IJANR
International Journal
of Agriculture
and Natural Resources

Int. J. Agric. Nat. Resour. 48(2):115-124. 2021
www.ijanr.cl

CROP SCIENCE AND PRODUCTION

DOI 10.7764/ijanr.v48i2.2255

RESEARCH NOTE

Transpiration-use efficiency of young cactus pear plants (*Opuntia ficus-indica* L.)

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Abstract

C. Kremer, C. Faúndez, V. Beyá-Marshall, N. Franck, and V. Muñoz-Aravena. 2021. Transpiration-use efficiency of young cactus pear plants (*Opuntia ficus-indica* L.). Int. J. Agric. Nat. Resour. 115-124. *Opuntia ficus-indica* is a versatile crop that is resilient to drought, making it perfect for semiarid to arid zones. However, the lack of knowledge associated with its benefits and the lack of simple crop growth simulation models to determine its potential development, among others, has prevented its expansion. Transpiration-use efficiency (w) has been used to evaluate crop performance under different water supplies; however, the lack of consistency in w values under different environmental conditions has impeded its use as a transferable parameter. To overcome this problem, w is estimated through the normalized water-use efficiency (k_{Da}) and the vapor pressure deficit (Da) as $w = k_{Da}\, D_a^{-1}$, where k_{Da} is a crop-dependent parameter. Therefore, the goals of this research were (i) to determine w and k_{Da} in young plants of *Opuntia ficus-indica* and (ii) to compare the obtained parameters with values from other species. The w and k_{Da} results were 18.57 (g kg^{-1}) and 6.48 (g kPa kg^{-1}), respectively. Here, w was more than two to six times the value for traditional cereals (maize, rice, wheat), while k_{Da} was larger than that of most C3 crops and fell in the range for C4 and CAM crops. This is the first study that explicitly determines k_{Da} for *Opuntia ficus-indica*; hence, more research should be carried out on its estimation, including under different agroclimatic conditions and in later stages of development. As a first approximation, the parameters obtained here can be used as a simple model to estimate yield projections of *Opuntia ficus-indica*.

Keywords: Arid zone agriculture, CAM, crops adapted to drought, simple crop growth models.

Introduction

Chile is under a serious water availability crisis, especially in semiarid to arid climate areas (central-northern zones of the country). In these zones, the demand/availability ratio for water is affected by rainfall scarcity in the last ten years and by the high demand for water among stakeholders (Garreaud *et al.*, 2017). In this scenario, the planting of fruit trees can be expanded via crops with low water requirements, good profitability and resistance to drought, such as *Opuntia*

Received May 04, 2020. Accepted Jul 14, 2021
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ficus-indica (cactus pear) (Sudzuki *et al*., 1993). *Opuntia ficus-indica* is a versatile crassulacean acid metabolism (CAM) species with diverse uses, such as fresh fruit and biofuel (Sáenz *et al*., 2006; Bernab & Lamas, 2011). This plant is also resilient to drought (Inglese *et al*., 2017), making it an excellent candidate for semiarid to arid zones. However, in Chile, according to the last agricultural and forestry census carried out in 2020, the area under cactus pear production was close to 596 ha, which incentivizes its expansion through the development of technical and scientific information available to farmers, especially information that allows them to make more efficient use of their water resources and to determine early indicators of the potential yield of cactus pear under different agroclimatic conditions.

Transpiration-based models of crop productivity, such as transpiration-use efficiency (w), defined as the amount of biomass expressed as dry matter produced for a unit of water transpired by a crop (Tanner & Sinclair, 1983), can be readily applied to a large number of crop species across the range of climatic conditions where these crops are grown. Katerji *et al.* (2008) pointed out that there are two approaches: an ecophysiological approach based on the analysis of the relationship between photosynthesis and transpiration per unit of leaf area at a given moment, called instantaneous water-use efficiency (w_i), and a seasonal approach based on the concepts of water consumption and biomass production (w). However, the lack of consistency in w values for a species under different environmental conditions has not allowed its use as a simple crop simulation model (Katerji *et al*., 2008, Kremer & Stöckle., 2012, Kremer *et al*., 2020). Among the reasons for this lack of consistency are experimental and methodological errors, agronomic management (Faustino *et al*., 2011), and major climate differences (Tanner & Sinclair, 1983; Kremer *et al*., 2008). On the other hand, simpler models have been developed to decrease the variability of w concerning climatic differences between sites, such as $w = k_{Da}\ Da^{-1}$, where Da corresponds to the vapor pressure deficit of the zone and k_{Da} is a crop-dependent parameter, also known as normalized water-use efficiency. Normalization by Da would correct the climatic variations in w, while k_{Da} would remain reasonably constant in different climatic zones (Condon, 1993; Kemanian *et al*., 2005; Steduto & Albrizio, 2005; Kremer *et al*., 2008).

