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*Botanical Gazette*, Volume 150, Issue 1 (Mar., 1989), 9-14.

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*Botanical Gazette*

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## INFLUENCE OF PHOTOPERIOD ON GROWTH FOR THREE DESERT CAM SPECIES

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*Agave deserti*, *Ferocactus acanthodes*, and *Opuntia ficus-indica* were maintained in environmental growth chambers under a constant total daily photosynthetically active radiation (PAR) for 1 yr to investigate the effects of photoperiod on growth of these Crassulacean acid metabolism (CAM) species. As the photoperiod was increased from 6 h to 18 h, growth increased 33% for *A. deserti*, 81% for *F. acanthodes*, and 50% for *O. ficus-indica*. Such increases were explained based on PAR saturation of the  $C_3$  photosynthetic carbon reduction cycle utilized by CAM plants during the daytime. In particular, the highest instantaneous PAR occurred for the shortest photoperiod and led to less growth for the same total daily PAR. Also, the total daily net  $CO_2$  uptake, which occurred primarily at night, increased 53% as the photoperiod was increased from 6 h to 18 h for *O. ficus-indica*, even though the accompanying night length decreased. The only other observed morphological effect was the sevenfold increase in the number of new cladodes initiated as the photoperiod was increased from 6 h to 18 h for *O. ficus-indica*. The influence of photoperiod on the daily pattern of net  $CO_2$  uptake and the lack of effect of drought on plant survival under long photoperiods for *O. ficus-indica* differ from previous reports on this and other CAM species.

### Introduction

Net  $CO_2$  uptake occurs primarily at night for Crassulacean acid metabolism (CAM) plants, so the effects of photoperiod on gas exchange and growth can be different for CAM plants than for  $C_3$  and  $C_4$  plants (KLUGE and TING 1978, pp. 102–104, 116–117, 199). For the CAM species *Aloe vera* (CREWS et al. 1976), *Portulacaria afra* (GURALNICK et al. 1984), and *Sedum morganianum* (BRULFERT et al. 1982b), increasing the photoperiod from about 9 h to 15 h has little effect on total  $CO_2$  uptake at night. Increasing the photoperiod over this range increases the maximal rate of net  $CO_2$  uptake at night for *Kalanchoë daigremontiana* (MARCELLE 1975) but reduces the maximal rate for *Ananas comosus* (NOSE et al. 1986). In all but one of these studies (NOSE et al. 1986) on CAM species, the instantaneous level of photosynthetically active radiation (PAR) was constant; that is, the total daily PAR varied when the photoperiod was changed. Very little information appears to have been published on the growth of CAM plants under various photoperiods.

The present study considers photoperiod effects on growth for three species of desert CAM succulents (*Agave deserti*, *Ferocactus acanthodes*, and *Opuntia ficus-indica*) subjected to a constant total daily PAR. Except when young or overwatered, these species have nearly all their net  $CO_2$  uptake at night, as expected for CAM plants (NOBEL 1976, 1977; ACEVEDO et al. 1983; NOBEL and HARTSOCK 1983). For *O. ficus-indica*, this predominance of

nocturnal  $CO_2$  uptake occurs under photoperiods of 9 h and 16 h (BRULFERT et al. 1984), and this was reexamined in the present study. A wide range in photoperiods was employed (6 h–18 h) for plants maintained under a constant thermoperiod, and possible morphological effects of photoperiod were also noted.

### Material and methods

Ramets of *Agave deserti* Engelm. (Agavaceae) and seeds of *Ferocactus acanthodes* (Lem.) Britton and Rose (Cactaceae) were collected from Agave Hill in the University of California Philip L. Boyd Deep Canyon Desert Research Center about 8 km south of Palm Desert, California. Terminal cladodes of *Opuntia ficus-indica* (L.) Miller (Cactaceae) were obtained from the Espinosa Cactus Farm near San Bernardino, California. Plants were initially maintained in a glasshouse in soil from Agave Hill (NOBEL 1976); they received 0.05-strength Hoagland solution no. 1 (HOAGLAND and ARNON 1950) approximately every other week such that the soil water potential in the root zone was always above  $-0.5$  MPa. For the 40 plants of each species selected at the beginning of the growth study, *A. deserti* was 24–26 cm tall with an average of seven leaves unfolded from the central spike of folded leaves, *F. acanthodes* was 3.7–4.3 cm tall, and the single cladodes of *O. ficus-indica* were 23.6–24.7 cm long, the basal one-third of which was placed in the soil.

