Water Relations, Diurnal Acidity Changes, and Productivity of a Cultivated Cactus, *Opuntia ficus-indica*[1]

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ABSTRACT

Physiological responses of the Crassulacean acid metabolism (CAM) plant *Opuntia ficus-indica* (Cactaceae) were studied on a commercial plantation in central Chile. Young cladodes (flattened stems) and flower buds exhibited daytime stomatal opening, whereas mature cladodes and fruit exhibited the nocturnal stomatal opening characteristic of CAM plants. Severe water stress suppressed the nocturnal stomatal opening by mature cladodes, but their high water vapor conductance occurring near dawn was not affected. Nocturnal acidity increases were not as sensitive to water stress as was the nocturnal stomatal opening. The magnitude of the nocturnal acidity increases depended on the total daily photosynthetically active radiation (PAR), being 90% PAR-saturated at 27 moles per square meter per day for a mean nighttime air temperature of 5°C and at 20 moles per square meter per day for 18°C. Inasmuch as the PAR received on unshaded vertical surfaces averaged about 21 moles per square meter per day, nocturnal acidity increases by the cladodes were on the verge of being PAR-limited in the field. The net assimilation rate, which was positive throughout the year, annually averaged 3.4 grams per square meter per day for 1.0- and 2.0-year-old plants. Plants that were 5.4 years old had 7.2 square meters of cladode surface area (both sides) and an annual dry weight productivity of 13 megagrams (metric tons) per hectare per year when their ground cover was 32%. This substantial productivity for a CAM plant was accompanied by the highest nocturnal acidity increase so far observed in the field, 0.78 mole H$^+$ per square meter.

CAM is generally associated with succulent species such as cacti that conserve water and are relatively slow growing (10, 23, 29). Stomatal opening occurs predominantly at night, when the drop in water vapor concentration from the air spaces within the chlorenchyma to the ambient air is less than during the daytime, thereby reducing transpiration (20). The CO_2 taken up at night is incorporated into four-carbon organic acids that are stored in the vacuoles of the chlorenchyma cells, leading to tissue acidity changes that can be readily measured in the field. Due to the lowered water vapor concentration drop at night and a relatively low stomatal conductance even when the stomata are fully open, the water use efficiency of CAM plants tends to be quite high (20, 28). Indeed, the cactus considered here, *Opuntia ficus-indica*, can

survive in areas with only 200 mm of rainfall year^{-1} (4).

Opuntia ficus-indica, which apparently originated in the American tropics (4), is cultivated on a limited basis in tropical and subtropical areas as well as in hot regions of the temperate zone. Its productivity can be relatively high, a total biomass of 50 Mg (wet weight) ha^{-1} year^{-1} being observed in North Africa (12) and 93 Mg ha^{-1} year^{-1} in Brazil (13; 1 Mg = 1000 kg = 1 metric ton). A fruit productivity of 16 Mg (wet weight) ha^{-1} year^{-1} was measured for approximately 18-year-old irrigated plants in central Chile (25), where about 700 ha of this plant are currently under cultivation. In Argentina, *O. ficus-indica* produced 2.5 Mg (dry weight) of stems and 0.2 Mg of fruit ha^{-1} year^{-1} with a rainfall of 300 mm (1). For comparison, above-ground seasonal productivities for major crops such as wheat and maize can reach 10 to 20 Mg (dry weight) ha^{-1}, of which about 30% is harvested as grain (2, 3, 14).

Relatively little is known about the physiology of the platyopuntia *O. ficus-indica*, although it has been shown that its mature cladodes (flattened stems) can have a fairly high nocturnal acidity accumulation of 0.63 to 0.67 mol H$^+$ m^{-2} in the field (19, 26). In the current study, attention was focused on the diurnal pattern of stomatal opening for various plant ages and parts under well watered and drought conditions. The influence of PAR and nocturnal temperature on diurnal acidity changes was also examined during field studies in central Chile from 1980 to 1982. Productivity measured as dry weight gain per unit area was found to vary markedly with time of year and with plant age.

