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Field validation of water-use efficiency of the CAM plant *Opuntia ellisiana* in south Texas

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In single plant studies, at time scales less than a growing season, the conversion efficiency of water to dry matter several times has been shown to be greater for CAM plants than either C_3 or C_4 plants. The objective of this work was to determine if this high conversion efficiency would occur at the field level over an entire growing season.

Thus, *Opuntia ellisiana* water-use efficiency values were obtained under field conditions in the third and fourth year of growth of a plantation. Although *O. ellisiana* is the slowest growing of all the spineless *Opuntias*, it was used because it is the only spineless *Opuntia* that is completely cold hardy in Texas. Above-ground dry matter production was obtained by complete harvest and by estimating above-ground biomass with regression techniques. Evapo-transpiration was estimated as the precipitation minus runoff, deep drainage, change in soil water content and water stored in the plant. In the fourth year, surface runoff was captured and measured in below-ground tanks. Based on the measurements, surface runoff in the third year was estimated using the regression technique. Soil evaporation was directly measured over a 2-week period, four times per year using microlysimeters. Using these direct soil evaporation measurements and companion meteorological data, yearly transpiration was computed using a Radial Basis Function (RBF) neural network. This yearly soil evaporation estimate allowed the separation of transpiration from evapo-transpiration.

At the beginning of the fourth years growth *Opuntia ellisiana* achieved a leaf area index (LAI) of 2·02. In the fourth year, 662 mm rainfall occurred. Soil evaporation (214 mm) and runoff (143 mm) were the major losses. A significant quantity of water (17 mm = 170,000 kg ha^{-1}) was stored in the cactus that could be of use for animal drinking water. The cactus transpired 285 mm of water producing 17,670 kg dry matter ha^{-1} for a transpiration water-use efficiency of 162 kg H_2O kg^{-1} dry matter. This is among the greatest water-use efficiency of any plant species (including C_3 and C_4) that has been measured under long-term field conditions. While this species is not particularly useful, other less cold hardy opuntias are widely used for fruit, vegetable and forage. Given water shortages on arid lands, much more development attention needs to be given to useful *Opuntia* species.

Keywords: cactus; forage; arid lands; cactus pears; nopalitos

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Introduction

Water-use efficiency (WUE) has been defined as the amount of water used per unit of plant material produced (Briggs & Shantz, 1914). This definition may be too broad in that it embraces water-use efficiencies obtained in diverse time and process scales. The plant material can be expressed as carbon dioxide assimilation, total biomass, or yield; the water use can be expressed as transpiration, evapo-transpiration or total water input to the ecosystem; and the timescale can be instantaneous, daily or seasonal (Sinclair *et al*., 1984). Sinclair *et al*. (1984) stressed that water-use efficiency obtained at different time and process scales should not be used interchangeably.

Frank & Barker (1987) compared WUE of field grown cultivars of crested wheatgrass (*Agropyron desertorum* (Fish. ex Link) Shultes), intermediate wheatgrass (*Elymus intermedium* (Fish. ex Link) Beauv. syn. *Thinopyrum intermedium* (Host) Barkworth & Dewey), and western wheatgrass (*Elymus smithii* (Rydb.) Gould syn. *Pascopyrum smithii* (Rybd.) Love to identical plants grown in a controlled environment. The results showed that the ratio, A/E, of the net CO_2 assimilation (A) to transpiration rate (E) were consistently larger than WUE calculated from dry matter accumulation and total evapo-transpiration for field grown plants for the three cultivars. Moreover, the rankings for these grass species between A/E values determined in the controlled environment and WUE values determined in the field were different, with crested wheatgrass having the smallest A/E but the highest WUE. Fisher & Turner (1978) also suggested that plant characters such as leaf morphology, leaf anatomy, stomatal apertures and plant ontogeny, in addition to the environment, can significantly affect WUE estimated from gas exchange ratios.

It has been widely accepted that, in general, plants possessing Crassulacean Acid Metabolism (CAM) have higher water-use efficiency than C_3 and C_4 plants. Black (1973) showed that the transpiration ratio for CAM plants ranged from 50 to 125 kg H_2O kg^{-1} CO_2, which is much higher than for C_3 plants (from 450 to 950 kg H_2O kg^{-1} CO_2) and for C_4 plants (from 250 to 350 kg H_2O kg^{-1} CO_2). A transpiration ratio of 50 kg H_2O kg^{-1} dry matter for pineapple was reported by Joshi *et al*. (1965). Neales *et al*. (1968) estimated transpiration ratios of 154 kg H_2O kg^{-1} CO_2 for *Aeonium hawarthii* (Salm-Dyck) Webb & Berth., 47 kg H_2O kg^{-1} CO_2 for *Agave americana* L. and 116 kg H_2O kg^{-1} CO_2 for pineapple. Meinzer & Rundel (1973) obtained a transpiration ratio of 135 kg H_2O kg^{-1} dry matter for *Echeveria pumila* Van Houtte (a CAM plant) in greenhouse experiments. These studies were conducted at leaf or single plant level in a controlled environment over a short period of time. Studies on water-use efficiency of CAM plants at plant community level under field conditions over a whole growing season have not often been reported in the literature. From an agronomical point of view, however, this kind of study is of great significance, both in theory and in practice.

