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J. E. Potzger

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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, Daubenmire, Potzger, and Billings served as Presidents of the Ecological Society of America.

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DIFFERENTIAL SELECTION IN JUNIPER POPULATIONS FROM THE BAUM LIMESTONE AND TRINITY SAND OF SOUTHERN OKLAHOMA

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ABSTRACT

Hall, Marion T. and **Claudia J. Carr.** (Stovall Museum, U. of Oklahoma, Norman, Oklahoma) Differential Selection in Juniper Populations from the Baum Limestone and Trinity Sand of Southern Oklahoma. Butler U. Bot. Studies 14(2):21-40. Illus. 1964.—Two markedly different geologic formations, the Baum limestone and Trinity sand and an area of intermixed talus were compared for several physical attributes and these correlated with the structure of the plant communities occupying them and with the variability of a conspicuous constituent for each of the three habitats. (1) *Juniperus Ashei* occupies the Baum limestone in nearly pure stands, but with wide spacing, while the general cover consists of *Bouteloua hirsuta* and *Andropogon scoparius*. The limestone has a high carbonate content, high hygroscopic coefficient, low soil moisture. (2) *Juniperus virginiana* occupies the Trinity sand on cleared, reverted land normally supporting a post-oak, black-jack oak forest. The junipers are widely spaced with oak forest in various stages of re-generation. Woody cover as well as ground cover is greater on the Trinity than on the Baum. The Trinity has low carbonate, low hygroscopic coefficient, high soil moisture. (3) The juniper population on the mixed talus sites are hybrid but closer to *Juniperus Ashei*. The various factors measured are intermediate between the other two habitats. (4) The data suggest that in southern Oklahoma *J. Ashei* develops plentifully in areas where the moisture content is low enough to limit *J. virginiana,* but as the habitats of the two species intergrade hybridization occurs, i.e., currently as well as historically, with only those hybrids surviving which are adapted to the intermediate habitats. (5) These mixed habitats are rich sources for continued hybridization and introgression until succession closes both the mixed habitats and the Trinity sand to junipers.

The Arbuckle Mountains of southern Oklahoma offer an important opportunity to study the influences of geology, soil types, and water relations on differential selection in complex plant populations. This paper is an

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analysis of population variation with respect to these factors for *Juniperus Ashei* Buchholz, *Juniperus virginiana* L. (Ozark race) and hybrid swarms between them. These populations occupy respectively distinct geological horizons or the talus between them: *J. Ashei* occurs on the Baum limestone, *J. virginiana* on the Trinity sand (Paluxy) and the hybrids on the alluvial mixtures of the two horizons wherever topography permits mutual erosion. To a limited extent hybrids may become established in each of the horizons, the Baum limestone and the Trinity sand, but ecologic factors are clearly strong barriers to the establishment of hybrids except where the alluvium is well mixed and consequently particularly limy. The data presented here express the relative strength of these ecologic barriers. Other woody plants show similar responses to habitat discontinuity in the Arbuckles even though these plants represent different levels of taxonomic categories. *Cercis reniformis* and *Cercis canadensis* respond similarly to *Juniperus* in this region. Races of *Forestiera* and *Celtis* behave similarly. The *Quercus breviloba, Quercus stellata* complex shows similar patterns. Where hybridization occurs among herbaceous species differential selection likewise produces variation patterns similar to those for *Juniperus*.

The Arbuckle Mountains (mountains in a structural sense only) comprises an area of 860 square miles, a low limestone plateau rising above the surrounding prairie, sloping from 1,350 feet on the west to 750 feet on the east. The plateau, characterized by numerous streams, springs, and waterfalls abounding in travertine deposits, is drained from north to south by the Washita River. Careful descriptions of the Arbuckle Mountains are known as early as 1856 from reports of exploration and surveys, U.S. House of Representatives documents.[3]

The geology of the Arbuckles is well-known (C. A. Reeds, 1910, 1927; C. E. Decker, 1939; J. A. Taff, 1903, 1904; G. D. Morgan, 1924; C. E. Decker and C. A. Merritt, 1928; E. O. Ulrich, 1911, 1932; W. E. Ham, 1949). In many sections of the Arbuckles, practically no major faulting has occurred, and one may look across more than 12,000 feet of sharply upturned sediments of Paleozoic rocks and rough stony land in almost unbroken sequence. Sedimentation began in the Cambrian and extended through the Mississipian. The Hunton Arch was formed, uplifting, folding and faulting in the Pennsylvanian era concomitantly with the uplifting of the Arbuckle Anticline. The erosion cycle following those events extended into the Cretaceous, when successive seas again covered the area. A late Cretaceous uplift

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[3] Reports of exploration and surveys, Vol. 4, House of Representatives Ex. Doc. No. 91, Washington, D.C. Exploration along the 35th parallel, search for railroad route from the Mississippi River to the Pacific coast, 33rd Congress, 2nd Session, U.S. Senate, 1856.

occurred and erosion proceeded again. The present minor topographic features are the result of erosion since the removal of the Cretaceous deposits. A core of porphyry and the granites of the Hunton Arch are surrounded by bands of limestones, conglomerates, sandstones, shales, cherts and other rocks in alternating sequences, a natural area for demonstrating selection pressures on plant populations.

