Great Basin Naturalist

Volume 45 | Number 3 Article 16

7-31-1985

High rates of photosynthesis in the desert shrub *Chrysothamnus nauseosus* ssp. *albicaulis*

Tim D. Davis
Brigham Young University

N. Sankhla
University of Jodhpur, India

W. R. Andersen
Brigham Young University

D. J. Weber
Brigham Young University

B. N. Smith
Brigham Young University

HIGH RATES OF PHOTOSYNTHESIS IN THE DESERT SHRUB *CHRYSOTHAMNUS NAUSEOSUS* SSP. *ALBICAULIS*

Tim D. Davis[1], N. Sankhla[2], W. R. Andersen[1], D. J. Weber[1], and B. N. Smith[1]

ABSTRACT.— Basic aspects of photosynthesis were investigated in white rubber rabbitbrush (*Chrysothamnus nauseosus* (Pallas) Britt. ssp. *albicaulis*), a common C_3 deciduous shrub native to arid regions of the western U.S. Under favorable field conditions, net photosynthesis (P_n) ranged from 36 to 73 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, which is relatively high for a woody species. The leaves from the actively growing flowering shoots exhibited higher P_n than those on the vegetative shoots. P_n also varied according to the age of the leaves and the location of the plants. P_n did not light saturate even at quantum flux densities (QFD) equivalent to full sunlight. The light compensation point was relatively high (ca 100 μmol $\cdot m^{-2} \cdot S^{-1}$), perhaps due to the presence of a tomentose vestiture on the leaf surface. At high QFD's, the stomatal conductance was high (ca 520 mmol $\cdot m^2 \cdot s^{-1}$) for a woody species. RUBP-carboxylase content of the leaves ranged from 20 to 22 mg per gram F.W., which is similar to that found in most C_3 crop species. These results suggest that rabbitbrush is able to maintain high rates of P_n, at least under nonstressed conditions.

The genus *Chrysothamnus* (rabbitbrush) consists of deciduous subshrubs or shrubs endemic to western North America in open plains, valleys, foothills, and mountains (McArthur et al. 1979). Like other species of the genus, *Chrysothamnus nauseosus* (Pallas) Britt. (rubber rabbitbrush) is an excellent plant for soil stabilization because of its deep roots, heavy litter, and ability to establish on severe sites. It can grow in the cold deserts of the Colorado plateau, the Great Basin plateau, and the warm deserts of the southwestern U.S. In fact, *Chrysothamnus* is able to survive and grow vigorously from Mexico to Canada, an area that represents a very wide range of environmental conditions.

Recently there has been a renewed surge of interest in rabbitbrush as a nontraditional source of rubber. Acquisitions containing up to 6% rubber per unit dry weight have been reported (Ostler 1980). As a part of an on-going project on the potential of *Chrysothamnus* as a rubber source, we became interested in evaluating factors controlling rubber production. Very little information is available on the photosynthetic potential and physiological characterization of rabbitbrush. This paper describes some basic aspects of the photosynthetic characteristics of this potentially important plant.

MATERIALS AND METHODS

For initial experiments, rates of net photosynthesis (P_n) were measured during September and October 1984 on vigorous, healthy, white rubber rabbitbrush plants growing in the Range Plant Garden at Brigham Young University (elevation approximately 1500 m) using the in situ CO_2 depletion technique (Ehleringer and Cook 1980). The cuvette was clamped onto the shoots for 45 sec. The CO_2 analysis system consisted of a Beckman 865 Infrared Analyzer through which N_2 gas was flowing. Samples were injected into the gas stream, and sample peaks were printed out by a Hewlett-Packard Model 3390-A Reporting Integrator. The rate of CO_2 exchange was calculated from the CO_2 depletion rate based on the chamber volume, using the ideal gas equation. Plants were about three years old and had been irrigated periodically throughout the summer. For comparative purposes, P_n was also measured on healthy, vigorous plants of several additional woody species growing under similar environmental conditions. P_n was also measured on rabbitbrush plants growing on three native sites in Utah County, Utah. These plants had received considerable rainfall about five days prior to measurement. Rates of P_n were expressed on leaf area, dry weight, and chlorophyll bases. Leaf