The main objective of this study was to determine whether the high water-use efficiency of CAM plants reported in greenhouse studies and short-term, single 'leaf' field studies could be obtained in the field. To accomplish this, the cold hardy, spineless *Opuntia ellisiana* Griffiths was grown in the field where precipitation, runoff, soil evaporation and moisture changes in the soil profile were measured to determine plant transpiration. Three plots were harvested at 1, 2, 3 and 4 years of age to determine dry matter productivity. From the annual dry matter productivity and plant transpiration, water-use efficiency was determined.

Methods and materials

Site description

The study site was located on the north-western part of the Texas A&M University — Kingsville campus, in Kingsville, Texas. The Hidalgo fine loam soil was well-drained and lacked a fluctuating ground-water table in its deep layer.

Mean daily maximum temperatures exceeded 30°C from April through October. Mean daily maximum temperatures were 35°C for June and 36°C for July and August. Mean annual precipitation was 700 mm with 22·8% occurring during May and June and 29·8% during August and September. September was the month with the greatest amount of precipitation (NOAA, 1991).

Experimental design

The experiment used a randomized complete block design with three blocks and four treatments (harvest dates) per block (total of 12 plots). Dry matter production was determined by harvesting three plots of cactus every year for 4 years on 15 April 1992, 1993, 1994 and 1995. Crop water use was obtained from a water budget involving measurements of soil water evaporation, soil water extraction in the profile, estimates of surface runoff and precipitation.

Opuntia ellisiana was planted using single cladodes on a 1·5 m between-row spacing and a 1 m in-row spacing on 1 April 1991. Although this species is slower growing than other spineless species such as *Opuntia ficus-indica*, (L.) Mill. it is the only spineless *Opuntia* species that survived the freeze in 1989 (–12°C) without any damage. Due to the necessity of working closely among the plants it was desirable to use a spineless species.

Plots were separated from field and each other by dikes (Fig. 1). Each 12-m long,

Figure 3. Illustration of the experimental plot, plant conditions and the neutron probe access tubes.

9-m wide plot had six rows of 12 plants per row. In each plot, five access tubes were placed between the two rows in the middle of the plots and three tubes were placed in the rows (Fig. 1). This was done to assess differences in moisture use within and between rows. The access tube was 130 cm above and below the ground.

To avoid fertility limitations on WUE 91 kg ha^{-1} of N, P_2O_5 and K and 2·4 kg ha^{-1} S, 0·81 kg ha^{-1} B, 1·92 kg ha^{-1} Cu, 4·5 kg ha^{-1} Fe, 4·8 kg ha^{-1} Mn, 0·024 kg ha^{-1} Mo and 2·7 kg ha^{-1} Zn were applied each spring.

Since unweeded cactus plots were shown to have 300% less biomass production in the first year of growth than weeded plots (Felker & Russell, 1988), herbicides were used for weed control. To control the troublesome perennial grasses, Johnson grass (*Sorghum halepense* (L.) Pers.) and Bermudagrass (*Cynodon dactylon* (L.) Pers.) the herbicide glyphosate (Roundup) (N-(phosphonomethyl) glycine) was used at a concentration of 1·5%. For long-term pre-emergence weed control, the herbicide tebuthiuron (Spike) (N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea) was used at a rate of 2·5 kg ha^{-1}. The plots were virtually free of grasses and broadleaf weeds during the entire experimental period.

The fungicide BANROT (5-ethoxy-3-trichloromethyl-1,2,4-thiadiazole and dimethyl 4,4'-O-phenylenebis), the bacteriacide agri-strep (streptomycin sulfate) and insecticide ORTHENE (acephate (O,S-dimethyl acetylphosphoramidothioate)) were also applied to prevent or control diseases and insects.

Determination of evapo-transpiration and plant transpiration

The soil water balance equation described by Fisher & Turner (1978) was used in determining evapo-transpiration and plant transpiration. Due to the fact that cacti can store a large amount of water in its above-ground part, in this study an additional component called plant water content change (ΔP_w) was included in the soil water balance equation.

$$P = ET + Rs + Rd + \Delta S + \Delta P_w = E + T + Rs + Rd + \Delta S + \Delta P_w \quad \text{(Eqn 1)}$$

where P is precipitation, ET is evapo-transpiration, E is soil evaporation, T is transpiration, ΔS is soil water content change, Rs is surface runoff, and Rd is deep drainage. When precipitation, surface runoff, soil water content change, plant water change and deep drainage are known, ET can be calculated as:

$$ET = P - (Rs + Rd + \Delta S + \Delta P_w) \quad \text{(Eqn 2)}$$

When soil evaporation is known, T can be calculated as:

$$T = ET - E = P - (Rs + Rd + \Delta S + \Delta P_w + E) \quad \text{(Eqn 3)}$$

Precipitation

Each rainfall event was measured with three Tenite rain gauges that had an accuracy of 0·21 mm.

Soil water content change

A Troxler 4300 neutron probe was used to measure volumetric soil water contents. The neutron probe was calibrated both in the laboratory and in the field. Our field calibration curve was chosen in preference to the laboratory calibration curve because it had a lower estimate error of regression. The field calibration curve was:

$$SWC = -0{\cdot}0435 + 0{\cdot}6793 \times CR \; (R^2 = 0{\cdot}83)$$

where SWC is volumetric soil water content (g cm^{-3}) and CR is the neutron probe count ratio. During the field calibration process, the soil bulk density was found to be 1·93 cm^{-3} g^{-1}, 1·75 cm^{-3} g^{-1}, 1·76 cm^{-3} g^{-1}, 1·80 cm^{-3} g^{-1} and 1·85 cm^{-3} g^{-1} for the 25, 50, 75, 100 and 125 cm depths, respectively.

