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THE COMPARATIVE ECOLOGY OF TWO CANYONS AND AN UPLAND AREA IN WEST CENTRAL OKLAHOMA

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BY

FRANK FITZHUGH WELBOURNE, JR.

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THE COMPARATIVE ECOLOGY OF TWO CANYONS AND AN UPLAND AREA IN WEST CENTRAL OKLAHOMA

APPROVED BY

Elroy L. Rice

Lawrence M Rohrbaugh

Norman Boke

George J. Goodman

Robert D. Burns

DISSERTATION COMMITTEE

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THE COMPARATIVE ECOLOGY OF TWO CANYONS AND AN UPLAND AREA IN WEST CENTRAL OKLAHOMA

INTRODUCTION

In recent years investigators have become increasingly interested in what respects local conditions may affect the more general vegetation of an area. Generally, an investigator who undertakes a study of an area will supply climatic data from the nearest weather bureau station with full realization that variations in degree and direction of slope, type of vegetation, soil color, and many other factors operating over very short distances may alter these data considerably. Other deficiencies of weather bureau data include gross generalizations, abstractness, unavailable data, and the fact that many important aspects of the weather are not measured, thus making such data difficult to apply to specific situations. An extensive microclimate study was done by Wolfe et al. (1949) in Neotoma Valley, located in Hocking County, Ohio. In the above study data were collected regarding maximum and minimum air temperatures beneath the leaf litter and five feet above ground, soil temperatures, plant temperatures, relative light intensities, precipitation, evaporation, vapor pressure, etc. Other investigations include projects conducted by Fritts (1959) and Rice (1960) relating growth and occurrence of certain species to microclimatic factors.

In addition to microclimatic studies, investigations concerning local edaphic variations have been useful in helping to explain vegetational patterns. Billings (1950), Blackman and Rutter (1950), Beadle (1953, 1954), Walker (1954), Coaldrake and Haydock (1958), and White (1961) have published results concerning vegetational distribution in relation to amounts and availability of minerals, particularly nitrogen and phosphorus. Rice et al. (1960) investigated the role of minerals in succession in abandoned fields in Oklahoma. In addition to the studies of minerals, other factors concerning the soil have also been related to plant distribution. One study was made by Welbank (1961) concerning root competition for soil water and nitrogen in *Agropyron repens*.

Local edaphic variations may be the result of climatic and topographical differences within an area. Russell (1958) states: "The effect of drainage on clay type and soil color can be seen all over the tropics wherever the rainfall is high enough to ensure some leaching. Even quite small changes in relief are enough to give the change from the red soils with kaolinitic clay in the better drained areas to the black soil with montmorillonitic (clay) in the less well drained depressions." These variations in soil color can affect local conditions and vegetation by affecting soil temperatures, which in turn influence the amount of organic matter and soil moisture relations and these are interrelated with such factors as quantity and availability of minerals, types and number of microorganisms, pH, erosion, and leaching.

One objective of this study was to obtain quantitative and qualitative information regarding differences in vegetation, soil factors, and microclimatic data in two canyons and the typical upland savannah in west central Oklahoma. Another objective was to determine through controlled experiments whether some of the encountered differences might be of significance in explaining the variations in vegetational composition observed in the three study areas.

DESCRIPTION OF STUDY AREAS

Three areas were chosen for comparison: two canyons, designated Devils and Howerton, and the upland around Devils Canyon. These canyons represent abrupt changes in topography and support a very different type of vegetation from the surrounding uplands (Fig. 1-7). Each canyon contains a small stream (Fig. 5) and each is cut in Rush Springs Sandstone, a loosely cemented red sandstone of Permian Age (Miser 1954). They are virtually "U" shaped except for occasional talus slopes caused by slumping of the sandstone cliffs. The cliffs are virtually barren (Fig. 4) except for an abundance of lichens on the west walls. Devils Canyon is the larger of the two canyons, averaging 359 feet in width with vertical walls averaging 58 feet in height. It is located near the Caddo-Canadian County line 7.5 miles east of Hinton, Oklahoma on State Highway 37 in Sect. 18, T11NR10W. Howerton Canyon averages only 100 feet in width and has an average vertical well height of 37 feet. It is located 3.5 miles west of Hinton on the continuation of SH 37 in Sect. 18, T11NR12W.

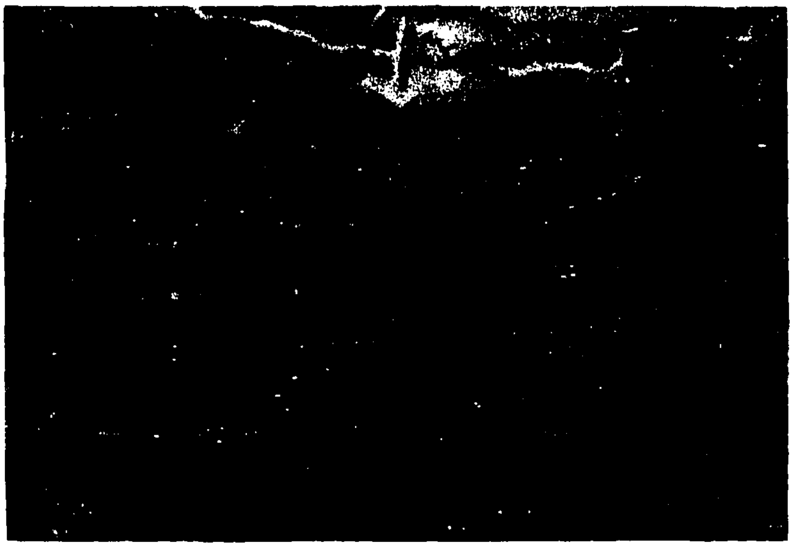

Fig. 1. Aerial photograph of study area in Devils Canyon.
Scale: One inch equals 660 ft.

