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Prediction and measurement of high annual productivity for *Opuntia ficus-indica*

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ABSTRACT

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Certain highly productive crops grown under optimal conditions can have annual aboveground dry matter productivities exceeding 30 Mg ha^{-1} year^{-1}. Recent modeling has predicted that the prickly pear cactus, *Opuntia ficus-indica* (L.) Miller, also can achieve such biomass productivity at close plant spacing. The objective of the present study was to test this prediction in the field during a 27 month experiment in central Chile. Mature cladodes of *Opuntia ficus-indica* were planted at 23 cm intervals along nine rows spaced 17 cm apart. Water and nutrients were not limiting; daily values of temperature and the photosynthetic photon flux density (PPFD) were recorded at the field site. Daily meteorological data were used in a model developed previously in order to predict PPFD interception and dry matter production per row based on the initial plant morphology and the morphology at 15 months. The number, average surface area, and dry weight of cladodes (stem segments) produced were determined by harvesting after 15 and 27 months. Both simulated and measured production per unit row length was highest for the outermost two rows. The central five rows acted as a relatively uniform field, for which measured productivities per unit ground area averaged 40 Mg ha^{-1} year^{-1}, in agreement with predicted values. Further analysis indicated that the dry matter productivity of *Opuntia ficus-indica* could reach 50 Mg h^{-1} year^{-1}.

INTRODUCTION

Productivity varies considerably among species and with their ambient environmental conditions, averaging as low as 1 Mg (1 t) aboveground dry matter per hectare per year for arid regions without irrigation (Leith and Whittaker, 1975). High annual productivities occur for the C_4 species *Saccharum officinarum* (sugar cane), which can produce 40–66 Mg ha^{-1} year^{-1} in regions with 2 m of annual rainfall (Evans, 1975; Beadle et al., 1985), and for the C_3 species *Medicago sativa* (alfalfa), which can produce 21–34 Mg ha^{-1}

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year^{-1} under irrigation (Loomis et al., 1971; Odum, 1971). The productivity of many agronomic crops, including *Glycine max* (soybean), *Oryza sativa* (rice), *Sorghum bicolor* (sorghum), *Triticum aestivum* (wheat), and *Zea mays* (maize), is 10–20 Mg ha^{-1} year^{-1} (Loomis et al., 1971; Odum, 1971; Evans, 1975; Beadle et al., 1985). Crassulacean acid metabolism (CAM) plants such as the prickly pear cactus *Opuntia ficus-indica*, the object of the present study, are often considered to have lower productivities than C_3 or C_4 plants. Indeed, the productivity of *Opuntia ficus-indica* under cultivation is generally below 10 Mg ha^{-1} year^{-1} worldwide (Nobel, 1988), although it and other opuntias can produce 20 Mg ha^{-1} year^{-1} (Griffiths, 1915; Monjauze and Le Houérou, 1965). *Opuntia ficus-indica* is cultivated in more than 20 countries for its fruits, young cladodes (stem segments) used as a vegetable, and mature cladodes used as cattle forage and fodder (Hernández Xolocotzi, 1970; Russell and Felker, 1987; Nobel, 1988).

For a commercial plantation near Santiago, Chile, *Opuntia ficus-indica* has a measured aboveground productivity of 14 Mg ha^{-1} year^{-1} when the stem area index (SAI; total area of both sides of the cladodes per unit ground area) is 1.4 (Garcia de Cortázar et al., 1985). For a close spacing with the planted cladodes nearly touching along rows spaced only 17 cm apart yielding an SAI of 4–6, its predicted productivity is 30 Mg ha^{-1} year^{-1} (Garcia de Cortázar and Nobel, 1986). The model underlying this prediction uses a ray-tracing technique to determine the interception of the photosynthetic photon flux density (PPFD, 400–700 nm) by individual cladodes; the direct solar beam is divided into a number of sub-beams, each of whose incidence on subsurfaces of the shoot is traced in the model. Environmental influences on net CO_2 uptake and hence productivity are then described quantitatively by a dimensionless environmental productivity index, EPI (Nobel, 1984, 1988). The environmental productivity index equals a PPFD index, multiplied by a temperature index, multiplied by a water index. Each component index indicates the fraction of maximal net CO_2 uptake expected based on the ambient value of that environmental factor, so a component index is unity when that environmental factor does not limit net CO_2 uptake over a 24 h period. Thus, EPI represents the fraction of maximal net CO_2 uptake expected under the prevailing environmental conditions, giving a first-order approximation of the influence of PPFD, temperature, and soil water status on net CO_2 uptake and hence on productivity. Nutrient effects on productivity can be incorporated using another multiplicative index, a nutrient index, which has been quantified for five soil elements (nitrogen, phosphorus, potassium, sodium, and boron) for various agaves and cacti (Nobel, 1989).

