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PHOTOSYNTHETIC DIVERSITY OF CEDAR GLADE PLANTS.

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ABSTRACT

The cedar glade flora spans the entire known range of photosynthetic pathway options, including C_3, C_4, and both obligate and facultative CAM species. This ecophysiological diversity is cataloged, and the contribution of CAM plants to the cedar glade plant community structure is emphasized.

INTRODUCTION

Plants have evolved a variety of photosynthetic mechanisms that differ in photosynthetic organ anatomy and biochemistry. Three main pathways of CO_2 fixation are now recognized: C_3, C_4, and CAM photosynthesis (Osmond et al., 1982). In addition to the anatomical and biochemical differences that these pathways exhibit, they also are known to differ in terms of ecophysiological adaptations and optima (Black, 1971; Kluge and Ting, 1978; Pearcy and Ehleringer, 1984). These ecophysiological differences have been shown to be useful in understanding species biogeography and patterns of species importance at the community level in a variety of ecosystems.

Photosynthetic pathway distributions and environmental correlations have been examined at several ecological scales. Teeri and colleagues have analyzed the biogeography of a number of C_4 and CAM groups in North America and have correlated the importance of the groups with environmental variables via stepwise multiple linear regression. They have examined C_4 grasses (Teeri and Stowe, 1976), C_4 dicots (Stowe and Teeri, 1978), the succulent CAM-dominated families Cactaceae and Crassulaceae (Teeri et al., 1978), and C_4 members of the Cyperaceae (Teeri et al., 1980). While each of these groups differs to some degree in response to environmental variables, they all appear to have their greatest adaptive advantage under hot, arid, high light conditions.

Studies conducted at the community level support these generalizations. Mooney et al. (1974), Syvertsen et al. (1976), and Eickmeier (1978) examined photosynthetic pathway distributions along desert aridity gradients and found that CAM, and to a lesser degree C_4, importance increased with increasing site aridity. Other studies in grassland ecosystems have clearly shown that C_3 species are replaced by C_4 species along environmental gradients towards the drier and/or lower elevation end of the gradients (Boutton et al., 1980; Hattersley, 1983; Tieszen et al., 1979).

Cedar glade ecosystems common to central Tennessee have complex spatial and temporal gradients of environmental variation. This is particularly true in terms of soil water potential which strongly influences photosynthetic pathway occurrence in other systems as described above. Glade environments become drier as soil depth decreases and during the summer months (Quarterman, 1950a, 1950b; Baskin and Quarterman, 1970). The purpose of this paper is to characterize the distribution of photosynthetis pathways of the vascular herbaceous flora of the cedar glades and in particular to examine the importance of CAM components.

MATERIALS AND METHODS

The photosynthetic pathway was determined for all the vascular herbaceous cedar glade species listed in Baskin et al. (1968) and supplemented by Baskin and Baskin (1975). A plant was assumed to be a C_4 species if it either has been reported to have Kranz anatomy (Welkie and Caldwell, 1970) or a stable carbon isotope ratio, expressed as delta ^{13}C value, of between -10 to -20°/oo (Smith and Epstein, 1971). A species that occurs in a genus (or subgenus for *Panicum)* known to contain only C_4 species was assumed to be C_4 if no direct pathway determiniation has been reported. A nonsucculent species which either lacked Kranz anatomy or which had a reported carbon isotope ratio delta ^{13}C value of between -22 to -33°/oo (Bender, 1971) was assumed to be C_3. A species that occurs in a genus or family known to contain only C_3 species was assumed to be C_3 if no direct pathway determination has been reported. In addition to the two sources given above, Baskin and Baskin (1981), Bender (1971), Bender and Smith (1973), Brown and Smith (1972), Downton (1975), and Smith and Brown (1973) contained information for species, genera, and families of plants that occur in the cedar glades that enabled a C_3 or C4 classification. Particular care was taken classifying species from genera or families where both C_3 and C_4 species have been found. Unless information was found for these species allowing an unambiguous pathway determination, they were listed as unknown.