Eight plants of each species were maintained in each of five environmental growth chambers with different photoperiods (table 1). Photosynthetically active radiation (wavelengths of 400–700 nm, as measured with a LiCor LI-190S quantum sensor) was provided 40% by General Electric LU-400 high-pressure sodium lamps and 60% by General Elec-

Manuscript received May 1988; revised manuscript received September 1988.

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TABLE 1  
MEAN INSTANTANEOUS LEVELS OF PHOTOSYNTHETICALLY ACTIVE RADIATION ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )

MEASUREMENT LOCATION	PHOTOPERIOD (h)				
	6	9	12	15	18
Horizontal plane near tops of plants . . . . .	1,800	1,200	900	720	600
<i>Agave deserti</i> . . . . .	761	516	396	312	263
<i>Ferocactus acanthodes</i> . . . . .	994	776	587	470	391
<i>Opuntia ficus-indica</i> . . . . .	692	461	339	276	230

NOTE.—Data were obtained midway through the 1-yr study period in the environmental growth chambers and represent the means of 10–12 PAR readings at representative locations on the photosynthetic surfaces (the 17% shading of the stem surface by spines for *F. acanthodes* was taken into account, while *O. ficus-indica* was spineless).

tric MV-400 metal halide lamps. PAR was varied using neutral density filters and by adjusting the distance from the lamps to the plants. To make the PAR distribution more uniform over the shoots and to enhance the PAR incident on certain photosynthetic surfaces, such as the vertical sides of the cladodes of *O. ficus-indica*, aluminum foil reflectors were placed around the inner sides of the environmental chambers and adjacent to individual plants. The total daily PAR (instantaneous PAR  $\times$  photoperiod) was maintained constant  $\pm 2\%$  for each species, except for *F. acanthodes*, for which the highest instantaneous PAR was kept below 1,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  to avoid stem bleaching (table 1). The PAR values for each species varied because of their differing shoot morphologies, with a mean total daily PAR on the photosynthetic surfaces of 16.8  $\text{mol m}^{-2}$  for *A. deserti*, 24.5  $\text{mol m}^{-2}$  for *F. acanthodes*, and 14.9  $\text{mol m}^{-2}$  for *O. ficus-indica*. The chambers were maintained at constant day/night air temperatures of 20 C/20 C and a constant relative humidity of approximately 50%. The watering protocol was the same as in the glasshouse.

To allow for acclimatization upon transfer of the plants from the glasshouse, the measurements constituting the beginning of the growth period were made 2 mo after the plants had been in the environmental chambers. Growth, which has been related to net  $\text{CO}_2$  uptake for each of the methods employed, was assessed by the number of leaves newly unfolding from the central spike of folded leaves for *A. deserti* (NOBEL 1984), by changes in stem height for *F. acanthodes* (JORDAN and NOBEL 1982), and by the volume of displaced water upon inverting the shoot to a premarked level near the soil surface into a water-filled chamber for *O. ficus-indica* (NOBEL and HARTSOCK 1987). Final growth measurements were made 1 yr after the initial measurements. After the growth study, the plants of *O. ficus-indica* were subjected to drought for 6 mo to compare with previously reported drought effects on this species (QUEIROZ and BRULFERT 1982).