MATERIALS AND METHODS

Plant Material, Soil, and Climate. *Opuntia ficus-indica* (L.) Miller (Cactaceae) is a perennial succulent native to Mexico, but also widely cultivated in a variety of soils ranging from an almost pure sand-gravel mixture to clay loam. Plants of various ages occur at the commercial plantation used as the study site in Til Til, Chile (33°2′ south latitude, 70°54′ west longitude, 570-m elevation, which is 50 km north-northwest of Santiago, Chile). The initial planting at the study site consisted of placing four cladodes in the ground approximately 1 m apart in a square array (just over half of the stem was placed underground). These arrays occurred at 4-m intervals along rows, which were spaced 5 m apart. The ground cover, determined from a polygon circumscribing the most extreme cladodes on the plants, was 5.6 ± 0.8% (SD, $n = 10$) for 1.9-year-old plants and 32.4 ± 3.9% for 5.4-year-old plants.

The plants were irrigated three times during the dry season (late spring-summer); each irrigation corresponded to a water depth of about 80 mm. The soil was a loamy sand and had the following average characteristics in the main root zone (5 to 40 cm depth): gravel, 30% (this fraction was removed for subsequent soil analy-

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sis); sand, 70% of the nongravel fraction; silt, 18%; clay, 12%; organic matter, 1.1%; pH 6.5; and electrical conductivity, 0.085 mho m^{-1}. Based on a 17-year average (1965–1981) for the Rungue meteorological station (700-m elevation) located 10 km north-northwest of the study site, annual rainfall averages 299 mm, with 68% occurring in the winter (June–August). The daily maximum/minimum air temperatures range from 29.5°C/10.9°C in January to 14.7°C/1.1°C in July.

Physiological Measurements. Physiological measurements were made for terminal, unshaded cladodes 5 to 6 months old on plants that were approximately 5 years old and under wet conditions (soil water potential ≥ −0.3 MPa in root zone), unless indicated otherwise. To measure acidity levels, cylindrical samples across a cladode were collected in triplicate using a cork borer (1.14 cm^2). The chlorenchyma on each side of the sample was separately ground with sand, 30 ml of distilled H$_2$O was added, and the slurry was titrated to pH 6.4 using 10 mM NaOH (7). Data are expressed as mol eq H$^+$ m^{-2} of tissue (surface areas refer to a particular side of a cladode). The nocturnal increase in acidity was the acid level 1 h before sunrise (dawn) minus the level 1 h after sunset (dusk).

Cladode temperatures were measured with copper-constantan thermocouples (0.15 mm in diameter) using a Wescor MJ-55 microvoltmeter and an electronic reference junction (accuracy of ±0.5°C). The thermocouples were inserted 1 mm below the surface in the center of the chlorenchyma. PAR (400 to 700 nm) was determined with a LI-COR LI-190S quantum sensor and an LI-170 meter; measurements were made normal to the cladode surface and were expressed either as instantaneous values (μmol m^{-2} s^{-1}) or integrals for the entire day (mol m^{-2} day^{-1}). Water vapor conductance was measured with a LI-COR LI-60 diffusive resistance porometer equipped with a LI-20S sensor that was calibrated immediately before and after each use. Plant and soil water potentials were measured with Wescor PT-05 thermocouple psychrometers read with an HR-33 dewpoint microvoltmeter.

Growth and Productivity. Surface area and dry matter were measured in the field at various times for plants initially 0.4, 1.4, or 4.9 years old. The area of both sides of a cladode (both sides were used because the cladodes are opaque) was calculated from 1.462 × length × width (r^2 = 0.98), a relationship derived using the projected areas of 33 cladodes of various sizes. Dry matter for each plant age was determined at each sampling time using about 20 cladodes from neighboring plants dried in a forced-air oven at 70°C until no further weight change occurred. Regressions of dry weight against area were performed for each cladode age and plant age, since the specific weight of the cladodes changed with time.

The NAR[3] was calculated using the following relationship (14):

$$\mathrm{NAR} = \frac{DW_2 - DW_1}{(t_2 - t_1)\bar{A}}$$

where DW_1 is the dry weight at time t_1, DW_2 the dry weight at t_2, and $\bar{A}$ is the average photosynthetic area for the time interval $t_2 - t_1$.