Fig. 2. Aerial photograph of Howerton Canyon study area.
Scale same as above.

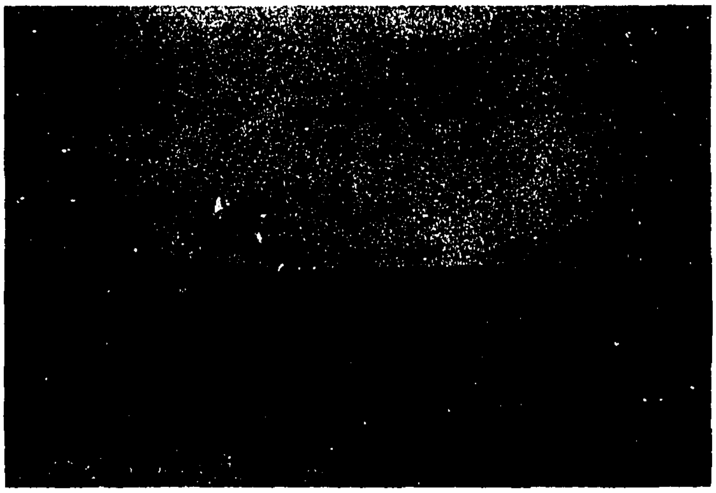

Fig. 3. Upland area of Devils Canyon.

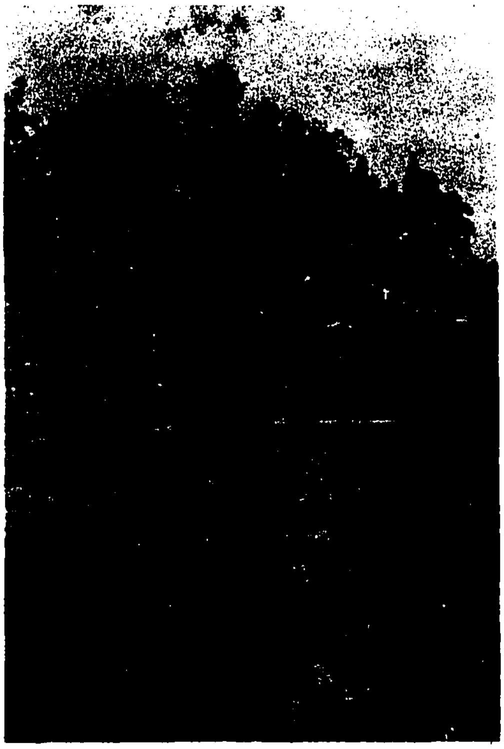

Fig. 4. Vertical sandstone cliff of Devils Canyon. Portions of the west facing wall, not shown here, are covered by numerous lichens.

Fig. 5. The small stream running through Devils Canyon. This stream is considerably wider than the one in Howerton Canyon.

Fig. 6. The vegetation in Devils Canyon. Several large sugar maples and a patch of Virginia wild rye are to be seen here.

Fig. 7. The vegetation of Howerton Canyon. Shrub cover in this canyon was highest of the three study areas.

This portion of Oklahoma is characterized by 28 - 30 inches of annual precipitation, high winds, few cloudy days, and low winter temperatures. It is covered for the most part by four distinct communities, three of which are savannahs and the other a tall grass prairie (Rice and Penfound 1959). The three savannah types are post oak (*Quercus stellata*)*-blackjack (*Q. marilandica*), blackjack, and blackjack - red cedar (*Juniperus virginiana*), the last being the most commonly represented in this area. The prairie is dominated by big bluestem (*Andropogon gerardi*), little bluestem (*A. scoparius*), switchgrass (*Panicum virgatum*), and Indian grass (*Sorghastrum nutans*). The prairie is found on the tighter soils underlain by shale, whereas the savannahs are located on the loose soils derived from sandstone. Forest type vegetation is present in the canyons and presents a marked contrast to the upland types in composition, physiognomy, and associated herbaceous species. Most of the trees in the canyons are slightly taller than the canyon walls in contrast to the short, scrubby appearance of the vegetation on the upland (Fig. 1-3). Some of the canyon species are disjunct over 180 miles from the east. The disjunct species are: Sugar maple (*Acer saccharum*), anise root (*Osmorhiza*

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*Nomenclature follows Waterfall (1960).

longistylis var. *villicaulis*), wood nettle (*Laportea canadensis*), figwort (*Scrophularia lanceolata*), panic grass (*Panicum clandestinum*), daisy fleabane (*Erigeron annuus*), and honewort (*Cryptotaenia canadensis*). Sears (1932, 1933) postulated that the canyon flora in Devils Canyon, the only area in this study to contain the disjunct species, represents the relict vegetation of a mesic forest that existed throughout the entire region during a more humid period in the past, perhaps about 4000 B. C. Further evidence that the canyons were present and supported vegetation in the past was obtained from a personal communication from U. A. Ireland, Professor of Geology at Kansas University, who found lignitized fossil wood at a depth of 125 feet in the floor of one of the canyons, very likely Devils Canyon. By C^{14} dating he determined the age of the piece to be 9000 $\pm$ 300 years old.