CAM species were established based on several criteria which included net nocturnal CO_2 uptake, substantial cell titratable acidity fluctuation from morning to evening, C_4-like carbon isotope ratio, and low ribulose bisphosphate carboxylase to phosphoenol pyuruvate carboxylase ratio (for explanation of criteria see Kluge and Ting, 1978).

Table 1.
Photosynthetic pathway distributions of the vascular herbaceous flora of the cedar glades. Floristic data are from Baskin et al. (1968) and Baskin and Baskin (1975). Pathway determinations are based on criteria and references given in the text.

Pathway	# Species	% of Flora
C_3		
Gramineae	21	
Non-Gramineae	283	
Total	304	88.8
C_4		
Gramineae	22	
Non-Gramineae	5	
Total	27	7.9
CAM		
Obligate	2	
Facultative	2	
Total	4	1.1
Unknown	7	2.0

CAM plants were identified using these criteria taken from Bender et al. (1973), Koch and Kennedy (1980), Martin and Zee (1983), Martin et al. (1982), Smith and Eickmeier (1983), and Szarek and Ting (1977). CAM plants were further identified as either obligate or facultative CAM species. In facultative CAM, CAM-like characteristics can be induced most often upon water stress in plants that behave as normal C_3 plants when well supplied with water (Kluge and Ting, 1978).

RESULTS

A total of 342 vascular herbaceous species were considered in the general photosynthetic pathway survey (Table 1). Pathway determinations were made at the family level for 246 species (all C_3), at the genus or subgenus level for 43 species (36 C_3, 7 C_4), and at the species level for 46 species (22 C_3, 20 C_4, and 4 CAM). Seven species were designated as unknown. Most cedar glade species utilize C_3 photosynthesis (88.8%). The C_4 pathway occurs in 7.9% of the species, most of them in the family Gramineae. The members of this family are about equally divided between the C_3 and C_4 pathways (49% and 51% respectively). Despite this numerical similarity, the ecologically dominant grass genera (i.e. *Andropogon, Aristida,* and *Sporobolus*) were all C_4. Four species have characteristics that are indicative of either obligate or facultative CAM, representing 1.1% of the glade flora.

Seven species could not be placed in the preceding categories. These include *Cyperus ovularis* (Michx.) Torr. and *Euphorbia obtusata* Pursh for which no specific information was found and which occur in genera that have been shown to contain more than one photosynthetic pathway. The species *Scleria pauciflora* Muhl., *Scirpus atrovirens* Willd., and *Scirpus lineatus* Michx., all in the Cyperaceae, occur in two genera where only a single species has been identified and classified as a C_4 species. With only one determination, no generalizations can be made at the generic level for these species and they are listed as unknown. In addition, *Mollugo verticillata* L. has been reported to have characteristics intermediate between C_3 and C_4 pathways (Kennedy and Laetsch, 1974; Sayre and Kennedy, 1977) and *Yucca filamentosa* L. has been reported as both a CAM (Szarek and Ting, 1977) and a C_3 (Bender, 1971; Martin et al., 1982) species so that its status cannot be determined accurately from the literature. All of

Table 2.
Summary of diagnostic photosynthetic characteristics of cedar glade CAM species.

Species	CO_2 Exchange[a] Night	Day	Acidity Fluctuation	Isotope Ratio $\delta\,^{13}C$ (^{o}/oo)	Carboxylase Ratio (RuBP/PEP Case)	Ref[b]
Agave virginica	0.1	0.2	4900	-16	ND	3
	[mg CO_2.gDW^{-1}.h^{-1}]		[μeq.gDW^{-1}]			
Opuntia compressa	ND		ND	-14	ND	1
	12.0	4.0	208	ND	ND	2
	[mg CO_2.dm^{-2}.h^{-1}]		[μeq.gFW^{-1}]			
	0.3	0.1	930	-12	ND	3
	[mg CO_2.gDW^{-1}.h^{-1}]		[μeq.gDW^{-1}			
	ND		140	ND	2.0	5
			[μeq.gFW^{-1}]			
Talinum teretifolium	0.0	0.0	400	-26	ND	3
	[mg CO_2.gDW^{-1}.h^{-1}]		[μeq.gDW^{-1}]			
calycinum	-1.0 to 0.7	5.7 to 0.0[c]	400	-28	ND	4
	[mg CO_2.gDW^{-1}.h^{-1}]		[μeq.gDW^{-1}]			
Sedum pulchellum	ND		ND	-30	ND	1
	-0.8 to 0.5	10.0 to 4.0[c]	46	ND	35.6 to 15.5[c]	5
	[mg CO_2.gDW^{-1}.h^{-1}]		[μeq.gFW^{-1}]			

