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CARBON REDUCTION PATHWAYS AND STANDING CROP IN THREE CHIHUAHUAN DESERT PLANT COMMUNITIES

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ABSTRACT. The complete floras of three Chihuahuan desert plant communities were surveyed to determine the relative numbers of species that possess either the C₃, C₄ or CAM carbon reduction pathway. There were more C₃ species in all three communities. Spring-flowering species were predominantly C₃ and CAM; C₄ species most commonly flowered in the summer. Plant standing crop data were used as an indication of the contribution of each pathway to the primary production of the communities. In the most geographically widespread of the three communities, an alluvial plain, CAM plants contributed 48% of the total biomass while only representing 10% of the possible species present. Less than 1% of the biomass was contributed by C₄ species although they comprised 24% of the possible species present. The C₄ pathway did make a substantial standing crop contribution in a very localized community, an ephemeral desert lake bottom, where one C₄ grass species accounted for 90% of the biomass present.

Early investigations by Bennett-Clark (1933) and more recent work by Kortschak et al. (1965) and Hatch et al. (1967) have shown that many plant species possess biochemical pathways whereby CO₂ can be supplied to the pentose or Calvin-cycle (C₃) pathway for carbon reduction much more efficiently than species which have only the C₃ pathway. Plants which possess Crassulacean acid metabolism (CAM) pathway are able to fix CO₂ initially into organic acids in the mesophyll chlorenchyma during the dark and then subsequently utilize the CO₂ for the formation of carbohydrate via the C₃ pathway during the light period. Plants which possess the C₄-dicarboxylic acid (C₄) pathway fix CO₂ into organic acids in the mesophyll chlorenchyma in the light. This carbon is then reduced to carbohydrates by the C₃ pathway in the bundle sheath chlorenchyma.

Since these supplemental pathways (CAM, C₄) have been elucidated there has been much study and speculation concerning the adaptive significance and competitive advantage these pathways may add to the C₃ pathway (Black et al. 1969; Bjorkman and Berry 1973).

Plants with only the C_3 pathway are the most common and they exhibit rates of CO_2 reduction intermediate to those of plants with the C_4 and CAM pathways (Mooney 1972). C_4 species have higher temperature optima for photosynthesis and better water use efficiency. They are most common in tropical grass taxa but are also found in a variety of dicotyledonous plant groups, especially those that are thought to have evolved in hot tropical areas of intermittent aridity (Downton and Tregunna 1968). Black et al., (1969) have pointed out that plants possessing the C_4 pathway have a competitive advantage because of their high rates of carbon gain and tend to be more successful “weeds” in hot, dry, high radiation environments. CAM plants have succulent tissues, exhibit diurnal fluctuations in organic acid content and are most common in hot, open arid areas with relatively low night temperatures (Ting et al. 1972). CAM are plants thought to be at a competitive disadvantage because of their lower rates of carbon reduction (Mooney 1972). Although authors have hypothesized that species exhibiting the C_4 pathway should be relatively more important in arid and tropical grassland communities (Caswell et al. 1973), information has not been reported which allows a critical test of this hypothesis. Importance can have several meanings. It may refer to the relative number of species present or their contribution to the primary productivity and standing crop or biomass of a plant community. To establish the relative importance of C_4 species will require extensive evaluations of many plant communities in various climates. The information reported here is intended as a step toward that goal.

Welkie and Caldwell (1970) presented an extensive C_3 - C_4 survey of selected taxa and pointed out the excellent correlation between the presence of chloroplast containing cells arranged radially around vascular tissue (Kranz anatomy) and the C_4 photosynthetic pathway that had been noted by previous workers (Hatch and Slack 1970). Leaf anatomy is a simple yet highly predictive method of ascertaining a plant's capability of fixing CO_2 via the C_4 pathway (Laetsch 1968, 1974). In all C_3 - C_4 surveys, whether by gas exchange, enzymatic techniques or the presence of Kranz anatomy, none has looked at the entire flora of a community to determine the relative number of C_3 , C_4 and CAM species present and their total biomass. Both the number of species of each type and their relative contribution to the total primary productivity and standing crop need to be elucidated to allow comparisons of the relative importance of the three CO_2 reduction pathways in different communities.

MATERIALS AND METHODS. In this study we utilized leaf anatomy to ascertain the total number of C₄ species. The presence of succulent tissues and diurnal organic acid accumulation data were used to identify CAM species. All other species were considered C₃ plants. Standing crop estimates were used as an indication of the relative importance of a species in the three desert communities studied.