Although general in principle, so far EPI has been applied only to CAM plants (Nobel, 1988). This is partly because of the nature of CAM plants, as their net CO_2 uptake occurs at night and as such is not related to the instantaneous PPFD level but rather to the total daily PPFD (Kluge and Ting, 1978;

Nobel and Hartsock, 1983; Nobel, 1984, 1988). Using EPI based on CO_2 exchange over 24 h periods, productivity has been predicted for the CAM species *Agave deserti, Ferocactus acanthodes*, and *Opuntia ficus-indica* in the southwestern United States (Nobel and Hartsock, 1986). Annual EPI has also been predicted for *Agave lechuguilla* in eleven states in Mexico and two in the United States (Quero and Nobel, 1987). Such predictions of productivity are within 5% of those measured using dry weight yields obtained upon harvesting the plants (Acevedo et al., 1983; Nobel, 1984).

A predicted productivity of 30 Mg ha^{-1} $year^{-1}$ for *Opuntia ficus-indica* is greater than productivities observed for most other agronomic plants and, indeed, has apparently not previously been measured for *Opuntia ficus-indica* in the field. Field experiments were therefore designed incorporating the close plant spacing predicted by the model to yield high productivities under conditions when EPI is relatively high (Garcia de Cortázar et al., 1985; Nobel, 1988; Garcia de Cortázar and Nobel, 1990). Annual productivities of *Opuntia ficus-indica* per unit ground area were measured and compared with predictions for the close plant spacing utilized.

MATERIALS AND METHODS

Mature cladodes of *Opuntia ficus-indica* (L.) Miller (Cactaceae) were obtained from a commercial plantation in El Noviciado, Chile (about 20 km west of Santiago) and were planted at La Rinconada Agricultural Experiment Station of the University of Chile (about 20 km southwest of Santiago at 33°19′S, 70°55′W, 500 m elevation). The cladodes, which averaged 38 cm in length and 22 cm in width, were planted on 20–22 January 1988 with half their length below ground at center-to-center intervals of 23 cm in nine rows spaced 17 cm apart. The rows were 12 m long and were oriented north–south with the cladodes facing east–west; the plants were not shaded by other vegetation.

Weeds were removed weekly and the soil in the root zone was kept wet (soil water potential greater than -0.3 MPa) by the seepage of water from adjacent irrigation channels. Soil and cladode analysis indicated no nutrient limitations. Specifically, in January 1988 the soil nutrient levels on a dry weight basis for ten pooled samples averaged 2500 mg N kg^{-1}, 59 mg P kg^{-1}, and 229 mg K kg^{-1}, leading to component indices of the nutrient index (Nobel, 1989) of 0.94, 1.00, and 0.99, respectively. For nine cladodes harvested in July 1989, mean $\pm$ SD values were $1.90 \pm 0.16\%$ for nitrogen, $0.27 \pm 0.04\%$ for phosphorus, and $5.05 \pm 0.29\%$ for potassium, all relatively high compared with other data for *Opuntia ficus-indica* and for other cactus species (Nobel, 1983).