Consequently, due to the affinity of the cactus pear fruit tree for growth in arid/semiarid regions and the lack of simple crop growth simulation models to determine its potential yield and development in different environments, the main objective of this research was to determine its w and k_{Da} parameters and to compare these values with data obtained for other species based on the literature.

Material and methods

Site, plant material and agronomic management

The experiment was performed at the experimental station "Las Cardas" of the University of Chile, Coquimbo region, Elqui Province (30°17′S, 71°15′W, 436 m.a.s). The zone's climate is temperate, arid Mediterranean with precipitation of 100 to 150 mm year^{1} in winter. The annual average temperature is 14.4 °C.

Forty-eight one-year-old cactus pear plants of ecotype "Blanco" were planted in 55 L pots (0.45 m in internal diameter and 0.5 m in height, Figure 1A) filled with 2 mm expanded perlite (bulk density: 0.155 Mg m^{-3}, water holding capacity base volume: 28%) up to a height of 40 cm. A layer of 4.5 kg of gravel was placed in the base of each pot to allow atmospheric seepage flow, and a 0.1 mm thick black polyethylene plastic was placed on the surface of each pot to avoid water loss by evaporation. Three drippers (2 Lh^{-1}) were used to irrigate. Irrigation was triggered when the water content was close to 70% of the water-holding capacity (WHC). The pots were weighed every two days using a scale to check the water content parameters (Izetta, mod. PK60, China). Irrigation was stopped when 95% of the WHC was reached. The pots were arranged in a row with a north-south orientation (Figure 1B), so all of them received similar light radiation. Other management practices, such as fertilization and pest control, were performed to ensure optimal development. Data were collected over a 503-day-long period that started on December 13, 2009, and ended on April 30, 2011.

Biomass

Four complete plants were extracted approximately every 40 days until 10/25/2010, and then two complete plants were extracted until the end of the trial (Figure 1B). In both cases, the fresh weight (*FM*) and the dry weight (*DM*) of the plants were determined using precise scales (Precisa mod. 3100c; accuracy of 0.01 g, Switzerland). To obtain *DM,* the plants were oven dried at 65 °C (Memmert model 800, Germany) until reaching a constant weight.

Transpiration

The transpired water was determined by mass lysimeters, where the unit to be weighed corresponded to each of the remaining 55 L pots at the end of each measurement interval. Crop transpiration was considered to be equal to the variation in the mass of the pot that occurred between each irrigation event once excess water was drained. For its determination, at the beginning of each measurement interval, a sufficient water load was applied to reach 95% of the WHC, and the water was allowed to drain freely for approximately 4 hours before pots were returned and weighed with a scale (Izetta, model PK60, China). At the end of the measurement interval and before watering, each pot was weighed again. Therefore, transpiration for the measurement interval (*Ati*) was determined as follows:

$$Ati = Mai - Mbi - Ei + Gf \qquad (1)$$

where *Mai* (kg) is the pot mass after irrigation, *Mbi* (kg) is the pot mass before irrigation, *Ei* is the loss by evaporation and *Gf* (kg) is the plant growth factor. The error produced in the estimation of transpiration by the increase in the plant's biomass over time was corrected once the study was finalized. The correction of *Gf* was determined through an exponential adjusted model of the total average *FM* as a function of time; with this information, the *FM* increment for the measurement interval was added to obtain *Ati*. Additionally, to avoid weight loss due to transpiration during drainage, water was applied to the plants in the morning due to their CAM metabolism. In turn, mass lysimeters were available under the same conditions as the previous ones but without plants to correct eventual losses due to evaporation. Daily