Neutron probe readings were taken at 25 cm depth increments from 25 cm to 125 cm, once a month. The measurements began on 15 April 1991 and ended on 15 April 1995. Because the top 15 cm soil water content could not be accurately measured by the neutron probe, the moisture content of this zone was measured by the oven-drying method (at 105°C). When the neutron probe readings were taken, three soil samples of the top 15 cm were taken from two widely separated plots, and converted into volumetric soil water content using the soil bulk density. The average volumetric soil water content for these two plots was used for all 12 plots.

The volumetric soil water content data obtained by the neutron probe from 12·5 to 137·5 cm and the oven-drying method of top 15 cm were combined to calculate the change of water stored in the entire soil profile from 0 to 137·5 cm. As there was very little change in neutron probe readings at the 137 cm depth throughout the year, we assumed the deep drainage to be negligible (Rd = 0).

Soil evaporation

To obtain yearly estimates of soil evaporation, daily soil evaporation was measured directly over a 15-day period in the spring (May–June 1994), summer (July–Aug 1994), fall (Oct–Nov 1994) and Winter (Jan–Feb 1995) with microlysimeter measurements. Then a radial basis function (RBF) artificial neural network was developed to estimate daily soil evaporation throughout the year from air temperature, relative air humidity, wind speed and soil water content (Han & Felker, in press). The RBF neural network was implemented using C programming language and trained based on 40 measured input–output pairs. The RBF neural network had a substantially lower standard error for prediction of soil evaporation than did a multiple linear regression with the same four input variables.

The 10-cm long, 4·9-cm diameter microlysimeters were made from 3-mm thick aluminum pipe. The portable electronic balance used to weigh the microlysimeter had an accuracy of 0·1 g (0·02 mm of water). The microlysimeters were weighed daily at about 0830h Central Daylight Time (CDT). Two lysimeters were placed between the row and two lysimeters were placed under the plant canopy. Soil cores in the four lysimeters were replaced every day.

For each microlysimeter measurement, a paired gravimetric soil water content (top 10 cm) was obtained at a site adjacent to the microlysimeter location. Three gravimetric soil samples were taken with a hand probe immediately after weighing the microlysimeters.

The daily average air temperature, relative humidity and wind speed were obtained from the Texas A&M University Research and Extension Center at Corpus Christi about 40 km away.

Surface runoff

Surface runoff was measured from two plots in the fourth year by collecting the runoff in cylindrical tanks 2·18 m in diameter and 1·82 m tall that were placed in below-grade pits (Fig. 1).

Based on the surface runoff measurement in the fourth year, a multiple linear regression technique was employed to establish a quantitative relationship between surface runoff, rainfall amount and top 10 cm soil water content prior to the rainfall. This regression was also used to estimate the surface runoff in the third year.

Plant water content change

Plant water content change is defined as the change of water stored in the above-ground plant materials over a given period of time. It can be measured by determining the above-ground fresh weight and plant water content at the beginning and the end of the period.

Dry matter production

Above-ground biomass production was measured by a complete above-ground harvest. While all six rows in the plots were harvested, to avoid a border row influence on the biomass estimation, biomass estimates excluded plants in the outer two rows and the two plants on the end of each row. Thus, the entire weight of the 16 individual plants in the interior two rows were measured. To determine the moisture content, sample plants were placed in a drying room at 70°C until no further change in weight was observed.

One estimate of yearly dry matter production was obtained by subtracting the dry matter production (average over three plots) from one harvest date from that (average over three plots) in the subsequent harvest date. However, some error was incurred due to the nonuniformity of soils and different microclimates between plots.

To avoid this problem, dry matter production in non-harvested plots was non-destructively estimated by regression techniques. Two types of regression were evaluated for use in non-destructive predictions of the standing biomass (Table 1). The first technique applied a regression equation between cladode width and cladode fresh weight to all the cladode widths on the chosen plant. The second technique involved harvest of about 50 plants to determine the relationship between total plant fresh weight and total plant cladode number.

For small plants in the first year, the cladode width approach gave the lowest standard error. However as the plants became larger, the total cladode weight per plant derived from cladode widths consistently underestimated the plant weight. Perhaps this was attributable to heavier cladodes in the lower portions of the plant that had the same cladode width as lighter, less mature cladodes.

Table 1. *Comparison of regression equations to predict biomass*

Year	Cladode width equations	R^2	SE	Cladode number equations	R^2	SE
1	$FW = 0.58\ (MW)^{2.40}$	0.93	54.0	$PFW = -0.349 + 0.394\ (PCN)$	0.83	79.2
2	$FW = 0.88\ (MW)^{2.27}$	0.90	62.0	$PFW = -1.466 + 0.407\ (PCN)$	0.90	49.9
3	$FW = 0.97\ (MW)^{2.58}$	0.81	71.3	$PFW = -7.795 + 0.497\ (PCN)$	0.88	56.6

FW = fresh weight of cladode (g); MW maximum width of cladode (cm); PFW = plant fresh weight (kg); PCN = plant cladode number.

