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THE PHOTOSYNTHETIC PATHWAY TYPE OF  
NORTH AMERICAN SHORTGRASS PRAIRIE SPECIES  
AND SOME ECOLOGICAL IMPLICATIONS

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ABSTRACT

Several dominant species of the shortgrass prairie were examined to identify their photosynthetic pathways. Dominant species of the Pawnee Grasslands, International Biological Program (IBP) site in northeastern Colorado, *Agropyron smithii*, *Bouteloua gracilis*, *Buchloe dactyloides*, *Artemisia frigida*, *Gutierrezia sarothrae*, and *Sphaeralcea coccinea* were grown in a greenhouse along with *Nicotiana tabacum*, a known C<sub>3</sub> plant, and *Zea mays*, a known C<sub>4</sub> plant. The photosynthetic pathways of the species were identified by determining the initial products of photosynthesis, CO<sub>2</sub> compensation points, and response of CO<sub>2</sub> compensation points to temperature. The experimental plants fell into two distinct groups: those which exhibited responses similar to *Nicotiana tabacum* (C<sub>3</sub>): *Artemisia frigida*, *Gutierrezia sarothrae*, *Sphaeralcea coccinea*, and *Agropyron smithii*, and those whose responses were similar to *Zea mays* (C<sub>4</sub>): *Bouteloua gracilis* and *Buchloe dactyloides*. The physiological characteristics associated with C<sub>3</sub> and C<sub>4</sub> pathways were discussed relative to the above-named species ability to perform efficiently under the conditions prevailing at the Pawnee Site.

## INTRODUCTION

The physiological and biochemical traits associated with  $C_3$  and  $C_4$  photosynthetic pathway types have been reviewed by many authors (Bjorkman 1971; Downton 1971; Zelitch 1971; Hatch and Slack 1970a; and Jackson and Volk 1970). The characteristics of adaptation, especially those concerned with water-use efficiency and temperature adaptation, have made the identification of a plant species as to type of photosynthesis ( $C_3$ ,  $C_4$  or C.A.M.) an important tool in studying the physiological ecology of the species in question. With this in mind a study of certain major plant species of the North American shortgrass prairie was undertaken to identify them as to type of photosynthesis. It was felt that this information would contribute to the interpretation of the ecology of the shortgrass prairie ecosystem.

## MATERIALS AND METHODS

For identification of photosynthetic type, plant species were analyzed to determine initial product of photosynthesis and carbon dioxide compensation point.

### Plant Material

Plant specimens used were all representative of the species as found on the Pawnee Site, International Biological Program intensive study site in northeastern Colorado. *Artemisia frigida* Willd., *Gutierrezia sarothrae* (Pursh) Britt. & Rusby, and *Sphaeralcea coccinea* (Pursh) Rydb. were transplanted from their natural habitat on the Pawnee Site to a greenhouse on the University of Denver campus. The three grasses, *Agropyron smithii*

Rydb, *Bouteloua gracilis* (H.B.K.) Lab., and *Buchloe dactyloides* (Nutt.) Engelm., were from the IBP site and also grown from seed purchased from the Rocky Mountain Seed Company, Denver, Colorado. Seed of *Zea mays* was obtained from Rocky Mountain Seed Company and seed of *Nicotiana tabacum* was kindly provided by James L. Tramel, Jr. of Virginia Polytechnic Institute, Blacksburg, Virginia. *Zea mays* was used as a control plant representative of  $C_4$  plants and *Nicotiana tabacum* was used as the representative of  $C_3$  plants.

All plants were grown in the greenhouse under natural Denver, Colorado, daylengths extended to a 15-hr photoperiod by incandescent light when natural daylengths were shorter than 15 hr. Plants were watered daily and given nutrient solution as needed. The nutrient solution contained 18.0 ml Hoagland's micronutrients, 40.0 g of Ra-pid-gro (Ra-pid-gro Corporation), and 16.0 g of chelated iron (Geigy Sequestrene 330) in 19 liters of tap water. The transplanted species were used within two weeks of collection and were replaced by fresh material when necessary.