Daily weather data at the field site for radiation, temperature, and rainfall were recorded with a LI-COR (Lincoln, NE) LI-1200S weather station. Such weather data were used to calculate daily values of the PPFD (photosynthetic photon flux density; wavelengths of 400–700 nm) index and temperature index based on responses of net CO_2 uptake over 24-h periods for *Opuntia ficus-indica* previously determined in the laboratory (Nobel and Hartsock, 1983, 1986; Garcia de Cortázar and Nobel, 1990). For instance, the PPFD index is 0.00 at a total PPFD of 2 mol m^{-2} day^{-1} (light compensation), 0.25 at 10 mol m^{-2} day^{-1}, 0.81 at 20 mol m^{-2} day^{-1} and 1.00 at 35 mol m^{-2} day^{-1} (light saturation). Net CO_2 uptake by CAM plants occurs predominantly at night (Kluge and Ting, 1978), so the temperature index is often related to minimum temperatures (Nobel, 1988). For *Opuntia ficus-indica*, the temperature index is 0.48 at a minimum nighttime temperature of 0°C, 0.98 at 10°C, 0.76 at 20°C, and 0.01 at 30°C. Because the plants were maintained under wet conditions, the water index was 1.00 throughout the study, so EPI was equal to the PPFD index multiplied by the temperature index.

The PPFD index was also calculated daily using a simulation model that incorporated a ray-tracing technique (Garcia de Cortázar et al., 1985) for a stem area index (SAI) of 4.0 and also for the initial plant morphology as well as the morphology observed after 15 months for the nine rows. The plants for the SAI of 4.0 represented a field with single cladodes on basal cladodes half-buried in the soil (structure I of Garcia de Cortázar and Nobel, 1986). The initial plant morphology corresponded to the basal cladode only. Based on the growth measured in the field, the morphology at 15 months was approximated by plants with four cladodes (in addition to the basal cladode) for the five interior rows, 12 cladodes for the two exterior rows, and six cladodes for the other row on each side; in the model such cladodes were placed vertically in pairs on the basal cladode with equal numbers facing north–south and east–west.

The model used cladodes that had the mean observed length and width (29 cm and 15 cm, respectively), and each side of each cladode was divided into approximately 150 subsurfaces whose Cartesian coordinates were known. The direct solar radiation was divided into approximately 20 000 evenly spaced parallel sub-beams for each plant; the first subsurface intercepting a sub-beam was counted as exposed to the sun and any other subsurfaces that intercepted the same sub-beam were counted as in shadow. If a sub-beam did not strike any subsurface of a particular plant, it might impinge upon the ground, leading to reflected radiation, or might impinge on a subsurface of an adjacent plant. Diffuse radiation from the sky and the ground was assumed to be isotropic, and occlusion by other parts of the same plant or by adjacent plants was taken into account for each subsurface. When a solar sub-beam was intercepted, the angle between the normal to the subsurface and the sub-beam was calculated, leading to a determination of the incident direct PPFD. Diffuse and direct PPFD were calculated hourly and then integrated over the daytime for each subsurface. Based on the response of net CO_2 uptake by *Opuntia ficus-indica* to total daily PPFD (Nobel and Hartsock, 1983, 1986), the PPFD index was calculated for each subsurface and then averaged over the shoot surface for each day.

To calculate productivity per unit row length for plants of the indicated geometry in each row, the PPFD index was determined daily for the 15 month period under field conditions for plants in each row. The environmental productivity index was then averaged daily over the 15 month period for the initial morphology (the planted cladode) and plants with the 15 month morphology for each row; each such EPI was multiplied by the total cladode area per unit row length, the maximum net CO_2 uptake per unit cladode area for *Opuntia ficus-indica* (0.344 mol CO_2 m^{-2} day^{-1}; Nobel and Hartsock, 1983), the 454 days in 15 months, and the conversion factor of 0.027 kg dry weight per mole of CO_2 fixed (Salisbury and Ross, 1991) to give the productivity per unit row length.

On 20 April 1989 and 20 April 1990, all cladodes on 36 plants (four plants chosen randomly from each of the nine rows) were harvested for determination of cladode area and dry weight. Also, fruits were harvested for measurement of both fresh weight and dry weight. Dry weights were determined after drying at 65 °C in a forced-draft oven until a constant weight was obtained (2–5 days; the surfaces of the larger cladodes were cut to facilitate drying).