MATERIALS AND METHODS

Vegetational Analyses

Quantitative samples of trees, shrubs, vines, and herbaceous species were taken in June and July 1958. The arboreal vegetation was sampled by means of the point center quarter method (Cottam and Curtis 1956), and the number of saplings (1 - 3 in. DBH) per acre was obtained by use of a 0.01 acre circle circumscribed about each point. Relative density, relative frequency, and relative cover obtained by this method were averaged for the calculation of the importance percentage. Forty points were taken in each of the two canyons and 30 points on the upland.

The shrubs and woody vines were sampled by means of the line intercept method described by Canfield (1941). Sixty lines of ten meters length were used in each area and the interceptions measured to the nearest millimeter. An importance percentage was calculated for each species on the basis of relative frequency and relative cover obtained by this method.

The herbaceous vegetation was sampled by means of the clip quadrat method using a 0.25 m^2 metal frame quadrat. Thirty quadrats were sampled in Devils Canyon and on the upland, and 20 in Howerton Canyon. Individual species were separated in the field and oven dried for 48 hours at 95° C prior to weighing. The importance percentage was calculated by averaging relative frequency and relative dry weight (relative cover) for each species.

Soil Studies

For subsequent analyses of organic carbon, mineral content, pH, and soil texture twelve samples were obtained from each area. Six of these were taken from the 0 - 6 in. level and six at the 18 - 24 in. level. Soil samples were air dried, cleared of rocks and pieces of undecayed organic matter, and ground with a mortar and pestle sufficiently to pass through a 2 mm sieve. A portion of each sample was weighed before and after oven drying to obtain the amount of moisture in the air dried soil. All analyses were made with air dry soil but all calculations were based on the oven dry weights of the samples. Except for about 60 g required for pH and textural analyses, the samples were pulverized in a hammer mill containing a 0.5 mm sieve. Duplicate samples were run in all of the determinations.

Soil samples for soil moisture determinations were collected from the 0 - 6 in. and 12 - 18 in. levels at ten points in each area in July and August. The samples were oven dried for 48 hours at 105^{o} C and the percentage of soil moisture based on the oven dry weight of the soil was calculated.

For determining soil reaction a suspension of 10 g of soil and 50 ml of aerated distilled water was prepared and the pH read directly by means of a Beckman pH meter. Soil texture was determined by the method of Bouyoucous (1936), organic carbon by a method modified slightly from Piper (1944), total nitrogen by the method of Noggle and Wynd (1941), and total phosphorus by the method of Shelton and Harper (1941). Soil extraction for the determination of exchangeable potassium was accomplished by the method of Peech and English (1944), and the measurement of exchangeable potassium was done by use of a Perkin-Elmer Flame Photometer, Model 146. The amounts of all elements were calculated as percentages of the oven dry weight of the soil.

Microclimates

Four stations, each equipped with white and black atmometer cups and a maximum-minimum thermometer located five feet above ground level, were spaced approximately equidistant in Howerton Canyon. A rain gauge was also placed at each end of the study area in this canyon. These instruments were checked weekly during the eight weeks comparison period and compared with five similar stations in Devils Canyon and five on the upland. In these two areas the maximum and minimum air temperatures were obtained from continuous recording thermographs. Relative light intensities in the two canyons were compared by means of 40 light meter readings taken four feet above ground level, from 2:30 P.M. until 4:29 P.M. June 18, 1959 and 10:00 A.M. until 11:23 A.M. August 8, 1959. Pairs of light meter readings were taken simultaneously in the two canyons by two persons with synchronized watches.

Mineral Nutrition and Water Requirements

Virginia wild rye (*Elymus virginicus*), spangle grass (*Uniola latifolia*), and six weeks fescue (*Festuca octoflora*), the herbaceous species having the highest importance percentages in Devils Canyon, Howerton Canyon, and the upland respectively, were compared as to relative requirements for nitrogen, phosphorus, and potassium. Plants of each species were grown in sand culture in four inch glazed pots in complete solution (Hoagland's No. 1) and in solutions containing one-twentieth, one-fortieth, or one-eightieth as much nitrogen, or phosphorus, or potassium, as was present in the complete solution. The pH of the solutions was adjusted to 5.8. Six pots of each species and each concentration were used and the number of plants per pot thinned to five soon after germination. Three months after planting the plants were harvested and dried at 95° C for 48 hours, after which dry weights of roots and tops were determined.

Soil moisture requirements of the three predominant herbaceous species were determined by placing several pots (Table VII) of each species on a 4, 12, and 20 day watering schedule. Each pot contained 20 individuals of a given species. The schedule was started when the seedlings were well established and the number of surviving individuals was determined at the end of three months.

Seed Germination Studies

Because of repeated difficulty in obtaining satisfactory germination of spangle grass seeds several agents were applied in varying concentrations. These included solutions of 3% thiourea, 3% and 6% ethylene chlorhydrin, gibberellic acid (4.5 mg per 100 ml of water), and absolute ethyl alcohol. One hundred seeds were soaked for two minutes in each solution and then allowed to stand in its vapors for 24 hours.