#### $CO_2$ Compensation Point Determination

The stems and leaves of the intact test plant were enclosed in a gas-exchange cuvette identical to one described by Mooney et al. (1971). Dead plant material was removed before placing the plant in the closed system and the potting soil was brought to field capacity. The cuvette was equipped with a radiator and fan to provide temperature control and adequate mixing of the internal air volume. A circulating water bath was connected to the radiator to control the temperature inside the cuvette within  $\pm 1^\circ C$  of the desired leaf and air temperatures. The dew-point temperature of air entering the chamber was regulated by bubbling the air supply through

water in sealed flasks in separate water baths prior to its entering the cuvette. The first water-bath temperature was slightly warmer (ca. 5°C) than the desired dew-point temperature and the second water-bath was set at the desired dew-point temperature. The inlet dew-point temperature could usually be maintained within  $\pm 0.5^\circ\text{C}$ ; however, fluctuations of  $\pm 2.5^\circ\text{C}$  were observed in a few instances. The dew point of the air supply into and out of the cuvette was monitored by narrow-range hygrometers (Hygrodynamics Model #15-3001). The dew-point of the air inside the cuvette was monitored by a Cambridge System Model 880 Dew Point Hygrometer installed in a circulating subsample loop (Fig. 1). A Brooks flowmeter (Model #R-2-15-B) was used to ensure proper air flow through the dew-point hygrometer. Copper-constantan thermocouples (diameter 0.015 inches) were used for continuous monitoring of leaf temperature, all air temperatures, and all water-bath temperatures (Fig. 1).

A Beckman model 315A differential infrared gas analyzer was used to measure the changes in  $\text{CO}_2$  concentration within the closed system. The analyzer was installed in a subsample loop, while the bulk of the air was being humidified and recirculated to the cuvette (Fig. 1). Only the outlet air passing through the sample side of the analyzer was dried by a potassium pentoxide ( $\text{P}_2\text{O}_5$ ) column. The air passing out of the analyzer was rehumidified and returned to the chamber (Fig. 1). The differential gas analyzer was calibrated before each experiment using standardized gases (Matheson) of known concentrations.<sup>1/</sup> Air flows into and out of the cuvette and analyzer were controlled by a reciprocator pump and by two Brooks R-6-25-A and R-2-15-D flow meters, respectively. The air flow through the cuvette was approximately