RESULTS

Daily and seasonal variations were apparent for EPI and its component indices for *Opuntia ficus-indica* under close spacing (Fig. 1). The simulated PPFD index reached a maximum of about 0.41 near the summer solstice (Fig. 1(A)). The great variation in the PPFD index, especially near the winter solstice, was a consequence of the variation in cloudiness; values slightly below zero occurred on heavily overcast days that generally were accompanied by rainfall. In contrast with the PPFD index, the temperature index was higher and more uniform, averaging 0.92 for the 15 month period (Fig. 1(B)). For much of the period, the temperature index was near unity, exceeding 0.95 on 61% of the days. In the winter, the temperature index could also be close to unity but it was more variable and occasional cold spells caused it to decrease below 0.6 (minimum air temperatures of 2 °C or less). Assuming a water index of unity for the well-watered field conditions, EPI was calculated for each day (Fig. 1(C)). The environmental productivity index tended to be highest in the summer, averaging 0.379 for 1 month on either side of the summer solstice, and lowest in the winter, averaging 0.098 for 1 month on either side of the winter solstice.

The PPFD index was next simulated for *Opuntia ficus-indica* growing in each of the nine rows (Fig. 2(A)). For plants consisting only of the initially planted cladode, which corresponded to an SAI of 1.6 for the interior rows, the PPFD index averaged over the 15 month period was 0.571 for the interior

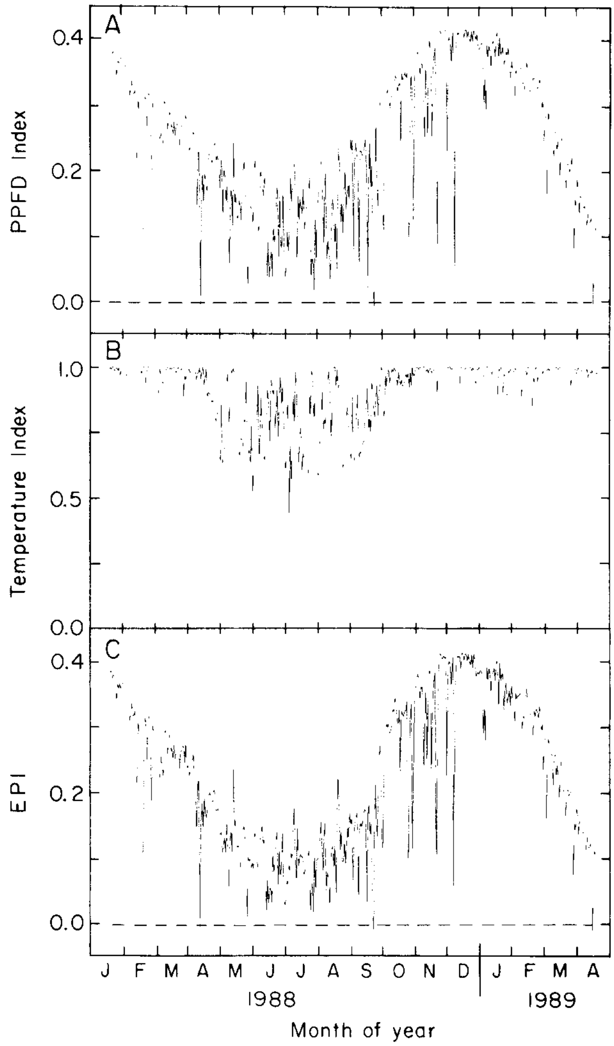

Fig. 1. Daily values over a 15 month period for *Opuntia ficus-indica* under field conditions near Santiago, Chile relating to: (A) photosynthetic photon flux density (PPFD) index; (B) temperature index; (C) environmental productivity index (EPI). The PPFD index was calculated for a field with a stem area index of 4.0.

rows, increasing 3% for rows 2 and 8 and 24% for the outermost rows (rows 1 and 9). Using the morphology appropriate for plants after 15 months, with an SAI of 7.9 for the interior rows, the PPFD index averaged over the year was 0.160 for the interior rows, increasing 8% for rows 2 and 8 and 18% for the outermost two rows (Fig. 2(A)).

