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WORLDWIDE ENVIRONMENTAL PRODUCTIVITY INDICES AND YIELD PREDICTIONS FOR A CAM PLANT, *OPUNTIA FICUS-INDICA*, INCLUDING EFFECTS OF DOUBLED CO_2 LEVELS

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ABSTRACT

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The productivity of *Opuntia ficus-indica* was predicted for 253 regions on a worldwide basis using data from 1464 weather stations within 60° of the equator. First, the climatic data were used to calculate daily values of a PAR index, a temperature index and a water index. These indices, each of which has a maximum value of unity when that environmental factor is not limiting net CO_2 uptake by *O. ficus-indica* over a 24-h period, were multiplied together to give an environmental productivity index, which indicates how the three environmental factors limit net CO_2 uptake and hence productivity. The photosynthetically active radiation (PAR) index for a canopy of closely spaced plants that have a high productivity per unit ground area was $\geqslant 0.20$ for 25% of the earth's land surface. The temperature index annually was $\geqslant 0.50$ for 81% of the earth's land surface, indicating that local temperatures do not greatly limit net CO_2 uptake by this species. The water index was $\geqslant 0.50$ for 79% of the earth's surface for *O. ficus-indica*, which exhibits Crassulacean acid metabolism with its accompanying high water-use efficiency. Predicted productivities for *O. ficus-indica* without irrigation were at least 10 metric tons ha^{-1} year^{-1}, the value for many important annual agronomic crops, for 41% of the earth's land area. Irrigation increased such high productivity regions to 77% of the earth's land surface area within 60° of the equator. For simulations that included the worldwide changes in PAR, temperature and rainfall patterns that will most likely accompany a doubling in the ambient CO_2 level, the high productivity of 10 tons ha^{-1} year^{-1} was predicted to occur for 54% of the earth's land surface area. Under elevated CO_2, the predicted productivity of *O. ficus-indica* increased for most of the U.S.A. and a productivity of 32 tons ha^{-1} year^{-1} was predicted for western South America.

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INTRODUCTION

Plant productivity depends on net CO_2 uptake by the shoot, which is influenced by water status, temperature and photosynthetically active radiation (PAR). The instantaneous responses of net CO_2 uptake to such environmental variables have been measured for many species. However, instantaneous rates are generally not as important for predicting productivity as are integrated responses over a 24-h period, especially for Crassulacean acid metabolism (CAM) plants whose CO_2 uptake occurs primarily at night when PAR is zero. For the CAM plants whose PAR responses have been studied in the most detail, *Agave deserti, A. fourcroydes, Ferocactus acanthodes* and *Opuntia ficus-indica*, net CO_2 uptake over 24 h depends on total daily PAR (Nobel, 1977, 1984, 1985; Nobel and Hartsock, 1983). For these species, net CO_2 uptake becomes positive at a total daily PAR of ~ 3 mol photons m^{-2} day^{-1}, is half-maximal at 12 mol m^{-2} day^{-1} and saturates at ~ 30 mol m^{-2} day^{-1} (Nobel, 1988). The PAR index (Nobel, 1984), which represents the fractional limitation by PAR on net CO_2 uptake over 24 h, can thus readily be calculated for these CAM species once the total daily PAR is known. The water index and the temperature index similarly are unity when these two environmental factors do not limit CO_2 uptake over 24-h periods and are proportionally lower under limiting conditions (Nobel, 1984). The product of the three indices is the environmental productivity index (EPI), which indicates the fraction of maximum CO_2 uptake over 24 h expected based on field values for soil water potential, ambient temperature and available PAR (Nobel, 1984, 1988).

Productivity has been predicted on a regional basis for *A. deserti, F. acanthodes* and *O. ficus-indica* using EPI (Nobel and Hartsock, 1986a). Based on weather data from 21 sites in the southwestern U.S.A., productivity is low in the Colorado River basin, which has low annual rainfall and high summer temperatures, as well as in the north-central part of the region, which has low temperatures and low PAR during winter, when the soil water potential leads to a water index of unity. Using data from 300 weather stations, isolines of annual EPI in 0.05 intervals have been constructed for *Agave lechuguilla* for 11 states in Mexico and two in the U.S.A. (Quero and Nobel, 1987). Besides indicating its productivity in specific regions, which is useful for evaluating where *A. lechuguilla* should be harvested from the wild for the hard fiber in its leaves, the EPI isolines also indicate that its distributional limits are not primarily determined by low productivity. Rather, other factors, such as low wintertime temperatures or competition from other species, are often of paramount importance for the range boundaries.

The previous studies have used average monthly minimum and maximum temperatures, average monthly radiation and algorithms based on average monthly rainfall to construct monthly values of the three component indices of EPI (Nobel, 1984, 1985; Quero and Nobel, 1987). Although this is useful as a first approximation and monthly average values of climatic data are commonly available, CO_2 uptake over 24-h periods is not linearly related to temperature or radiation and rainfall does not have the same daily pattern each year. Errors caused by using average monthly values, instead of daily values, to calculate EPI have been recognized for PAR for *O. ficus-indica* (Garcia de Cortázar et al., 1985) and for temperature for *A. deserti* (Nobel and Hartsock, 1986b). To generate daily temperatures, radiation and rainfall events from monthly data, special climatological models (Richardson and Wright, 1984; Geng et al., 1986) were used in the present study. Also, monthly and annual values were averaged over 10 years to provide more reliable productivity estimates than those based on single years.