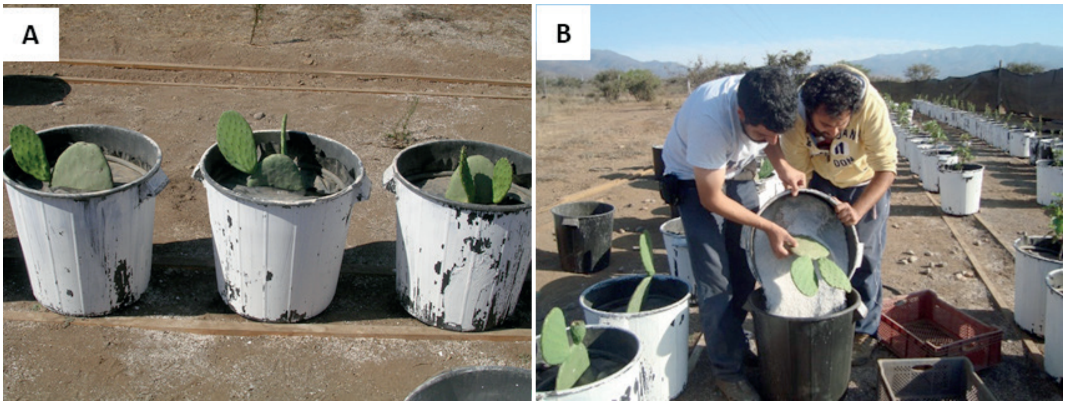

Figure 1. A: 55 L pots, B: Arrangement of pots in the north-south direction and plant extraction procedure.

transpiration (*Td*) was inferred as *Ati*/n, where n is the number of days between each measurement interval "i". The cumulative transpiration (*T*) was estimated as follows:

$$T = \sum_{i=1}^{i=m} Ati \qquad (2)$$

Transpiration-use efficiency (w)

Transpiration-use efficiency (*w*) was computed as the slope of the linear regression between the average cumulative *DM* (g) and the average cumulative *T* (kg) as follows (Tanner & Sinclair, 1983; Condon, 1993; Kemanian *et al.*, 2005; Steduto & Albrizio., 2005; Kremer & Stöckle, 2012; Kremer *et al.*, 2008, 2020):

$$w = \frac{dDM}{dT} \qquad (3)$$

where *w*= Transpiration use efficiency (g kg^{-1}), *DM* = cumulative dry matter (g) and *T* = cumulative transpiration (kg).

Normalized water-use efficiency (k_{Da})

The normalized water-use efficiency k_{Da} (g kPa kg^{-1}) was estimated as the slope of the linear regression between the average cumulative *DM* (g) and the daily integration of the quotient between average *Td* (kg) and air vapor pressure deficit during the night ($Td\ D_{an}^{-1}$; kg kPa^{-1}; Eq 4, Tanner & Sinclair, 1983; Condon, 1993; Kemanian *et al.*, 2005; Steduto & Albrizio., 2005; Kremer & Stöckle, 2012; Kremer *et al.*, 2008, 2020) as follows:

$$k_{Da} = \frac{dDM}{d\left(\frac{Td}{Dan}\right)} \qquad (4)$$

where *DM* = cumulative dry matter (g), *Td* = daily transpiration (kg) and D_{an}= daily air vapor pressure deficit at night (kPa). To calculate D_{an}, the maximum and minimum relative humidity (RH (max) and RH (min)) and maximum and minimum temperature (T(max) and T(min)) during the night were used. The climatic variables were obtained from a weather station located 300 m away from the study site (Campbell Scientific, U.S.A.). The methodology for the computation of D_{an} is fully described in FAO-56 (2006).

Statistical analysis

A regression analysis was performed to obtain *w* and k_{Da} with INFOSTAT statistical software ($p<0.05$). In both cases, the statistical significance of the y-axis interception was analyzed. Additionally, an exponential regression to obtain *Gf* was adjusted where the dependent variable was *FM* and the independent variable was days after planting. The coefficient of determination (R^2) was used to evaluate the accuracy of these regressions.

Results and discussion

Figures 2 and 3 show the results obtained from the growth and transpired water tests. Exponential increases in both *DM* and *FM* was observed, which was also reflected by *T* (Figure 2). The exponential adjustment of *Gf* (Figure 1, *FM* graph) showed a high coefficient of determination (R^2: 0.99), which gave confidence in its use for the estimation of *T*.

