REDCEDAR (*Juniperus virginiana* L.) COMMUNITIES IN THE KENTUCKY RIVER GORGE AREA OF THE BLUEGRASS REGION OF KENTUCKY[1/]

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Abstract.--Clifftop redcedar (*Juniperus virginiana* L.) communities in the gorges of the Kentucky River and its tributaries were studied. Average density was high (766 trees/ha), but basal area (14-18 m^2/ha) was lower than for nearby hardwood stands. Because of the clear dominance of redcedar (52-65% of the importance values), species diversity was low and evergreenness high. The small tree-shrub associates in these communities form a distinct and characteristic component. The harsh clifftop environments (S-, W-, SW-facing exposures; thin, clayey soils over limestone; low soil moisture; low nutrient levels) serve to reduce competition from more site-demanding species. Those factors, plus fire protection, have served to select for redcedar. The coefficients of determination and species replacement patterns indicate that these clifftop communities are rather stable and long persisting.

Keywords: *Juniperus virginiana*, redcedar, Kentucky

INTRODUCTION

According to Braun (1950) the only areas of natural vegetation that remain in the Inner Bluegrass of Kentucky are confined to the gorges of the Kentucky River and its tributaries. Braun wrote that, "In these gorges communities range from the most mesophytic on deep talus of sheltered slopes to dry and open redcedar communities on exposed cliffs." Martin et al. (1979) found the mesic slope communities to have sugar maple (*Acer saccharum*), white ash (*Fraxinus americana*), northern red oak (*Quercus rubra*), basswood (*Tilia americana*) and bitternut hickory (*Carya cordiformis*) as the dominants, whereas on the dry, exposed slopes, the dominants were redcedar (*Juniperus virginiana*), chinquapin oak (*Q. muehlenbergii*), blue ash (*F. quadrangulata*), sugar maple, northern red oak, and white ash. The gorge communities are distinct and not representative of the open savanna-woodland that formerly occupied the rolling, fertile uplands away from the gorges (Braun 1950, Bryant et al. 1980, Campbell 1985).

Figure 1.--View of a redcedar community on a clifftop in the Kentucky River gorge area.

The redcedar communities associated with the Kentucky River gorge area have long been known (fig. 1). In fact, the earliest descriptions of the Bluegrass Region made mention of the groves of redcedar that crowned the Kentucky River cliffs (McAfee 1773, Filson 1784, Morse 1789, Imlay 1792, McMurtire 1819, Flint 1822); however, since that time only a few brief accounts of these communities have appeared

[1/] Paper presented at the Seventh Central Hardwood Forest Conference, Carbondale, IL. March 5-8, 1989.

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(Evans 1889, Harper 1912, Martin et al. 1979). These stands are generally small in size and are somewhat scattered in their distribution. For the most part they are dense and the open glade so prominent in other geographical areas is less well developed; e.g. Alabama (Mohr 1901, Harper 1920), the Nashville Basin of Tennessee (Gattinger 1901, Harper 1926, Picklesimer 1927, Freeman 1933, Quarterman 1950a,b), east Tennessee (Cain 1931), the Ozarks of Missouri and Arkansas (Palmer 1921, Turner 1935, Steyermark 1940, Erickson et al. 1942, Kucera and Martin 1957, Keeland 1978), southern Ohio (Braun 1928), northwestern Georgia (Van Horn 1980), southern Wisconsin (Curtis 1959, Bray 1960), and elsewhere in Kentucky (Baskin and Baskin 1975, 1978, 1985, Johnson 1981). Only Picklesimer (1927), Curtis (1959), Keeland (1978) and Fralish (1976) for Illinois, presented quantitative information on the redcedar component of these communities.

This paper summarizes the results of my studies of the redcedar communities on the soil borders of the exposed clifftops in the Kentucky River gorge area of central Kentucky. Emphasis is placed on the structure and composition of these stands as well as the apparent environmental complex operating on these clifftop habitats that may serve to select for redcedar and its associates while reducing competition from more site-demanding hardwoods.

The Study Area

The Bluegrass Region of Kentucky is a central lowland formed on limestone of Ordovician age. It is flat to rolling except near large streams because it is the uplifted peneplain still in the first stages of dissection (McFarlan 1943). Erosion has been slow and mainly by solution. The geologic history of the Kentucky River involves uplift, abandonment of former (Pliocene) channels, rejuvenation and downcutting which have created a rugged landscape with massive limestone cliffs forming the gorge. Tributaries are similarly deep, cliff-bound gashes in the upland. There is a 100-125 m difference in elevation from the tops of many of the cliffs to the current river level. The slopes are sheer drops or 50-70% slopes. Meander loops of the river account for the multitude of slope exposures.

Caves, sinks, and springs dot the uplands and runoff is through these. In places, remnants of the Irvine gravels (deposits from the abandoned channels) and clays are common.