The species chosen, *O. ficus-indica*, is cultivated in ~20 countries worldwide for its fruits, its young cladodes (stem segments) used as a human food and its mature cladodes used as animal forage or fodder (Russell and Felker, 1987a; Nobel, 1988). Prediction of productivity based on EPI closely agrees with that based on the dry weight of harvested material for *O. ficus-indica* studied over a 16-month period near Santiago, Chile (Garcia de Cortázar et al., 1985; Nobel, 1988). Moreover, month-by-month shoot dry weight increases of *O. ficus-indica* growing under controlled conditions of PAR, temperature and soil water status that were changed monthly to simulate environmental conditions at another field site agreed well with monthly values of EPI (Nobel and Hartsock, 1986a). PAR interception by *O. ficus-indica* can be modeled for various plant shapes, including a potentially high productivity, low-profile structure consisting of a basal cladode, partially buried in the soil, on which another mature cladode occurs (Garcia de Cortázar and Nobel, 1986) using a ray-tracing method that has been validated in the field (Garcia de Cortázar et al., 1985). Based on climatic conditions for irrigated commercial plantations of this platyopuntia near Santiago, Chile, an extremely high above-ground productivity of 28 metric tons ha^{-1} $year^{-1}$ is predicted for relatively closely spaced plants that have a stem area index (SAI, total area of both sides of the cladodes per unit ground area) of 4.0.

An objective of the present study is to predict the productivity of *O. ficus-indica* on a global scale using the EPI approach for an optimum plant spacing. For this condition, component indices of EPI are also presented. In addition, the effects on productivity are considered for an approximate doubling in atmospheric CO_2 levels (Nobel and Hartsock, 1986c), which is expected within 100 years (Gates, 1983; Cure and Acock, 1986), including the effects on productivity of the associated changes in temperature and rainfall patterns (Hansen et al., 1984; Schlesinger and Mitchell, 1986).

MATERIALS AND METHODS

Climate

Average monthly data from 1464 weather stations within 60° latitude of the equator (the land surface area considered in all calculations) included daily global radiation, percent of maximum sunshine hours, maximum and minimum temperature, maximum and minimum relative humidity, and total rainfall (Great Britain Meteorological Office, 1960, 1972; Löf et al., 1966). Global radiation, when not available for a particular station, was estimated from the percent of maximum sunshine hours (Doorenbos and Pruitt, 1977). The generation of the necessary daily data was based largely on the WGEN (Weather Generator) model of Richardson and Wright (1984) with the rainfall modification of Geng et al. (1986). For a specific location and time of year, the model first generates either dry days or wet days (>2 mm of rainfall), depending on the probability of rainfall. Then it generates a corresponding value for global radiation and temperature.

Daily rainfall probability is generated using a Markov chain and the amount of daily rainfall is predicted with a gamma function (Richardson and Wright, 1984), both based on the fraction of wet days per month and the total monthly rainfall (Geng et al., 1986). The fraction of wet days was available for 888 of the weather stations; for the other stations, an algorithm relating monthly rainfall to the mode (most frequent value of a series) of the fraction of wet days per month was used. The monthly average potential evapotranspiration was generated using monthly solar irradiation, temperature, relative humidity and assumed moderate wind speeds of 2–5 m s^{-1} at 2 m above the vegetation (Doorenbos and Pruitt, 1977); daily values were simulated using daily global radiation.

Daily global radiation and temperature is generated in WGEN by combining a sinusoidal wave, representing the average variation of the parameter during the year for any site, with a noise factor. The mean value of global radiation for dry days averaged 12% more and for wet days 28% less than the 30-year averages for 31 sites in the U.S.A. (Ruffner, 1978; Richardson and Wright, 1984); the amplitude of the sinusoid averaged 7% more on dry days and 15% less on wet days than the 30-year averages. For daily minimum temperature (the temperature necessary to predict CO_2 uptake for *O. ficus-indica*; Garcia de Cortázar et al., 1985), no differences in the sinusoid occurred between dry and wet days. The phase of the sinusoid was the same as that used by Richardson and Wright (1984) for sites in the northern hemisphere, with a 180° shift for the southern hemisphere. The noise factor is a coefficient from -2.5 to $+2.5$ times the standard deviation for a daily value, these standard deviations used in the model being based on data for the 31 U.S. sites (Richardson and Wright, 1984). For global radiation, 24% of the coefficient is derived from the value on the previous day and 76% is from a normally distributed random number (between -2.5 and $+2.5$); for minimum temperature, weighting of the previous day's value is 68% (Richardson and Wright, 1984).

After calculations were made for all 1464 weather stations, the data were averaged for those stations within a particular square region of land area. The weather stations ranged from 60°N to 47°S, and the 253 regions had limits of 60°N and 50°S. The data were plotted at the center of each region, whose vertical dimension was 7.86° of latitude, which is equal to 874 km (the degrees of longitude for each square varied with latitude, but the horizontal dimension was always ~874 km).

EPI

The simulated daily global radiation was partitioned into direct and diffuse components (Bristow et al., 1985); the total of both components intercepted by the crop was calculated using a ray-tracing technique that determined the instantaneous values of PAR (400–700 nm) for ~600 subsurfaces of the cladodes (Garcia de Cortázar et al., 1985; Garcia de Cortázar and Nobel, 1986). The PAR index was obtained from the relationship between net CO_2 uptake over a 24-h period for *O. ficus-indica* and the integral of incident instantaneous PAR for the cladode surfaces, the maximum value of unity occurring for PAR saturation of daily net CO_2 uptake (Nobel and Hartsock, 1983). The temperature index (TI) was determined from the response curve for *O. ficus-indica* (Nobel and Hartsock, 1986a)

$$\mathrm{TI}=0.559+0.0750\,T-0.00319\,T^2$$

where T is the average night-time temperature of the tissue, which is 2°C higher than the minimum air temperature (Garcia de Cortázar et al., 1985).

The water index for *O. ficus-indica* is 1.00 when the soil water potential (ψ^{soil}) in the root zone is > -0.5 MPa, which is representative of the shoot water potential of this species under hydrated conditions when water uptake from the soil is thermodynamically possible (Nobel, 1988). Because of water storage in the succulent stem, the water index is also unity for the first 6 days of drought ($\psi^{\mathrm{soil}} < -0.5$ MPa), after which it decreases approximately linearly with time, becoming 0.00 after 40 days of drought (Nobel and Hartsock, 1986a). ψ^{soil} in the root zone was determined from the balance of daily input (rainfall) and output (evapotranspiration, percolation) together with the water-holding capacity and hydraulic conductivity of the sandy loam described by Young and Nobel (1986), which is representative of soils used for the cultivation of *O. ficus-indica* (Nobel, 1988).