There is a lack of information about *w* in CAM plants. The available information is mainly related to water-use efficiency (WUE), which includes evapotranspiration and, in some cases, gross irrigation, making it a poor parameter for transferability among climatically different sites and for comparison with our results. Figure 4 displays the results for *w* and k_{Da} for cactus pear plants. The interception with the y-axes was not statistically significant ($p<0.05$); therefore, both values start at zero. The value of *w* obtained was 18.58 g kg^{-1}, which is in the lower range of the values reported by Silva and Acevedo (1995, Table 1). This values is also approximately 2 to 4 times greater than the values reported for C4 crops such as maize and

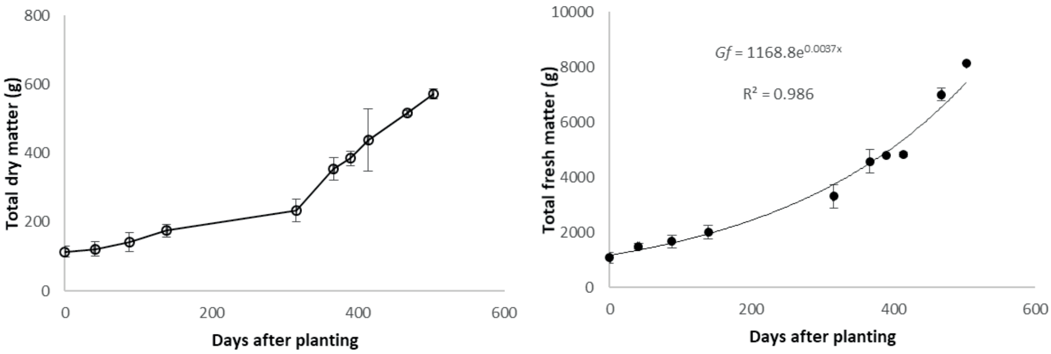

Figure 2. Cumulative dry matter (*DM*) and fresh matter (*FM*) during the whole trial. Dots represent the average weight, and error bars represent the standard deviation for each sample interval.

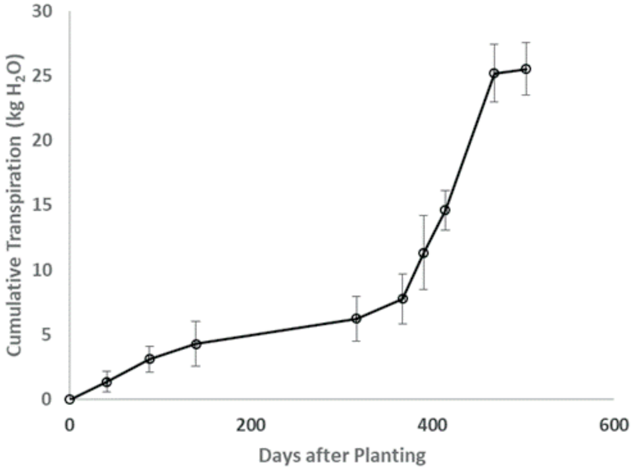

Figure 3. Cumulative transpiration during the whole trial. Dots represent the average transpiration, and error bars represent the standard deviation for each sample interval.