[1]College of Biological and Agricultural Sciences, Brigham Young University, Provo, Utah 84602.
[2]Permanent address: Department of Botany, University of Jodhpur, India.

area was determined using Li-Cor model LI-3000 and LI-3100 area meters. Because of the narrowness of rabbitbrush leaves, it was found that the LI-3000 area meter underestimated leaf area by 45%. Hence leaf area data obtained by the LI-3000 area was multiplied by 1.82 to correct for this error. Chlorophyll content was determined using the method of Lichtenthaler et al. (1982), and the dry weights were determined by oven drying at 70 C for at least 16 hours.

To determine the response of rabbitbrush P_n to light, shoots from plants growing in the Range Plant Garden were excised under water and placed in an open gas exchange system as described in detail by Ehleringer (1983). Shoots were first exposed to a quantum flux density (QFD) of 2650 $\mu mol \cdot m^{-2} \cdot S^{-1}$. The QFD was then lowered in steps down to 80 $\mu mol \cdot m^{-2} \cdot S^{-1}$. Shoots remained at a given QFD until a stable photosynthetic rate was achieved (usually about 45 min.). Leaf temperature was held constant at 25 C, and CO_2 concentration was about 350 $\mu l \cdot l^{-1}$ during the measurements. Stomatal conductance and intercellular CO_2 concentrations were calculated as described previously (Ehleringer 1983).

For enzyme assays, fully expanded leaves were collected from young vigorous shoots. One-gram samples were each ground in 5 ml buffer (0.1 M Tris-Cl, pH 8.2 (25 C), 20 mM $MgCl_2$, 4 mM ethylendiaminetetraacetic acid, 4 mM dithiothreitol, and 5% acid and deionized H_2O-washed polyvinylpolypyrrolidone (Sigma). Assay and activation of ribulose bisphosphate carboxylase (RuBPCase) followed the method of Lorimer et al. (1977). Concentration of $NaH^{14}CO_3$ was 10 mM in the activation and assay media. Concentration of ribulose-1,5-bisphosphate was a 0.4 mM with $MgCl_2$ at 20 mM in the activation and assay media. Determination of amount of enzyme followed the Beckman Model-E ultracentrifuge method of Andersen et al. (1970) using the Schlieren optical system at a bar angle of 50°. Amount of enzyme as mg $\cdot$ ml^{-1} extract was determined by dividing the 15× magnified area of the Schlieren peak by a factor of 4.107.

For scanning electron microscopy (SEM), leaf tissue was fixed in glutaraldehyde-acrolein (Hess 1966). After dehydration to acetone, tissue was critical-point dried and sputter coated with gold.

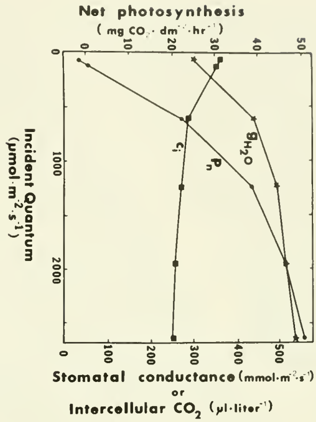

Fig. 1. Response of net photosynthesis (P_n), stomatal conductance (gH_2O), and intercellular CO_2(C_i) of rabbitbrush to incident quantum flux.