The study area is on the northern edge of the Chihuahuan Desert and includes an alluvial fan (bajada) which drains into an ephemeral desert lake (playa). The three communities studied, the bajada, playa bottom and playa fringe, comprise the US/IBP Desert Biome Jornada Site located in northeastern Doña Ana County, New Mexico. The dominant shrubs of the bajada community are *Larrea tridentata* (DC) Cov., *Prosopis glandulosa* Torr. var. *torreyana* (L. Benson) M. C. Johnston and *Flourensia cernua* DC. The playa bottom is vegetated almost exclusively by *Panicum obtusum* HBK, whereas the playa fringe area is dominated by *Hilaria mutica* (Buckl.) Benth. and *Prosopis*. A complete plant species list for the area has been compiled by Spellenberg (unpubl.). Plant biomass data for 1970-1972 was estimated by Ludwig and Nickell (1973).

Initial observations of the leaf anatomy were made by freehand or freeze-microtome sectioning of fresh leaves and examining them immediately with a microscope. It was later found that the Kranz anatomy could be observed with equal reliability on whole leaves under a dissection microscope by the contrast of the veins with the mesophyll. C₄ plants appear to have relatively darker veins whereas C₃ plants have veins which are conspicuously lighter than the mesophyll. Both fresh and hydrated leaves from herbarium sheets were subsequently examined in this manner. Several leaves were observed both microscopically in cross section and as whole mounts under a dissection microscope; observations made by the former method confirmed those made by the latter. Plants were categorized as CAM species chiefly by the subjective evaluation of the presence of succulent tissues. Diurnal fluctuation in titratable acidity were measured (Sideris et al. 1948) in plants which were not cacti but suspected of being CAM species because of their inclusion in taxa in which the CAM pathway predominates (Ting et al. 1972).

RESULTS. The entire plant species lists for each of the three communities are presented. Each angiosperm species is followed by a (+) for the presence of the Kranz leaf anatomy — C₄, a (–) for the absence of the Kranz leaf anatomy — C₃, or a (C) for the CAM pathway. An asterisk follows those species that were encountered during the biomass sampling. *Cuscuta* has been included for completeness even though it is considered nonphotosynthetic. The list is arranged alphabetically within each community. Subspecific names have been omitted; nomenclature follows that of Correll and Johnston (1970) or Kearney and Peebles (1960) for species not included in the former.

PLAYA BOTTOM

Amaranthus blitoides (+), *A. palmeri* (+), *A. pubescens* (+), *Calliandra humilis* (–), *Chenopodium incanum* (–), *Cirsium ochrocentrum* (–), *Corydalis aurea* (–), *Cuscuta umbellata*, *Cy-*

*perus esculentus** (+), *Eragrostis arida* (+), *E. cilianensis* (+), *Euphorbia serpyllifolia* (+), *Gaura parviflora* (-), *Helianthus ciliaris* (-), *Hoffmanseggia glauca** (-), *Hymenoxys odorata* (-), *Kallstroemia parviflora* (+), *Panicum obtusum** (+), *Portulaca oleracea* (+), *Sida leprosa** (-), *Sphaerophysa salsula* (-), *Xanthium strumarium* (-).