RESULTS

Stomatal Conductance. The diurnal pattern of stomatal opening depended on the age of the plant part (Fig. 1). For 2-week-old cladodes, stomatal opening occurred during the daytime and the maximal and the minimal water vapor conductances were both relatively large. For a 6-month-old cladode, nocturnal stomatal opening characteristic of the CAM mode was observed (Fig. 1A); very similar diurnal patterns were observed for cladodes 2 months old and 3.5 years old (data not shown; cladode length was about
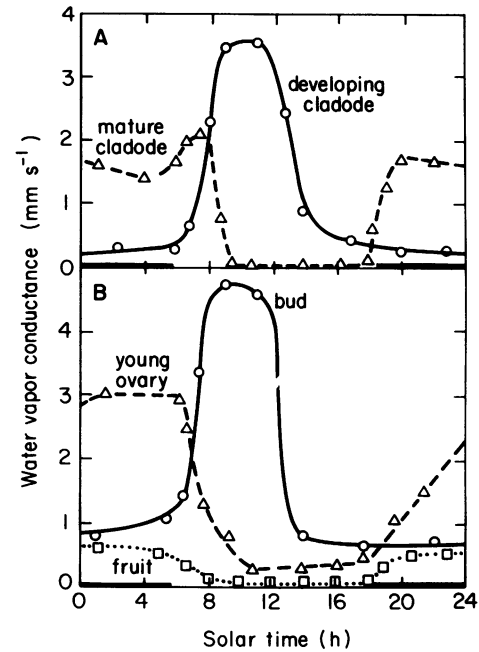
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[3] Abbreviation: NAR, net assimilation rate.

FIG. 1. Diurnal changes in water vapor conductance. A, Developing cladode (2 weeks old) and mature cladode (6 months old); B, flower bud (1 week old), pericarp of young ovary (about 3 weeks old), and maturing fruit (about 1.5 months old). Data were obtained on east-facing side of unshaded plant parts on February 25, 1981 (soil water potential ≥ −0.3 MPa).
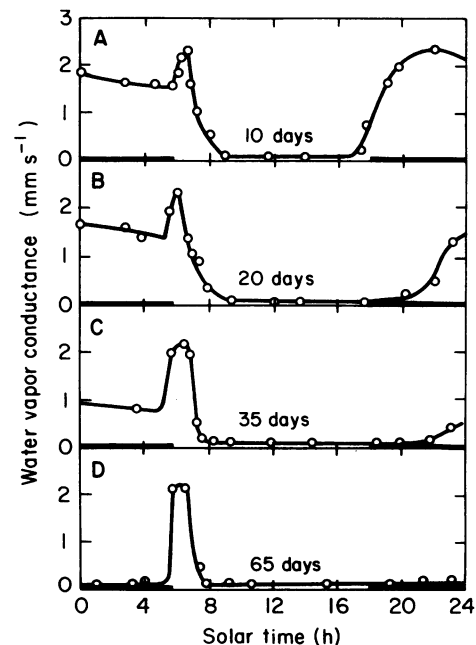

FIG. 2. Effect of drought period (indicated in days) on water vapor conductance of mature cladodes (about 5 months old). Data were obtained on March 17, 1982 for east-facing side of cladodes on plants that had been irrigated at various times. A, Irrigated 10 d earlier (soil water potential in root zone of −0.1 MPa); B, 20 d (−0.3 MPa); C, 35 d (−0.8 MPa); and D, irrigated 65 d earlier (−2.5 MPa).