Because of the extensive limestones similar in properties to those of the Edwards Plateau of south central Texas and the bald knob areas of southwestern Missouri, the vegetation of the Arbuckles, both structurally and floristically, is remarkably similar in these three areas so well isolated from one another. Palmer, 1934; Hopkins, 1938, 1942; Steyermark, 1940; Hall, 1952b; Dale, 1956, have discussed these floristic affinities. Bruner, 1931, writing about the Arbuckles, stated, "Climatically the area should be dominated by grasses, but the open porous soil permits the growth of trees, and in places, turns the balance decidedly in their favor." In southern Oklahoma in the ecotone between oak-woodland and prairie, limestones weather into dark soils with a high colloidal content, good soil moisture retention, but high hygroscopic coefficients. These soils support prairie vegetation. On the other hand the sandstones weather into light soils with poorly developed colloidal fractions, low water retention, but low hygroscopic coefficients. These sandy soils do not hold water against the vegetation and consequently black-jack, post-oak forest develops readily. In occasional areas where talus of mixed limestone and sands is situated, the vegetation itself is intermediate, typically forming juniper-oak savanna.

There are frequent modifications of this generalized vegetational pattern which adds to the structural and floristic complexity. This study presents a few of these complications.

THE HABITATS

This study was made along the southern edge of the Arbuckle Mountains where the Baum limestone forms five outcrops between Baum, Carter County, and eastward to Ravia, Johnston County, a distance of twelve miles. Here the Baum limestone forms mesas from ten to forty feet above the highly sandy Washita River alluvium to the south. A large portion of the alluvial sand is derived from more elevated Trinity sandstone bordering the Washita River to the south. In numerous sites along this commissure erosion has produced a limy, sandy mixture of these substrates of several acres in extent. These studies were made at stations selected in typical Baum limestone, typical Trinity sand, and the aprons where they mix.

Baum Limestone. The Baum limestone, described by Wayland, 1954, refers to the basal member of the Paluxy formation of the lower Cretaceous. The limestone is pinkish gray to white, compact, fine grained, with patches of calcite and chert pebbles, occasionally with pebbles of limy conglomerate on slopes. The Baum weathers to a rubbly surface of rounded masses, either brown-banded or bright white. The measured thickness of the Baum varies from 13 feet to 73 feet, thin on the west and east edges, thickest in the Ravia-Mannsville or central area. The parent materials belong to the Paleozoic carbonate rocks of the Arbuckle Mountains just north of the Baum. The authors made analyses of carbonate content, water content, and hygroscopic coefficient (see TABLE 3). There is a slight west-east gradient, high for each factor to lower, probably the result of the greater quartz and feldspar content of the arkosic limestone at the eastern edge of the Baum (Ravia area).

Trinity Sand. This group is part of the Comanchean series of the Cretaceous constituting its basal member lying unconformably over the Arbuckle Mountain's Paleozoic formations which are capped by Sycamore limestone. The member of the Trinity sand concerned with this study is the Paluxy formation. Overlying the Trinity sand are occasional outcrops of Goodland limestone, Fredricksburg Group, mostly farther to the south in Marshall County and along the Red River. Taff, 1903, and Bullard, 1926, have described the geologic features of the Trinity sand. It is a massive bedded, fine, white to yellow pack sand forty to fifty feet thick. Scattered throughout the formation are lentils of yellowish purple clay which are hard enough to permit a rugged relief; i.e., escarpments, bluffs, and steep-sided ravines. The pack sand itself weathers easily into loose debris, adding extensively to the Washita River alluvium. The hilly terrain of the Trinity sand is covered by a thick growth of black-jack and post-oak forest. The authors made analyses of carbonate content, water content, and hygroscopic coefficient (TABLE 3). Carbonate is quite low, water content slightly higher than for the Baum, hygroscopic coefficient very low.

Aprons. These alluvial aprons are best developed on more gentle slopes where the mesas of the Baum are lowest in elevation above the surrounding terrain. These areas are also the greatest distance from the nearby Washita River channel. Where the channel runs close to the face of the Baum, it cuts away and carries the apron material in its waters. The best of these dissected aprons are at the western and southwestern edges of the Baum. The aprons are limy mixtures of Trinity (Paluxy) sand and rubble from the Baum. Carbonate content, water content, and hygroscopic coefficient proved to be intermediate between the two formations.