PLAYA FRINGE

*Allionia incarnata** (+), *Ammocodon chenopodioides** (-), *Amaranthus blitoides** (+), *A. fimbriatus* (+), *A. palmeri** (+), *A. pubescens** (+), *Aristida adscensionis** (+), *Asclepias brachystephana* (-), *Astragalus tephrodes** (-), *Atriplex canescens* (+), *Bahia absinthifolia** (-), *Berlandiera lyrata* (-), *Boerhavia spicata** (+), *Bouteloua aristiodoides* (+), *B. barbata** (+), *B. eriopoda* (+), *Calliandra humilis** (-), *Cassia bauhinoides** (-), *Chenopodium incanum** (-), *Chloris virgata** (+), *Chilopsis linearis** (-), *Croton pottsii** (-), *Cucurbita foetidissima* (-), *Cuscuta umbellata*, *Datura meteloides* (-), *Distichlis stricta* (+), *Ephedra trifurca** (-), *E. torreyana* (-), *Eragrostis arida** (+), *E. curtipedicellata* (+), *Eriogonum abertianum** (-), *E. rotundifolium** (-), *E. trichopes** (-), *Erioneuron pulchellum** (+), *Euphorbia albomarginata** (+), *E. glyptosperma** (+), *E. micromera** (+), *E. serpyllifolia** (+), *E. serrula** (+), *E. setiloba* (+), *Flourensia cernua* (-), *Hilaria mutica** (+), *Hoffmanseggia glauca* (-), *Hymenoxys odorata** (-), *Iva ambrosiaefolia** (=), *Kallstroemia parviflora** (+), *Krameria lanceolata* (-), *Leucelene ericoides** (-), *Machaeranthera tanacetifolia* (-), *Muhlenbergia arenacea* (+), *Oenothera albicaulis* (-), *Panicum hirticaule* (+), *Pectis papposa** (+), *Perezia nana** (-), *Plantago patagonica* (-), *Portulaca mundula* (+), *P. oleracea** (+), *Proboscidea parviflora* (-), *Prosopis glandulosa** (-), *Salsola paulsenii** (+), (and intergrades towards *S. iberica*; = *S. kali* of authors), *Sarcostemma cynanchoides** (-), *Senecio longilobus* (-), *Sida leprosa** (-), *S. physocalyx* (-), *Solanum elaeagnifolium* (-), *Sphaeralcea subhastata** (-), *Sporobolus cryptandrus** (+), *Stephanomeria pauciflora* (-), *Talinum angustissimum** (-), *Tidestromia lanuginosa** (+), *Tragus berteronianus* (+), *Tribulus terrestris** (+), *Verbesina encelioides* (-), *Xanthium strumarium** (-), *Xanthocephalum sarothrae** (-), *X. sphaerocephalum* (-), *Yucca elata** (C), *Zephyranthes longifolia* (-), *Zinnia acerosa** (-).

BAJADA

Acacia constricta (-), *Allionia incarnata* (+), *Ammocodon chenopodioides* (-), *Amaranthus palmeri* (+), *Aphanostephus ramosissimus* (-), *Aristida adscensionis* (+), *A. glauca* (+), *A. hamulosa* (+), *A. longiseta* (+), *A. purpurea* (+), *Asclepias brachystephana* (-), *Astragalus allochrous* (-), *A. mollissimus* (-), *A. nuttallianus** (-), *A. tephrodes* (-), *A. wootoni* (-), *Atriplex canescens* (+), *Bahia absinthifolia** (-), *B. biternata* (-), *B. pedata* (-), *Baileya multiradiata** (-), *Boerhavia coccinea* (+), *B. gracillima* (+), *B. intermedia* (+), *B. spicata** (+), *Bothriochloa barbinodis* (+), *Bouteloua aristidoides* (+), *B. barbata** (+), *B. curtipendula* (+), *B. eriopoda* (+), *Brickellia laciniata* (-), *Calycoseris wrightii* (-), *Carlowrightia linearifolia* (-), *Cassia bahinioides* (-), *Ceratoides lanata* (-), *Chaenactis stevioides** (-), *Chenopodium incanum* (-), *Chilopsis linearis* (-), *Condalia spathulata* (-), *Coryphantha macromeris* (C), *C. vivipara* (C), *Croton pottsii** (-), *Cryptantha angustifolia** (-), *C. crassisepala** (-), *C. jamesii* (-), *C. micrantha** (-), *Cucurbita foetidissima* (-), *Cuscuta umbellata*, *Dalea formosa* (-), *Descurainaea pinnata** (-), *Dithyrea wislizenii** (-), *Draba cuneifolia* (-), *Dyssodia acerosa* (-), *Echinocereus horizonthalonius* (C), *E. fendleri* (C), *E. pectinatus* (C), *E. triglochidiatus* (C), *Enneapogon desvauzii* (+), *Ephedra trifurca* (-), *Eragrostis curtipedicellata* (+), *Eriastrum diffusum* (-), *Erigeron divergens* (-), *Eriogonum abertianum** (-), *E. rotundifolium** (-), *E. trichopes** (-), *E. wrightii* (-), *Erioneuron pulchellum** (+), *Erodium texanum** (-), *Eschscholtzia mexicana* (-), *Euphorbia albomarginata* (+), *E. micromera** (+), *E. serpyllifolia** (+), *E. serrula** (+), *E. setiloba** (+), *Fallugia paradoxa* (-), *Ferocactus wislizenii* (C), *Flourensia cernua* (-), *Fouquieria splendens* (-), *Gilia ophthalmoides* (-), *Happlopappus gracilis* (-), *Heterotheca fulcrata* (-), *Hybanthus verticillatus* (-), *Ibervillea tenuisecta* (-), *Ipomoea cristulata* (-), *Iva ambrosi-aefolia** (-), *Krameria parvifolia* (-), *Lappula redowskii* (-), *Larrea tridentata** (-), *Lepidium lasiocarpum** (-), *L. medium* (-), *Lesquerella fendleri* (-), *L. gordonii* (-), *Lotus neomexicanus* (-), *Lupinus concinnus* (-), *Mammillaria gummifera* (C), *Malacothrix fendleri* (-), *Melampodium leucanthum* (-), *Menodora scabra* (-), *Mentzelia albicaulis* (-), *M. pumila* (-), *Mollugo cerviana** (-), *Muhlenbergia porteri** (+), *Nama hispidum* (-), *Neolloydia intertexta* (C), *Nicotiana trigonophylla* (-), *Oenothera primiveris* (-), *Opuntia imbricata* (C), *O. leptocaulis* (C), *O.*