After 6 mo in the environmental chambers, net  $\text{CO}_2$  exchange of basal cladodes of *O. ficus-indica* over 24-h periods was determined using a modified Siemens compensating closed-circuit gas exchange system (NOBEL and HARTSOCK 1978). All conditions were the same as in the environmental growth chambers, with a mean  $\text{CO}_2$  level of 350  $\mu\text{L L}^{-1}$ , as measured with an Anarad AR-500R infrared gas analyzer. Net  $\text{CO}_2$  uptake was expressed on a total photosynthetic surface area basis (both sides of the cladodes).

## Results

Under a constant total daily PAR, growth tended to increase with the length of the photoperiod for all three species over the 1-yr study period. From the shortest photoperiod of 6 h to the longest of 18 h, leaf unfolding of *Agave deserti* increased by 33% (fig. 1A), the stem height increment of *Ferocactus acanthodes* increased by 81% (fig. 1B), and cladode volume increment of *Opuntia ficus-indica* increased by 50% (fig. 2A). When *O. ficus-indica* was subjected to a 6-mo drought after the growth period, all plants survived for each photoperiod.

Besides the effects on growth, the only other observed morphological influence of photoperiod was on the number of cladodes that developed on the basal cladode of *O. ficus-indica*. In particular, the number of new cladodes increased nearly sevenfold from an average of less than one over the 1-yr study period at a photoperiod of 6 h to more than four at a photoperiod of 18 h (fig. 2B).

The daily pattern of net  $\text{CO}_2$  exchange was also influenced by photoperiod for *O. ficus-indica*. For the shortest photoperiod (6 h), the net rate of  $\text{CO}_2$  uptake decreased 57% from the maximal value by the middle of the night, compared with declines of 34% in the instantaneous rate for a 12-h photoperiod and only 2% for an 18-h photoperiod (fig. 3). For photoperiods of 6 h, 12 h, and 18 h, the maximum rate of net  $\text{CO}_2$  uptake at night was 2.9, 4.1, and 6.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively, and the total  $\text{CO}_2$  uptake over the 24-h period was 73, 96, and

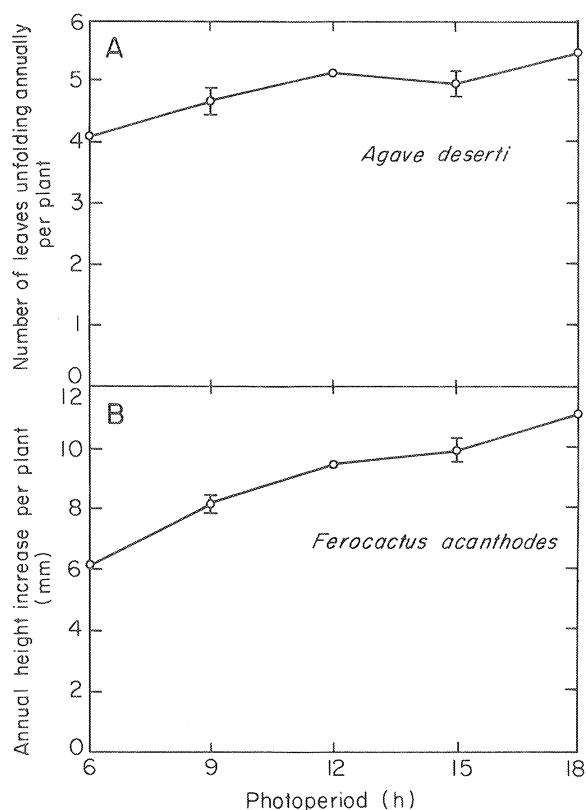


FIG. 1.—Growth of *Agave deserti* (A) and *Ferocactus acanthodes* (B) over a 1-yr period at various photoperiods. The total daily PAR and the air temperature were constant for eight well-watered plants under each condition. Representative standard errors of the mean are presented; one-way analysis of variance indicated significant photoperiod effects on growth ( $P < .001$  for both species).

112 mmol m<sup>-2</sup>. About 95% of the net CO<sub>2</sub> uptake occurred at night for all three photoperiods (fig. 3).