Based on the PPFD index determined for field conditions (Fig. 2(A)), on EPI, and on the cladode area applicable to each row, dry matter production

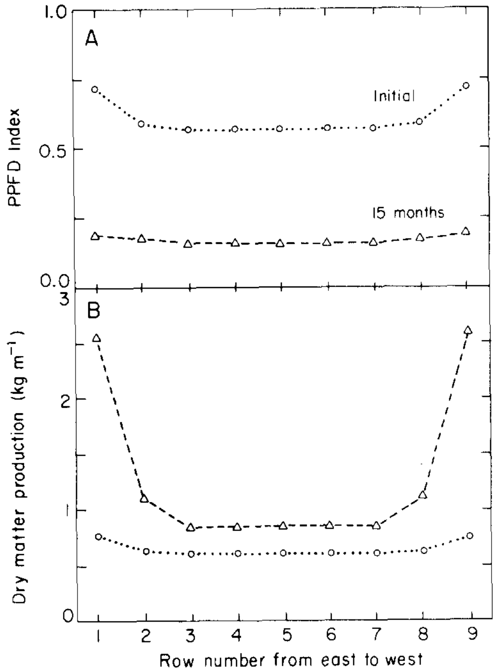

Fig. 2. Simulated values of the average daily photosynthetic photon flux density (PPFD) index (A) and the dry matter production per unit row length (B) over a 15 month period for *Opuntia ficus-indica* in nine rows in the field. Simulations used the morphology of the initial plants (○) or that representing the plants after 15 months (△).

was predicted assuming a particular plant morphology over the 15 month period considered (Fig. 2(B). For plants consisting of the initially planted basal cladode, dry matter production per unit row length for the interior row was 0.605 kg m^{-1}, increasing 3% for rows 2 and 8 and 24% for the outermost two rows. Because the greater growth experienced by the outer rows over the 15 month period led to more cladode surface area than for the inner rows, the dry matter production varied more from row to row for the simulations using the morphology of the 15 month plants than for the initial morphology. In particular, production per unit row length for the 15 month morphology was 0.845 kg m^{-1} for the interior rows, increasing 31% for rows 2 and 8 and 204% for the outermost two rows (Fig. 2(B)).

Dry matter production was also measured in the field upon harvesting plants after 15 months (Fig. 3(A) and 27 months (Fig. 3(B)). As indicated by the simulations (Fig. 2), border effects extended over two rows on each side of the plot, so these rows were considered separately from the five interior rows. For the interior rows (rows 3–7) after 15 months, the dry matter production per unit row length averaged 0.803 kg m^{-1}, increasing 50% for rows 2 and 8 and 174% for the outermost two rows (Fig. 3(A)). After 12 more months of

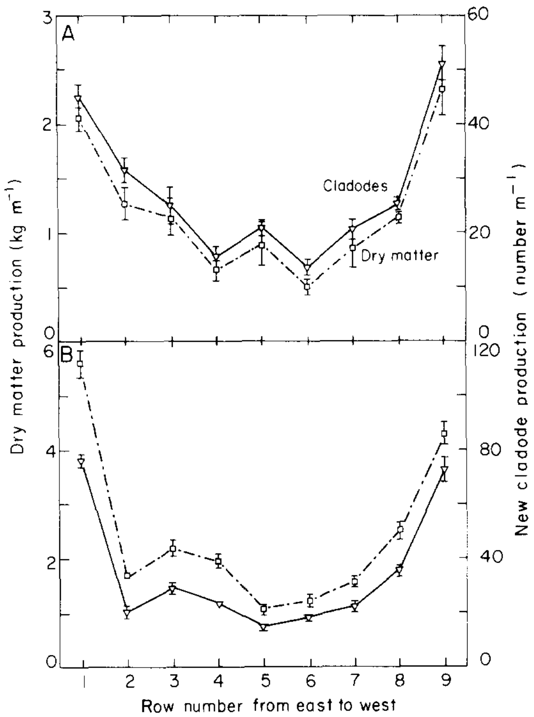

Fig. 3. Measured dry matter (□) and cladode (▽) production per unit row length for *Opuntia ficus-indica* in nine rows over: (A) a 15 month period; (B) a 27 month period. Plants were planted on 20–22 January 1988 and were harvested on: (A) 20 April 1989; (B) 20 April 1990. Data are presented as mean ± 1 SE for the four plants harvested from each of the nine rows (absence of a bar indicates that the SE was smaller than the symbol).