SE = the standard error of regression (g per cladode).

Leaf (cladode) area index (LAI)

Leaf area index was determined by applying the regression equation: A = –110·69 + 23·54 × MW (where A is leaf (cladode) area (cm^2) and where MW is maximum cladode width (cm)) to the maximum width of all cladodes on two of the 16 sample plants. This equation was based on paper tracings of 53 randomly selected cladodes. The cladode area of the remaining 14 plants per replicate was obtained based on the ratios of their cladode number to the cladode number of the two sample plants.

Calculation of evapo-transpiration water-use efficiency (WUEet) and transpiration water-use efficiency (WUEt)

Evapo-transpiration and transpiration water-use efficiency were calculated as:

$$\text{WUEet (evapo-transpiration efficiency)} = \frac{\text{Evapo-transpiration}}{\text{Dry matter production}}$$

$$\text{WUEt (transpiration efficiency)} = \frac{\text{Transpiration}}{\text{Dry matter production}}$$

Results

Dry matter production and leaf area index

The standing dry biomass, annual growth, leaf area index and rainfall for the 4-year period are presented in Tables 2 and 3. The annual growth increased by about 250% from the first to second year and from the second to third year, but there was only a 30% increase in the fourth growing season. There is no apparent trend between the annual rainfall of 1016, 675, 833 and 622 mm in the first to fourth year and growth. In contrast, these growth rates parallel the leaf area indices of 0·06 ± 0·01, 0·39 ± 0·08, 2·02 ± 0·49 and 3·88 ± 0·50 at the end of the first to fourth years growth, respectively.

Evapo-transpiration and plant transpiration

Due to the low leaf area index and high soil evaporation during the first 2 years, we only present evapo-transpiration and plant transpiration for the last 2 years.

Rainfall that occurred during the last 2 years growth is presented in Fig. 2. The total rainfall was 833 mm for the third year and 662 mm for the fourth year. We considered a rainfall event whose amount was equal to or greater than 40 mm as a heavy rainstorm and a rainfall event whose amount was less than or equal to 5 mm as a light rain. In the third year, there were 44 rainfall events. Of these seven were heavy rainstorms with a total rainfall of 452 mm, which accounted for 54% of the 833 mm annual rainfall. In the fourth year, there were 51 rainfall events. Of these, four were heavy rainstorms with a total rainfall of 240 mm, which accounted for 36% of the annual rainfall of 662 mm.

The number of light rainfall events in the third year was 15, which accounted for 34% of the total 44 rainfall events, for a total rainfall of 38 mm. The number of light rainfall events in the fourth year was 23, which accounted for 45% of the total rainfall events, for a total rainfall of 61 mm.

The predicted total surface runoff in the third year was 252 mm, which was 30% of the annual rainfall. The measured total surface runoff in the fourth year was 143 mm, which was 22% of the annual rainfall.

The yearly change in soil water content, grouped according to year of harvest, is presented in Table 4. In the fourth growing season, the change in soil water content for the profile was nearly the same whether the plots had never been harvested (standing dry biomass ranging from 36,454 to 41,926 kg ha^{-1}) or whether the plots were nearly bare with a harvest only 1 year earlier. The 4-year results (data are not included in this paper) showed that water stored in the soil profile did not increase more than 15 mm in the rainy season or decrease more than 10 mm in the dry season. We believe the small changes in soil moisture in the 15 to 135 cm depth are the result of the occurrence of significant amounts of surface runoff and soil evaporation. The lack of soil moisture changes deeper than 15 cm confirms Nobel's (1988) earlier finding that the cactus root system is very shallow (where unfortunately is not possible to use neutron probes).

Based on the precipitation characteristics and the surface runoff measurements for each rainfall event in 1994 (Table 5), rainfall events less than 15 mm would not result in significant surface runoff. Correlation coefficients between surface runoff and rainfall amount and between surface runoff and antecedent soil water content were 0·85 (p = 0·001 and N = 11) and 0·52 (p = 0·106 and N = 11). Stepwise regression found that the partial regression coefficient for the rainfall amount was 0·73 (p = 0·0008) and for the antecedent soil water content 0·18 (p = 0·0035). This

Table 2. *Standing dry biomass for* Opuntia ellisiana *for the 1-year, 2-year, 3-year and 4-year growth periods*

	Dry matter production (kg ha^{-1})			
Plot	1-year	2-year	3-year	4-year
1	1622*	–	–	–
2	1805†	6486*	–	–
3	1902†	6419‡	20658§	37794*
4	1901†	7768‡	23036§	41926*
5	1880†	6573*	–	–
6	1581†	5909‡	18821*	–
7	1942*	–	–	–
8	1210†	4337‡	17184*	–
9	1307†	4272§	16695*	–
10	848*	–	–	–
11	1751†	6170‡	19465§	36454*
12	1643†	6515*	–	–

*Total dry matter harvested.

†Estimated using equation: $FW = 0{\cdot}58\ (MW)^{2{\cdot}40}$; FW = cladode fresh weight; MW = cladode maximum width. Total dry weight = R_1×total fresh weight. R_1 = 0·071: ratio of dry weight to fresh weight for the first harvest. R_1 was determined by the harvest method.