The soils are developed in residuum or colluvium from the limestone. These soils are shallow, azonal with a high clay and rock content. Their water-holding capacity is low. The process of soil formation on the clifftops is similar to that for the glades of the Nashville Basin (Galloway 1919).

The climate of the Bluegrass Region is of the humid continental type, with sharp contrasts between the winter and summer. The average temperature for the region is 12.8 C (Palmquist and Hall 1961). Rainfall averages 109 cm annually for the Bluegrass. The annual runoff is 38 cm and the discharge by evapotranspiration is about 71 cm (Hendrickson and Kreiger 1964). Although precipitation is rather evenly distributed throughout the year, drought conditions occasionally prevail for several weeks during the summer (Palmquist and Hall 1961).

METHODS

Redcedar communities on the Kentucky River cliffs in Anderson, Fayette, Franklin, Jessamine, Madison, Mercer, and Woodford counties were located. Some grazing and logging had occurred in the past in a number of these stands. Only the least disturbed stands are presented for analysis here.

Trees were sampled in 0.04 ha circular plots spaced at 30 m intervals throughout the stands. Trees were those woody species with diameters at breast height (dbh) of $\geq$8.9 cm (3.5 inches).

Seedlings were sampled in 0.004 ha circular plots and saplings in 0.01 ha circular plots. Size classes follow Bryant (1978). Class 1 seedlings ranged from $\geq$15.2 cm to <1.37 m (6 inches - 4.5 feet) in height. All other seedlings and saplings were >1.37 m in height. Class 2 seedlings <1.27 cm (0.5 inch) diameter at ground level. Diameter ranges for Class 3 saplings were >1.27 <3.81 cm (0.5 <1.5 inches); Class 4, >3.81 <6.35 cm (1.5 <2.5 inches); and Class 5, >6.35<8.9 cm (2.5 <3.5 inches). Shrubs were sampled with with seedlings and saplings.

Trees were analyzed to relative frequency (RF), relative density (RD), and relative dominance (RDo) which were summed to give an importance value (IV) for each species. Density (trees/ha) and basal area (m^2/ha) were determined. The coefficients of similarity between stands were determined by the equation: $C = (2w)/(a+b)$, where a = the sum of importance values of all species in one stand, b = a similar sum for a second stand, and w = the sum of lesser values for only those species which are in common to the two stands.

Species diversity patterns were calculated using the Shannon-Wiener index:

$$H' = -\sum_{i=1}^{s} pi \log_2 pi,$$

where s is the number of species and pi is the proportion of each species in the forest (Shannon and Weaver 1949). The evergreen character of a stand was expressed as the sum of importance values of all evergreen species divided by the sum of importance values of all species (Monk 1965, 1966).

Stem counts were plotted against their size classes on semi-log paper and a regression line was fitted to the plotted data using the methods of Schmelz and Lindsey (1965). The coefficient of determination ($100r^2$), which defines how much the variation of the dependent variable (density) is accounted for by the variation of the independent

variable (diameter), was used as an index of the degree of past disturbance of the stand structure still detectable at the time of study, a high value indicating little disturbance (Schmelz and Lindsey 1965).

For a limited number of stands, soil cores were taken on a seasonal basis. These soils were sent to the University of Kentucky Soil Testing Laboratory for analysis of pH, organic matter(%), soil moisture (%), Ca, P, K, and Mg.

RESULTS

Eastern redcedar (IV 174.65) clearly dominates the soil borders on the exposed limestone cliffs in the Kentucky River gorge area (table 1). In those stands sampled, the frequency of redcedar was 100% and it accounted for ≈76% of the density and ≈79% of the basal area. Its major associates were white ash (F. americana, IV 42.07), redbud (Cercis canadensis, IV 17.02), slippery elm (Ulmus rubra, IV 14.79), honey locust (Gleditsia triacanthos, IV 10.71), and chinquapin oak (Q. muehlenbergii, IV 6.33). Overall tree density averaged 766 trees/ha and basal area ranged from 13.7-18.3 m^2/ha.

Because of the dominance of redcedar, species diversity (H') was low, ranging from 1.2-1.7, relative to hardwood stands in the gorge. The degree of evergreenness, 52%-65%, was also an indication of the dominance of redcedar. Although there was some variability among stands, the average similarity was 75%.

The coefficients of determination ($100r^2$) for the three least disturbed stands were 97, 96, and 94. Some trees were >120 years old, however, most of those that were cored for age analysis were ≈90 years.

There were 19 species of tree seedlings/saplings in the plots, but individuals of only 5 species, redcedar, chinquapin oak, slippery elm, redbud, and hackberry (Celtis occidentalis) reached tree-replacement size (table 2). This varied among stands with redcedar and redbud being the only species with numbers that seemed significant. Openings in the woodland, many created by windthrow, were frequent enough to allow the establishment of redcedar seedlings/saplings. Many of the other tree species represented here are pioneer or early successional species and usually fail to reach the tree stratum.