Crop characteristics

For all simulations, 2-cladode plants of *O. ficus-indica* (Structure I of Garcia de Cortázar and Nobel, 1986) were arranged in rows oriented north–south with cladodes facing east–west. The lower cladode (half buried in the soil) was 0.46

m long and 0.23 m wide, and the upper cladode was 0.40 m long and 0.20 m wide. The distance between plant centers was 0.25 m along rows spaced 0.19 m apart, leading to a SAI of 4.0. The maximum rooting depth was 0.3 m (Nobel, 1988).

Transpiration, which occurs primarily during the night for *O. ficus-indica*, was represented as 15% of daily evapotranspiration (day+night), which is approximately the ratio of night evapotranspiration to total daily evapotranspiration for a wet surface (Campbell, 1985). When soil water was limiting ($\psi^{soil} < -0.5$ MPa in the root zone), this value was multiplied by the water index. Soil evaporation was simulated according to the bare surface evaporation model of Campbell (1985), corrected by the fraction of global radiation hitting the ground as calculated by the PAR interception model for *O. ficus-indica* (Garcia de Cortázar et al., 1985). Under non-limiting water conditions, evapotranspiration was between 0.30 and 0.45 of the potential evapotranspiration, consistent with the 0.35 average for two other CAM crops, agave and pineapple (Doorenbos and Pruitt, 1977).

To account for the annual variability of climate, the model was run on a daily basis for a period of 10 years for every weather station. The mean annual EPI was obtained from the integration of the daily product of the three component indices reflecting PAR, temperature and water limitations. Productivity, in metric tons of dry matter produced per hectare per year, was calculated from the mean annual EPI × the maximum CO_2 uptake per unit area of cladode for *O. ficus-indica* (0.344 mol CO_2 m^{-2} day^{-1}; Nobel and Hartsock, 1983) × SAI × 365.25 days $year^{-1}$, assuming an average composition of 27 g dry weight per mol of CO_2 fixed (Salisbury and Ross, 1985) and noting that 1 kg m^{-2} equals 10 metric tons ha^{-1}.

Enhanced CO_2 levels

To simulate the effects on climate caused by an approximate doubling of the atmospheric CO_2 level, the GISS (Goddard Institute for Space Studies) model of Hansen et al. (1984), as presented by Schlesinger and Mitchell (1986), was used. Changes in temperature and rainfall for two periods of the year (December–February and June–August) were digitized in 10° latitude × 10° longitude squares (resolution of GISS model); intervening months were assigned the mean value for these two periods. The changes were added to the mean data for each weather station inside these squares to reflect temperature and rainfall conditions for an atmosphere with 630 p.p.m. CO_2. Because changes in rainfall changed the number of wet days, which have a lower radiation than dry days, the PAR index was also affected. Thus, new values were obtained for the PAR, temperature and water indices for each weather station, leading to new values of EPI. The effect of increasing CO_2 concentration by itself on net CO_2 uptake by *O. ficus-indica* was based on the measured response of other

CAM plants (*A. deserti* and *F. acanthodes*) to elevated CO_2 maintained for 1 year, for which net CO_2 uptake per unit surface area increases by 30% when the level of atmospheric CO_2 increases from 350 to 650 p.p.m. (Nobel and Hartsock, 1986c).

RESULTS

As an example of monthly measured values versus simulated values of climatic parameters as well as monthly component indices and EPI, data are presented for dryland conditions at Santiago, Chile, where *O. ficus-indica* is extensively cultivated (Table 1). Predictions of total daily PAR on a horizontal surface, minimum air temperature and rainfall were close to the actual values; the average absolute monthly differences were 2 mol m^{-2} day^{-1} for total daily PAR, 0.3 °C for temperature and 7 mm for rainfall. The annual averages were 38 mol m^{-2} day^{-1} versus a predicted value of 37 mol m^{-2} day^{-1} for total daily PAR, 7.2 °C for both measured and predicted minimal daily temperatures, and 376 mm versus a predicted value of 331 mm for rainfall (Table 1).

The PAR index for *O. ficus-indica* at Santiago had a maximum monthly

TABLE 1

Comparison between actual and simulated average daily values of PAR, minimum temperature and rainfall for 10 years at Santiago, Chile (33°27′S, 70°42′W, 520 m elevation). Also included are the average daily values of the PAR index (PI), temperature index (TI), water index (WI) and environmental productivity index (EPI) for the 10-year period (EPI and the other indices were calculated daily and then the daily values were averaged for each month). PAR values are for a horizontal surface, whereas PI is based on the accompanying PAR in the planes of the cladodes (Garcia de Cortázar and Nobel, 1985)