4 cm at 2 weeks, 21 cm at 2 months, 30 cm at 6 months, and 35 cm at 3.5 years). Similarly, young flower buds had a non-CAM stomatal rhythm, while the young ovary and the fruit (mature ovary) had CAM rhythms (Fig. 1B). As the fruit matured, the
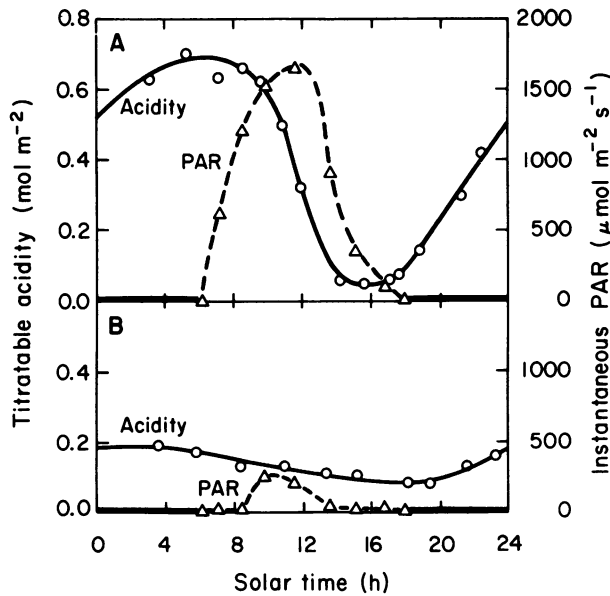
FIG. 3. Diurnal changes in titratable acidity and incident PAR. Data were obtained on September 9, 1980 for (A) an approximately north-facing unshaded cladode receiving a total daily PAR of 36 mol m^{-2} d^{-1}, and (B) a shaded cladode receiving 3.5 mol m^{-2} d^{-1}.
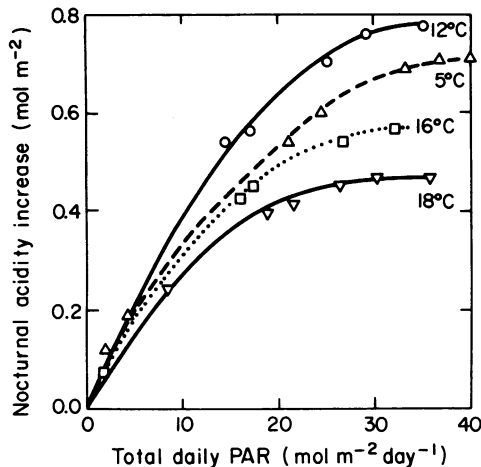

FIG. 4. Influence of total incident daily PAR on nocturnal acidity increases at various temperatures. Mean nocturnal air temperatures are indicated next to the curves (cladode temperatures were generally within ±1°C of air temperatures). Dawn minus dusk acid levels were determined under wet conditions (soil water potential ≥ −0.3 MPa) for cladodes of various orientations and shading (and hence various PAR values) on September 9, 1980 (mean nocturnal air temperature of 5°C; minimum nocturnal air temperature of 0°C), December 22, 1980 (16°C; 9°C), January 9, 1981 (12°C; 7°C), and February 26, 1981 (18°C; 11°C).

stomata became progressively nonfunctional, e.g. the maximal water vapor conductance was only 0.2 mm s^{-1} for mature green fruit (about 2.5 months old).

The diurnal stomatal rhythm was also influenced by water status. To vary water status, groups of plants were irrigated at various times before the diurnal pattern of stomatal opening was determined (Fig. 2) during a period with no rainfall. Tissue water potential was relatively uninfluenced by up to 20 d of drought (remaining −0.73 ± 0.15 MPa, SD for five measurements in each case), but decreased substanially after 65 d of drought (to −1.12 ± 0.11 MPa). (The dry matter averaged 10.9 ± 1.3% of the wet weight for up to 20 d of drought and 20.6 ± 0.5% for 65 d of drought.) The main influence of progressively greater drought on
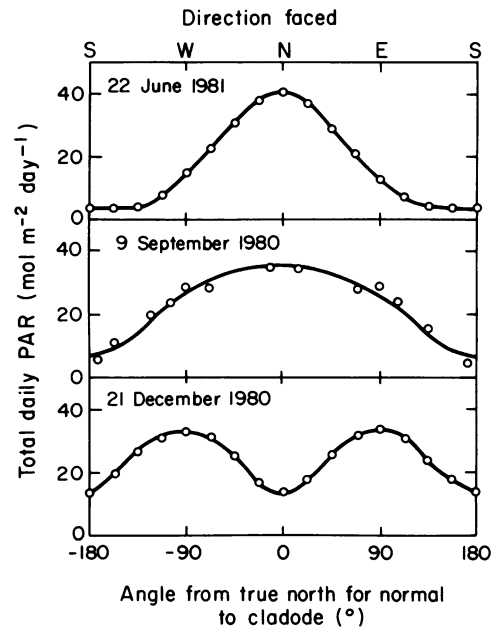