RESULTS

White rubber rabbitbrush consistently exhibited high P_n rates for a woody species (Fig. 1; Tables 1–4). Rates obtained with intact shoots in the field using the CO_2 depletion technique compared favorably with those obtained with excised shoots in the open gas exchange system. On a leaf area basis, the P_n in this plant was considerably higher than that of the other woody C_3 species (Table 1). Even on a dry weight basis, the P_n in rabbitbrush equaled that of *Atriplex canescens*, a C_4 species, and was nearly twofold or more than that of the other C_3 species. When calculated on chlorophyll basis, only the C_4 *A. canescens* exhibited a higher P_n rate than that of rabbitbrush. The P_n rates in plants growing on the nonirrigated native sites were found to be somewhat lower than those recorded for the plants maintained at the Range Plant Garden (Table 2).

In rabbitbrush the stem is also photosynthetic, and leaf senescence progresses acropetally. To assess the contribution of stem photosynthesis in overall P_n as well as to evaluate the role of leaf senescence, additional

TABLE 1. Net photosynthetic rates (P_n) of *Chrysothamnus nauseosus* ssp. *albicaulis* and six other woody species under similar environmental conditions. All plants were growing outdoors under irrigated conditions except for *A. tridentata*, which was measured on a native site after a heavy rainfall. Plus/minus values indicate standard of error of the mean (n = 4).

	P_n			Environmental conditions	
Species	$mgCO_2 \cdot dm^{-2} \cdot hr^{-1}$	$mgCO_2 \cdot g^{-1} D.W. \cdot hr^{-1}$	$mgCO_2 \cdot mg^{-1} Chl \cdot hr^{-1}$	QFD ($\mu mol.m^{-2} \cdot s^{-1}$)	Temp. (°C)
Chrysothamnus nauseosus	45.9±1.2	31.3±1.8	5.9±0.3	1050	20
Acer saccharinum	16.8±1.9	21.0±2.4	6.4±0.7	1700	24
Artemisia cana	26.8±2.9	17.4±2.3	3.1±0.4	1150	20
Artemisia tridentata	30.0±3.8	13.9±1.0	5.3±0.4	1600	26
Atriplex canescens	55.8±2.7	30.2±2.0	8.3±0.6	1050	20
Ephedra viridis	—*	5.2±0.5	3.7±0.4	1600	20
Malus domestica "Red Delicious"	23.1±2.1	18.9±1.7	4.0±0.4	1800	26

*This species has photosynthetic stems and bears no leaves. Hence P_n on a leaf area basis was not calculated.

TABLE 2. Net photosynthesis by *Chrysothamnus nauseosus* at three native locations in Utah County, Utah. Plus/minus values indicate standard error of the mean (n = 4). All measurements made at QFD of 1800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and on nonflowering shoots.

	P_n	
Location	$mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$	$mg\ CO_2 \cdot g^{-1}\ D.W. \cdot hr^{-1}$
1. Provo Canyon—partially shaded, southern slope, near Provo River (temp. = 20 C)	39.5±4.3	42.0±4.6
2. Provo Canyon—open field, flat, full sun (temp = 20 C)	36.1±2.1	28.7±1.6
3. Mouth of Rock Canyon—slight western slope, full sun (temp. = 26 C)	40.9±2.2	28.6±1.6

TABLE 3. Net photosynthesis rates (P_n) of nonflowering and flowering shoots of *Chrysothamnus nauseosus* with and without leaves. Plus/minus values indicate standard error of the mean (n = 5).

	P_n		
Shoot type	$mgCO_2 \cdot dm^{-2} \cdot hr^{-1}$	$mgCO_2 \cdot g^{-1} D.W. \cdot hr^{-1}$	$mgCO_2 \cdot gChl^{-1} \cdot hr^{-1}$
Nonflowering, leaves intact	54.3±3.7	45.2±3.1	10.5±0.7
Flowering, leaves intact	73.3±6.7	61.5±5.6	16.8±1.5
Nonflowering, leaves removed	—	3.1±1.2	2.7±1.0
Flowering, leaves removed	—	4.7±1.6	4.3±1.5

TABLE 4. Net photosynthesis of the terminal 10 cm and the adjacent 10 cm below *Chrysothamnus nauseosus* shoots. Plus/minus values indicate standard error of the mean (n = 4). Environmental conditions during measurement: QFD = 1700 $\mu mol \cdot m^2 \cdot s^{-1}$, Temp. = 20 C.