### Discussion

Growth tended to increase with the length of the photoperiod at a constant total daily PAR for all three CAM species examined—*Agave deserti*, *Ferocactus acanthodes*, and *Opuntia ficus-indica*. This growth increase occurred despite the accompanying decrease in length of the night, the time when the net CO<sub>2</sub> uptake was predominantly occurring, at least for *O. ficus-indica*, in agreement with a previous study on this species (BRULFERT et al. 1984). However, to maintain the constant total daily PAR with increasing photoperiod, the instantaneous PAR was decreased, which could have affected growth.

To analyze the effect of instantaneous PAR on growth, the relative growth of the plants per unit time in the light was determined. The shortest photoperiod with its accompanying highest instantaneous PAR led to the greatest growth per unit of photoperiod time (fig. 4), although it led to the least

growth over the entire year (figs. 1, 2A). Moreover, the curve relating growth to instantaneous PAR for all three species had the shape expected for CO<sub>2</sub> fixation by C<sub>3</sub> photosynthesis, approaching saturation at higher levels for which individual photons cannot be as efficiently used in carbon reduction (fig. 4). A similar C<sub>3</sub>-like dependence of the rate of nocturnal acid accumulation on daytime instantaneous PAR has previously been noted for *O. ficus-indica* (NOBEL and HARTSOCK 1983). Therefore, the observed increase in growth with photoperiod at constant total daily PAR apparently represents the PAR-saturation effects of the C<sub>3</sub> photosynthetic carbon reduction cycle taking place in these CAM plants during the daytime. Actually, the same conclusion applies both to any daytime CO<sub>2</sub> uptake, which is directly supported by C<sub>3</sub> photosynthesis, and also to the nighttime CO<sub>2</sub> uptake in the CAM mode, for which the C<sub>3</sub> photosynthesis takes place during the daytime behind closed stomata, leading to the refixation of CO<sub>2</sub> released internally by the decarboxylation of malate.

As the photoperiod was increased from 6 h to 18 h for *O. ficus-indica*, the 53% increase in net CO<sub>2</sub> uptake over a 24-h period was consistent with the

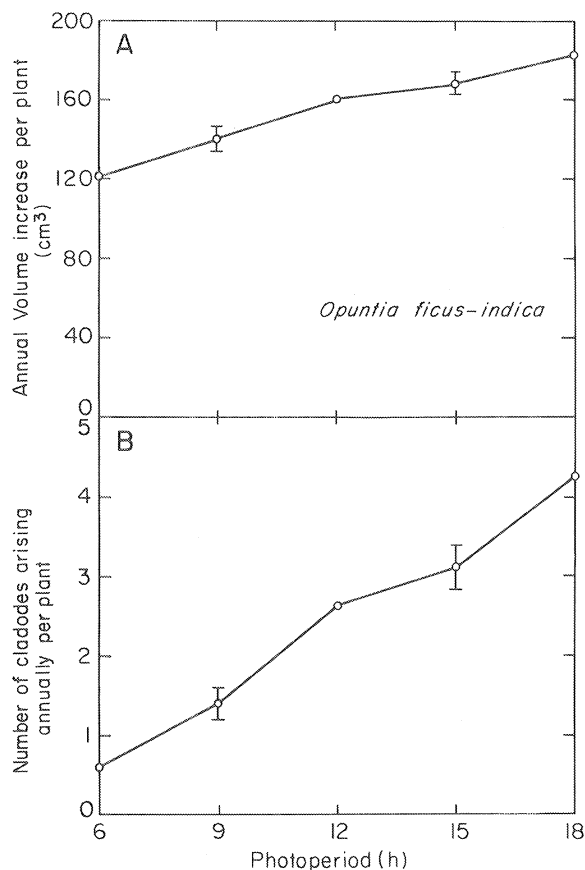


FIG. 2.—Growth (A) and new cladodes formed (B) for *Opuntia ficus-indica* over a 1-yr period at various photoperiods. Conditions are as for fig. 1, including  $P < .001$ .