phaeacantha (C), *O. violacea* (C), *Parthenium incanum* (−), *Pectis angustifolia* (+), *Pectis papposa** (+), *Perezia nana** (−), *P. wrightii* (−), *Phacelia coerulea** (−), *Plantago patagonica* (−), *Polanisia trachysperma* (−), *Porophyllum scoparium* (−), *Portulaca mundula** (+), *Proboscidea parviflora* (−), *Prosopis glandulosa** (−), *Rhus microphylla* (−), *Scleropogon brevifolius* (+), *Senecio longilobus* (−), *Setaria leucopila* (+), *Sida filicaulis* (−), *Sporobolus cryptandrus* (+), *Streptanthus arizonicus** (−), *Talinum angustissimum** (−), *Tecoma stans* (−), *Tidestromia lanuginosa* (+), *Tragia stylaris* (−), *Tribulus terrestris* (+), *Verbena wrightii* (−), *Verbesina encelioides* (−), *Xanthocephalum microcephalum* (−), *X. sarothrae** (−), *X. sphaerocephalum* (−), *Yucca baccata** (C), *Y. elata** (C), *Zephyranthes longifolia* (−), *Zinnia acerosa** (−), *Z. grandiflora* (−), *Ziziphus obtusifolia* (−).

Species of angiosperms within the three communities were characterized by flowering period as spring, summer or spring-summer. The species that comprise the spring floras flower from March to May. The presence and biomass of each is extremely variable from year to year due to the irregularity in timing and amount of winter and spring rains. The greatest number of species appear in the summer floras, which flower from July to September. These large numbers are probably due to the greater regularity of summer precipitation. The spring-summer flowering period contains those species which bloom in the spring and/or summer.

The 13 species of Cactaceae and the two species of *Yucca* were grouped into the CAM category. All have succulent tissue and *Y. elata* exhibits diurnal fluctuations in titratable acidity (Syvertsen and Smith, unpubl.).

Because the number of species present varies from year to year, those species listed are actually the total that are known to occur in each of the communities. The playa bottom community has 11 C₃ and 10 C₄ species. All the C₄ species bloom during the summer and account for a total of 62% of that flora. The spring and spring-summer floras are entirely C₃ and comprise 52% of the species on the playa (Table 1).

The percentages of species listed for the playa fringe are also essentially split evenly between the C₃ and C₄ pathways. The C₄ category has the largest percentage of the summer flora whereas the C₃ species dominate the spring and the spring-summer floras. There are many more species present on the playa fringe than on the playa bottom. This is probably due to a greater diversity of micro-habitats on the playa fringe. The only CAM species that occurs on the playa fringe is *Yucca elata* (Table 1).

TABLE 1

Percent C_3 , C_4 and CAM of the total species present in each of the three communities during the three flowering periods.

Flowering period	Species present	% C_3	% C_4	% CAM
PLAYA BOTTOM				
Spring	1	100	0	0
Summer	16	38	62	0
Spring-Summer	4	100	0	0
Total	21	52	48	0
PLAYA FRINGE				
Spring	6	83	0	17
Summer	52	42	58	0
Spring-Summer	19	79	21	0
Total	77	54	44	1
BAJADA				
Spring	48	77	2	21
Summer	65	54	45	1
Spring-Summer	31	74	13	13
Total	144	66	24	10

The bajada has the greatest number of species in any of the three communities. All the CAM species which flower during the spring and spring-summer periods are found in this community. CAM species account for 10% of the total species present. Two-thirds of the total are C_3 ; they too most commonly bloom during the spring and spring-summer periods. The summer flora possesses the most species and is essentially split evenly between C_3 and C_4 (Table 1). Over half the C_4 species belong to the Gramineae.