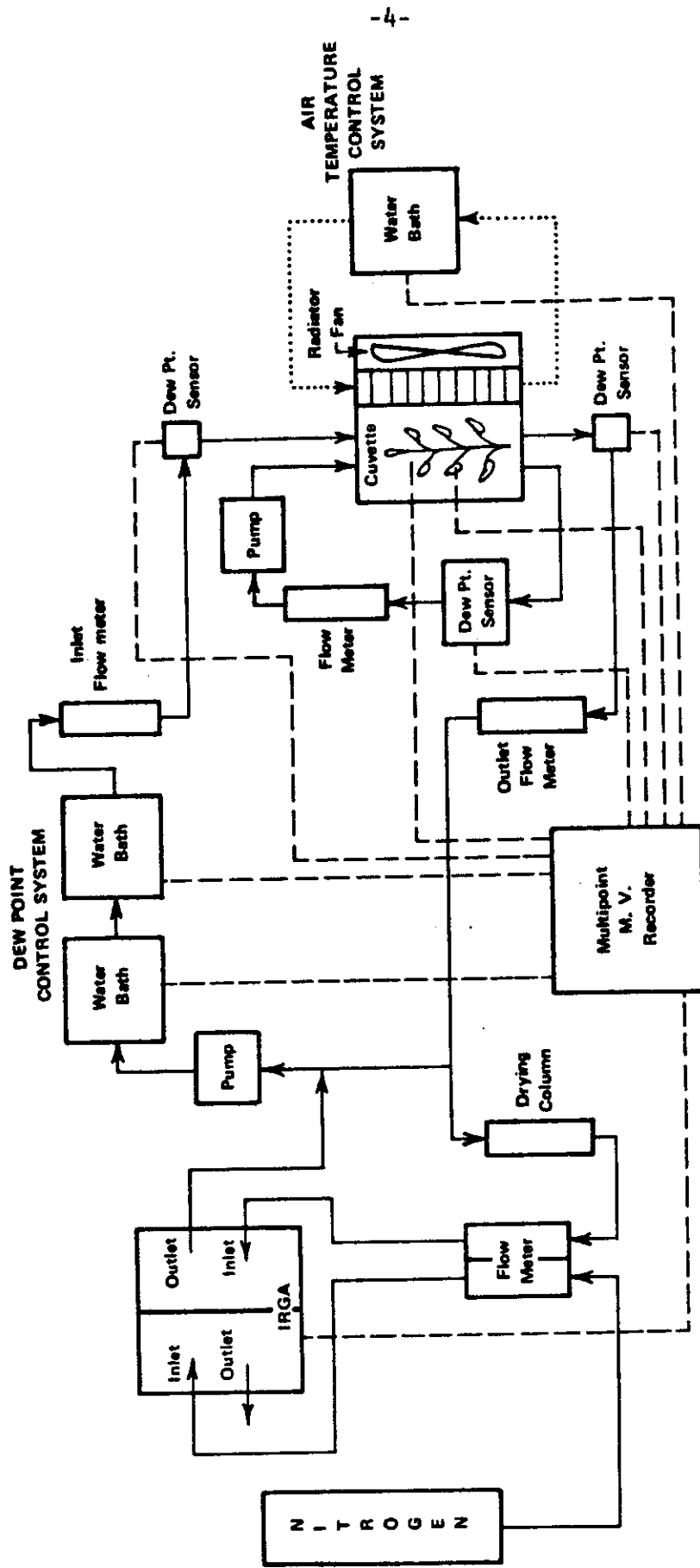


Fig. 1. Simplified schematic diagram of the system used to determine CO<sub>2</sub> compensation points. The solid lines show the air flow pattern in the closed system. The dashed lines represent thermocouples measuring air, leaf, and water temperatures and/or instrument output leads. The dotted lines indicate the flow of water in the air temperature control-system.

10.7 SLPM (standard liters per minute) and the airflow through the analyzer was approximately 390 cc/min. The air pathways of the entire system were built with stainless-steel 3/8-inch tubing and brass fittings (68-FL mini-flex, Imperial Eastman). Stainless-steel tubing was used to reduce the usual diffusion of CO<sub>2</sub> which is experienced when Tygon or other types of polyvinyl tubing are used. Irradiation was provided by three General Electric lamps; a 400-w multivapor, a 400-w mercury vapor, and a 400-w lucalox, and eight Vitalight ultra high output, power groove fluorescent lights. The lighting complex was fitted with plexiglass shields coated with reflective mylar (Solar-X) to provide maximum irradiance. The irradiance measured by a Yellow Springs Radiometer Model 65 was  $5.12 \times 10^5$  ergs cm<sup>-2</sup> sec<sup>-1</sup> outside the cuvette (at plant level) and  $3.375 \times 10^5$  ergs cm<sup>-2</sup> sec<sup>-1</sup> inside the cuvette (at plant level). Measurements of all parameters of the system were recorded by a multichannel recorder. Under the above conditions, the plant was allowed to remove CO<sub>2</sub> from this closed system until an equilibrium value was established.

#### Identification of Initial Products of Photosynthesis

Initial products of photosynthesis were determined as described by Williams and Markley (1972).