FIG. 5. Influence of direction faced by unshaded vertical surface on the interception of PAR. Instantaneous values of PAR were measured approximately hourly on clear days near the winter solstice (June 22, 1981), spring equinox (September 9, 1980), and summer solstice (December 21, 1980). Total daily PAR was determined graphically as the integral of the hourly values (17).
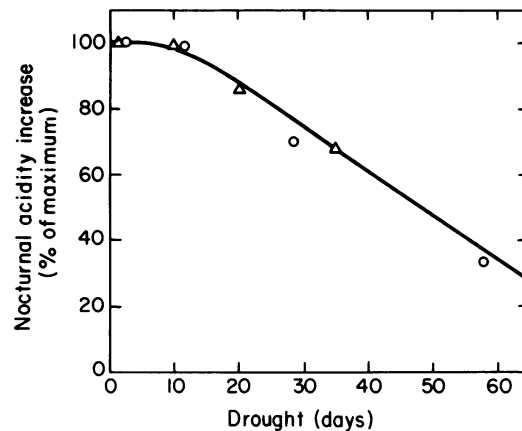

FIG. 6. Effect of drought period on nocturnal acidity increase. Data were obtained on April 8–9, 1980 (○) and March 16–17, 1982 (△; see Fig. 2) for cladodes receiving an incident PAR of at least 23 mol m^{-2} d^{-1}.

stomatal opening was to delay the onset of nocturnal opening and to decrease the maximum water vapor conductance at night. The stomatal opening observed at dawn and the maximum water vapor conductance at this time were little influenced by water stress (Fig. 2).

Diurnal Acidity Changes. The chlorenchyma of *O. ficus-indica* exhibited the characteristic CAM pattern for titratable acidity, having a minimum at dusk and a maximum at dawn (Fig. 3). The CAM pattern depended on cladode age, since a 2-week-old developing cladode (Fig. 1A) had essentially no diurnal change in acidity, while a 2-month-old cladode had the same pattern as a mature 6-month-old cladode (Fig. 3) or a 3.5 year-old cladode (the latter had 18% less nocturnal acid accumulation than the 6-month-old cladode). A 4-week-old cladode was intermediate, exhibiting both daytime and nighttime stomatal opening and 20% as much nocturnal acid increase as a 6-month-old cladode. The diurnal acidity changes were also affected by the PAR intercepted
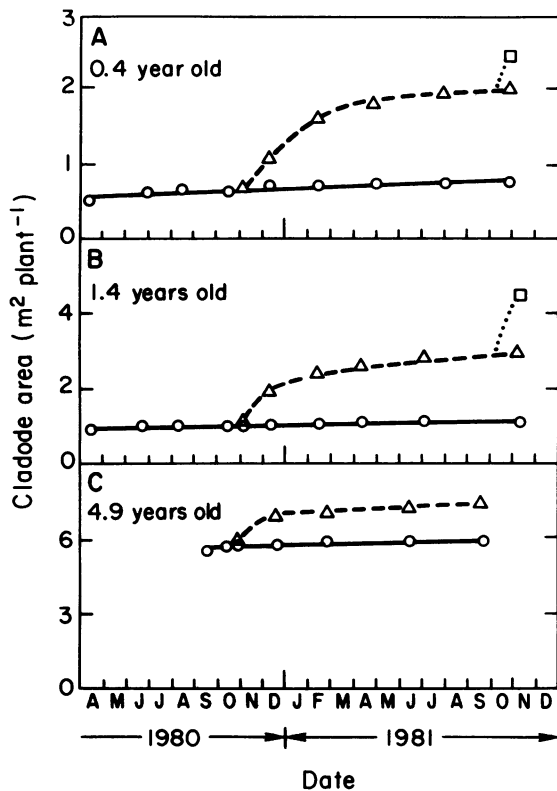
FIG. 7. Changes in cladode area (both sides) with time for plants of various ages (initial ages indicated). The initial average number of cladodes per plant was 9.7 (n = 16) for the plants 0.4 year old, 11.8 (n = 12) for those 1.4 years old, and 55.5 (n = 4) for those 4.9 years old (growth of these original cladodes indicated by O). These three age groups added an average of 16.8, 15.7, and 27.0 cladodes, respectively, during the next year of growth (△). At the beginning of the next growth season (□), the plants initially 0.4 year old added an additional 10.4 cladodes/plant and those initially 1.4 years old added 38.0 cladodes.
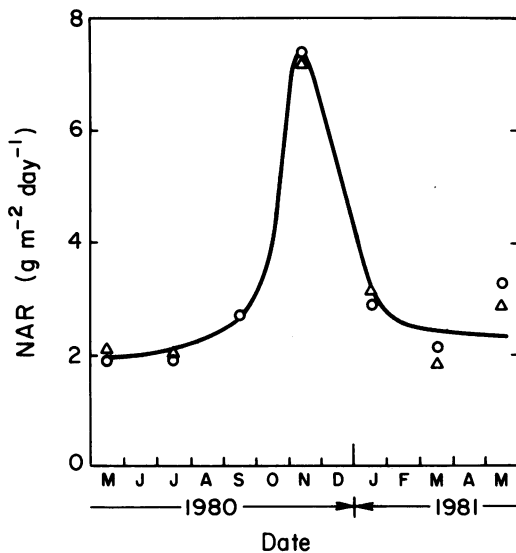