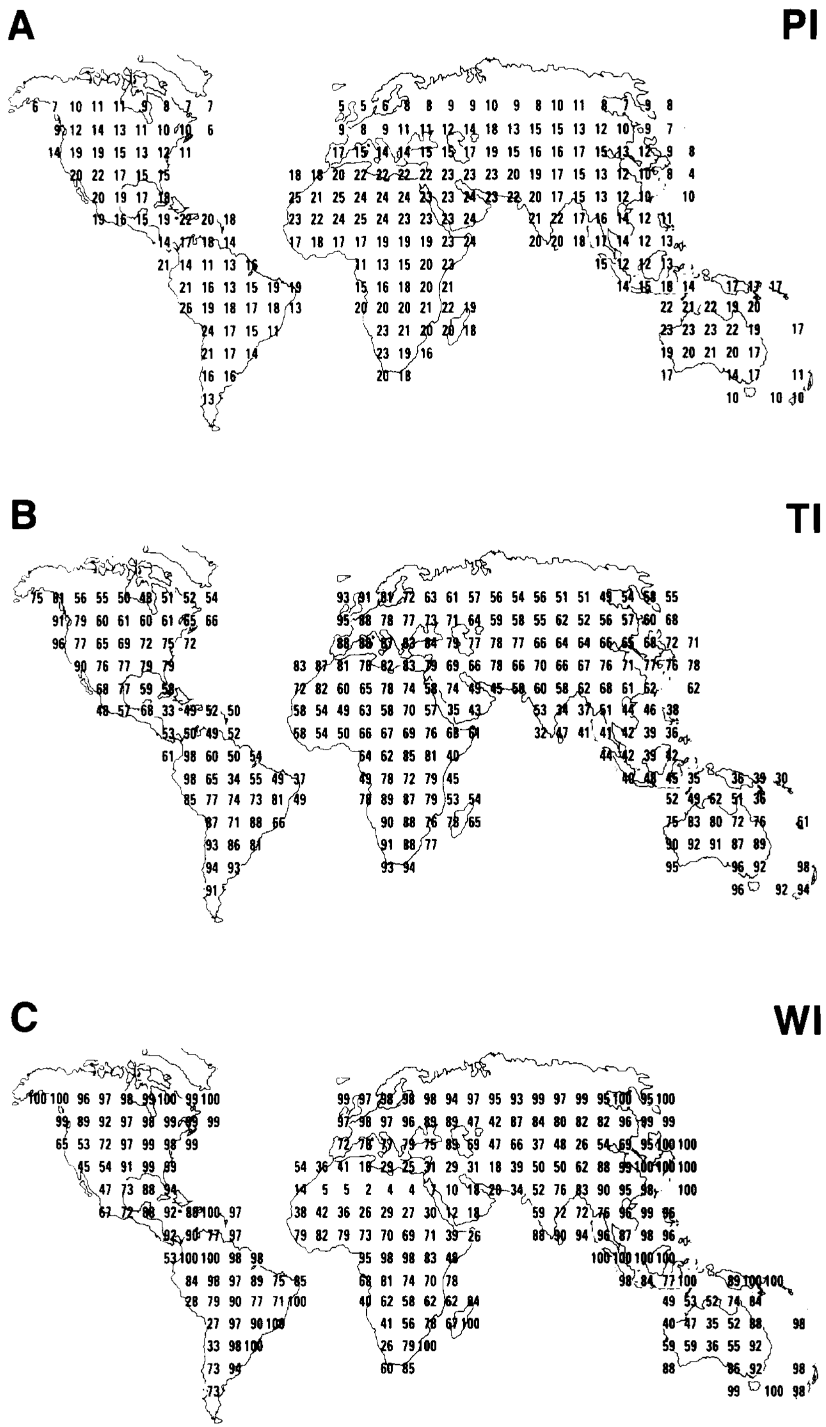
Month	Total daily PAR (mol m^{-2} day^{-1})		Minimum temperature (°C)		Rainfall (mm)		PI	TI	WI	EPI
	Actual	Model	Actual	Model	Actual	Model				
Jan.	58	58	11.7	11.4	1	5	0.35	0.98	0.04	0.014
Feb.	56	54	11.1	10.8	2	5	0.34	0.99	0.11	0.034
Mar.	43	45	9.4	9.2	5	1	0.26	0.99	0.03	0.009
Apr.	31	33	7.2	7.2	17	4	0.14	0.97	0.13	0.016
May	19	21	5.0	5.1	55	44	0.05	0.92	0.43	0.015
Jun.	14	16	2.8	3.1	75	58	0.02	0.86	0.86	0.013
Jul.	16	17	2.8	3.1	91	100	0.02	0.86	1.00	0.018
Aug.	21	22	3.9	4.1	70	67	0.06	0.89	1.00	0.052
Sep.	28	31	5.6	5.7	30	19	0.13	0.94	1.00	0.118
Oct.	44	46	7.2	7.2	17	21	0.26	0.97	0.94	0.233
Nov.	49	51	8.9	8.9	7	6	0.29	0.99	0.51	0.138
Dec.	59	59	10.6	10.6	5	1	0.36	0.99	0.08	0.027

value of 0.36 in the summer (Table 1), when there is a high proportion of clear days; the relatively low maximum value is a consequence of the close spacing of the plants, which led to a low PAR index, but a high productivity per unit ground area (Garcia de Cortázar and Nobel, 1986). The monthly PAR index in the winter was very low, averaging only 0.03 for June–August (Table 1), reflecting the high proportion of cloudy days then. The temperature index had a minimum monthly value of 0.86 and averaged 0.95 (Table 1), indicating only slight limitation on the annual productivity of *O. ficus-indica* at this site by adverse temperatures. The water index was near unity ($\geqslant 0.86$) in the winter and early spring (June–October), but was very low ($\leqslant 0.13$) during the summer and early autumn (December–April), when rainfall was slight (Table 1). The product of these three indices, EPI, was substantial ($\geqslant 0.100$) for the closely spaced plants considered only in the spring, which in the absence of irrigation is the best time of the year for net CO_2 uptake by *O. ficus-indica* near Santiago.

The component indices were next calculated on a worldwide basis for current values of the climatic variables and in the absence of irrigation (Fig. 1). The highest average annual PAR index was associated with regions just north or south of the equator, especially deserts with low cloud cover. Specifically, the average annual PAR index for the fields of closely spaced *O. ficus-indica* was $\geqslant 0.20$ for the southwestern U.S.A., northern Mexico and the Caribbean, northern Chile plus western Ecuador and Peru, northern and southern Africa, the Middle East plus the Indian subcontinent, and most of Australia [Fig. 1(a)]. The average annual PAR index was $\leqslant 0.10$ only for latitudes $>44°$N or $<42°$S and some northern Pacific islands. On a worldwide basis, 25% of the land surface within 60° of the equator had a PAR index of $\geqslant 0.20$, 60% was between 0.10 and 0.20, and 15% was $\leqslant 0.10$ or less [Fig. 1(a)].