The species of the small tree and shrub stratum consisted of redbud, fragrant sumac (Rhus aromatica), Carolina buckthorn (Rhamnus caroliniana), lanceleaf buckthorn (R. lanceolata), blackhaw viburnum (Viburnum rufidulum), roughleaf dogwood (Cornus drummondi), coralberry (Symphoricarpos orbiculatus), and Carolina rose (Rosa carolina). The dwarf hackberry (Celtis tenuifolia), wafer ash (Ptelea trifoliata), ninebark (Physocarpus opulifolius), and prickly ash (Zanthoxylum americana) were occasional and generally few in numbers. These twelve species are here considered to be characteristic of the redcedar communities of the Kentucky River clifftops. As many as seven of these species were present together in some stands. Table 3 summarizes the size class distributions of the small tree and shrub stratum. The presence of two introduced species, Lonicera and Ligustrum, is a remnant of some past disturbance.

Table 1.--The average importance values (IV) for three of the largest and least disturbed stands of redcedar in the Kentucky River gorge area.

Species	IV
Juniperus virginiana	174.65
Fraxinus americana	42.07
Cercis canadensis	17.02
Ulmus rubra	14.79
Gleditsia triacanthos	10.71
Quercus muehlenbergii	6.33
Diospyros virginiana	5.16
Acer saccharum	5.11
Robinia pseudoacacia	4.55
Celtis occidentalis	3.91
Quercus rubra	2.25
Juglans nigra	2.14
Sassafras albidum	2.10
Prunus serotina	2.03
Morus rubra	1.74
Viburnum rufidulum	1.61
Aesculus glabra	1.27
Fraxinus quadrangulata	1.15
Quercus stellata	0.85
Carya glabra	0.55

Table 2.--Size class distribution of seedlings (Class 1 & 2) and saplings (Classes 3, 4, & 5) per hectare in the redcedar communities of the Kentucky River gorge area.

Size Classes	1	2	3	4	5
Juniperus virginiana	518.7	127.6	333.5	227.2	46.1
Cercis canadensis	325.2	185.3	77.4	11.5	9.9
Fraxinus americana	592.8	172.9	133.4	0	4.9
Quercus muehlenbergii	279.9	8.2	0	4.9	3.3
Ulmus rubra	119.3	0	21.4	0	4.9
Celtis occidentalis[3/]	148.2	0	41.2	19.8	4.9
Prunus serotina	16.5	0	0	3.3	0
Acer saccharum	24.7	16.5	4.9	3.3	0
Acer negundo	28.8	0	4.9	0	0
Diospyros virginiana	24.7	24.7	0	0	0
Gleditsia triacanthos	16.5	0	0	0	0
Morus rubra	32.9	0	16.5	0	0
Juglans nigra	41.2	0	0	0	0
Liriodendron tulipifera	16.5	0	0	0	0
Fraxinus quadrangulata	12.4	0	0	0	0
Sassafras albidum	74.1	0	0	0	0
Robinia pseudoacacia	12.4	0	0	0	0
Carya glabra	16.5	0	0	0	0
Quercus rubra	8.2	0	0	0	0
Totals	2309.5	535.2	633.2	274.9	74.0

[1/] May include Celtis tenuifolia.

Table 3.--Size class distribution of seedlings (Class 1 & 2) and saplings (Classes 3,4 & 5) of shrubs/hectare in the redcedar communities of the Kentucky River gorge area.

Size Classes	1	2	3	4	5
Rhus aromatica	2091.3	551.6	42.8	0	0
Rhamnus caroliniana	1671.4	185.3	126.8	8.2	0
Rhamnus lanceolata	284.1	0	0	0	0
Symphoricarpos orbiculatus	1564.3	0	0	0	0
Cornus drummondi	222.3	49.4	6.6	0	0
Viburnum rufidulum	160.6	82.3	13.2	6.6	0
Rubus sp.	370.5	0	0	0	0
Rosa carolina	45.3	0	0	0	0
Euonymus atropurpureus	12.4	0	0	0	0
Celastrus scandens	37.1	0	0	0	0
Lonicera tartarica	12.4	24.7	9.9	0	0
Ligustrum sp.	65.9	12.4	0	0	0
Totals	6537.6	905.7	199.3	14.8	0

Soil properties varied somewhat among stands and seasonally within stands. Table 4 summarizes these properties. In general, P was significantly lower and Ca significantly higher in certain redcedar stands than for adjacent hardwood communities (table 4). Soil depth ranged from 0 cm on exposed outcrops to 50 cm, and averaged about 20 cm.

