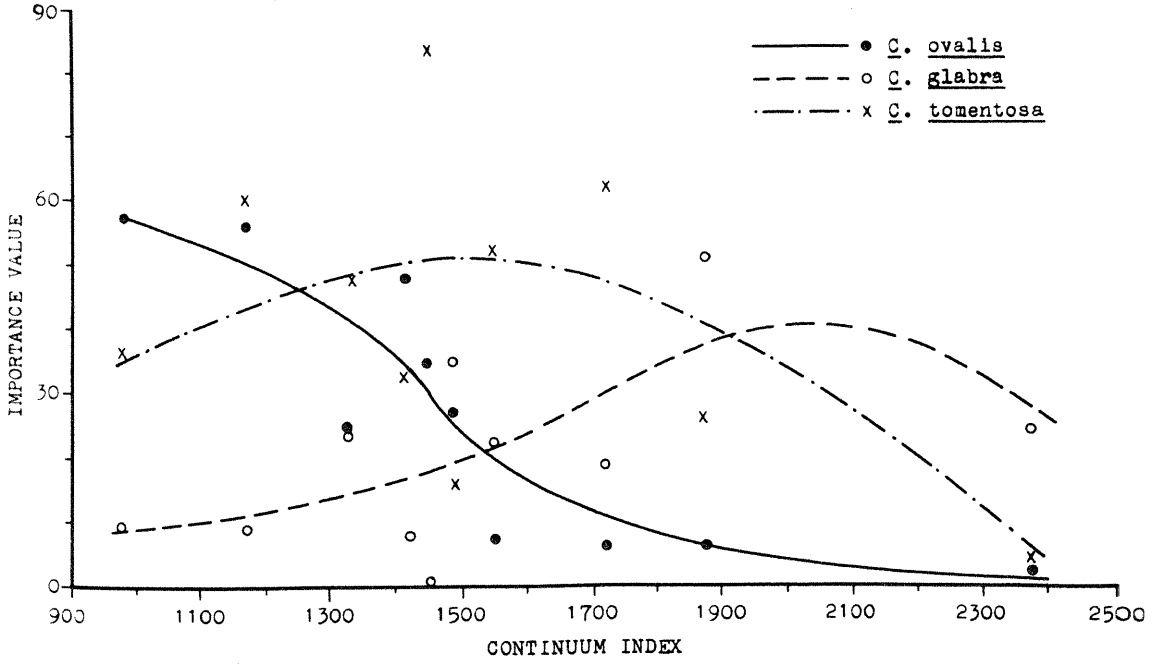

Figure 3. Importance value curves for three Carya species. Each point is an average for four stands that are sequential in continuum indices. The smooth lines are free-hand curves through the points.

Relationships with Site Factors

A search was undertaken for relationships between measured site variables and the coenocline quantified by stand continuum indices. Plotting of slope steepness, aspect, texture and consistence of the A horizon, texture and consistence of the B horizon, depth to subsoil, and total soil depth against continuum index revealed no direct relationships. Only topographic position and parent material type appeared to be directly related to continuum index.

Thirty-eight of the stands were on either a slope or ridge topographic position. Slope gradients ranged from 2 to 49%, averaging 12%. Two stands were located in broad coves without stream channels. Mean continuum index of the ridge stands was significantly higher (5% level) than those on slopes (Figure 4).