	P_n		
Shoot location	$mgCO_2 \cdot dm^{-2} \cdot hr^{-1}$	$mgCO_2 \cdot g^{-1} D.W. \cdot hr^{-1}$	$mg \cdot mgChl^{-1} \cdot hr^{-1}$
Upper 10 cm	48.2±8.2	28.1±4.6	9.2±1.3
Section between 10 and 20 cm below apex	28.4±7.2	13.9±4.8	6.8±2.3

measurements of P_n were undertaken. The results indicate that stem P_n, on a dry weight basis, was only about 7% of that observed for leaves on both flowering and nonflowering shoots (Table 3). Leaves on flowering shoots at anthesis exhibited about a 35% higher P_n than

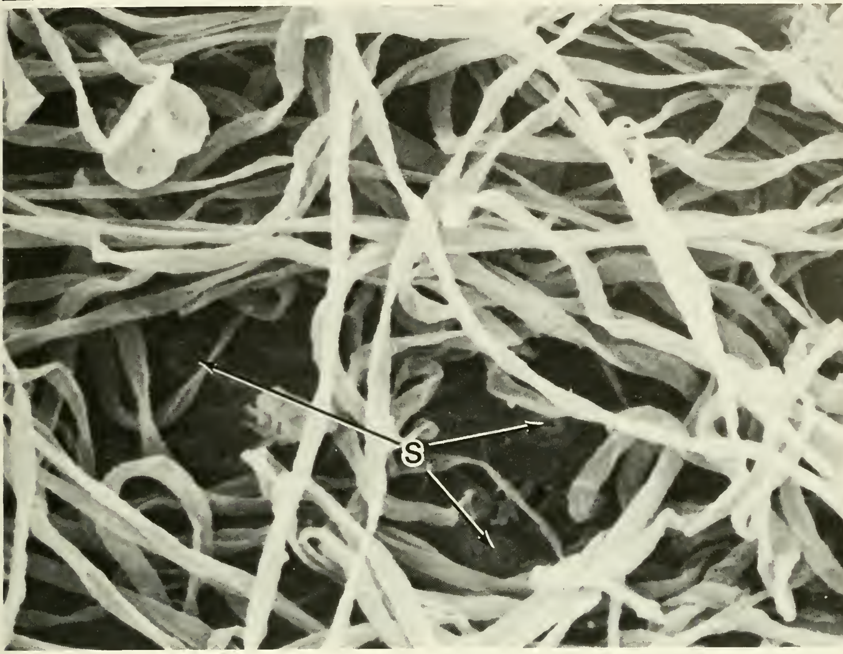

Fig. 2. Scanning electron micrograph of rabbitbrush leaf surface (X300) showing pubescence. Arrows point to stomata(s).

the leaves on nonflowering shoots on the same plant.

Results relating to the effect of leaf senescence on P_n are presented in Table 4. The leaves on the terminal 10 cm of rabbitbrush shoots exhibited a P_n rate that was about twofold higher that observed on the same shoots just 10 cm below the terminal section that had senescing leaves.

In this plant P_n did not light saturate at QFD's near full sunlight (Fig. 1). The light compensation point was also found to be relatively high (ca 100 $\mu mol \cdot m^{-2} \cdot S^{-1}$). A SEM of the leaf surface revealed that rabbitbrush leaves are covered with a dense pubescence (Fig. 2). High P_n rates in rabbitbrush were accompanied by high stomatal conductance values (Fig. 1). The intercellular CO_2 concentrations in rabbitbrush leaves were similar to those found in other C_3 drought-deciduous shrubs that exhibit high P_n and stomatal conductance (Ehleringer and Björkman 1978, Comstock and Ehleringer 1984).