Table 4.--A comparison of the seasonal range of plant nutrients (P,K,Ca, and Mg in ppm), pH, organic matter (%), and soil moisture (%) between a redcedar community and a deciduous hardwood community on a N-facing slope in the Kentucky River gorge area.

	Redcedar Community	N-facing Slope
P 4/	1-5 ppm	111.5-150 ppm
K	111-137 ppm	129.0-192 ppm
Ca 5/	4375-5875 ppm	3250-4575 ppm
Mg 6/	101.5-163.5 ppm	154-179.5 ppm
pH	7.4-7.8	6.4-7.5
Organic Matter	7.2-8.9%	7.1-7.9%
Soil Moisture	31-38%	35-53%

4/ (P<0.001) t-test
5/ (P<0.01) t-test
6/ ()<0.05) t-test

DISCUSSION

Although eastern redcedar (Juniperus virginiana) is a common tree in old field communities over much of eastern United States, in many parts of its range, especially limestone outcrop areas of the Interior Low Plateaus and the Limestone Valleys and Uplands Soils Province (Bennett 1921), it forms long persistant stable communities. These communities have been regarded as climax (Picklesimer 1927), subclimax (Freeman 1933, Quarterman 1950a,b, Steyermark 1940), and edaphic climax (Erickson et al. 1942). In addition, stable redcedar communities occur along the Mississippi River from Missouri to Minnesota (Curtis 1959) and in the Great Valley Province (Carr 1944, Braun 1950). However, in those areas where redcedar forms stable communities, most of the ecological work has centered on the open, rocky herb-dominated glade rather than the redcedar woodland. As a consequence, less is known about the structure, dynamics, and environmental relationships of the redcedar woodland communities.

Historically, redcedar has long been known as a major species on the Kentucky River cliffs of central Kentucky where it occurs on the soil borders of exposed clifftops and ledges. These are long persistant stands which suggest climax, probably edaphic climax. On similar sites in southern Illinois, Winterringer and Vestal (1956) considered the small tree-shrub communities on the soil borders of exposed sandstone cliffs to be climax. The high coefficients of determination (Schmelz and Lindsey 1965) and the replacement patterns shown by redcedar suggest that these are relatively stable communities.

Many writers have considered the characteristic habitat for redcedar to be shallow limestone soils on rough topography. The characteristic habitats for members of the shrub and small tree component, Rhus aromatica, Rhamnus caroliniana, R. lanceolata, Cercis canadensis, Viburnum rufidulum, Ptelea trifoliata, Cornus drummondi, Celtis tenuifolia, Zanthoxylum americana, Ceanothus americanus, and Physocarpus opulifolius, include "bluff escarpments, limestone glades, rocky open wooded slopes, borders of glades" (Steyermark 1964). In the Kentucky River area, V. rufidulum, P. trifoliata, and C. tenuifolia, occur as disjunct populations (Little 1977). The ranges of many of the other shrubs extend just into central Kentucky where they overlap in the gorge.

According to McDougal (1949) some plants "tolerate" rather than "prefer" certain habitats. This means that, under ordinary conditions, they are not able to compete with other plants in more favorable habitats, but are able to meet competition in unfavorable ones. Redcedar appears to be such a species. It shows best growth on the better soils, but on these is unable to compete with succeeding hardwoods (Fowells 1965). On the dry, infertile limestone outcrops it forms stable communities and the environmental complex that develops on these sites selects against potential competitors. In the redcedar-hardwood stands in the Central Basin of Tennessee, McKinney and Hemmerly (1984) considered white ash to be a successional species. On the Kentucky River clifftops, white ash showed slight increases in importance with increasing P, soil moisture, and organic matter. However, it is doubtful that white ash will displace redcedar in the clifftop communities.

The factor or factor complex that is responsible for the maintenance of redcedar communities has not been determined (Curtis 1959, Massey 1968). It seems probable that a number of factors, either singly or in combination, interact to produce an environmental complex that may select for redcedar

in this harsh environment. These factors include shallow, azonal clayey soil; limestone, often dolomitic, bedrock that funnels off water through subterranean passageways resulting in reduced soil moisture; pH >7; limited or excessive plant nutrients; limited organic matter; great exposure to wind and sunlight; and protection from fire.

> Beadle (1953) wrote that, "Soil properties can affect vegetation in two ways: firstly, by controlling structure. Floristic composition is controlled by selection of species suitable to the area. Plants that have become adapted to low nutrient levels are capable of surviving in the low nutrient media, while those with higher requirements are excluded. Selection may occur at the germination stage, or more frequently in the early stages of the seedling, or even at the near-maturity stage through competition. On the other hand, community structure is determined partly by the habit of the species that succeed in the area, partly by the relative levels of the various plant nutrients (including water) which determine the size attained by the individual plants, and partly by the manner in which the various species have become adapted to the limited factor of the environment. Consequently, in some areas of uniform climate and physiography distinct patterns of vegetation develop, which are determined by the concentration of the limiting nutrient."