The worldwide pattern for the temperature index was quite different than for the PAR index, values typically ranging from 0.40 to 0.70 for the warm regions with 20° latitude of the equator. In equatorial regions of high elevation or of continental climate caused by great distances from the oceans, lower temperatures led to values >0.70 [Fig. 1(b)]. The temperature index was also $\leqslant 0.70$ at latitudes $>44°$N as well as in adjacent continental regions of high elevation, in this case representing a decrease in net CO_2 uptake by *O. ficus-*

Fig. 1. Predicted daily values averaged over the year for the three component indices of EPI for *O. ficus-indica.* (a) PAR Index (PI); (b) temperature index (TI); (c) water index (WI) for a 10-year period with current average climatic conditions and using rainfall as the only source of water. Each number shows the average annual value for the weather stations included in the square, whose vertical dimension is 7.86° of latitude (874 km). Numbers in the oceans correspond to islands and/or coastal stations falling within the limit of the square. For clarity of presentation, values were multiplied by 100, effectively meaning that each component index is presented as a percentage of the maximum net CO_2 uptake caused by that environmental factor.


A
PI
B
TI
C
WI

indica caused by low temperatures. For the other latitudes, mostly from 20° to ~44° from the equator, the temperature index often exceeded 0.80 [Fig. 1(b)]. On a worldwide basis, 19% of the earth's land area within 60° of the equator had a temperature index <0.50, 59% was from 0.50 to 0.80, and 22% was $\geqslant 0.80$. The water index for *O. ficus-indica* was quite high on a worldwide basis, even in the absence of irrigation, reflecting its use of the water-conserving CAM pathway. Specifically, the water index was $\geqslant 0.50$ for 79% of the land surface area and $\geqslant 0.80$ for 55% [Fig. 1(c)]. Values <0.20 for the annual average water index were restricted to the large desert regions of northern Africa.

The product of the PAR index, the temperature index and the water index (Fig. 1) leads to the EPI for *O. ficus-indica*, here presented worldwide [Fig. 2(a)]. Because EPI is expressed on the basis of cladode surface area, values are much lower than for widely spaced plants that would have a much higher PAR index, but a lower productivity per unit ground area. EPI was $\geqslant 0.10$ (representing a dry weight productivity of 14 tons ha^{-1} year^{-1} for the closely spaced plants considered) for the middle and southern U.S.A., various countries in South America, central and southern Africa, and eastern Australia [Fig. 2(a)]. Limitations on EPI were often the consequence of inadequate rainfall, because raising the water index to unity, such as can occur by irrigation, quadrupled the land area within 60° of the equator where EPI was $\geqslant 0.10$ [Fig. 2(b)]. Indeed, EPI then became $\geqslant 0.10$ for most of the world, except for hot areas in central America, northern and eastern South America, west-central Africa, and southeastern Asia, as well as cold areas in northern North America, northern Europe and northern Asia [Fig. 2(b)].

Because EPI (Fig. 2) represents the fraction of maximum net CO_2 uptake per unit cladode area, it can readily be converted to productivity per unit ground area for *O. ficus-indica* with a known stem area index. Predicted productivities of at least 10 tons ha^{-1} year^{-1} occur for 41% of the earth's land surface area within 60° of the equator, including much of all six continents considered [Fig. 3(a)]. Indeed, predicted productivities were at least 15 tons ha^{-1} year^{-1} for middle North America, middle and southern South America, southern Africa and eastern Australia [Fig. 3(a)]. The land areas for such high predicted productivities increased substantially when the water index was made unity, as can occur by irrigation [Fig. 3(b)]. Predicted productivities for *O. ficus-indica* were then at least 10 tons ha^{-1} year^{-1} for 77% of the earth's land surface area and at least 15 tons ha^{-1} year^{-1} for 45%. Productivities were at least 20 tons ha^{-1} year^{-1} for the southwestern U.S.A., northwestern Mexico, most of western South America, northern and southern Africa, and 70% of Australia [Fig. 3(b)].

The changes in net CO_2 uptake caused by changes in climatic conditions associated with an approximate doubling in atmospheric CO_2 levels, as well as by the direct effects of the new ambient atmospheric CO_2 level on net CO_2 uptake, were also predicted for *O. ficus-indica*. The PAR index was little af-

