PHOTOSYNTHETIC DIVERSITY OF CEDAR GLADE PLANTS.

WILLIAM G. EICKMEIER
Vanderbilt University
Nashville, TN 37235

Proofs and offprint requests to: Dr. William G. Eickmeier, Department of General Biology, Vanderbilt University, Nashville, TN 37235

ABSTRACT

The cedar glade flora spans the entire known range of photosynthetic pathway options, including C3, C4, 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 CO2 fixation are now recognized: C3, C4, 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 C4 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 C4 grasses (Teeri and Stowe, 1976), C4 dicots (Stowe and Teeri, 1978), the succulent CAM-dominated families Cactaceae and Crassulaceae (Teeri et al., 1978), and C3 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 C4, importance increased with increasing site aridity. Other studies in grassland ecosystems have clearly shown that C3 species are replaced by C4 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 photosynthetic 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 C3 species if it either has been reported to have Kranz anatomy (Welkie and Caldwell, 1970) or a stable carbon isotope ratio, expressed as delta 13C value, of between -10 to -20‰ (Smith and Epstein, 1971). A species that occurs in a genus (or subgenus for Panicum) known to contain only C3 species was assumed to be C3 if no direct pathway determination has been reported. A nonsucculent species which either lacked Kranz anatomy or which had a reported carbon isotope ratio delta 13C value of between -22 to -33‰ (Bender, 1971) was assumed to be C3. A species that occurs in a genus or family known to contain only C4 species was assumed to be C4 if no direct pathway determination has been reported. In addition to the two sources given above, Baskin and Baskin (1981), Bender (1971), Baskin 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 C3 or C4 classification. Particular care was taken...
classifying species from genera or families where both C3 and C4 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 CO2 uptake, substantial cell titratable acidity fluctuation from morning to evening, C4-like carbon isotope ratio, and low ribulose bisphosphate carboxylase to phosphoenol pyruvate 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.

<table>
<thead>
<tr>
<th>Pathway</th>
<th># Species</th>
<th>% of Flora</th>
</tr>
</thead>
<tbody>
<tr>
<td>C3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gramineae</td>
<td>21</td>
<td></td>
</tr>
<tr>
<td>Non-Gramineae</td>
<td>283</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>304</td>
<td>88.8</td>
</tr>
<tr>
<td>C4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gramineae</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td>Non-Gramineae</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>27</td>
<td>7.9</td>
</tr>
<tr>
<td>CAM</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Obligate</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Facultative</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>4</td>
<td>1.1</td>
</tr>
<tr>
<td>Unknown</td>
<td>7</td>
<td>2.0</td>
</tr>
</tbody>
</table>

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 C3 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 C3), at the genus or subgenus level for 43 species (36 C3, 7 C4), and at the species level for 46 species (22 C3, 20 C4, and 4 CAM). Seven species were designated as unknown. Most cedar glade species utilize C3 photosynthesis (88.8%). The C4 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 C3 and C4 pathways (49% and 51% respectively). Despite this numerical similarity, the ecologically dominant grass genera (i.e., Andropogon, Aristida, and Sporobolus) were all C3. 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 Scirpia praecox a Muhl., Scirpus atrovirens Wild., and Scirpus linearis Michx., all in the Cyperaceae, occur in two genera where only one single species has been identified and classified as a C4 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 C3 and C4 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 C4 (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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Night</th>
<th>CO2 Exchangea/</th>
<th>Day</th>
<th>Acidity Fluctuation</th>
<th>Isotope Ratio d13C (‰/oo)</th>
<th>Carboxylase Ratio (RubP/PEP Case)</th>
<th>Refb/c</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agave virginica</td>
<td>0.1</td>
<td>[mg CO2 gDW⁻¹ h⁻¹]</td>
<td>0.2</td>
<td>[µeq gDW⁻¹]</td>
<td>-16</td>
<td>ND</td>
<td>3</td>
</tr>
<tr>
<td>Opuntia compressa</td>
<td>12.0</td>
<td>[mg CO2 dm⁻² h⁻¹]</td>
<td>4.0</td>
<td>ND</td>
<td>-14</td>
<td>ND</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>0.3</td>
<td>[mg CO2 gDW⁻¹ h⁻¹]</td>
<td>0.1</td>
<td>[µeq gFW⁻¹]</td>
<td>-12</td>
<td>ND</td>
<td>3</td>
</tr>
<tr>
<td>Talinum terefolium</td>
<td>0.0</td>
<td>[mg CO2 gDW⁻¹ h⁻¹]</td>
<td>0.0</td>
<td>[µeq gDW⁻¹]</td>
<td>-26</td>
<td>ND</td>
<td>3</td>
</tr>
<tr>
<td>calycinum</td>
<td>-1.0 to 0.7</td>
<td>[mg CO2 gDW⁻¹ h⁻¹]</td>
<td>5.7 to 0.0c</td>
<td>[µeq gDW⁻¹]</td>
<td>-28</td>
<td>ND</td>
<td>4</td>
</tr>
<tr>
<td>Sedum pulchellum</td>
<td>-0.8 to 0.5</td>
<td>[mg CO2 gDW⁻¹ h⁻¹]</td>
<td>10.0 to 4.0c</td>
<td>[µeq gFW⁻¹]</td>
<td>ND</td>
<td>35.6 to 15.5c</td>
<td>5</td>
</tr>
</tbody>
</table>

a Positive values represent net CO2 uptake and negative values represent net CO2 efflux
b 1 = Bender et al. (1973); 2 = Koch and Kennedy (1980); 3 = Martin et al. (1982)
c 4 = Martin and Zee (1983); 5 = Smith and Eickmeier (1983)

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 CO₂ uptake, large titratable acidity fluctuations, and C₃-like carbon isotope ratios (Bender et al., 1973; Koch and Kennedy, 1980; Martin et al., 1982; Smith and Eickmeier, 1983) and C₃-like characteristics never have been reported to develop. In addition, Smith and Eickmeier (1983) reported that the RuBP carboxylase to PEP carboxylase ratio of *O. 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 Kansa 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 C₃ species until exposed to substantial water stress in situ on the cedar glades (Smith and Eickmeier, 1983).

**ACKNOWLEDGEMENTS**

This material was first presented at an Association of Southeastern Biologists symposium entitled “Biota, Ecology and Ecological History of Cedar Glades,” on April 12, 1985 at Middle Tennessee State University, Murfreesboro, TN. I would like to thank Drs. Jerry Baskin and Elsie Quarterman for their many helpful comments concerning this study.

**LITERATURE CITED**