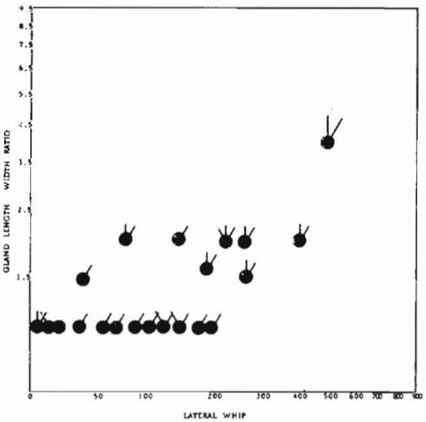
METHODS

The rationale of this study involves an objective view of the interaction of species variability and variability in plant community structure correlated with the major differences in the habitats. These trends present a broad view of the dynamics in the ecology of juniper-savanna, juniper-woodland, and oak-forest in southern Oklahoma. Methods required were those presenting useful comparative data for the three main features stated above.

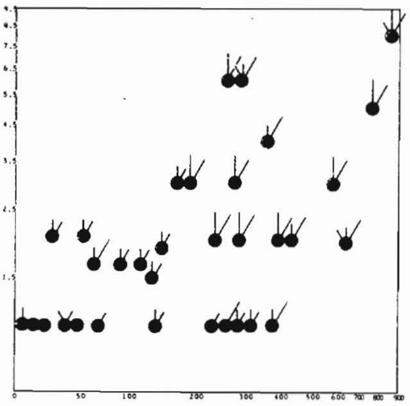
Species variability. Analyses of variation in *Juniperus Ashei* and *J. virginiana* have been presented elsewhere (Hall, 1952a, 1952b, 1955). A summary of some morphological differences between the two species follows.

JUNIPERUS ASHEI	JUNIPERUS VIRGINIANA
1. Trunk more or less branched near the base; aspect generally bush-like, height to 35 feet	1. Trunk single, erect; aspect generally pyramidal; height to 80 feet
2. Foliage dense	2. Foliage more or less open, green to bluish-green
3. Whip or long shoot leaves average 3.4 mm. in the Arbuckle Mtns; range 2.0-6.2	3. Whip or long shoot leaves average 8.8 mm. in eastern race; range 6.0-12.0
4. Glands on leaves nearly round to short elliptic; raised well above the leaf in a convex hemisphere; average length width ratio is 1.25, range 1.0-2.0	4. Glands much elongated on certain leaf-types, elliptic on others; seldom raised above the leaf; average length width ratio is 6.4, range 4.3-9.0
5. Fruit large (6-8 mm. in diam.) with slightly resinous juicy pulp	5. Fruit small (4.5-6 mm. in diam.) with strongly resinous dry pulp
6. Seed 4-5 mm. diam.; 1, rarely 2 per berry-cone, sharply pointed tip, no pits, smooth white hilum conspicuous, covering at least ¼ length of seed	6. Seed 2-3 mm. in diam., 1 or 2 per berry-cone, rarely 3-6, blunt tip, numerous pits, small inconspicuous hilum.

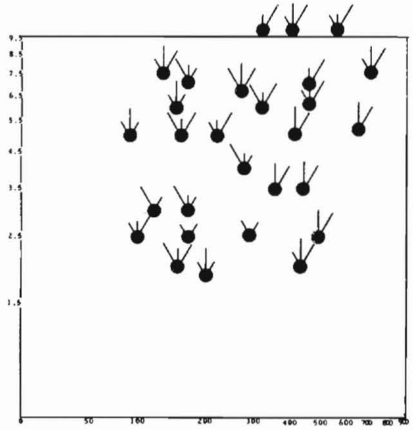
The scatter diagrams, FIGURE 1, show the nature of *Juniperus* populations in Baum limestone, Trinity sand, and mixed lime and sand from an alluvial apron with respect to the following five characters: (1) gland length-width ratio, (2) length of lateral whip, (3) length of terminal whip, (4) length of whip leaf, (5) percent of decussate leaves. The relative genetic bases and the environmental responses of these five characters were analyzed in detail in a previous paper, Hall, 1952b. The data obtained may be grouped into three separate categories: *Ashei*-like characters, hybrid characters, and *virginiana*-like characters as shown in FIGURE 1. Through the use of the scatter diagrams in the study, a direct comparison between the population variations and habitat factors may be made. Along the abscissa is plotted



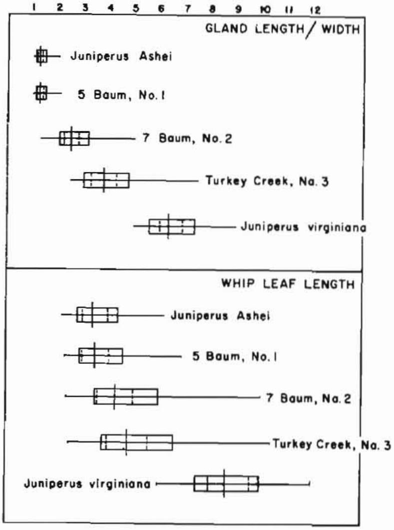
POPULATION I. 5 Baum, Juniperus Ashei



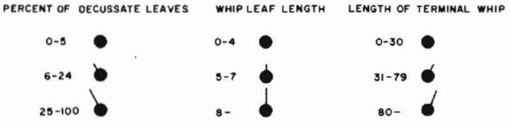
POPULATION 2. 7 Baum, Hybrids: J. Ashei X J. virginiana