RuBPCase content and catalytic activities at V_{max} were measured for separate extractions of six samples of fully expanded leaves from actively growing shoots. Amount of RuBPCase was 21 ± 1.25 $mg \cdot g^{-1}$ F.W., 12.93 ± 0.74 $mg \cdot mg^{-1}$ chlorophyll, and 1.07 ± 0.06 $mg \cdot cm^{-2}$ leaf area. The catalytic activities of RuBPCase at V_{max} levels of substrate were 712 ± 96 nmol $^{14}CO_2 \cdot mg^{-1}$ enzyme $\cdot$ min^{-1}, 9.66 ± 0.87 μmol $^{14}CO_2 \cdot mg^{-1}$ chlorophyll $\cdot$ min^{-1}, and 761 ± 102 nmol $^{14}CO_2 \cdot cm^{-2} \cdot min^{-1}$.

Discussion

Desert ecosystems are inhabited by a variety of plant life forms including ephemerals, drought-deciduous and desiccation-tolerant evergreen shrubs and herbaceous perennials (Walter and Stadelmann 1974, Ehleringer and Mooney 1983). Moisture stress is a continual limiting factor for the photosynthetic process in most desert plants. Therefore, it is not surprising to note that desert plants adapt the photosynthetic apparatus to desiccation tolerance and/or drought avoidance. It appears that white rubber rabbitbrush has resorted to drought avoidance in its photosynthetic adaptation. Like ephemerals (Mooney et al. 1976), this deciduous shrub is able to maintain high rates of P_n during nonstress periods. In fact, the rates of P_n exhibited by rabbitbrush were found to be similar to those observed in well-watered, drought-deciduous shrubs of warm deserts that typically exhibit very high P_n rates for woody species (Ehleringer and Mooney 1983). The rates of P_n in rabbitbrush even compared well with those found in many herbaceous C_3 crop species (Leopold and Kriedemann 1975). Rates of P_n were particularly high in flowering shoots at anthesis. The reason for this is not clear, but the presence of reproductive sinks is known to stimulate P_n in at least some plants (Milthorpe and Moorby 1974).

The higher amounts of RuBPCase per unit leaf area in rabbitbrush could also be a significant factor contributing to high rates of P_n in this species. In seedling leaves of *Pisum sativum* and in fully expanded leaves of *Medicago sativa*, the estimated amounts of RuBPCase were 11 and 21 mg · g^{-1} F.W., respectively (Gordon et al. 1978, Meyers et al. 1982). Thus, on a fresh weight basis, the amount of enzyme in rabbitbrush leaves is similar to that found in C_3 crop species. Based upon mass of enzyme per unit leaf area, however, RuBPCase in rabbitbrush is relatively high (1.07 mg · cm^{-2}). Some of the highest amounts of this enzyme on a leaf area basis (0.5 mg · cm^{-2}) for C_3 species have been measured in desert winter annuals (Seemann et al. 1980). Depending upon leaf age, RuBPCase amounts in soybean were 0.1 to 0.4 mg · cm^{-2} (Wittenbach et al. 1980). Similarly, in fully expanded leaves of spinach the amount of this enzyme was 0.3 mg · cm^{-2} (Seemann and Berry 1981). The amount of RuBPCase on a leaf area basis measured in our study of rabbitbrush exceeds the extremes of these values by more than twofold. However, on the bases of chlorophyll or fresh weight, rabbitbrush values are similar to those in other C_3 species. The carboxylation activities for rabbitbrush per mg RuBPCase or per mg chlorophyll are also similar to that found in other C_3 species (Koivuniemi et al. 1980, Seemann et al. 1980, Seemann and Berry 1981). However, carboxylation activities in rabbitbrush at V_{max} were high on a leaf area basis compared to other C_3 species showing high RuBPCase activities per unit leaf area (Mooney et al. 1976).