‡Estimated using equation: PFW=–1·466+0·407 (PCN); PFW=plant fresh weight; PCN=plant cladode number. Total dry weight=R_2×total fresh weight. R_2=0·074: ratio of dry weight to fresh weight for the second harvest. R_2 was determined by the harvest method.

§Estimated using equation: PFW=–7·795+0·497 (PCN); PFW=plant fresh weight; PCN=plant cladode number. Total dry weight=R_3×total fresh weight. R_3=0·089: ratio of dry weight to fresh weight for the third harvest. R_4 was determined by the harvest method.

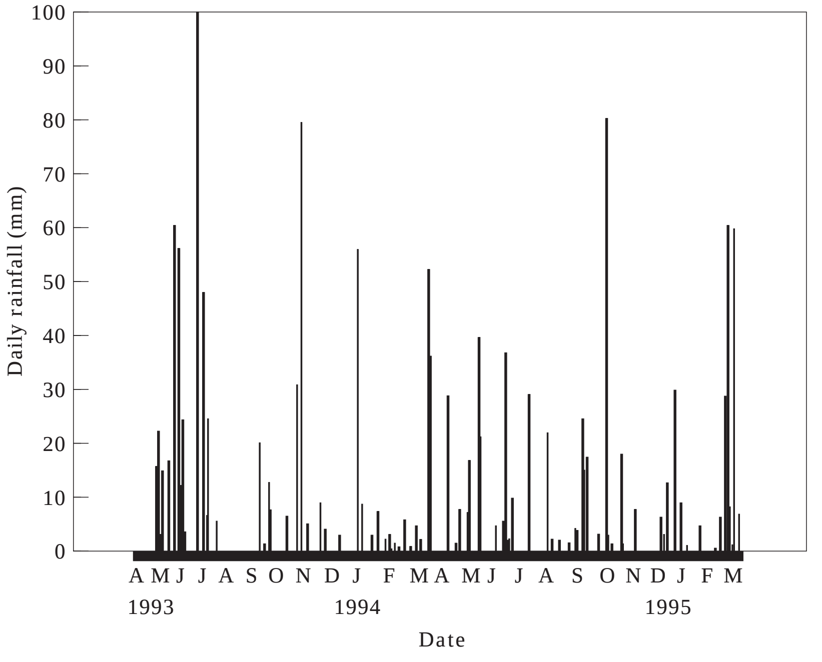

Figure 2. Distribution of daily rainfall from April 1993 to April 1995.

indicated that both rainfall amount and antecedent soil water content had a significant effect on surface runoff. The estimation equation was:

$$S_R = -23{\cdot}9129 + 0{\cdot}6438 \times P + 143{\cdot}0971 \times ASWC$$

where S_R is surface runoff (mm), P is rainfall amount (mm) and ASWC is antecedent soil water content (g g^{-1}). The R^2 value for this model was 0·91 and the root mean square error (MSE) of this model was 5·69 mm. This equation was used to estimate the surface runoff generated by the rainfall events in the third year (Table 6).

Examples of the daily soil evaporation obtained in the third and fourth year with the trained RBF neural network (Han & Felker, in press) are presented in (Table 7). It was assumed that the daily soil evaporation was negligible when the daily rainfall was greater than 5 mm as the high relative humidity during the rains would inhibit soil water evaporation. The estimated daily soil evaporation ranged from 0·20 mm day^{-1} to

Table 3. *Annual growth of* Opuntia ellisiana *for plots 3, 4 and 11, annual rainfall and leaf area index for the 4 consecutive years*

Year	Dry matter production (kg ha^{-1} $year^{-1}$) plot 3	plot 4	plot 11	Rainfall (mm)	LAI*
1	1902	1901	1751	1016	0·06
2	4517	5867	4419	675	0·39
3	14239	15268	13295	833	2·02
4	17136	18890	16989	622	3·88

*LAI is measured at the end of the year.

Table 4. *Average soil water content change over three plots which were harvested in the same year for four 1-year periods*

Plots and year of harvest	Change in soil water content (mm)			
	Year 1	Year 2	Year 3	Year 4
First year (1, 7, 10)	21	–26*	4	2
Second year (2, 5, 12)	1	–29	2	3
Third year (8, 9, 6)	30	–34	7	1
Fourth year (3, 4, 11)	14	–35	8	3

*The negative value indicates plot lost water during that period.

2·5 mm day^{-1}. Total soil evaporation (E) (the sum of the daily soil evaporation) was 249 mm for 339 days (average daily soil evaporation was 0·73 mm) in the third year and 214 mm for 337 days (average daily soil evaporation was 0·64) in the fourth year.

The average actual evapo-transpiration (ET) over plots 3, 4 and 11 was 559 mm in the third year and 499 mm in the fourth year. The computed average transpiration was 310 mm in the third year and 285 mm in the fourth year.

The water balance for the third and fourth year of this trial (Table 8) shows that less than half of the precipitation was transpired. In the third year, which had higher rainfall, the runoff and soil evaporation were nearly identical, while in the fourth year with lower rainfall the soil evaporation was considerably greater than the runoff. In both years the soil water content change was relatively insignificant.