POPULATION 3. Turkey Creek, Juniperus virginiana (Ozark race)



EXPLANATION OF PICTORIALIZED SCATTER DIAGRAM



PLOTTED VERTICALLY: GLAND LENGTH-WIDTH RATIO.
PLOTTED HORIZONTALLY: LENGTH LATERAL WHIP

length of lateral whip and along the ordinate, gland length-width ratio. Each dot represents a single individual sampled at random from the stand locality. The left-quadrant bar represents percent of decussate leaves, the vertical bar represents length of whip leaf, and the right quadrant bar expresses length of terminal whip. The bars, designed from grouped data, represent limits of variation typical for the species or intermediate. These limits were derived from statistical analyses from an earlier work, Hall, 1952b. In general dots in the lower left of the graphs represent *J. Ashei,* in the upper right, *J. virginiana,* in between, hybrids. Weak linkage produces a lower left-upper right axis for hybrid populations.

TABLE 1 shows the parameters of two characters for each of these three populations from the Baum area and for two populations typical for the species elsewhere. Typical *J. Ashei* is represented by Population A from the Viola limestone of the Arbuckle Mountains. Here *J. Ashei* is essentially identical to stands from the Edwards and Comanche Plateaus of central Texas. Population 1, from the Baum, is slightly more variable than A and carries some genes of red cedar. The means, ranges and 95% confidence limits for whip leaf length and gland length-width ratio for these five populations are listed in TABLE 1. The confidence limits of a population mean based on small samples are usually obtained from the standard deviation estimate, S, which requires the summing of squares. Lord, 1947, determined that the range of the sample could be used instead with high statistical efficiency. The confidence limits for the two-sided probabilities shown may be obtained from $\overline{x} \pm kw$, where $\overline{x}$ is the sample mean, w is the sample range and k is obtained from a table of scale factors and equivalent degrees of freedom for x-approximation to range in normal samples. The scale factors are from TABLE III of Hall and Thomson from Hall, 1955. Standard deviations are listed only for Populations A and V, i.e., for each species of *Juniperus.*

FIGURE 1. Pictorialized scatter diagrams of Juniper populations in southern Oklahoma. Population 1 represents *Juniperus Ashei* with few hybrids (*J. Ashei* X *J. virginiana*). The stand occurred on pure Baum limestone at a site five miles east of Baum, Carter County, Oklahoma. Population 2 represents a hybrid swarm, *J. Ashei* X *J. virginiana,* occurring on mixed Baum limestone detritus and Trinity sand at a site seven miles east of Baum, Johnston County, Oklahoma. Population 3 is a stand of *Juniperus virginiana* (Ozark race) occurring in pure Trinity sand at a site three miles southeast of Mannsville on Turkey Creek, in northwest Marshall County, Oklahoma. The habitat of Population 2 is intermediate in several features between those of Populations 1 and 3. Each dot on the graphs represents a single juniper plotted for five characters. In the bar graphs for Gland length-width and Whip leaf length the horizontal lines represent the ranges, the vertical lines represent the means, the rectangles about the means correspond to the fifty percent probability levels, the dotted lines indicate the ninety-five percent confidence limits of the means.

TABLE I

POPULATION (Number in sample in parentheses)	LOCALITY	WHIP LEAF LENGTH (mm.)			GLAND LENGTH — WIDTH RATIO		
		Mean	Range	95% Confidence Limits	Mean	Range	95% Confidence Limits
A (25)	*J. Ashei* from the Arbuckle Mtn., Oklahoma	3.4	2.2- 6.2	(2.97-3.82) st. dev. 0.500	1.25	1.0-2.0	(1.14-1.35) st. dev. 0.045
V (25)	*J. virginiana* from Interior Low Plateau, eastern United States. . .	8.8	6.0-12.0	(8.10-9.60) st. dev. 0.088	6.4	5.0-9.0	(6.0-6.9) st. dev. 0.100
1 (21)	5 miles east Baum, Carter Co., Oklahoma, on pure limestone. . .	3.5	2.3- 7.0	(2.90-4.09)	1.25	1.0-2.0	(1.123-1.38)
2 (33)	7 miles east Baum, Johnston Co., Oklahoma, mixed lime and sand .	4.4	2.4-10.0	(3.74- 5.05)	2.5	1.7-5.0	2.22-2.78)
3 (28)	3 miles southeast of Mannsville on Turkey Creek, in northwest Marshall Co., Oklahoma, nearly pure sand.	4.8	2.5-10.4	(4.02- 5.60)	3.8	2.5-7.5	(3.30-4.30)

Plant community structure. Vegetational variation from stand to stand was determined by the line strip method where cover is determined by the line, frequency, density and basal area by the strip. A 400′ line strip (elbed) averaging ten per stand gives suitably low standard errors for the dominant species in the juniper woodland of Oklahoma. Wooten and Lindsay, 1954, used 800′ elb-strips in studies of juniper-pinyon in the southern Rockies, but they used fewer per stand and worked farther west where spacing is greater. Each strip was divided into eight units. Herbaceous species values were recorded for the first and last units; woody species values were recorded throughout. Frequency, density, cover, and basal area for the woody species are presented here in TABLE 2. These attributes are converted to relative values and combined to produce a predominance index for each major species of the community. The predominance value places a distinct emphasis on cover, and it serves as a good index of the relative importance of a given species in a stand.