### RESULTS

#### Initial Products of Photosynthesis

Radioactivity of the 3-phosphoglycerate-hexose phosphate to the malate-aspartate fraction (3:1) from *Nicotiana tabacum* samples indicates that the majority of <sup>14</sup>C<sub>2</sub> was fixed in 3-phosphoglycerate-hexose phosphate (Table 1). In *Zea mays*, the majority of radio-activity is contained in the malate-aspartate



Table 1. CO<sub>2</sub> compensation points and initial products of photosynthesis of grassland species.

Species	CO <sub>2</sub> Compensation Point in ppm <sup>a/</sup>	Initial Products 3-phosphoglycerate- hexose phosphate malate-aspartate Ratio <sup>b/</sup>	Leaf Temperature (°C)
<i>Zea mays</i>	3	1:3	27
<i>Bouteloua gracilis</i>	10	1:8	25
<i>Buchloe dactyloides</i>	18	1:2	28
<i>Nicotiana tabacum</i>	65	3:1	28
<i>Artemisia frigida</i>	39	9:1	23
<i>Gutierrezia sarothrae</i>	56	6:1	23
<i>Agropyron smithii</i>	57	9:1	28
<i>Sphaeralcea coccinea</i>	75	2:1	23

<sup>a/</sup> CO<sub>2</sub> compensation points are all means based on five replicates at the indicated leaf temperatures.

<sup>b/</sup> The ratio values are means based on:

counts per minute of radioactively labeled 3-phosphoglycerate-hexose phosphate  
counts per minute of radioactively labeled malate-aspartate

after a 10 second exposure to <sup>14</sup>CO<sub>2</sub> of three replicates.

fraction (1:3). Species with ratios similar to *Nicotiana tabacum* included *Artemisia frigida*, *Gutierrezia sarothrae*, *Agropyron smithii*, and *Sphaeralcea coccinea*; and those like *Zea mays* were *Buchloe dactyloides* and *Bouteloua gracilis* (Table 1).

#### Carbon Dioxide Compensation Point

The two control plants, *Nicotiana tabacum* (C<sub>3</sub>) and *Zea mays* (C<sub>4</sub>), had different CO<sub>2</sub> compensation points and of the species tested *Nicotiana tabacum* had one of the highest (65 ppm) and *Zea mays* one of the lowest values (3 ppm) (Table 1). Experimental plant species whose CO<sub>2</sub> compensation points were similar to *Nicotiana tabacum* were *Artemisia frigida*, *Gutierrezia sarothrae*, *Agropyron smithii*, and *Sphaeralcea coccinea*; species with compensation points similar to *Zea mays* were *Buchloe dactyloides* and *Bouteloua gracilis*.

The effect of temperature on the CO<sub>2</sub> compensation points of the different species can also be compared to the response of the control plants. *Nicotiana tabacum* (C<sub>3</sub>) and *Zea mays* (C<sub>4</sub>) have response curves to temperature of steep slope and no slope, respectively (Fig. 2). Species for which CO<sub>2</sub> compensation point temperature response curve is similar to that of *Nicotiana tabacum* are *Gutierrezia sarothrae* and *Agropyron smithii* and species with curves similar to *Zea mays* are *Artemisia frigida*, *Buchloe dactyloides*, and *Bouteloua gracilis* (Fig. 2). *Sphaeralcea coccinea* was not included as wilting occurred, making accurate CO<sub>2</sub> compensation points impossible to determine.