sorghum (Table 1) and up to 2 to 6 times greater than some values reported for C3 crops such as alfalfa, barley, wheat, rice and jatropha (Table 1). This result agrees with Nobel (2003) and his study on ecophysiology in cactus pears, where he concluded that CAM plants have a *w* three times larger than that of highly productive C4 plants, such as maize or sugar cane, and 5 times larger than that of highly productive C3 plants, such as alfalfa, cotton or wheat. This higher efficiency was also noted by Carvajal *et al.* (2010), who presented a study on CO_2 absorption (g of CO_2 fixed per kg of transpired H_2O) by C3, C4 and CAM plants. Their findings showed CO_2 absorption rates of 1-3, 2-5 and 10-40 g kg^{-1} for C3, C4 and CAM plants, respectively. Silva and Acevedo (1995) and Nobel (2003) mentioned that one of the mechanisms that explains the higher *w* of cactus pear with respect to C3 and C4 plants is related to its CAM metabolism, where the smallest difference in vapor pressure between the plant and the atmosphere during the night coincides with its period of maximum stomatal opening, decreasing its transpiration rate and consequently increasing *w*. In this study, we found that *Dan* was practically half of *Dad* (vapor pressure difference during the day) throughout the whole trial, which supports Noble´s (2003) comments (Figure 5). Conversely, Felker and Han (1997) conducted an open-field experiment in Texas (USA) for four years using *Opuntia ellisiana* (CAM plant) to estimate *w*. They measured the biomass without including the roots and estimated the transpiration with indirect methods. They reported a *w* value of 6.17 g kg^{-1}, which is practically one-third the value obtained in the present study and closest to the values reported for maize (Table 1). Silva and Acevedo (1995) and Nobel (2003) point out that the roots represent only 12% of the total biomass of *Opuntia ficus-indica*, which coincides with our results (12.48% ± 3.59, data not shown). After including 12% of the root biomass in the estimation of *w* by Felker and Han (1997), *w* increases up to 6.91 g kg^{-1}, showing that the lack of root biomass in the determination of *w* in this case does not by itself explain the difference with the result obtained here. We believe that the difference in *w* could be explained by different species and climatic differences between the test sites and mainly by differences in the estimation of crop transpiration. Silva and Acevedo (1995) determined *w* for 10 Opuntia taxa in a greenhouse in the same area where this study was performed. They obtained *w* values ranging from 22.18 ± 2.41 (*Opuntia streptacantha*) to 54.88 ± 2.91 (*Opuntia pumila*) g kg^{-1} (Table 1) for well-watered plants. Specifically, for *Opuntia ficus-indica,* they obtained values ranging from 40.64 ± 2.81 to 49.63 ± 3.31 for water-restricted and well-watered plants, respectively. These values were 2 to 3 times greater than those obtained in this study. This difference could be explained mainly because Silva and Acevedo (1995) carried out their experiments in a greenhouse. They mentioned that the average night temperature and the average relative humidity between July and March were between 15 and 20 °C and 80 and 90%, respectively. Considering a simple comparative analysis with an average night temperature of 17.5 °C and a relative humidity close to 90%, the average *Dan* would be 0.2 KPa, which is close to half of the average *Dan* obtained for the same period in this investigation (0.39 KPa, data not shown). Based on this result, we hypothesize that our plants transpired two times more (Fick's law) than theirs and in turn had a lower *w*. Accepting this gross relationship when comparing the values of *w* estimated by Silva and Acevedo (1995) for *Opuntia ficus-indica* with ours, their values must decrease by half, resulting in 20.32 g kg^{-1} and 24.92 g kg^{-1} for water-restricted and well-watered plants, respectively, which are closer to our results. Furthermore, in certain studies, a low WUE of *Opuntia ficus-indica* has been reported during the first year of establishment (Ratsele, 2003, Snyman, 2013), while the opposite occurs when the WUE is estimated in older plants (Snyman, 2013). However, the latter was not observed with our results; extrapolating *w* from the data only from the second season (8-month-old plants, similar to Silva and Acevedo plants) resulted in an even lower *w* (data not shown). Despite this result, plant age should be a topic to consider for further investigation.

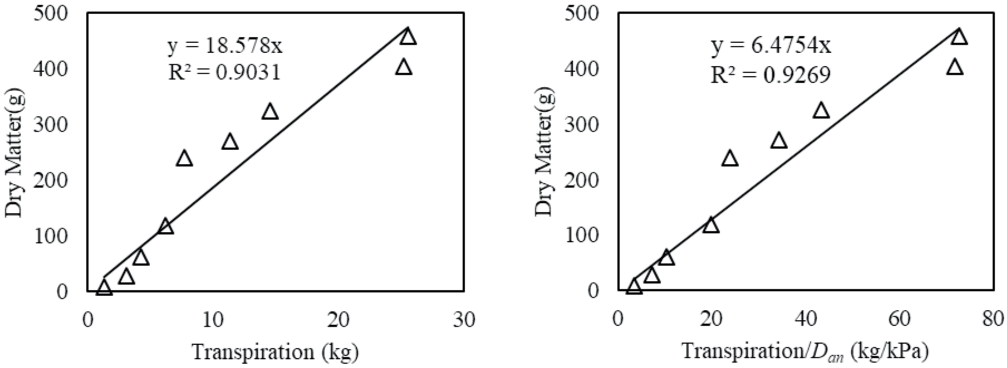

Figure 4. Dry matter as a function of cumulative transpiration (A) and cumulative transpiration normalized by the air vapor pressure deficit at night (B) for cactus pear grown in Las Cardas, Coquimbo Region.