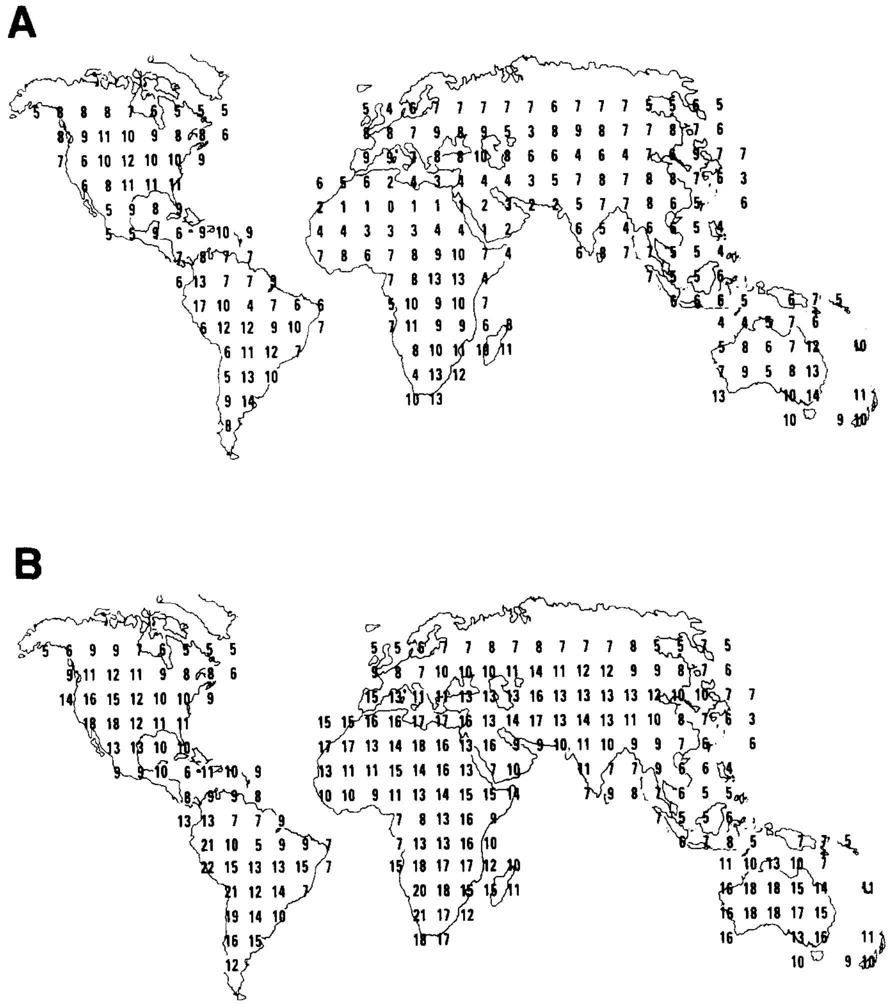


Fig. 2. Predicted annual EPI for *O. ficus-indica* for a 10-year period with current average climatic conditions. (a) Rainfall as the only source of water (Fig. 1); (b) irrigation supplying water leading to a water index of unity. For clarity of presentation, values were multiplied by 100.

fected by the increased atmospheric CO_2 level, the average worldwide value decreasing 3% compared with today's climatic conditions. Because of rising temperatures associated with an elevated CO_2 level, the temperature index decreased an average of 44% for latitudes within 20° of the equator (where the temperature for the regions considered increased by an average of 3.6°C), decreased 16% for 20 to ~44° (temperature increase of 4.1°C) and increased 10% for latitudes >44°N or <42°S (temperature increase of 4.3°C). Because of increased rainfall (an increase of 14% for regions within 20° of the equator,

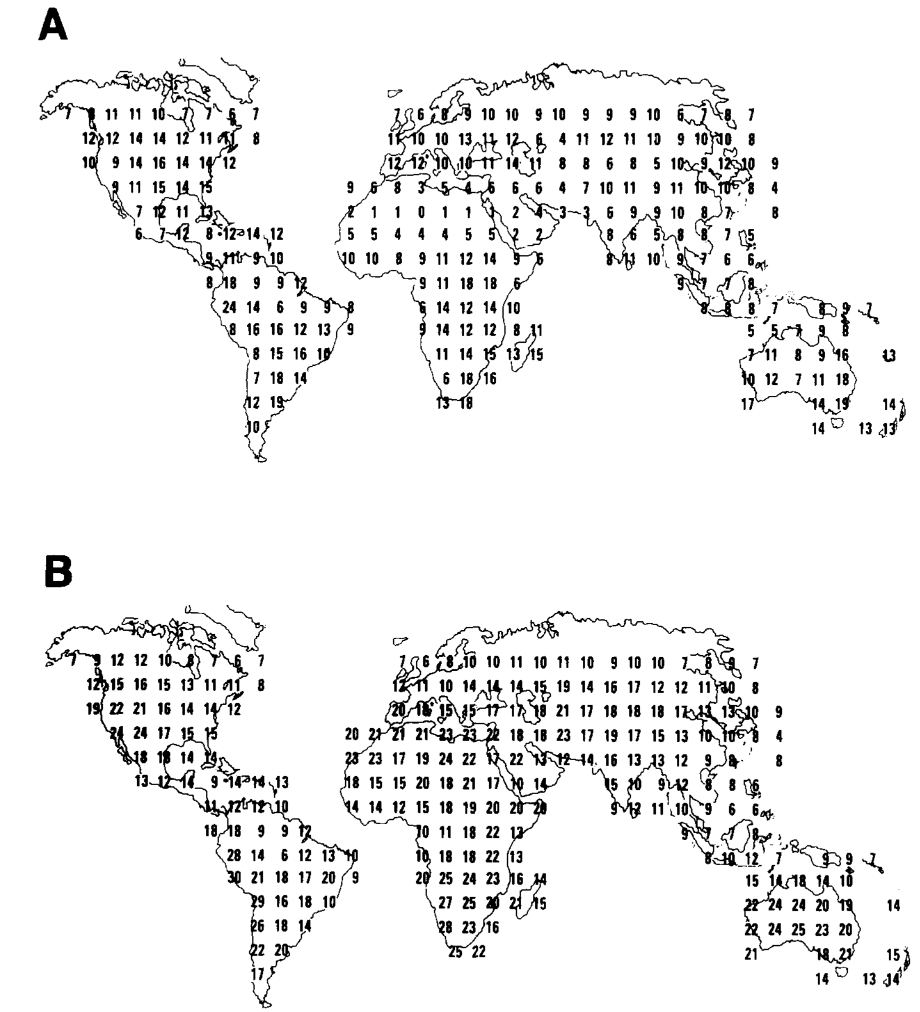


Fig. 3. Predicted annual productivity (metric tons ha^{-1} $year^{-1}$) for *O. ficus-indica* with current average climatic conditions. (a) Rainfall as the only source of water; (b) irrigation leading to a water index of unity.

14% for 20–44° and 19% for the other regions), the water index tended to be higher under elevated CO_2, the worldwide average increasing 11%.