Among the different desert life forms, the highest photosynthetic rates and leaf conductances have been recorded for ephemerals (Mooney et al. 1976, Mooney and Ehleringer 1978, Ehleringer et al. 1979). Some of the drought-deciduous shrubs and herbaceous perennials, which are active for somewhat longer periods than ephemerals, also have high P_n rates (Ehleringer and Björkman 1978). High P_n rates in rabbitbrush were also accompanied by high stomatal conductance. However, it should be pointed out that these high conductance values were measured on well-watered plants. Under more dry native conditions, such high values may not be observed. Even the intercellular CO_2 concentrations in rabbitbrush leaves were found to be similar to C_3 drought-deciduous shrubs, which exhibit high P_n and high stomatal conductance (Ehleringer and Mooney 1983).

Leaves of many desert plants are pubescent. The presence of pubescence not only modulates leaf spectral characteristics and leaf boundary layer resistance, but it also reduces leaf absorptance resulting in reduced heat load, lower leaf temperatures, and lower transpiration rates (Ehleringer and Björkman 1978, Ehleringer and Mooney 1978) and may have adaptive significance. In rabbitbrush the shoot is covered with a green, yellow-green, gray-green to white, feltlike tomentum, and the leaves are clothed with a tomentose vestiture. A characteristic feature of P_n in rabbitbrush is that it is not light saturated at QFD's near full sunlight. In addition, the light compensation point is relatively high. Similar responses of P_n to light have also been recorded in some C_3 species native to the Sonoran desert (Ehleringer and Björkman 1978). In *Encelia farinosa*, the high light saturation point has been attributed to the pubescent nature of the leaf surface. It is likely that the nonsaturation of P_n at near full sunlight and the high light compensation point in rabbitbrush is due to its tomentose vestiture.

In conclusion, this study indicates that rabbitbrush is capable of maintaining high photosynthetic rates during nonstress periods. Thus, at least under favorable environmental conditions, a potential exists for high rates of dry matter accumulation per unit of biomass. The extent to which the dry matter production can be partitioned into rubber as well as an elucidation of the factors promoting rubber production should be a worthwhile subject for future investigation. It will also be of interest to determine how P_n responds on a seasonal basis to water stress and other environmental parameters.

Acknowledgments

Gratitude is expressed to J. Ehleringer and J. Comstock (University of Utah) for their helpful comments and the use of their open gas exchange system. We also express appreciation to W. M. Hess (Brigham Young University) for the SEM of the rabbitbrush leaf surface. This research was supported in part by a grant from Brigham Young University.

Literature Cited

ANDERSEN, W. R., G. F. WILDNER, AND R. S. CRIDDLE. 1970. Ribulose diphosphate carboxylase III. Altered forms of ribulose diphosphate carboxylase from mutant tomato plants. Arch. Biochem. and Biophys. 137:84–90.

COMSTOCK, J., AND J. EHLERINGER. 1984. Photosynthetic responses to slowly decreasing leaf water potentials in *Encelia fruitescens*. Oecologia 61:241–248.

EHLERINGER, J. 1983. Ecophysiology of *Amaranthus palmeri*, a sonoran desert summer annual. Oecologia 57:107–112.

EHLERINGER, J., AND O. BJÖRKMAN 1978. A comparison of photosynthetic characteristics of *Encelia* species possessing glabrous and pubescent leaves. Plant Physiol. 62:185–190.

EHLERINGER, J., AND C. S. COOK. 1980. Measurements of photosynthesis in the field: utility of the CO_2 depletion technique. Plant, Cell, and Environment 3:479–482.

EHLERINGER, J., AND H. A. MOONEY. 1978. Leaf hairs: effects on physiological activity and adaptive value to a desert shrub. Oecologia 37:183–200.

_____. 1983. Productivity of desert and mediterranean-climate plants. Pages 205–231 *in* O. L. Lange, P. S Nobel, C. B. Osmond, and H. Ziegler, eds., Encyclopedia of plant physiology. Vol. 120. Springer-Verlag, Berlin.