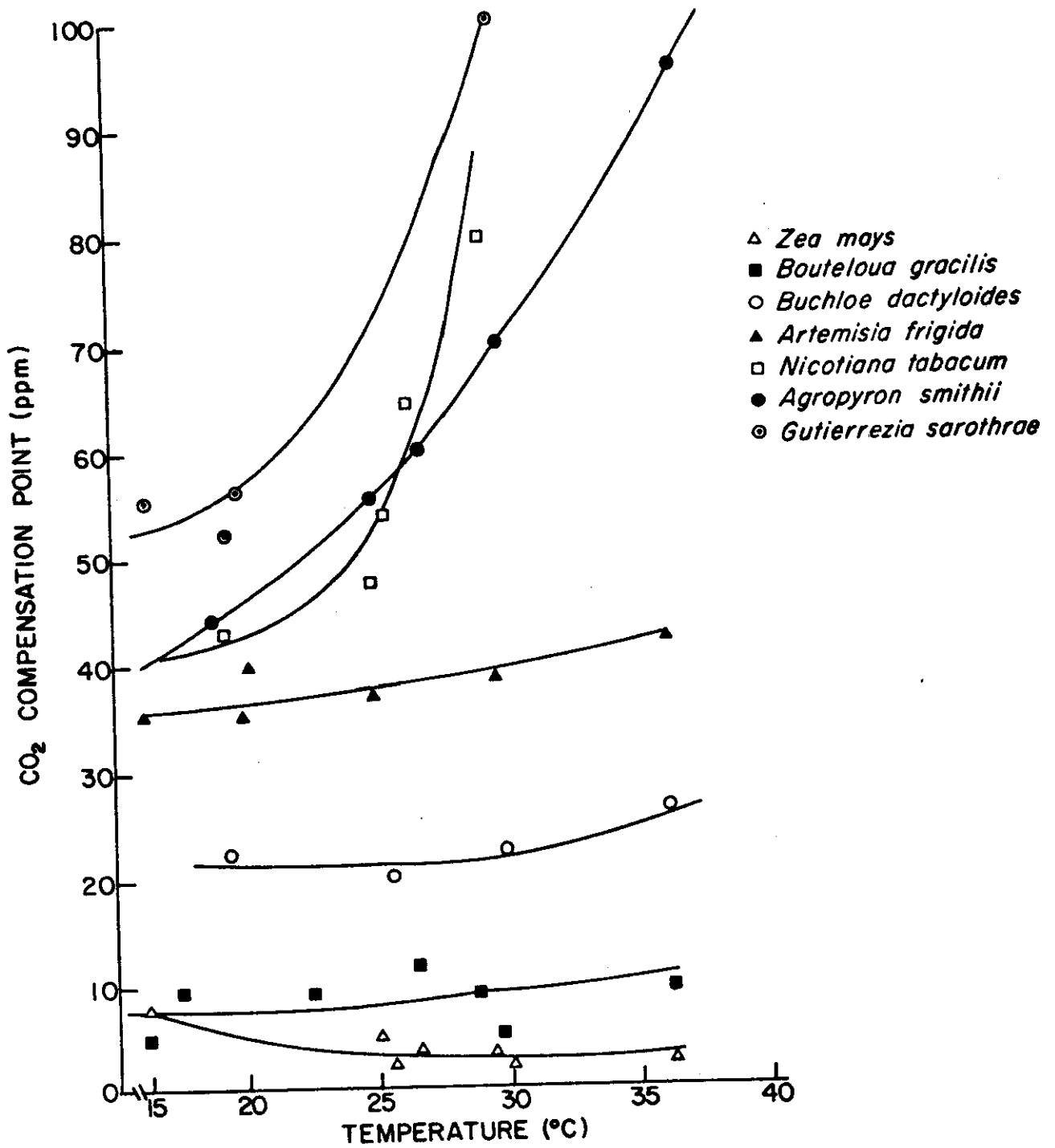


Fig. 2. The CO<sub>2</sub> compensation points of control and experimental plants. The points are means of replicates of five plants at each leaf temperature. The greatest range of values for any plant was 10 ppm CO<sub>2</sub>.