The areas sampled were the precise areas represented by the population variation diagrams of FIG. 1: Population 1, *Juniperus Ashei* from 5 miles east of Baum, Carter County, Oklahoma; Population 2, intermediates from the alluvial apron 7 miles east of Baum, Johnston County; Population 3, *Juniperus virginiana,* from the Trinity sand, 3 miles southeast of Mannsville, on Turkey Creek, in northwestern Marshall County.

Because this study involved a general survey of a rather sizable area, a method which was economical, yet insured accuracy, was needed. A square quadrat method was impractical, as the trees are often widely spaced and large bare areas frequently occur. Furthermore, although cover is certainly one of the most important phytosociological factors to be considered when characterizing a community, the square quadrat method is a time-consuming means to determine cover accurately. The line-interception method provides an excellent way of measuring cover, but it is poorly adapted for measuring other characters, e.g., frequency, density. By combining the line-interception and quadrat methods into a "line-strip" method, the advantages of both are utilized. Cover was quickly determined from the line, while density, frequency, and basal area of woody species was obtained from the strip. The line-strip was laid out by placing the line at random within a stand. For this study, a width of 21.4 feet was chosen for the strip, which makes the sample area a convenient fraction of an acre. The bent form of the line was sufficient to compensate for any gullies, ridges or other atypical topography or disturbance in the region which may entirely encompass a straight line. The bent form consisted of 200 feet in both halves, forming a right angle at their point of intersection. After placing a tape in the approximate position of the randomized elb-transect, cover was measured by recording the points of interception of each species on the tape. In deter-

TABLE 2

Population 1 — 5 Baum

Species	Frequency	Relative Frequency	Relative Density	Importance	Relative Cover	Percent Ground Cover	Basal Area	Predominance
Juniperus Ashei	100	27.7	62.3	540.8	76.2	13.5	25,793.7	19.7
Juniperus virginiana ...	40	11.1	5.6	23.4	3.3	0.6	649.5	0.2
Quercus Shumardii	70	19.4	6.2	36.8	5.2	0.9	112.6	0.4
Diospyros virginiana ...	40	11.1	0.4	5.4	0.7	0.1	41.5	(0.001)
Bumelia lanuginosa	30	8.3	0.01	8.3	1.1	0.2	27.1	(0.004)
Quercus marilandica ...	20	5.5	6.2	20.5	2.8	0.5	98.8	0.1
Quercus stellata	20	5.5	12.3	52.0	7.3	1.3	490.6	0.4
Carya texana	10	2.7	0.005	9.0	1.3	0.2	95.0	(0.002)
Ulmus crassifolia	20	5.5	5.0	6.0	0.8	0.1	38.0	0.08
Fraxinus americana	10	2.7	(0.005)	9.0	1.3	0.2	4.5	.002

Population 2—7 Baum

Species	Frequency	Relative Frequency	Relative Density	Importance	Relative Cover	Percent Ground Cover	Basal Area	Predominance
Juniperus Ashei	100	23.8	0.4	233.5	40.4	5.8	14,671.8	1.1
Juniperus virginiana ...	100	23.8	0.3	198.0	34.2	4.9	4,896.3	0.7
Diospyros virginiana ...	40	9.5	0.2	56.6	9.8	1.4	40.5	0.07
Bumelia lanuginosa	10	2.4	(.005)	11.0	1.9	0.3	21.4	....
Quercus stellata	50	11.9	(.04)	37.0	6.4	0.9	2,718.4	0.04
Ulmus crassifolia	50	11.9	0.05	20.5	3.5	0.5	193.4	0.01

TABLE 2 (*Continued*)

Population 2—7 Baum (*Continued*)

Species	Frequency	Frequency Relative	Relative Density	Importance	Relative Cover	Percent Ground Cover	Area Basal	Predominance
Fraxinus americana	20	4.8	0.01	1.5	0.2	(0.03)	10.7	....
Juniper hybrids (Putative F_1)	70	5.5	3.1	17.5	2.4	0.4	335.3	0.1
Cercis canadensis	10	2.4	(0.01)	3.0	0.5	0.1	3.8	....
Celtis laevigata	10	2.4	(0.01)	0	0	0	0	....