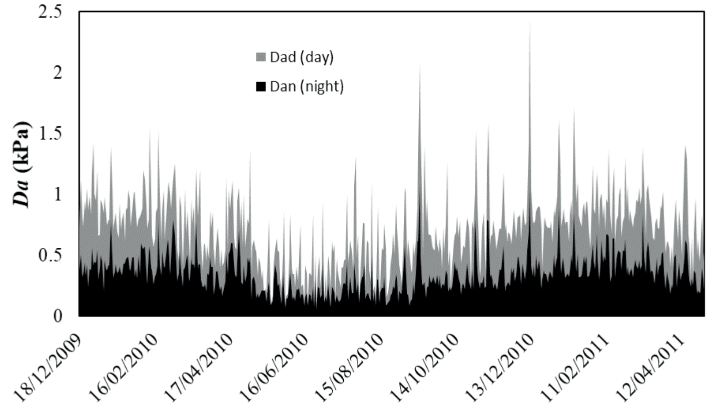

Figure 5. Day (*Dad*) and night (*Dan*) vapor pressure deficit (*Da*).

Table 1. Transpiration-use efficiency (w) and k_{Da} for different species reported or calculated from data obtained from the literature and the present study.

Photosynthetic metabolism	Common name	Species	w	k_{Da}	Source
			g kg^{-1}	g kPa kg^{-1}	
C4	Maize	*Zea mays*	4.12-8.25	6.1-8.4	a^{1,2}
		Miscanthus	11.5-14.2	6.6	b^{1}
	Sorghum	*Sorghum bicolor L.*	4.1-4.85	8.6-10	c^{2}
C3	Alfalfa	*Medicago sativa*	4.1	4.3	d^{1}
	Barley	*Hordeum vulgare L.*	3.2-5.69	3.0-6.9	e^{1,2}
	Wheat	*Triticum aestivum L*	3.1-8.61	2.7-5.9	f^{1,2}
	Rice	*Oryza sativa L.*	2.2-4.0	1.3-5.0	g^{1}
	Jatropha	*Jatropha curcas L.*	4.3	3.3	h^{1}
CAM	Tuna blanca	*O. hyptiacantha*	30.04	5.76	j^{2,3}
	Cardella	*O. pumila*	54.88	10.43	j^{2,3}
	Tuna cardona	*O. streptacantha*	31.82	9.3	j^{2,3}
	Nopal cochinero	*O. cochinillifera*	35.73	6.04	j^{2,3}
	Nopal	*O. ficus indica*	49.63	9.42	j^{2,3}
	Nopal	*O. ficus indica*	18.58	6.5	k^{1}

a: Tanner and Sinclair, 1983; Howell *et al.*, 1988; Kremer *et al.*, 2015; b: Clifton-Brown and Lewandowski, 2000; c: Thapa et al (2017); d: Tanner and Sinclair (1983); e: Kemanian et al (2005); f: Kemanian et al (2005); Kremer *et al.*, (2015); g: Haefele et al (2009); h: Kremer *et al.*, (2020); j: Silva and Acevedo (1995); k: present research. 1 w and k_{Da} were estimated with the same methodology used in the present research, 2 w and k_{Da} were estimated considering total crop transpiration and biomass for the whole period, and D_a is the average for the same period, according to (Kemanian *et al.*, 2005), and 3 for k_{Da}, an average *Dan* of 0.2 KPa was utilized.