growth, production averaged 1.60 kg m^{-1} for the interior rows, increasing 30% for rows 2 and 8 and 209% for the outermost two rows (Fig. 3(B)). For both the 15 and the 27 month plants, production for the outer row on each side was significantly higher than for each of the inner five rows, whereas the variation among the inner rows was not significant ($P<0.01$, four replicates per row, Student's *t*-test). On a row-by-row basis, the number of cladodes initiated closely paralleled the variations in the dry matter production, but the average dry matter per cladode varied for the two growth periods (Fig. 3). In particular, the dry matter per cladode initiated was 42.9 ± 3.0 g (SD for $n=9$ rows) for the 15 month period and 72.1 ± 7.3 g for the 27 month period.

Fruits also contributed to the dry matter, although the contributions were relatively small. Specifically, the dry weight of fruits over the 15 month period amounted to 0.086 kg m^{-1} for the outermost two rows on each side (rows 1, 2, 8, and 9) and 0.006 kg m^{-1} for the interior five rows. Over the 27 month period, production was 0.160 kg m^{-1} for the outer rows and 0.008 kg m^{-1} for the interior rows.

DISCUSSION

Plant productivity is generally influenced by water status, temperature, photosynthetic photon flux density, and soil nutrients. Indices to predict productivity have been proposed, with most emphasizing the specific factor of greatest importance. For instance, some productivity indices and yield predictions are based solely on the soil water balance (Nix and Fitzpatrick, 1969; Duncan and Woodmansee, 1975; Le Houérou, 1984; McBride and Mackintosh, 1984), although productivity at a particular site can vary more from year to year than does rainfall (Le Houérou et al., 1988). Growth indices are often based on the accumulated time that the temperature is above some value, the so-called 'degree-day' approach (Castonguay and Dubé, 1985; Long and Woodward, 1988). Crop growth may also be proportional to intercepted radiation (Monteith, 1977; Jones, 1983). Although the environmental productivity index (EPI) and its associated nutrient index incorporate four factors (Nobel, 1988), for the present study the productivity of *Opuntia ficus-indica* was influenced mainly by PPFD. In particular, the water index was essentially unity, as were the component indices measured for the nutrient index, and the temperature index averaged 0.92. However, the PPFD index varied substantially with season, cloudiness, and plant morphology.

Daily and seasonal variations occurred in EPI and its component indices. For instance, daily changes in cloudiness caused the PPFD index to vary more than 50% from day to day, and even in the summer it could become nearly zero; consequently, this index must be based on daily weather data rather than on monthly averages, as has previously been indicated (Garcia de Cortázar et al., 1985; Garcia de Cortázar and Nobel, 1990). The temperature index was lowest in the winter, averaging 0.76 for 1 month on either side of the winter solstice, but was usually not a major limitation on productivity for *Opuntia ficus-indica* in central Chile. At other locations where *Opuntia ficus-indica* is commercially cultivated, such as tropical regions, the temperature index is generally reduced more by high temperatures during the summer than by low temperatures during the winter (Nobel, 1988; Garcia de Cortázar and Nobel, 1990). The day-to-day scatter in EPI during the winter was less than the day-to-day scatter in the temperature index and the PPFD index. In particular, on clear days with a high PPFD index, the minimum temperatures tended to be lower and substantially decreased the temperature index, whereas cloudy days with a lower PPFD index had higher minimum temperatures leading to a higher temperature index. Because of lower temperatures and less available PPFD, EPI was lowest in the winter, which is also the rainfall season in central Chile. Thus, management practices, such as irrigation and fertilizer application, would be more advantageous if undertaken during the other seasons.