Population 3—Turkey Creek

Species	Frequency	Frequency Relative	Relative Density	Importance	Relative Cover	Percent Ground Cover	Area Basal	Predominance
Juniperus Ashei	0	0	0	0	0	0	0	0
Juniperus virginiana	100	22.2	51.3	370.0	50.1	9.2	15,753.3	10.9
Quercus Shumardii	60	13.3	6.6	70.9	9.6	1.8	753.3	0.5
Diospyros virginiana	0	0	0	1.0	0.1	(0.02)	90.6	....
Quercus marilandica	10	2.2	2.6	16.0	2.2	0.4	96.7	(0.03)
Quercus stellata	40	8.9	10.6	60.0	8.1	1.5	108.4	0.5
Ulmus crassifolia	30	6.7	10.2	43.9	5.9	1.1	187.1	0.3
Fraxinus americana	20	4.4	1.3	12.0	1.6	0.3	15.2	(0.02)
Juniper hybrids (Putative F_1	40	9.5	(0.02)	17.0	2.9	6.4	29.7	(0.01)
Bumelia lanuginosa	10	2.2	0.4	0.7	6.1	(0.01)	3.1	...
Quercus muhlenbergii	20	4.4	0.9	19.0	2.6	0.5	0	(0.02)

mining coverage of woody species, an imaginary line was dropped from the two places where the crown edge intersected the line and the figures were recorded. Each half of the elb consisted of four quarters, making a total of eight sub-divisions. The herbaceous coverage was recorded only in the first and last of these, whereas that of woody species was recorded in all eight. Woody species occurring within the strip (10.7 feet to either side of the line) were recorded and their basal areas computed by measuring the diameter of each at ground level (necessary because of a high degree of branching at the ground level in *J. Ashei*). Necessary calculations were made to convert these measurements to basal area. Thus, cover, frequency, density and basal area of the trees in the area were obtained. After converting these values into relative terms, they were considered in combination with each other, and a predominance value for each species was calculated by the following formula: $O_5 = \frac{(F_3 + C_3)\ (D_3 + C_4)}{400}$, with the symbols of this formula standing for the following values: O_5 = predominance value, D_3 = relative density, C_3 = relative cover, F_3 = relative frequency, C_4 = percent ground cover.

Physical characteristics of the habitats. Carbonate content, percent

TABLE 3

LOCALITY	POPULATION 1 Baum limestone		POPULATION 2 Alluvial apron		POPULATION 3 Trinity Sand	
	Mean	**Range**	**Mean**	**Range**	**Mean**	**Range**
Carbonate content	95.2	92.9–97.6	54.6	45.1–69.3	11.4	8.3–14.4
Percent water						
*Horizon "A"	12.3	9.3–15.6	18.6	14.9–22.0	26.3	20.1–32.0
Horizon "B"	9.6	7.1–12.4	16.0	13.1–19.7	22.7	17.3–28.5
Hygroscopic coefficient						
Horizon "A"	7		5		2	
Horizon "B"	9		7		3	

* Not true horizons. Horizon "A" refers to upper three inches of "soil" in what is classified for the Baum as rough stony land. Horizon "B" samples were at one foot depth.

(weight) water content, and hygroscopic coefficient of the soils from these three stands were obtained. These values are presented in TABLE 3. Water content samples were taken at one week intervals for the months of June and July, 1963.

RESULTS

Examination of the data, FIG. 1, TABLES 1 through 4, shows a fairly precise correlation between direction of variation in the juniper populations and differences in the habitats, both structurally and in physical characteristics. The Baum limestone supports a stand of relatively pure *Juniperus Ashei,* widely spaced, with relatively lower general cover than the other habitats. The limestone has a high carbonate content, a requirement for *J. Ashei,* a low soil moisture trend, and a high hygroscopic coefficient which adds to its xeric quality.

Population 1 of FIG. 1 shows a scatter diagram representing the population of *J. Ashei* from the Baum limestone. *Ashei* characteristics are shown by the clumping of specimens to the lower left corner of the graph. A few specimens of those sampled showed some genes of red cedar, particularly the specimen to the upper right of Population 1. Reference to TABLE 4 shows the Baum limestone supporting a good stand of prairie grasses composed primarily of *Bouteloua hirsuta* and *Andropogon scoparius.*

The Trinity sand normally supports a post-oak, black-jack oak woodland except on land cleared by fire or grazing or on old fields. Population 3 of FIG. 1 from the Trinity represents a mature stand of *Juniperus virginiana,* Ozark race, on previously burned and grazed pasture. The burning had occurred in the early 1940's and killed most of the post-oak except those near the bluffs of Turkey Creek. The bluff-top flora was much less disturbed and supported red cedar stands with an average age of thirty-five years. The sampled stand was in the least disturbed area. This stand, Population 3 of FIG. 1, shows a typical population of Ozark red cedar with some hybrids appearing in the lower left of the graph. The population is quite distinct from that of the Baum limestone. The Trinity sand as a habitat is likewise different from the Baum. The Trinity has a low lime content, higher water content, and a low hygroscopic coefficient. It is a considerably more mesic situation than the Baum limestone. Clearly red cedar has a considerably greater water requirement than *J. Ashei.*

A look at Population 2 of FIG. 1 shows a juniper population nearly intermediate between *J. Ashei* and *J. virginiana.* The alluvial apron habitat is likewise nearly intermediate, in lime content, water content, and hygroscopic coefficient. In each case the apron habitat is a little more similar to the Baum limestone, expressing a strong correlation. Both species and numerous hybrids occupy these aprons or zones of substrate mixing. The apron habitat again is primarily a juniper-oak savanna with a well developed prairie grassland ground cover composed of more mesic species than the Baum. The aprons also have a greater floristic diversity and a greater woody cover.