Based on observations in the Kentucky River gorge area, it appears that a situation similar to Beadle's predictions may be occurring. However, there are a number of problems in determining the relationship of soil chemical properties and forest trees because of the lack of information on forest tree requirements, forest tree-forest soil interrelationships, and confusion of methodology in forest soil analysis (Gessel 1962). This is further compounded by the fact that the total of a nutrient in the soil may be determined with great accuracy, yet its availability is susceptible to little more than a rough approximation (Buckman and Brady 1969).

The soils of the Inner Bluegrass are known for their great fertility, largely attributable to their unusually high P content (McFarlan 1943). However, the P content in the soils of some of the redcedar stands was significantly lower than for adjacent hardwood sites. Low P levels are known to influence the distribution of evergreen or sclerophyllous vegetation (Billings 1950, Beadle 1954, 1966, Wright and Mooney 1965). Monk (1965, 1966) found evergreen species in Florida to be most abundant on soils low in Ca, K, P, and N, while Westman (1975) found P to be low in the pygmy forest of California. Goldberg (1983) equated nutrient-poor soils and evergreenness.

pH influences nutrient absorption and plant growth especially by its influence on nutrient availability. P, which is never readily soluble in soil, seems to be held with less tenacity in a pH centering around 6.5, thus plants are able to extract it with less difficulty (Buckman and Brady 1969). The soil pH on the clifftops was generally >7. In the adjacent hardwood slope communties, the pH was in the 6.5 range although this was variable.

Redcedar and many of its tree and shrub associates are calciophilous species. Calcium was significantly higher in the soils under the redcedars than in the surrounding hardwood stands. Buckman and Brady (1969) noted that excess calcium carbonate may have a detrimental influence on plants by reducing phosphate availability through the formation of complex and insoluble calcium phosphates. Fletcher and Ochrymochych (1955) however, found that an increase in exchangeable soil calcium leads to increased root development in redcedar seedlings resulting in greater nutrient uptake, especially P.

Other nutrients, organic matter, and their interactions may exert influence on the plant community, but the combination of low P, high Ca, and pH >7 may favor redcedar. It is this combination of factors that is found in the redcedar communities of Arkansas (Keeland 1978), Missouri (Fletcher and Ochrymochych 1955), Tennessee (Turner 1972), and Wisconsin (Curtis 1959). The differentiating effects of parent material are greatest on immature soils which may be chemically unbalanced or deficient (Lutz and Chandler 1946).

Limited soil moisture, the result of rapid underground drainage and high evaporation, has been cited most often as controlling cedar glades (Freeman 1933, Quarterman 1950a,b, Erickson et al. 1942, Bray 1960). Total soil moisture was lower in the redcedar communities than in adjacent hardwood communities. This may be attributed to drainage and evaporation, but also to the shallow, clayey soils. The clay dries hard and develops cracks during periods of drought, but during rainy periods the clay swells and the cracks close. The result is that the water stands on the soil surface where it is unavailable to plants. Erickson et al. (1942) considered standing water to cause winter rotting in the Missouri glades. This might serve to eliminate potential competitors. Also, the short periods of drought may be more disastrous on the clifftops than longer periods in less severe habitats. Quarterman (1950a) found a rapid water loss from saturation levels to near zero in two or three day periods in the cedar glades of the Nashville Basin.

The nature of the limestone bedrock may also influence the establishment and distribution of redcedar communities. The nutrients released through weathering have already been mentioned. The denseness of the bedrock poses problems for root penetration and in some areas limits this to cracks and crevices. Since the bedrock is dotted with sinks, it also serves to funnel off much of the water underground. The heating action of the limestone adds to the xeric conditions (Dansureau 1957).

In all of the stable redcedar communities, the soils are shallow and azonal which poses problems for the anchorage of large trees. The seedlings of many species possess deep penetrating taproots, however, because of the thin soil and dense bedrock, a lateral taproot may be essential if trees are to successfully occupy these outcrops. Redcedar has a penetrating taproot in the seedling stage and in later stages may develop a lateral taproot system. This was observed in a number of overturned trees and a similar condition was reported by Winterringer and Vestal (1956) on the xeric sandstone cliffs in Illinois.

The clay soils may also present a barrier to root growth. The soils of the Missouri glades were clayey and droughty (Kucera and Martin 1957). In addition to the residual clays, deposits of the high terrace clays are local along the Kentucky River uplands. These clays have been used in pottery production, thus the baking action of the sun on them may be critical.

The position of these redcedar communities atop the S-, W-, and SW-facing slopes may exaggerate the effects of temperature and evaporation. During the summer, day time air temperatures may be as much as 8 C higher in the redcedar communities than in less exposed hardwood sites. Exposure must be critical because hardwoods dominate the N-, E-, and NE-facing slopes. There redcedar is absent or of only minor importance.