RESULTS

Vegetational Analyses

The dominant arborescent species (Table I) in Devils Canyon were sugar maple and red elm (*Ulmus rubra*), both of which had an importance percentage greater than 16. On this basis black walnut (*Juglans nigra*) was the only species that could be considered a dominant in Howerton Canyon. Chestnut oak (*Q. muehlenbergii*) and American elm (*U. americana*) were important secondary species. The dominants on the upland were blackjack oak and red cedar. Howerton Canyon had the greatest density of the three areas with 203 trees per acre, but did not contain as much basal area per acre as Devils Canyon. The upland was lowest in basal area and density. Sugar maple and hackberry (*Celtis occidentalis*) were reproducing well in Devils Canyon as indicated by the number of saplings, whereas red elm, a codominant, had a very low reproductive rate (Table I). In Howerton Canyon, the dominant species, black walnut, was reproducing very little

Table I. Results of quantitative sampling of arborescent species in the three study areas.

SPECIES	TREES PER ACRE			BASAL AREA PER ACRE*			PERCENTAGE FREQUENCY			IMPORTANCE PERCENTAGE**			SAPLINGS PER ACRE		
	D. Can.	H. Can.	Upland	D. Can.	H. Can.	Upland	D. Can.	H. Can.	Upland	D. Can.	H. Can.	Upland	D. Can.	H. Can.	Upland
Acer negundo	20.8	1.7	-	12.7	0.3	-	45.0	3.3	-	13.0	0.7	-	0.0	0.0	-
Acer saccharum	39.8	-	-	25.2	-	-	62.5	-	-	22.5	-	-	32.5	-	-
Celtis occidentalis	15.3	6.8	0.3	8.8	0.8	0.0	37.5	13.3	3.3	10.0	2.7	1.1	25.0	10.0	0.0
Cercis canadensis	0.0	35.5	-	0.0	3.8	-	0.0	40.0	-	0.0	11.3	-	5.0	43.3	-
Juglans nigra	19.0	25.4	-	18.0	32.0	-	37.5	36.7	-	13.1	17.4	-	2.5	0.0	-
Juniperus virginiana	0.0	23.7	11.0	0.0	7.2	2.8	0.0	33.3	70.0	0.0	9.6	36.9	2.5	60.0	3.3
Quercus marilandica	-	-	21.5	-	-	3.8	-	-	90.0	-	-	57.4	-	-	66.7
Quercus muehlenbergii	4.5	27.0	-	5.8	18.2	-	12.5	46.7	-	3.9	14.8	-	0.0	10.0	-
Ulmus americana	13.6	18.6	-	20.1	27.3	-	25.0	30.0	-	11.0	14.2	-	0.0	3.0	-
Ulmus rubra	19.0	18.6	-	29.8	13.5	-	45.0	30.0	-	16.9	10.2	-	2.5	3.0	-

*Square feet.

**Average of relative density, relative frequency, and relative basal area.

Table I. Continued.

SPECIES	TREES PER ACRE			BASAL AREA PER ACRE			PERCENTAGE FREQUENCY			IMPORTANCE PERCENTAGE			SAPLINGS PER ACRE		
	D. Can.	H. Can.	Upland	D. Can.	H. Can.	Upland	D. Can.	H. Can.	Upland	D. Can.	H. Can.	Upland	D. Can.	H. Can.	Upland
Bumelia lanuginosa	3.6	15.2	0.3	0.9	3.3	0.0	10.0	23.3	3.3	2.2	6.0	1.0	0.0	10.0	10.0
Catalpa speciosa	-	16.9	-	-	4.3	-	-	26.7	-	-	6.9	-	-	13.3	-
Celtis reticulata	-	3.4	0.6	-	0.2	0.0	-	3.3	3.3	-	1.0	1.9	-	13.3	10.0
Gymnocladus dioca	0.8	-	-	-	-	-	6.7	-	-	0.1	-	-	0.0	-	-
Morus rubra	5.5	10.2	-	2.7	4.2	-	12.5	20.0	-	3.3	5.4	-	0.0	10.0	-
Quercus macrocarpa	1.7	-	-	6.7	-	-	5.0	-	-	2.7	-	-	0.0	-	-
Quercus shumardii	0.8	-	-	1.0	-	-	-	-	-	0.4	-	-	0.0	-	-
Quercus stellata	-	-	1.2	-	-	1.0	-	-	10.0	-	-	-	-	-	0.0
Totals	144.4	203.0	34.9	131.7	115.1	7.6				99.1	100.2	98.3	70.0	175.9	90.0

whereas redbud (Cercis canadensis) and red cedar were reproducing well. On the upland blackjack oak was reproducing well with only a low rate of reproduction being noted for red cedar.

The predominant woody vines (Table II) were Virginia creeper (Parthenocissus quinquefolia) in Devils Canyon; Virginia creeper and catbrier (Smilax tamnoides) in Howerton Canyon, and Virginia creeper and red-berried moonseed vine (Cocculus carolinus) on the upland. The predominant shrubs in the three areas were dogwood (Cornus drummondii) and coralberry (Symphoricarpus orbiculatus) in Devils Canyon, coralberry in Howerton Canyon, and skunkbush (Rhus aromatica var.) and coralberry on the upland. The cover of shrubs and woody vines was very low on the upland, intermediate in Devils Canyon, and highest in Howerton Canyon.

Virginia wild rye was the most important herbaceous species in Devils Canyon (Table III). Spangle grass was the predominant herbaceous species in Howerton Canyon with Virginia wild rye occurring as an important secondary species. On the upland six weeks fescue and Texas bluegrass (Poa arachnifera) had the highest importance percentages, 13.7 and 13.1 respectively. Thirty-four herbaceous species were sampled in Devils Canyon and two of these, daisy fleabane

Table II. Quantitative analysis of the shrubs and woody vines in the three study areas.