Based on the combined climatic changes, the EPI for *O. ficus-indica* decreased an average of 15% worldwide for elevated CO_2 compared with the present CO_2 level. Taking into consideration the 30% enhancement in net CO_2 uptake at the elevated CO_2 level, productivity of *O. ficus-indica* under elevated CO_2 was predicted to be at least 10 tons ha^{-1} $year^{-1}$ for 54% of the earth's land surface area within 60° of the equator [Fig. 4(a)]. In particular, predicted productivity in the absence of irrigation then increased substantially for most of the U.S.A., western South America, southwestern Africa, central Asia and southern Australia [Fig. 3(a) versus 4(a)]. Partly because of the expected increase in the water index, irrigation would have less effect in increasing productivity under elevated CO_2 [Fig. 4(b)] compared with present climatic conditions [Fig. 3(b)]. Nevertheless, predicted productivity of irrigated *O. ficus-*

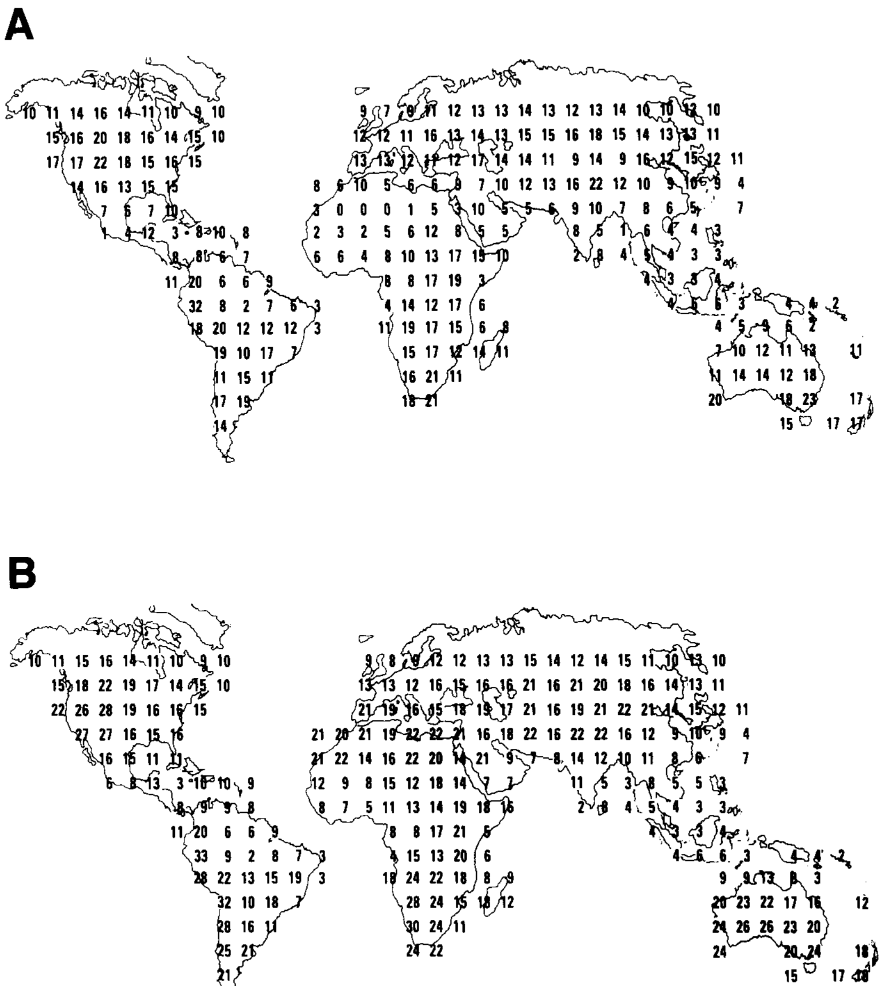


Fig. 4. Predicted annual productivity (tons ha^{-1} year^{-1}) for *O. ficus-indica* for an approximately doubled atmospheric CO_2 level with its accompanying changes in climatic conditions: (a) Rainfall as the only source of water; (b) irrigation leading to a water index of unity.

indica was at least 10 tons ha^{-1} $year^{-1}$ under elevated CO_2 for 68% of the earth's land area within 60° of the equator and three regions (two in western South America, one in southern Africa) had predicted productivities of at least 30 tons ha^{-1} $year^{-1}$ [Fig. 4(b)].

DISCUSSION

Based on data from 1464 weather stations and methods for predicting daily values of climatic variables from monthly data, an EPI was calculated daily and averaged annually for *O. ficus-indica* and then presented for 253 regions distributed uniformly over the earth's land surface for latitudes within 60° of the equator. EPI represents the fraction of maximum net CO_2 uptake per unit cladode area expected for the environmental conditions in each region, so EPI values were converted to annual productivities using the appropriate stem area index of 4.0. Even though annual EPI is positive for a particular region, *O. ficus-indica* may not be able to grow there (Nobel and Hartsock, 1986a; Quero and Nobel, 1987). For instance, its establishment may not be possible without special conditions, such as supplemental watering until the plants obtain sufficient shoot volume per unit surface area to survive drought (Nobel, 1988). Also, winter temperatures may be too low for the survival of *O. ficus-indica*, which generally succumbs to freezing damage at ~ -10°C (Russell and Felker, 1987a). Although low temperature limitations are not a problem for most regions in the southern hemisphere or up to ~36°N, temperatures dropped below -10°C at some time during the year for essentially all regions above 44°N (upper two lines of data in the figure panels) and for many regions centered at 40°N. Indeed, the identification of cultivars of *O. ficus-indica* and other platyopuntias that are tolerant to subzero temperatures is an important objective in efforts to extend the area suitable for the cultivation of these cacti to higher latitudes or greater elevations (Russell and Felker, 1987a).

Even when the cultivation of presently available cultivars of *O. ficus-indica* above ~40°N is dismissed (except in coastal regions) because of wintertime temperatures < -10°C, much of the land surface of the earth is still potentially suitable. In particular, productivity was at least 10 tons ha^{-1} $year^{-1}$ for 40% of the land surface area with minimum temperatures > -10°C. This percentage rose to 79% with supplemental irrigation, irrigation that need not involve massive amounts of water per unit ground area for this shallow-rooted CAM plant. Thus, under conditions of natural rainfall, nearly half of the earth's land area with minimum temperatures > -10°C had a predicted annual productivity for *O. ficus-indica* of at least 10 tons ha^{-1} $year^{-1}$, which is higher than for most agricultural crops and terrestrial ecosystems (Leith and Whittaker, 1975; Loomis, 1983). Regions with minimum wintertime temperatures > -10°C that can have productivities of at least 10 tons ha^{-1} $year^{-1}$ when irrigated comprise 32% of the entire area of North America considered, 84%

of South America, 100% of Africa, 41% of Europe, 38% of Asia and 100% of Australia.