Normalized water-use efficiency (k_{Da}) has been widely reported in cereals. However, there is little information on CAM plants (Table 1). We are the first study that explicitly presents k_{Da} for *Opuntia ficus-indica*, which was 6.48 ± 0.85 g kPa kg^{-1}. The relevance of this parameter is related to the close link between w and D_a (Vadez *et al.*, 2014). Consequently, normalization by D_a is fundamental to be able to compare w in different climatic zones and periods of the year and to estimate biomass production and water use among zones. In this sense, as observed by Kemanian *et al.* (2005) in barley, normalization by D_a decreased the dispersion of the data (Figure 3). The k_{Da} value obtained for cactus pear in this study was larger, and the values for alfalfa, rice, and jatropha were surprisingly close to the highest values for wheat and barley (Table 1, C3 plants). In a comparison with C4 plants, k_{Da} fell in the lower range of values for *Zea mays,* was similar to values for *Miscanthus,* and was less than values for *Sorghum bicolor L.* It is interesting to note that our k_{Da} value falls in the lowest k_{Da} range inferred from Silva and Acevedo (1995) for Opuntia taxa (Table 1), and as happened in the analysis of *w* in the case of *Opuntia ficus-indica*, their value is still higher than that obtained here. The reasons that may explain these differences are the same as those mentioned to explain *w*. Table 1 shows the impact of climate on the estimation of *w* and how normalization by a variable such as *Da* allows this impact to be moderated and values obtained in different regions through k_{Da} to be more comparable. A clear example of this is the comparison of *w* in the higher range of *Zea mays* (8.25 g KPa kg^{-1}) with the value obtained for *Opuntia ficus-indica* in this study (18.58 g KPa kg^{-1}). Initially, one would choose Opuntia as the more efficient plant; however, when the climate effect is included in the determination of *w* through the use of k_{Da}, both species have a more similar *w* value. These results are somewhat contradictory to Nobel's (2003) comments on *w* comparisons among C3, C4 and CAM plants. We expected to obtain larger values, at least those in the higher C4 range (Table 1), which is closer to the k_{Da} values inferred for *Opuntia ficus-indica* by Silva and Acevedo (1995). Different authors have mentioned that although k_{Da} is a more reliable and transferable parameter to estimate *w*, it is also influenced by climatic conditions (Kemanian *et al.*, 2005, Steduto & Albrizio, 2005, Kremer & Stockle., 2012). Therefore, more research is needed on the estimation of k_{Da} in different agroclimatic conditions and in later stages of development to increase the database for comparison.

Conclusions

The values for transpiration-use efficiency (*w*) and the normalized water-use efficiency (k_{Da}) for young cactus pear were 18.58 g kg^{-1} and 6.48 g kg^{-1}, respectively. The *w* value was within the ranges for CAM plants inferred from previous studies and was high enough for use in cactus pear under semiarid conditions, as an alternative to C3 plants. However, when k_{Da} was compared with values for C4 plants, it fell within their lower range. This is the first study that explicitly determined k_{Da} for *Opuntia ficus-indica*; therefore, more research should be carried out on the estimation of *w* and $k_{Da,}$ including under different agroclimatic conditions and during later stages of development of the crop, which will allow more confidence in the range of variation of these parameters. We are confident that the parameters obtained here can be used as a first approximation to estimate yield projections of *Opuntia ficus-indica*.

Resumen

C. Kremer, C. Faúndez, V. Beyá-Marshall, N. Franck, y V. Muñoz-Aravena. 2021. Eficiencia de uso de la transpiración en plantas jóvenes de nopal (*Opuntia ficus-indica* L.). Int. J. Agric. Nat. Resour. 115-124. *Opuntia ficus-indica* es un cultivo versátil, resistente a la sequía, ideal para zonas semiáridas y áridas. Sin embargo, la falta de conocimiento de sus beneficiosos usos y la falta de modelos de crecimiento para estimar su potencial, entre otros, ha impedido su expansión. La eficiencia de uso de la transpiración (*w*) se ha utilizado para evaluar el rendimiento de los cultivos con diferentes suministros de agua. Sin embargo, la falta de consistencia de *w* en diferentes condiciones ambientales ha impedido su uso como parámetro transferible. Para superar esto, *w* se estima a través de la eficiencia de uso de agua normalizada (k_{Da}) y el déficit de presión de vapor (*Da*) como; $w = k_{Da}\ Da^{-1}$, donde k_{Da} es un parámetro dependiente del cultivo. Por lo tanto, los objetivos fueron (i) determinar *w y* k_{Da} en plantas jóvenes de *Opuntia ficus-indica* y (ii) comparar estos con valores de otras especies. Los resultados de w y k_{Da} fueron 18.57 g kg^{-1} y 6.48 g kPa kg^{-1}, respectivamente. w excedió de dos a seis veces el valor de los cereales tradicionales (maíz, arroz, trigo); mientras que k_{Da} fue mayor que la mayoría de los cultivos C3 y cayó en el rango de los cultivos C4 y CAM. Este es el primer estudio que determina k_{Da} para *Opuntia ficus-indica*, por lo que se deben realizar más investigación incluyendo diferentes condiciones agroclimáticas y etapas posteriores de desarrollo. Los parámetros obtenidos se pueden utilizar como un modelo simple para estimar las proyecciones de rendimiento de *Opuntia ficus-indica.*

Palabras claves: Agricultura de zonas áridas, CAM, cultivos adaptados a la sequía, modelos simples de crecimiento de cultivos.

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