While the water content of the plant is normally not reported in water balance studies, in the case of cacti with very high moisture content the amount of water contained in the annual growth was greater than the soil water content change. The water content for the 4-year-old *Opuntia ellisiana* was 90·9%. It is obvious that the

Table 5. *Measured surface runoff for the rainfall events occurring from 15 April 1994 to 15 April 1995*

Date	Rain (mm)	ASWC (g g^{-1})	Runoff (mm)
1994			
2 May	16·7	0·125	4·4
13 May	39·1	0·063	5·8
14 May	21·2	0·152	5·8
14 May	36·4	0·074	1·7
1 Aug	21·8	0·023	0·3
10 Sep	24·5	0·027	0·2
15 Sep	16·2	0·113	1·1
7 Oct	80·4	0·054	33·6
1995			
24 Feb	28·6	0·087	5·9
27 Feb	60·5	0·144	36·5
6 Mar	58·9	0·178	47·3

ASWC = Antecedent (before rain) soil water content.

Table 6. *Predicted surface runoff for the rainfall events occurring from 15 April 1994 to 15 April 1995*

Date	Rain (mm)	ASWC ($g\ g^{-1}$)	Runoff (mm)
1993			
28 Apr	22·2	0·141	10·6
17 May	60·3	0·099	29·1
22 May	56·1	0·115	28·6
12 Jun	42·2	0·065	12·6
13 Jun	48·8	0·165	31·1
14 Jun	23·1	0·177	16·3
21 Jun	47·7	0·101	21·3
25 Jun	24·3	0·125	9·6
8 Oct	55·9	0·045	18·5
19 Dec	65·3	0·187	44·8
1994			
14 Mar	52·3	0·028	13·7
16 Mar	36·0	0·112	15·3

water contained in the fourth year's growth (176,516 kg H_2O ha^{-1}) could greatly reduce water requirements for livestock in water-short arid lands.

To facilitate comparison of our data with other reports where soil evaporation was not measured, we have included the water-use efficiency based on both the transpiration and evapo-transpiration in Table 8.

The mean transpiration water-use efficiency of 162 kg H_2O kg^{-1} dry matter for the fourth year is greater than that obtained for any plant in any other replicated field trials where the influences of border effects were taken into account.

Discussion and conclusions

While the biomass productivity of this cold hardy cactus was very low in the first 2 years, after the cacti reached a leaf area index of 2·02, a dry biomass productivity of 17,670 kg ha^{-1} $year^{-1}$ was achieved that is comparable to many C_3 and C_4 plants. The low productivity in the early years of planting seems due to a low LAI and not rainfall since the rainfall was highest in the first year. Moreover, de Cortazar & Nobel (1986) found that *Opuntia ficus-indica* required a leaf area index of about 4 for high productivity.

Other studies with cacti have reported productivities even greater than the 17,670 kg dry matter ha^{-1} $year^{-1}$ that we measured, i.e. a rain use efficiency (RUE) of 26·7 kg DM mm^{-1} ha^{-1} $year^{-1}$. In a replicated, non-irrigated fertility trial, Gonzalez (1989) obtained a dry matter productivity of 62,000 kg dry matter ha^{-1} $year^{-1}$ ha over the last 4 years of his experiment where the annual rainfall was 430 mm $year^{-1}$. When irrigated and fertilized, *Opuntia ficus-indica* and *O. ficus-indica* forma *amyclea* (Ten.) Weber syn. *O. amyclea* Ten. had productivities of 47,000 and 45,000 kg ha^{-1} $year^{-1}$, respectively, in Santiago, Chile and Saltillo, Mexico (Nobel, 1991, 1992).

However, caution must be exercised with these high productivities since the full disclosure of experimental details regarding control of border influences on productivity of small plots was not provided in these reports. To illustrate the problems of

Table 7. *Estimated daily soil evaporation data obtained from average air relative humidity, air temperature, wind speed and soil water content using RBF neural network*

Date	Relative humidity (%)	Air temperature (°C)	Wind speed (km h^{-1})	Soil water content (g g^{-1})	Soil evaporation (mm)
1993					
29 Apr	82·8	20·9	5·7	0·141	1·57
2 May	95·9	22·2	3·5	0·115	1·99
3 May	92·4	22·7	2·7	0·095	1·72
11 May	88·4	21·3	3·7	0·123	2·02
16 May	88·8	23·9	4·6	0·069	0·80
16 Jun	89·6	26·5	2·5	0·130	2·05
20 Jun	88·0	26·6	6·4	0·055	0·47
4 Jul	82·5	28·4	6·1	0·045	0·31
9 Aug	80·2	29·2	2·7	0·024	0·31
13 Aug	78·3	29·3	3·6	0·024	0·25
6 Sept	79·2	27·5	1·8	0·125	1·69
8 Sept	76·9	28·8	2·7	0·075	0·58
9 Oct	70·6	27·1	3·9	0·091	0·69
11 Oct	63·2	26·1	4·6	0·068	0·46
6 Nov	69·2	10·8	7·6	0·084	0·67
9 Nov	85·5	16·9	5·3	0·057	0·59
1 Dec	70·6	21·1	5·9	0·038	0·36
1994					
7 Jan	67·9	11·2	7·8	0·070	0·65
13 Jan	84·2	14·2	4·6	0·114	1·49
14 Feb	62·4	10·9	4·1	0·038	0·58
24 Feb	57·2	9·8	3·4	0·053	0·61
7 Mar	90·4	21·3	7·1	0·050	0·53
17 Mar	91·3	16·8	3·1	0·148	1·81
1 Apr	71·5	17·1	4·5	0·037	0·29
8 Apr	80·4	19·3	6·5	0·108	1·14
5 May	87·9	23·1	4·3	0·110	1·31
6 May	92·6	24·0	4·4	0·101	1·01
7 Jun	83·3	28·2	3·9	0·053	0·37
16 Jun	89·6	27·8	5·7	0·130	1·77
10 Jul	83·4	28·0	3·6	0·141	1·19
19 Jul	76·6	28·1	5·3	0·062	0·46
5 Aug	89·9	26·6	2·1	0·081	0·59
15 Aug	78·6	27·9	2·4	0·061	0·21
6 Sept	79·2	28·0	2·6	0·045	0·20
13 Sept	91·8	25·8	1·9	0·135	1·91
13 Oct	75·7	18·6	2·1	0·101	0·81
14 Nov	76·7	24·1	4·0	0·103	1·00
18 Dec	84·1	13·4	3·6	0·107	1·43