[a]/Positive values represent net CO_2 uptake and negative values represent net CO_2 efflux
[b]/1 = Bender et al. (1973); 2 = Koch and Kennedy (1980); 3 = Martin et al. (1982)
4 = Martin and Zee (1983); 5 = Smith and Eickmeier (1983)
[c]/First value for low water stress and second value for high water stress

these unknown species, except for *E. obtusata*, have been reported as either rare or infrequent by Baskin et al. (1968) or Baskin and Baskin (1975) and so are probably of minor ecological importance.

The four CAM species, while a small percentage of the glade flora, are ecologically dominant in shallow soil glade habitats adjacent to open limestone (Quarterman, 1950b). Two of the four species are obligate in their CAM physiology (Table 2). Both *Agave virginica* L. and *Opuntia compressa* (Salisb.) Macbr. have substantial nocturnal net CO_2 uptake, large titratable acidity fluctuations, and C_4-like carbon isotope ratios (Bender et al., 1973; Koch and Kennedy, 1980; Martin et al., 1982; Smith and Eickmeier, 1983) and C_3-like characteristics never have been reported to develop. In addition, Smith and Eickmeier (1983) reported that the RuBP carboxylase to PEP carboxylase ratio of *0. compressa* was low throughout the growing season in support of the obligate CAM nature of this species.

The remaining two species, the annual *Sedum pulchellum* Michx., and the perennial *Talinum calcaricum* Ware, appear to have a variable physiology indicative of facultative CAM (Table 2). While the glade species *T. calcaricum* itself has not yet been investigated, its close relatives *T. teretifolium* of the granite outcrops (Martin et al., 1982) and *T. calycinum* from Kansan sandstone outcrops (Martin and Zee, 1983) have characteristics that indicate a flexible CAM capability when under water stress. Undoubtedly, *T. calcaricum* will follow this pattern. *Sedum pulchellum* has clearly been shown to operate as a normal C_3 species until exposed to substantial water stress in situ on the cedar glades (Smith and Eickmeier, 1983).

DISCUSSION

A knowledge of the pattern of photosynthetic pathway distributions over time and space is important to a full understanding of the ecology of the cedar glades. This information contributes to our appreciation of both individual species autecology and community-level interactions. The results of this initial cedar glade flora analysis are similar in many respects to those obtained from the analysis of desert communities. In these cases, including Sonoran, Chihuahuan, and Chilean deserts, C_3 species are numerically dominant. This supports the contention of Baskin and Baskin (1981, 1985) that C_4 or CAM photosynthesis is not prerequisite for adaptation to the hot, dry, high-light environment of the glades.

Mooney et al. (1974 found that even in the driest parts of both Baja California and the Chilean coastal deserts greater than 70% of the species were C_3 while 25% or less were CAM. The C_4 pathway was virtually unrepresented in both of these areas. Similar results were reported by Syvertsen et al. (1976) for the bajada community of the Chihuahuan desert (66% C_3, 24% C_4, and 10% CAM species) and by Eickmeier (1978) for an elevational gradient in Big Bend National Park, TX (72% C_3, 3% C_4, and 25% CAM species). Thus, the photosynthetic diversity in plants of the cedar glades matches that seen in more arid ecosystems.

Another similarity between the present analysis and that of Syvertsen et al. (1976) concerns the ecological significance of the CAM portion of the community. They found that while representing only about 10% of the species, plants with the CAM pathway made up 48% of the total community biomass. The biomass contribution of CAM species to shallow soil, glade environments is similarly greater than its species number contribution would suggest.

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