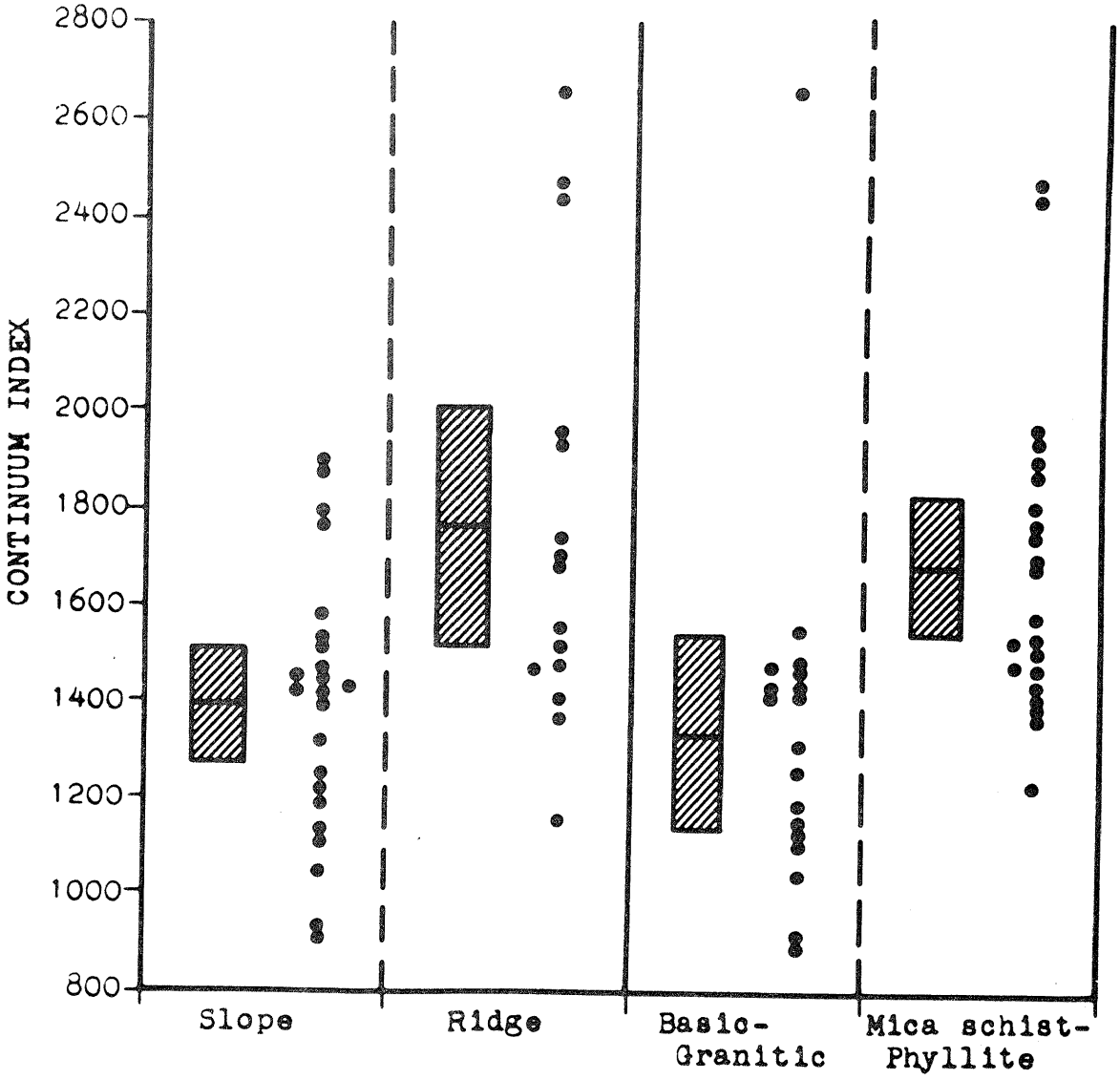

Figure 4. Continuum indices of stands, separated into groups according to topographic position and nature of underlying rock strata. Points are individual stands. Heavy mid-lines are the group means; shaded areas show 95% confidence limits for each mean.

Parent materials underlying the stands were classified as mica schist, phyllite, granite, or basic rocks (dark rocks high in ferro-magnesium minerals). Sites were classed into two parent material groups, granitic-basic and mica schist-phyllite. The mica schist-phyllite group mean continuum index, 1760, is significantly higher (5% level) than the granitic-basic rock group mean of 1390 (Figure 4).

Most of the soils sampled were Typic Hupludults or Rhodic Paleudults. Surface soil depths ranged from 7 to 58 cm (averaged 28 cm) and were most commonly sandy loams or clay loams. Subsoils were clays, sandy clays, or clay loams, and were predominantly friable or semi-plastic. Only one site had a total soil depth less than 50 cm, but 13 of the 40 soil depths were between 50 and 100 cm.