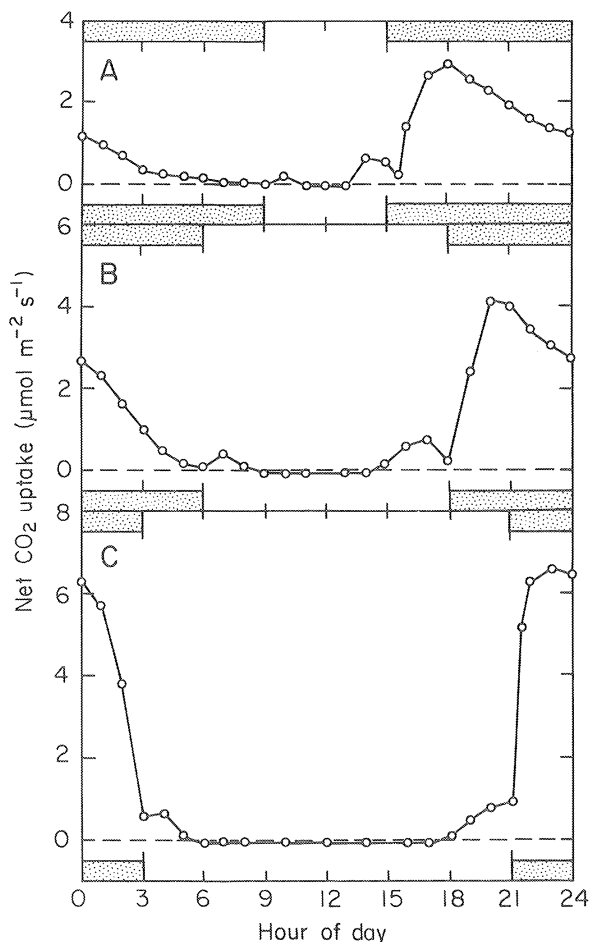


Fig. 3.—Net CO<sub>2</sub> uptake over 24 h for *Opuntia ficus-indica* with photoperiods that were 6 h (A), 12 h (B), and 18 h (C) in duration. Stippled bars indicate night.

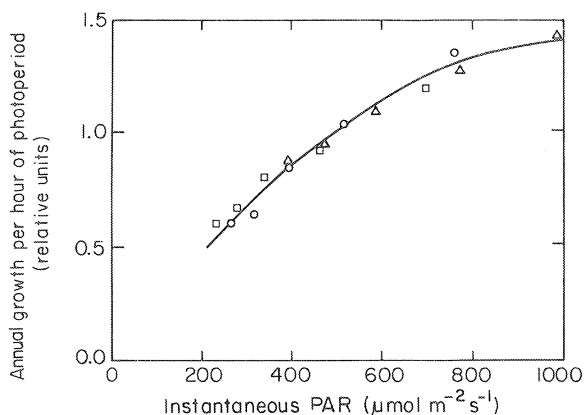


Fig. 4.—Relative growth per unit time of the photoperiod at various PAR levels for *Agave deserti* (○), *Ferocactus acanthodes* (Δ), and *Opuntia ficus-indica* (□). The response (annual growth in figs. 1, 2A divided by photoperiod length in hours) of each species was normalized to unity at an instantaneous PAR of 500 μmol m<sup>-2</sup> s<sup>-1</sup>.

50% increase in annual growth. The longer photoperiod with its accompanying shorter night was associated with higher maximal rates of net CO<sub>2</sub> uptake, similar to results for *Kalanchoë daigremontiana* (MARCELLE 1975) but not for *Ananas comosus* (NOSE et al. 1986). Increasing the photoperiod from 9 h to 16 h for *Kalanchoë blossfeldiana* causes a switch from CAM to C<sub>3</sub> (BRULFERT et al. 1982b), in agreement with early studies on this species (GREGORY et al. 1954) but contrary to the present results with *O. ficus-indica*. For *K. blossfeldiana* and *Kalanchoë velutina*, CAM is promoted by short photoperiods for the young leaves, because aging tends to lead to CAM behavior, even under long-day conditions (BRULFERT et al. 1982a). *Peperomia camptotricha* under an 8-h photoperiod has slightly more nocturnal CO<sub>2</sub> uptake for its older leaves than those with a 14-h photoperiod (SIPES and TING 1985). Thus, photoperiod has different influences on the daily pattern of net CO<sub>2</sub> uptake for different CAM plants.