FIG. 8. Net assimilation rates at various times of the year. Data are for plants that were initially 0.5 (O) or 1.5 (△) years old.

by the cladode. A 10-fold increase in total daily PAR from 3.5 to 36 mol m^{-2} day^{-1} caused the nocturnal acid accumulation to increase from 0.11 to 0.64 mol m^{-2} (Fig. 3).

The influence of PAR on nocturnal increases in acidity was also

Table I. *Annual Biomass Productivity (Dry Weight) for O. ficus-indica of Various Ages*

All cladodes were measured on 16 plants with a mean age of 1.2 years, on 12 plants of 2.2 years, and on 4 plants of 5.4 years. Cladode area was regressed against dry weight determined on about 20 cladodes from neighboring plants of the same age at each sampling date, and fruit dry weights were determined on 15 fruits under each condition (1 Mg = 1000 kg = 1 metric ton).

Mean Plant Age	Sampling Period	Productivity		
		Cladodes	Fruit	Total
years		*Mg ha^{-1} year^{-1}*		
1.2	August 1980–August 1981	3.75	0.10	3.85
2.2	August 1980–August 1981	5.31	0.34	5.65
5.4	October 1980–October 1981	10.50	3.15	13.15

examined for nights of various temperaures (Fig. 4). The PAR responses were independent of cladode age from 2 months to 14 months, the data reported referring to cladodes 5 to 6 months old. Nocturnal acidity increases reached 90% of maximal for 27 mol m^{-2} d^{-1} at 5°C mean nocturnal temperature, 23 mol m^{-2} d^{-1} at 12°C, 21 mol m^{-2} d^{-1} at 16°C, and 20 mol m^{-2} d^{-1} at 18°C (Fig. 4). Nocturnal acidity increases were greatest near a mean nocturnal temperature of 12°C.

Inasmuch as PAR levels have such a major influence on nocturnal acid accumulation, values expected for vertical surfaces (appropriate for the cladodes of *O. ficus-indica*) were determined in the field at various times of the year (Fig. 5). Near the summer solstice, unshaded cladodes facing east-west intercept the highest PAR, while near the winter solstice a side facing north intercepts the most although its opposite side receives very litle PAR. Near an equinox, an east-west-facing cladode intercepts about 30% more PAR than a north-south-facing one (Fig. 5).

As would be expected from its effect on stomatal opening (Fig. 2), drought also affected the diurnal acidity changes of *O. ficus-indica* (Fig. 6). The nocturnal rise in acidity decreased after about 2 weeks of drought, and it was only one-third of the maximum value after 2 months.

Growth and Development. The total cladode area per plant increased approximately linearly with plant age up to 6 years, e.g. it was 0.6 m^2 at 6 months, 4.5 m^2 at 36 months, and 7.4 m^2 at 72 months (Fig. 7). However, the development and expansion of new cladodes was seasonal, most of the area expansion occurring in the late spring and early summer (October to January). Once past the initial expansion phase of about 3 months, individual cladode area increased approximately linearly with time, although it varied with plant age. The annual increase in area averaged 30% for all the cladodes on plants initially 0.4 year old, 14% for those 1.4 years old, and 3% for those 4.9 years old (Fig. 7). Due to the fairly slow growth of older cladodes, most of the source of new photosynthetic area for a plant is from the expansion of the new cladodes. Floral bud and initial fruit development tended to occur in late spring and early summer, hence overlapping with cladode development.