Although not generally recognized, certain perennial CAM plants, such as agaves, cacti and pineapple, can have higher productivities than most annual crop plants, partly because CAM plants have a high water-use efficiency (CO_2 fixed per water transpired). The comparatively high productivity per unit ground area is apparent when the canopy architecture of the CAM plants allows for nearly complete interception of incident PAR, especially in arid and semi-arid regions where the low annual rainfall limits the productivity of unirrigated C_3 and C_4 plants (Nobel, 1988). The C_3 species *Medicago sativa* can have an annual productivity of 21–34 tons ha^{-1} $year^{-1}$ when cropped multiple times in a year (Odum, 1971; Loomis et al., 1971) and the C_4 species *Saccharum officinarum* can yield 40–60 tons ha^{-1} $year^{-1}$ (Evans, 1975). On the other hand, other common agronomic crops, such as *Glycine max, Oryza sativa, Sorghum vulgare, Triticum aestivum* and *Zea mays*, generally have aboveground productivities of $\sim$10 tons ha^{-1} $year^{-1}$ (Odum, 1971; Evans, 1975; Monteith, 1977; Fischer and Turner, 1978; Loomis, 1983). Certain CAM plants can have substantially higher measured productivities, such as 20 tons ha^{-1} $year^{-1}$ for *Ananas comosus* (Bartholomew and Kadzimin, 1977) and *O. ficus-indica* (Griffiths, 1915; Monjauze and Le Houérou, 1965; Flores Valdez and Aguirre Rivera, 1979) and 25 tons ha^{-1} $year^{-1}$ for *Agave tequilana* (Nobel and Valenzuela, 1987). In the present study, annual productivities for unirrigated *O. ficus-indica* approaching 20 tons ha^{-1} $year^{-1}$ were predicted for southern South America, southern Africa and southeastern Australia under present climatic conditions.

The productivities of *O. ficus-indica* predicted for an atmospheric CO_2 level approximately double the present level are uncertain, in part reflecting the uncertainty of the accompanying climatic changes. If no climatic changes were to accompany a doubling in the ambient CO_2 level (Newell and Dopplick, 1979; Idso, 1980), then the productivity of *O. ficus-indica* would increase by $\sim$30% over the estimates for the current atmospheric CO_2 level, if this species responded to elevated CO_2 in the same way as other CAM species (Nobel and Hartsock, 1986c). Assuming that certain specific climatic changes do occur (Hansen et al., 1984; Schlesinger and Mitchell, 1986), annual productivity would also tend to increase and major changes in relative productivity would occur among geographical regions. The regions where predicted productivity was nearly 20 tons ha^{-1} $year^{-1}$ for current CO_2 levels would expand and new areas, such as the center of the North American continent, would also achieve such high productivities.

The direct effect of an elevated atmospheric CO_2 level on net CO_2 uptake by *O. ficus-indica* is the primary reason that the average annual productivity of this CAM plant is expected to increase when the ambient CO_2 level doubles. The accompanying increase in rainfall, averaging 15% annually for earth's land surface area within 60° of the equator (Schlesinger and Mitchell, 1986), raised the water index; the associated increase in cloudiness lowered the PAR index slightly. The increasing air temperatures that are expected to accompany the increasing CO_2 levels averaged 4.0 °C for the earth's land surface area considered (Schlesinger and Mitchell, 1986), which has major implications for the growth of *O. ficus-indica* in different regions. The rise in temperature for the already warm sites within 20° of the equator will substantially lower their temperature index; hence, even with irrigation most of this region will not have productivities exceeding 10 tons ha^{-1} $year^{-1}$. On the other hand, the rise in temperatures will make regions further from the equator more suitable for growing *O. ficus-indica*. Despite these general trends, the highest productivity under elevated CO_2 in the absence of irrigation, 32 tons ha^{-1} $year^{-1}$, was predicted to occur near the equator in western South America. This occurred for a PAR index of 0.20 (the maximum anywhere for the closely spaced plants considered was 0.24 for the elevated CO_2 condition), a temperature index of 0.96 (the maximum was 0.97) and a water index of 0.97 (the maximum was 1.00). As expected from the value of the water index, irrigation raised the predicted productivity for *O. ficus-indica* in this high productivity region by only 3%, but irrigation for the elevated CO_2 condition often increased the predicted productivity by > 60% for southwestern North America, western South America, southwestern Africa and Australia.

Platyopuntias such as *O. ficus-indica* can be expected to become increasingly important agronomically for human consumption and animal fodder, especially if certain cultivation, management and cultural issues are addressed (Russell and Felker, 1987a, b; Felker and Russell, 1988; Nobel, 1988). Very little breeding has been attempted in a systematic way, especially with regard to cold hardiness, which has major implications for extending the cultivation of this species to higher latitudes. Information is needed on nutrient responses to test a recently proposed nutrient index, which multiplies EPI to account for the effects on productivity of five key soil elements (Nobel, 1989). The advantages of the cultivation of CAM plants with their high water-use efficiencies will be increasingly recognized for arid and semi-arid regions, especially when water for irrigation becomes unavailable or salinization from previous irrigation becomes so severe that continued irrigation of C_3 or C_4 species becomes unfeasible. When certain CAM plants have been cultivated, often little attention has been paid to weeding or pest control, with a consequent decrease in productivity. The reduction of water loss from the soil surface accompanying a closed canopy of CAM plants is also often not achieved. In any case, using climatic data together with EPI, productivity can be predicted region by region for *O. ficus-indica*, other platyopuntias and other crops whose responses of net CO_2 uptake to environmental factors have been determined.

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