Although the junipers and habitats of the Baum limestone are primarily *Ashei*-like, introgression of genes of *J. virginiana* becomes progressively more significant as moisture conditions show a transition from xeric to mesic. That is, *J. Ashei* develops more plentifully in areas where the moisture content is low enough to become a limiting factor to the survival of *J. virginiana,* but as the habitats of the two species intergrade, hybridization occurs, with only those hybrids surviving which are suitably adapted to the new moisture conditions. Both species are calciphiles, but *J. Ashei's* requirement is obligatory.

The extensive hybridization between *J. Ashei* and *J. virginiana* in the Baum limestone is illustrated by the scatter diagrams. Gene interchange between the species is not very evident in the area 5 miles east of Baum, and this habitat supports chiefly *J. Ashei,* but the increasing importance of *J. virginiana* becomes evident in the 7 miles east of Baum area, where *J. virginiana* nearly balances *J. Ashei* in abundance.

TABLE 4, concerning herbaceous coverage, demonstrates some significant differences in the vegetation of the 7 and 5 Baum areas. A considerably greater total herbaceous coverage, as well as woody coverage, occurs in the 7 Baum site. This might be expected, as the area represents a more mesic environment, while no woody species other than *J. Ashei* were noted in the 5 Baum area, perhaps due to the lack of adaptation of other woody species to the very low moisture and high carbonate content. Although the two locations support approximately the same number of herbaceous species, and grasses are dominant in both, forbs are far more prominent in the *J. virginiana* area. Rather notable differences concerning the herbaceous dominants may be seen between the two locations; although the major herb layer dominant (*Bouteloua hirsuta*) occurs as such in both, other species of primary importance vary greatly between the two areas, e.g., *Bouteloua curtipendula, B. rigidiseta,* and *Andropogon scoparius.*

DISCUSSION

The study of variation received great empetus with William Bateson's "Materials for the Study of Variation", which appeared in 1894 and presented lucidly the problems pursuant to Lamarkian and Darwinian theories of evolution. The principle that specific diversity of form is consequent upon diversity of environment, and diversity of environment is thus the ultimate measure of diversity of specific form is an efficient ground rule provided

TABLE 4

SPECIES	LOCALITY	
	5 Baum (pure lime, xeric)	7 Baum (mixed, mesic)
Bouteloua hirsuta	34.4	30.0
Bouteloua rigidiseta	...	19.7
Bouteloua curtipendula	...	12.0
Andropogon scoparius	28.4	19.9
Sporobolus asper	0.5	...
Buchloe dactyloides	...	2.5
Neptunia lutea	...	2.1
Acacia angustissima	0.4	2.0
Panicum scribnerianum	0.2	1.7
Andropogon saccharoides	2.2	1.5
Carex sp.	2.4	1.2
Sorghastrum nutans	0.1	0.1
Krameria lanceolata	...	0.5
Daleo purpurea	0.1	0.5
Heliotropium tenellum	...	0.4
Euphorbia corollata	...	0.4
Ruellia humilis	0.1	0.3
Cirsium texanum	...	0.1
Hymenopappus scabiosa	...	0.1
Linum rigidiseta	0.1	0.1
Echinacea pallida	2.3	...
Houstonia nigricans	10.8	...
Aristida intermedia	2.7	...
Oenothera missouriensis var. *oklahomensis*	12.8	...
Psoralia linearifolia	0.7	...

the melange of forces which produce discontinuity are brought into perspective. Since the works of the great nineteenth century naturalists, a vast literature on the subject has developed exploring the nature of variation from many viewpoints, genetic, cytogenetic, morphologic, morphogenetic, physiologic, ecologic and biochemical, among others. General principles elucidating the major forces responsible for variation have been elaborated. It is not only valid but essential that field studies utilize as many kinds of data as possible for the purpose of expressing the interrelations between variations within species and variations within the communities which they compose. Kerner (1891), Bonnier (1889, 1890, 1895, 1920), MacDougal (1907, 1921a, b), Turesson (1922a, b, 1925, 1929, 1930a, b, 1931a, b, 1938), Clements (1908, 1929), laid the groundwork by bringing nature into the experimental plot while Clausen, Keck, and Hiesey (1940, 1945, 1948) placed plants of uniform heredity in varied environments and those of varied heredity into uniform environments. With the rapid growth of experimental taxonomy and ecology, we now have enough facts to analyze interactions between species variability and the environmental complex. Many such studies are underway. One of the primary values of this study of the Baum area is to point out that few sites have potential for analyses equal to the Arbuckle Mountains of southern Oklahoma where habitat differences are marked and discontinuities are knife-line. I propose that the Arbuckles be studied intensively as a field station for natural history. The excellent facilities of the University of Oklahoma Biological Station are within easy reach.