An increase in dry weight occurred throughout the year, as evidenced by a positive net assimilation rate (Fig. 8). The highest NAR, exceeding 7 g m^{-2} d^{-1}, was attained in the late spring, a time when dry matter was accumulating rapidly but before the rapid expansion in total cladode area (Fig. 7) and before the increasing environmental temperatures in the summer. A moderately low NAR of about 2 g m^{-2} d^{-1} occurred during the winter (Fig. 8).

The annual productivity of *O. ficus-indica* in three fields is summarized in Table I. The productivity per unit ground area tended to increase with plant age, especially for the fruit. The

annual productivity for plants of mean age 5.4 years, which led to a ground cover of 32.4%, was over 13 Mg (dry weight) ha^{-1} $year^{-1}$.

DISCUSSION

Mature cladodes of *O. ficus-indica* exhibit characteristic CAM behavior (10, 23, 29), as indicated by diurnal stomatal rhythms and changes in acidity levels observed in the field. Both the nocturnal stomatal opening and the nocturnal acid accumulation were diminished by water stress (Figs. 2 and 6), as also occurs for other CAM plants (*e.g.* 5, 15). Stomatal opening was affected to a greater degree, since a 65-d drought nearly eliminated nocturnal stomatal opening but considerable nocturnal acid accumulation still occurred, in agreement with studies on *O. ficus-indica* under laboratory conditions (22) as well as studies on other cacti (6, 24, 27, 28). Contrary to the case for mature organs, young organs such as flower buds and 2-week-old developing cladodes exhibit day-time stomatal opening (Fig. 1) and essentially no diurnal acidity fluctuations, presumably reflecting C_3 photosynthesis. Analogous observations of C_3 photosynthesis for young plants gradually changing to CAM as the plants mature have been made for a number of species (10) including *Agave deserti* (8) and *Mesembryanthemum crystallinum* (30).

The dawn stomatal opening of mature cladodes, which may support C_3 photosynthesis, occurs when the cladodes are at their lowest daytime temperature, and hence transpiration is then less for a given water vapor conductance than it would be during the rest of the day. Such stomatal opening was relatively unaffected by water stress in *O. ficus-indica*, although it decreased markedly with water stress for another cactus, *Ferocactus acanthodes* (16). The progressive decrease in nocturnal water vapor conductance with increasing drought clearly conserves water, as does the delay after dusk for the limited stomatal opening that does occur, because the cladode temperature steadily decreases through the night (also observed for *F. acanthodes*; Ref. 16). For the conditions of Figure 2, delaying a given degree of stomatal opening for 2 h after dusk reduces the calculated transpiration rate by 40% compared to opening at dusk, and a delay of 6 h reduces it by 80%. The water vapor conductance for the developing organs during the daytime was greater than the water vapor conductance during the nighttime for mature organs (Fig. 1). This higher water vapor conductance for the young organs is most likely accompanied by higher rates of CO_2 upake at a time when the advantage of increased carbon gain apparently outweighs the disadvantage of increased water loss.

Tissue acidity, which increases approximately linearly with time over the first half of the night, is markedly influenced by PAR (Fig. 3). Although instantaneous values of PAR have an effect, because a high PAR for a short time leads to less acid accumulation by *O. ficus-indica* than does the same total PAR over a longer time (22), total daily PAR has proved to be a convenient index for nocturnal acid accumulation in the field (17, 18). A 90% saturation of nocturnal acid accumulation and CO_2 uptake generally occurs for a total daily PAR of 20 to 25 mol m^{-2} d^{-1} for CAM plants (9, 16, 18, 19, 21). For *O. ficus-indica*, the PAR for 90% saturation steadily decreased from 27 to 20 mol m^{-2} d^{-1} as the mean nighttime temperature increased from 5°C to 18°C (Fig. 4). Evidently, the limitation on acid accumulation by some temperature-dependent process(es) at lower temperatures can be overcome by a higher PAR, or perhaps higher temperatures may enhance the photoinhibition that can occur at high PAR levels (22).