SPECIES	PERCENTAGE COVER			IMPORTANCE PERCENTAGE*		
	D. Can.	H. Can.	Upland	D. Can.	H. Can.	Upland
Celastrus scandens	0.1	0.0	-	0.6	0.4	-
Cissus incisa	-	-	0.0	-	-	0.8
Cocculus carolinus	-	-	0.4	-	-	7.6
Cornus drummondii	2.5	2.8	-	11.5	7.8	-
Euonymous atropurpureus	0.6	0.4	-	2.6	1.6	-
Forestiera pubescens	0.0	0.4	0.6	0.1	0.9	7.4
Parthenocissus quinquefolia	4.2	7.0	0.3	36.5	31.4	4.6
Rhus aromatica var.	-	-	2.2	-	-	40.0
Rhus glabra	-	-	0.6	-	-	9.4
Rhus radicans	2.3	2.6	-	10.4	10.8	-
Sambucus canadensis	0.2	0.1	-	1.4	0.6	-
Smilax bona-nox	0.2	0.1	-	1.3	0.4	-
Smilax tamnoides	2.1	5.1	-	14.0	20.0	-
Symphoricarpos orbiculatus	1.5	3.8	1.4	11.4	19.7	30.2
Vitis spp.	2.7	2.3	-	10.2	6.5	-
Totals	16.4	24.6	5.5	100.0	100.0	100.0

*Average of relative frequency and relative cover.

Table III. Results of sampling of herbaceous vegetation in the three study areas. Species with an importance percentage of greater than two in at least one area are listed.

SPECIES	IMPORTANCE PERCENTAGE*		
	Devils Canyon	Howerton Canyon	Upland
Acalypha sp.	2.3	0.7	-
Andropogon scoparius	-	-	4.5
Aphanostephus skirrobasis	-	-	4.6
Bidens bipinnata	5.6	-	0.2
Bouteloua gracilis	-	-	5.6
Bromus purgans	4.3	9.8	-
Carex microdonta	4.5	2.7	-
Elephantopus carolinianus	2.1	-	-
Elymus villosus	3.3	-	-
Elymus virginicus	40.0	25.2	-
Erigeron strigosus	-	-	2.8
Equisetum hyemale	-	7.4	-
Festuca octoflora	-	-	13.7
Iresine paniculata	3.4	2.0	-
Lactuca canadensis	1.3	2.4	-
Menispermum canadense	8.5	2.9	-
Paspalum pubescens	-	-	5.9
Plantago purshii	-	-	7.2
Poa arachnifera	-	-	13.1
Polygonatum canaliculatum	0.3	3.9	-
Tovara virginiana	2.7	-	-
Sanicula canadensis	3.4	3.8	-
Uniola latifolia	1.7	33.6	-

*Average of relative frequency and relative cover.

(Erigeron annuus) and panic grass (Panicum clandestinum) were disjunct species which were recorded for the first time from this canyon. Seventeen herbaceous species were sampled in Howerton Canyon and 47 on the upland.

Soil Studies

Organic carbon, total nitrogen, and soil moisture were highest in both the 0 - 6 in. and 18 - 24 in. levels in Devils Canyon, intermediate in Howerton Canyon, and lowest on the upland (Table IV). On the basis of Student's "t" Test (Snedecor 1946), the differences in the mean amounts of organic carbon were significant at both the 0 - 6 in. and the 18 - 24 in. levels between all areas except Howerton Canyon and the upland. The "t" values for the differences in mean amounts of nitrogen between plots were very close to the 0.05 level of significance for all areas except Howerton Canyon and the upland. Total phosphorus was highest in the two levels in Devils Canyon but was about equal in Howerton Canyon and on the upland. The differences in the mean amounts of phosphorus between plots at both levels were generally statistically significant except between Howerton Canyon and the upland. The soil texture at both levels in all three areas was similar and would be classified as sand (Lyon and

Table IV. Results of soil analyses in Devils Canyon, Howerton Canyon, and the upland around Devils Canyon.

Area	Level	% Org. Carbon	% Total Nitrogen	% Total Phos.	% Exc. K	pH	% Soil Moisture	Texture
Devils Canyon	0-6 in.	0.900	0.081	0.015	0.007	7.0	12.7	93.1% sand 4.8% silt 2.1% clay
	18-24 in.	0.412	0.045	0.013	0.004	7.1	12.0	93.5% sand 3.8% silt 2.7% clay
Howerton Canyon	0-6 in.	0.654	0.064	0.011	0.006	7.0	7.9	94.1% sand 3.6% silt 2.4% clay
	18-24 in.	0.279	0.029	0.009	0.004	6.7	7.5	95.0% sand 2.0% silt 3.1% clay
Upland	0-6 in.	0.601	0.057	0.012	0.008	6.5	6.0	92.6% sand 3.3% silt 4.2% clay
	18-24 in.	0.236	0.027	0.008	0.005	6.4	7.4	90.3% sand 3.5% silt 6.2% clay

Buckman 1948). Amounts of exchangeable potassium were similar in the three areas also, with no differences between plots being statistically significant. Differences in soil reaction were small and were in a range favoring availability of the required minerals.

Microclimatic Measurements

Relative light intensities were higher in Howerton Canyon than in Devils Canyon in the August readings and very nearly the same in June. The average of the 40 points in June was 831 ft-c in Devils Canyon and 841 ft-c in Howerton Canyon, and the August readings were 661 ft-c and 995 ft-c respectively. No readings were taken on the upland but the average would have been very nearly that of full sunlight, 7200 - 8400 ft-c.