Windthrow may also be related to exposure and shallow soils. The periodic opening of the stands by blow downs undoubtedly favors redcedar as does the high light intensity on the exposed clifftops. Harper (1912) did not feel that the denseness of certain redcedar stands should be viewed as one preventing reproduction and seedling development. More recent studies (Lassoie et al. 1983) have found redcedar to persist under an oak-hickory canopy which may suggest that it is not as intolerant as generally accepted.

The absence of fires is another factor that must be considered in the maintenance of stable redcedar communities. In fact, Harper (1912) suggested that "redcedar dreads fire more than it likes lime". Curtis (1959) considered some form of fire barrier, especially from the southwest, as an essential feature of those sites where redcedar is old-growth. Prior to and at the time of settlement of the Bluegrass Region, fire was of common occurrence (Roosevelt 1900). Perhaps the upper slopes and clifftops in the Kentucky River gorge served as refugia for redcedar and its associates. Nigh et al. (1985) referred to those sites in the River Hills of Missouri where redcedar and sugar maple were associates as fire refugia. Fralish (1988) supports the refugia view in southern Illinois. Conditions such as rocky, shallow soils and low fuel loads do not promote fires (Arend 1950). However, with the cessation of fires and the changes in land use that accompanied settlement, redcedar spread from its confines on the clifftops onto the rolling uplands where it has assumed a successional role. Hall (1952) reasoned that this was the way that redcedar spread and Beilmann and Brenner (1951) reported a similar situation for the Ozarks.

The success of redcedar on these limestone outcrops also involves those ecomorphological and ecophysiological adaptations that give it an advantage over hardwoods. At least three such interconnected adaptations are drought tolerance, evergreenness, and mineral conservation.

Whittaker (1975) stated that plant communities on limestone are often more xeric, or drought-adapted, than those on other substrates. This is paralleled by Wells (1976) who stated that, "The most likely places for the evolution of the more extreme xeromorphic characters under humid conditions would have been on sunny scarps with bedrock outcrops..". The drought-tolerance of redcedar is well-known (Ormsbee et al. 1976). One character associated with that tolerance is its double-membraned tonoplast (Parker 1971). The scale-like evergreen leaves of redcedar represent a xeromorphic adaptation (Harper 1912) and Monk (1966) regarded evergreen leaves as sclerophylls.

A number of metabolic adaptations of redcedar may be related to its evergreenness. In the old fields of Illinois, Ormsbee et al. (1976) found redcedar to show active photosynthesis under low soil moisture in the summer and the ability to photosynthesize during the winter even at 0 C. Because of these attributes, redcedar individuals prolong their effective growing season to essentially the entire year.

> In Florida, Monk (1965) pointed out that, "An evergreen species might have selective advantages over deciduous species in sterile soils. If a soil has a limited amount of nutrients, a community might be assembled, through natural selection, which would then to be more conservative. Although many evergreen species are tolerant to low nutrient levels, it is possible that this fact is secondary. Perhaps the cardinal point is the gradual return of nutrients to the soil through slow year-round-leaf-fall. This implies that an assemblage of evergreen species on sterile sites is a product of natural selection permitting a nearly closed cycle to exist."

Stable redcedar communities occur as small "evergreen islands" scattered throughout the eastern deciduous forest. More detailed experiments are needed to sort out those factors that determine the structure and composition of the vegetation of such "insular sites".

LITERATURE CITED

Arend, J.L. 1950. Influence of fire and soil on the distribution of eastern redcedar in the Ozarks. J. Forest. 48:129-130.