The 90% PAR saturation of nocturnal acid accumulation occurred at approximately the average PAR received by a randomly oriented vertical surface at various times of the year, 21 mol m^{-2} d^{-1} (Fig. 5). Increases above the average PAR do not enhance acid accumulation or the underlying CO_2 uptake that it represents because of the proximity to PAR saturation, whereas any decrease below the average PAR, such as on cloudy days, for shaded cladodes, or for cladodes facing in a nonoptimal direction, will decrease nocturnal acid accumulation and, hence, productivity. This case of incipient PAR limitation in putatively high radiation environments has been pointed out for other CAM plants (17, 18). In a matter related to PAR limitations, the cladodes of *O. ficus-indica* are not randomly oriented in the field, but rather they tend to face in a direction that maximizes PAR interception at a time of the year favorable for growth (19). For the irrigated fields in Chile, new growth is greatest in the late spring and early summer (Fig. 7), similar to field data on *Opuntia humifusa* (11), when facing east-west leads to more PAR absorption by a cladode (Fig. 5). Indeed, 2.7 times more cladodes faced within ±15° of east-west than north-south on 5-year-old plants at Til Til (19).

The use of an analogy to leaf area index (total leaf area per ground area) is not really appropriate for vertically oriented surfaces, such as the cladodes of *O. ficus-indica*, unless the vertical distribution in space and, hence, mutual shading is also indicated. Nevertheless, a cladode area index can give some idea of the photosynthetic surface area available. For 5.4-year-old plants, the total cladode area of both sides is 7.2 m^2 (Fig. 7), and based on the observed ground cover, each plant occupies an average area of 1.62 m^2. The cladode area index is thus 4.4 based on the ground area under the cladodes of the plants and 1.4 based on the total ground area in the field (there were 2000 plants ha^{-1}).

The dry matter gain by *O. ficus-indica* over the year can be related to nocturnal increases in acidity. The net assimilation rate for plants averaging 1.0 and 2.0 years in age ranged from 2 to 7 g m^{-2} d^{-1}, with a mean of 3.43 g m^{-2} d^{-1} (Fig. 8). For 5.4-year-old plants, the annual productivity was 13.15 Mg (dry weight) ha^{-1} $year^{-1}$ (Table I), which for their surface area of 7.2 m^2 corresponds to a NAR of 2.50 g m^{-2} d^{-1}. The somewhat lower NAR for the older plants may be primarily due to a lower PAR for them than for the younger plants, because the older plants have more cladode self-shading, and the fact that PAR is on the verge of being limiting, even for unshaded cladodes. Inasmuch as at least $2H^+$ are produced per CO_2 taken up at night by *O. ficus-indica* (22) and assuming that the dry matter is carbohydrate (mol wt of 30/C), then a NAR of 3 g m^{-2} d^{-1} corresponds to a nocturnal acidity increase of at least 0.2 mol m^{-2}. This number represents dry matter production, which due to respiration probably accounts for only about 60% to 70% of the assimilated carbon. Hence, an actual nocturnal acidity increase of about 0.3 mol m^{-2} might be expected. This is a substantial nocturnal acidity increase to be maintained over an entire year, *e.g.* it corresponds to that expected at a PAR on the cladodes of about 10 mol m^{-2} d^{-1} when soil moisture is not limiting (Fig. 4).

The annual productivity of *O. ficus-indica* can be substantial and at more than 13 Mg ha^{-1} $year^{-1}$ for 5.4-year-old plants is comparable to that of one growing season for conventional crops such as wheat and maize (2, 3, 14). For plants of this age, the fruits represent 24% of the annual gain in biomass (Table I) and are a commercial crop in Chile. The high productivity of *O. ficus-indica* is reflected in its high amount of nocturnal acid accumulation of up to 0.78 mol m^{-2} (Fig. 4), which apparently surpasses other field measurements on this species (19, 26) as well as on all other CAM plants, *e.g.* maximum uptake in the field is 0.65 mol m^{-2} for *A. deserti* (31), 0.70 mol m^{-2} for *Opuntia inermis* (24), and 0.76 mol m^{-2} for *Opunta chlorotica* (17). Furthermore, irrigated *O. ficus-indica* can maintain a substantial net assimilation rate throughout the year (Fig. 8), and individual cladodes can remain photosynthetically active for at least 4 years. Because of these attributes, this species may assume greater agronomic importance in the future as well as provide physiological information on the interrelationships between water status, temperature, and PAR of CAM plants.

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