## DISCUSSION

The purpose of this study was to identify the photosynthetic pathways of selected dominant species in the shortgrass prairie. The classification was based on initial carboxylation products,  $\text{CO}_2$  compensation points, and  $\text{CO}_2$  compensation points as a function of temperature. This arbitrary division into either a  $\text{C}_3$  type or  $\text{C}_4$  type may soon be considered a rather dogmatic view and one which should be accepted only in a guarded manner. As previously mentioned one of the species tested in this study served to illustrate this point; *Artemisia frigida* was a difficult species to place into an either/or category using the criteria of initial carboxylation products,  $\text{CO}_2$  compensation point and temperature response of  $\text{CO}_2$  compensation point. As more species are tested, this could be a recurring result. To date, other exceptions to our scheme of separating species into  $\text{C}_3$  or  $\text{C}_4$  types based on physiological response have been noted. For example, certain  $\text{C}_3$  species do not exhibit low-light intensity saturation of photosynthesis (*Helianthus annuus*, Hesketh and Moss 1963; *Aegilops* spp. and some diploid *Triticum* spp., Evans and Dunstone 1970) and old and shade-grown leaves of a  $\text{C}_4$  species (*Amaranthus edulis*) exhibit light saturation of photosynthesis at levels similar to  $\text{C}_3$  species (El-Sharkawy et al. 1968). Photosynthetic rates of old and shade-grown leaves of *A. edulis* were comparable to  $\text{C}_3$  species (El-Sharkawy et al. 1968) again demonstrating an exception to the present dogma of high rates in  $\text{C}_4$  types and low rates in  $\text{C}_3$  types. *Typha latifolia*, a  $\text{C}_3$  species, was shown to have rates comparable to  $\text{C}_4$  species (McNaughton and Fullem 1970), thus providing another example of the departure from the either/or dogma. In our desire to generalize we often set up criteria for organizing our knowledge (i.e., photosynthetic

types C<sub>3</sub>, C<sub>4</sub> and C.A.M.) and place organisms into our scheme without always appreciating their deviance from our organization scheme. Thus, it is the authors' hope that we do not bury these exceptions but exploit them by continuing to point to them with the hope that they will spark biological curiosity. We, therefore, point to one species (*Artemisia frigida*) as being a difficult species to place into either a C<sub>3</sub> or a C<sub>4</sub> type; we did finally do so for the sake of generalizing our information. The results indicated that in the shortgrass prairie at least two basic groups of plants, each with a different photosynthetic pathway, can be distinguished. All species but one were readily identified as C<sub>3</sub> or C<sub>4</sub> type. Plants similar in response to *Nicotiana tabacum* were identified as C<sub>3</sub> plants; those similar to *Zea mays* were classified as C<sub>4</sub> plants.

The use of <sup>14</sup>C<sub>2</sub> for the labeling of initial products demonstrates that the control plants, *Nicotiana tabacum* and *Zea mays*, compare favorably with results reported by Hatch, Slack, and Johnson (1967). The greater ratio of labeled 3-phosphoglycerate-hexose phosphate to labeled malate-aspartate as an initial product is a positive indication of the C<sub>3</sub> pathway (Hatch et al. 1967). It is also known that the initial photosynthetic product of *Nicotiana tabacum* (C<sub>3</sub>) is 3-phosphoglycerate, while in *Zea mays* (C<sub>4</sub>) it is malate-aspartate (Hatch and Slack 1970b; Hatch, Osmond, and Slayter, 1971). These plants were used as controls and the dominant species from the grassland site were compared to these controls for initial products ratios. The resultant division of the grassland species into C<sub>3</sub> and C<sub>4</sub> types on the basis of initial products are as follows: C<sub>3</sub> species--*Artemisia frigida*, *Gutierrezia sarothrae*, *Agropyron smithii*, and *Sphaeralcea coccinea*; C<sub>4</sub> species--*Bouteloua gracilis* and *Buchloe dactyloides* (Table 1).