Average weekly maximum temperatures were highest on the upland, intermediate in Howerton Canyon, and lowest in Devils Canyon in all eight weeks under consideration (Table V). Average weekly minimum temperatures were generally lowest in Howerton Canyon and highest on the upland with Devils Canyon intermediate. These data were not as consistent as the average weekly maximum temperatures.

Average daily evaporation losses were not significantly

Table V. Results of microclimatic measurements in the three study areas during an eight week period in 1958.

Microclimatic Measurements	Date	Devils Canyon		Howerton Canyon		Upland	
Weekly Maximum Air Temperatures °F	July 26	95.4		98.0		98.2	
	Aug. 2	92.4		94.2		95.8	
	Aug. 9	92.8		95.2		98.8	
	Aug. 16	95.0		98.0		103.2	
	Aug. 23	90.8		92.0		97.2	
	Aug. 30	93.2		97.2		102.0	
	Sept. 6	93.0		96.0		97.0	
	Sept. 13	88.2		90.8		93.6	
	Avg.	92.6		95.2		98.2	
Weekly Minimum Air Temperatures °F	July 26	65.4		64.3		64.4	
	Aug. 2	66.4		66.2		67.4	
	Aug. 9	68.4		67.1		70.4	
	Aug. 16	66.6		65.9		69.8	
	Aug. 23	63.8		62.8		63.0	
	Aug. 30	57.8		58.0		60.4	
	Sept. 6	63.6		62.8		65.8	
	Sept. 13	61.0		59.5		62.0	
	Avg.	64.1		61.0		65.4	
		White cup	Black cup	White cup	Black cup	White cup	Black cup
Avg. Daily Evaporation ml	July 26	14.7	17.4	9.9	14.4	35.0	38.7
	Aug. 2	7.6	17.8	12.6	15.7	35.8	45.8
	Aug. 9	18.9	21.2	15.0	18.1	48.1	62.0
	Aug. 16	19.4	21.6	19.4	22.4	50.3	64.4
	Aug. 23	12.3	13.7	11.1	13.5	30.0	39.4
	Aug. 30	14.5	17.9	20.1	23.2	54.4	62.5
	Sept. 6	29.1	30.5	27.0	30.9	59.6	78.8
	Sept. 13	11.3	15.8	14.3	15.4	28.8	40.8
	Avg.	16.0	19.5	16.2	19.2	42.7	54.0

different in the two canyons but were three times as great on the upland (Table V). Average insolation was over three times as high on the upland as in the canyons based on comparative evaporation rates from white and black cups in each area. It was about the same in the two canyons, however.

Mineral Nutrition and Water Requirement

The results of the mineral nutrition experiment (Table VI) show that six weeks fescue in low nitrogen solutions attained a larger percentage of its control weight of both shoots and roots than Virginia wild rye or spangle grass. Six weeks fescue also had a higher percentage of tillers than the other two grasses based on their respective controls. Except for the shoot weight and tillering in the N/80 solutions, spangle grass showed better growth than Virginia wild rye in the low nitrogen solutions. These results suggest that the order of species based on an increasing requirement for nitrogen is six weeks fescue, spangle grass, and Virginia wild rye.

The results concerning phosphorus nutrition (Table VI) were not as clear cut as with nitrogen but spangle grass had poorer growth of both shoots and roots in almost every low phosphorus solution than did Virginia wild rye or six

Table VI. Relative requirements of the three predominant herbaceous species for nitrogen, phosphorus, and potassium.

Mineral Conc.	Plant Part	Elymus virginicus		Uniola latifolia		Festuca octoflora	
		% of control weight	% of control tillering	% of control weight	% of control tillering	% of control weight	% of control tillering
Control	Shoots	100.0	100.0	100.0	100.0	100.0	100.0
	Roots	100.0		100.0		100.0	
N/20 10.5 ppm	Shoots	35.6	46.3	37.1	26.2	39.8	56.5
	Roots	44.0		79.1		102.0	
N/40 5.25 ppm	Shoots	16.8	30.6	18.4	8.3	26.2	44.5
	Roots	20.3		55.6		76.5	
N/80 2.62 ppm	Shoots	11.4	18.6	10.5	4.2	13.6	32.2
	Roots	16.4		26.1		39.2	
P/20 1.55 ppm	Shoots	45.1	43.1	35.6	41.7	42.4	48.6
	Roots	44.9		57.4		68.6	
P/40 0.78 ppm	Shoots	16.8	11.0	15.9	16.7	18.8	31.2
	Roots	18.4		30.0		41.2	
P/80 0.39 ppm	Shoots	22.6	16.1	6.0	15.4	12.0	26.4
	Roots	23.7		16.5		21.6	
K/20 11.72 ppm	Shoots	84.2	82.2	96.8	98.8	46.1	43.8
	Roots	53.1		85.2		68.6	
K/40 5.86 ppm	Shoots	68.5	70.9	66.0	73.8	40.3	57.2
	Roots	40.6		44.4		72.6	
K/80 2.93 ppm	Shoots	62.8	67.6	79.4	72.1	69.1	68.2
	Roots	33.8		59.1		50.1	

weeks fescue. The percentage of tillering also was generally lower in spangle grass than in the other species. Virginia wild rye had slightly better shoot growth but poorer root growth than six weeks fescue. Six weeks fescue attained a larger percentage of tillers with respect to the controls than Virginia wild rye. These results suggest that spangle grass has a slightly higher requirement for phosphorus than the other species. The results concerning the relative phosphorus requirements of six weeks fescue and Virginia wild rye are inconclusive.