Plant morphology markedly influenced the PPFD index and the production per unit row length for *Opuntia ficus-indica*. Plants in the outermost two rows on each side of the nine-row plot had a greater number of cladodes. Because of this and a slightly higher PPFD index, predicted and measured dry matter production per unit row length was greatest for the outer rows, decreasing substantially for the second row from each side. Because essentially no lateral penetration of PPFD occurred to the five interior rows, border effects were limited to the outermost two rows on each side. Thus, productivity per unit row length of the interior five rows was assumed to resemble the productivity of a uniform field, which is generally expressed on a unit area basis. Based on the row spacing of 17 cm, the annual predicted productivities (over the 15 month period) for the initial morphology and the 15 month morphology were 28 Mg ha^{-1} $year^{-1}$and 40 Mg ha^{-1} $year^{-1}$, respectively, or an average of 34 Mg ha^{-1} $year^{-1}$. This is in close agreement with the measured productivity for the same five interior rows of 38 Mg ha^{-1} $year^{-1}$ for the 15 month period. Also, the simulated annual productivity of 40 t ha^{-1} $year^{-1}$ for the 15 month morphology is similar to the measured productivity of 42 Mg ha^{-1} $year^{-1}$ over the 27 month period.

The increase in productivity from the first to the second harvest reflects the significant degree of incidence of PPFD on soil for the first few months. In particular, the stem area index was 1.6 initially, 7.9 after 15 months, and 12.0 after 27 months. Such SAI are predicted to lead to annual productivities that are 52%, 4%, and 10% lower, respectively, than the maximal productivity of *Opuntia ficus-indica* that occurs at an SAI of 4.0 (Garcia de Cortázar et al., 1985; Garcia de Cortázar and Nobel, 1986). After 27 months, the number of cladodes per plant was 17% greater than for the 15 month plants, and such cladodes were 28% greater in area and 68% greater in dry weight. If all cladodes had had the same area and dry weight as for the 15 month plants, SAI would have been 15.1 at 27 months, causing more cladodes in the canopy to be below the PPFD compensation level. Apparently, new cladode induction under the high SAI was reduced; similarly, fruit production was lower for the central rows, where the PPFD was lower.

Predicted productivities range from 27 to 34 Mg ha^{-1} $year^{-1}$ for different morphologies of *Opuntia ficus-indica* when the water index is 0.84 (Garcia de Cortázar et al., 1985; Garcia de Cortázar and Nobel, 1986). For a water index of 1.00 as in the present study, such productivities would increase to 32–40 Mg ha^{-1} $year^{-1}$. For an SAI of 7.9, the model predicted 40 Mg ha^{-1} $year^{-1}$, which is the average measured value in the present study for 2 years in the field. Higher values should be possible: for the 12 months between the first and second harvests, the difference in dry matter production was equivalent to 47 Mg ha^{-1} $year^{-1}$, which might have reached 50 Mg ha^{-1} $year^{-1}$

had the canopy been maintained at an SAI near 4.0. Such high productivities would be difficult to obtain in large-scale agriculture because of management requirements, especially for harvesting, but even half of the maximum value would exceed the productivity of most C_3 and C_4 crops (Loomis et al., 1971; Odum, 1971; Evans, 1975; Beadle et al., 1985). A high productivity similar to that reported here can also be estimated from a measured cladode fresh weight yield of 400 Mg ha^{-1} $year^{-1}$ for *Opuntia ficus-indica* in Mexico (observation of V. Riquelme, cited in Russell and Felker, 1987); using the 9.8% dry matter content measured in the present study, the estimated dry matter production would be 39 Mg ha^{-1} $year^{-1}$. Moreover, a possible productivity of 50 Mg ha^{-1} $year^{-1}$ for *Opuntia ficus-indica* is similar to the values observed for sugar cane, which up to now has one of the highest measured productivities among all plants, further emphasizing the potential for high biomass productivity of this prickly pear cactus.

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