Baskin, J.C. and C.C. Baskin. 1975. The cedar glade

flora of Bullitt County, Kentucky. Castanea 40:184-190.
_____. 1978. Plant ecology of cedar glades in the Big Barrens region of Kentucky. Rhodora 80:545-557.
_____. 1985. A floristic study of a cedar glade in Blue Licks Battlefield State Park, Kentucky. Castanea 50:19-25.
Beadle, N.C.W. 1953. The edaphic factor in plant ecology with a special note on soil phosphates. Ecology 34:426-428.
_____. 1954. Soil phosphate and the delimitation of plant communities in eastern Australia. Ecology 35:370-375.
_____. 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecology 47:992-1007.
Beilmann, A.P. and L.G. Brenner. 1951. The recent intrusion of forests in the Ozarks. Ann. Mo. Bot. Gard. 38:261-282.
Bennett, H.H. 1921. The Soils and Agriculture of the Southern States. Macmillan Co. N.Y.
Billings, W.D. 1950. Vegetation and plant growth as affected by chemically altered rocks in the western Great Basin. Ecology 31:62-74.
Braun, E.L. 1928. Vegetation of the Mineral Springs Region of Adams County, Ohio. Ohio Bio. Surv. 15:383-517.
_____. 1950. Deciduous Forests of Eastern North America. Blakiston Co. Philadelphia, Pa.
Bray, J.R. 1960. The composition of savanna vegetation in Wisconsin. Ecology 41:721-732.
Bryant, W.S. 1978. Vegetation of the Boone County Cliffs Nature Preserve, a forest on a Kansan outwash deposit in northern Kentucky. Trans. Ky. Acad. Sci. 39:12-22.
_____., M.E. Wharton, W.H. Martin and J.E. Varner. 1980. The blue ash-oak savanna-woodland, a remnant of presettlement vegetation in the Inner Bluegrass of Kentucky. Castanea 45:149-165.
Buckman, H.O. and N.C. Brady. 1969. The Nature and Properties of Soils. Macmillan Co. N.Y.
Cain, S.A. 1931. Ecological studies of the vegetation of the Great Smoky Mountains of North Carolina and Tennessee. I.-Soil reaction and plant distribution. Bot. Gaz. 91:22-41.
Campbell, J.J.N. 1985. The Land of Cane and Clover. Rept. Univ. Ky. Herbarium. Lexington, Ky. 93p.
Carr, L.G. 1944. A new species of Houstonia from the cedar barrens of Lee County, Virginia. Rhodora 46:306-310.
Curtis, J.T. 1959. The Vegetation of Wisconsin. Univ. of Wisc. Press. Madison, Wisc.
Dansureau, P. 1957. Biogeography-an ecological perspective. Ronald Press. N.Y.
Erickson, R.O., L.G. Brenner and J.W. Wraight. 1942. Dolomitic glades of east-central Missouri. Ann. Mo. Bot. Gard. 29:89-101.
Evans, H.A. 1889. The relation of the flora to the geological formations in Lincoln County, Kentucky. Bot. Gaz. 14:310-314.
Filson, J. 1784. The Discovery, Settlement and Present Site of Kentucke. James Adams Printer. Wilmington, Del.
Fletcher, P.W. and J. Ochrymowych. 1955. Mineral nutrition and growth of eastern redcedar in Missouri. Mo. Agr. Exp. Sta. Bull. 577.
Flint, J. 1822. Letters from America. W. & C. Tait. Edinburgh.
Fowells, H.A. 1965. Silvics of Forest Trees of the United States. Agr. Handbook 271.
Fralish, J.S. 1976. Forest site-community relationships in the Shawnee Hills region, southern Illinois. pp. 67-87. In: J. Fralish, G. Weaver and R. Schlesinger (eds.). Proc. First Central Hardwood Conference. Carbondale, Ill.
_____. 1988. Predicting potential stand composition from site characteristics in the Shawnee Hills Forest of Illinois. Amer. Midl. Nat. 120:79-101.
Freeman, C.P. 1933. Ecology of cedar glade vegetation near Nashville, Tennessee. J. Tenn. Acad. Sci. 8:135-228.
Galloway, J.J. 1919. Geology and natural resources of Rutherford County, Tennessee. Tenn. Geol. Bull. 22.
Gattinger, A. 1901. Flora of Tennessee and Philosophy of Botany. Bur. Agr., Stat., and Mines. Nashville, Tenn.
Gessel, S.P. 1962. Progress and problems in mineral nutrition of forest trees. pp. 221-235. In: T. Kozlowski (ed.). Tree Growth. Ronald Press. N.Y.
Goldberg, D.E. 1983. The distribution of evergreen and deciduous trees relative to soil type: An example from the Sierra Madre, Mexico, and a general model. Ecology 63:942-951.
Hall, M.T. 1952. Variation and hybridization in Juniperus. Ann. Mo. Bot. Gard. 39:1-64.
Harper, R.M. 1912. The diverse habitats of the eastern redcedar and their interpretation. Torreya 12:145-154.
_____. 1920. The limestone prairies of Wilcox County, Alabama. Ecology 1:198-203.
_____. 1926. The cedar glades of middle Tennessee. Ecology 7:48-54.
Hendrickson, G.E. and R.A. Kreiger. 1964. Geochemistry of natural waters of the Blue Grass Region. Ky. Geol. Surv. Water-Supply Pap. 1700.
Imlay, G. 1792. A Topographical Description of the Western Territory of North America. J. Debrett. London.
Johnson, G. 1981. An undescribed cedar glade in Warren County, Kentucky. Trans. Ky. Acad. Sci. 42:101-105.
Keeland, B.D. 1978. Vegetation and soils in calcareous glades of northwest Arkansas. M.S. thesis. Univ. Arkansas. Fayetteville, Ark.
Kucera, C.L. and S.C. Martin. 1957. Vegetation and soil relationships in the glade region of the southwestern Missouri Ozarks. Ecology 38:285-291.
Lassoie, J.P., P.M. Dougherty, P.B. Reich, T.M. Hinckley, C.M. Metcalf and S.J. Dina. 1983. Ecophysiological investigations of understory eastern redcedar in central Missouri. Ecology 64:1355-1366.
Little, E.L., Jr. 1977. Minor Eastern Hardwoods. Vol. 4. USDA Forest Service Misc. Publ. 1342.
Lutz, H.J. and R.F. Chandler. 1946. Forest Soils. J.C. Wiley and Sons Co. N.Y.