The experiment did not demonstrate any evidence of differential requirements for potassium in the three species. Although none of the species in reduced potassium solutions exceeded its respective control in root and shoot weights or tiller counts, growth was better in some of the lower concentrations than in the higher concentrations.

On the basis of relative survival on various watering schedules, Virginia wild rye appeared to have the highest water requirement, spangle grass was intermediate, and six weeks fescue had the lowest requirement (Table VII). This was particularly apparent in the group watered every 20 days, but several Virginia wild rye plants died on the 12 day schedule. This experiment was repeated with virtually the

Table VII. Relative soil moisture requirements of the herbaceous species having the highest importance percentage in each area.

Species	Watering Schedule	Number of pots of 20 plants each	Percentage of individuals surviving
Elymus virginicus	4 Day	2	100
Festuca octoflora		2	100
Elymus virginicus	12 Day	3	80
Uniola latifolia		4	95
Festuca octoflora		3	98
Elymus virginicus	20 Day	4	39
Uniola latifolia		3	47
Festuca octoflora		4	68

same results.

Seed Germination Studies

Soaking spangle grass seeds for two minutes in 3% thiourea and then allowing the seeds to stand in the vapors for 24 hours brought about almost 100% germination in less than ten days. A very slight improvement in germination was noted after application of a gibberellic acid solution.

DISCUSSION

Results of the vegetational analyses showed that Devils Canyon contained more mesic species than the other areas. Howerton Canyon was intermediate in this respect in that none of the disjunct herbaceous species was found in this area, and such mesic species as bur oak (Q. macrocarpa) and Shumard's red oak (Q. shumardii) did not occur in this canyon. The greater abundance of red elm than American elm in Devils Canyon and the reverse situation in Howerton Canyon is also indicative of a more mesic situation in Devils Canyon in that Rice (1961) found American elm to be more abundant on the drier sites and red elm to be more abundant on the more mesic sites in Oklahoma. The vegetation of the upland was definitely the most xeric of the three areas. Basal area per acre was greatest in Devils Canyon, intermediate in Howerton Canyon, and lowest on the upland indicating greater production of plant material in the more mesic areas.

Results of the soil and microclimatic studies suggest several reasons why Devils Canyon supports the most mesic vegetation and greatest basal area of the three areas. Organic carbon, total nitrogen, total phosphorus, and soil moisture were all highest in this area and average weekly maximum air temperatures were lowest. The intermediate position of Howerton Canyon with respect to mesic vegetation and basal area is probably related to the intermediate amounts of organic carbon, total nitrogen, and soil moisture found in this area. Average weekly maximum air temperatures were also intermediate in this area. Evaporation studies did not show any significant difference in evaporation or insolation in the two canyons but evaporation and insolation were much greater on the upland. Average light intensity was found to be higher in Howerton Canyon than in Devils Canyon in spot checks with Weston Light Meters. In a more extensive study by Rice (1960) comparing Devils Canyon with the upland, average daily maximum air temperatures were found to be 3^{o} - 5^{o} F lower in the canyon than on the upland each week, evaporation to be 2 - 4 times as high on the upland as in the canyon each week, and average daily air movement was from 3.5 - 15 times as high each week outside the canyon as inside.

The fact that soil conditions were more favorable in the canyons is probably related to the microclimatic aspects of the canyons. The lowered environmental stresses would cause such factors as soil moisture and organic matter to be higher with consequent increase in minerals and greater availability of these minerals. It appears that these conditions are related to the ability of the areas to support a more mesic vegetation and produce greater basal area than the upland. In the Sydney district of Australia, Beadle (1954) found that with decreasing soil fertility, the number of species decreases, the trees are shorter, and the canopy becomes more open. He concluded that ". . . the higher the phosphate content of the soil, the more mesic and taller is the vegetation."

The favorable soil conditions and microclimate in Howerton Canyon make it reasonable to assume that at least some of the disjunct species would have survived in this canyon had they ever been present. Norris (1951) states that the canyons in this portion of Oklahoma were first excavated during the Pleistocene and have been filled and reexcavated several times since. It is probable that the most recent reexcavation of Howerton Canyon occurred subsequent to the latest reexcavation of Devils Canyon, and after the disjunct species had become extinct on the upland. If so, such species would not have been available for the invasion of Howerton Canyon after its most recent reexcavation.

In considering the reasons for the distribution of the herbaceous species in the study areas, it appears that the relative requirements for water and nitrogen are of great importance. Virginia wild rye was found to have the greatest requirements for these factors, spangle grass was intermediate, and six weeks fescue had the lowest requirements. Moreover, Virginia wild rye was the predominant herbaceous species in the area of highest soil moisture and nitrogen, spangle grass was predominant in the area of intermediate content of these factors, and six weeks fescue was the predominant species on the upland, the area of lowest soil nitrogen and moisture.

It appears that relative soil phosphorus requirements do not play a very important role in determining the distribution of herbaceous species in the study areas. The results showed spangle grass to have the highest requirement for this element with six weeks fescue and Virginia wild rye having about the same requirement. Virginia wild rye was the most important herbaceous species, however, in the area with the highest amount of total phosphorus. Spangle grass and six weeks fescue were the predominant herbaceous species in the areas with similar amounts of total phosphorus. These inconsistencies are not surprising in that differences in soil phosphate were not great in the three areas.