Broad patterns of variation within species suggest correlation with different kinds of habitat diversification. In geologic time variation was greatest following periods of mountain formation, the higher the mountains the greater the diversification, and probably least in periods approaching base-level. Our own time is clearly one of great diversification. In the American west the correlation of great differences in altitude with latitude produce astonishing diversity. Also arms of the north Mexican plateau flora have their well differentiated western and eastern floristic segments as demonstrated in species of organisms like *Juniperus, Cercis, Veronica, Prunus, Gaillardia, Artemisia, Pinus, Quercus* and *Populus* among others. Elements of the Antilles flora have influenced variation patterns in plants of the southern coastal plain, e.g., *Phytolacca octandra* into *Phytolacca americana* and *Juniperus barbadense* into *Juniperus virginiana.* Segments of the Rocky Mountain flora have influenced variation patterns not only of the plains but of the oak forests farther eastward, e.g., *Acer grandidentatum* into *Acer saccharum* var. *Schneckii, Juniperus scopulorum* into *Juniperus virginiana* and *Quercus breviloba* into *Quercus stellata.*

Species of the southwestern United States have likewise added to the variation of Ozarkian and Interior Low Plateau relatives, *Cercis reniformis* into *C. canadensis, Juniperus Ashei* into *J. virginiana.* Genes of *Juniperus Ashei* appear in red-cedar populations of the granite outcrops along the fall line of the Piedmont upland in Georgia.

Northern species have interacted to ameliorate variability in more southern ones, e.g., *Tilia americana* has influenced variation in *Tilia heterophylla* resulting in the "species complex" *Tilia neglecta* in Ohio (Braun, 1960). *T. americana* probably moved into contact with *T. heterophylla* from refugia to the west or southwest of Ohio, possibly from the Driftless area of Wisconsin along the ice margin. A similar pattern exists for *Hudsonia* but with migration along the ice margin predominately east to west. Hybrid swarms between *Hudsonia tomentosa* and *H. ericoides* were formed on the Atlantic coast from New Jersey to Maine and Prince Edward Island. Hybrids, along with apparently pure *H. tomentosa,* migrated westward along the ice margin eventually reaching into the northwest as far as Lake Athabaska (Hall, 1957). A similar pattern is evident for *Iris setosa* var. *interior* into *I. virginica* var. *Schrevei* producing *I. versicolor*, the variation indicating a north, south axis (Edgar Anderson, 1936). *Primula mistassinica* and *P. intercedens* form another glacial border variation spectrum.

There are many other patterns of variation among vascular plants involving close to continental dimensions, some of these suggested but yet unanalyzed. The various levels of complication caused by hybridization and differential selection from distances of influence of a thousand miles to a very few reiterates the idea that the only particularly stable element of the communities characterized by these species is its physiognomy. The phenotypic homogeneity of dominants from these communities mask a great deal of genetic heterogeneity and ecologic diversity.

These larger patterns of interspecific and interracial influences contribute to the concept of the continuum or a statistical expression of the nature of associations and are in turn further complicated by very local interactions demonstrated by this study of the Baum limestone and Trinity sand. From preliminary studies it is evident that cedar glades whether on the banks of the Red River in Grayson County, Texas, or on the bluffs of the Ohio River near Cincinnati, support populations of red-cedar more similar in spite of distance than those cedar populations close by but occupying differing habitats such as sandy, old-fields. This pattern is the result of genes contributed by another species through introgression followed by differential selection.

Environmental factors do not operate independently of one another but produce a concerted and simultaneous or perhaps a holistic response. It is not safe to suppose that independent controls operate in the vegetational array. Correlations between any specific factor and either boundaries or behavior of vegetation must be accepted with reservations. Yet, it seems useful to note the correlations of species and community variations shown in this paper with variations in water relations. The trends are clear and suggest a means for predicting environmental attributes from species interactions.

The Baum limestone shows no evidence of succession to oak forest. Its woody aspect is made up by *Juniperus Ashei* with occasional specimens of hybrids with red-cedar. Other woody plants found, primarily along drainageways, are *Bumelia lanuginosa, Celtis reticulata, Cercis canadensis, Diospyros virginiana, Forestiera pubescens, Fraxinus americana, Prunus mexicana, Viburnum rufidulum, Lonicera albiflora, Smilax bona-nox, Symphoricarpos orbiculatus* and *Rhus aromatica*. Woody cover or basal area is predominantly contributed by *J. Ashei*. What variation one does find is in spacing.

Populations of *Juniperus virginiana* on the Trinity sand are clearly successional. Eventually they are replaced by oak forest. Wherever the mixed talus occurs hybrids between the two juniper species are relatively abundant.

These hybrid populations are rich sources for continued introgression until succession closes those habitats capable of supporting oak forest.

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