EHLERINGER, J., H. A. MOONEY, AND J. A. BERRY. 1979. Photosynthesis and microclimate of *Camissonia claviformis*, a desert winter annual. Ecology 60:280–286.

GORDON, K. H. J., M. B. PEOPLES, AND D. R. MURRAY. 1978. Aging-linked changes in photosynthetic capacity and in fraction I protein content of the first leaf of pea *Pisum sativum* L. New Phytol. 81:35–42.

HESS, W. M. 1966. Fixation and staining of fungus hyphae and host plant root tissues for electron microscopy. Stain Technology 41:27–35.

KOIVUNIEMI, P. M., N. E. TOLBERT, AND P. S. CARLSON. 1980. Ribulose-1,5-bisphosphate carboxylase/oxygenase and polyphenol oxidase in the tobacco mutant su/SU and three green revertant plants. Plant Physiol. 65:828–833.

LEOPOLD, A. C., AND P. E. KRIEDEMANN. 1975. Plant growth and development. McGraw-Hill, New York.

LICHTENTHALER, H. K., T. J. BACK, AND A. R. WELLBURN. 1982. Cytoplasmic and plastidic isoprenoid compounds of oat seedlings and their distinct labelling from ^{14}C- mevalonate. Pages 489–500 *in* J. F. Winternans, G. M. Kuiper, and P. J. C. Kuiper, eds., Biochemistry and metabolism of plant lipids. Elsevier Biomedical Press, Amsterdam.

LORIMER, G. H., M. R. BADGER, AND T. J. ANDREWS. 1977. D-ribulose-1,5-bisphosphate carboxylase-oxygenase: improved method for the activation and assay of catalytic activities. Anal. Biochem. 78:66–75.

MCARTHUR, E. D., A. C. BLAUER, A. P. PLUMMER, AND R. STEVENS. 1979. Characteristics and hybridization of important intermountain shrubs. III. Sunflower family. USDA Forest Service Research Paper INT-220, U.S Dept. of Agriculture.

MEYERS, S. P., S. L. NICHOLD, G. R. BAER, AND W. T MOLIN. 1982. Ploidy effect in isogenic populations of alfalfa. I. Ribulose-1,5-bisphosphate carboxylase, soluble protein, chlorophyll and DNA in leaves. Plant Physiol. 70:1704–1709.

MILTHORPE, F. L., AND J. MOORBY. 1974. An introduction to crop physiology. Cambridge Press.

MOONEY, H. A., AND J. R. EHLERINGER. 1978. The carbon gain benefits of solar tracking in a desert annual. Plant Cell Environ. 1:307–311.

MOONEY, H. A., J. E. EHLERINGER, AND J. A. BERRY. 1976. High photosynthetic capacity of a winter annual in Death Valley. Science 194:322–324.

OSTLER, W. K. 1980. Selection of acquisitions of *Chrysothamnus* for rubber production. Native Plants Inc., Salt Lake City. NSF Report.

SEEMAN, J. R., AND J. A. BERRY. 1981. Interspecific differences in the kinetic properties of RuBP carboxylase protein. Carn. Inst. Yr. Bk. 81:78–83.

SEEMAN, J. R., J. M. TEPPERMAN, AND J. A. BERRY. 1980. The relationship between photosynthetic performance and levels and kinetic properties of RuBP carboxylase oxygenase from desert winter annuals. Carn. Inst. Yr. Bk. 80:67–72.

WALTER, H., AND E. STADELMANN. 1974. A new approach to the water relations of desert plants. *In* G. W Brown, ed., Desert biology, Vol. 2. Academic Press, New York.

WITTENBACK, V. A., L. C. ACKERSON, R. T. GIAQUINTA, AND R. R. HEBERT. 1980. Changes in photosynthesis, ribulose bisphosphate carboxylase, proteolytic activity, and ultrastructure of soyabean leaves during senescence. Crop. Sci. 20:225–231.