It is unlikely that potassium plays an important role in determining the distribution and occurrence of natural vegetation in this portion of Oklahoma inasmuch as most of the samples analyzed from this area by Harper (1950) showed high amounts of potassium, as did the samples taken in this study. Moreover, no clear cut differences in potassium requirements were demonstrated for the predominant herbaceous species in the study areas.

Other workers have also obtained evidence that variations in soil nitrogen, phosphorus, and moisture have a bearing on the presence and importance of certain species. Rice et al. (1960) showed that plants occurring in different stages of succession in abandoned fields in Oklahoma had different requirements for nitrogen and phosphorus. They also obtained inconsistent results with potassium nutrition.

Evans (1960) showed by mineral nutrition experiments that differential ability to compete for nitrogen in three species of the annual grassland type in California correlated well with changes observed in the field when various amounts of nitrogen fertilizers were added. It was observed that *Festuca megalura* decreased and *Bromus mollis* and

Erodium botrys increased in importance when nitrogen was added. Greenhouse experiments showed differential ability to take up and utilize soil nitrogen as the principal factor in competition between the two grass species, but shading was also important when E. botrys was grown with the two grasses. White (1961) found that the presence of little bluestem on certain xeric areas was due to its ability to compete successfully there for nitrogen, phosphorus, and potassium with western wheatgrass (Agropyron smithii). A study by Welbank (1961) showed root competition for water to be greater than for nitrogen in Agropyron repens. This is interesting in that the most definite correlation in the present study between the presence of the predominant herbaceous species in the three study areas and soil conditions was with the factor of soil water. Another study relating the occurrence of certain species to variations in soil moisture was made by Mueller and Weaver (1942). Dominant species of the true and mixed prairie were arranged according to decreasing drought resistance by field observations and actual experiments.

An investigation by Beadle (1953, 1954) indicated that the delimitation of plant communities in the Sydney district of Australia is primarily controlled by soil fertility, and soil phosphate is the factor exerting the greatest influence. The absence of the species with a low requirement for the element on the more fertile soils is explained on the basis of their inability to compete with the more vigorous species native to these soils. Billings (1950) found that soils under patches of yellow pine (Pinus ponderosa) and Pinus jeffreyi in the predominantly sagebrush-pinyon-juniper zones to the east of the Sierra Nevadas showed gross mineral deficiencies and high acidity as compared with the surrounding areas. These patches were on light colored soils derived from the weathering products of hydrothermally altered igneous rocks. It was found that tobacco and tomato plants did not grow in soils from these areas with only distilled water added but matured and flowered after additions of nitrogen and phosphorus. It was concluded that the pine stands are relicts which have remained because of the inability of the sagebrush zone dominants to invade these mineral deficient soils.

SUMMARY

1. The arborescent species, shrubs, woody vines, and herbaceous species were sampled in three relatively undisturbed areas in west central Oklahoma. Two of these areas were canyons, Devils and Howerton. These canyons were found to support mesic forest vegetation in marked contrast to the savannah and prairie vegetation found typically in this portion of Oklahoma. The third study area was a savannah upland located in the vicinity of Devils Canyon.

2. The most mesic species of the three areas were found in Devils Canyon, and several of the species were disjunct from the East. The dominant species in Devils Canyon were sugar maple and red elm. Howerton Canyon contained none of the disjuncts, supported fewer mesic species, and had less basal area than Devils Canyon. The dominant species in Howerton Canyon was black walnut. The species on the upland were more xeric than those in either canyon, the arborescent species consisting almost entirely of blackjack oak and red cedar.

3. Soil analyses and microclimatic studies were made in the three areas in an effort to explain the reasons for the differences in vegetation. The soil analyses showed Devils Canyon to be highest in organic carbon, total nitrogen, total phosphorus, and soil moisture. Howerton Canyon was intermediate in amounts of all of these factors except phosphorus, and the upland was the most deficient except for phosphorus, which was virtually the same as in Howerton Canyon. Differences in exchangeable potassium, soil texture, and soil reaction were not significant in the three areas. Microclimatic comparisons showed average daily maximum temperatures to be lowest in Devils Canyon, intermediate in Howerton Canyon, and highest on the upland. Differences in evaporation and insolation were not great in the two canyons but were about three times as great on the upland as in either canyon.

4. The presence of the more mesic species and greater basal area found in Devils Canyon are probably related to the more favorable soil and microclimatic conditions found in this canyon. The less mesic vegetation found in Howerton Canyon is associated with somewhat less favorable soil and microclimatic conditions, although the absence of the disjunct species could be a result of a more recent

reexcavation of this canyon subsequent to the time when the species were present on the upland. The upland supported the most xeric species, produced less basal area, and showed the poorest soil conditions and the most severe microclimate of the three areas.

5. Controlled greenhouse experiments indicated that Virginia wild rye, the predominant herbaceous species from the area of highest soil nitrogen and moisture (Devils Canyon), had the highest requirement for these two factors. The predominant herbaceous species in Howerton Canyon, spangle grass, was intermediate in its requirement for soil nitrogen and soil moisture and amounts of these factors were intermediate in Howerton Canyon. Six weeks fescue had the lowest requirements for soil nitrogen and soil moisture and was the predominant herbaceous species in the area with the lowest amounts of these materials. Studies concerning the relative requirement of these species for potassium and phosphorus were inconclusive. Thus, it appears that soil nitrogen and soil moisture exert great influence in determining the presence and abundance of the predominant herbaceous species in the three study areas.

6. Seed germination studies showed that treating spangle grass seeds with a 3% solution of thiourea greatly improved germination.

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