Table 8. *Summary of soil water balance and water-use efficiency of* Opuntia ellisiana *for plots 3, 4 and 11 during the third year, fourth year and the 2-year period*

Parameter	Year 3		Year 4		Year 3+Year 4	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
Rainfall (mm)	833	–	662	–	1495	–
Soil water content change (mm)	10	2	3	2	13	4
Plant water content change (mm)	12	3	17	4	29	6
Surface runoff (mm)	252	–	143	–	395	–
Soil evaporation (mm)	249	–	214	–	463	–
Evapo-transpiration (mm)	559	5	499	6	1058	10
Transpiration (mm)	310	4	285	6	595	10
Dry matter production (kg ha^{-1})	14267	987	17671	1057	31939	1998
WUEet (kg kg^{-1})	393	30	283	19	332	23
WUEt (kg kg^{-1})	218	18	162	12	187	14

–S.D. does not apply.
WUE = water-use efficiency.

influence of border on productivity, Zavitkovski (1981) found that for closely planted trees (0·3 m × 0·3 m) the outer row had 800% greater biomass than the plot interior and that the border influence extended five rows into the plot.

Opuntia ellisiana is a slower growing species compared to other *Opuntia* species such as *Opuntia ficus-indica*. For example, while these *O. ellisiana* were less than 1·5 m tall at the end of 4 years, other less cold-tolerant *Opuntia ficus-indica* planted at the same time in adjacent plots for fruit production were over 4 m tall in same time period. Thus it would be very interesting to repeat this experiment in a frost-free region where the WUE of faster growing cacti could be measured. Dry-matter-based WUEt of these species can be expected to be higher than *Opuntia ellisiana*. In contrast to these managed *Opuntia* plantations, the productivity of non-managed arid zones is typically much less, i.e. of the order of 1000 kg above-ground dry matter ha^{-1} $year^{-1}$ (Leith & Whittaker, 1975).

More significantly than the high production of biomass, the cacti achieved this productivity while only transpiring 285 mm water, giving a water-use efficiency of 162 kg H_2O kg^{-1} dry matter. Neither the comprehensive review of Fisher & Turner (1978) or the classic work of Briggs & Shantz (1914) report dry matter-based water-use efficiencies as high as those reported here.

The transpiration ratio (equivalent to transpiration water-use efficiency) has been reported to range from 50 to 125 kg H_2O kg^{-1} dry matter for CAM plants, from 250 to 350 kg H_2O kg^{-1} dry matter for C_4 plants and from 450 to 950 kg H_2O kg^{-1} dry matter for C_3 plants (Black, 1973). Joshi *et al*. (1965) reported that for an 80-day period, pineapple growing in a greenhouse in North Carolina during the winter had a transpiration ratio of 50 kg H_2O kg^{-1} dry matter. The pineapple is the fastest growing species among CAM plants (Kluge & Ting, 1978). Neales *et al*. (1968) reported transpiration ratios of 154 mg H_2O mg^{-1} CO_2 for *Aeonium hawarthii*, 47 mg H_2O mg^{-1} CO_2 for *Agave americana* and 116 mg H_2O mg^{-1} CO_2 for pineapple. Nobel (1977) found that the barrel cactus, *Ferocactus acanthodes* (Lemaire) Britton & Rose, growing in natural stands, had transpiration ratios of 105 mg H_2O mg^{-1} CO_2 during the hot months and 18 to 24 mg H_2O mg^{-1} CO_2 during the cooler season.

Because of the difficulty of partitioning evapo-transpiration into soil evaporation and plant transpiration, evapo-transpiration water-use efficiencies were most often obtained in the field studies. In addition, the efficiency of total precipitation in producing dry matter has been termed rain-use efficiency and worldwide values for rain-use efficiency have been extensively reviewed (Le Houérou, 1984).