Martin, W.H., W.S. Bryant, J.S. Lassetter and J.E. Varner. 1979. The Kentucky River Palisades--Flora and Vegetation. The Nature Conservancy.

Massey, A.B. 1968. Notes relative to plant ecology in Virginia. Castanea 33:161-162.

McAfee, J.J. 1773. The Journal of James J. McAfee. pp. 8-9. In: A.B. Burr. 1931. Panther Rock. Cincinnati, O.

McFarlan, A.A. 1943. Geology of Kentucky. Univ. Ky. Press. Lexington, Ky.

McKinney, L.F. and T.E. Hemmerly. 1984. Preliminary study of deciduous forests within the Inner Central basin of Tennessee. J. Tenn. Acad. Sci. 59:40-42.

McMurtrie, H. 1819. Sketches of Louisville and its Environs. S. Penn, Jr. Co. Louisville, Ky.

Mohr, C.O. 1901. Plant Life of Alabama. Contr. U.S. Nat. Herb. 6.

Monk, C.D. 1965. Southern mixed hardwood forest in north-central Florida. Ecol. Monogr. 35:335-354.

_____. 1966. The ecological significance of evergreenness. Ecology 34:504-505.

Morse, J. 1789. The American Universal Geography. Wm. Williams. Uttica, N.Y.

Nigh, T.A., S.G. Pallardy and H.E. Garrett. 1985. Sugar maple-environment relationship in the River Hills and Central Ozark Mountains of Missouri. Amer. Midl. Nat. 114:235-251.

Ormsbee, P., F.A. Bazzaz and W.R. Boggess. 1976. Physiological ecology of Juniperus virginiana in oldfields. Oecologia 23:75-82.

Palmer, E.J. 1921. The forest flora of the Ozark region. J. Arn. Arb. 2:216-232.

Palmquist, W.N., Jr. and F.R. Hall. 1961. Reconnaissance of ground-water resources in the Blue Grass Region Kentucky. Geol. Surv. Water-Supply Pap. 1533.

Parker, G. 1971. Unusual tonoplast in conifer leaves. Nature 234:231.

Picklesimer, B.C. 1927. A quantitative study of the plant successions of the cedar glades of middle Tennessee. M.S. thesis. George Peabody Teachers College. Nashville, Tenn.

Quarterman, E. 1950a. Major plant communities of Tennessee cedar glades. Ecology 31:234-254.

_____. 1950b. Ecology of cedar glades. I. Distribution of glade flora in Tennessee. Bull. Torrey Bot. Club 77:1-9.

Roosevelt, T. 1900. The Winning of the West. Part II. G.P. Putnam's Sons Co. N.Y.

Schmelz, D.V. and A.A. Lindsey. 1965. Size-class structure of old-growth forests in Indiana. Forest Sci. 11:258-264.

Steyermark, J.A. 1940. Studies of the vegetation of Missouri. I. Natural plant associations and succession in the Ozarks of Missouri. Field Mus. Nat. Hist. Bot. Ser. o:345-475.

_____. 1964. Flora of Missouri. Iowa State Univ. Press. Ames, Iowa.

Turner, B.H. 1972. Allelopathic effects of Petalostemon gattingeri on the distribution of Arenaria patula in cedar glades. Ph.D. Diss. Vanderbilt Univ. Nashville, Tenn.

Turner, L.M. 1935. Notes on forest types of northwestern Arkansas. Amer. Midl. Nat. 16:417-421.

Van Horn, G.S. 1980. Additions to the cedar glade flora of northwest Georgia. Castanea 45:134-137.

Wells, P.V. 1976. A climax index for broadleaf forest: An n-dimensional ecomorphological model of succession. pp. 131-176. In: J.S. Fralish, G.T. Weaver and R.C. Schlesinger (eds.). Proc. First Central Hardwood Conference. Carbondale, Ill.

Westman, W.E. 1975. Edaphic climax patterns of the pygmy forest region of California. Ecol. Monogr. 45:109-135.

Whittaker, R.H. 1975. Communities and Ecosystems. Macmillan Co. N.Y.

Winterringer, G.S. and A.G. Vestal. 1956. Rock-ledge vegetation in southern Illinois. Ecol. Monogr. 26:105-130.

Wright, R.D. and H.A. Mooney. 1965. Substrate-oriented distribution of bristlecone pine in the White Mountains of California. Amer. Midl. Nat. 73:257-284.