Due to higher precipitation in both the spring and summer of 1972, this growing season produced the greatest plant biomass of the three years (1970, 1971, 1972) sampled (Ludwig 1973). Only the 1972 data were used in this study because it appears to provide the best estimate of maximum standing crop for each of the communities. When a particular species was sampled on more than one of the sampling days (27 June, 22 August or 26 October 1972), the maximum biomass value was used as the estimation of the annual standing crop potential for that species.

The playa fringe community had the greatest total biomass (11,-200.01 kg·ha⁻¹) with a total of 48 species sampled. *Hilaria* is a C_4 summer blooming grass making up 50% of the playa fringe standing crop. In addition, 7% of the total fringe standing crop is *Ephedra trifurca*, a spring blooming gymnosperm that we considered C_3 and 30% *Prosopis*, a spring-summer blooming C_3 shrub. Only four species

TABLE 2

C₃, C₄ and CAM biomass percentages of the total standing crop in the three communities during each flowering period. NE refers to not encountered in the biomass sampling.

Communities	Spring	Summer	Spring-Summer	Total
%C ₃ BIOMASS				
Playa Bottom	NE	7	3	10
Playa Fringe	7	<1	34	41+
Bajada	<1	3	48	51+
%C ₄ BIOMASS				
Playa Bottom	NE	90	NE	90
Playa Fringe	NE	50	<1	50+
Bajada	NE	<1	NE	<1
%CAM BIOMASS				
Playa Bottom	NE	NE	NE	NE
Playa Fringe	8	NE	NE	8
Bajada	48	NE	NE	48

were encountered and subsequently used in the standing crop estimates for the playa bottom. Of the total standing crop on the playa bottom (1,243 kg·ha⁻¹), 90% was *Panicum obtusum*, a C₄ summer blooming grass. On the bajada, 37 species were encountered and of the total plant biomass (2,087.91 kg·ha⁻¹), 36% was *Larrea*, which is a spring-summer blooming C₃ shrub; 47% was produced by *Yucca elata*, a spring blooming succulent with the CAM pathway. In all three communities one or two perennial species account for the bulk of the standing crop (Table 2).

DISCUSSION. The three communities studied all occur in a hot, nonsaline arid, high radiation environment. In addition, all three communities have been subjected to past and present grazing which might favor colonizing weedy species. If the hypothesis concerning the competitive advantage of the supplemental C₄ pathway in these types of communities is true, one might expect the C₄ species to be most important and hence, contribute substantially more to the standing crop of these three plant communities than in communities of many other areas. We cannot, of course, accept or reject the hypothesis on the basis of these limited data. However, our results indicate that although C₄ species may be relatively important in terms of numbers, the C₄ pathway may not be as important to the standing crop in all of these communities as previous speculation might have led us to suspect. Data is sorely needed to compare the relative im-

portance of each carbon reduction pathway to the total primary production of a community.

The bulk of the C_4 species are perennial herbs or annuals that are most important in terms of biomass in the wettest communities, the very localized playas and playa fringes. The bajada community is the driest and is found over large areas in this region. The bajada C_4 plants account for 24% of the total species present but represent only a minute portion of the total standing crop. This partly is a function of the fact that there are no C_4 shrubs in this flora other than *Atriplex*, which in this area was not common enough to be encountered in the biomass studies. It appears however, that the idea that C_4 plants have a competitive advantage in the relatively arid plant communities needs to be re-evaluated.

We did not expect the CAM biomass to be very large as there are few cacti that occur on the bajada and during summer, when moisture is usually not limiting, the nights are relatively warm. Moist days and warm nights tend to negate any advantage that these plants might gain by being able to exchange gases during the night. The large CAM biomass values are due almost entirely to *Yucca elata*. These data may be misleading in that they represent relatively few individuals that impart an apparent large importance to the CAM pathway because of massive individual biomass.

The presence of the C_4 pathway does not automatically enable a species to be a more efficient competitor nor does it enable a plant to accumulate enough biomass to appear to play a dominant role in the relatively arid bajada community. The perennial habit obviously contributes more to the standing crop in this flora than the particular photosynthetic pathway that a species possesses.

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