Snyman (1989) reported the WUEet for grass species *Cymbopogen pospischilii* (K.Schum.) C.E. Hubb. syn. *C. plurinodis* (Stape) Burtt-Davy and *Panicum stapfianum* Fourc. during the 1986–1987 season was 1277 kg H_2O kg^{-1} dry matter and 2119 kg H_2O kg^{-1} dry matter, respectively. When given a high rate of N fertilizer (168 kg ha^{-1}), a mixed prairie plant community whose major species were western wheatgrass (*Elymus smithii* syn. *Agropyron smithii* Rydb.) and needleandthread (*Stipa comata* Trin. & Rupr.) in Montana had a dry matter production of 2389 kg ha^{-1} and WUEet of 1160 kg H_2O kg^{-1} dry matter when it reached maturity (Wight & Black, 1978). Wight & Black (1978) also reported that the annual precipitation use efficiency for a fertilized mixed prairie plant community in eastern Montana ranged from 987 kg H_2O kg^{-1} dry matter to 3184 kg H_2O kg^{-1} dry matter over a 10-year period. Under favorable water and nutrient conditions, a plant community comprising blue grama (*Bouteloua gracilis* (Kunth) Lag. ex Steud.) and western wheatgrass in Mandan, North Dakota had a WUEet of 2236 kg H_2O^{-1} kg dry matter (Smika *et al.*, 1965). WUEet of corn with a population density of 74,000 plants ha^{-1} from planting to harvest (about 6 months) was about 385 kg H_2O kg^{-1} dry matter (Alessi & Power, 1976).

The relationship between WUE obtained at different process and timescales are complicated. For a given plant species, the WUEt based on the dry matter production will necessarily be lower than the WUEt at gas exchange level (Fisher & Turner, 1978). For example, some CO_2 fixed during the day will be respired during the night and in non-photosynthetic tissue. The photosynthetic activity ceases at night while the transpiration is still active. Dry matter might be lost due to water stress, diseases and insects. Root dry matter is usually not included as is the case in this study. Also the WUE for the same crop (such as summer and winter wheat) will be lower in the summer than in the winter due to the greater vapor pressure deficit in the summer (Fisher & Turner, 1978).

In field water balance studies one of the major difficulties is the separation of evapo-transpiration into plant transpiration and soil evaporation (Fisher & Turner, 1978; Boast, 1986). Fortunately, the ratio of E to ET decreases as the crop matures and the LAI increases (Ritchie, 1972; Sinclair *et al.*, 1984; Jagtap & Jones, 1989) making it easier to accurately estimate transpiration. Ritchie (1972) reported that when the soil water supply to plant roots was not limited, the plant transpiration was negligible when the LAI was less than 0·1; transpiration accounted for 25% of total water loss when the LAI was 0·5; plant transpiration accounted for nearly 100% of the total water loss when the LAI reached 3. Sinclair *et al.* (1984) reviewed that for a fully developed leaf canopy, E/ET is generally in the range of 0·15 to 0·25. In our study, LAI was 0·39 at the beginning of the third year, 2·02 at the end of the third year and 3·88 at the end of the fourth year. Due to the greater precision in estimating E and thus T at a greater LAI, we have greater confidence in our fourth year's measurements than the third year' measurements.

The average transpiration water-use efficiency (WUEt) and evapo-transpiration water-use efficiency (WUEet) of *Opuntia ellisiana* over plots 3, 4 and 11 were 218 kg kg^{-1} and 393 kg kg^{-1} in the third year and 162 kg kg^{-1} and 283 kg kg^{-1} in the fourth year, respectively. As discussed above, surface runoff and soil evaporation might be underestimated in the third year. As a result, values of WUEt and WUEet in the third year should be smaller than those reported here.

Neutron probe measurements to estimate the change in stored soil moisture from 15 to 125 cm depth found no differences among non-harvested or harvested cactus plots. Thus it appears as if all water uptake by the cactus is from the top 15 cm.

Precipitation is the only water input into this plant–soil system. The availability of rain water to plants depends on the characteristics of the rainfall event such as intensity, duration and amount (Fisher & Turner, 1978). In this study area, precipitation had the following two prominent properties which greatly limited the availability of rain water to plants. First, a large proportion of the rainfall occurred in heavy storms which caused significant surface runoff. Second, the number of light rainfall events accounted for a large percentage of the total rainfall events. When the vegetation cover was incomplete most of the water from these light rainfall events was evaporated from soil surface. When the vegetation had a high LAI, the light rains were intercepted by the plant canopy and evaporated from the plant surfaces. In both cases the light rains were not effectively used by the plant.

Whether cropping systems in arid regions are rain-fed or irrigated, pressure on the water resource base mandates that water be used with the greatest efficiency possible. The *Opuntia ellisiana* cactus in this study is not economically promising as it does not produce edible fruit and produces insufficient immature growth on a year-round basis to be a vegetable (nopalito) variety. However *Opuntia ellisiana* could be a useful forage variety in locations that are too cold for *O. robusta* Wendl. or *O. ficus-indica*. Indeed, the yearly fresh weight of 194,187 kg ha^{-1} in the fourth year would be sufficient for 4315 cows day^{-1} at a feeding rate 45 kg day^{-1} (Felker, 1995). While this variety was chosen because it was spineless and sufficiently cold hardy to live through the required 4-year growth period, there are many other much faster growing cacti (Inglese *et al.*, 1995) that produce excellent quality fruit and vegetables. As nearly all of the 130 accessions in our germplasm collection have greater height growth than *Opuntia ellisiana* under the same rainfall conditions, it would appear that they might have even greater water-use efficiencies.

Now that a long-term field study, with adequate control over border influences, has clearly demonstrated that cacti have greater conversion efficiency of water to dry matter than any widely used C_3 and C_4 species, we suggest that serious efforts be made to develop cactus-based fruit, vegetable and forage systems for arid lands.

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