Our results show the CO<sub>2</sub> compensation points of *Nicotiana tabacum* to be 65 ppm (at 27°C) and *Zea mays* to be 3 ppm (at 27°C) which compared to those of Moss (1962) who found CO<sub>2</sub> compensation points of 60 ppm for *Nicotiana tabacum* and less than 10 ppm for *Zea mays*. Heichel (1971) also reported a value of 60 ppm for *Nicotiana tabacum*. Downton and Tregunna (1968) reported values of 37 to 50 ppm for *Nicotiana tabacum* and less than 5 ppm for *Zea mays*. Heichel and Musgrave (1969), with 15 varieties of maize, reported a range of 9 to 25 ppm. Later Moss (1971) repeated the experiment with 33 genotypes including the 15 varieties of Heichel and Musgrave. His findings revealed all genotypes had low compensation points with a mean of 1.3 ppm with a standard error of ±1.2 ppm. Our study of CO<sub>2</sub> compensation points grouped certain species with *Nicotiana tabacum* on that basis and identified them as C<sub>3</sub> types. They were *Artemisia frigida*, *Gutierrezia sarothrae*, *Agropyron smithii*, and *Sphaeralcea coccinea*. Those grouped with *Zea mays* and classified as C<sub>4</sub> were *Bouteloua gracilis* and *Buchloe dactyloides*.

Results of the effect of temperature on CO<sub>2</sub> compensation points also confirm that control plants followed expected responses. Zelitch (1966) showed that the CO<sub>2</sub> compensation point is greater at higher temperatures in plants with apparent photorespiration (those exhibiting the Calvin cycle). His graphs for *Nicotiana tabacum* closely resemble those presented in this study. Hofstra and Hesketh (1969) and El-Sharkawy and Hesketh (1964) found that plants without apparent photorespiration (plants with the C<sub>4</sub> dicarboxylic acid pathway) did not show any consistent CO<sub>2</sub> evolution at elevated temperatures. Bjorkman, Gauhl, and Nobs, (1968), working with *Atriplex*, a genus

in which both  $C_3$  and  $C_4$  species occur, found a similar response pattern. They reported in *Atriplex patula* ( $C_3$ ) that the compensation point increases exponentially with increasing leaf temperature, whereas in *Atriplex rosea* ( $C_4$ ) it remains very low throughout the entire temperature range of 5 to 35° C.

The species investigated in this experiment, with one exception, had response curves to temperature either like *Zea mays* ( $C_4$ ) or like *Nicotiana tabacum* ( $C_3$ ). Those plants whose responses were similar to *Nicotiana tabacum* were classified as  $C_3$  and included *Gutierrezia sarothrae* and *Agropyron smithii*. *Bouteloua gracilis* and *Buchloe dactyloides*, whose responses were similar to *Zea mays*, can be identified as having the  $C_4$  dicarboxylic acid pathway. *Artemisia frigida* represents the anomalous case as the  $CO_2$  compensation point is intermediate and no temperature effect is apparent.

By combining the results of the initial products of photosynthesis,  $CO_2$  compensation points, and response curve of  $CO_2$  compensation points as a function of temperature, identity of the experimental species can be made. One method alone is not always conclusive as the data for *Artemisia frigida* exemplify, and anomalous results based on one test are often resolved by the composite result of the three. For example, *Artemisia frigida* appeared to respond like a  $C_4$  plant to increased temperature effect on  $CO_2$  compensation point, but based on the combined results of the fairly high  $CO_2$  compensation point at all temperatures and the ratios of initial products (3:1 phosphoglycerate-hexose to malate-aspartate), it was concluded that *Artemisia frigida* is a  $C_3$  plant.

It has been established that plants with different biochemical pathways have different physiological responses. On the basis of results

reported in this study, meaningful correlations can now be drawn for the species tested and habitat parameters at the Pawnee Site. Of the experimental species studies, the existing literature focuses on only the three grasses: *Agropyron smithii*, *Buchloe dactyloides*, and *Bouteloua gracilis*.