Photoperiod has many effects on the development and morphological expression of CAM plants. For instance, *Peperomia camptotricha* is about twice as tall after 4 mo with a photoperiod of 8 h compared with 14 h because the shorter photoperiod leads to much greater internodal elongation as well as larger leaves (SIPES and TING 1985). Short photoperiods of 8 h can induce *Kalanchoë blossfeldiana* to flower, whereas photoperiods of 16 h do not (CHATURVEDI and ZABKA 1977). Also, an 8-h photoperiod induces *Ananas comosus* to flower whereas a 16-h photoperiod leads to no flowering but double the number of leaves initiated (FRIEND and LYDON 1979). On the other hand, a 16-h photoperiod leads to flowering of *Sedum telephium* while 8 h does not (LEE and GRIFFITHS 1987). For *Echinopsis* sp. supplied with nutrients, a 14-h photoperiod induces two to three times as many floral buds as 8 h but no change in stem elongation (PUSHKARAN et al. 1980). Flowering of *Mammillaria longicoma* can also be induced by long photoperiods (RÜNGER 1968), but for *Schlumbergera truncata* progressively shorter photoperiods are required for flower induction as the temperature increases from 10 C to 30 C (RÜNGER and FÜHRER 1981).

The present study showed that increasing the photoperiod from 6 h to 18 h at a constant total daily PAR greatly stimulated the production of daughter cladodes for *O. ficus-indica*. The seven-fold enhancement in cladode initiation caused by going from the shortest to the longest photoperiod was proportionally much greater than the accompanying 50% increase in growth. This could reflect the limited expansion possible for the basal cladode so that the additional volume increment under the longer photoperiod might then be diverted to small daughter cladodes, leading to many of them. For *O. ficus-indica* in the field in Chile, cladodes

tend to be initiated in mid- to late spring when the photoperiod is about 13 h (ACEVEDO et al. 1983). Such timing would allow for rapid cladode expansion during the favorable climatic conditions, including higher PAR, of late spring and early summer. For *O. ficus-indica* at certain locations in Israel and California where winter rainfall predominates, cladodes are mainly initiated near the winter solstice (NOBEL 1982), a time when the photoperiod is shortest (about 10 h). This is again consistent with the suggestion that cladode initiation occurs in response to favorable growing conditions, not photoperiod length.

Much remains to be learned and certain discrepancies need to be resolved concerning the photoperiodic responses of CAM plants. For instance, *O. ficus-indica* has been proposed to develop tolerance to drought imposed during long photoperiods when grown under wet conditions for short photoperiods but not for long photoperiods (QUEIROZ and BRULFERT 1982). Specifically, when plants under a 16-h photoperiod (27 C/17 C day/night air temperatures, 70% relative humidity) were subjected to drought (27 C/17 C, 10% relative hu-

midity) they reportedly died in 70 d (QUEIROZ and BRULFERT 1982; J. BRULFERT, personal communication). However, when *O. ficus-indica* under photoperiods of 15 h and 18 h were subjected to drought for 6 mo in the present study, no death occurred. Although useful as a first approximation, especially under field conditions where the instantaneous PAR varies considerably (NOBEL 1977, 1984), the present study shows that net CO<sub>2</sub> uptake and growth are not always uniquely related to total daily PAR. The differing influences of photoperiod and PAR level on such diverse responses as daily patterns of net CO<sub>2</sub> uptake and flowering among CAM plants also need to be better understood through future research.

### Acknowledgments

Technical assistance was competently performed by Mr. TERRY L. HARTSOCK. Financial support was provided by the Ecological Research Division of the Office of Health and Environmental Research, U.S. Department of Energy, contract DE-FC03-87-ER60615.

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