DISCUSSION

One of the primary objectives of the ordination of stands was to provide a basis for determining which major environmental factor or factors might be related to species composition in these stands. The absence of correlation between continuum index and any single measured variable can be explained by one or more of several hypotheses.

One possibility is that the ordination does not reflect a real coenocline and is simply an artifact of the method or an accident of sampling. The general agreement of the RA ordinations with those of the LDA is evidence that weakens the validity of this hypothesis. Though the placement and value of each species in the LDA ordination is subjective to some extent and may be interpreted in different manners, it seems reasonable to accept the general accuracy of the species ordination and the stand ordination derived from it.

Another hypothesis is that the most important environmental factor or factors may not have been measured. Since the site factors were limited in number, it is possible that the ordination might be more closely related to some unmeasured variables (e.g., soil available water holding capacity, soil pH, soil fertility, microclimatic conditions). The variables actually measured are only indirectly associated with environmental factors which act directly to favor or limit species occurrence (e.g., soil moisture availability, nutrient availability).

A third hypothesis is that the gradient of species composition is most directly related to a "complex-gradient" (Whittaker 1956, 1967) which comprises gradients of many particular environmental factors that change together in space but frequently at different rates. For some complex-gradients, a convenient environmental measurement is available which can be related to a vegetation coenocline. A good example is elevation in both the Great Smoky Mountains (Whittaker 1956, Golden 1974) and the Santa Catalina Mountains (Whittaker and Niering 1956). Occasionally it is possible to devise indices that are related to an apparent

complex-gradient and that in turn exhibit a direct relationship to a vegetation coenocline, e.g., the "environmental scalars" of Loucks (1962), the "site gradient index" of Golden (1974).

In this study, topographic position and type of soil parent material appear to be quite imprecise indices of complex-gradients. Neither topographic position nor parent material has a direct effect on species success at a site, but each is related to a complex of factors which may be direct in effect.

One of the more probable directly-limiting factors related to topographic position is available soil moisture. Mid-slope positions usually receive some runoff or subsurface moisture flow from upper slopes and ridges above, which conversely lose water to runoff and subsurface flow. Increased exposure to drying winds on ridges and upper slopes may cause higher evapotranspirational loss of soil moisture, thereby increasing soil moisture differences between mid-slope and ridge sites. Such differences may become critical to drought-sensitive species during periods of low rainfall. It is recognized that periods of summer drought combined with high potential evapotranspiration commonly lead to significant soil moisture deficiencies (38-50 cm) on many forest sites in the mid-south (Zahner 1956).

Available soil moisture may also be one of the more important factors resulting from the difference between parent material types. Topography is typically more rugged in the areas underlain by mica schist and phyllite rocks. The mean slope angle of mica schist-phyllite sites (15.5%) was significantly higher (5% probability level) than the mean slope angle of basic-granitic sites (9.2%). It is reasonable to expect greater surface runoff and subsurface soil water loss with increasing slope angle. With an arbitrary depth of 152 cm assigned to all soils deeper than the maximum sampled value of 122 cm, the mica schist-phyllite sites have a significantly lower (5% level) mean soil depth (108 cm) than the basic-granitic sites (138 cm). With decreased soil depth, root space and soil moisture storage capacity are reduced.

The correlation between individual site factors and the vegetation gradient is probably reduced by compensating effects commonly called interaction. For example, a cooler northerly aspect may compensate somewhat for the increased drainage and exposure of ridges or the low moisture storage capacity of thin soils. All of the ridge position stands with continuum indices lower than 1,500 were found on northerly aspects (WNW to NNE). Similarly, all stands underlain by mica schist-phyllite parent materials and with continuum indices below 1,500 were on north-to-east aspects (WNW to E).

Within the limitations of the data and from field observation, it seems a reasonable conclusion that the species and stand compositional gradients quantified in the ordinations are related to a complex-gradient that involves soil moisture availability as a major factor.

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