*Agropyron smithii* has been referred to as a "cool season" grass, while *Buchloe dactyloides* (C<sub>4</sub>) and *Bouteloua gracilis* (C<sub>4</sub>) have been classed as "warm season" grasses (Dickinson and Baker 1972; Arnold 1964). Julander (1945) grew grasses at various temperatures and reported *Buchloe dactyloides* to be the most heat resistant of those tested, while *Agropyron smithii* grew best in 15.6°C/10°C and 10°C/4.4°C day/night temperature regimes, and *Bouteloua gracilis* and *Buchloe dactyloides* had their best growth in 32.2°C/26.7°C day/night chambers.

The effect of drought on these grasses has also been tested. During the "Great Drought" that lasted from 1933 to 1940 in the Midwest, many observations were made. Albertson and Weaver (1944) observed that as a result of the drought *Buchloe dactyloides* was found to increase greatly but was less drought-resistant than *Bouteloua gracilis*. In three plant communities near Hays, Kansas, Albertson and Tomanek (1965) reported that the shortgrass community was dominated by *Buchloe dactyloides* and *Bouteloua gracilis* in 1932, but was dominated only by *Bouteloua gracilis* in 1961. In other studies Hulett, Sloan, and Tomanek (1968) in northwestern Kansas and southwestern Nebraska observed *Bouteloua gracilis* dominating the level uplands (dry site), while *Agropyron smithii* dominated the mesic lowlands where more run off occurred. Studies by Branson, Miller, and McQueen (1970) on tolerance of species to total soil water stresses confirmed these observations. They found *Bouteloua*



*gracilis* could withstand 30 bars. The only study available including one of the other experimental plants, *Gutierrezia sarothrae*, was done by Arnold (1964). He found in zones of decreasing moisture content around a juniper tree that *Agropyron smithii* and *Gutierrezia sarothrae* occupied the zone where moisture conditions were favorable, while only *Bouteloua gracilis* was found in the drier zones. These responses to water stress can be compared with the growth patterns of these plants on the Pawnee Site and the existing climatological records. Of the 15 inches or less of moisture that occur during the year at the Pawnee Site, 80% falls as rain from 3 to 4 major summer thunderstorms (Rasmussen, Bertolin, and Almayda 1971). Of that 80%, 50% falls in May and June during the peak growing periods of the plants with only the C<sub>3</sub> Calvin cycle. During the hot months of July, August, and September when plants with the C<sub>4</sub> pathway reach their peak, only 30% of the precipitation occurs. The above-mentioned responses to temperature and water stress can be correlated to the phenology of the grasses on the Pawnee Site. *Agropyron smithii* first initiates growth on the prairie in May when the maximum temperature is 20°C and the minimum 4.4°C and reaches maximum growth in late June when the temperature variation is 25.6°C to 7.2°C. *Buchloe dactyloides* and *Bouteloua gracilis* begin growing later in the spring and remain later in the summer where temperatures reach 30.6°C during the day with 11.7°C temperatures at night. Therefore, it would appear probably that the growing season of the species with the C<sub>3</sub> pathways would coincide with the cool, moist months while the physiological traits of C<sub>4</sub> plants would allow them to grow during the hotter, drier months.

Based on the information above, one can speculate that the selective advantages of physiological characteristics associated with C<sub>3</sub> and C<sub>4</sub>

photosynthetic pathways would enable each species to perform efficiently under the conditions prevailing in the shortgrass prairie habitat. This type of selection would thus allow many species to occupy the same site with minimal interspecific competition. The two species which represent upwards of 60% of the total aboveground plant biomass on the Pawnee Site are *Bouteloua gracilis* and *Agropyron smithii*.

The evidence suggests that these shortgrass prairie species possess the unique physiological traits of known  $C_3$  and  $C_4$  species. The above hypothesis of minimal interspecific competition based on phenologies which allow use of habitat factors in periods of the growth season matched to physiological attributes remains to be tested, but the species of *Bouteloua gracilis* and *Agropyron smithii* would make ideal test plants.

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FOOTNOTES

- 1/ With the help of Dr. A. J. Dye of Colorado State University our standards were compared with those of the National Oceanic and Atmospheric Administration in Boulder, Colorado.

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